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MEASURING AQUATIC ORGANISM RESPONSES TO GRASSLAND RESTORATION: DOES THE *FIELD OF DREAMS* REALLY EXIST?

BY

DAVID A. SCHUMANN

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This dissertation is approved as credible and independent investigation by a candidate for the Doctor of Philosophy in Wildlife and Fisheries Sciences degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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ABSTRACT

MEASURING AQUATIC ORGANISM RESPONSES TO GRASSLAND RESTORATION: DOES THE *FIELD OF DREAMS* REALLY EXIST?

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Landscape homogenization and the degradation of riparian areas has greatly impaired stream ecosystems throughout North America. Conservation programs may repair riparian ecosystems to indirectly improve water quality and instream habitat heterogeneity in hopes to elicit biological responses. However, focused manipulations on isolated stream fragments have rarely achieved biological goals. Prairie streams with restored riparian areas were appraised (chemical, physical, and biological variables) to quantify the indirect effects of prevalent grassland conservation practices on aquatic resources. Riparian rehabilitation, via passive methods, promoted bank-stabilizing vegetation along all conservation stream reaches. Riparian vegetation and function quickly recovered from previous agricultural disturbances at conservation reaches. Substantial animal trampling and grazing pressure persisted at reference sites and restricted vegetation growth. Grassland conservation actions improved water quality and restored processes that create diverse instream habitat complexes in adjacent streams.

Despite dramatic changes to riparian areas and subsequent improvements to instream environments, benthic invertebrate and fish assemblages have yet to respond to conservation. Restoration efforts that assume that ‘if you (re-)build it, they will come’ (‘field of dreams’ hypothesis), may underestimate the many other barriers to the restoration of biotic diversity. Restored stream reaches were not *created* equally and each have different colonization prospects when environmental pressures were removed. By considering the local effects of riparian restoration and the riverscape properties that dictate biotic responses, I was better able to explain conservation outcomes. I evaluated three alternative hypotheses to explain the limited biotic response to restoration efforts: (1) connections to newly available habitats remained severed; (2) regional assemblages lack species adapted to utilize opened niches; and (3) the niche space created did not benefit local species.

The fragmentation of stream networks has severed historic movement pathways and potentially limited opportunities for fish to colonize restored stream reaches. To describe the relative likelihood that prairie fishes bypass anthropogenic barriers I quantified their swimming and jumping abilities. Stream fishes are not equally vulnerable to instream barriers, but all failed to circumvent relatively minor obstacles. Small vertical barriers (> 5 cm) blocked most fish passage and, with access, all species were unable to traverse relatively short obstacles with moderate water velocities. Abundant barriers to recolonization and limited tools to improve passage for small-bodied prairie fishes will restrict colonization of nearby habitats when they are improved.

Interpreting biological responses requires consideration of the regional species pools from which restored reaches would recruit individuals. Conservation efforts in watersheds with small, impoverished species pools are unlikely to elicit a measurable response from aquatic assemblages. By considering the regional species pool, I identified many areas with few aquatic taxa available for colonization. Future colonization by many aquatic taxa is unlikely at a large number conservation sites throughout the James River basin.

The determination of specific environmental targets for stream restoration efforts to benefit particular taxa and biotic diversity is critical but often addressed with limited data. My results suggest that benthic invertebrates and fishes strongly respond to changes to the riparian area that increase ground vegetation and tree cover. Fish and benthic invertebrate diversity was highest when instream cover (woody debris and overhanging vegetation) was available in areas with large substrates and abundant aquatic plants. Grassland conservation efforts created niche space that is beneficial to local aquatic fauna and rare in degraded reaches, but that are not utilized in inaccessible areas. Managers can supplement riparian rehabilitation efforts by providing large substrates and woody debris in areas with abundant aquatic and overhanging vegetation.

Although the cumulative protected area exceeds 81,000 acres, each conservation easement only represents a sliver of the riverscape. Grassland conservation improved water quality and indirectly created heterogeneous stream habitats, but not all restored stream reaches were *created* equally. Stream fragmentation and ongoing, degenerative land practices may outdo the positive effects of restoring minority fractions of watersheds. The development of niche space didn’t directly translate to successful colonization and occupation by aquatic life. Strategic investments in species rich areas with few instream barriers are most likely to achieve aquatic diversity goals.

INTRODUCTION AND LITERATURE REVIEW

LANDSCAPE PERSPECTIVES APPLIED TO STREAM ECOLOGY: IMPLICATIONS FOR CONSERVATION EFFECTIVENESS IN A RIVER NETWORK

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Aquatic Systems on the Prairie

Prairie landscapes are among the most topographically simple biomes in North America and are characterized by abundant grassland areas and annual extremes in temperature and moisture (Matthews 1988; Covich et al. 1997). The Great Plains were once one of the largest biomes in North America, encompassing > 160 million hectares and multiple vegetative and climatic ecoregions (Covich et al. 1997). Currently, prairie areas are among the most endangered ecosystems worldwide, having been replaced largely by agriculture (Samson and Knopf 1994), and streams of the region are especially endangered (Covich et al. 1997; Dodds et al. 2004). Many remaining fragments of prairie are too small to serve as functional watersheds, and vast aquifers that once supplied the plains have been exploited and no longer provide water to many streams (Dodds et al. 2004; Cooke et al. 2012). Highly variable mid-continental weather patterns affect hydrology and influence the distribution and quality of water resources in the region (Covich et al. 1997; Dodds et al. 2004).

Prairie ecosystems have diverse aquatic systems, which include springs and wetlands, intermittent and ephemeral streams, and large rivers, all of which are dynamic and responsive to climatic variability (Matthews 1988; Covich et al. 1997). Prairie drainage networks historically were a critical component of prairie ecosystems (Harding et al. 1998), and were once characterized by shallow, wide systems with many braided channels (Matthews 1988; Covich et al. 1997; Harding et al. 1998; Dodds et al. 2004). Lotic habitats have been altered greatly in the last century by agricultural and urban development which exploited underground and surface waters (Covich et al. 1997; Dodds et al. 2004; Hrodey et al. 2009; Cooke et al. 2012). Greater understanding of prairie stream ecology and the benefits of restoration processes are essential to reverse this degradation and restore ecosystem function (Dodds et al. 2004; Cooke et al. 2012).

Grassland Stream Ecology

Prairie stream systems are typically eutrophic, with high gross primary productivity, although some systems are light limited due to high turbidity (Matthews 1988; Covich et al. 1997). The upper reaches of grassland streams tend to have sparse riparian canopy cover and few organic litter inputs, diverging from stream trophic ecology in forested reaches where allochthonous inputs are much greater (Wiley et al. 1990; Dodds et al. 2004). Autochthonous production and limited particulate matter input provide the trophic base for food web interactions in prairie streams (Matthews 1988; Dodds et al. 2004). However, many prairie streams receive additional nutrient inputs through overland flow in highly fertilized drainages and localized nutrient rich additions from cattle operations (Covich et al. 1997). In these systems, primary production is highly driven by primary consumers and omnivores (Gido and Matthews 2001; Bertrand and Gido 2007), by means of reducing algal biomass through consumption and stimulating algal development by recycling limited nutrients (Dodds et al. 2004; Bertrand et al. 2009).

Disturbance is a regular aspect of the hydrograph in the region and streams often fluctuate drastically in both physical and chemical properties (Poff and Ward 1989; Dodds et al. 2004). Prairie streams occur in a non-equilibrium state between flooding and drought (Matthews 1988; Dodds et al. 2004; Franssen et al. 2006), which are often exacerbated by anthropogenic land and water use (Covich et al. 1997; Scheurer et al.

2003). Recurrent disturbance events and extreme environmental conditions regulate the distributions and abundance of aquatic organisms (Poff and Ward 1989; Poff and Allan 1995; Matthews and Zimmerman 1990; Fritz and Dodds 2005; Franssen et al. 2006). Plains fishes are normally tolerant of wide fluctuations in chemical and physical states and have life history characteristics that allow dispersal over large scales to rapidly recover after disturbance (Matthews 1988; Matthews and Marsh-Matthews 2003; Dodds et al. 2004; Franssen et al. 2006; Gido et al. 2010). Connections to refugia throughout stream networks offer means for recolonization of extirpated reaches when suitable conditions return (Dodds et al. 2004; Franssen et al. 2006). However, barriers to fish movement have fragmented stream habitats and isolated fish populations, potentially eliminating recolonization opportunities (Perkin and Gido 2012; Perkin et al. 2013; Rolls et al. 2013; Perkin et al. 2014).

The Demise of Prairie Streams

Prairie streams and the fish assemblages maintained within are at continued risk of decline in direct response to land and water use in the region, principally motivated by agricultural practices, but also from prevalent channel modification and the widespread introduction of nonnative species (Richter et al. 1997; Ricciardi and Rasmussen 1999; Burkhead 2012). Prairie streams are subject to numerous pressures; however, the entire process of prairie stream degradation can be summarized as landscape and local habitat homogenization (Wiley et al. 1990; Scott and Helfman 2001). Alterations and degradation to available instream habitats, decreased water quality, and the proliferation of barriers have imperiled many stream fishes in North America (Wilcove et al. 1998;

Reynolds et al. 2002; Olden and Poff 2005). Few undisturbed stream reaches remain in the plains region, as those not impacted by row crop agriculture and urbanization are typically maintained for cattle grazing (Bonner and Wilde 2002; Fischer and Paukert 2008).

Particularly strong negative effects are realized in areas where riparian vegetation and proximate terrestrial ecosystems are removed (Scott and Helfman 2001). Decreased riparian cover directly reduces instream habitat diversity and the capacity for surplus nutrients and sediments to be intercepted before reaching the stream channel (Scott and Helfman 2001). As a result, these now homogenous habitats typically cease to provide refugia from regular stochastic events and further endanger these delicate ecosystems (Dodds et al. 2004). Collectively, these disturbances have resulted in reductions to nongame native species diversity and facilitated assemblage homogenization (Fairchild et al. 1998; Rahel 2000, 2002).

Freshwater Fishes at Risk

North America once had among the greatest diversity of temperate freshwater fishes in the world (Jelks et al. 2008). Freshwater fishes are now midst the most imperiled vertebrate groups worldwide; approximately one-third are currently protected by federal or state legislation (Ricciardi and Rasmussen 1999; Reynolds et al. 2002; Saunders et al. 2002). The rapid and widespread loss of biodiversity throughout North America is a severe threat to the quality of life enjoyed by society in terms of reduced aesthetics, ecological benefit, economic value, and ethics (Angermeier and Winston 1999).

Accelerated rates of species extinctions have made ecologists consider the consequences of diversity loss in stream ecosystems (Bertrand and Gido 2007; Bertrand et al. 2009). Although the loss of complete feeding functional groups is expected to change ecosystem processes (Schwartz et al. 2000), the unique ecosystem contributions of individual species have been realized in several recent studies (Cardinale et al. 2002; Bertrand and Gido 2007; Bertrand et al. 2009). The impact of grazing fishes on autochthonous primary productivity in prairie aquatic ecosystems can be considerable since outside organic matter contributions are relatively low (Dodds et al. 2004; Bertrand and Gido 2007; Gido et al. 2010; McIntyre and Flecker 2010). Sequestering rare nutrients permits fish to regulate nutrient availability and reduce the rate of nutrient turnover in streams (McIntyre and Flecker 2010).

Management of Nongame Fishes

Fish species that seemingly provide little direct economic, recreational, or other benefits to human society are commonly known as *nongame* species (Cooke et al. 2012). Nongame fishes generally lack comprehensive management plans and populations can deteriorate to near extinction before management actions are undertaken (Winter and Hughes 1997; Ricciardi and Rasmussen 1999; Cooke et al. 2012). Historically, only a small portion of all species have been managed and focus has been on species that are commercially or recreationally important (Winter and Hughes 1997; Reynolds et al. 2002; Cooke et al. 2012). Concern for nongame fishes has increased in recent years in response to their widespread imperilment and the need to develop recovery plans due to the passing of the Endangered Species Act (ESA) in 1973, which offered protection to nearly 1,100 species (Campbell et al. 2002; Cooke et al. 2012). Except for those species granted special protection, there are few specific regulations to protect or manage the majority of nongame species (Winter and Hughes 1997; Norris 2004; Cooke et al. 2012). In order to effectively manage nongame fishes, many researchers favor the use of alternative strategies, including the development of freshwater protected areas, habitat rehabilitation, and the maintenance of natural processes such as flow regimes (Olden and Poff 2005; Palmer et al. 2005; Suski and Cooke 2006). These conservation efforts create opportunities to manage communities of native fishes, rather than individual species, by focusing limited resources on the management or restoration of habitats that sustain the integrity of lotic systems (Rinne and Stefferud 1999).

Stream Restoration

Although habitat restoration efforts typically share similar goals of improving conditions for both terrestrial and aquatic resources, it remains unclear whether many projects are achieving such claims (Bash and Ryan 2002). Commonly, stream and riparian restoration projects strive to restore processes that maintain habitat heterogeneity and thereby increase biological diversity; however, the effectiveness of most managements practices to meet desired ecological goals is poorly understood (Palmer et al. 2005; Palmer and Bernhardt 2006). This is in part because monitoring and evaluation is generally limited or unreported (~10%) after implementation (Bernhardt et al. 2005). Agencies often allocate resources to the establishment of protected areas with perceived benefits to aquatic environments, rather than to research program effectiveness (Palmer and Bernhardt 2006). A large-scale evaluation of restoration monitoring procedures and subsequent assessments can offer resource managers identify progress toward achieving ecological goals and facilitate improvements to future stream conservation practices (Bash and Ryan 2002; Roni et al. 2008).

The "*Riverscape*"

The small-scale focus of past management actions on species, populations, or short stream reaches has not addressed broad-scale factors that influence populations of rare aquatic organisms and have failed to alleviate issues challenging stream ecosystems (Angermeier and Schlosser 1995; Labbe and Fausch 2000; Fausch et al. 2002). Researchers have studies these issues at small spatial scales (50-500 m) for short time periods (two to four years), which typically has not been useful for ameliorating large-scale anthropogenic disturbances (Allan and Flecker 1993; Fausch et al. 2002). Greater emphasis on landscape-level ecosystem function has been included in contemporary conservation strategies for lotic fishes (Schlosser 1991; Schlosser and Angermeier 1995; Labbe and Fausch 2000).

Awareness of the governing, *riverscape* framework, which regulates local instream conditions, allows managers to link important physical and biotic processes in streams and their riparian areas at a spatial scale pertinent to human disturbance (Schlosser 1991; Fausch et al. 2002). To be effective, management needs to recognize and maintain ecosystem processes and dispersal pathways while accepting the ephemeral nature of local populations and planning for regional species persistence (Labbe and Fausch 2000). Refinement of the *riverscape* paradigm explicitly embraces the continuous, hierarchical, and heterogeneous nature of lotic aquatic habitats and considers ecological processes that operate primarily at landscape scales (Taylor et al. 1993; Fausch et al. 2002). Lotic systems are hierarchical, where climate, geology, and topography drive processes that generate and maintain habitats at small scales (Fausch et al. 2002). Because streams habitats are inherently heterogeneous, with critical elements for stream fish development separated, awareness of spatial and temporal organizations of these habitat patches is essential (Schlosser 1991; Fausch et al. 2002). Researchers must understand how these disparate habitats are arranged, created, and destroyed at multiple scales and how they are related to fish population ecology along the linear gradient (Schlosser and Angermeier 1995; Fausch et al. 2002).

RESEARCH OBJECTIVES

Landscape homogenization and the degradation of proximate ecosystems have impaired local aquatic environments and catchments throughout North America. Conservation and incentive programs have the potential to mitigate lost ecological functions. A loosely defined collection of aquatic species are expected to respond to riparian conservation efforts and improved instream environments. However, focused manipulations on isolated stream fragments have rarely achieved desired biological goals. Modern conservation of stream fishes has recently placed greater emphasis on riverscape-level processes that operate at spatial scales in which ecosystem recovery is largely mediated. We appraised the indirect effects of prevalent prairie conservation practices that restored landscapes and reestablished riparian corridors on local water quality, physical habitat availability, and the response of aquatic resources in the James River basin, South Dakota. Although restoration projects assume that the creation of habitat is the key to restoring aquatic biota (‘field of dreams’ hypothesis, Palmer et al. 1997), numerous other factors that interrupt the link between habitat and biotic restoration. We evaluated three alternative hypotheses that potentially explain the limited biotic response: (1) connections to newly available habitats will remain severed; (2) regional assemblages will lack species adapted to use opened niches; and (3) the niche space created will not benefit local species. Finally, we assessed novel tagging methods for small-bodied fishes to benefit future studies of species microhabitat affinities and catalog species-specific responses to niches created by grassland restoration actions. By integrating riverscape and local, stream reach perspectives, managers will better understand the effectiveness of actions used to counter pervasive and widespread pressures on stream ecosystem integrity.

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CHAPTER TWO

INDIRECT IMPACTS OF GRASSLAND CONSERVATION ON AQUATIC ECOSYSTEMS

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ABSTRACT

Landscape homogenization and the degradation of riparian areas has greatly impaired stream ecosystems throughout North America. Conservation programs may repair sensitive riparian areas to indirectly improve water quality and instream habitat heterogeneity, and elicit biological responses. However, previous conservation efforts that focus on isolated stream fragments have rarely achieved biological goals. Modern conservation practices place greater emphasis on riverscape-level processes that largely mediate stream ecosystem recovery. We evaluated the effects of grassland conservation practices and the reestablishment of riparian corridors on aquatic resources in a prairie landscape. Grassland conservation improved water quality and created diverse stream habitats in adjacent stream reaches compared to nearby reaches still under agricultural influence. Despite dramatic changes to riparian function and favorable alterations to local stream environments, aquatic taxa did not, thus far, respond to conservation actions. Restoration efforts that assume that ‘if you (re-)build it, they will come’ (‘field of dreams’ hypothesis), may underestimate the many other barriers to the biotic restoration. Stream fragmentation and ongoing, degenerative land practices may outdo the positive effects of restoring minority fractions of watersheds. The development of niche space didn’t directly translate to successful colonization and occupation by aquatic life. Grassland conservation improved water quality and indirectly created heterogeneous stream habitats, but not all restored stream reaches were *created* equally. Strategic investments in species rich areas with few instream barriers are most likely to achieve aquatic diversity goals.

INTRODUCTION

Agricultural development has degraded terrestrial and aquatic environments throughout North America (Ricciardi and Rasmussen 1999; Palmer and Bernhardt 2006; Burkhead 2012). In aquatic systems, many negative effects resulted from the removal of riparian ecosystems that once supported important ecological functions (Wiley et al. 1990; Ricciardi and Rasmussen 1999; Scott and Helfman 2001; Palmer and Bernhardt 2006; Teels et al. 2006). Riparian areas regulate water availability and disturbance, cycle nutrients, trap mobile sediments, and provide habitat for diverse biota (Dodds et al. 2004; Cooke et al. 2012). The rate of decline to functional riparian ecosystems was greatest prior to 1985 (Gray and Teels 2006; Dodds et al. 2008). Widespread restoration efforts and protections for native landscapes and riparian areas are now subsidized by a variety of federal and state conservation programs (Gray and Teels 2006; Teels et al. 2006; Dodds et al. 2008), which appeal to many landowners (Kurzejeski et al. 1992; Pfrimmer et al. 2017).

The US spends $1 billion annually to support aquatic restoration; a minor sum relative to the cost of terrestrial landscape restoration (Bernhardt et al. 2005). Despite being a new interdisciplinary field, descriptions of aquatic restoration efforts are extensive, but rarely quantitative (Buijse et al. 2002). Project designs and implementation techniques are diverse and usually unique to specific agency programs (Roni et al. 2008). Generally, these programs retire agricultural land to increase the extent of native landscapes and rehabilitate streams and riparian areas (Bernhardt et al. 2005; Palmer and Bernhardt 2006). Agencies generally allocate disproportionate resources to establishing riparian buffers and little is spent researching program effectiveness (Palmer and Bernhardt 2006).

Although stream and riparian restoration efforts share similar goals improving habitat and increasing biological diversity, it is unclear whether many projects are achieving their goals (Bash and Ryan 2002; Palmer et al. 2005; Palmer and Bernhardt 2006). This is in part because monitoring and evaluation is rare or unreported after implementation (~10%; Bernhardt et al. 2005). Ecological structure and function of restored systems are expected to be similar to those of natural stream ecosystems (Kaufmann et al. 1997; Teels et al. 2006; Dodds et al. 2008; Roni et al. 2008). Although riparian restoration efforts are thought to benefit numerous species, little quantitative research has validated this assumption (Bash and Ryan 2002; Parkyn et al. 2003). When reported, focused restoration efforts on isolated stream fragments have rarely achieved desired biological goals (Bernhardt et al. 2005; Palmer et al. 2005; Palmer and Bernhardt 2006).

Modern stream restoration emphasizes the riverscape-level processes that regulate local stream environments and largely mediate ecosystem recovery (Angermeier and Schlosser 1995; Labbe and Fausch 2000; Fausch et al. 2002). By incorporating the riverscape framework, managers can link local stream conditions to largescale conservation programs by prioritizing easements in areas most likely to succeed (Fausch et al. 2002). To maximize the benefits of restoration, we must understand this link between large-scale ecological dynamics and local management actions (Kauffman et al. 1997; Sear et al. 1998; Palmer and Bernhardt 2006; Teels et al. 2006). Few research programs have evaluated the effects of grassland restoration programs on streams, and fewer still have integrated local and riverscape perspectives to contextualize aquatic organism responses to conservation (Hughes et al. 1990; Meyerson et al. 2005; Teels et al. 2006).

We compared stream reaches flowing through restored grasslands with reestablished riparian areas to neighboring reaches flowing through active agricultural lands. Specifically, we assessed riparian condition, water chemistry, instream habitat availability, and benthic invertebrate and fish assemblage structure at conservation and reference stream reaches. Our objectives were to compare: (1) riparian condition and instream habitats; (2) benthic invertebrate and fish assemblage structure; (3) size structure of abundant fish species; (4) age structure of a native intolerant species between conservation and reference stream reaches, and; (5) to describe taxa-habitat relationships for habitats provided by grassland conservation. Prevalent grassland conservation practices are likely to improve riparian conditions, provide clean water, and diverse instream habitat, to which aquatic fauna are expected to respond via colonization. Stream restoration may alter fish size structure and facilitate the dominance of larger adult fish. By separating perception and reality when implementing stream restoration, these analyses will guide future habitat rehabilitation efforts.

METHODS

Grassland management in South Dakota. – The Conservation Reserve Enhancement Program (CREP) partners federal and state agencies to enhance restoration programs nationwide by addressing conservation priorities in sensitive or economically important ecosystems (Richards and Grabow 2003). The South Dakota CREP partnership (initiated: Nov. 2009) strives to eliminate agriculturally related environmental concerns by establishing 100,000 acres of permanent vegetation and riparian buffers, dispersed indiscriminately throughout the James River basin (Appendix A). Voluntarily program participants receive financial incentives to enroll under long-term contracts (i.e., 10-15 years) to transition cropland or marginal pastureland from agricultural production. Specific benefits sought include reductions to peak flooding, improved water quality (i.e., reduced sedimentation and nutrient loading), and enhanced wildlife habitat; however, additional benefits also may accrue as restored habitat patches are colonized in response to the altered environment (Sear et al. 1998; USDA 2011). The James River is the second largest catchment in the Great Plains ecoregion (54,760 km^2) and was historically comprised of both tallgrass and mixed grass prairie; however, agricultural disturbances (i.e., pasture and row crop) now impact >95% of the basin (Wimberly et al. 2017).

Study reaches and experimental design. – We selected HUC-12 watersheds (*n* = 12) using two-stage stratified sampling design and PROC SURVEYSELECT in SAS v9.2 (SAS Institute, 2008) to quantify the effects of grassland management on local aquatic habitat patches (Figure 1). Each subwatershed represented one experimental unit and each was selected in a stratified manner based on the proportion of protected area in the catchment. We selected four subwatersheds from three enrollment categories (*i.e.,* low [25th percentile], moderate, and high [75th percentile]). Although >81,000 acres were restored in the James River basin, conservation areas were relatively small portions of each subwatered and never exceeded 11%. Low enrollment subwatersheds had <1.5% conservation land, moderate enrollment was >1.5% and <4%, and high subwatersheds were comprised of >4% conservation area. Stream reaches were then randomly selected from each subwatershed, but to be included, specific conservation enrollments had to encompass both stream banks. Within each subwatershed, we sampled two stream reaches: (1) an agricultural production “reference” site, and (2) “conservation”, CREP enrolled site. Reference sites were dominated by row crop or pasture agriculture and were upstream from the restoration sites. The 24 stream reaches were sampled up to three times annually for three years (*i.e.*, spring, summer, fall) and, when logistically feasible, conservation and reference site pairs were sampled on the same day. Each sampling reach was delineated as 40 times the average wetted stream width at five randomly selected points; however, a minimum of 150 m and maximum of 300 m was established (Patton et al. 2000; Reynolds et al. 2003).

Field sampling and laboratory processing

Riparian and instream habitats. – To describe the impact of grassland conservation on stream ecosystems, we measured a suite of chemical characteristics, and quantified riparian condition and available instream habitat using standard methods (South Dakota Department of Environment and Natural Resources 2005). Dissolved oxygen (mg/L), temperature (ºC), pH, specific conductance (µS), and turbidity (NTU), salinity (ppt) were measured mid-stream using commercially available digital meters. All water chemistry sampling activities were conducted before fish, macroinvertebrate, and habitat sampling efforts to minimize disturbance to the system.

Qualitative observations of riparian condition (10 m from water’s edge on both banks) were made along 11 equally spaced transects at each stream reach. The riparian vegetation was conceptually divided into three classes: canopy (>5 m), understory (0.5-5 m), and ground cover (<0.5 m) in which vegetation type, size, and density were visually assessed. Estimates of cover within each of the vegetative zones and by each vegetation type were characterized using a categorical scale: absent (zero), sparse (<10%), moderate (10-40%), heavy (41-75%), and very heavy (>75%).

Physical habitat was subsampled along the same 11 equally spaced transects. At each transect, we measured wetted width (m), bar width (m), and bankfull width (m); bank angle was measured on the right and left stream banks. Depth (cm) and water velocity (cm/s) were measured at five equally spaced points along each transect. At each point, water velocity was measured at the water's surface and at 60% of the water's depth. In addition, the presence and density of specific habitat types (*i.e.*, undercut banks, aquatic macrophytes and algae, woody debris, and overhanging vegetation) and dominant substrate were measured within 15 equally spaced sections along each transect. Substrate coarseness was visually classified by the percentage composition of silt/muck (< 0.06 mm), sand (0.06-2 mm), fine gravel (2-16 mm), coarse gravel (16-64 mm), and cobble (64-240 mm). The density of cover available for fish and macroinvertebrate taxa was also estimated within 15 equally spaced sections along each transect.

Benthic invertebrate and fish assemblages and fish population dynamics. – We sampled benthic macroinvertebrates using a stovepipe core sampler (20 cm diameter) at the same transects used for habitat assessment, excluding the middle transect (*n* = 10 per site). Sampling started at the most downstream transect (Whiles and Goldowitz 2005; Meyer et al. 2011). The sample collection area was standardized by pressing the stovepipe 20 cm into the substrate (Sklar 1985; Meyer et al. 2011). We agitated the substrata inside the corer (6,283 cm^3 of water) and used a 500 µm mesh dip net to transfer the macroinvertebrates from the core to a 500 µm sieve (Sklar 1985; Meyer et al. 2011). We preserved macroinvertebrates in a 70% ethanol solution in 0.25L Whirlpaks®, for sorting and identification in the laboratory. Common benthic invertebrates were identified to genus and rare individuals were grouped into order or family taxonomic groups prior to analyses.

We sampled fish using standardized single-pass, pulsed DC backpack electrofishing in an upstream direction (Kauth et al. *in review*), then identified, counted, measured (100 individuals of each species; total length; mm) and noted external abnormalities, prior to release. We installed block nets at the upstream and downstream ends of the sampling reach to prevent fish emigration and immigration during sampling. Up to 30 Creek Chub *Semotilus atromaculatus* were sacrificed from all sampling reaches during 2015 summer samples and later processed to recover otoliths and determine age. Saggital otoliths were removed, dried, and adhered to glass microscope slides. We polished each otolith using wetted 1000 grit sandpaper. Two readers examined otoliths and independently estimated ages. When readers disagreed, an otolith was re-examined until a consensus was reached. Only consensus ages were used for analysis.

Data analysis

Riparian condition and instream habitats. – We first compared conservation and reference reaches using a nearest-neighbor Discriminant Function Analysis (DFA). We described differences in riparian condition and instream habitat between reference and conservation sites using reclassification accuracy. Variables were only included in this analysis if encountered at greater than 10% of all sampling events. To identify specific changes to riparian and instream conditions at conservation reaches, we used to logistic with a stepwise forward selection procedure to compare the binary treatment groups. Multi-collinearity was assessed for the resultant model using the intercept-adjusted cumulative condition index (<10) and, when collinearity was detected the most practically measured variable was retained.

Benthic invertebrate and fish assemblages and fish size structure. – We described differences in benthic invertebrate and fish assemblages between reference and conservation stream reaches using the reclassification accuracy from two separate DFAs. We compared several measures of community structure (richness, evenness, and diversity) and region-specific indices of biotic integrity (Bertrand and Troelstrup 2013) between conservation and reference sites using general linear models. These indices were calculated for benthic invertebrates and fish assemblages. One-way ANOVA, blocked by season, was used to compare the percent of abnormalities in the captured fish population between treatment groups.

Fish population dynamics. – We used Kologorov-Smirnov tests to compare length-frequency distributions, (10 mm length groups) for all fish species, between treatments. Separate tests were conducted for each season and species combination. We calculated Creek Chub mean length-at-age for each reach using all individuals captured in summer 2015. We used the aged individuals to create a probability matrix to estimate the proportion of individuals of each age within each length-class. Ages were assigned to unaged individuals following the method of Isermann and Knight (2005). This age-length key was used to convert our length-frequency data to age-frequency and increase the sample size. We evaluated differences in mean length of Creek Chub captured at reference and conservation stream reaches using ANOVA, blocked by age. All analyses were conducted using SAS v9.2 (SAS Institute, 2008).

Taxa-habitat relationships. – Canonical Correspondence Analyses (CCA) were used to describe the effect of riparian condition and instream habitat on fish and invertebrate assemblages. This multivariate technique identifies the relative influence of environmental variables (vectors) on specific benthic invertebrate and fish taxa without regard to treatment (Jongman et al. 1995). By identifying environmental variables that influence benthic invertebrate and fish abundances we described potential environmental targets for further restoration efforts. Rare habitats or species (<10% of sample events) and redundant variables (Spearman r >0.60) were removed to reduce the dimensionality of these datasets prior to analyses (D'Ambrosio et al. 2009). We created ordination biplots to visually demonstrate the relationship between assemblage structure and informative environmental variables.

RESULTS

Riparian condition and instream habitats. – Conservation efforts, in surrounding grasslands, restored riparian processes (DFA reclassification rate = 82.1%) which improved local water quality and created diverse instream habitat complexes (DFA reclassification rate = 69.4%). Significant differences in riparian condition (Logistic regression, forward selection: Residual χ^2 = 9.2, df = 15, P = 0.87) and instream environments (Residual χ^2 = 8.1, df = 6, P = 0.23) were apparent between conservation and reference sites (Table 1).

Reference sites were characteristically more homogeneous, with less riparian vegetation compared to conservation sites. Siltation, stream bank degradation, and riparian vegetation trampling were rampant at reference sites (Table 1). Within in the riparian area, reference sites were 20 times more likely to have a high proportion of bare soil ($\chi^2 = 12.4$, $P < 0.01$), potentially related to the four-fold increase in animal damage ($\chi^2 = 13.8$, $P < 0.01$). Turbidity was approximately three times greater at agricultural sites (reference: 33.3 ± 6.9; conservation: 10.0 ± 2.1), where exposed soil and banks damaged by animal trampling were prevalent (Table 1). Although conservation stream reaches had well vegetated riparian areas, invasive plant species' dominance was 4 times more likely than at reference sites ($\chi^2 = 9.7$, $P < 0.01$).

The effects of conservation on instream habitat availability were less clear (Table 1). Although mean discharge increased ($\chi^2 = 4.7$, $P = 0.03$), and aquatic vegetation ($\chi^2 = 11.9$, $P < 0.01$) and large detritus materials ($\chi^2 = 4.0$, $P = 0.04$) were ubiquitous after conservation, the effects sizes were quite small (<5%; Table 1). Owing to riparian vegetation development, overhanging vegetation ($\chi^2 = 5.0$, $P = 0.03$) was close to two times more likely at conservation reaches (Table 1). Woody debris ($\chi^2 = 6.2$, $P = 0.01$) was approximately 50% more likely to occur in conservation stream reaches than in control sites, where trees were rare in the riparian area (Table 1).

Fish and benthic invertebrate assemblages. – We collected 15,804 fish representing six orders, eight families, and 25 species. We collected and identified 32,412 individual benthic invertebrates from 22 different taxonomic groups. No South Dakota Species of Greatest Conservation Need (SGCN; SDGFP 2014) were captured. Fish (DFA reclassification rate = 56.4%) and benthic invertebrate (DFA reclassification rate =

54.9%) assemblages were indistinguishable between conservation and reference reaches. No measure of fish or benthic invertebrate diversity nor biotic integrity differed significantly between treatment groups (Table 2). External abnormalities were rare throughout the study, and the percent of abnormalities in the fish community was similar for both conservation and reference sites ($F_{1, 44} = 0.29$, $P = 0.59$).

Fish population dynamics

Fish size structure. – There was no effect of sampling year on fish size structure so data were combined across years. Length-frequency distributions of two common fishes were significantly different between treatment groups. Fathead Minnow *Pimephales promelas* were significantly larger at conservation sites during all sampling seasons (Figure 2). Creek Chub were larger at conservation sites in spring and summer (Figure 3). Length frequency histograms for all other species captured were similar between conservation and reference stream reaches.

Age structure of a native intolerant fish. – Despite being regularly captured at additional sites, Creek Chub were only abundant enough at twelve sites, six conservation-reference pairs, for age structure analyses ($N = 327$). Regardless of treatment, Creek Chub populations were primarily composed of two age groups; 53% of all individuals were ages 0 or 1 (Figure 4). Although the oldest individuals collected at either treatment were estimated to be 5 years old, these fish represented <3% of their populations (Figure 4). In general, Creek Chub were older and larger at conservation reaches than reference sites (Figure 4). Creek Chub were more abundant at reference sites, but reference populations were dominated by small, young individuals (Figure 4). Mean length was larger at conservation sites (94.0 ± 5.3 mm) than at reference sites (69.8 ± 2.5 mm), but mean length-at-age did not differ between treatments ($F_{1,5}$ = 1.29, P = 0.26; Figure 5).

Taxa-habitat relationships

Thirteen macroinvertebrate taxa (Figure 6) and 16 fish species (Figure 7) were included in the taxa-environment CCAs; others were excluded for rarity. Ten environmental explanatory variables that represent both riparian condition (bare soil, vegetated ground cover, and trees) and instream environments (turbidity, overhanging vegetation, large substrate, canopy cover, woody debris, large coarse organic materials, and aquatic plants) were retained. Variables included in the taxa-environment CCAs were not redundant and none had variation inflation factors greater than 7.

Benthic invertebrates. – Variation in invertebrate assemblage structure explained by local environmental conditions was 39.3% along axis 1 and 29.7% along axis 2 (Figure 6). Bare soil and abundant vegetated ground cover were the most influence variables we measured in the riparian area (Figure 6). In the stream channel, large substrates, woody debris, overhanging vegetation, canopy cover, and turbidity in the stream channel were the strongest of the analyzed variables (Figure 6).

A strong horizontal gradient along the first CCA axis was explained by variation in turbidity, woody debris, overhanging vegetation, substrate richness, and large substrates (Figure 6). Increased turbidity was located on the left side of axis 1, whereas abundant overhanging vegetation, woody debris, substrate richness, and large substrate classes were positive and located on the right side of axis 1 (Figure 6). The horizontal axis, left to right, well represents a transition from homogenous fine substrates, common in turbid environments, to diverse instream habitats (Figure 6). Although conservation actions are able to influence instream habitat diversity, conservation and reference site centroids were distributed throughout the horizontal gradient and likely more closely associated to subwatershed than treatment (Figure 6).

The second CCA axis was strongly influenced by riparian condition; variation was explained by bare soil, trees, canopy cover, and vegetated ground cover (Figure 6). This vertical axis, top to bottom, generally represents common prairie successional processes, from bare soil to short vegetation and, eventually to tree establishment, suggesting that riparian age may influence invertebrate assemblages (Figure 6). Conservation centroids were largely clustered near the bottom of the vertical axis, suggesting that riparian areas are generally well developed after conservation efforts (Figure 6). However, numerous reference sites are grouped nearby, illuminating the potential influence of subwatershed on riparian condition (Figure 6).

Taxa centroids identified unique and sometimes intimate relationships between several benthic invertebrate groups and specific environmental conditions (Figure 6). Leeches (Archynchodellida) were most abundant in areas with bare soil and abundant coarse organic materials (Figure 6). Conversely, Caddisflys (Trichoptera) larvae were more abundant in areas with trees that provide canopy cover and vegetated ground cover (Figure 6). Sideswimmers (Amphipoda) were closely associated with overhanging vegetation, woody debris, and large substrates (Figure 6). A weaker relationship was recognized between the same environmental variables and Mayfly naiads (Ephemeroptera; Figure 6). In contrast, Planorbidae snails, true bugs (Hemiptera), crayfishes, and the aquatic worms (Naididae and Lumbriculida) were common in homogenous, turbid environments (Figure 6). Fingernail clams (Sphaeriidae) and beetles (Coleoptera) were, to a lesser extent, also associated with turbidity (Figure 6). Freshwater snails (Physidae and Lymnaeidae) and Odonata were closely associated with increased aquatic vegetation (Figure 6).

Fish. – Variation in fish assemblage structure explained by local environmental conditions was 32.5% along axis 1 and 26.2% along axis 2 (Figure 7). Few riparian conditions were strongly associated with fish assemblage structure (canopy cover; Figure 7). In the stream channel, overhanging vegetation, large substrates, aquatic plants, and woody debris were the most influential variables analyzed (Figure 7).

The first CCA axis was explained by variation in overhanging vegetation, coarse organic materials, large substrates, and aquatic plants (Figure 7). Stream reaches with abundant aquatic vegetation and large coarse organics were on the right side of CCA axis 1, whereas areas with more overhanging vegetation and larger substrates were located on the left (Figure 7). The horizontal gradient represents to common stable states in stream ecosystems. Established vegetation in the riparian zone can intercept excess sediments, improve water clarity, and help expose embedded large substrates, whereas coarse organics materials are generally common in over productive areas with abundant aquatic vegetation (Figure 7). Although conservation centroids are dispersed widely along this horizontal access, a large proportion are located on the left side and not in close proximity to their specific reference site pair, suggesting a change to the improved stable state (Figure 7).

The second CCA axis was explained best by riparian condition (Figure 7). Reaches with more woody debris and trees that provide canopy cover were located near the bottom of CCA axis 2, whereas areas with bare soil exposed in the riparian zone were positioned near the top of CCA axis 2 (Figure 7). Similar to the invertebrate analysis, this vertical axis, top to bottom, describes grassland successional process that start with bare soil and, in the absence of disturbance, end with tree establishment (Figure 7). Most reference site centroids were located near the top of the vertical axis, while many conservation sites were near the bottom (Figure 7). Stream reaches with well developed, mature riparian areas seem to strongly influence fish assemblages (Figure 7).

Species centroids identified habitat associations of several fishes in the James River basin (Figure 7). Increased overhanging vegetation and larger substrates were closely related to the abundance of three native nontolerant coolwater fish species (*i.e.*, Creek Chub, Iowa Darter *Etheostoma exile*, and Johnny Darter *Etheostoma nigrum*). In addition, Tadpole Madtom *Noturus gyrinus* abundance was associated with the same environmental features (Figure 7). Each of these species were only weakly associated with axis 2 (Figure 7). In contrast, Common Carp *Cyprinus carpio* and Yellow Perch *Perca flavescens* responded to increased aquatic plant cover and abundant large coarse organic materials (Figure 7). Blacknose Dace *Rhinichthys atratulus* influences local Index of Biotic Integrity (IBI) values (Krause et al. 2013) and responded strongly to increased canopy cover and woody debris (Figure 3). Fathead Minnow and Black Bullhead *Ameiurus melas* were abundant in turbid stream reaches with bare soil in the riparian area (Figure 7). Northern Pike *Esox lucius* were common in environments with bare soil in the riparian area and abundant aquatic plants (Figure 7). Bluegill *Lepomis macrochirus* and Green Sunfish *Lepomis cyanellus* negatively impact IBI scores and seem to respond positively to increased turbidity and overhanging vegetation (Figure 7).

White Sucker *Catostomus commersonii* and Brook Stickleback *Culaea inconstans* were located near the origin indicating no strong association with any habitat factor (Figure 7).

DISCUSSION

Grassland management improved local water quality and restored processes that create and maintain diverse habitat complexes in conservation stream reaches. Despite these changes to riparian function and improvements to local stream environments, aquatic taxa did not, thus far, respond to conservation actions. For two species, population size structure was skewed to larger individuals in response to conservation actions. Further research may demonstrate whether local population dynamics were changed or large individual were attracted from nearby areas. We identified several environmental features to which fish and benthic invertebrate taxa responded positively, many of which can be directly influenced by management. Below, we summarize the effectiveness of grassland restoration practices to improve riparian condition, instream water quality and habitat, and aquatic biota.

Riparian and instream habitats. – Riparian rehabilitation, generally via passive methods (*e.g.,* cattle exclusion, buffer strips), facilitated the development of vegetation along conservation stream banks. Similar to other short-term (< 10 years) stream restoration studies, our research demonstrates the propensity for riparian ecosystems to quickly recover following anthropogenic disturbance (Jorgensen et al. 2000; Robertson and Rowling 2000; Roni et al. 2008). Riparian vegetation was well developed at conservation sites, which presumably restored many ecosystem functions (*i.e.,* temperature regulation, sediment storage, organic inputs, nutrient cycling). Substantial grazing pressure and row-crop encroachment persisted at nearby reference reaches. As with other restoration programs, grassland management shows initial promise toward developing hardwood rich riparian zones that are expected to benefit both fish and benthic invertebrate diversity (Sprenger et al. 2002). However, 25% of conservation sites were dominated by non-woody invasive plant species that can hinder further improvements via successional processes if left unmanaged (Sprenger et al. 2002). Riparian plantings are thought to improve instream environments and benefit aquatic taxa; however, relatively little research has connected rehabilitation efforts to specific instream habitats and fish responses, and even fewer have examined other lotic fauna (Penczak 1995; Roni et al. 2008; Sass et al. 2017).

Restored riparian areas can improve water quality, reduce sedimentation, and increase channel stability (Parkyn et al. 2003; Dosskey et al. 2005; Puckett and Hughes 2005). Although instream conditions are expected to recover more slowly than riparian areas, conservation reaches in this study were clearer with more heterogeneous habitat than reference reaches. The newly developed riparian ecosystems effectively reduced stream turbidity by reducing the local influx of sediments carried by overland flow (Kauffman et al. 1997; Sovell et al. 2000; Voichick et al. 2016). Uninterrupted sediments continue to pollute the non-vegetated and actively disturbed (*i.e.*, cattle grazing and row crop agriculture) reference reaches. Suspended sediments degrade the visual environment in turbid systems (Utne-Palm 2002; Shoup and Wahl 2009), impact survival of early life stages and reproductive success (Fiksen et al. 2002), and alter fish assemblage structure (Rodriguez 1997). Following riparian restoration, the abundance of coarse organic materials has in the stream bed increased in this study and others (Robertson and Rowling

2000). These organic materials are often the foundation of prairie stream trophic systems and provide important habitat for more fish and benthic invertebrate food source (Dodds et al. 2004). By restoring diverse vegetation in the riparian area, managers provided dense root structures that stabilized stream banks at conservation reaches and helped increase mean water discharge; results often reported in other regions (Myers and Swanson 1995; Dosskey et al. 2005). Increased inputs and improved retention of woody debris was directly related to the prominence of trees at conservation reaches (Myers and Swanson 1995). The abundance of woody debris in streams is commonly linked to benthic invertebrate and fish diversity, but had little effect on biota in the current study (Roni 2003; Johnson et al. 2005; Miller et al. 2010).

Benthic invertebrate and fish assemblages. – Efforts to quantify the responses of stream biota to riparian rehabilitation projects are rare and have largely focused on fish (Roni et al. 2008). When measured, diversity has either only slightly increased or been unchanged by restoration (Rinne 1999; Bond and Lake 2003a; Medina et al. 2005; Lepori et al. 2005). It is suspected that aquatic macroinvertebrates respond to conservation efforts quicker than fish (Miller et al. 2010); however, for both taxa, recovery depends on the proximity of source populations and the regional species pool (Bond and Lake 2003a; Stoll et al. 2014; Tonkin et al. 2014). Our research has yet to demonstrate changes to benthic invertebrate and fish assemblage structure in response to conservation; however, some evidence suggests that aquatic invertebrate assemblages differ more between treatments than fish. The development of isolated niche space doesn’t directly translate to successful colonization and subsequent occupation by aquatic life. Instead, the recovery of local aquatic diversity after restoration efforts may be strongly dictated by the sites position on the landscape.

Nearly 20% of the taxa we collected were not well distributed throughout the James River basin and, in most cases, were only encountered at one conservation-reference stream reach pair. Variations in abundance and occurrence of these taxa (*e.g.,* Blacknose Dace and Tadpole Madtom) could be explained by stream system alone. Future colonization by these taxa is unlikely at a large number of conservation sites throughout the James River basin. However, many taxa occurred throughout the basin so their distributions and local abundances were potentially more sensitive to conservation efforts that were scattered throughout the region. To successfully increase biodiversity and benefit at-risk species, that are often poorly distributed, management efforts should target areas most likely to achieve these goals. For example, Topeka Shiner *Notropis topeka,* a federally endangered cyprinid, are present in the James River basin but none were captured during our sampling efforts. Nearly 60% of conserved landscapes in the James River basin are located in subwatersheds where the probability of Topeka Shiner occurrence is < 20% (M. Wagner, Mississippi Department of Wildlife, Fisheries, and Parks, personal communication). Only ~15% of conservation sites are located in areas where the probability of Topeka Shiner occurrence is > 40% (M. Wagner, personal communication). Strategic conservation investments in areas most likely to be colonized by unique or rare species may better achieve management objectives related to diversity.

Fish population dynamics. – Although changes to fish assemblage structure were minimal after conservation efforts, the size structures of two species were significantly altered. For both species, larger individuals were encountered more frequency at conservation reaches than the reference sites. Although rare, similar studies have identified changes to fish population size structure, particularly adult salmonids (Binns 2004; White et al. 2011), after restoration efforts, but most studies have found negligible effects (Riley and Fausch 1995; Roni and Quinn 2001; Vehanen et al. 2010). Disagreement persists as to whether measured effects are in response to changed local population dynamics or the attraction of large, presumably dominate, individuals from adjoining areas (Riley and Fausch 1995).

We found no evidence that Creek Chub growth rates or age structure were changed in response to conservation actions. Two generations are usually necessary before population level response to conservation actions are detected at individual stream reaches (Reeves et al. 1991). Because Creek Chub mature rapidly, up to six generations have come to be at the conservation reaches without measurable changes to mean length-at-age.

Taxa-habitat relationships. – Reduced habitat availability and poor water quality are often regarded as the primary factors that limit populations and assemblages in degraded stream ecosystems (Bond and Lake 2003b; Sass et al. 2017). By restoring that ecosystems processes in riparian areas that improve water quality and provide additional habitat in streams, managers plan to elicit a biological response from targeted species or assemblages (Palmer et al. 2005; Roni et al. 2008). However, this requires an understanding of which environmental features favor occupancy by specific aquatic taxa. The determination of specific environmental targets for stream restoration efforts to benefit particular taxa and increase biodiversity is critical but often addressed with limited data (Bond and Lake 2003b; Roni et al. 2008). We identified several environmental features that impact fish and macroinvertebrate diversity and are influenced by grassland conservation efforts. We provide a component of the restoration framework described by Hobbs and Norton (1996) by generating evidence of important organism-habitat relationships necessary to generate realistic goals for restoration actions. Our results suggest that benthic invertebrates and fishes respond strongly to changes to the riparian area that increase ground vegetation and tree cover. In addition, fish and benthic invertebrates responded to patches of structural habitat near vegetation; conditions that were rarely met in degraded stream reaches. Managers can supplement riparian rehabilitation efforts by providing large substrates and woody debris in areas with abundant aquatic and overhanging vegetation. Grassland conservation efforts created niche space that is beneficial to local aquatic fauna, but that were not utilized in inaccessible areas.

Restoration projects often assume that the creation of habitat is the key to restoring aquatic biota (‘field of dreams’ hypothesis, Palmer et al. 1997); however, many other factors may interrupt the link between habitat and biotic restoration (Bond and Lake 2003a; Roni et al. 2008). Although grassland management actions improved local stream conditions, they do not address stream connectivity issues or overcome damaging land and water practices elsewhere in the riverscape that may govern animal responses. Although the cumulative protected area exceeds 81,000 acres, each conservation easement only represents a sliver of the riverscape. Not all restored sites were *created* equally; each have local and riverscape scale constraints that dictate biotic response patterns. Three alternative hypotheses potentially explain the limited biotic response: (1) connections to newly available habitats remain severed; (2) regional assemblages lack species adapted to utilize opened niches; and (3) the niche space created does not benefit local species. The development of niche space does not directly translate to successful colonization and subsequent occupation by aquatic life.

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Table 1. Significant environmental measures used to differentiate between "conservation" (Conservation Reserve Enhancement Program) and paired "reference" sites. Riparian condition (intercept: 1.82 [0.53], $\chi^2 = 8.12$, df = 6, $P = 0.23$) and instream habitat (intercept: -2.98 [0.75], $\chi^2 = 9.19$, df = 15, $P = 0.87$) were analyzed separately using forward selection, stepwise logistic regression.

Environmental Condition	Coefficient (SE)	Wald Chi-Square	*P* value	Odds Ratio	Conservation (mean ± SE)	Reference (mean ± SE)
Riparian Zone						
Bare Soil (Index)	-3.02 (0.86)	12.4	< 0.01	0.05	0.17 (0.04)	0.86 (0.11)
Animal Damage (Index)	-1.27 (0.34)	13.8	< 0.01	0.28	0.62 (0.16)	1.98 (0.17)
Invasive Species (Index)	1.39 (0.45)	9.7	< 0.01	4.01	1.21 (0.18)	0.49 (0.12)
Instream Habitat						
Mean Discharge ($m^3 s^{-1}$)	0.05 (0.02)	4.7	0.03	1.05	19.3 (4.9)	4.4 (1.4)
Overhanging Vegetation (Index)	0.65 (0.29)	5.0	0.03	1.92	1.1 (0.15)	1.0 (0.15)
Aquatic Vegetation (% area)	0.04 (0.01)	11.9	< 0.01	1.04	47.5 (4.7)	17.5 (4.2)
Large Coarse Organics (% area)	0.03 (0.01)	4.0	0.04	1.03	32.4 (4.0)	11.1 (3.0)
Woody Debris (% area)	0.31 (0.12)	6.2	0.01	1.36	3.4 (0.97)	0.69 (0.30)

Table 2. Benthic invertebrate and fish measures of assemblage structure (mean ± SE) from collections, 2013-2015, at "conservation" (Conservation Reserve Enhancement Program) and "reference" stream reaches and located throughout the James River basin, South Dakota.

Taxa	Assemblage Metric	Conservation	Reference
Benthic Invertebrates	Richness	6.4 (0.69)	5.7 (0.52)
	Evenness	0.11 (0.01)	0.10 (0.01)
	Simpson's D	2.62 (0.25)	2.29 (0.22)
	IBI Score	39.8 (2.0)	40.5 (2.5)
Fishes	Richness	3.4 (0.34)	4.3 (0.37)
	Evenness	0.11 (0.01)	0.11 (0.01)
	Simpson's D	1.75 (0.11)	1.76 (0.11)
	IBI Score	50.2 (1.9)	48.3 (1.6)

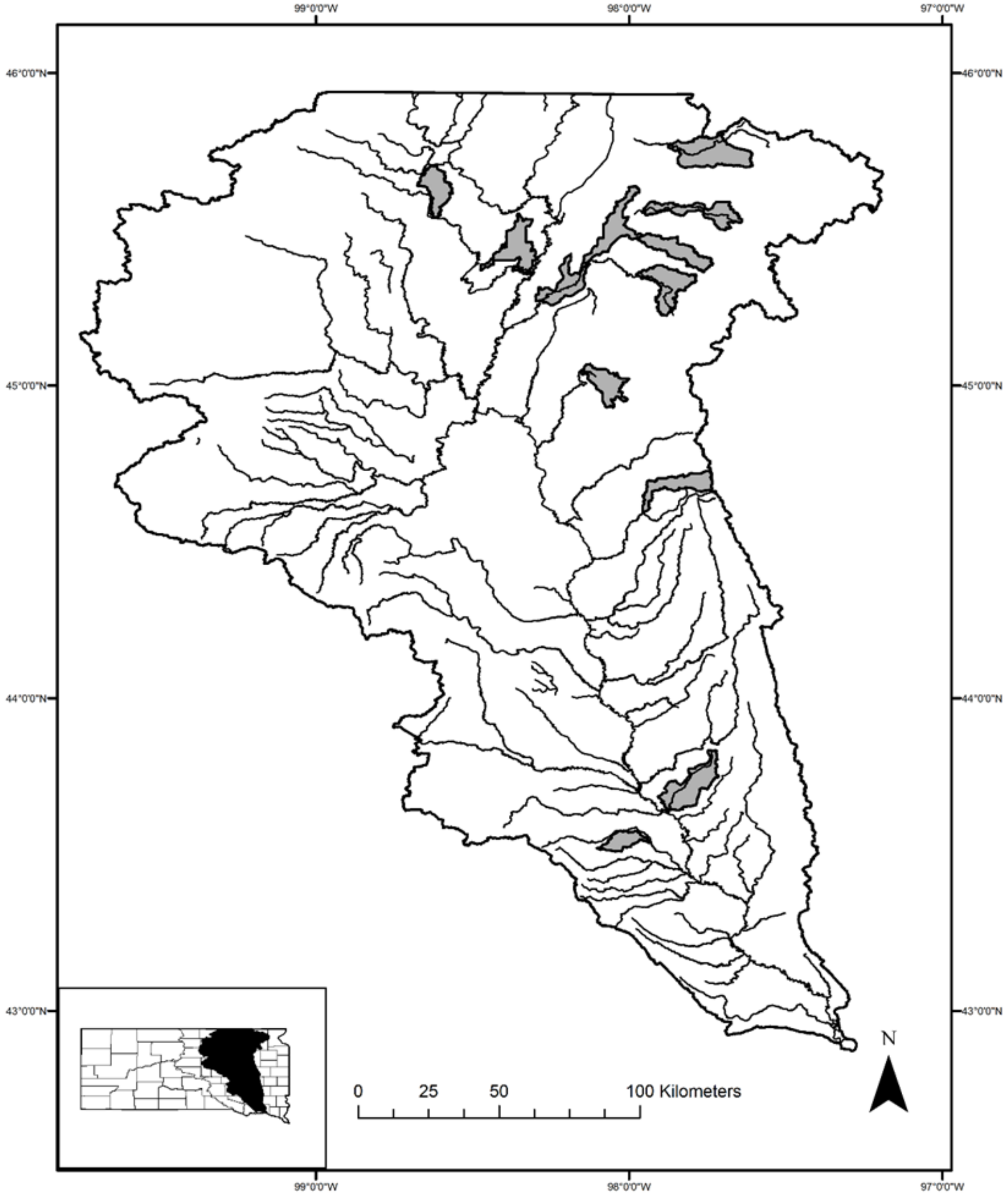

Figure 1. Twelve selected subwatersheds (HUC-12) used to describe local aquatic resource response to grassland conservation in the James River basin of eastern South Dakota. Within each subwatershed a pair of "conservation" and upstream "reference" sites were sampled three times annually from 2013-2015.

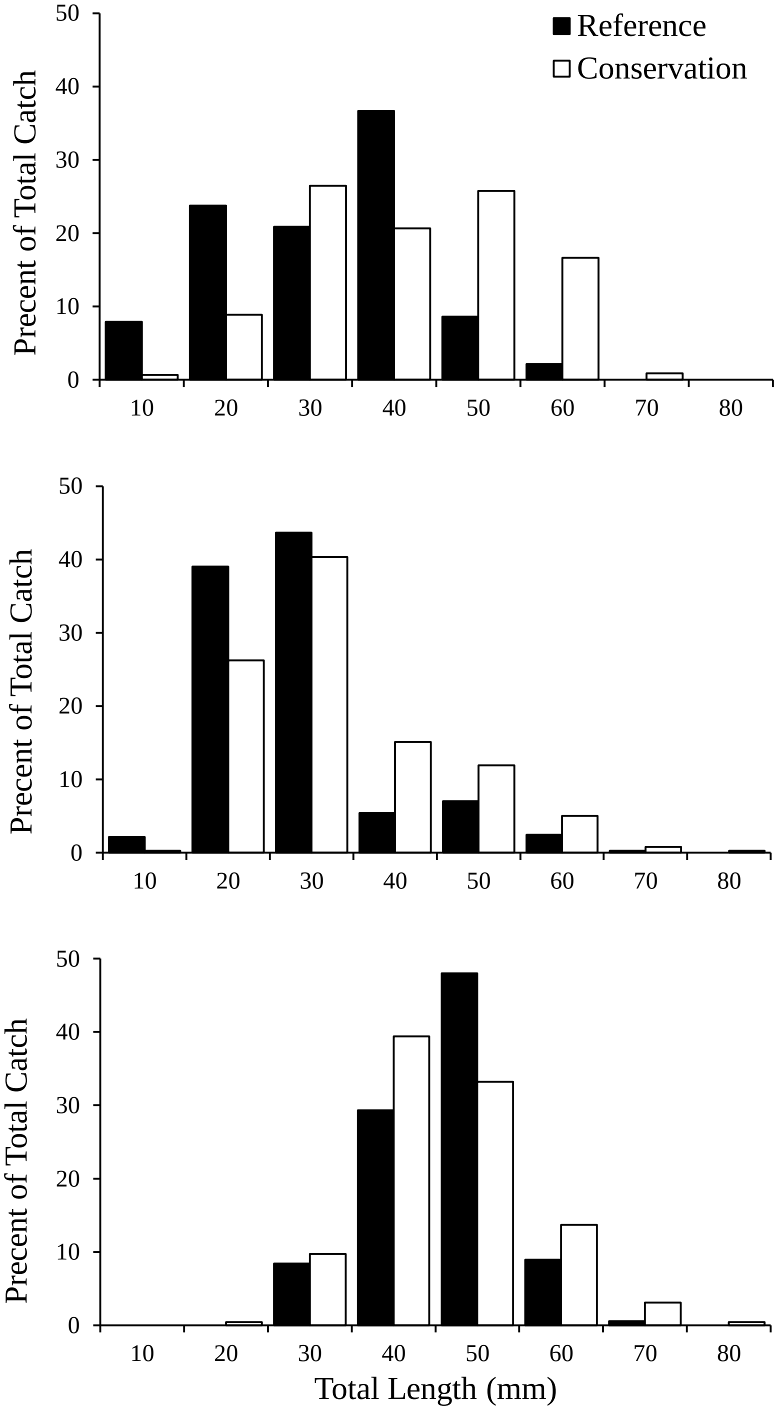

Figure 2. Fathead Minnow *Pimephales promelas* length frequency histograms from “conservation” and “reference” stream reaches within the James River basin, South Dakota during 2015, spring (top), summer (middle), and fall (bottom).

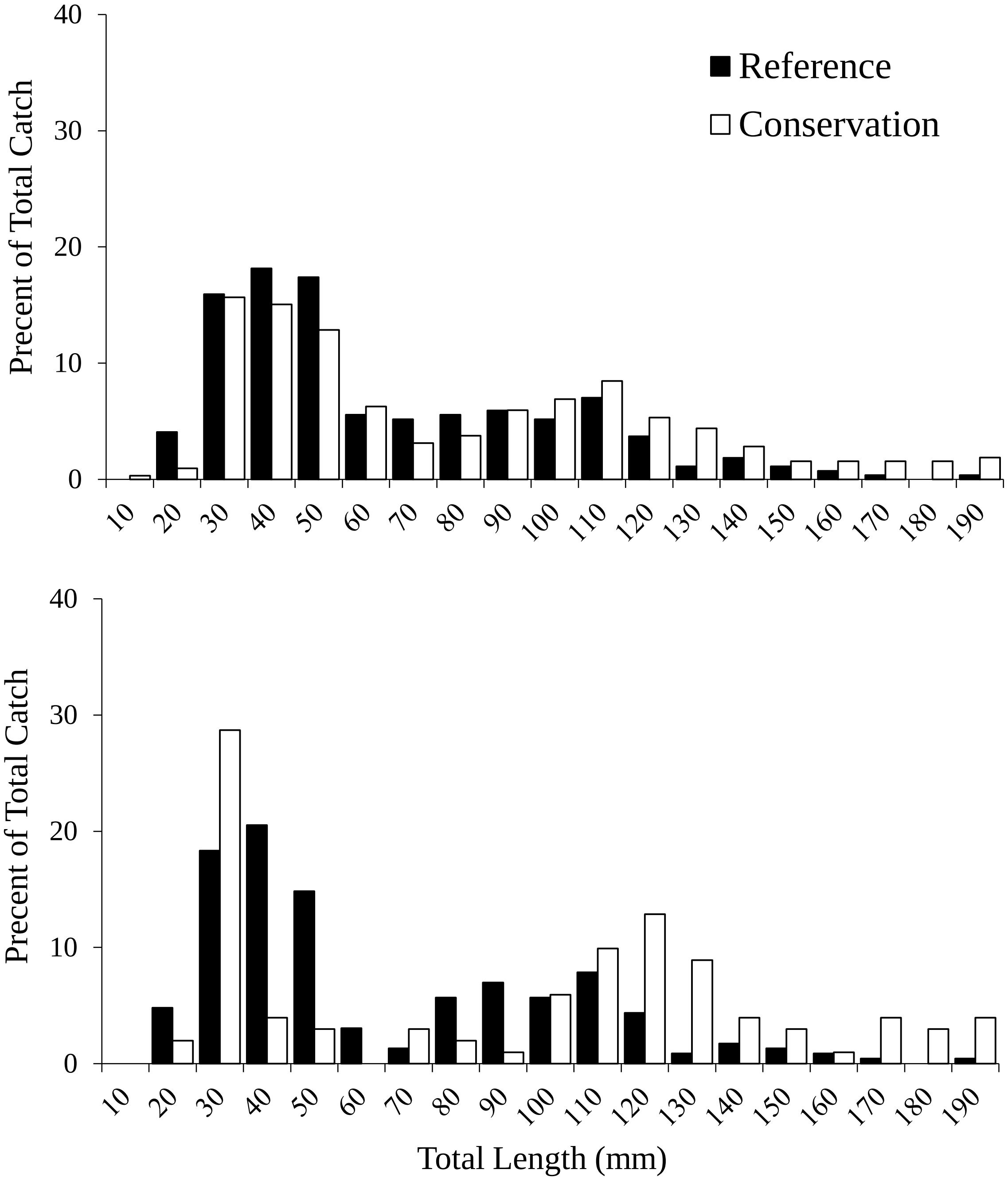

Figure 3. Creek Chub *Semotilus atromaculatus* length frequency histograms from “conservation” and “reference” stream reaches within the James River basin, South Dakota during 2015, spring (top) and summer (bottom).

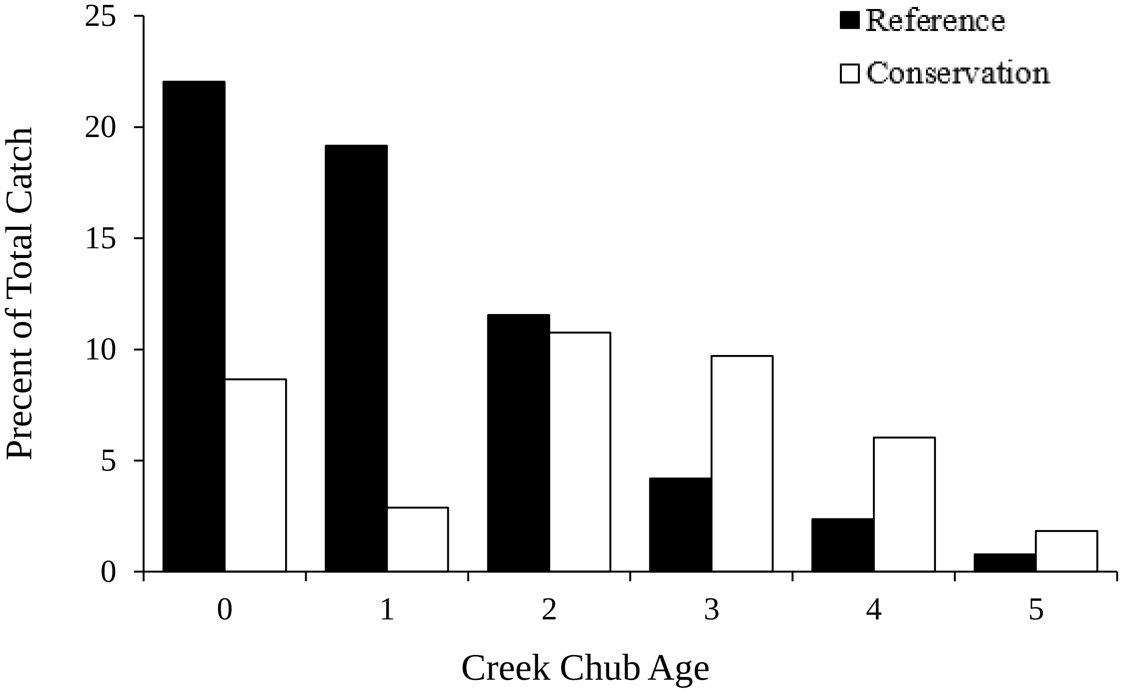

Figure 4. Age composition of Creek Chub *Semotilus atromaculatus* captured during summer 2015 at six paired “conservation” and “reference” stream reaches in the James River basin, South Dakota.

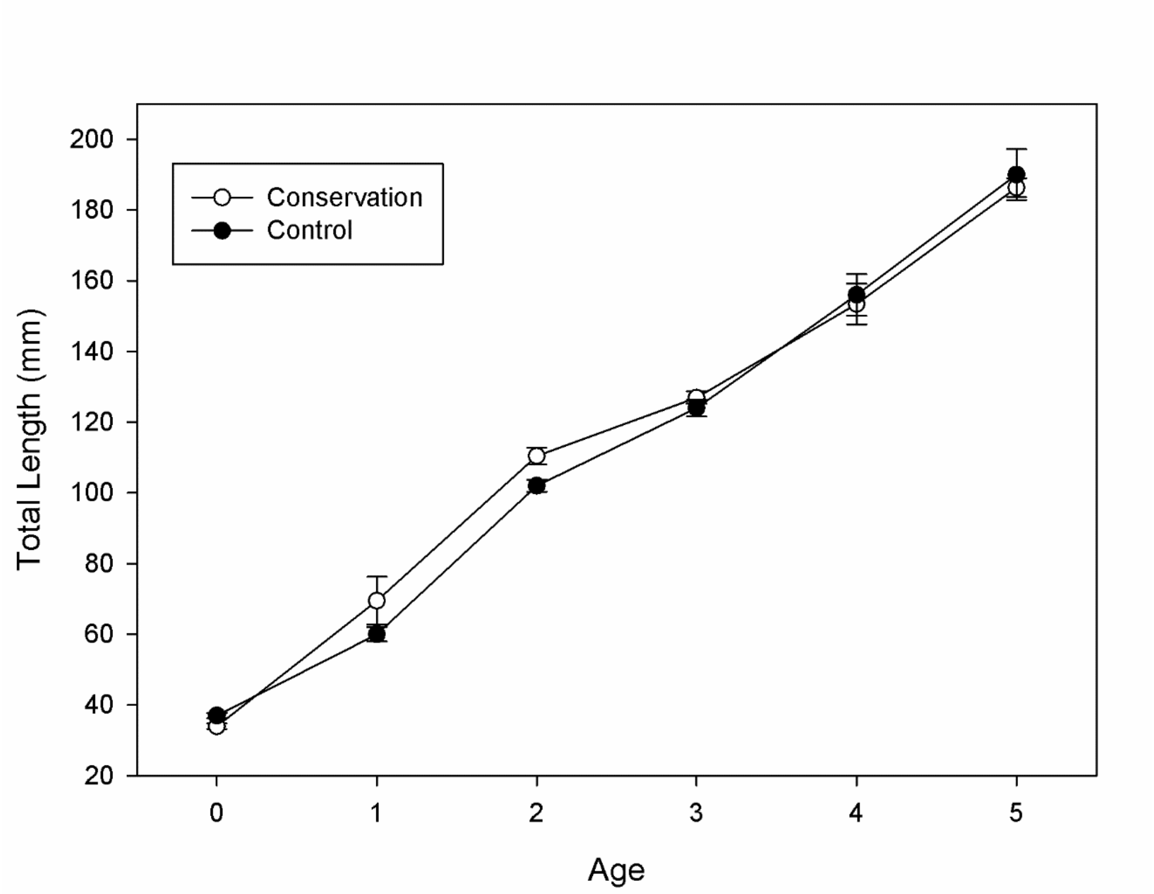

Figure 5. Mean length-at-age and standard error for Creek Chub *Semotilus atromaculatus* (*N* = 327) collected in summer 2015 from “conservation” and “reference” stream reaches in the James River basin, South Dakota.

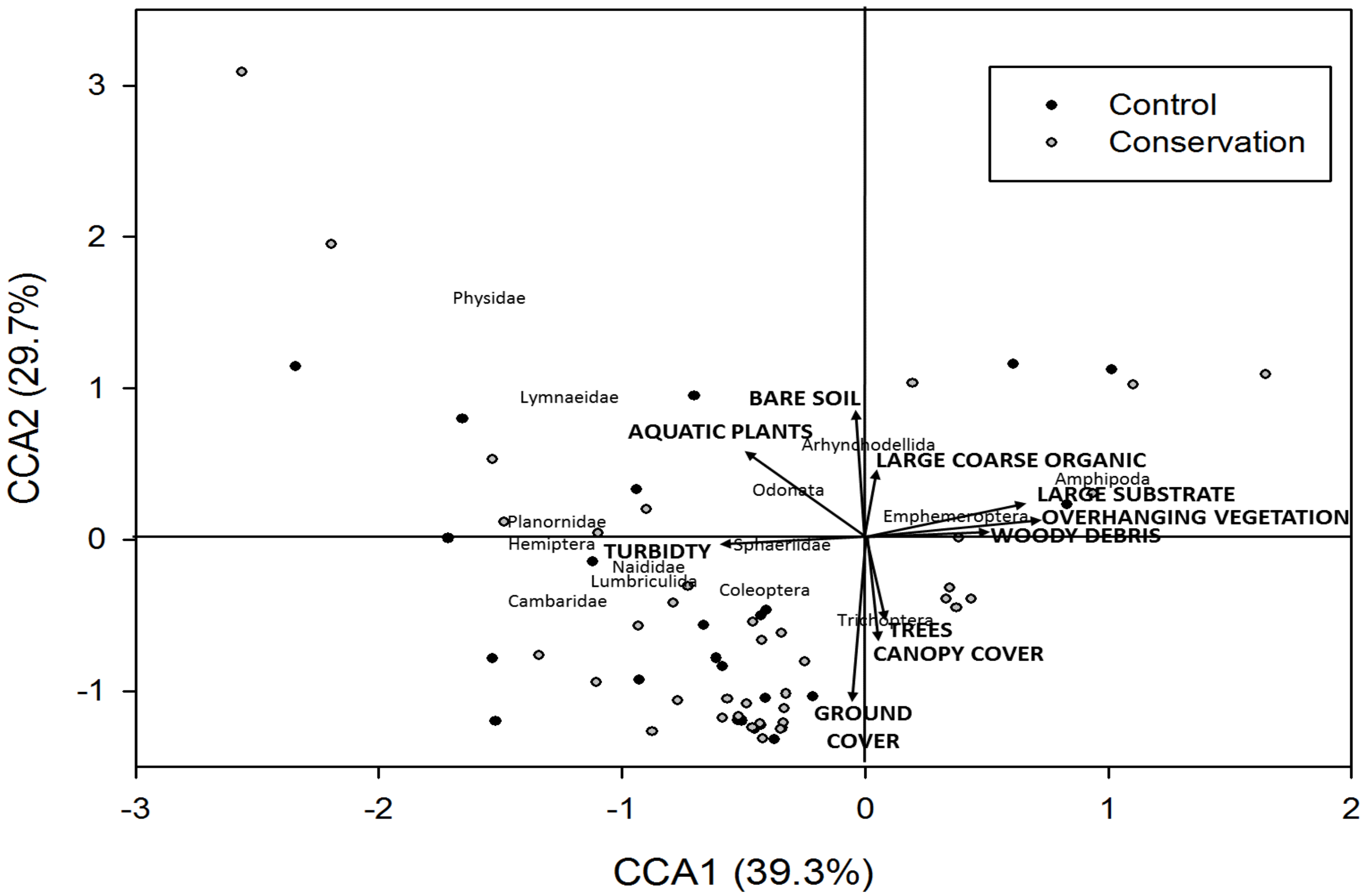

Figure 6. Canonical Correspondence Analysis of retained environmental measures with benthic invertebrate assemblage features plotted as species. Environmental vectors describe the direction and magnitude of their effect on benthic invertebrate assemblage structure in the James River basin, South Dakota.

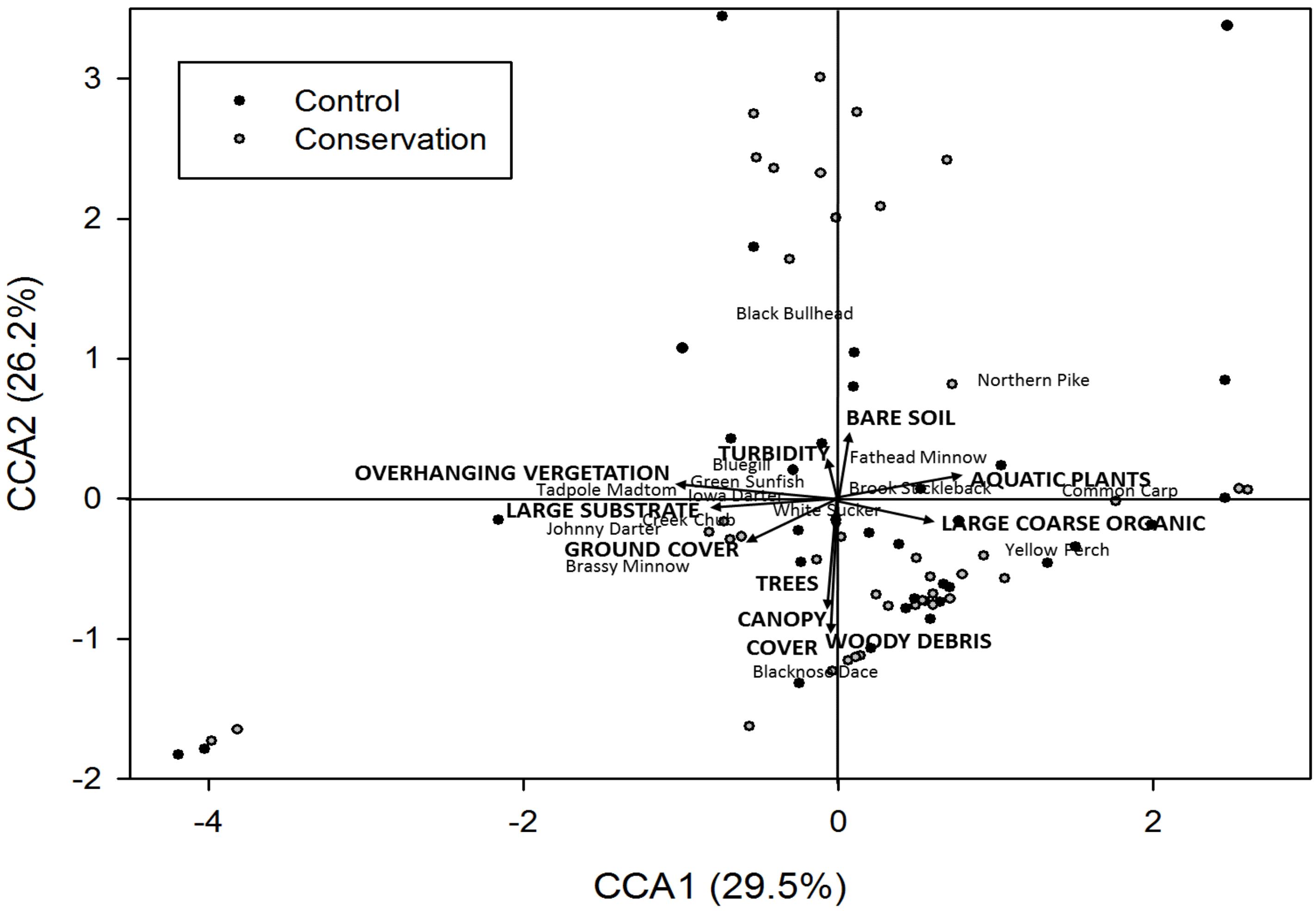

Figure 7. Canonical Correspondence Analysis of retained environmental measures with fish assemblage features plotted as species. Environmental vectors describe the direction and magnitude of their effect on fish assemblage structure in the James River basin, South Dakota.

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CHAPTER THREE

MOVEMENT OF PRAIRIE FISHES IN A FRAGMENTED RIVERSCAPE: ECOSYSTEM PROCESSES RISK BEING *RATCHETED DOWN*STREAM

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ABSTRACT

Prairie streams are dynamic systems wherein habitat patches are sporadically created and lost during extreme hydrologic events. Strong environmental pressures commonly result in local fish extirpation and species persistence depends on life history traits that facilitate dispersal over large areas. Lost connectivity throughout stream networks has severed historic movement pathways and may limit recolonization opportunities for fishes. Although barriers are thought to fragment and ultimately ratchet fish populations downstream, the relative vulnerability and ecological consequences of lost prairie fish diversity above barriers are largely unknown. We describe the susceptibility of four small-bodied prairie fishes to stream fragmentation and the consequent risk to stream ecosystems. The selected species exhibit wide tolerances to environmental stressors and represent unique functional feeding guilds and habitat affinities. Extirpation-recolonization potential likely varies among species and each are expected to have different effects on local stream ecosystem processes. We quantified each species' ability to access (jumping aptitude) and successfully traverse (swimming endurance) simulated instream barriers. Experimental stream complexes were used to isolate the unique effects of each species on ecosystem processes with replication. In these 'knockout' experiments each treatment imitated the extirpation of one species that was unable to recolonize and a 'no fish' control was used. Prairie fishes are not equally vulnerable to instream barriers, but all failed to circumvent relatively minor obstacles. Small vertical barriers (> 5 cm) blocked most fish passage and, with access, all species were unable to traverse relatively short obstacles with moderate water velocities. Without colonization opportunities from neighboring source populations, disturbance events will

alter headwater fish assemblage structuring. Lost fish diversity above barriers will hinder stream ecosystem processes as species were not ecologically redundant and each impacted ecosystem structure differently. The risk of systematic species loss above barriers greatly outweighs the opportunity for improvement (*i.e.*, ecological ratchet) suggesting that ecosystem structure could be moving downstream. Abundant barriers to recolonization with limited tools to improve passage for small-bodied prairie fishes will interact with a range of stochastic and human-mediated disturbances to further threaten fish assemblage structuring and ecosystem processes in headwater streams.

INCTRODUCTION

Prairie streams are dynamic systems, wherein habitat patches are sporadically created and lost as a result of highly variable hydrologic episodes (Matthews 1988; Dodds et al. 2004; Fritz and Dodds 2005). Prairie fish assemblages are structured by this erratic hydrology and extreme environmental pressures that regulate local abundance and distribution (Poff and Ward 1989; Kelsch 1994; Lohr and Fausch 1997; Franssen et al. 2006). Local species persistence depends on unimpeded fish movement behaviors that balance regular stochastic extinctions and recolonization (Scheuer et al. 2003; Dodds et al. 2004; Dunham et al. 2004). However, fragmented stream habitats have isolated fish populations and interrupted dispersal pathways, potentially eliminating colonization opportunities (Perkin and Gido 2012; Rolls et al. 2013; Perkin et al. 2014).

The widespread proliferation of barriers in river networks has constrained critical fish dispersal events and has been implicated in the decline of stream fishes worldwide (Perkin and Gido 2011; Liermann et al. 2012; Wilde and Urbanczyk 2013). Road crossings are commonly considered barriers to fish movement because they increase water velocities through constrained stream channels that provide little refuge (Bouska and Paukert 2010; Anderson et al 2012; Perkin et al. 2013). Waterfalls, located on the downstream end of many culverts, potentially further segregate fish assemblages and limit access by species physically unable or unmotivated to jump (Kondratieff and Myrick 2005; Burford et al. 2009; Ficke 2011; Prenosil et al. 2015). Thus, road crossings may confine fish to downstream reaches if they are unable to traverse barriers in two dimensions (*i.e.*, vertical and longitudinal). Although studies of fish dispersal relative to road crossings are common, research that directly quantify the ability of small-bodied fish to both access (vertical) and navigate (longitudinal) barriers are relatively rare (Ficke 2011; Perkin et al. 2013; Prenosil et al. 2015). By understanding obstacles to stream fish movement in two dimensions, the threat of instream barriers will be more apparent.

Accelerated extinction rates of freshwater fishes have required ecologists to consider the consequences of diversity loss to stream ecosystem structure and function (Loomis et al. 2000; Kreman 2005; Burkhead 2012). Researchers have identified 'large and pervasive' effects and unique ecological contributions of fish feeding guilds and individual species on stream ecosystem processes (Schwartz et al. 2000; Cardinale et al. 2002; Vanni 2002; Bertrand and Gido 2007; Bertrand et al. 2009). Some fishes are known to impact primary production, decomposition rates, and nutrient sequestration in prairie streams, but it is unclear if these results can be generalized to other species (Grimm 1988; Bertrand and Gido 2007; Gido et al. 2010; McIntyre and Flecker 2010). Without colonization from nearby source populations, episodic disturbance events will alter headwater fish assemblages and may degrade the ecosystem goods and services provided above barriers.

Directional (*i.e.,* downstream) disruptions to stream fish assemblage structuring by stochastic disturbance and interrupted fish movement corridors reflect an 'ecological ratchet' (Covich et al. 1997; Birkeland 2004; Roberts et al. 2013; Perkin et al. 2014). The ratchet concept describes self-reinforcing spatial or temporal and irrevocable system change in response to natural or human disturbance (Birkeland 2004; Perkin et al. 2014). The system is unable to reverse the change as a result of introduced blockades and degradation continues without management intervention (Birkeland 2004; Perkin et al. 2014). In stream systems, ratcheting begins when longitudinal habitat connections are lost to fragmentation and regional immigration is removed from community structuring processes in headwater reaches (Angermeier and Winston 1998; Perkin and Gido 2012; Wilde and Urbanczyk 2013). Although upstream habitats recover from disturbance events and can be improved by restoration efforts, ecosystem effects persist because local diversity is lowered (Dodds et al. 2004; Roni et al. 2008; Perkin et al. 2014).

The widespread fragmentation of riverscapes has likely detached immigration from community structuring and risked alteration to the ecosystem products provided by headwater prairie streams. The systematic and irreversible (*i.e.*, ecological ratchet moving downstream) reduction in stream fish diversity may plague countless riverine systems given that potential barriers are numerous and solutions to improve passage for small-bodied fishes are limited (Bouska and Paukert 2010; Ficke 2011; Lorenzen 2016). To better understand the ecological threat of instream barriers, we assessed the relative vulnerability and ecosystem consequences of lost prairie fish diversity. Specifically, we: (1) estimated the ability of four ecologically important small-bodied fishes to bypass simulated vertical and longitudinal barriers, and; (2) describe the unique ecosystem effects of each species. This information will be useful when predicting changes to stream ecosystems where riverscape connectivity issues are not alleviated. Distinct ecological effects and movement capabilities of each species likely alter ecosystem processes above barriers and may eliminate or displace ecosystem services downstream.

METHODS

Study species. — We quantified the swimming and jumping abilities and ecological role of four dissimilar small-bodied prairie fishes; Brassy Minnow *Hybognathus hankinsoni*, Iowa Darter *Etheostoma exile,* White Sucker *Catostomus commersonii*, and Central Stoneroller *Campostoma anomalum*. The species evaluated, excluding Brassy Minnow, belong to the native coolwater guild, but all represent unique functional feeding guilds (Krause et al. 2013). Brassy Minnow are more tolerant to anthropogenic stressors and are less likely to be extirpated from prairie streams (Distler et al. 2014). Each species occupies different stream habitats, consume different prey, and likely have unique influences on local ecosystem processes (Distler et al. 2014).

Fish collection and husbandry. — We collected a representative pool of each species using seine nets from local streams in eastern South Dakota. We transported individuals to the South Dakota State University (SDSU) Fisheries Ecology Research Center in 113-L aerated containers, taking care to minimize handling stress (Harmon 2009). Fish were slowly acclimated to laboratory conditions before being transferred to species-specific segregated portions of a temperature controlled 20,000-L recirculating system (Harmon 2009). We offered fish a daily mixture of frozen bloodworms, frozen brine shrimp, and flake foods during a two-week acclimation period before experimental procedures.

Swimming performance (longitudinal barriers). — We evaluated fish swimming performance using a time-to-fatigue endurance test protocol with a 10-L Brett-type swimming chamber (Peake et al. 1997; Ficke et al. 2011). We measured fish endurance at water velocities of 16, 32, 48, 64, and 80 cm s^{-1} for all species. We sampled five replicate individuals for each species and velocity increment combination. Once assessed, we removed individuals from the experimental population to avoid training effects (Farlinger and Beamish 1978). Prior to experiments, specimens were fasted for 36 h to ensure that they were in a post-absorptive state (Peake et al. 1997). Only fish to be used for upcoming swimming trials were starved. We conducted swimming endurance tests at ~15°C.

For each replicate, we place a single fish into the swimming chamber and allowed it to orientate to the experimental chamber for 5 min. We maintained the water velocity at approximately 0.5 body lengths per second during this acclimation period. Following acclimation, we increased the water velocity to the treatment level and measured the time until the fish became fatigued. The trial was ended when the fish could no longer maintain its position in the water column and was impinged against the downstream grid for 10 s. If a fish maintained its position in the flume for more than 200 min it was assumed it could do so indefinitely and the trial was ended (Peake et al. 1997; Ficke et al. 2011). We classified fish that refused to swim or were reluctant to do so as "nonperformers" and did not include them in analyses. Swimming performance data were analyzed using a survival analysis (PROC LIFEREG in SAS). We used chi-square tests to test the significance of measured variables (total length [TL] and water velocity) at $\alpha <$ 0.05. Swimming endurance was estimated using multiple regression as follows (Peake et al. 1997):

$$\log(E) = \beta_0 + \beta_1 L + \beta_2 V + \beta_3 LV + e$$

where E is endurance (minutes), L is total length (TL; mm), V is water velocity (cm s^{-1}), and e is a normally distributed error term with mean 0 and variance σ^2. Significance was determined at $\alpha \leq 0.05$.

We used the endurance equation to estimate the maximum barrier length each species is able to pass as a function of water velocity. Maximum barrier length was calculated as:

$$V_f = V_s - (d * E_{V_s}^{-1})$$

where V_f is the water velocity in the barrier (cm s^{-1}), V_s is the swimming speed of the focal species (cm s^{-1}), d is the barrier length (cm), and E_{v_s} is the endurance for the species at the given velocity (seconds) (Peake et al. 1997). This formula provides combinations of distance and water velocity in which passage beyond a potential barrier is possible for each species.

Jumping abilities (vertical barriers). — We measured fish jumping ability using artificial waterfalls (*n* = 3) originally designed by Kondratieff and Myrick (2005). This original design has been modified and improved upon to meet particular study objectives by (Ficke et al. 2011), Prenosil et al. (2015), and the current study. However, the internal dimensions (60 x 120 [divided by weir] x 120 cm), weir design, and protocol for use have remained consistent through each study. We conducted all trials between 17 and 20°C. Weir heights evaluated were 0, 5, 10, 15, and 20 cm; however, we only tested Iowa Darter at 0 and 5 cm. We never observed an Iowa Darter successfully jump past 5 cm barriers in pilot studies. We conducted four replicate trials of ten individuals each for every species and weir height combination. Sampling was done without replacement to the experimental population. We maintained the water velocity through the weir at 76-L per min and fixed the plunge pool depth at 30 cm.

We allowed fish to acclimate to the conditions in the lower chamber of the artificial waterfall for 24 h. After the acclimation period, we adjusted the weir to the treatment height and allowed fish 24 h to access the upper chamber of the waterfall. Following each trial, we removed fish from both chambers, measured all individuals to TL, and recorded the proportion that successfully passed the barrier and accessed the upper chamber. We provided no incentive to motivate fish passage into the upper chamber. We used an information theoretic multi-model interference approach to describe the relative influence of water temperature, dissolved oxygen, TL, and weir height on passage. Models were ranked by ΔAIC_c and we used a $\Delta\text{AIC}_c \geq 4$ threshold to scale candidate model performance (Burnham and Anderson 2002). We valued individual predicator support by summing AIC_c weights (Σw) of candidate models that included the predictor (MacKenzie et al. 2006). We used logistic regression to model the response form for informative variables as:

$$Y_i = e^{(\beta_0+\beta_1 X_i)}/[1+e^{(\beta_0+\beta_1 X_i)}]\,,$$

where Y_i is passage probability, β_0 is the regression intercept, β_1 is the regression slope, and X_i is the value for the predictor variable.

Ecosystem effects. — We quantified the effects of each species on stream ecosystems by isolating their ecological role in a series of replicated 'knockout' experiments. Experimental streams helped us simplify the complexity of stream ecosystems and identify the ecological contributions of each species with replicated treatments. The experimental streams at the SDSU Fisheries Ecology Research Center were designed following Matthews et al. (2006). These systems are functionally and physically very similar to pool-riffle complexes in nearby natural streams (Gelwick and Matthews 1992; Gido and Matthews 2001; Bertrand et al. 2009).

Each experimental stream unit (n = 24) consisted of one 2.54 m^2 pool connected to a 0.84 m^2 riffle. Water was supplied continuously by an on-site well which maintained the temperature near 17°C and water was recirculated at a rate of 0.15 m/s. A uniform amount of large gravel substrate was available in each pool and riffle. Prior to experiments each unit was drained, pressure washed, and allowed to dry for seven days prior to filling. Stream units were filled seven days prior to the beginning of the experiment to facilitate algal and invertebrate colonization. Previous studies have found algae and invertebrate taxa with mobile adults to readily colonize similar systems (Matthews et al. 2006).

We measured fish (TL) and stocked the experimental streams at ‘natural’ local densities of 5-10 g m^{-2} on day 0 (26 June 2013). We replicated each fish species treatment 5 times, except White Sucker (4 replicates) in a randomized design. A ‘no fish’ control treatment was also replicated five times. We ended the experiment and removed all fish after 7 weeks.

We measured ecosystem function every other week using wholestream metabolism (GPP, NEP, and CR; Murdock et al. 2011), and once-per-month we measured nutrient retention (TN and TP). Every other week, we measured ecosystem structure with algal filament length and algal biomass (benthic chlorophyll *a*). Response variables were compared among treatments and control using repeated measures ANOVA (SPSS version 21).

RESULTS

Swimming performance. — The number of “nonperformers” was low for all species, but highest for Central Stoneroller (N = 2). There was no apparent pattern to the prevalence of nonperforming individuals. The species exhibited different behaviors in the swimming flume. Brassy Minnow, Central Stoneroller, and White Sucker sustained their position in the water column throughout the experiments. Iowa Darter did not swim continuously, and instead avoided constant motion by affixing their fins to the bottom of the chamber. At higher velocities, all species maintained their position through erratic bursts or with continuous sprints.

Swimming endurance time (*E*, seconds) was significantly influenced by water velocity for all species (Figure 1A-D). Median endurance varied by species (Figure 1A-D). Species specific regression equations are found in Figure 1A-D. Brassy Minnow maintained longer than the other species at all water velocities (Figure 1A). Central Stoneroller and Iowa Darter endurance times were similar at all trial velocities (Figure 1B & C). The weakest performer at any given water velocity was White Sucker (Figure 1D). All species could pass barriers up to 15 meters in length if the water velocity was below 30 cm s^{-1} (Figure 2). White Sucker are most vulnerable to barriers that increase water velocity which are prevalent on the landscape (Figure 2). For example, White Sucker could traverse a 40 m barrier only at water velocities approximately 40% less than what would allow the other three species to pass (Figure 2). Central Stoneroller and Iowa Darter would succumb to barriers of similar length and water velocity (Figure 2). Brassy Minnow would successfully pass more barriers than any of the other species (Figure 2).

Jumping abilities. — Prairie fishes exhibited diverse jumping abilities with some species substantially outperformed others at moderate weir heights (Figure 3). Candidate models provided evidence that both weir height and total length impact fish passage probability (Table 1). Summed model weights demonstrated the effect of weir height on jumping success for all species, but also recognized the influence of total length on Central Stoneroller and Iowa Darter passage at low (< 5 cm) weir heights (Table 1). Larger Central Stoneroller and smaller Iowa Darter were more likely to ascend vertical barriers.

(Figure 3). Little explanatory value was gained by considering water temperature and dissolved oxygen concentration in the lower chamber. The probability that any species ascend a 5 cm weir was < 50% (Figure 3). At 20 cm, no species had a > 20% chance of successfully jumping past a barrier (Figure 3).

Ecosystem effects. — Native prairie fishes affected stream ecosystem structure. Algal filaments in stream pools were shortest in Central Stoneroller treatments, followed by Brassy Minnow, no fish, and Iowa Darter ($F_{4,19} = 7.87$, $P < 0.01$; Figure 4). Algal filament lengths in the White Sucker treatment were intermediate and not significantly different from the other fish and no fish treatments in *post hoc* comparisons. Riffle algal filament lengths ($F_{4,19} = 0.73$, $P = 0.58$) and algal biomass were similar among treatments (pools: $F_{4,18} = 1.92$, $P = 0.15$; riffles: $F_{4,18} = 2.20$, $P = 0.11$).

There was no evidence to suggest that individual species had distinct effects on ecosystem function. Net primary productivity was similar among fish treatments and the no fish control ($F_{4,2} = 2.75$, $P = 0.28$). Nutrient retention was also similar among treatments and control tanks (TN: $F_{4,19} = 0.91$, P = 0.48; TP: $F_{4,\,19} = 0.26$, $P = 0.90$).

DISCUSSION

Fragmented riverscapes have detached immigration from stream fish community structuring and endangered ecosystem processes in headwater reaches. Prairie fishes are not equally vulnerable to instream barriers, but all failed to circumvent relatively minor obstacles. Diversity loss will hinder stream ecosystem processes as fishes were not ecologically redundant and each impacted ecosystem structure differently. The risk of systematic species loss above barriers greatly outweighs the opportunity for improvement (*i.e.*, ecological ratchet moving downstream) suggesting that ecosystem structure could be moving downstream (Perkin et al. 2014). Because barriers are very prevalent the methodical changes to fish assemblage structuring and ecosystem processes we forecast may disturb innumerable river systems (Bouska and Paukert 2010; Ficke 2011; Lorenzen 2016).

Unequal abilities to bypass both vertical and longitudinal obstacles associated with road crossings suggest that prairie fishes are uniquely vulnerable to stream fragmentation. Roads bisect streams at nearly every mile on the landscape and every road crossing has the potential to block fish movement and fragment critical habitats (Warren and Pardew 1998; Bouska and Paukert 2010; Perkin et al. 2013). Fragmentation is expected to impact each species slightly differently and alter upstream fish assemblage composition by first removing poorer performing species. However, small vertical barriers (> 5 cm) block most fish passage and, with access, all species are unable to traverse relatively short obstacles with moderate water velocities.

Prior research has effectively quantified the swimming endurance and jumping abilities of numerous salmonids (Kondratieff and Myrick 2006; Mueller et al. 2008) and other large-bodied species (Ward et al. 2003; Haro et al. 2004), with less consideration of ecologically significant small-bodied fishes (*c.f.*, Adams et al. 2000; Ficke et al. 2011; Prenosil et al. 2015). Our swimming endurance estimates generally correspond well to literature values for similar species (Leavy and Bonner 2009; Billman and Pyron 2005; Ficket et al. 2011). Our estimates suggest White Sucker are much weaker swimmers (81% less endurance at 64 cm s^{-1}) than Sonoran Sucker *Catostomus insignis*; however, this value was partly attributed to behaviors used to adhere to the flume (Ward et al.

2003). Our results suggest that White Sucker and Iowa Darter are very susceptible to population fragmentation by longitudinal obstacles. Although Central Stoneroller and Brassy Minnow performed better, no species is expected to pass relatively short reaches with moderate water velocities. Some species jumped better than others (*i.e.*, poor performance of Central Stoneroller), but none are likely to bypass vertical barriers > 5 cm. Passage by all species, except Central Stoneroller, was high when the weir was at the water surface. Similar to observations by other researchers, passage probability decreased rapidly for all species with slight increases in weir height (Ficke et al. 2011; Prenosil et al. 2015). Unique to this study, Central Stoneroller and Iowa Darter length largely influenced passage of vertical barriers; patterns that potentially reveal dispersal motivations (Agostinho et al. 2007). Our estimates of fish vulnerability only consider the physical capability of each species to bypass barriers without respect to other factors that influence their motivation to do so (*i.e.*, dark tunnel, food availability, density-dependence, etc.). Because prairie fishes are not equally able to navigate instream barriers, fish assemblages will be altered in predictable ways. Minor constraints on the stream channel will select for more mobile species (*i.e.*, Brassy Minnow); however, road crossings will more often impede immigration by all species.

Worldwide declines to freshwater fish diversity have raised concern about the integrity of stream ecosystem processes after extinction (Bertrand and Gido 2007; Bertrand et al. 2009; Burkhead 2012). Unique ecological contributions of fish species have been quantified prior to this research, but ours is among the first to find little support for ecological redundancy within a guild of closely related fishes (Cardinale et al. 2002; Bertrand and Gido 2007; Bertrand et al. 2009; Vanni 2010). Each species we evaluated had slightly different impacts on the stream mesocosms owing from their different habitat preferences and diets (Hargrave 2009; Vanni 2010). Similar to other research, the simulated extirpation of a grazing minnow, in our example Central Stoneroller, caused great increases to algal filament length and altered ecosystem structure (Grimm 1988; Matthews 1988; Dodds et al. 2004; Reisinger et al. 2011). Without colonization opportunities from neighboring source populations, disturbance events will alter headwater fish assemblages and degrade ecosystem structure above barriers.

We hypothesize that fragmented riverscapes interact with harsh disturbance regimes to form an ecological ratchet mechanism in dendritic prairie streams. Extirpation of vulnerable headwater fishes and consequent changes to ecosystem structure moves the ratchet toward a new ecological state and recolonization to reverse the motion is blocked by fragmentation (Schlosser 1990; Fausch and Bramblett 1991). Continued ratcheting will systematically move ecosystem goods and services downstream until being eliminated when environmental tolerances of ecologically relevant fishes are exceeded (Vannote et al. 1980). Although upstream habitats recover from disturbance events and can be improved by restoration efforts, legacy effects will impede ecosystem reset because the local diversity has been reduced (Dodds et al. 2004; Roni et al. 2008; Perkin et al. 2014). The ratchet mechanism describes the process in which fish diversity is reduced in fragmented riverscapes and has great conservation value as we enter a more extreme environmental future (Covich et al. 1997; Perkin et al. 2014).

Abundant barriers to recolonization with limited tools to improve passage for small-bodied prairie fishes will interact with a range of stochastic and human-mediated disturbances to further threaten fish assemblage structuring and ecosystem processes (Bouska and Paukert 2010; Ficke et al. 2011; Lorenzen 2016). This ecological ratchet could be slowed by maintaining suitable flow regimes during dry periods (Cooke et al. 2012; Perkin et al. 2014), rescuing and re-releasing populations during disturbances (Hammer et al. 2013), or by reintroducing individuals after environmental conditions improve (Seddon et al. 2007; George et al. 2009). Each of these management tools require substantial resources that are rarely available for the conservation of small-bodied stream fishes. Improving recolonization pathways via prioritized barrier removal (Kornis et al. 2015; Magilligan et al. 2016) or implementing novel fish passage structures (Ficke et al. 2011; Lorenzen 2016), should prioritized to reverse the ratchet without further intervention (Perkin et al. 2014). The future prognosis for small-bodied prairie fishes and the headwater ecosystems they support is grim unless steps are taken to move ecosystem structure upstream.

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fisheries and stream ecosystem in the Northern Great Plains), and the David W. Willis Fisheries Research Award.

Table 1. Top candidate models and associated AIC_c values and those with strongly differentiated performances to evaluate species-specific jumping performance. W_i is the AIC_c weight and ΣW_i are the summed model AIC_c weight for influential predictors by species

Species	Predictors	K	ΔAIC_c	w_i	Σw_i
Brassy Minnow					
	Weir height	3	0	0.46	Weir height = 0.74
	Weir height x Mean total length	4	3.10	0.10	Total length = 0.23
Central Stoneroller					
	Mean TL	3	0	0.59	Total length = 0.66
	Weir height	3	2.09	0.21	Weir height = 0.27
Iowa Darter					
	Mean TL	3	0	0.45	Total Length = 0.65
	Weir height	3	0.65	0.32	Weir height = 0.44
White Sucker					
	Weir height	3	0	0.47	Weir height = 0.71
	Mean TL	3	1.54	0.22	Total length = 0.45

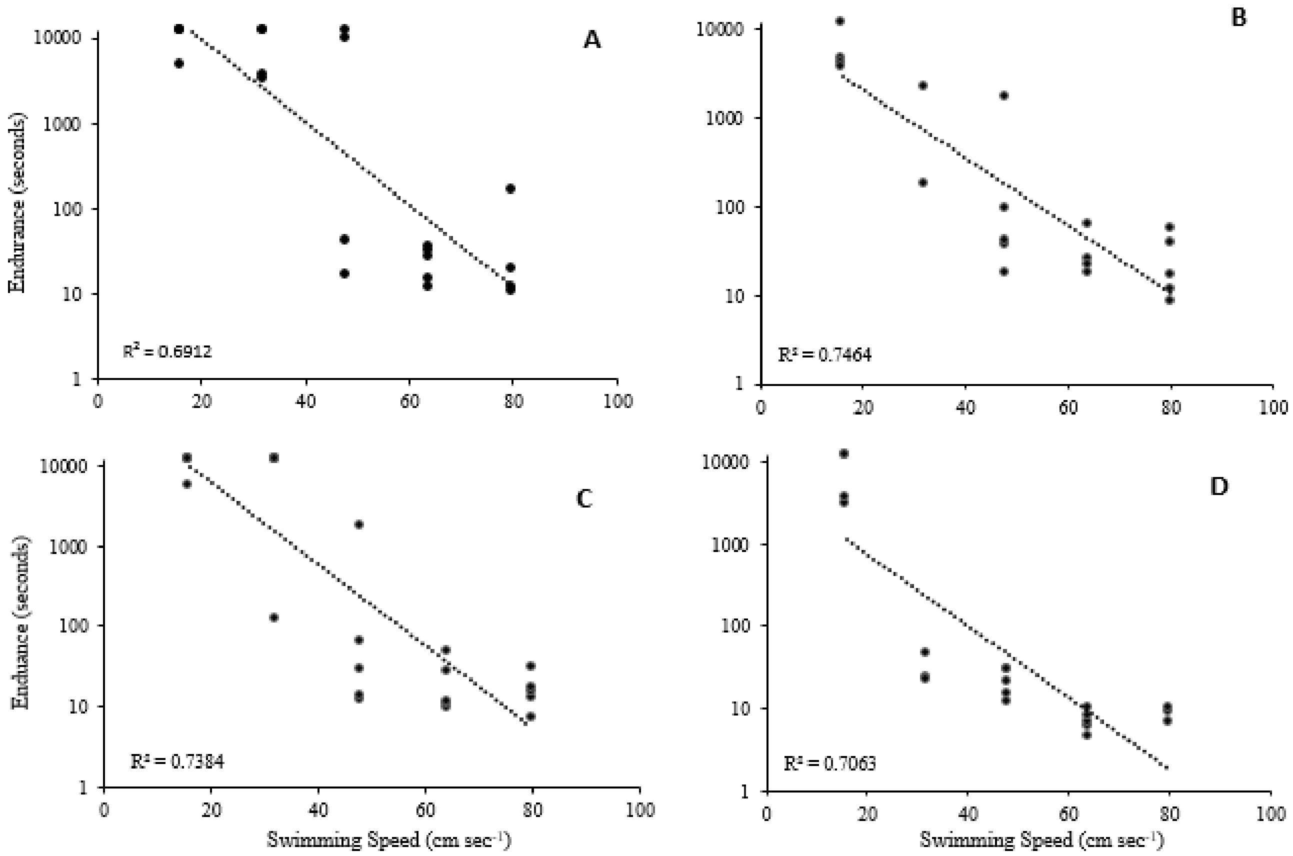

Figure 1. Predictive endurance curve (seconds) estimated using multiple regression as follows (Peake et al. 1997): Brassy Minnow (A), Log(*E*) = 3.101 + (-0.0485 * water velocity); Central Stoneroller (B), Log(*E*) = 2.71 + (-0.0434 * water velocity); White Sucker (C), Log(*E*) = 2.358 + (-0.0486 * water velocity); and Iowa Darter (D), Log(*E*) = 2.991 + (-0.0508 * water velocity).

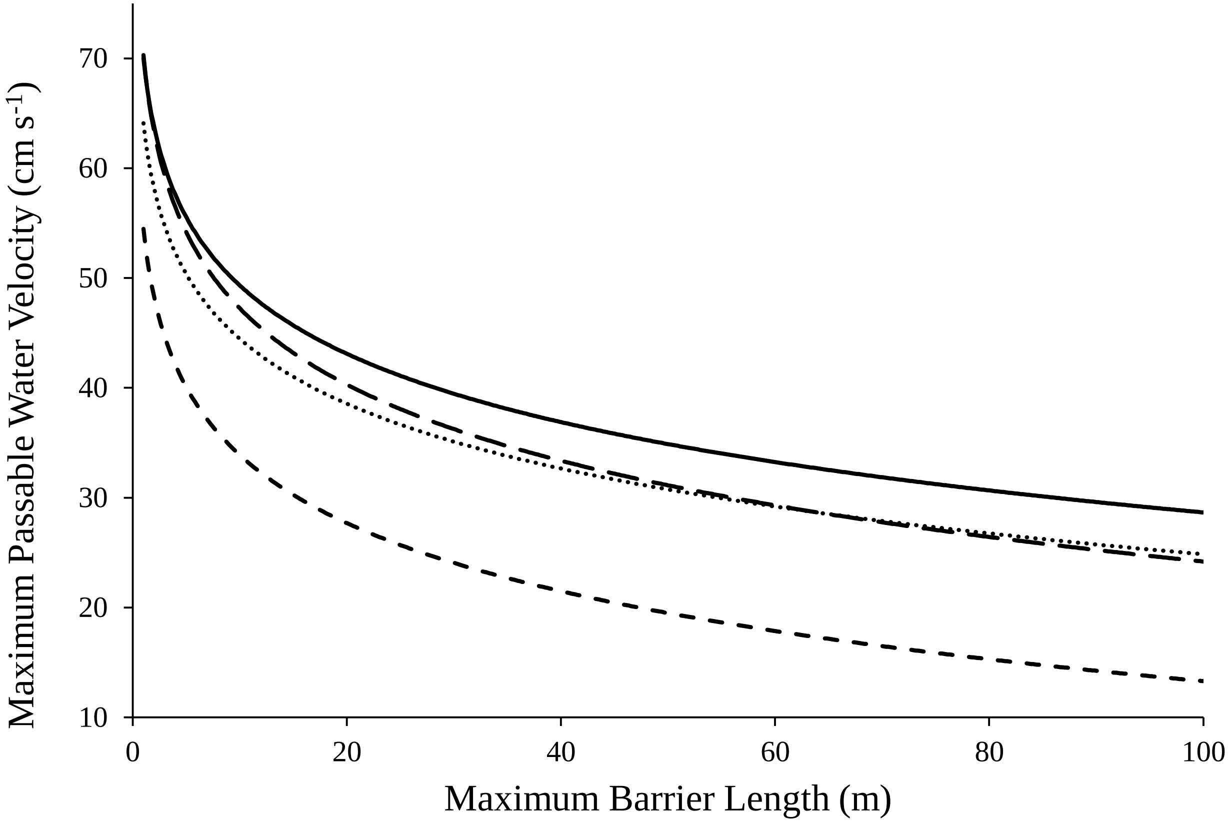

Figure 2. Combinations of barrier length (m) and water velocity (cm s^{-1}) in which passage is possible for Brassy Minnow (solid line), Central Stoneroller (large dashes), Iowa Darter (dotted line), and White Sucker (small dashes). The area under the plotted points for each species represents passable combinations of length and velocity. Estimated median endurance times were used to generate estimates (Peake et al. 1997).

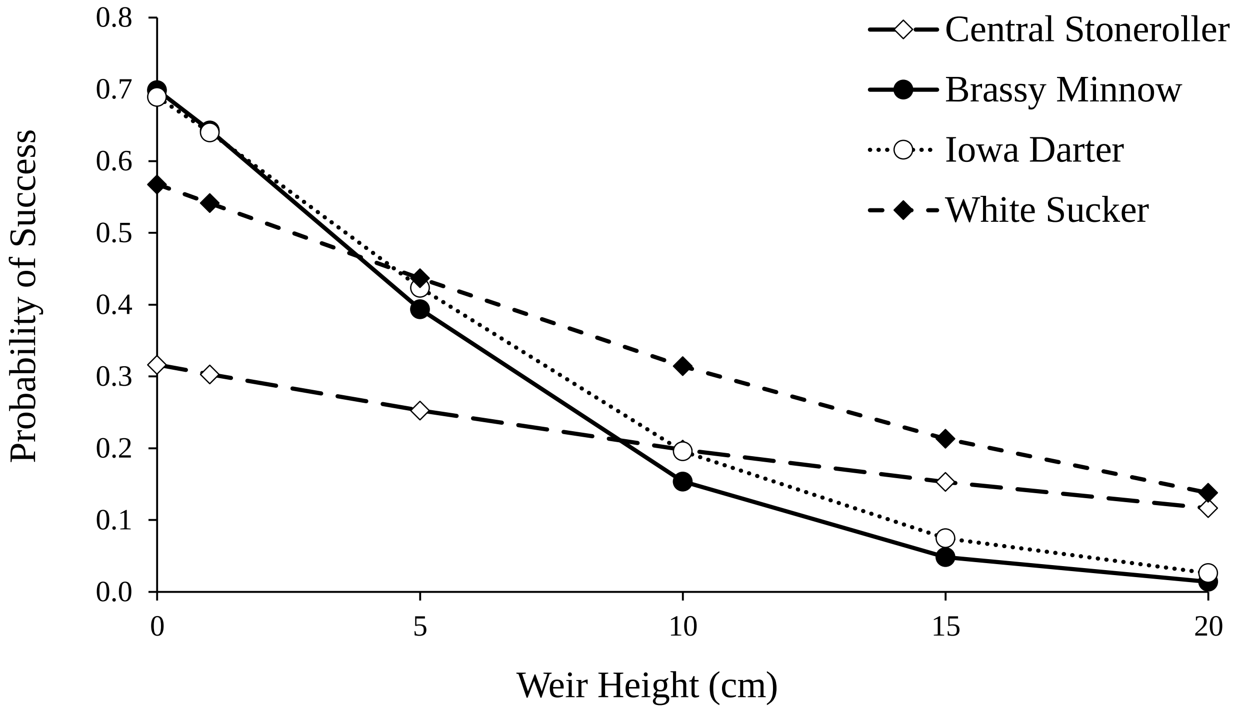

Figure 3. Probability of jumping success as a function of weir height for Brassy Minnow, Central Stoneroller, Iowa Darter, and White Sucker.

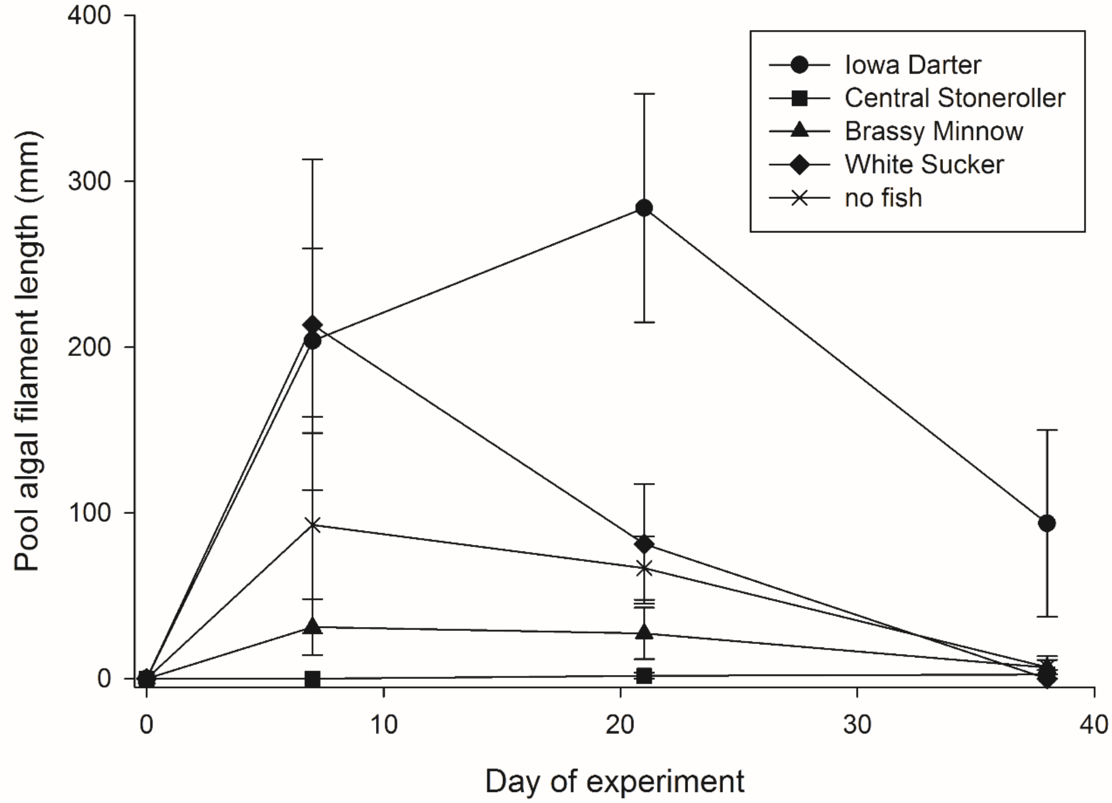

Figure 4. Mean algal filament length measured in pools of experimental streams, used to describe impact of species loss, during June-August 2013.

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CHAPTER FOUR

PASSIVE INTEGRATED TRANSPONDER (PIT) TAGS SURGICALLY IMPLANTED INTO SMALL-BODIED FISHES

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ABSTRACT

Innovative tools that inform conservation are critical as freshwater fishes are lost at unprecedented rates. Although mark-recapture methods can characterize population ecology and describe life history traits of rare species, techniques for tagging small fishes have been limited. Recent advances in passive integrated transponder (PIT) tag technology may provide opportunities to tag small-bodied fishes and benefit fisheries research. Despite the potential value of new PIT tags (8.4 x 1.4 mm), 30% smaller than those previously available, little research has evaluated their suitability when implanted into small fishes. We evaluated the effectiveness of these tags when surgically implanted into representative small-bodied species from eight taxonomic groups with different body shapes. Fish of each species were randomly assigned to one of three equally sized treatment groups (handled [control], surgical incision [sham], or surgical incision plus PIT tag implantation [PIT]). During a six-week study period, mortalities and expelled tags were counted daily and growth was measured weekly. Effects of surgically implanted PIT tags varied by taxonomic group and by initial fish length for some species. Managers can expect little tag loss and uncompromised growth rates for a variety of small-bodied fishes signifying the wide applicability of this technology. Significant tag loss suggests that PIT tags aren’t yet suitable for Johnny Darter *Etheostoma nigrum* and other related species. Small PIT tags offer opportunities for ecological and behavioral studies and fisheries scientists now have critical information concerning their suitability for several groups of small-bodied fishes that was previously unavailable.

INTRODUCTION

As extinction reaches unprecedented rates conservation biology is more critical than ever (Richter et al. 1997; Cardinale et al. 2012). Human induced stressors exacerbate declines in distribution and local abundance of freshwater fish species worldwide and threaten aquatic ecosystem stability (Richter et al. 1997; Ricciardi and Rasmussen 1999; Cardinale et al. 2012). Conservation of fishes has lagged behind that of terrestrial animals as a result of less reliable techniques to estimate population demographics and life history characteristics of aquatic organisms (Allan and Flecker 1993; Cooke et al. 2012).

Mark-recapture techniques are important to studies of fish population ecology (Jolly 1965; Pollock et al. 1990). Recapturing tagged individuals can help characterize life history traits, estimate demographic rates, document behavior, or describe survival (Nielsen 1992; Ruetz et al. 2006; Kaemingk et al. 2011; Hamel et al. 2012). Important assumptions mark-recapture studies include: (1) a known tag retention period, (2) tags have negligible effects on life history traits and behaviors, and (3) tags do not affect the direction or magnitude of results (Gibbons and Andrews 2004; Bolland et al. 2009). No known tagging technique is universally applicable for all fish species and life stages so researchers must carefully select tagging methods that meet study objectives (Ruetz et al. 2006) and balance the constraints of time and cost (Gibbons and Andrews 2004; Lower et al. 2005; Bolland et al. 2009).

Biologically inert passive integrated transponder (PIT) tags are common in mark-recapture studies of large-bodied fishes (Gibbons and Andrews 2004; Knaepkens et al. 2007; Archdeacon et al. 2009). Their indefinite life span, internal placement, high detection efficiency, and unique identification numbers make PIT tags versatile and convenient (Gibbons and Andrews 2004; Knaepkens et al. 2007; Archdeacon et al. 2009; Ficke et al. 2012). Passive integrated transponder tags rarely have had significant effects on life history characteristics and behavior when implanted into large-bodied fishes (Baras et al. 2000; Ruetz et al. 2006; Archdeacon et al. 2009; Dixon and Mesa 2011). However, inconsistent physical and behavioral responses after PIT tag implantation has prompted concern for their application to new taxonomic groups and life stages without prior evaluation (Prentice et al. 1990; Baras et al. 2000; Archdeacon et al. 2009; Tiffan et al. 2015; Schumann et al. 2017). Detrimental tag effects are expected to increase with the tag size to fish size ratio for smaller fish (Jepsen et al. 2002; Bolland et al. 2009; Pennock et al. 2016). Novel PIT tag technology, a smaller (8.4 x 1.4 mm) PIT tag, may transform our understanding of small-bodied fish ecology but their suitability has not been tested extensively for many species or taxonomic groups (but see Clark 2016; Pennock et al. 2016). Knowledge of tag loss (mortality + tag ejection) and the effects on fish growth is required before widespread use.

New, small PIT tags may improve mark-recapture studies of small-bodied fishes and provide new insights into fish ecology that was previously unavailable, but studies of their safety and effectiveness are necessary first. Therefore, the objectives of this study were to evaluate the effects of small (8.4 x 1.4 mm) PIT tags on fish survival and growth and measure tag retention time when implanted into eight small-bodied fish species that represent a variety of taxonomic groups and may act as surrogates for similar species. Conclusions generated will provide fisheries scientists with critical information concerning the suitability of PIT tags that is applicable to many taxonomic groups.

METHODS

Study species. — We evaluated the effectiveness of surgically implanted PIT tags on representative small-bodied species from eight taxonomic groups with different body shapes. Species were: Common Shiner *Luxilus cornutus*, Sand Shiner *Notropis stramineus*, Creek Chub *Semotilus atromaculatus*, Blacknose Dace *Rhinichthys atrtulus*, White Sucker *Catostomus commersonii*, Plains Topminnow *Fundulus sciadicus*, Johnny Darter *Etheostoma nigrum*, and Tadpole Madtom *Noturus gyrinus*. Without additional investigation, our broad generalizations may be applied to closely related small-bodied species (e.g., Sand Shiner as a substitute for federally endangered Topeka Shiner *Notropis topeka*). We did not tag any fish < 30 mm total length (TL) because pilot investigations recognized 100% mortality of smaller individuals (D. Schumann, unpublished data).

We captured most species by seine or with backpack electrofishing from local streams in eastern South Dakota, but Plains Topminnow were obtained from an extensive aquaculture pond constructed to house a refuge population near Wilcox, NE (Schumann et al. 2012). We transported fish in 113-L aerated containers to a temperature controlled 20,000-L recirculating system at the Fisheries Ecology Research Center (South Dakota State University, Brookings). We took care to minimize stress associated with handling, transportation, and confinement (Harmon 2009). We slowly acclimated fish to laboratory water conditions (~17°C) and transferred to species specific holding tanks. We maintained a consistent photoperiod of 12:12 h light/dark using incandescent lighting and fed fish once daily with a mixture of frozen chironomid larvae and dry food (70% Otohime and 30% Cyclopeeze) during the 14 d acclimation period.

Study design. — Two treatment groups were evaluated for each species: (1) incision only [sham], and (2) incision plus PIT tag implantation [PIT]. Treatments were compared to a control groups that were handled in a similar manner but not treated with an incision or PIT tag implantation. We randomly selected individuals from our acclimated source populations and assigned each to one of the two treatments or control groups. We selected 30 individuals for both treatments and 30 control fish for each species. We housed all fish in species-specific 946-L tanks in the original recirculating system. We monitored tanks for 42 d following the procedure because previous studies observed complete healing and recovery after 6 weeks (Kaemingk et al. 201l; Tiffan et al. 2015).

Tagging technique. — We withheld food for 36 h prior to PIT tag implantation to allow for consistent gut fullness (i.e., completely evacuated; empty) among individuals. Prior to each procedure, we sanitized all PIT tags and surgical equipment in 95% ethyl alcohol to decrease the risk of infection (Dixon and Mesa 2011). All fish were removed from the acclimation tanks, anesthetized in tricaine methanesulfonate (MS-222; 100 mg L^{-1}), measured to TL (mm), and weighed (0.1 g) before the procedure. We marked each fish with a treatment specific visible implant elastomer (VIE) tag to identify treatment groups through time. Visible implant elastomer marks have negligible physiological effects on small-bodied fishes (Sutphin et al. 2007). Fish assigned to the control group were immediately placed into treatment specific recovery tanks. We made a 2-3 mm medial incision near the midventral line and anterior to the pelvic girdle of treatment fish using a 3.0 mm microsurgical scalpel. For PIT treatment fish, we implanted a PIT tag (HPT8 MiniChip; 8.4 mm x 1.4 mm, 0.036 g; Biomark, Boise, Idaho) into the abdominal cavity manually (Knaepkens et al. 2007; Archdeacon et al. 2009). To decrease handling time, we left all surgical wounds open (Archdeacon et al. 2009). We placed all individuals in heavily aerated treatment-specific recovery tanks for 10 min before transferring them to trial tanks. In pilot investigations respiration rate, movement behaviors, and righting response returned within 10 minutes. We did not feed fish on day zero or one of the trial. All fish were offered a daily ration of chironimid larvae equal to 10% of the tank biomass beginning on day two.

Estimating survival, tag retention, and growth. — Initial mortality included fish that died during the procedure or recovery period and was expressed as a percentage by treatment without variation. We monitored tanks for mortalities and expelled PIT tags daily during the 42 d study period. Any individuals that ejected a PIT tag were removed from the experiment as the tag was no longer inflicting a physiological response. Mortality from the surgical procedure and PIT implantation was considered the difference between survival of treatment and control groups. Survival and PIT tag retention were expressed as the percentage of individuals within each treatment.

We conducted failure-time analyses (LIFETEST procedure in SAS version 9.4) to compare cumulative survivorship among treatments with a Wilcoxon chi-square test by species (Fox 2001). This statistical technique was also used to compare PIT tag retention and survival rates of PIT tagged individuals among taxonomic groups. This analysis compares survivorship (or retention rates) among treatment groups and species throughout the trial (0-42 d) rather than solely on the final trial day. It manages right-censored data and does not assume that data are normally distributed (Fox 2001). All individuals that survived or retained their tag through day 42 were considered right-censored. For each analysis, we set $\alpha = 0.05$. If differences were observed in survivorship or retention, we performed a Šidák multiple-comparison *post hoc* tests between among treatment groups and species pairs (Fox 2001).

We used logistic regression (SAS version 9.4) to assess the effect of initial TL on survival and tag retention of PIT tagged individuals. The logistic response form is:

$$Y_i = e^{(\beta_0+\beta_1 X_i)}/[1+e^{(\beta_0+\beta_1 X_i)}] \text{ ,}$$

where Y_i is the survival or tag retention probability of fish *i* on day 42, β_0 is the regression intercept, β_1 is the regression slope, and X_i is the TL of fish *i*.

We weighed (g) all fish prior to tagging and on a weekly basis for the duration of the study to evaluate the effects of the surgical procedure (sham) and PIT tag implantation (PIT) on growth. We calculated relative daily growth rate (RDGR) for each control and replicate group and for all PIT tagged individuals as:

$$\text{RDGR} = ((m_t - m_0)/m_0)/\Delta t,$$

where m_t is the mass (minus the mass of the PIT tag) of a fish at time *t* and m_0 is initial mass of the same fish measured at the time of the surgical procedure. Two-way repeated measures ANOVA (SAS version 9.4) was used to test the null hypothesis that RDGR did not differ among treatments through time or by species ($\alpha \leq 0.05$). If differences were observed, we performed a Student-Newman-Keuls *post hoc* test to partition treatment effects into distinct groups (Zar 2010).

RESULTS

We successfully implanted PIT tags into fish ranging from 39 to 169 mm TL (Table 1). No significant differences existed in initial TL among treatment groups for all species except Tadpole Madtom (Table 1). Tadpole Madtom individuals in the sham treatment were generally about 8 mm shorter than PIT tag fish ($F_{2, 87} = 3.1$, $P = 0.02$; Table 1). Initial weight did not vary among treatments for any species evaluated (Table 1). The initial PIT tag: fish weight ratio was < 3% (i.e., the recommended maximum; Jepsen et al. 2005) for all species except Johnny Darter (Table 1). The mean (± standard error [SE]) tag: fish weight ratio was 3.0% ± 0.29% in Johnny Darters in this study; ratios for Plains Topminnows and Tadpole Madtoms were between 2 and 3% (Table 1). The mean tag: fish weight ratio was less than 2% for all other fish evaluated (Table 1).

Survival, tag retention, and growth. — Initial mortality was rare, except for White Suckers in the PIT tag treatment group (23%; Table 1). Johnny Darters in the PIT tag treatment group also succumbed to the procedure, but at a much lower rate (7%; Table 1). Few sham individuals (3%; Blacknose Dace and Sand Shiner) and control fish (3%; White Sucker) perished during the initial procedure (Table 1).

Impacts of the surgical procedure and PIT tag implantation were species-specific and generally minor. However, survival of PIT tagged individuals was significantly lower than controls for two fishes (Figure 1). Dace that were implanted with PIT tags were 25% less likely to survive than the control fish (Figure 1; $\chi^2 = 7.82$, df = 2, $P = 0.02$). Darters in the PIT group were 30% less likely to survive than their conspecifics in the control group (Figure 1; $\chi^2 = 6.22$, df = 2, $P = 0.04$). Although PIT tagged fish of the other six taxonomic groups perished during the study, these mortalities paralleled those in the corresponding controls. Expected survival of these diverse taxonomic groups after PIT tag implantation is high (> 97%). No differences in survival were apparent between the sham and control treatments for any group of fishes. Initial fish length strongly influenced darter ($\chi^2 = 3.86$, df = 1, $P = 0.04$), dace ($\chi^2 = 5.49$, df = 1, $P = 0.02$), and sucker ($\chi^2 = 5.01$, df = 1, $P = 0.03$) survival. To improve survival, researchers would have to tag larger individuals of these three fishes (Figure 2). By tagging 74 mm TL darters, 91 mm TL dace, and 160 mm TL suckers, researchers could expect 90% survival (Figure 2).

Most tag ejections (97%) occurred during the first 2 weeks of the study, a period in which many wounds were not fully healed (Figure 3). Retention of PIT tags during the study varied significantly among taxonomic groups ($\chi^2 = 50.6$, df = 7, $p < 0.01$) and ranged from 57% for madtoms to 100% for dace (Figure 3). PIT tag retention exceeded 90% for daces, topminnows, chubs, and suckers (Figure 3). Sand Shiner PIT tag retention was >15% less likely than the upper tier species (Figure 3). Retention was poor (< 70%) for darters, Common Shiner (the only dorsally-laterally compressed fish evaluated), and madtoms (Figure 3). No relationship was identified between initial TL and tag retention for any taxonomic group.

Growth rates of small-bodied fish varied significantly during the study (Figure 4; $F_{6,\ 345} = 5.5$, $P < 0.01$); however, within species growth was unaffected by the surgical procedure or tag implantation (Figure 4; $F_{2,\ 345} = 1.02$, $P = 0.36$). Throughout the study Creek Chub growth was significantly higher than all other species (Figure 4). Madtom growth rates were greater than dace during the last two trial weeks (Figure 4). The interaction term (species*treatment) was not significant (Figure 4). Although time did not significantly impact small-bodied fish growth ($F_{5,\ 1725} = 2.65$, $P = 0.07$), negative growth rates were apparent early in the trial for several taxonomic groups (Figure 4).

DISCUSSION

Few studies have tested the potential limitations of newly developed, small (8.4 x 1.4 mm) PIT tags with fish and, to our knowledge, no research has evaluated their suitability for many of the small-bodied fishes evaluated in this study (but see Ficke et al. 2012; Pennock 2017). Impacts of surgically implanted PIT tags on small-bodied fish survival and growth were taxa specific, but generally minimal. Managers can expect little tag loss and uncompromised growth rates for diverse small-bodied fishes signifying the wide applicability of this technology. However, managers tagging darters and dace should expect lower survival. Tag loss resulting from poor retention (< 70%) was prevalent for darters, dorsal-laterally compressed minnows, and madtoms. This research addresses many concerns when PIT tagging several groups of small-bodied fishes making managers better able to study small fish ecology.

Survival and tag retention. — Initial mortality was relatively high for White Sucker (23%) and notable for Johnny Darter (7%). Although initial mortality rates aren't available, survival of larger White Sucker (> 100 mm TL) tagged to evaluate swimming performance was low in previous research (~32%; Ficke et al. 2012). No individuals of any other taxonomic group perished during the surgical procedure. Significant initial mortality has been rarely reported after incision and insertion of small PIT tags (Ward et al. 2015; Tiffan et al. 2015; Pennock et al. 2016; Schumann et al. 2017); however, injecting tags with gauged needles has resulted in increased initial mortality of small fishes (Archdeacon et al. 2009). Managers tagging small fishes (particularly suckers) should consider supplementing released populations with additional individuals or observe and replace fish during a short (< 10 min) recovery period.

Short-term survival (42 d) was impacted by the implanted PIT tags for only two taxonomic groups, dace and darters. Survival of these fishes was low compared to developing standards for success when implanting PIT tags into similar small-bodied fishes (Bolland et al. 2009; Pennock et al. 2016). The authors are unaware of similar research that evaluates survival of PIT tagged darters. Short-term survival of the other PIT tagged fishes evaluated was high (> 97%) and well aligned with literature values for small-bodied fishes that generally range from 50-100% (Dixon and Mesa 2011; Bangs et al. 2015; Clark 2016; Pennock et al. 2016; Pennock 2017). We tagged smaller individuals than previous researchers and improved survival of Creek Chub and White Sucker by using smaller PIT tags (Johnson and Smithson 1999; Ficke et al. 2012). Consistent with other research of surgically implanted PIT tags, mortality ceased on day 28 for most fishes (Archdeacon et al. 2009; Bangs et al. 2015; Pennock 2017). However, darters and Common Shiners died throughout the study when incision wounds became inflamed and some Creek Chub escaped the tanks.

Tag retention was relatively low (< 60%) for species with small mean body widths or pliable skin without scales (i.e., darters, dorsal-laterally compressed minnows, and madtoms). All other fishes retained PIT tags at relatively high rates that were consistent with literature values for similarly sized fishes. Retention of surgically implanted PIT tags has varied considerably for other small fishes (Clark 2017; Pennock 2017; Schumann et al. 2017) but has rarely been reported below 70% (Johnson and Smithson 1999; Pennock et al 2016; Pennock 2017). Retention of PIT tags was about 20% higher for Sand Shiner when inserted via our surgical incision than previous research that used a hypodermic needle to puncture the peritoneal cavity (Pennock 2017).

Retention rates may have improved if we inserted PIT tags into the intramuscular locations typical for PIT tag implantation in larger fishes. We selected the abdominal cavity because the tag: muscle ratio tissue was considered inadequate for implantation. When small PIT tags were implanted into the abdominal cavity and dorsal musculature of Humpback Chub (Ward et al. 2015), Chinook Salmon (Tiffan et al. 2015), and Pikeperch *Sander lucioperca* (Hopka et al. 2010) ejection rates were equivalent.

Tag-ejection typically occurred within 14 d of implantation before wounds were completely healed (Baras et al. 1999; Pennock 2017). Darter wounds stayed open throughout the study and tags were ejected up to 35 d following the procedure. Although we may have increased retention rates by using sutures or cyanoacrylate to close incision wounds, these techniques were not applied to reduce handling stress and potential mortalities (Skov et al. 2005; Archdeacon et al. 2009). Supplemental research found that using cyanoacrylate to close incisions can greatly improve retention for darters, dorsal-laterally compressed minnows, and madtoms (>80%; J. Hoekwater, unpublished data). However, doing so resulted in substantially more darter mortality and reduced short-term survival to 22% (J. Hoekwater, unpublished data). Survival of the other two fishes was increased when cyanoacrylate was used to close surgical wounds (J. Hoekwater, unpublished data).

Tag loss is of interest to mark-recapture studies as each remove PIT tagged individuals from the released population. Although survival of a diverse group of small-bodied fishes after PIT tag implantation, tag retention was more variable. Cumulative success (survival + retention) provides a direct measure of the suitability of PIT tags when surgically implanted into small-bodied fishes. Tagging success ranged from 43%

(darters) to 97% (topminnow) and was strongly influenced by tag retention issues. Notably low success (< 60%) was identified for the three species with tag retention problems. However, success rates exceeded 90% for topminnows, suckers, and chubs. No universally accepted standard exists for tagging success rates so investigator judgment must be used to decide if each taxonomic group's predicted tag loss rate is acceptable for a given project

Survival and PIT tag retention have commonly been linked to fish size at the time of tagging (Bolland et al. 2009; Ficke et al. 2012; Bangs et al. 2013; Pennock et al. 2016; Schumann et al. 2017). Although survival is expected to substantially increase if tagging of suckers, dace, and darters is limited to larger individuals, we didn't identify any relationship between initial length and tag retention. We recognized the same length effect as Ficke et al. (2012) for White Sucker, despite implanting smaller PIT tags. Larger individuals with a smaller tag: body size ratios may be better able to tolerate the surgical procedure (Jepsen et al. 2005; Pennock et al. 2016). Although we subjected some fish to tag burdens higher than conventional standards (Table 1), recent studies have reported high survival rates with tag loads up to 11% (Skov et al. 2005; Bolland et al. 2009; Ward et al. 2015; Pennock et al. 2016). Pennock et al. (2016) suggested that a tag load < 5% is acceptable for most fishes. By incorporating length, managers can now better predict taxa specific survival after PIT tag implantation.

Relative daily growth. — Growth rates of these dissimilar fishes were unaffected by PIT tag implantation. Although some fish lost weight during the early phases of the experiment, all individuals were able to gain weight after a short recovery period (< 14 d). Impacts of this tagging technique on small fish growth are uncommon and, when identified, have been acute (Baras et al. 2000; Ruetz et al. 2006; Tiffan et al. 2015; Clark 2017; Schumann et al. 2017). When recognized, impacts to fish growth have been attributed to morphological differences and initial size at tagging (Knudsen et al. 2009; Tiffan et al. 2015; Schumann et al. 2017).

Tagging success is highly variable among small-bodied fishes and appears to be size dependent for specific taxonomic groups. However, negative effects of surgically implanted PIT tags were often negligible. This tagging technique is widely applicable to a diverse group of small fishes and researchers can reasonably expect limited tag loss and uncompromised growth rates. Variable responses among different fishes complicate the establishment of appropriate guidelines for all small-bodied species, but assuming that closely related species respond similarly, these results can act as a surrogates for tagging studies involving other fishes. However, substantial tag losses may limit future applications of PIT tag technology for Johnny Darter and similar *Etheostomine* darters. By tagging larger individuals and using cyanoacrylate to close surgical wounds, researchers can improve survival and tag retention for select fishes. Small PIT tags offer opportunities for ecological and behavioral studies of small fishes and fisheries scientists now have critical information concerning the suitability and their impacts on several fishes that was previously unavailable.

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Table 1. Mean (± SE) and range of initial total lengths (TL; mm), weight (g), percent tag to wet fish weight ratio, initial mortality (%), and cumulative success (survival and retention) after the surgical passive integrated transponder (PIT) tag implantation to eight species of small-bodied warmwater fishes.

Species	Treatment	Initial TL (mm)	TL range (mm)	Initial weight (g)	Initial tag to fish weight (%)	Initial mortality (%)	Cumulative Success (%)
Plains Topminnow	Control	51.7 (1.4)	40 - 70	1.8 (0.1)	No tag	0	
	Sham	50.0 (1.3)	37 - 63	1.7 (0.1)	No tag	0	
	PIT	51.4 (1.3)	39 - 66	1.8 (0.1)	2.3 (0.2)	0	97
Tadpole Madtom	Control	50.6 (2.1)^{ab}	37 - 85	1.8 (0.3)	No tag	0	
	Sham	49.4 (1.4)^{a}	41 - 79	1.5 (0.2)	No tag	0	
	PIT	57.2 (2.6)^{b}	38 - 95	2.6 (0.4)	2.2 (0.2)	0	57
Johnny Darter	Control	55.3 (1.0)	46 - 66	1.5 (0.1)	No tag	0	
	Sham	53.2 (1.2)	40 - 64	1.4 (0.1)	No tag	0	
	PIT	54.1 (1.4)	39 - 69	1.5 (0.1)	3.0 (0.3)	6.7 (NA)	43
Common Shiner	Control	84.6 (2.9)	53 - 119	6.5 (0.8)	No tag	0	
	Sham	84.1 (3.2)	49 - 133	6.3 (0.9)	No tag	0	
	PIT	85.9 (4.0)	44 - 123	7.2 (0.9)	1.0 (0.2)	0	60
Sand Shiner	Control	62.0 (1.1)	43 - 70	2.6 (0.1)	No tag	0	
	Sham	63.2 (1.1)	48 - 75	2.7 (0.1)	No tag	3.3 (NA)	
	PIT	63.8 (1.0)	47 - 71	2.8 (0.1)	1.5 (0.2)	0	77
Blacknose Dace	Control	78.0 (1.9)	51 - 96	5.6 (0.1)	No tag	0	
	Sham	77.8 (1.9)	47 - 89	6.0 (0.5)	No tag	3.3 (NA)	
	PIT	78.4 (2.0)	45 - 90	6.3 (0.5)	0.94 (0.3)	0	67
White Sucker	Control	79.3 (3.6)	61 - 148	5.7 (1.0)	No tag	3.3 (NA)	
	Sham	84.0 (3.1)	59 - 162	6.6 (1.1)	No tag	20.0 (NA)	
	PIT	83.9 (3.4)	52 - 169	5.7 (0.6)	0.87 (0.1)	23.3 (NA)	90
Creek Chub	Control	91.8 (4.5)	41 - 165	5.7 (0.7)	No tag	0	
	Sham	95.1 (4.8)	38 - 172	6.9 (0.9)	No tag	0	
	PIT	92.2 (4.2)	46 - 159	5.5 (0.7)	1.4 (0.2)	0	95

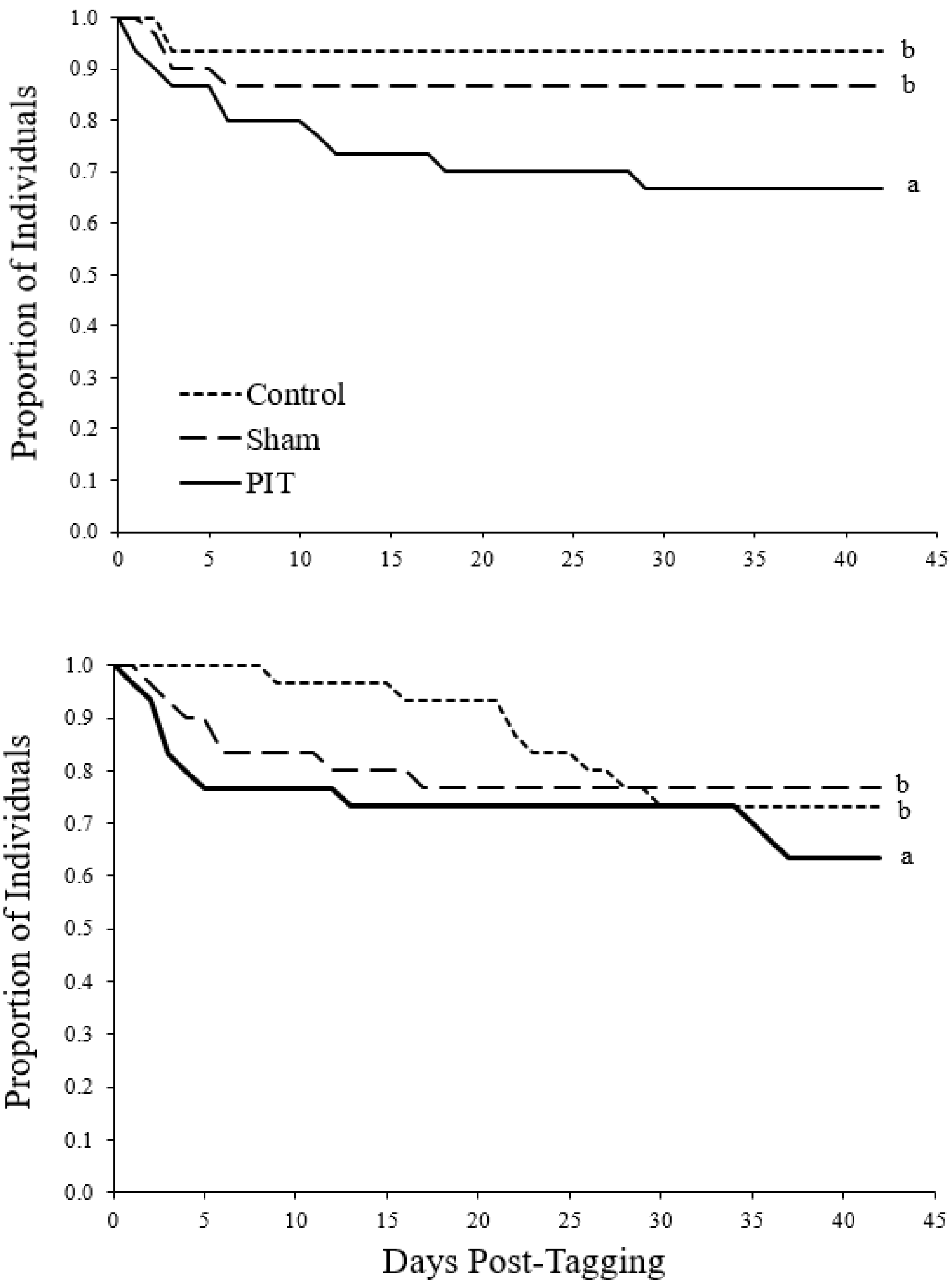

Figure 1. Daily survival of small-bodied Blacknose Dace *Rhinichthys atratulus* (top) and Johnny Darter *Etheostoma nigrum* (bottom) by treatment procedure (*n* = 30 per treatment. Different letters denote statistically significant differences among treatments ($P < 0.05$).

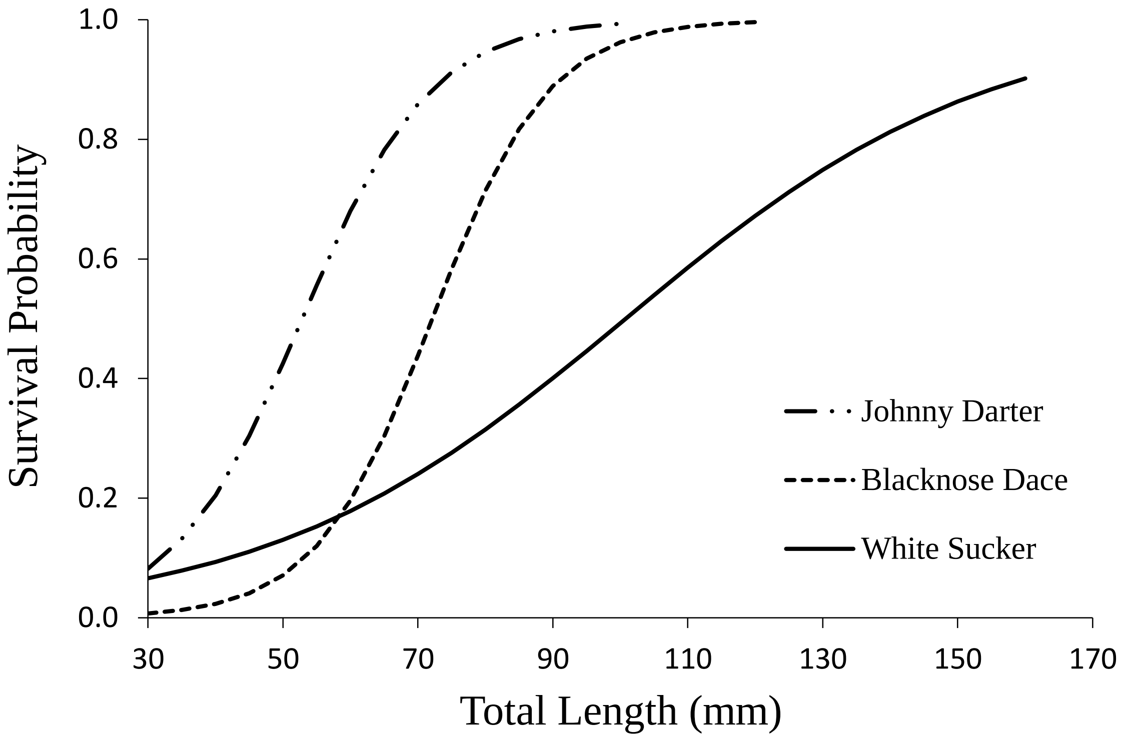

Figure 2. Significant relationships between initial total length (mm) and probability of survival to day 42 for Johnny Darter *Etheostoma nigrum* (slope: 0.11, intercept: -5.58), Blacknose Dace *Rhinichthys atratulus* (slope: 0.12, intercept: -8.39), and White Sucker *Catostomus commersonii* (slope: 0.04, intercept: -3.77) that received passive integrated transponder tags via surgical incision.

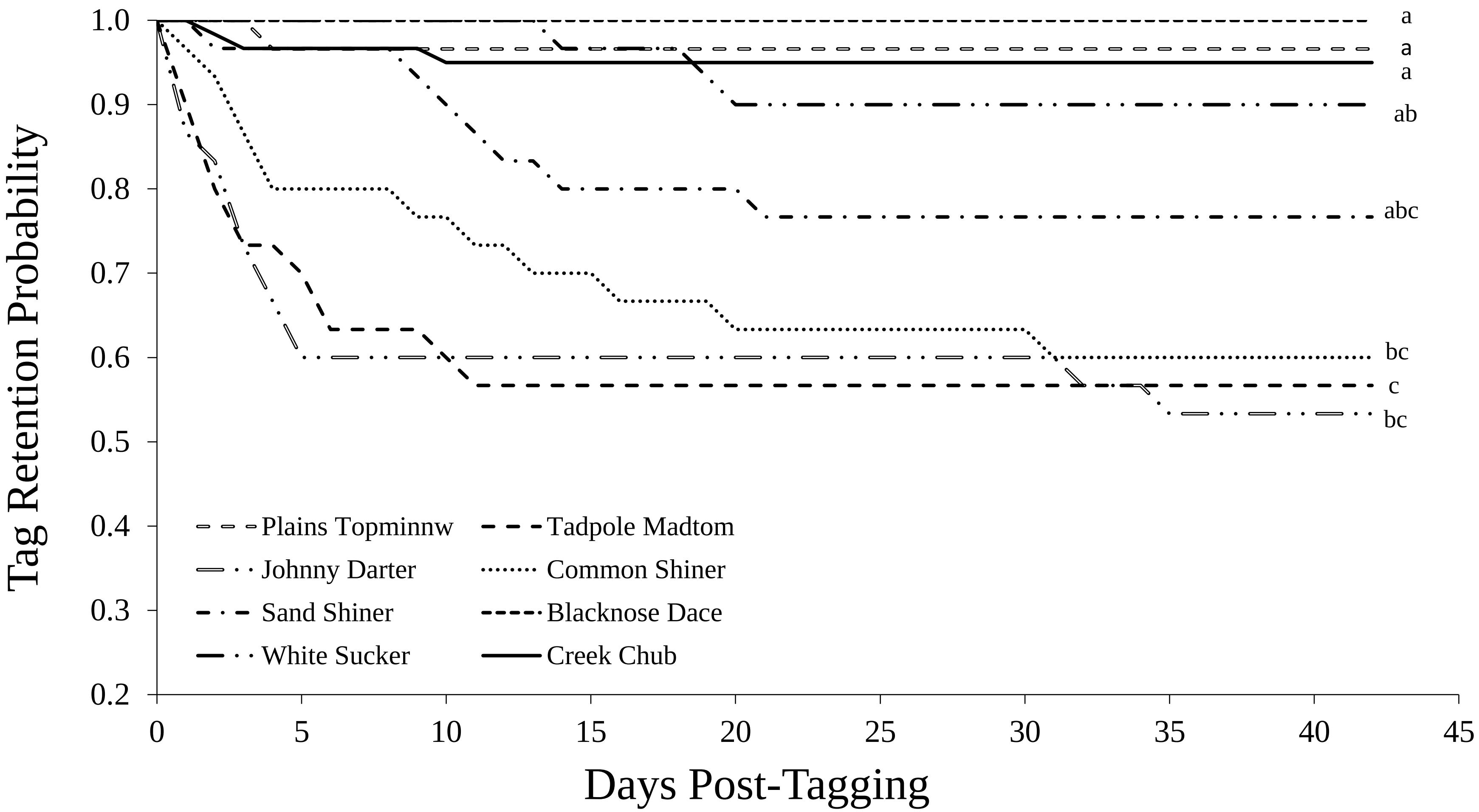

Figure 3. Daily retention of passive integrated transponder (PIT) tags for eight species of small-bodied warmwater fishes that received tags via surgical implantation. Tag retention was calculated only for living fish. Different letters denote statistically significant differences among species (*P* < 0.05).

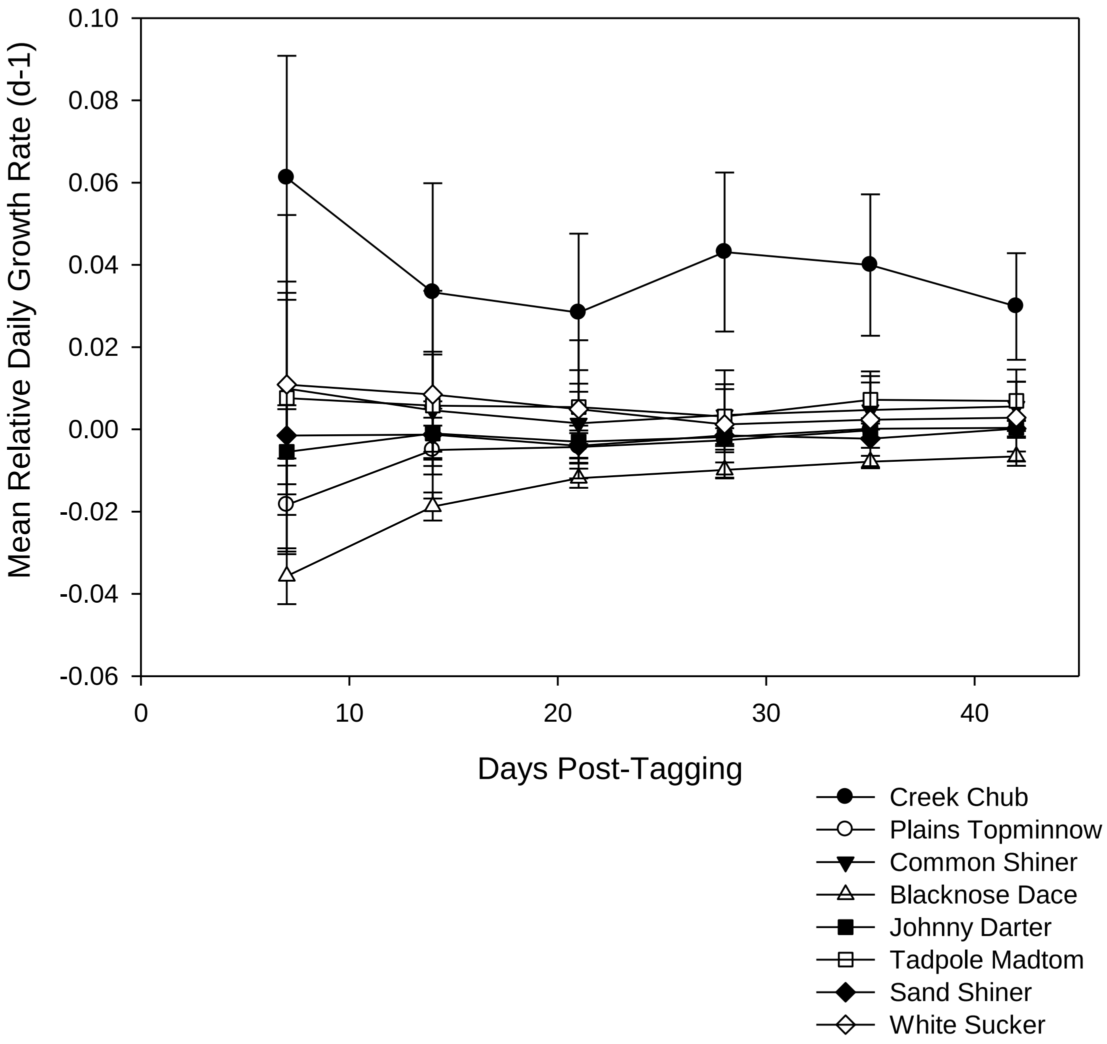

Figure 4. Mean relative daily growth rates (error bars = 2 SE) during the 42-d trial for eight species of small-bodied warmwater fishes (*n* = 90 per species).

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CHAPTER FIVE

INTEGRATING LANDSCAPE AND LOCAL PERSPECTIVES TO UNDERSTAND ECOSYSTEM RESPONSE TO STREAM RESTORATION

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Introduction

Numerous conservation programs exist to reverse landscape homogenization and restore ecological function in riparian areas. A loosely defined collection of aquatic species are expected to respond to riparian conservation efforts and improved instream environments. However, focused manipulations on isolated stream fragments have rarely achieved desired biological goals. Modern conservation of stream fishes has recently placed greater emphasis on riverscape-level processes that operate at spatial scales in which ecosystem recovery is largely mediated. Prairie landscapes with reestablished riparian corridors were appraised to quantify the indirect effects of prevalent grassland conservation practices on aquatic resources. I contextualized the results using riverscape perspectives to better understand organismal response patterns to landscape conservation efforts. Additional research efforts addressed three hypotheses that we generated to explain stream reach level observations.

Impact of grassland management on local stream ecosystems

Riparian rehabilitation, via passive methods (*e.g.*, cattle exclusion), promoted bank-stabilizing vegetation along conservation stream reaches. Riparian vegetation and function recovered quickly from agricultural disturbance and provided conservation streams with important shade, sediment storage, and organic input. Substantial animal trampling and grazing pressure persisted at reference sites and limited vegetation growth in riparian areas. Although instream conditions are expected to recover slower than riparian features, I identified changes to instream habitat availability at conservation sites. Restoration efforts effectively reduced turbidity, increased coarse organic and woody debris inputs, provided overhanging vegetation, increased water discharge. Localized grassland conservation actions improved local water quality and restored processes that create diverse instream habitat complexes.

Much of our knowledge of riparian protections and their impacts on aquatic life have been developed indirectly by studying the effects of riparian rehabilitation on water quality and instream habitat availability. Direct measures of biotic response patterns have rarely been the focus of riparian improvement projects. My research was unable to demonstrate strong changes to benthic invertebrate and fish assemblage structure in response to conservation actions. However, changes to invertebrate taxa were more apparent than for fishes at conservation sites. Restoration efforts generally assume that by creating habitat aquatic biota diversity will be improved (‘field of dreams’ hypothesis), but numerous other factors may interrupt the link between habitat and biotic restoration. It is clear that improvements to isolated prairie stream fragments do not directly result in colonization by aquatic fauna. Stream restoration programs must also consider the specific habitat needs of target species and the accessibility of newly available habitats.

Although changes to fish assemblage structure were minimal, the size structure of two species was influenced by restoration efforts. Larger Fathead Minnow *Pimephales promelas* and Creek Chub *Semotilus atromaculatus* were encountered more frequently at conservation stream reaches. It is unclear whether these observations represent altered local population dynamics or the attraction of large, presumably dominate, individuals from adjoining areas. Similarities in mean length-at-age of Creek Chub between conservation and reference stream reaches suggest that population growth rates have not changed in response to conservation efforts.

By integrating riverscape and local, stream reach perspectives, managers will better understand the effectiveness of actions used to counter pervasive and widespread pressures on stream ecosystem integrity. Ultimately, restored sites were not *created* equally and each have different colonization prospects when environmental pressures are removed. By considering the local effects of riparian restoration and riverscape properties that dictate biotic response, I was better able to explain conservation outcomes. I evaluated three alternative hypotheses to explain the limited biotic response to restoration efforts: (1) connections to newly available habitats remain severed; (2) regional assemblages lack species adapted to utilize opened niches; and (3) the niche space created do not benefit local species.

Hypothesis One

Prairie streams are dynamic systems wherein habitat patches are sporadically created and lost from regular hydrologic variability. Extreme environmental pressures impact fish assemblage structure in prairie streams by regulating species abundance and distribution. Local extirpation is common so species persistence is dependent on dispersal over large areas to recolonize available habitats. The fragmentation of stream networks has severed historic movement pathways and potentially limited opportunities for fish to colonize restored stream reaches. To describe the relative likelihood that small-bodied fishes bypass anthropogenic barriers and the consequent risk to ecosystem function if they are unable, the swimming and jumping abilities and ecosystem effects of four representative plains fishes were quantified. These evaluations provide an indirect measure of each species' colonization potential following riparian rehabilitation efforts.

Prairie fishes are not equally vulnerable to instream barriers, but all failed to circumvent relatively minor obstacles. Small vertical barriers (> 5 cm) blocked most fish passage and, with access, all species were unable to traverse relatively short obstacles with moderate water velocities. Without colonization opportunities from neighboring source populations, disturbance events will alter headwater fish assemblage structuring. Restoration efforts above barriers are unlikely to be colonized despite improvements to stream conditions. Lost fish diversity above barriers will hinder stream ecosystem processes as species were not ecologically redundant and each impacted ecosystem structure differently. Algal filament length was greatly increased by the simulated extirpation of a grazing minnow, Central Stoneroller *Campostoma anomalum*. Abundant barriers to recolonization with limited tools to improve passage for small-bodied prairie fishes will limit the effectiveness of conservation efforts in areas where fish are unable to reach.

Hypothesis Two

Various conservation programs have the potential to alleviate environmental impacts that reduce fish diversity and alter ecosystem function in streams. These conservation tools usually attempt to improve water quality and increase instream habitat heterogeneity. By restoring riparian processes and indirectly providing additional habitat features, managers hope to elicit a biological response by individual species or assemblages. As found in this study, stream restoration programs have failed to improve biological diversity. Interpreting biological responses requires consideration of the regional species pool from which restored reaches would recruit individuals.

Conservation efforts in watersheds with small, impoverished species pools are unlikely to elicit a measurable response from aquatic assemblages or targeted species. The identification of regional species pools and species-specific environmental tolerances should be considered a prerequisite to management.

Of the benthic invertebrate and fish taxa encountered in this study, ~20% were only captured at a few isolated stream reaches and were not well distributed. In almost all cases, these organisms occurred at a single conservation and reference stream reach pair in distinct regions of the James River basin. The variation in the abundance and occurrence of some taxa, such as Blacknose Dace *Rhinichthys obtusus* and Tadpole Madtom *Noturus gyrinus*, was explained by stream system alone. Other taxa occurred throughout the basin suggesting that their occurrence and local abundance were subject to grassland conservation efforts. Although not encountered at any conservation or reference stream reaches in the current study, the Topeka Shiner *Notropis topeka* distribution in South Dakota represents the importance of targeted management actions (Figure 1). Nearly 60% of conserved landscapes in the James River basin are located in subwatersheds where the probability of Topeka Shiner occurrence is < 20% (Figure 1). Only ~15% of conservation sites are located in areas where the probability of Topeka Shiner occurrence is > 40% (Figure 1). Future colonization by many aquatic taxa is unlikely at a large number conservation sites throughout the James River basin.

Hypothesis Three

The determination of specific environmental targets for stream restoration efforts to benefit particular taxa and biotic diversity is critical but often addressed with limited data. Our results suggest that benthic invertebrates and fishes strongly respond to changes to the riparian area that increase ground vegetation and tree cover. Fish and benthic invertebrate diversity was highest when instream cover (woody debris and overhanging vegetation) was available in areas with large substrates and abundant aquatic plants.

We identified several environmental features that effect fish and macroinvertebrate diversity that are influenced by grassland conservation efforts. Fish and benthic invertebrates responded to patches of structural habitat which were relatively rare in degraded stream reaches. Grassland conservation efforts created niche space that is beneficial to local aquatic fauna, but that are not utilized in inaccessible areas. Managers can supplement riparian rehabilitation efforts by providing large substrates and woody debris in areas with abundant aquatic and overhanging vegetation.

A Tool to Further Evaluate Hypothesis Three

Innovative conservation tools are critical as freshwater fishes are lost at unprecedented rates. Mark-recapture can describe fish-habitat relationships at small spatial scales, but techniques for tagging small-bodied fishes are very limited. Recent advances in passive integrated transponder (PIT) tag technology may facilitate the tagging of small species and early life stages of larger species. Despite the potential value of new, smaller PIT tags (8.4 x 1.4 mm), little research has evaluated their suitability when surgically implanted into small fishes. We evaluated the effectiveness of these tags when surgically implanted into representative small-bodied species from eight taxonomic groups with different body shapes.

Effects of surgically implanted PIT tags varied by taxonomic group and by initial fish length for some species, but negative effects were often negligible. Managers can expect little tag loss and uncompromised growth rates for a variety of small-bodied fishes signifying the wide applicability of this technology. Significant tag loss suggests that PIT tags aren’t yet suitable for Johnny Darter *Etheostoma nigrum* and other related species. Small PIT tags offer opportunities for ecological and behavioral studies and fisheries scientists now have critical information concerning their suitability for several groups of small-bodied fishes that was previously unavailable.

Conclusions

Prairie conservation efforts improved local stream environments and provided instream features to which aquatic organisms depend. Despite dramatic changes to riparian ecosystems and subsequent improvements to instream habitat availability, benthic invertebrate and fish assemblages have yet to respond to conservation efforts. Not all restored sites are *created* equally; each have both local and riverscape scale constraints that dictate biotic response patterns. Although the cumulative protected area exceeds 81,000 acres, each conservation easement only represents a sliver of the riverscape. Every stream reach is subject to degradation that impacts water availability and quality throughout the watershed and severs colonization pathways from neighboring source populations. Although grassland management actions were able to improve local stream conditions, they do not address stream connectivity issues or overcome the sizeable impact of nearby land practices that govern animal responses. The development of niche space does not directly translate to successful colonization and subsequent occupation by aquatic life.

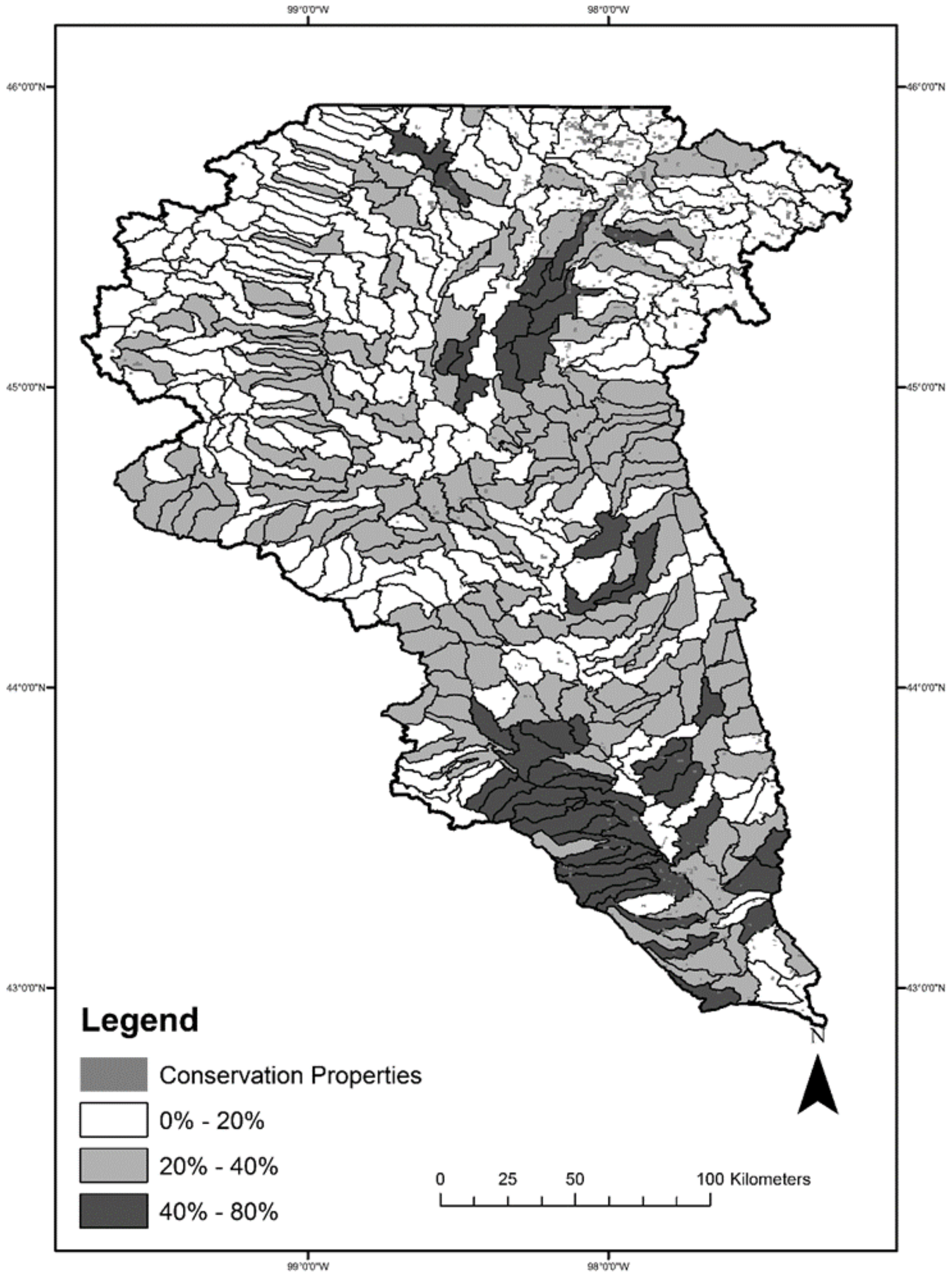

Figure 1. Predicted occurrence probability of Topeka Shiner *Notropis topeka* in subwatersheds (HUC-12) of the James River basin, South Dakota (data used with permission from Matt Wagner).

APPENDIX A

James River Watershed CREP—Major Aquatic Resource Goals

Provide a variety of environmental benefits and improvements through the reduction of sediments and nutrients entering waterways from adjacent land due to agricultural practices on previously utilized agricultural landscapes

1. Reduce soil erosion on fields planted in row crops to reduce sedimentation of waterways by 90 percent or 54,000 tons/year
2. Reduce phosphorous and nitrogen pollution from row crop agriculture by 65 percent or 144,000 lbs/year for phosphorous and 546,000 lbs/year for nitrogen
3. Reduce excess sediment and nutrients entering waterways from lands adjacent to enrolled riparian buffers by 50 percent or 2,100 tons/year for sediment, 5,200 lbs/year for phosphorous, and 28,000 lbs/year for nitrogen
4. Stabilize 90 percent of the channels in reaches where riparian buffers are installed by removing livestock and establishing riparian vegetation