Environmental factors associated with long-term trends of mountain sucker populations in the Black Hills, and an assessment of their thermal tolerance

BY

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A thesis submitted in partial fulfillment of the requirements for the

Master of Science

Major in Wildlife and Fisheries Sciences

South Dakota State University

2011

Environmental factors associated with long-term trends of mountain sucker populations in the Black Hills, and an assessment of their thermal tolerance

This thesis is approved as a creditable and independent investigation by a candidate for the Master of Science degree and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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Acknowledgements

I would like to extend my deepest gratitude to my parents, Michael E. Schultz and Teresa Black whose support has inspired me to continually strive to do great things. I cannot think of two more important people in my life, and I hope that their support continues for many years to come. They instilled in me an astounding work ethic, passion for the outdoors, and compassion for people. I cannot think of two better parents on Earth and they have done a remarkable job of raising two tremendous sons. On that note, I would also like to recognize my brother, Dustin Schultz, unquestionably my oldest and one of my dearest friends. In addition, I would like to acknowledge the support of my close friends in the Hayward, WI area: Mike, Larry, and Mary Glodoski, Chris, Wayne and Mary Westerhoff, Mike Siverling and Laura Fafara Siverling, Roger Burger, Dave Eckstrom, and Tom Heinrich.

I consider myself fortunate to have spent time in Ely, MN while attending Vermilion College. While there, in addition to receiving a first class natural resource education, I gained numerous friendships with first class people. I would like to acknowledge the wisdom and guidance that I have received from P. Doran, C. Tikkanen, D. Marshall, T. Sertich, J. Greene, M. Thompson, A. Maves, and K. Turner. I would also like to acknowledge the support and love that I have received from S. Thompson, who treated me like a son and will be forever in my heart.

Something must also be said of some of the influential people I have had the privilege knowing from UWSP. They include: E. Anderson, R. Hauer, B. Bell, L. Roffler, B. Spude, J. Hammen, B. Cross, A. Smith, A. Musch, M. Hughes, S. Schmidt,

and B. Sloss. Professionally, I owe much to M. Bozek for allowing me to learn form, work with, and listen to the 'wisdom' he provided. While in Wyoming, I was greatly aided by the guidance and friendship of J. Luginbill and R. Compton.

Since coming to South Dakota in 2009, many people have provided innumerable support professionally and personally. First off, I would like to thank Sarah Jane Lewis for two years of faithful service while working in the Black Hills. I would be hard-pressed to find a better technician, idea sounding board, guide to all things Black Hills, car loan service, comic relief expert, and friend – and she accomplished all of these with ease. I would also like to acknowledge the support provided by my Black Hills network of friends including Chuck and Judy Lewis, Lee and Lisa Erickson, Lindsay Bressler, and Angela and Mike Jarding. While in Brookings, I owe a good deal to the special friendships that were provided by McLain Johnson, Landon 'P.I.C' Pierce, Will 'Bestie' Schreck, Bre VanDeHey (co-adventurer and dog advice consultant), and Aaron 'Bromance' VonEschen. These people have always been there for me whether it be emotionally, comically, or for hunting (elk, ducks, pheasants…other things). In addition, I would like to thank: R. Andvik, T. Bacula, J. Baker, J. Bender, T. Berdan, M. Blaalid, I. Csargo, J. Davis, D. Dembkowski, E. Felts, M. Fincel, B. Fincel, W. French, M. Greiner, C. Hayer, M. Hennen, H. Heyer, A. Hitt, J. Howell, D. James, A. Jansen, J. Jolley, M. Kaemingk, J. Krause, A. Letvin, C. Mehls, C. Mosby, K. Mosel, N. Peterson, E. Phillips, T. Rapp, S. Shaw, J. Sholly, M. Thul, D. Toy, J. VanDeHey, J. White, M. Wuellner, and anyone that ever gave me food.

I have also had the privilege to work with top-notch people while here at SDSU. South Dakota Game, Fish and Parks fisheries biologist J. Wilhite provided logistical support, exceptional guidance, tremendous humor, and good friendship to me for two years, and I look forward to any additional interactions with him. Without the constant help and friendship of Terri Symens, Carol Jacobson, and Di Drake my time here would have been much more difficult and fruit(candy)less – I thank them for all they have done and continue to do. Great help on this and numerous other projects was generously provided by B. Graeb, M. Brown, S. Pederson, D. Auger, J. Jenks, S. Chipps, P. Tille, and D. Willis. My advisor, K. Bertrand, and I have endured numerous growing pains together. Looking back, she has been tremendous every step of the way by challenging me and pushing me to achieve all that I am capable of, and I admire her ability to balance everything she does while remaining good spirited and keeping her sense of humor intact. I can only hope that I have not let her down, and that her following students are not as 'rough around the edges'.

My personal development was largely shaped by the influences of several additional people that are worthy of mention. In no particular order they include: M.J. Keenan, J. Chancellor, D. Carey, A. Jones, D. Draiman, N. Young, D. Abbott, K.W. Shepherd, E. Vedder, M. McCeady, S. Gossard, J. Ament, M. Cameron, J. Fogerty, N. Peart, S. Weiland, T. Morello, C. Cornell, B. Seger, K. Cobain, M. Manson, A. Young, R.J. Dio, Flea, D. Mustaine, B. Smith, J. Todd, W. Scantlin, P. Loeffler, C. Taylor, J. Lennon, M. Collins, Slash, S. Erna, Z. Wylde, T. McIlrath, B. Dickinson, L. Staley, J.J.

Walker, J. Cantrell, L. Kilmister, J. Hetfield, K. Hammet, L. Ulrich, C. Burton, and to a lesser extent J. Newsted.

Finally, I would like to thank tectonic uplift and glacial events for creating and shaping a landscape rich in topographic, botanical, scenic, and faunal diversity that refreshes my soul and rejuvenates my body. Without these simple releases, completion of this work would have been immensely more difficult, and I was privileged to have an advisor that allowed me to partake in these multiple pursuits "as long as I got my stuff done." For that, Katie, I am indebted and thank you.

Additional field work for this project was provided by South Dakota Game, Fish and Parks personnel including J. Wilhite, J. Davis, M. Bucholz, C. Cudmore, and M. Barnes, K. Wintersteen, and the NcNenny State Fish Hatchery crew. Helpful comments to a previous draft of Chapter 4 were provided by P. Bettoli. Funding for this project was provided by South Dakota State Wildlife Grant T2-2-R to K. Bertrand in the Wildlife and Fisheries Sciences Department at South Dakota State University.

Abstract

Environmental factors associated with long-term trends of mountain sucker populations in the Black Hills, and an assessment of their thermal tolerance

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May 2011

Addressing the global loss of biodiversity is the penultimate challenge for conservation biology. In western North America, the decline of native fishes is well-documented and resulted from burgeoning water resource development, habitat alteration, introduction of non-indigenous fishes, and riverscape changes resulting from impoundment of large river systems. Understanding population trends and addressing the causative factors involved in species declines is critical to recovery and management actions. Mountain sucker *Catostomus platyrhynchus* is a stream fish native to the Intermountain Region of western North America, and populations in the Black Hills of South Dakota represent the easternmost range of the species. Recent stream fishery surveys raised concerns about the status of mountain sucker populations in South Dakota. In addition, little information exists on the basic ecology of the species, which precludes informed management and conservation. The objectives of this study were to 1) document the current (2008-2010) distribution and abundance of mountain sucker in South Dakota for comparison with historical data, 2) evaluate the potential influence of physical and biological factors on the abundance and distribution of mountain sucker, and

3) assess their thermal tolerance. I analyzed stream fisheries survey data collected between 1960 and 2010 and found that mountain sucker density generally declined at three nested spatial scales: sample reach, stream, and watershed. At 14 sample reaches and two streams mountain sucker appear extirpated, whereas they persisted at densities ranging from 0.002-0.7 fish m^{-2} in 12 streams and eight watersheds. In 2008-2010, populations exceeding densities of 0.01 fish m^{-2} persisted only in Whitewood, Elk, Boxelder, and Bear Butte Creeks, and Rapid Creek and its tributaries above Pactola Reservoir, and mountain sucker appear to have been extirpated from all but one sample reach in the southern Black Hills. To explain the distribution of mountain sucker, I modeled mountain sucker presence and density as functions of geomorphic, sample reach habitat, and fish assemblage variables. Candidate models were evaluated for relative support using an information theoretic approach. Mountain sucker presence was best predicted by a combination of sample reach habitat, geomorphic, and fish assemblage variables, whereas trout density greater than 0.15 fish m^{-2} was associated with absence of mountain sucker. In sample reaches with mountain sucker, their density was positively associated with periphyton coverage, a food resource. Mountain sucker thermal tolerance was assessed using the lethal thermal maxima (LTM) procedure, a standard measure of thermal tolerance that is easily compared across species. The LTM of mountain sucker was greater than that of the three co-occurring salmonids, but lower than three co-occurring cypriniforms in the Black Hills. These results indicate that mountain sucker are not currently thermally limited in the Black Hills, but may lose suitable habitat as climate change persists. This study documents the decline of a native fish in the Black

Hills of South Dakota, and a comprehensive ecosystem management approach could mitigate further loss of mountain sucker. Furthermore, the results of this study can be used to prioritize conservation areas for mountain sucker and aid in the understanding of mountain sucker ecology across their range.

TABLE OF CONTENTS

ACKNOWLEDGMENTS iii

ABSTRACT vii

LIST OF TABLES xii

LIST OF FIGURES xiv

CHAPTER 1. Introduction 1

CHAPTER 2. Long term trends and outlook for mountain sucker in the Black Hills of South Dakota 7

Abstract 7

Introduction 8

Study Site 10

Methods 12

Results 14

Discussion 15

CHAPTER 3. Historical biogeography, autecology and biotic interactions influence the distribution of an imperiled fish 29

Abstract 29

Introduction 30

Methods 34

Results 41

Discussion 44

CHAPTER 4. An assessment of the lethal thermal maxima for mountain sucker 59

Abstract 59

Introduction 60

Methods 66

Results 65

Discussion 66

CHAPTER 5. Summary, management implications, and research needs 76

LITERATURE CITED 81

LIST OF TABLES

Table 2-1. Location and density of sample reaches where mountain sucker were collected 2008-2010 20

Table 2-2. Regression analysis of mountain sucker density for the years 1960-2010 in the Black Hills of South Dakota at three nested spatial scales 22

Table 2-3. Sample reaches and streams where mountain sucker were captured historically and years since last detection in the Black Hills of South Dakota. 25

Table 3-1. Sample reach-habitat, geomorphic and fish assemblage variables included in predictive models and multivariate analyses of mountain sucker distribution and fish assemblage patterns 51

Table 3-2. Predictive models, AIC_c, ΔAIC_c, w_i, and ROC values for *a priori* models used to predict mountain sucker presence/absence with logistic regression in the Black Hills of South Dakota. 52

Table 3-3. Model-averaged parameter estimates (b_i) and standard error for four logistic regression models used to predict presence of mountain sucker for streams in the Black Hills, South Dakota, including the number of models (k) that each parameter occurred in. 53

Table 3-4. Predictive models, AIC_c, ΔAIC_c, and w_i values for *a priori* linear models used to predict mountain sucker density in the Black Hills of South Dakota. 54

Table 3-5. Weighted correlation matrix of stream habitat variables and species values with canonical ordination axes. 55

Table 4-1. Measured lethal thermal maximum temperatures at four measured endpoints for mountain sucker acclimated to 20.0°C, 22.5°C, and 25.0°C 72

Table 4-2. Comparison of the laboratory thermal tolerance for fishes that are sympatric with mountain sucker in the Black Hills, fishes that may occur with mountain sucker across their range, and other catostomids. 73

LIST OF FIGURES

Figure 1-1. Distribution of mountain sucker in North America. 6

Figure 2-1. Current distribution (black) and locations of historic collection (red) of mountain sucker in the Black Hills of South Dakota. 27

Figure 2-2. Significant stream- (a), and watershed spatial scale (b) mountain sucker density regression trends in the Black Hills of South Dakota since routine sampling began in the 1960s 28

Figure 3-1. Mountain sucker density as a function of trout density for 100m sample reaches in the Black Hills, South Dakota sampled 2008-2010.. 56

Figure 3-2. Individual species-habitat factor ordination from canonical correspondence analysis (CCA) ordination of fish assemblages in the Black Hills, South Dakota sampled 2008-2010..... 57

Figure 3-3. Sample reach fish assemblage-habitat factor ordination from canonical correspondence analysis (CCA) ordination of fish assemblages in the Black Hills, South Dakota sampled 2008-2010.. 58

Figure 4-1. Lethal thermal maxima (LTM ± 95% confidence intervals) for mountain sucker acclimated to three different acclimation temperatures..... 75

Chapter 1.

Introduction

The number of imperiled freshwater and diadromous fishes in North America has increased 92% since the late 1980s (Jelks et al. 2008), and the rate of extinction for freshwater fauna will likely increase into the future (Ricciardi and Rasmussen 1999). Causes for declines include habitat loss, overexploitation, and hybridization and competition with introduced species. In western North America, extirpation and imperilment of the native fishes resulted from a combination of these stressors (Minckley and Deacon 1991). Despite being a relatively species poor region, fishes that occur west of the Continental Divide comprise nearly half of all described forms that have been listed, or considered for listing, as threatened or endangered by the U.S. Fish and Wildlife Service. Conservation action is critical in the recovery of these species and an understanding of population trends is paramount to prioritizing management activities to address these declines (Williams 1991).

Mountain sucker *Catostomus platyrhynchus* occur throughout the western United States and Canada from southern Saskatchewan and Alberta in the north, south and west to eastern California, and east through the Intermountain region to western Nebraska and the Black Hills of South Dakota (Figure 1-1, Scott and Crossman 1973). They inhabit cool mountain streams with mostly rocky substrates (Hauser 1969, Scott and Crossman 1973, Sigler and Sigler 1996), but are also found in large rivers (Smith 1966), lakes (Baxter and Stone 1995) and as adfluvial reservoir populations in headwater areas

(Erman 1973, Marrin and Erman 1982, Decker 1989, Wydoski and Wydoski 2002). Populations in the Black Hills of South Dakota and Wyoming are hypothesized to be either glacial relicts or present due to a stream capture event of the Little Missouri River headwaters by the Belle Fourche River (Bailey and Allum 1962) and represent the easternmost range of the species.

The current status of mountain sucker throughout its range is secure (G5; Natureserve 2009), but regional trends suggest that the species is declining at finer spatial scales. A series of long-term studies on Sagehen and Martis Creeks and Stampede Reservoir in Eastern California indicated declines in mountain sucker abundance, relative abundance, and spatial distribution (Erman 1973, 1986, Gard and Flittner 1974, Marrin and Erman 1982, Moyle and Vondracek 1985, Decker 1989). In the Missouri River drainage of Wyoming, Patton et al. (1998) found that mountain sucker had declined on at least three spatial scales since the 1960s, and increases were not detected at any of the four spatial scales analyzed. Of local importance, the South Dakota Department of Game, Fish and Parks lists the mountain sucker as a species of greatest conservation need (S3; SDGFP 2006) and the U.S. Forest Service designates the mountain sucker as a sensitive species and a Management Indicator Species (MIS) in the Black Hills National Forest (BHNF). Additionally, recent stream fishery surveys raised concern about potential declines of mountain sucker in the Black Hills of South Dakota (SDGFP unpublished data).

The long-term persistence of mountain sucker in the Black Hills of South Dakota depends on informed management decisions based on their biology. Overall, little published information exists on mountain sucker biology throughout their range in North America. Reviews of mountain sucker biology and status in Canada (Campbell 1992) and across their range (Belica and Nibbelink 2006) indicated that available data is insufficient to conclusively assess population trends across the range of mountain sucker, particularly in the Black Hills. These reviews identified the most pressing research needs: document the current distribution of mountain sucker in the Black Hills for comparison with existing data, monitor trends in abundance, identify habitat and landscape features that promote the existence of mountain sucker, investigate their community ecology, and increase the knowledge of the basic biology of the species (Isaak et al. 2003, Belica and Nibbelink 2006).

Initial assessments to address these information gaps occurred at a broad spatial scale and can be used to direct finer scale evaluations. Dauwalter and Rahel (2008) used a modeling approach to evaluate associations between four habitat and landscape features and mountain sucker presence. The distribution of mountain sucker in the BHNF of South Dakota and Wyoming was most strongly influenced by stream permanence (intermittency). However, a model with stream permanence and the interactions of three geomorphic habitat variables (stream order, channel slope, and elevation) improved the overall predictive value. In addition, the density of brown trout *Salmo trutta* negatively influenced mountain sucker presence when added to the combined model (Dauwalter and

Rahel 2008). These model predictions of distributions have yet to be field validated and could be refined with the addition of sample reach-specific habitat and fish assemblage structure metrics that were indicated as potential areas of information need (Belica and Nibbelink 2006).

Stream temperature may further limit distributions of coolwater fishes like mountain sucker, especially as global temperatures increase with climate change (Eaton and Scheller 1996). The thermal tolerance of a species is important in understanding its biology, and identifying thermal refugia is a critical step in establishing conservation areas for imperiled fishes (e.g., Smith and Fausch 1997, Selong et al. 2001, Harig and Fausch 2002). White sucker *Catostomus commersonii* are considered a coolwater fish rarely occupying habitats that exceed 27.3°C in weekly mean temperature (Eaton et al. 1995), and bridgelip sucker *Catostomus columbianus* (which are in the sub-genus *Pantosteus* with mountain sucker), had a realized thermal niche center of 21.9°C, and were not found in streams exceeding 25.7°C (Huff et al. 2005). Mountain sucker are thought to be replaced by bridgelip sucker along thermal gradients in Pacific Northwest streams (Li et al. 1987). Because mountain sucker inhabit mostly coolwater streams and other catostomids show temperature-regulated distribution, high water temperatures likely constrain the distribution of mountain sucker. Increasing stream temperatures, resulting from climate change, might further limit mountain sucker distribution.

This study addressed many of these research needs and may be used to better inform stream management decisions in the Black Hills of South Dakota. In Chapter 2, I

document the current distribution of mountain sucker in South Dakota's Black Hills and compared it to historic records. In Chapter 3, I evaluated the influence of physical and biological variables on the distribution of mountain sucker. Finally, Chapter 4 contains an assessment of the thermal tolerance of mountain sucker. Chapter 5 summarizes the major findings of this research and addresses the potential management applications of this work. The results of this study increase our understanding of mountain sucker ecology and may be used to assess conservation areas in the Black Hills. In addition, our approach can be adopted in other systems. Concurrent evaluation of multiple scales improved predictive models, and illustrated that multiple environmental filters (*sensu* Tonn 1990) need to be considered to most effectively predict species distributions. In addition, managers using this multiple-scale approach can identify spatial scales that management actions can effectively target (Quist et al. 2005).

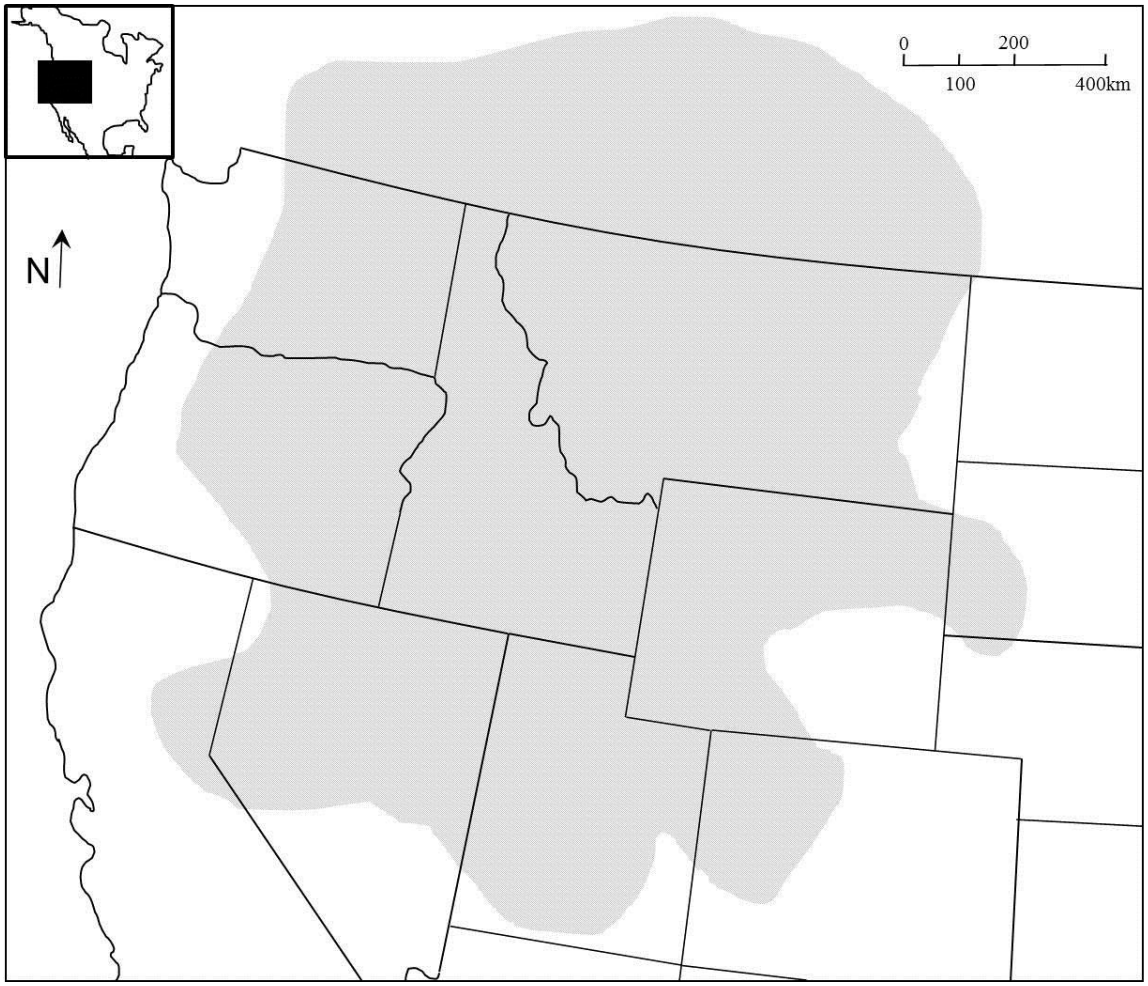

Fig. 1-1. Distribution of mountain sucker in North America. Adapted from Scott and Crossman (1973).

Chapter 2.
Long term trends in mountain sucker populations and spatial distribution in the Black Hills of South Dakota

This chapter was submitted as a manuscript to the American Midland Naturalist and was co-authored by Dr. Katie N. Bertrand.

ABSTRACT

The extirpation of native fishes is a major concern in North America, and an understanding of population trends of imperiled fishes is critical to their management and recovery. Mountain sucker *Catostomus platyrhynchus* is a stream fish native to the Intermountain Region of western North America, and populations in the Black Hills of South Dakota represent the easternmost range of the species. Recently, stream surveys raised concerns about the status of mountain sucker populations in South Dakota. The purpose of this study was to document the current distribution of mountain sucker in the Black Hills of South Dakota for comparison with historic records. We analyzed stream fisheries survey data collected between 1960 and 2010 and found that mountain sucker density generally declined at three nested spatial scales: sample reach, stream, and watershed. At 14 sample reaches and two streams, mountain sucker appear extirpated, whereas in remaining areas they persist at a wide range of densities. In 2008-2010, populations exceeding densities of 0.01 fish m^{-2} persisted only in Whitewood, Elk, Boxelder, and Bear Butte Creeks, and tributaries to Upper Rapid Creek. Our study documents the decline of a native fish in the Black Hills of South Dakota, and a comprehensive ecosystem management approach is needed to mitigate further loss of

mountain sucker and co-occurring native species, while at the same time maintaining a highly valued salmonid fishery.

INTRODUCTION

Recent studies documented an increase in the number of imperiled freshwater and diadromous fishes in North America since the late 1980s (Jelks et al. 2008). Causes for declines include habitat loss, overexploitation, hybridization, and competition with introduced species. Other recent literature suggests that the rate of extinction for freshwater fauna will increase into the future (Ricciardi and Rasmussen 1999). Fish extinctions (e.g., Snake River sucker *Chasmistes muriei*) and extirpations (e.g., Colorado Pikeminnow *Ptychocheilus lucius* from the lower Colorado River) in North America are most numerous in the West where reservoir construction, nonnative fish introductions and water withdrawals altered habitat and established new predators and competitors for native fishes (Minckley and Douglas 1991).

Quantifying long term population trends is the first step in prioritizing conservation actions for imperiled fishes (Williams 1991). Population parameters including density, natality, immigration/emigration, and mortality are useful in understanding the dynamics of an imperiled population (Bestgen et al. 2007), and comparing a species' present and historic distribution is critical for addressing changes in the status of a species of interest (e.g., Allendorf and Leary 1988, Dobson et al. 1997). Quantifying population trends and parameters has been used to assess status and set conservation priorities for a variety of declining taxa including: amphibians (Stuart et al.

2004), birds (Kochert and Steenhof 2002), mammals (Cofré and Marquet 1999), and fish (Williams et al. 1989, Jelks et al. 2009).

The current status of mountain sucker *Catostomus platyrhynchus* throughout its range is secure (G5, Natureserve 2010), but regional trends suggest that the species is in decline at finer spatial scales. In the Black Hills of South Dakota, recent stream fishery surveys raised concern about potential declines in localized mountain sucker populations and extirpations. Mountain sucker occur throughout the western United States and Canada from southern Saskatchewan and Alberta in the north, south and west to eastern California, and east through the Intermountain region to western Nebraska and the Black Hills of South Dakota (Scott and Crossman 1973). They inhabit cool mountain streams with mostly rocky substrates (Hauser 1969, Scott and Crossman 1973, Sigler and Sigler 1996), but are also found in large rivers (Smith 1966), lakes (Baxter and Stone 1995) and as adfluvial reservoir populations in headwater areas (Erman 1973, Marrin and Erman 1982, Decker 1989, Wydoski and Wydoski 2002). A series of long term studies on Sagehen and Martis Creeks and Stampede Reservoir in Eastern California indicated declines in mountain sucker total abundance, relative abundance, and spatial distribution (Erman 1973, 1986, Gard and Flittner 1974, Marrin and Erman 1982, Moyle and Vondracek, 1985, Decker 1989). In the Missouri River drainage of Wyoming, Patton et al. (1998) found that mountain sucker distribution declined on at least three spatial scales since the 1960s. In South Dakota, the Department of Game, Fish and Parks (SDGFP) listed mountain sucker in the State Wildlife Action Plan as a species of greatest conservation need (SDGFP 2006), and the U.S. Forest Service designated mountain

sucker as a sensitive species and a management indicator species in the Black Hills National Forest (USDA Forest Service 2005).

Reviews of mountain sucker biology and status in Canada (Campbell 1992) and across their range (Belica and Nibbelink 2006) indicated that available data is insufficient to conclusively assess population trends across the range of mountain sucker, particularly in the Black Hills. To better inform management decisions, the objective of this study was to document the current distribution of mountain sucker in South Dakota's Black Hills for comparison with historic records. Furthermore, analyzing historic density data at nested spatial scales allowed assessment of broad- and fine-scale density trends.

STUDY AREA

The Black Hills of South Dakota and Wyoming are a 100km wide (east-west) by 200km (north-south) forested dome-shaped uplift surrounded by short and midgrass prairie, leading some to call them an "island on the plains" (Koth 2007). Because of this "island" effect, many of the species present in the Black Hills, terrestrial and aquatic, are isolated from other conspecific populations across their range. In the Black Hills, Bailey and Allum (1962) attributed mountain sucker presence to either isolation following the retreat of the Pleistocene glaciers or stream capture of the Little Missouri River headwaters by the Belle Fourche River, which drains the northern Black Hills. The Black Hills are part of the Level III Middle Rockies Ecoregion which includes open ponderosa pine *Pinus ponderosa* stands and abundant spring-fed, perennial streams (Omernik 1987). Geologically, the center of the dome is characterized by Precambrian metamorphic and intrusive rocks, and is surrounded by a ring of Cretaceous sedimentary formations that

completely encircle the core (DeWitt et al. 1989). These sedimentary formations have substantial effects on the stream hydrology of the region. The limestone formations to the west of the core serve as groundwater recharge zones with little or no surface discharge, and streams that arise in the center of the Black Hills lose much of their surface discharge to the porosity of the formations as they flow north or east off the core of uplift (Williamson and Carter 2001). These zones of stream intermittency are known as the Loss Zone and can limit the distribution and dispersal of fishes between watersheds, especially in dry years.

Streams in the Black Hills of South Dakota have variable morphology and biological characteristics. Channel widths in small, headwater streams (e.g., Deer, South Boxelder, Tillson Creeks) average 1-4 m and average depth is between 5 and 15 cm. Larger streams (e.g., Spring, French, Boxelder Creeks) have average widths from 3-10 m, and average depths range from 15-30 cm. The largest streams (e.g., Rapid and Spearfish Creeks) average 7-15 m in width and 20-50 cm in depth, getting larger as they flow downstream onto the plains. Substrate in streams is generally cobble and rubble, but slack water portions of channels can accumulate finer sediments and organic debris. Native stream fish assemblages generally contain mountain sucker, white sucker *Catostomus commersonii*, longnose dace *Rhinichthys cataractae*, creek chub *Semotilus atromaculatus*, and fathead minnow *Pimephales promelas*. There are no native representatives of the family Salmonidae in this region, but introduced brook trout *Salvenlinus fontinalis*, brown trout *Salmo trutta*, and rainbow trout *Oncorhynchus mykiss* dominate many fish assemblages throughout Black Hills streams. From 1988-2001,

increased stream discharge in the Black Hills region connected previously disjunct fish populations. Discharge data (monthly mean, m^3s^{-1}) recorded between 1996 and 2001 was significantly different from data recorded between 2002 and 2007 in Spearfish Creek in the northern Black Hills at Spearfish, SD (2.51 vs. 1.50, $t_{129} = 10.97$, $P < 0.01$) and in Rapid Creek in the central Black Hills at Rapid City, SD (4.02 vs. 1.15, $t_{75} = 7.99$, $P < 0.01$). Between 2002 and 2007, these conditions decreased brown trout biomass in Rapid and Spearfish Creeks (James et al. 2010). Effects of the drought on native fishes were not studied.

METHODS

We assessed mountain sucker abundance at standardized sample reaches with repeated fish survey data from SDGFP. Comprehensive reports of fish assemblages from the Black Hills are available from historical data collected in the late 1950s and early 1960s (Bailey and Allum 1962, Stewart and Thilenius 1964), 1984 and 1985 (Ford 1988), and 1988-2008 (SDGFP 1988-2008). To describe current distributions of mountain sucker, we conducted region-wide inventories of streams in the Black Hills of South Dakota. We began sampling where mountain sucker were previously collected, then searched unsampled reaches up and downstream to comprehensively assess their distribution. In each 100 m sample reach, we used single-pass electrofishing to collect fish. Single-pass and multiple-pass catch per unit effort strongly correlate in the Black Hills and in other regions, and density estimates based on single-pass samples provide a reliable approximation of absolute abundance and species diversity (Bertrand et al. 2006, Reid et al. 2009). We counted, measured (total length; mm), and identified each fish to

species following completion of each pass and then released them back into the sample reach. Based on species-specific models relating single- and multiple-pass catch per unit effort, we computed density (fish m^{-2}) for each species in each sample reach. Voucher specimens of each species and any unidentified individuals were anaesthetized and preserved in a 10% formalin solution in the field, transferred to a 70% ethanol solution for later processing, and archived in the South Dakota State University fish reference collection. Field identification was verified with voucher specimens in the laboratory using a dissecting light microscope.

We modeled mountain sucker density as a function of sampling period using simple linear regression. If parameter estimates for the slope of the linear regression differed significantly ($\alpha = 0.05$) from zero, we inferred a population trend. We analyzed data at three spatial scales: sample reach, stream, and watershed. We defined sample reaches as locations were stream fishery assessments have routinely occurred since the late 1950s (typically 100 m in length). We defined streams as waterbodies having different names on USGS topographic maps (scale 1:24000) and potentially comprising multiple sample reaches. We defined watersheds as major drainages (11-digit hydrologic unit code) of the Black Hills which empty into larger rivers on the plains (i.e., Cheyenne, Belle Fourche, Redwater), and could contain multiple streams. We used this system of watersheds because mountain sucker are unlikely to travel into prairie portions of streams to disperse into adjacent watersheds and often are unable to do so because of a lack of surface flow in the Loss Zone. We performed linear regressions for datasets that had at least seven sampling events and included 16 sample reach-level, 16 stream-level, and 10

watershed-level regressions. We also compared the number of valley segments (Frissell et al. 1986) in which mountain sucker were present 2008-2010 to the number of valley segments that mountain sucker historically occupied.

RESULTS

Mountain sucker historically occurred throughout the Black Hills of South Dakota, but persisting mountain sucker populations occur only in the northern Black Hills. Sampling in 2008-2010 detected mountain sucker in 27 of 104 (26%) valley segments where fishery biologists historically found mountain sucker (Figure 2-1), and their range appears to have contracted considerably since routine sampling began in the late 1950s. At every scale, mountain sucker distributions appear to be shrinking towards the center of their previous extent. For example, across the Black Hills, mountain sucker currently are not found in peripheral stream reaches they historically occupied. At the stream spatial scale, mountain sucker were not found in many headwater stream segments or downstream segments from which they were previously sampled (Figure 2-1). Mountain sucker were not collected in many reaches of southern Black Hills streams including Cascade, Beaver (south), French, and Spring Creeks, as well as large portions of Castle, Lower Rapid, and Spearfish Creeks. In the southern Black Hills, mountain sucker persisted only in small numbers in Battle Creek. Currently, mountain sucker persist in densities exceeding 0.01 fish m^{-2} in Whitewood, Elk, Boxelder, and Bear Butte Creeks, near the center of their current distribution in the Black Hills. At the periphery of their current distribution in the Black Hills, mountain sucker are present in modest densities (0.0017-0.0624 fish m^{-2}) in portions of the Rapid Creek watershed above

Pactola Reservoir (i.e., Upper Rapid and North Fork Rapid Creeks, Swede Gulch) and in low densities (0.0017-0.0048 fish m^{-2}) in portions of Annie, Battle, Crow, and Castle Creeks (Table 2-1).

Significant decreases in mountain sucker density ($P < 0.05$) were detected at all three spatial scales (Table 2-2). One sample reach (Rapid Creek - 44.079N, 103.255W), seven streams (Annie, Spearfish, Castle, Iron (south), Grace Coolidge, Rapid downstream of Pactola Reservoir, Spring; Figure 2-2), and five (of 10) watersheds (Spearfish, Rapid-above Pactola Reservior, Rapid – below Pactola Reservoir, Spring, Battle; Figure 2-2) have significantly fewer mountain sucker than they had historically. In addition, fourteen sampling reaches (in Annie, Castle, Rapid, Spring and Iron (south) Creeks) and two streams (South Fork Rapid and Spearfish) had biologically significant declines, but we didn't apply linear regression because mountain sucker were detected once (usually early in historical records) and never detected at that sample reach again (Table 2-3). We found no significant temporal trend (i.e., $P > 0.05$) in17 sample reaches, 8 streams, and 5 watersheds and, most notably, observed no significant increases at any spatial scale (Table 2-2).

DISCUSSION

These results strongly indicate that mountain sucker in the Black Hills of South Dakota have declined since the 1960s. No sample reaches, streams, or watersheds showed increasing trends in mountain sucker density. Whitewood, Elk, Boxelder, and Bear Butte Creeks and portions of the Rapid Creek watershed above Pactola Reservoir appear to have persistent populations, but mountain sucker appear to have been extirpated

from most of the southern Black Hills and substantial portions of Spearfish, Rapid (downstream of Pactola Reservior), and Castle Creeks since the 1960s. Other watersheds across the Black Hills lacked trends or infrequent sampling precluded analysis. Our results indicate a more critical situation than was suggested by Isaak et al. (2003). They concluded that mountain sucker were relatively secure across the Black Hills, but their dataset was based primarily on presence/absence data current through 1999, with limited quantitative density data available.

The patterns in distribution and population trends quantified herein are alarming but two confounding factors warrant discussion. Mountain sucker were not the target species in historic fisheries assessments, hence their population size and density estimates may have been negatively biased. Bias against mountain sucker and other non-sportfish species in stream population assessments is common and can influence accuracy and precision of population size estimates (Zalewski and Cowx 1990). However, since our assessments targeted mountain sucker more specifically than historic samples, these biases should be minimized or reversed in the most recent samples, implying that the "true" population trend may actually be steeper than our estimates. Additionally, because the movement patterns of mountain sucker are largely unknown (Belica and Nibbelink 2006), it is unclear to what degree, and over what time scale, mountain sucker are truly 'absent' from (versus not currently occupying) a given sample reach. Despite these potentially confounding factors, there were no sample reaches, streams, or watersheds with significant positive increases in density, which provides evidence that our analyses have described real trends.

Across North America, many native fishes share similar patterns of distributional changes and conservation threats with mountain sucker, including salmonids and other catastomids. For example, Westslope cutthroat trout *Oncorhynchus clarkii lewisii* have been restricted to 60% of their historic range and populations at the core of the range were much denser than those at the periphery (Shepard et al. 2005). Numerous catostomid species have similarly experienced range contractions and population declines (Cooke et al. 2005). Like numerous other catostomid species in western North America, mountain sucker in the Black Hills are locally disjunct from conspecific populations due to orographic and/or glacial events. Also, like other sucker species, a paucity of basic biological information and understanding of their ecological roles inhibits effective conservation of mountain sucker, and a prevailing perception of suckers as "trash" fish can impede management actions (Cooke et al. 2005). Cooke et al. (2005) identified multiple threats faced by imperiled catostomids including habitat loss and degradation, inter-specific hybridization, environmental contaminants, and negative interactions with exotic species, including hybridization (McDonald et al. 2008). Loss of habitat connectivity and fragmentation also contribute to imperilment of two sucker species in Wyoming (Compton et al. 2008). Although less common, overexploitation of sucker species can be a significant issue in the conservation of sucker populations, particularly lacustrine sucker species (e.g., cui-ui *Chasmistes cujus*; Scoppettone and Vinyard 1991).

Translocations (e.g., Harig et al. 2000, 2002), habitat rehabilitation and restoration, removal of exotic species (e.g., Shepard et al. 2002), and isolation management (i.e., the construction of barriers to artificially isolate fish populations of

conservation interest; Novinger and Rahel 2003) have been used extensively in the recovery of imperiled salmonid species. Fisheries biologists encounter mixed success when implementing these actions, and identifying potential areas of conservation interest and prioritizing areas for management action can be complex (Peterson et al. 2008). Similar recovery efforts have been applied in the conservation of native non-game species, including suckers (Minckley 1995, Tyus and Saunders 2000). Hendrickson and Brooks (1991) report two instances of translocations saving species from extinction, and removal of nonnative fishes is a common practice in native fish conservation and restoration (Meuller 2005). Isolation management activities directed towards non-game fishes are in their infancy (e.g., Muddy Creek, WY; Compton et al. 2008, Beatty et al. 2009). Thus, there is a critical need for novel predictive analytical tools, increased understanding of factors that influence project success, and continued refinement of implementation strategies, all of which should increase the chances of success in future actions (Polasky and Solow 2001).

This conservative analytical approach has documented a decline of a native fish in the Black Hills of South Dakota, and action is needed to proactively address these trends. Belica and Nibbelink (2006) identified some of the most pressing gaps in mountain sucker knowledge for their proper management: understanding stream and landscape habitat factors promoting their existence, better information on their basic demographic characteristics, and an improved understanding of their community ecology. The quantitative assessment herein can be used by managers to prioritize critical areas for mountain sucker conservation in the Black Hills of South Dakota. Similar analyses in

other peripheral portions of the range of mountain sucker would elucidate their broad-scale status and increase the understanding of mountain sucker ecology. Of additional interest is an investigation of interactions between mountain sucker and introduced salmonids and the mechanisms underlying observed patterns of distribution. This basic biological information would help address potential causes of decline, and aid in identifying areas of conservation interest toward their recovery.

Table 2-1. Location (Stream - latitude/longitude) and density of sample reaches where mountain sucker were collected 2008-2010. Date = year of collection.

Sample Reach	**Date**	**MTS density (fish m^{-2})**
Crow - 44.562N 104.01W	2008	0.002
Annie - 44.331N, 103.878W	2010	0.005
Annie - 44.318N, 103.871W	2010	0.004
Whitewood - 44.412N, 103.694W	2009	0.107
Whitewood - 44.356N, 103.739W	2008	0.173
Whitewood - 44.518N, 103.608W	2009	0.168
Whitewood - 44.590N, 103.520W	2009	0.006
Whitewood - 44.622, 103.472W	2009	0.003
Whitewood - 44.473N, 103.625W	2009	0.075
Whitewood - 44.459N, 103.626W	2008	0.331
Whitewood - 44.396N, 103.702W	2009	0.134
Whitewood - 44.517N, 103.605W	2009	0.034
Bear Butte - 44.334N, 103.625W	2010	0.004
Bear Butte - 44.324N, 103.650N	2010	0.014
Bear Butte - 44.298N, 103.677W	2010	0.018
Bear Butte - 44.307N, 103.669W	2010	0.003
Bear Butte - 44.315N, 103.652W	2010	0.054
Bear Butte - 44.288N, 103.693W	2010	0.013

Elk - 44.280N, 103.634W	2008	0.078
Elk - 44.277N, 103.695W	2009	0.393
Elk - 44.276N, 103.668W	2009	0.703
Elk - 44.302N, 103.553W	2009	0.034
Elk - 44.298N, 103.582W	2009	0.435
Meadow - 44.287N, 103.562W	2010	0.006
Boxelder - 44.157N, 103.466W	2010	0.023
Boxelder - 44.198N, 103.523W	2010	0.079
Boxelder - 44.229N, 103.599W	2010	0.012
Rapid - 44.106N, 103.652W	2010	0.002
Rapid - 44.106N, 103.652W	2010	0.017
Rapid - 44.111N, 103.671W	2010	0.010
Swede Gulch - 44.178N, 103.776W	2008	0.005
Swede Gulch - 44.174N, 103.799W	2009	0.040
N. Fork Rapid - 44.178N, 103.756W	2010	0.062
N. Fork Rapid - 44.132N, 103.736W	2010	0.028
N. Fork Rapid - 44.197N, 103.761W	2010	0.030
Castle - 44.078N, 103.718W	2009	0.002
Battle - 43.889N, 103.363W	2009	0.002

Table 2-2. Regression analysis of mountain sucker (MTS) density (fish m^{-2}) for the years 1960-2010 in the Black Hills of South Dakota at three nested spatial scales. num df = numerator degrees of freedom, den df = denominator degrees of freedom, # points = total times sampled since routine sampling began in 1960s. Sample reach includes stream and latitude and longitude of sampling location. Last year w/ MTS indicates when mountain sucker were last detected (last year sampled). Sample reaches include: ANN – Annie Creek, BBC – Bear Butte Creek, STRW – Strawberry Creek, WWC – Whitewood Creek.

Location	N	*F*	*P*	r^2	num df	den df	Model	Last year w/ MTS
Sample Reach								
ANN - 44.331N, 103.878W	10	0.10	0.7551	0.0129	1	8	y = -1.461 + 7.47E-3(yr)	2010 (2010)
BBC - 44.334N, 103.625W	10	0.27	0.6153	0.0330	1	8	y = -2.138 + 1.086E-3(yr)	2010(2010)
BBC - 44.335N, 103.629W	8	2.71	0.1487	0.3138	1	6	y = 22.70 – 1.13E-2(yr)	2004 (2004)
BBC - 44.324N, 103.650W	19	0.01	0.9110	0.0008	1	17	y = -0.646 + 3.71E-4(yr)	2010(2010)
BBC - 44.325N, 103.652W	7	0.99	0.3644	0.1659	1	5	y = -27.81 + 1.40E-2(yr)	1997 (1997)
BBC - 44.328N, 103.644W	14	0.04	0.8385	0.0036	1	12	y = -1.90 + 9.73E-4(yr)	2004 (2010)
BBC - 44.328N, 103.645W	12	0.83	0.3824	0.0770	1	10	y = -4.172 + 2.10E-3(yr)	2007 (2007)
BBC - 44.326N, 103.652W	10	2.54	0.1498	0.2408	1	8	y = 85.32 – 4.25E-2(yr)	2004 (2007)
STRW - 44.323N, 103.652W	8	1.59	0.2542	0.2094	1	5	y = 4.123 – 2.06E-3(yr)	2002 (2010)
Rapid - 44.085N, 103.227W	9	0.24	0.6402	0.0330	1	7	y = 0.563 – 2.77E-4(yr)	2003 (2005)
Rapid - 44.085N, 103.239W	10	3.81	0.0869	0.3223	1	8	y = 1.679 – 8.37E-4(yr)	2003 (2005)
Rapid - 44.079N, 103.255W	17	11.53	**0.0040**	0.4346	1	15	y = 1.464 – 7.30E-4(yr)	2003 (2008)
Rapid - 44.064N, 103.276W	11	2.75	0.1319	0.2337	1	9	y = 0.0845 – 4.21E-5(yr)	1999 (2008)

WWC- 44.385N, 103.719W	15	0.06	0.8057	0.0048	1	13	y = 1.31 – 6.33E-4(yr)	2008 (2008)
WWC - 44.366N, 103.734W	11	0.03	0.8760	0.3118	1	9	y = -0.38 + 1.95E-4(yr)	2000 (2008)
WWC - 44.363N, 103.738W	10	2.23	0.1736	0.2181	1	8	y = -23.82 + 0.012(yr)	2000 (2000)
WWC - 44.622N, 103.471W	14	2.43	0.1450	0.1684	1	12	y = -0.616 + 3.08E-4(yr)	2009 (2009)
WWC - 44.589N, 103.520W	8	4.35	0.0822	0.4200	1	6	y = -0.67 + 3.36E-4(yr)	2009 (2009)
Stream								
Annie	27	10.74	**0.0031**	0.3005	1	25	y = 26.46 – 1.32E-2(yr)	2010 (2010)
Battle	19	0.92	0.3508	0.0514	1	17	y = 1.099 - 5.42E-4(yr)	2009 (2009)
Bear Butte	97	0.09	0.7642	0.0010	1	88	y = 1.55 – 7.30E-4(yr)	2010 (2010)
Boxelder	19	1.35	0.2622	0.0733	1	17	y = -1.12 + 5.73E-4(yr)	2010 (2010)
Castle	92	19.1	**<0.0001**	0.1751	1	90	y = 0.277 - 1.38E-4(yr)	2009 (2009)
Elk	15	0.01	0.9105	0.0010	1	13	y = 1.71 – 6.73E-4(yr)	2010 (2010)
French	33	1.04	0.3154	0.0325	1	31	y = -0.68 + 3.53E-4(yr)	1996 (2009)
Grace Coolidge	12	5.52	**0.0407**	0.3558	1	10	y = 42.67 – 0.021(yr)	1997 (2009)
Iron (south)	35	7.78	**0.0087**	0.1908	1	33	y = 0.948 – 4.73E-4(yr)	1994 (2010)
North Fork Rapid	13	3.10	0.1061	0.2198	1	11	y = 3.257 – 1.61E-3(yr)	2010 (2010)
Rapid – upstream Pactola Res.	19	7.81	**0.0124**	0.3148	1	17	y = 0.687 – 3.395E-4(yr)	2010 (2010)
Rapid – downstream Pactola Res.	172	25.55	**<0.0001**	0.1307	1	170	y = 0.535 – 2.67E-4(yr)	2005 (2009)
Slate	10	49.92	**0.0001**	0.8619	1	8	y = 3.24 – 1.61E-3(yr)	1995 (2010)
Spring	57	6.62	**0.0128**	0.1074	1	55	y = 2.97 – 1.48E-3(yr)	1997 (2009)
Strawberry	8	1.59	0.2542	0.2094	1	6	y = 2.85 – 1.42E-3(yr)	2002 (2010)
Whitewood	94	0.49	0.4843	0.0053	1	92	y = -2.42 + 1.23E-3(yr)	2010 (2010)
Watershed (HUC-11)								
Spearfish	41	16.21	**<0.001**	0.2935	1	39	y = 12.84 – 6.39E-3(yr)	2010 (2010)
Whitewood	94	0.49	0.4843	0.0053	1	92	y = -2.43 + 1.23E-3(yr)	2010 (2010)
Bear Butte	105	0.29	0.5943	0.0028	1	103	y = 2.53 – 1.22E-3(yr)	2010 (2010)

Elk	19	0.38	0.5444	0.0220	1	17	y = 6.91 – 3.31E-3(yr)	2010 (2010)
Boxelder	37	0.003	0.9600	7.3E-5	1	35	y = -2.67E-2 + 2.4E-5(yr)	2010 (2010)
Rapid – upstream Pactola Res.	159	10.27	**0.0016**	0.0614	1	157	y = 1.04 – 5.16E-4(yr)	2010 (2010)
Rapid – downstream Pactola Res.	174	25.69	**<0.0001**	0.1300	1	172	y = 0.538 – 2.68E-4(yr)	2005 (2009)
Spring	63	6.45	**0.0136**	0.0957	1	61	y = 2.83 – 1.41E-3(yr)	1998 (2009)
Battle	69	5.81	**0.0187**	0.0798	1	67	y = 9.30 – 4.65E-3(yr)	2009 (2010)
French	33	1.04	0.3154	0.0325	1	31	y = -0.68 + 3.53E-4(yr)	1996 (2009)

Table 2-3. Sample reaches and streams where mountain sucker were captured historically but never detected again despite intensified sampling effort since initial detection in the Black Hills of South Dakota. Sample locations are the stream and latitude and longitude of sample reach. Density is the estimate of density at last collection.

Location (stream lat/long)	N	Last detection (yr)	Last sampled (yr)	Density (fish m^{-2})
Sample reach				
Rapid - 44.076N, 103.484W	17	1960	2008	0.025
Rapid - 44.055N, 103.406W	18	1959	2008	0.0296
Rapid - 44.080N, 103.430W	9	1960	2008	0.0221
Rapid - 44.076N, 103.476W	18	1960	2008	0.027
Rapid - 44.072N, 103.475W	20	1960	2008	0.032
Rapid - 44.068N, 103.271W	8	1990	2006	0.009
Castle - 44.043N, 103.772W	10	1959	2000	0.025
Castle - 44.044N, 103.774W	13	1959	2006	0.025
Castle - 44.057N, 103.764W	10	1959	2000	0.014

Castle - 44.030N, 103.783W	9	1959	2006	0.025
Spring - 43.984N, 103.429W	8	1959	2009	0.0428
Spring - 43.990N, 103.408W	7	1959	2009	0.087
Iron(south) - 43.828N, 103.461W	7	1962	2006	0.0311
Annie - 44.327N, 103.894W	8	1995	2007	0.1535
Stream				
South Fork Rapid	7	1959	2006	0.0684
Spearfish	8	1959	2005	0.27 – 0.44

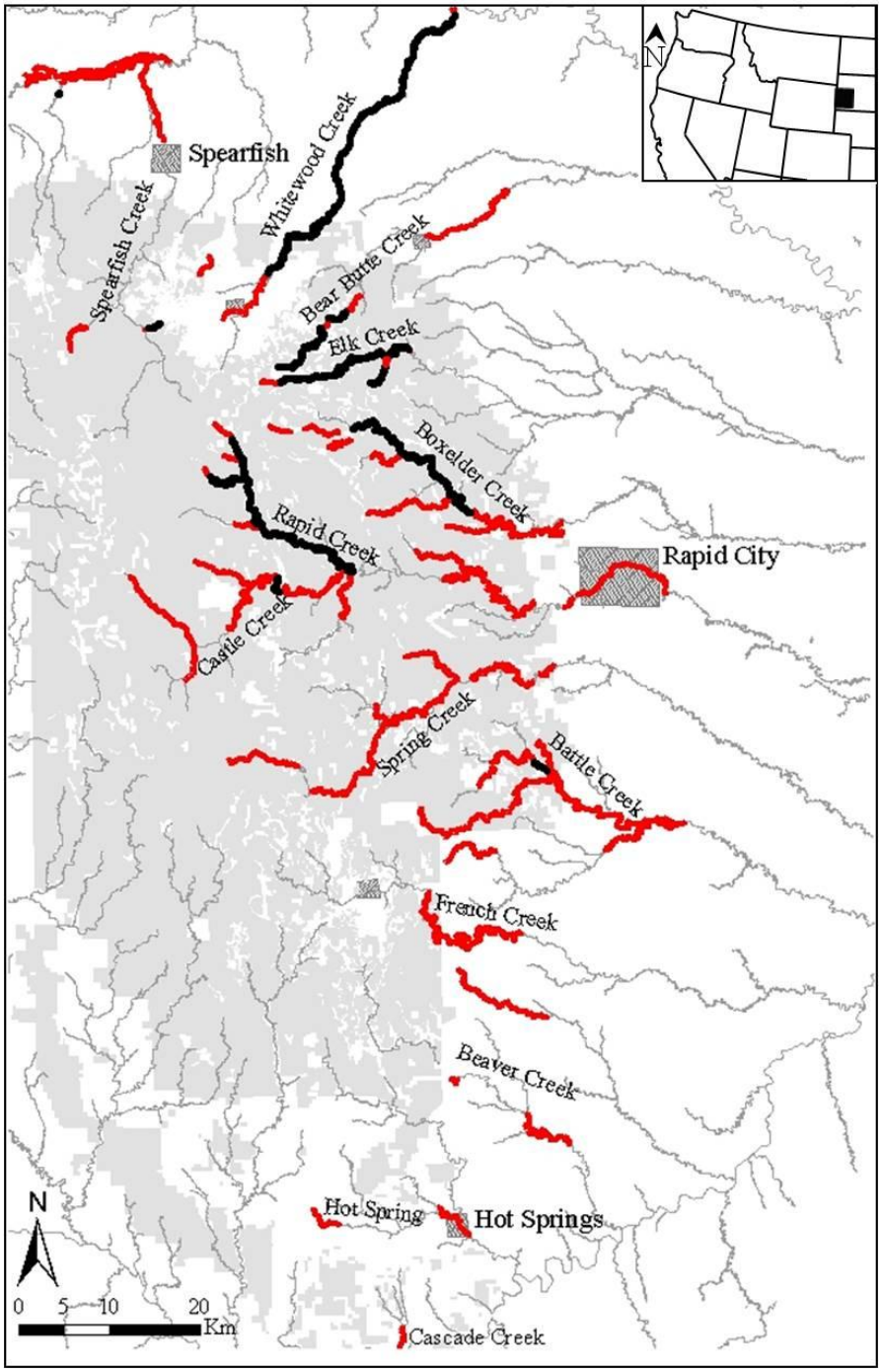

Fig. 2-1. Current distribution (black) and locations of historic collection (red) of mountain sucker in the Black Hills of South Dakota.

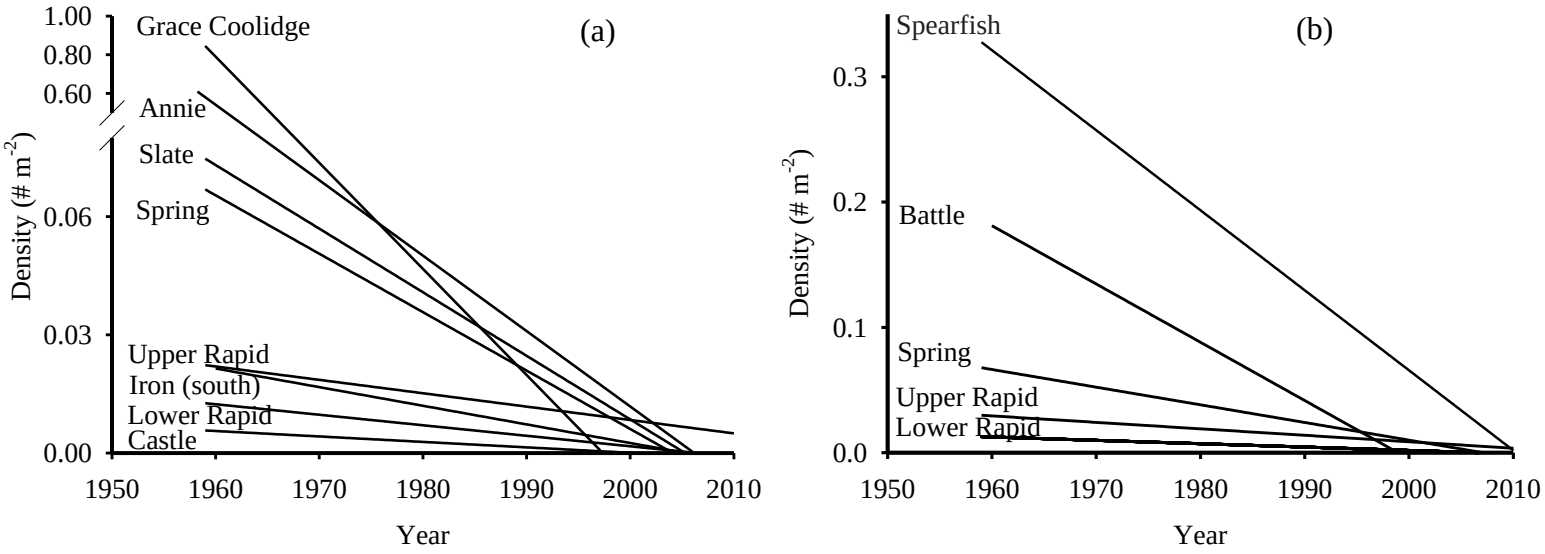

Fig. 2-2. Significant stream- (a), and watershed spatial scale (b) mountain sucker density regression trends in the Black Hills of South Dakota since routine sampling began in the 1960s. Stream names in (a) represent mainstems, whereas watersheds in (b) include mainstems and tributaries. Upper Rapid = Rapid Creek upstream of Pactola Reservoir, Lower Rapid = Rapid Creek downstream of Pactola Reservoir. Note: axis break on stream spatial scale due to the considerably steeper regression trends in Grace Coolidge and Annie Creeks.

Chapter 3.

Historical biogeography, autecology and biotic interactions influence the distribution of an imperiled fish

ABSTRACT

An understanding of the factors associated with the distribution of fishes is a fundamental question in ecology, and can be used to assess and prioritize potential conservation areas for imperiled species. Although broad-scale landscape variables are influential to species distributions, inclusion of finer scale habitat data and biotic interactions may improve the predictive value of distribution models. Mountain sucker *Catostomus platyrhynchus* are stable across their range, but recent studies have documented declines at finer spatial scales on the periphery of their range, including the Black Hills. In addition, little information exists on their basic autecology and community dynamics. The objective of this study was to evaluate the influence of physical and biological variables on the distribution of mountain sucker in the Black Hills of South Dakota. Candidate models were developed *a priori* to predict mountain sucker presence and density, and evaluated for relative support using an information theoretic approach. Mountain sucker presence was best predicted by a combination of study reach-specific habitat, geomorphic, and fish assemblage variables, with the density of trout having a negative influence. Mountain sucker density was highest where periphyton was most abundant. These results can be used to assess and prioritize areas of conservation interest for this native fish in the Black Hills, and provides an increased understanding of

mountain sucker ecology across their range. Concurrent evaluation of multiple scales illustrated that multiple environmental filters need to be considered to most effectively predict species distributions. In addition, managers using this multiple-scale approach can identify what scale of factors management actions can effectively target.

INTRODUCTION

An understanding of the factors involved in the presence and abundance of species across the landscape is a fundamental challenge in ecology. The occurrence of a fish species in a stream reach may be the result of historic (e.g., geologic and/or evolutionary) and local (e.g., coarse/fine-scale habitat, biotic interactions) processes (Matthews 1998) that function as interactive faunal 'filters' (Tonn 1990). These 'filters' operate hierarchically over time and space creating predictable fish assemblages, whereas human-mediated introductions result in non-coevolved assemblages. For example, plate tectonics and glacial events shaped the distribution and evolution of fishes in western North America over millions of years (Smith 1981). At finer spatial and temporal scales, fish distributions reflect longitudinal physicochemical gradients in factors such as water temperature (e.g., De Staso and Rahel 1994, Tanguchi et al. 1998, Ostrand and Wilde 2001), and predator-prey interactions can influence fish assemblage structure within a stream reach (e.g., Power et al. 1985).

Because processes that regulate fish distributions operate concurrently across scales, accurately predicting species occurrence patterns requires sampling species and

their environment at coarse and fine scales (Poff 1997, Jackson et al. 2001). Although both presence-absence and abundance data can be used effectively to detect trends in species distribution, abundance data increases predictive power (Joseph et al. 2006). The development of geographic information systems (GIS) has allowed researchers to evaluate broad-scale landscape variables influential to species occurrence (Guisan and Zimmerman 2000). For example, Johnson et al. (2004) used multiple spatial scale vegetative and topographic factors to predict endangered mountain caribou *Rangifer tarandus caribou* occurrence in British Columbia and identify and rank available habitats for forest management planning. Refining and improving the utility of predictive models may involve the addition of finer spatial scale abiotic data (Rabeni and Sowa 1996) and the incorporation of biotic filters (Quist et al. 2005). Models that evaluate the relative importance of abiotic and biotic filters and anthropogenic effects can be used to prioritize conservation tactics for species of concern (Moyle and Sato 1991, Rodríguez et al. 2007). Additionally, fish-habitat models can identify potential threats to imperiled fishes by assessing the influence of habitat and/or biotic conditions on species of interest (Shrank et al. 2001), and be used to guide management decisions (Belk and Johnson 2007).

Mountain sucker *Catostomus platyrhynchus* is a native catostomid that occurs throughout the western United States and Canada from southern Saskatchewan and Alberta in the north, to eastern California in the south and west, and through the Intermountain region to western Nebraska and the Black Hills of South Dakota in the east (Scott and Crossman 1973). They inhabit cool mountain streams with mostly rocky

substrates (Hauser 1969, Scott and Crossman 1973, Sigler and Sigler 1996), but are also found in large rivers (Smith 1966), lakes (Baxter and Stone 1995) and as adfluvial reservoir populations in headwater areas (Erman 1973, 1986, Marrin and Erman 1982, Decker 1989, Wydoski and Wydoski 2002). Populations in the Black Hills of South Dakota and Wyoming represent the easternmost range of the species, and resulted from either post-glacial isolation or stream capture of the Little Missouri River headwaters by the Belle Fourche River, which drains the northern Black Hills (Bailey and Allum 1962). Like numerous other fish species in western North America (Jelks et al. 2008), mountain sucker are currently declining in portions of their range (Decker 1989, Patton et al. 1998), including the Black Hills of South Dakota (Schultz and Bertrand *in review*) where mountain sucker is listed as a species of greatest conservation need (South Dakota Department of Game Fish and Parks (SDGFP) 2006).

The long-term persistence of mountain sucker depends on informed management decisions based on the qualitative and quantitative assessment of multi-scale factors that regulate their occurrence and abundance. Reviews of mountain sucker biology (Campbell 1992, Isaak et al. 2003, Belica and Nibbelink 2006) emphasized the need for current distribution data in the Black Hills, an evaluation of habitat and landscape features that promote the existence of mountain sucker, and assessment of their interspecific interactions, particularly with piscivorous salmonids. We evaluated the influence of three scales of factors on the presence and abundance of mountain sucker in the Black Hills of South Dakota. The coarsest habitat scale we examined included

geomorphic factors that should operate at the segment spatial scale (i.e., 10^2-10^3 m, Frissell et al. 1986). We built on the previous work of Dauwalter and Rahel (2008) in the Black Hills where a combination of four geomorphic variables (i.e., stream order, gradient, permanency, and elevation) interacted to influence mountain sucker presence. In addition to coarse scale geomorphic variables, we evaluated finer-scale habitat factors within sample reaches, which should operate at the reach spatial scale (i.e., 10^1-10^2m, Frissell et al. 1986). We hypothesized that the addition of local physical habitat variables would better explain mountain sucker distribution and abundance across the Black Hills relative to only coarse-scale geomorphic data. At the finest scale, we evaluated potential biotic interactions (i.e., predation, competition) between fish species present in each sample reach. Since mountain sucker in other regions have shown a negative association with introduced salmonids (Decker 1989, Giddings et al. 2006, Dauwalter and Rahel 2008), we hypothesized a similar relationship would be observed in our study. Furthermore, we hypothesized that competition with white sucker *Catostomus commersoni* might negatively influence mountain sucker. We evaluated the predictive model of Dauwalter and Rahel (2008) throughout the Black Hills of South Dakota, and compared model precision with the addition of further variables. Habitat conservation, restoration, and species translocation are three potential options fisheries biologists can strategically prioritize based on our model predictions, and we suggest our approach as a template for prioritizing conservation actions for species facing similar threats in other areas.

METHODS

Study Area

The Black Hills of South Dakota and Wyoming are a 100 km wide (east-west) by 200 km (north-south) forested dome-shaped uplift surrounded by short and mid-grass prairie, leading some to call them an "island on the plains" (Koth 2007). Because of this "island" effect, many of the species present, including mountain sucker, are isolated from other conspecifics. The Black Hills are part of the Level III Middle Rockies Ecoregion which includes open ponderosa pine *Pinus ponderosa* stands and abundant mountain-fed, perennial streams (Omernik 1987). Geologically, the center of the uplift is characterized by Precambrian metamorphic and intrusive rock that is surrounded by a ring of Cretaceous sedimentary formations that completely encircle the core (DeWitt et al. 1989), which has a substantial effect on the stream hydrology of the region. The limestone formations to the west of the core serve as groundwater recharge zones with little or no surface flow, and streams that arise in the center of the Black Hills lose much or all of their surface flow to the porosity of the formations as they flow north or east off the core of uplift (Williamson and Carter 2001). These zones of stream discharge loss are known as the Loss Zone and can limit the distribution and dispersal of fishes, especially in dry years.

Streams in the Black Hills of South Dakota have variable morphology and fish assemblages. Channel widths in small, headwater streams (e.g., Deer, South Boxelder,

Tillson Creeks) average between 1 and 4 m and average depth is between 5 and 15 cm. Larger streams (e.g., Spring, French, Boxelder Creeks) average 3 to 10 m in width, and average depths range from 15-30 cm. The largest streams (e.g., Rapid and Spearfish Creek) average 7 to 15 m in width and 20-50 cm in depth, getting larger as they flow downstream onto the plains. Substrate in streams is generally cobble and rubble, but slack water portions of channels can accumulate finer sediments and organic debris. Water quality impacts and habitat degradation from mining activities have been identified as potential causes for decreased species richness in some Black Hills streams (Rahn et al. 1996). Native stream fish communities generally contain mountain sucker, white sucker, longnose dace *Rhinichthys cataractae*, creek chub *Semotilus atromaculatus*, and fathead minnow *Pimephales promelas*. Introduced salmonids (i.e., brown trout *Salmo trutta*, brook trout *Salvenlinus fontinalis*, and rainbow trout *Oncorhynchus mykiss*) are present across the Black Hills and represent more than 90% of total fish abundance in many areas.

Fish and habitat sampling

To evaluate which geomorphic, local habitat, and biotic factors best explain presence of mountain sucker, we sampled fish and physical habitat in 2008-2010 at historically sampled locations throughout the Black Hills. We began sampling where mountain sucker were detected in 2007-2009 and continued sampling up- and downstream to delineate their spatial distribution. Block nets were placed at the upstream end of each 100 m sample reach, and sample reaches were single-pass electrofished in an

upstream direction with one or two backpack electrofishers, depending on stream width (Halltech HT-2000, Smith Root LR-24, ETS ABP-3-300); output was adjusted at each sample reach to a level that allowed fish to be captured with dipnets. Mountain sucker is vulnerable to this sampling method (Dauwalter et al. 2008). Following completion of electrofishing, captured fish were identified to species, counted, measured, and released outside of the sample reach. Based on species-specific models relating single- and multiple-pass catch per unit effort, we estimated density (fish m^{-2}) for each species in each sample reach. Single-pass and multiple-pass catch per unit effort strongly correlate in the Black Hills and in other regions, and density estimates based on single-pass samples provide a reliable approximation of absolute abundance and species diversity (Bertrand et al. 2006; Reid et al. 2009).

In each sample reach we quantified physical stream habitat. Habitat transects were measured at the midpoint of each electrofished sample reach, and 25 m upstream and downstream from the midpoint. Along each transect, water depth, dominant substrata (after Platts et al. 1983), embeddedness, mean velocity, vegetation (including submergent, emergent, terrestrial, and floating), and periphyton coverage were quantified within each of five evenly-spaced 33 cm by 33 cm quadrats. Periphyton coverage was visually estimated as the percent of substrate within each quadrat containing algal filaments or an adnate algal turf. At the middle transect of the sample reach, additional metrics included: primary productivity (see Gelwick and Matthews 1992 for methodology), canopy cover (%), riparian vegetation type (i.e., deciduous, mixed,

coniferous trees, grass/open; 10 m from wetted stream edge on either bank), and general grazing condition (grazed/non-grazed; 10 m from wetted stream edge on either bank). Throughout the sample reach, we measured, counted, and mapped the size and location of large structural habitat features including undercut banks, log complexes, root wads, and boulders. Geomorphic metrics that were not conducive to measurement in the field (i.e., channel gradient, stream permanency, stream order, elevation) were inferred from GIS data layers (Dauwalter and Rahel 2008). Correlation analyses identified biologically meaningful covariates. For any pair of redundant variables ($r > 0.60$), we chose one as an explanatory variable based on which was more biologically encompassing; the remaining factor was eliminated from further analyses (Table 3-1). For example, mean and maximum depth and velocity and discharge were strongly correlated ($r = 0.88$ and $r = 0.78$, respectively), so maximum depth and velocity were omitted from further analyses.

Analyses

Hierarchical modeling. —We evaluated the relative performance of three classes of *a priori* models to predict the distribution of mountain sucker across Black Hills streams in South Dakota. A suite of biologically-inferred candidate models were developed and divided into geomorphic, sample reach, and fish assemblage classes of factors. By developing models for each class of factors, the total number of potential parameters was reduced in models. We used these models to predict mountain sucker presence and abundance (density) across our study area (Meyer et al. 2010). To evaluate factors that influence the presence of mountain sucker in a particular sample reach, we

predicted mountain sucker presence using logistic regression. To identify the strongest relationships between measured environmental variables and mountain sucker abundance in a given sample reach, we predicted mountain sucker density with linear regression. We evaluated the same candidate models for their performance when predicting presence and density.

We combined all landscape, sample reach, and fish assemblage factors into a global model for each class of factors, which were the most-parameterized models tested and should explain the most variation in the data. Mountain sucker are primarily benthic grazers (Hauser 1969, Baxter and Stone 1995), thus their presence should track primary producers. Furthermore, mountain sucker abundance should increase with greater periphyton coverage and primary productivity. Because canopy cover can decrease incoming solar irradiance leading to decreased productivity (e.g., Hill and Boston 1991), mountain sucker abundance should be negatively influenced by increasing canopy cover. The effect of land use and riparian vegetation on mountain sucker should be variable due to influences on nutrient inputs, carbon sources, and habitat perturbations (Schlosser 1991). Conditions that support higher stream primary productivity (e.g., open riparian areas, watershed nutrient inputs) should also support greater densities of mountain sucker. Competition from similar species (i.e., white sucker) and predation from large trout (Decker and Erman 1992, Dauwalter and Rahel 2008) may negatively influence mountain sucker distribution. The global geomorphic model included the landscape factors permanency, channel slope, stream order, elevation and their interactions

(Dauwalter and Rahel 2008). The global sample reach model included the factors mean depth, mean substrate size, embeddedness, discharge, in-channel vegetation, periphyton, primary productivity, % canopy cover, riparian vegetation, and grazing condition. The global fish assemblage model included factors white sucker density, trout density (all spp.), and the density of trout >200 mm TL.

Although the global model would likely explain the most variance, we proposed a set of reduced models for each class that contained more parsimonious combinations of predictor variables. We used multimodel inference to evaluate which of the candidate models best predicted presence and density of mountain sucker (Burnham and Anderson 2002). Akaike's information criterion adjusted for small sample bias (AIC_c) and Akaike weights (w_i) were computed for competing models to rank the relative support for each model (Burnham and Anderson 2002). With *a priori* analyses, we identified models and variables from each category of factors that had strong predictive support.

To further refine predictor models and potentially increase the overall explanatory value of these models, we developed a set of models *post hoc* that combined informative *a priori* factors. We compared explanatory performance of *post hoc* models (i.e., multiple classes of factors) to the "best" *a priori* model in each class using AIC_c. The most plausible models were judged as those having the highest w_i values, although model selection uncertainty was addressed by averaging model parameters between competing models that were within 2.0 ΔAIC_c values of the most plausible model (Burnham and Anderson 2002). We computed model parameter estimates to show the relationship

between model variables and mountain sucker presence and density. We assessed logistic regression model performance based on a receiver-operator-characteristic (ROC) curve, where ROC values from 0.5-0.7 indicate low, 07.-0.9 indicate medium, and 0.9-1.0 indicate high model accuracy (Manel et al. 2001).

Multivariate Fish Assemblage Analysis.—We used canonical correspondence (CCA) to analyze the multivariate response of fish assemblage structure to multiple habitat factors across the Black Hills. This technique is a direct gradient analysis that uses empirically-derived species and environmental data to create multivariate gradients that maximize dispersion among species and environmental (habitat) variables in ordination space and identify important variables in community composition (ter Braak 1995, ter Braak and Verdonschot 1995).

We selected variables that were well-supported from our explanatory models to include in the CCA; auto-correlated variables ($r > 0.60$) were eliminated from further analyses. We standardized the fish species matrix for the CCA to the density of fish of each species captured in each sample reach. To eliminate heteroscedasticity, we logarithmically ($\log_{10} + 1$) transformed periphyton data. Species were only considered in the CCA if they were present in more than five sample reaches (>5% of total sample reaches). Ordination biplots were constructed to help visualize dispersion of species along eigenvectors weighted by environmental variables.

RESULTS

Mountain sucker were present in 39 of 108 sample reaches sampled in 2008-2010; density ranged from 0.0017 to 0.703 fish m^{-2}. Streams with mountain sucker included Crow, Annie, Whitewood, Bear Butte, Elk, Meadow, Boxelder, North Rapid, Upper Rapid, and Battle Creeks, and Swede Gulch, and the highest densities occurred in Whitewood and Elk Creeks. Sampling locations captured variability of streams throughout the Black Hills; sample reaches were distributed widely across the study area, stream order ranged from 2 to 5, and elevation ranged from 862 to 1,916 m above sea level. Mean stream width ranged from 0.9 to 10.6 m (mean = 4.1 m). In general, brook trout dominated the fish assemblage in cold, narrow first-order streams, and as water temperature, stream width and stream order increased, peak abundance transitioned from brook trout to longnose dace, brown trout, mountain sucker, and finally redhorse *Moxostoma spp.* as streams flowed out of the highlands and onto the prairie. Stream fish assemblages were variable across watersheds. In the northern Black Hills, Crow, Spearfish, and Lower Rapid Creek watersheds were dominated by introduced salmonids (primarily brown trout). Watersheds in the southern Black Hills (i.e., Spring, Battle, French, and Beaver) were characterized by eurythermal generalists (e.g., creek chub and longnose dace).

Mountain sucker presence

The presence of mountain sucker was best predicted by an *a priori* model that included depth, substrate size and embeddedness, in-channel terrestrial and submergent vegetation, periphyton coverage, primary productivity, canopy cover, and discharge; however, this model was only 1.4 times more likely to be the best than a competing model without the variables embeddedness, in-channel terrestrial and submergent vegetation, and canopy cover (Table 3-2). In the other classes of models, the density of all trout, brown trout, brook trout, and brook trout >200 mm were well-supported factors from the fish assemblage class of models, and stream order was supported more than other models from the geomorphic class.

When well-supported geomorphic and fish assemblage factors were combined with the two sample reach habitat models *post hoc*, the predictive performance of models improved (i.e, AIC_c values were 7.16-9.69 lower, 3-14% higher ROC values; Table 3-2). Two competing *post hoc* models showed strong support and explained about the same variation in data ($\Delta AIC_c < 0.30$, Table 3-2). These two models included a sample reach habitat model, stream order, and the density of trout, indicating that mountain sucker presence was best predicted by a combination of multiple spatial scales and the associated fish assemblage (Table 3-2). Averaged model parameters included negative effects of trout density, depth, substrate size, submergent vegetation, canopy and discharge and positive effects of periphyton coverage, productivity, embeddedness, terrestrial vegetation, and stream order (Table 3-3). Competing models had ROC values

ranging from 0.81 - 0.92 (Table 3-2). There appeared to be a threshold response with the density of trout and mountain sucker. Where trout density exceeded 0.15 fish m^{-2}, mountain sucker density was less than 0.0125 fish m^{-2} or zero (Figure 3-1).

Mountain sucker density

Periphyton coverage alone was the best predictor of mountain sucker density (y = 0.276(x) – 8.68E-03, $r^2 = 0.19$, $F_{37, 1} = 8.86$, $P < 0.01$, Table 3-4). Competing models ($\Delta AIC_c < 5.0$) from the sample reach habitat class showed less support and all included the periphyton coverage variable, which had a positive influence on mountain sucker density. The most strongly supported fish assemblage models included the densities of brown trout, brown trout > 200 mm, and brook trout > 200 mm. The geomorphic class of models was generally not strongly supported when predicting density in the sample reach. The density of white sucker was also not strongly supported when used to predict mountain sucker density. When the density of brown trout, brown trout > 200mm, and brook trout >200 mm were combined with two different sample reach habitat models (i.e., Peri, Peri+Disch), the predictive performance of *post hoc* models did not improve (i.e., AIC_c was higher for *post hoc* models, Table 4). Because *a priori* models were more supported than *post hoc* models, a linear relationship with periphyton coverage alone was the top overall model, and all competing models included periphyton coverage, we did not average model parameters in density analyses.

Species-habitat relationships

For CCA, the first two axes explained 70.9 and 19.3% of the variation in species abundance among sample reaches, respectively. Deeper sample reaches with higher discharge were clustered to the left on CCA axis 1, whereas sample reaches with higher periphyton coverage were clustered toward the top of CCA axis 2 (Table 5, Figure 3-2). Depth and periphyton coverage had stronger gradients than discharge, however, all habitat vectors were fairly short relative to sample reach scores. Sample reaches with mountain sucker were evenly spread along CCA axis 1, but tended to be positively associated with CCA axis 2 (Figure 3-3).

Species centroids elucidated habitat associations of species across the Black Hills (Figure 3-2). Brown trout and longnose dace were positioned close to the origin of both CCA axes. Brook trout were positioned furthest right on CCA axis 1. In contrast, rainbow trout and green sunfish *Lepomis cyanellus* were associated with higher discharge and depth. The mountain sucker centroid was neutrally associated with CCA axis 1, but located distal to the origin on CCA axis 2. Other species displayed variable sensitivities to habitat characteristics (Figure 3-2).

DISCUSSION

The presence and density of mountain sucker, a species of greatest conservation need, were influenced by a combination of geomorphic, sample reach habitat, and biotic interaction factors in the Black Hills of South Dakota. Results from both predictive

modeling and multivariate analyses were highly congruent, and indicated multiple habitat factors and spatial scales were influential for predicting the presence of mountain sucker. Mountain sucker rarely occurred where trout densities exceeded 0.15 fish m^{-2}, but as periphyton coverage increased, so did mountain sucker density. These results can be used to better inform management decisions to predict and prioritize suitable conservation, restoration, or translocation areas for this declining native fish.

Stream habitat conditions were influential to the distribution and density of mountain sucker in this study, which has also been observed in the limited number of other studies pertaining to mountain sucker. A habitat model that included depth, substrate, in-channel vegetation, periphyton coverage, primary productivity, discharge, and canopy cover predicted presence of mountain sucker across the Black Hills. When assessing mountain sucker micro-habitat selection, Decker (1989) found that mountain sucker selected areas of rubble and cobble substrates, with cover being influential. Periphyton coverage and primary productivity relate to food resources for mountain sucker, a benthic grazer. Primary productivity, as indexed with our methodology, correlates well with community productivity (Young and Huryn 1999), which influences distribution and biomass of fishes along a stream continuum (Vannote et al. 1980). Canopy cover constrains the solar radiation reaching the stream segment, which can affect system and periphyton productivity (Hetrick et al. 1998). Discharge limits the volume of habitat available and the reach permanency, and streams with relatively greater baseflow are less likely to be dewatered during periods of drought and probably represent

source populations for reestablishment during fish assemblage recovery from these natural disturbances (Magoulick and Kobza 2003). Personal communication with landowners adjacent to sample reaches with mountain sucker present indicated that these reaches retained flowing water during a recent extended drought period (i.e., 2002-2007).

Periphyton coverage was the best predictor of mountain sucker density in sample reaches across the Black Hills of South Dakota. These results indicate that when conditions are suitable for mountain sucker presence, food availability drives density. Periphyton and algal standing crop influenced the distribution of central stoneroller *Campostoma anomalum* (Lennon and Parker 1960, Power and Matthews 1983, Power et al. 1985, Matthews et al. 1987), and in a California stream, mountain sucker movements tracked algal blooms (Decker 1989).

Although competitive interactions between white sucker and mountain sucker were not supported, these results provide clear, quantitative evidence of a negative relationship between mountain sucker and introduced salmonids. Diet analyses of white sucker and mountain sucker voucher specimens did not suggest competition for food resources between these two species; white sucker were invertivorous (predominantly consumed Diptera larvae) whereas mountain sucker were herbivorous (predominantly consumed algae and detritus). Our study is not the first to suggest negative interactions between introduced trout, particularly brown trout, and mountain sucker (Moyle and Vondracek 1985, Decker and Erman 1992, Giddings et al. 2006, Dauwalter and Rahel 2008) and other native species (Moyle and Marciochi 1975, Garman and Neilsen 1982,

Crowl et al. 1992). Extirpation of native fish has occurred throughout the Mountain West in managed salmonid fisheries, including the Black Hills (Schultz and Bertrand *in review*). The ecological mechanisms underlying this relationship remain largely inferential, but are likely a combination of multiple effects. One explanation is predation by trout. Brown trout ontogenetically switch to piscivory earlier than other salmonids (Mittelbach and Persson 1998), but rainbow trout, although less common in the Black Hills, likely have similar effects on native fish as brown trout (Crowl et al. 1992). Salmonid (i.e., brown and rainbow trout) diets in the Black Hills include mountain sucker (Schultz personal observation), but the effect of predation on mountain sucker population mortality rates has not been quantitatively assessed relative to other causes of mortality (Belica and Nibbelink 2006).

Another potential explanation for negative interactions with trout is different physical habitat preference between these species. Although the thermal tolerance of mountain sucker is higher than co-occurring salmonids (Schultz and Bertrand *in review*), their thermal habitat preference is not well understood. Giddings et al. (2006) found that sites with fish assemblages dominated by mountain sucker were warmer than assemblages characterized by brown trout in Utah. Li et al. (1987) reported that mountain sucker are replaced along a thermal and channel slope gradient in Oregon streams by bridgelip sucker *Catostomus columbianus*, which has a realized thermal niche center considerably higher than most salmonids (Huff et. al 2005). From these studies, it can reasonably be inferred that the thermal preference of mountain sucker is slightly

higher than trout in the Black Hills, and therefore mountain sucker likely segregate into warmer habitats than salmonids. Brook trout, in particular, tended to be associated with headwater habitats and longitudinally segregated from mountain sucker. Mountain sucker in Whitewood Creek were found well downstream of the lower extent of all trout species (Schultz and Bertrand *in review*), providing support for this explanation. A quantitative field assessment of mountain sucker temperature preference would identify the degree of thermal overlap between mountain sucker and trout, and may be used to predict areas where negative interactions between these species are likely to occur.

Our incorporation of sample reach habitat and fish assemblage variables into mountain sucker distribution and density models improved predictive performance in comparison with models containing only geomorphic variables (i.e., Dauwalter and Rahel 2008). When predicting the density of mountain sucker in sample reaches across the Black Hills, geomorphic variables generally performed poorly. Models derived from GIS data (i.e., Dauwalter and Rahel 2008) are best suited to identify the factors with the most influence on watershed scale presence (Guisan and Zimmerman 2000; Frissell et al. 1986). Patch scale habitat factors are often more appropriate for predicting sample reach scale fish presence (Harig and Fausch 2002). Combining watershed, sample reach and biotic interaction factors is the most comprehensive approach because it accounts for variability of ecological processes operating within each scale (e.g., Rabeni and Sowa 1996).

This study identified factors influential to the distribution of mountain sucker and areas of conservation interest in the Black Hills of South Dakota, and the results could be further applied to prioritize suitable habitats for restoration. In the Black Hills, suitable conservation and translocation areas would contain low densities of introduced salmonids, environmental conditions supportive of high periphyton standing crops, and maintain baseflow through drought periods. Complete or selective removal of nonnative fishes could improve conservation or translocation areas for mountain sucker, and strike a balance between salmonid fisheries and maintaining biodiversity in Black Hills coldwater habitats. Physical habitat restoration for mountain sucker conservation would be most effective in areas characterized by open riparian canopy and annual high discharge events ($> 8\ m^3\ s^{-1}$) that deepen pools and promote export of fine sediment. Future research in the Black Hills should build on our work to address the basic ecology of mountain sucker and the ecological mechanisms involved in the negative relationship with introduced trout. In addition, understanding movement patterns of mountain sucker should include assessment of mountain sucker responses to periphyton dynamics and barriers, and identify important spawning locations, overwintering areas, and refugia during drought. Filling these knowledge gaps in mountain sucker ecology would aid the interpretation of these results and conservation of this declining native fish.

Our approach can be adopted in other systems as well. Concurrent evaluation of multiple scales improved predictive models and illustrated that multiple environmental filters (*sensu* Tonn 1990) need to be considered to most effectively predict species

distributions. Typical species distribution modeling work relies on coarse scale factors to predict species occurrence across broad geographic areas (e.g., Guisan and Zimmerman 2000, Dauwalter and Rahel 2008) to focus future sampling effort and prioritize areas of conservation interest. Classical species-habitat relationships have relied on local physical habitat conditions (e.g., Platts et al. 1983), and biotic interactions may strongly influence observed fish assemblages in some systems (e.g., Crowl et al. 1992, Jackson et al. 2001). This study illustrates that multiple spatial and temporal scales, combined with potential biotic interactions, need to be considered to best predict distributions (and abundance at suitable locations) of species of conservation interest and evaluate suitable conservation or restoration areas. In addition, managers using this multiple-scale approach can identify what scale of factors management actions can effectively target (Quist et al. 2005). Managers have little control over large-scale geomorphic factors structuring fish assemblages (except for species introductions from outside the basin), but may be able to ameliorate limiting habitat (e.g., in-stream cover, large woody structure) or negative interactions with other species (e.g., discontinue stocking of predatory fishes, invasive fish removal).

Table 3-1. Geomorphic, sample reach habitat, and fish assemblage variables (unit) included in predictive models and multivariate analyses of mountain sucker distribution and fish assemblage patterns in the Black Hills of South Dakota.

Variable	**Description**
Geomorphic	
Perm	permanency (1-perrenial, 0-intermittent)
Ord	Strahler order (categorical, 1-5)
Elev	elevation (m)
Grad	gradient, channel slope (m/km)
Sample reach habitat	
Dep	Depth, mean (cm)
Subsz	substrate, mean particle size (mm)
Embed	embeddness, mean (log_{10})transformed
VegSub	in-channel submergent vegetation (mean %)
VegTerr	in-channel terrestrial vegetation (mean %)
Peri	periphyton coverage (%), mean (log_{10} +0.001) transformed
Can	canopy cover (%)
Prod	primary productivity (gO2/L/hour) (Gelwick and Matthews 1992)
Disch	discharge (m^3/s)
Fish assemblage	
TRT	trout density (all species; fish m^{-2})
TRT200	trout >200mm TL density (fish m^{-2})
WTS	white sucker density (fish m^{-2})
BNT	brown trout density (fish m^{-2})
BNT200	brown trout >200mm TL (fish m^{-2})
BKT	density of brook trout (fish m^{-2})
BKT200	brook trout >200mm TL density (fish m^{-2})
RBT	rainbow trout density (fish m^{-2})
RBT200	rainbow trout >200mm TL density(fish m^{-2})

Table 3-2. Predictive models, AIC_c, ΔAIC_c, w_i, and ROC values for *a priori* models used to predict mountain sucker presence/absence with logistic regression in the Black Hills of South Dakota. *Post hoc*, models H1 and H2 were combined with strongly supported variables from other variable classes to assess whether combining variables from different classes improved the predictive performance of models. Variable descriptions can be found in Table 1. All models that were run are not included in this table.

Model	**AIC_c**	**ΔAIC_c**	**w_i**	**ROC**
A priori				
Dep + Subsz + Embed + VegSub + VegTerr + Peri + Can + Prod + Disch (H1)	118.97	-	0.41	0.86
Dep + Subsz + Peri + Prod + Disch (H2)	119.93	0.96	0.25	0.81
Post hoc				
H1 + TRT	110.24	-	0.30	0.89
H1 + TRT + Ord	110.75	0.51	0.23	0.92
H2 + TRT	110.77	0.53	0.23	0.86
H2 + TRT + Ord	111.81	1.57	0.14	0.89
H1	118.97	8.73	0.003	0.86
H2	119.93	9.69	0.002	0.81

Table 3-3. Model-averaged parameter estimates (b_i) and standard error for four logistic regression models used to predict presence of mountain sucker for streams in the Black Hills, South Dakota, including the number of models (k) that each parameter occurred in. Variable descriptions can be found in Table 3-1. Competing models were < 2.0 ΔAICc units than the best model.

Variable	***k***	b_i	**SE**
Intercept	4	-8.57E+00	1.76E+03
Dep	4	-4.79E-03	4.19E-02
Subsz	4	-6.90E-03	3.37E-03
Embed	2	2.89E 00	2.32E 00
VegSub	2	-1.31E-01	4.98E-02
VegTerr	2	3.69E-03	3.16E-02
Peri	4	5.42E 00	1.51E 00
Can	2	-5.90E-03	6.51E-03
Prod	2	8.67E-02	2.36E-01
Dish	2	-1.84E-01	7.57E-01
TRT	4	-8.40E-00	3.28E-00
Ord	2	7.95E+01	1.76E+03

Table 3-4. Predictive models, AIC_c, ΔAIC_c, and w_i values for *a priori* linear functions used to predict mountain sucker density in the Black Hills of South Dakota. *Post hoc*, variables from each category were combined to assess whether combining variables from different classes improved the predictive performance of models. Variable descriptions can be found in Table 3-1. All models that were run are not included in this table.

Model	**AIC_c**	**ΔAIC_c**	**w_i**
A priori			
Peri	676.23	-	0.49
Peri + Disch	677.39	1.15	0.28
Post hoc			
Peri	676.23	-	0.33
Peri + BKT200	676.29	0.05	0.32
Peri + BNT200	676.79	0.55	0.25

Table 3-5. Weighted correlation matrix of stream habitat variables and species values with canonical ordination axes. Eigenvalues equal the dispersion of species scores on the axis and indicate the importance of the axis.

	Canonical axis		
Variable	**1**	**2**	**3**
Habitat factors			
Depth	-0.90	-0.34	0.29
Periphyton	-0.23	0.97	0.09
Discharge	-0.78	0.02	-0.63
Species			
Mountain sucker, *Catostomus platyrhynchus*	-0.08	0.49	0.06
Longnose dace, *Rhinichthys cataractae*	0.07	0.03	0.10
Brown trout, *Salmo trutta*	-0.09	-0.01	0.01
Brook trout, *Salvelinus fontinalis*	0.58	-0.10	-0.11
Rainbow trout, *Oncorhynchus mykiss*	-1.04	0.15	-0.68
White sucker, *Catostomus commersoni*	-0.41	-0.17	0.06
Creek chub, *Semotilus atromaculatus*	-0.43	-0.38	-0.02
Fathead minnow, *Pimephales promelas*	-0.31	-0.25	0.07
Green sunfish, *Lepomis cyanellus*	-1.55	-0.25	0.30
Rock bass, *Ambloplites rupestris*	-0.07	-0.38	0.38
Eigenvalue (% variation explained)	0.174 (70.9)	0.048 (19.3)	0.024 (9.8)

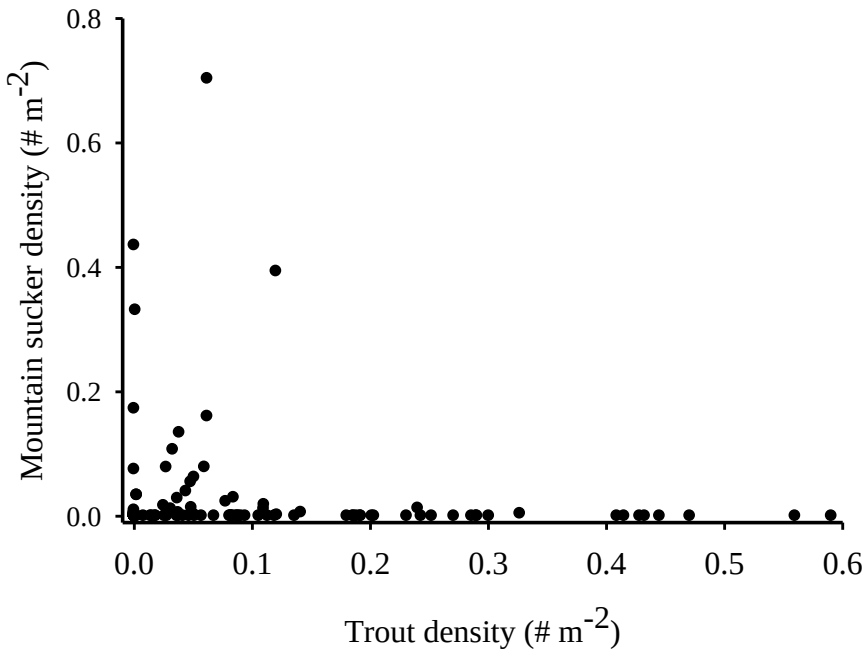

Fig. 3-1. Mountain sucker density as a function of trout density for 100m sample reaches in the Black Hills, South Dakota sampled 2008-2010.

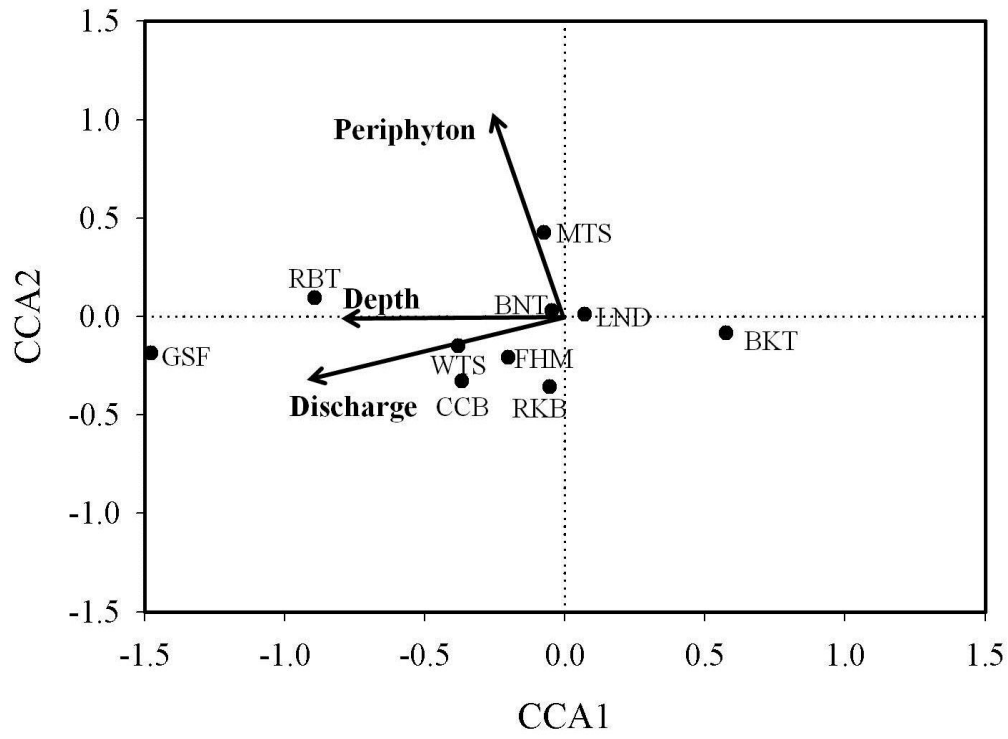

Fig. 3-2. Individual species-habitat factor ordination from canonical correspondence analysis (CCA) ordination of fish assemblages in the Black Hills, South Dakota sampled 2008-2010. The ordination biplot illustrates the influence of three habitat variables on the distribution of 10 fish species in the Black Hills. Stream habitat variables are represented by vectors and species are represented by their abbreviations. Species codes: BKT –brook trout, *Salvelinus fontinalis*, BNT – brown trout, *Salmo trutta*, CCB – creek chub, *Semotilus atromaculatus*, FHM – fathead minnow, *Pimephales promelas*, LND – longnose dace *Rhinichthys cataractae*, MTS – mountain sucker, *Catostomus platyrhynchus*, RBT – rainbow trout, *Oncorhynchus mykiss*, RKB – rock bass, *Ambloplites rupestris*, WTS – white sucker, *Catostomus commersoni*.

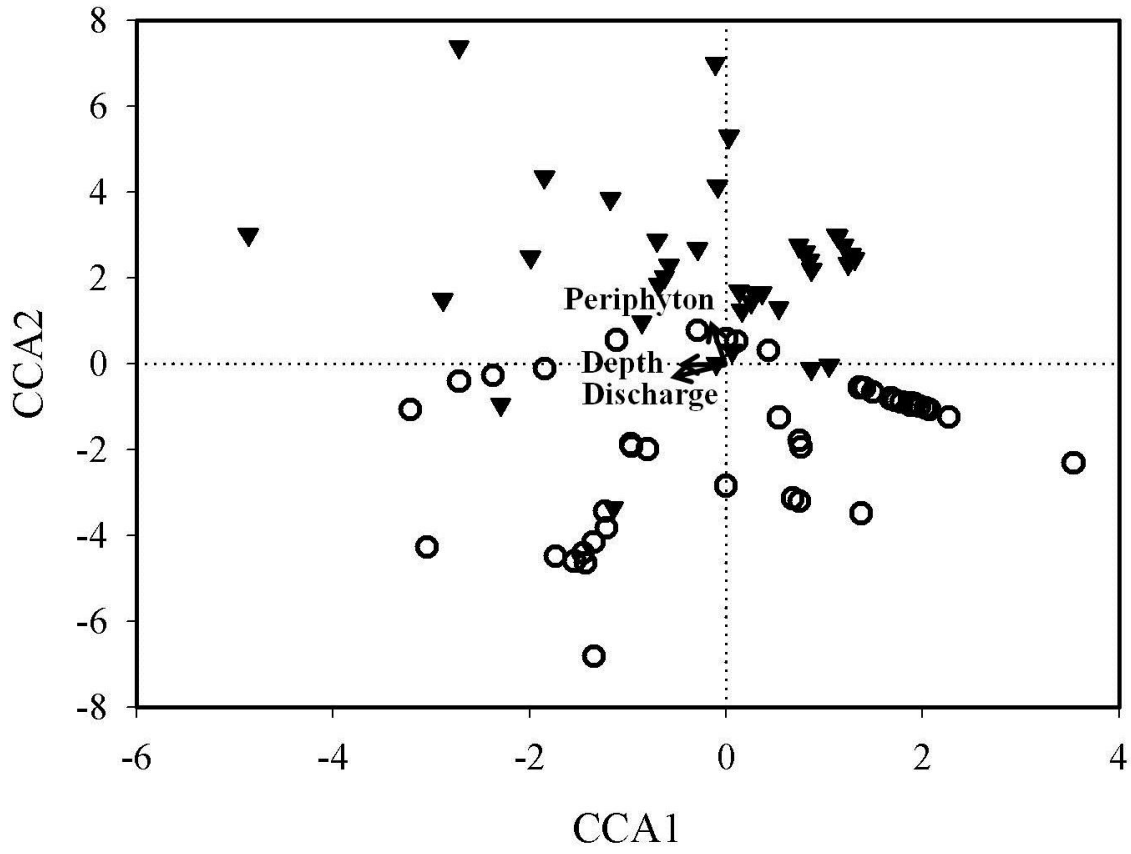

Fig. 3-3. Sample reach fish assemblage-habitat factor ordination from canonical correspondence analysis (CCA) ordination of fish assemblages in the Black Hills, South Dakota sampled 2008-2010. Stream habitat variables are represented by vectors, and sample reaches by open circles (mountain sucker absent) and closed triangles (mountain sucker present).

Chapter 4.

Assessment of the lethal thermal maxima for mountain sucker

This chapter was submitted as a manuscript to the Western North American Naturalist and was co-authored by Dr. Katie N. Bertrand.

ABSTRACT

Temperature is a critical factor in the distribution of stream fishes and from laboratory studies of thermal tolerance fish ecologists can assess whether species distributions are constrained by tolerable thermal habitat availability. The objective of this study was to assess the upper thermal tolerance for mountain sucker *Catostomus platyrhynchus*, a species of greatest conservation need in the state of South Dakota, with lethal thermal maxima (LTM) methodology. Adult fish were captured from wild populations in the Black Hills, and acclimated to 20°C, 22.5°C, or 25°C. Four endpoints (three sublethal, one lethal) were recorded, with death being the most precise. The LTM for mountain sucker was 34.0°C at 25°C acclimation, 33.2°C at 22.5°C acclimation, and 32.9°C at 20°C acclimation. Mountain sucker had an intermediate ability to increase thermal tolerance with increased acclimation temperature and, when compared to co-occurring species in the Black Hills, the LTM of mountain sucker was higher than that of salmonids, but lower than that of three cypriniforms. Mountain sucker LTM was intermediate when compared to other species in the family Catostomidae. These results suggest that mountain sucker are not currently limited by water temperatures in the Black Hills, but may be affected by stream warming as a result of climate change.

INTRODUCTION

Climatologists predict that global air temperatures will continue to increase into the future (Bates et al. 2008) and individual species, communities, and ecosystems will be forced to respond to these changes or face extirpation (Thomas et al. 2004, Parmesan 2006). In fisheries biology, recent work has focused on the thermal criteria of fishes to address the anticipated impacts of climate change (Eaton et al. 1995). Water temperature regulates the distribution of stream fishes through direct and indirect effects (Ferguson 1958, Matthews 1998). Temperature directly affects fish metabolism, feeding, growth, and reproductive physiology (Hutchinson and Maness 1979, Clarke and Johnston 1999, Matthews 1998) and indirectly affects food availability (Brylinsky and Mann 1973, Hinz and Wiley 1998) and condition-specific competition (Baltz et al. 1982, De Staso and Rahel 1994, Tanguchi et al. 1998). For these reasons, temperature is one of the most commonly measured and manipulated variables in laboratory (e.g., Fry 1947, Brett 1952, Feminella and Matthews 1984, Smith and Fausch 1997) and field studies (e.g., Eaton et al. 1995, Welsh et al. 2001, Huff et al. 2003, Wherly et al. 2007).

Fish abundance in a stream reach is a response to abiotic variables, including temperature. Species can persist where conditions are within its range of tolerance, but the abundance of a species should be greatest when conditions are closest to its optima (Huey and Stevenson 1979). Laboratory assessments of thermal tolerance can be used to draw inferences about a species' distribution along a temperature gradient. Great Plains stream fishes adapted to habitats often characterized by high temperatures, high salinity,

and low dissolved oxygen (Dodds et al. 2004), and the distribution of fishes reflect interspecific differences in physicochemical tolerance (Matthews 1987). In the Brazos and South Canadian Rivers, species distributions and abundances in warm and drying pools matched their estimated temperature and salinity tolerances from laboratory studies (Matthews and Maness 1979, Ostrand and Wilde 2001). Thus, thermal tolerance measured in the laboratory is a predictor of fish presence and abundance in the field. Estimation of individual species' thermal criteria can be important in the conservation of imperiled fishes (e.g., Smith and Fausch 1997, Torgersen et al. 1999, Selong et al. 2001, Harig and Fausch 2002).

Low and high water temperatures limit fish distributions. Cold temperatures have sub-lethal effects, including delayed egg and larval development (Harig and Fausch 2002), whereas warm temperatures may increase susceptibility to predation or increase direct mortality, in addition to numerous negative sub-lethal effects (e.g., reduced growth and fecundity; Selong et al. 2001). Based on an evaluation of stream water temperatures and fish distributions in the U.S., a global mean surface air temperature increase of 4.4°C would reduce available habitat for cold and cool water fish by 50% rangewide (Eaton and Scheller 1996). Laboratory studies can estimate thermal tolerance, assess the relative vulnerability of different fishes to increasing water temperatures (e.g., Smith and Fausch 1997), and predict habitat overlap between native and nonnative species (Carveth et al. 2006), all of which aid in selecting suitable conservation areas.

This study empirically derived the lethal thermal maxima for mountain sucker *Catostomus platyrhynchus*. Although mountain sucker are secure across their range (G5; Natureserve 2011), regional trends suggest declines at finer scales. A series of long-term studies on Sagehen and Martis Creeks and Stampede Reservoir in Eastern California indicated declines in mountain sucker total abundance, relative abundance, and spatial distribution (Erman 1973, 1986, Gard and Flittner 1974, Moyle and Vondracek 1985, Decker 1989). In the Missouri River drainage of Wyoming, Patton et al. (1998) found that mountain sucker distribution declined on at least three spatial scales since the 1960s. In South Dakota, mountain sucker are listed as a species of greatest conservation need (SDGFP 2006), and a long-term analysis indicated the species had significantly declined in density and spatial distribution since routine sampling began in the 1960s (Schultz and Bertrand *in review*).

Since mountain sucker inhabit mostly coolwater streams (Hauser 1969, Scott and Crossman 1973, Baxter and Stone 1995, Sigler and Sigler 1996, Belica and Nibbelink 2006) and other catostomids show temperature-regulated distribution (e.g., Li et al. 1987, Eaton et al. 1995, Huff et al. 2005), high water temperatures likely constrain the distribution of mountain sucker. As the climate warms (Bates et al. 2008), mountain sucker distribution may be further limited by warming stream temperatures. To better inform management decisions and understanding of mountain sucker biology in the Black Hills of South Dakota, the objective of this study was to assess the thermal tolerance of mountain sucker in the laboratory. These results will improve the understanding of factors that threaten peripheral populations of mountain sucker and

inform predictions of the consequences of elevated stream temperatures resulting from climate change in the Black Hills of South Dakota and across their range.

METHODS

Field collection and laboratory acclimation

Mountain sucker (TL 78-179 mm) were captured by electrofishing from Whitewood Creek near Whitewood, SD (44.472N, 103.624W) and Elk Creek near Lead, SD (44.277°N, 103.696°W) in the Black Hills in August 2010. Mean August water temperature in Whitewood Creek was 18.1°C (± 0.2°C) for the period 2007-2010. Fish were transported in an aerated transport truck and placed into holding tanks located at South Dakota State University (Brookings, SD). Prior to beginning experiments, we allowed fish to adjust to our laboratory conditions (temperature, feeding, dissolved oxygen) for 6 days. Pilot studies identified proper feeding and handling protocols. Fish were held in 5000-L rectangular tanks that were supplied with rock and wood cover, exposed to a 12 h light:12 h dark photoperiod, and fed a diet of attached periphyton collected from local waterbodies supplemented with live and frozen chironomid larvae. Water was circulated using small submersible pumps to ensure homogeneous water temperatures throughout the holding tank. Mortality associated with transport and adjustment to laboratory conditions was less than 3%. Following the initial adjustment period, 18 fish each were placed into separate tanks and acclimated (i.e., <1°C/hr) to three different temperatures: 20, 22.5, or 25°C. These acclimation temperatures were based on field data from streams across the Black Hills, and should represent the highest

prolonged (12+ hr) temperatures that mountain sucker experience in natural conditions (Simpson 2007). To mimic natural diel conditions that fish would be exposed to, daily temperature fluctuations (± 1.5°C) occurred during the acclimation period; the mean daily temperature in each tank remained constant. Water was continuously aerated and replaced every 3 days to reduce non-temperature related stress. Following the onset of acclimation conditions, fish were held for at least ten days before further testing.

Lethal thermal maxima procedure

We used the lethal thermal maxima (LTM) procedure to assess the upper thermal tolerance of mountain sucker. With the LTM method, fish are subjected to progressively higher water temperatures until they reach the death endpoint (Becker and Genoway 1979); we generated one lethal and three sublethal estimates of thermal tolerance (Carveth et al. 2006) for mountain sucker. The temperature was recorded at: (1) initial loss of equilibrium (the ability to maintain an upright position); (2) final loss of equilibrium (no longer able to self-right) (Becker and Genoway 1979, Lutterschmidt and Hutchinson 1997); (3) flaring opercula (fish movement except for opercula ceased) (Beitinger et al. 2000); and (4) death (no heartbeat or other motion visible). Our definition of initial loss of equilibrium is an ecologically relevant point because it is the temperature when fish might not be able to effectively escape predation or other lethal conditions.

Assessment of LTM involved randomly selecting and removing one fish from acclimation tanks and transferring it to a 3.8L glass container on an electric hot plate

filled with water from the acclimation tank. The container was continuously monitored (digital thermometer) and aerated to ensure consistent and homogeneous temperature and oxygen levels. Water temperature in the container was raised at a constant rate of 0.3°C/min, as Beitinger et al. (2000) recommended for small-bodied fishes. Hot plate settings were adjusted to maintain a constant rate of increase. The four endpoints (Carveth et al. 2006) were recorded to the nearest 0.1°C and each individual was measured (total length, mm) following death.

Statistical analyses

We assessed the influence of total length on thermal tolerance using linear regression. We used a one-way ANOVA to compare temperature endpoints between acclimation temperatures. To assess the ability of mountain sucker to alter their upper thermal tolerance with changes in acclimation temperature, we computed the acclimation response ratio (ARR) by dividing the difference between mean endpoint temperatures at the highest and lowest acclimation temperatures (i.e., 25°C and 20°C) by the temperature difference between endpoints (i.e., 5°C). To infer the relative thermal tolerance of mountain sucker, we compared the LTM of mountain sucker to other co-occurring species in the Black Hills and across their range, and those of other catostomids.

RESULTS

The LTM for mountain sucker was 34.0°C when acclimated to 25°C, 33.2°C when acclimated to 22.5°C, and 32.9°C when acclimated to 20°C (Figure 4-1, Table 4-1). LTM did not vary significantly with total length ($r^2 = 0.03$, $P = 0.25$), so all fish tested

were pooled in subsequent analyses. Ending temperatures increased significantly with acclimation temperature for all endpoints (initial equilibrium loss – $F_{2,52}$ = 46.95, P <0.01; final loss of equilibrium – $F_{2,52}$ = 40.23, P <0.01; flaring opercula – $F_{2,52}$ = 33.38 , P <0.01; death – $F_{2,52}$ = 42.09, P <0.01; Figure 4-1). All fish reacted similarly during the LTM procedure; swimming activity increased as temperature approached the endpoints. The most precise endpoint was death (SE = 0.094), followed closely by final loss of equilibrium (SE = 0.106) and flaring opercula (SE = 0.107). Initial loss of equilibrium, a commonly used endpoint in other studies, was difficult to discern and provided the least precise endpoint (SE = 0.156). The ARR of mountain sucker was 0.23.

When compared to other fishes in the Black Hills region and other stream-dwelling catostomids, mountain sucker have intermediate thermal tolerance (Table 4-2). In contrast, the thermal tolerance of mountain sucker is relatively high when compared to other potentially co-occurring western North American stream fishes (Table 4-2).

DISCUSSION

The lethal thermal maxima provided the most precise estimate of upper tolerance estimates of the four endpoints we examined for mountain sucker. Although the rapid rate of temperature change we employed does not mimic those predicted to occur under climate change, it provides an empirical measure of thermal tolerance that is easily comparable with other studies. For mountain sucker, the LTM was 34.0° when acclimated to 25°C. Mountain sucker appear to have intermediate thermal tolerance among fishes in the Black Hills, but are considerably more tolerant to high temperatures

than the three co-occurring species of salmonids (i.e., brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, rainbow trout *Oncorhynchus mykiss*) in the Black Hills and elsewhere. These results are consistent with field studies of mountain sucker-dominated assemblages, which occupied warmer habitats in Utah than assemblages characterized by introduced brown trout (Giddings et al. 2006).

Based on recent available field temperature data from eleven streams (Simpson 2007, L.S. unpublished data), mountain sucker do not appear to be thermally limited in the Black Hills of South Dakota. During the drought summer of 2005, Simpson (2007) sampled streams across the Black Hills and observed a maximum stream temperature of 27.4°C in Whitewood Creek (44.417N, 103.693W), which is 5.0°C less than the mean temperature at which we observed initial loss of equilibrium. Furthermore, of the eight streams in the Black Hills where mountain sucker still occur, Whitewood Creek contains the highest densities of mountain sucker (Schultz and Bertrand *in review*). From 2008-2010, we collected mountain sucker from the warmest streams in the Black Hills (i.e., highest mean weekly stream temperatures were 20.5°C; L.S., unpublished data).

In warmer areas of their range, mountain sucker have the potential to be thermally limited but habitat overlap with other native and nonnative species is more important in explaining their distribution and abundance. Mountain sucker are thought to be replaced by bridgelip sucker *Catostomus columbianus* (both belong to sub-genus *Pantosteus*) along thermal and channel slope gradients in Pacific Northwest streams (Li et al. 1987). In Oregon, bridgelip sucker were not found in streams exceeding 25.7°C, had a realized

thermal niche center of 21.9°C, and showed a strong relationship with stream temperature (Huff et al. 2005). White sucker *Catostomus commersonii* are a cool water fish with a 95th percentile presence weekly mean temperature of 27.3°C (Eaton et al. 1995), which suggests that white sucker could outcompete mountain sucker in warmer stream segments, and might represent a threat to mountain sucker (and other catostomids) outside their native range.

When compared to other species in the western U.S., the ARR of mountain sucker is intermediate. The ability of an organism to alter its thermal tolerance has implications for how well it is able to respond to climate change (e.g., Stillman 2003, Calosi et al. 2008). Calosi et al. (2008) and Eaton and Scheller (1996) provided evidence that the thermal tolerance of a species is positively related to the geographic range size of the species, although these findings have not been examined extensively in many taxa. In a study that included two Arizona catostomids, razorback sucker *Xyrauchen texanus* and desert sucker *Catosomus clarkii*, Carveth et al. (2006) found ARR values of 0.33 and 0.16, respectively. In the same study, ARR values for other Arizona fishes ranged from 0.02 (loach minnow *Rhinichthys cobitis*) to 0.54 (green sunfish *Lepomis cyanellus*). This indicates that mountain sucker (ARR = 0.23, moderate geographic range) have intermediate ability to increase thermal tolerance with increasing acclimation temperature and intermediate vulnerability to stream warming as a result of climate change.

One criticism of the LTM procedure is the potential for pseudoreplication as a result of acclimation of all fish from one acclimation temperature in a single holding

tank. This practice is very common in LTM and CTM studies (e.g., Matthews and Maness 1979, Smith and Fausch 1997, Currie et al. 1998, Rajaguru 2002). Some researchers have attempted to circumvent this issue by acclimating fish individually or splitting individual fish among several acclimation tanks (Carveth et al. 2006). Due to equipment and laboratory limitations, the practice of acclimating individual fish is often not feasible. Although we could not completely eliminate this issue, in our study each fish was individually transferred to the test beaker, so we considered each individual an experimental unit.

The LTM is a common method for assessing thermal tolerance in fishes. Critical thermal maximum (CTM) and upper incipient lethal temperature (UILT) are two common alternatives to LTM. Both LTM and CTM provide a standard measure of thermal tolerance for an organism with a limited number of individuals and are often used to make comparisons among species and infer ecological patterns (e.g., Matthews and Maness 1979, Carveth et al. 2006). In both procedures, test fish are subjected to linearly increasing or decreasing temperature to a predefined endpoint (Beitinger et al. 2000). With the CTM method, the predefined endpoint is generally sub-lethal (e.g., loss or failure of equilibrium, flaring opercula). The UILT procedure involves acclimatizing fish at different temperatures prior to exposure to a series of constant test temperatures and tracking fish survival over time (Fry 1947). Although numerous researchers have tried to predict UILT using CTM or LTM data (e.g., Kilgour et al. 1985, Kilgour and McCauley 1986, Lohr et al. 1996), the two procedures measure different things. Abrupt transfer procedures (UILT) measures only mortification, while CTM/LTM procedures measures

both mortification and partial acclimation (Kilgour and McCauley 1986, Beitinger et al. 2000). The LTM/CTM procedures are advantageous because they generate a standardized measurement of thermal tolerance that is easily comparable across species. Because these procedures require smaller numbers of animals to complete the test, they are especially valuable for species of concern (Beitinger et al. 2000).

An understanding of mountain sucker thermal criteria will aid in the conservation of these native stream fish and help explain observed patterns of distribution in the Black Hills and across their range. An assessment of the realized thermal niche (e.g., Betolli 2005, Huff et al. 2005) for mountain sucker would further aid in understanding the ecological mechanisms underlying observed fish assemblages in the Black Hills. Of particular interest would be the overlap of preferred temperature ranges between mountain sucker and introduced salmonids to evaluate negative interactions between these species. Finally, these results aid in the identification of thermally suitable habitat for mountain sucker across their range and contribute to predictions of the potential consequences of elevated stream temperatures resulting from climate change (Mohseni et al. 1999). In the Black Hills, the distribution of mountain sucker currently does not appear to be constrained by temperature. Although a myriad of interacting factors influence observed stream temperature, future conditions may exceed the temperature at which we estimated initial loss of equilibrium for mountain sucker. Climate change scenarios (IPCC 2007) predict mean annual global air temperature increases of 1.8-4.0°C (range: 1.1-6.4°C), which could limit thermally suitable habitat for mountain sucker in the Black Hills. In addition, the potential consequences of altered flood and drought

intensity and duration from climate change, industrial thermal pollution, and interactions with introduced species are likely to increase the sensitivity of these native fish to warming stream temperatures.

Table 4-1: Measured lethal thermal maximum temperatures at four measured endpoints for mountain sucker acclimated to 20.0°C, 22.5°C, and 25.0°C. Confidence intervals (95%) are reported for each value.

	Acclimation Temperature		
Endpoint	20	22.5	25.5
Initial equilibrium loss	31.5 ± 0.7	32.4 ± 0.2	33.4 ± 0.2
Final equilibrium loss	32.3 ± 0.3	32.6 ± 0.2	33.6 ± 0.3
Flaring opercula	32.5 ± 0.4	32.7 ± 0.3	33.7 ±0.2
Death	32.9 ± 0.3	33.2 ± 0.2	34.0 ± 0.2

Table 4-2. Comparison of the laboratory thermal tolerance for fishes that are sympatric with mountain sucker in the Black Hills, fishes that may occur with mountain sucker across their range, and other catostomids. Endpoints include: EQ loss – final loss of equilibrium, FO – flaring opercula.

	Critical Thermal Maxima (°C)	Acclimation temperature (°C)	Endpoint	Reference
Co-occurring Species (Black Hills region)				
Fathead minnow *Pimephales promelas*	36.1	25	EQ loss	Carveth et al. (2006)
Creek chub *Semotilus atromaculatus*	35.7	26	EQ loss	Smale and Rabeni (1995)
White sucker *Catostomus commersoni*	34.9	26	EQ loss	Smale and Rabeni (1995)
Mountain sucker	33.6	25	EQ loss	this study
Longnose dace *Rhinichthys cataractae*	31.4	15	FO	Kowalski et al. (1978)
Brown trout *Salmo trutta*	29.8	20	EQ loss	Lee and Rhinne (1980)
Brook trout *Salvelinus fontinalis*	29.8	20	EQ loss	Lee and Rhinne (1980)
Rainbow trout *Oncorhynchus mykiss*	29.4	20	EQ loss	Lee and Rhinne (1980)
Co-occurring Species (rangewide)				
Northern leatherside chub *Lepidomeda copei* (juvenile)	34.6	23	EQ loss	Billman et al. (2008)
Mountain sucker	33.6	25	EQ loss	this study
Speckled dace *Rhinicthys cataratae*	32.4	20	EQ loss	Castleberry and Cech (1992)
Mottled sculpin *Cottus bairdi*	30.9	15	FO	Kowalski et al. (1978)
Arctic grayling *Thymallus arcticus*	29.3	20	EQ loss	Lohr et al. (1996)
Cutthroat trout *Oncorhynchus clarkii clarkii*	27.6	10	EQ loss	Heath (1963)

Other Catostomids				
Desert sucker *Catostomus clarkii*	35.1	25	EQ loss	Carveth et al. (2006)
White sucker	34.9	26	EQ loss	Smale and Rabeni (1995)
Mountain sucker	33.6	25	EQ loss	this study
Shortnose sucker *Catostomus brevirostris*	32.7	20	EQ loss	Castleberry and Cech (1992)
Klamath largescale sucker *Catostomus snyderi*	32.6	20	EQ loss	Castleberry and Cech (1992)
Northern hogsucker *Hypentelium nigricans*	30.8	15	FO	Kowalski et al. (1978)

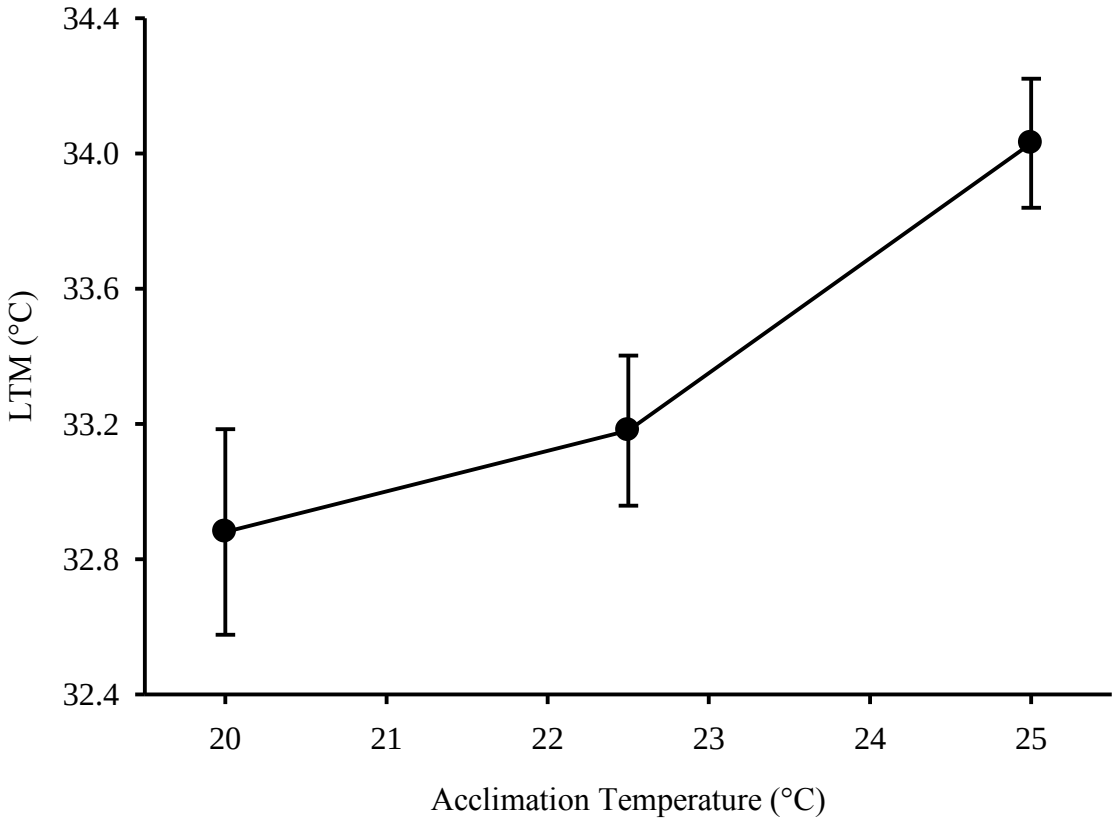

Fig. 4-1. Lethal thermal maxima (LTM ± 95% confidence intervals) for mountain sucker acclimated to three different acclimation temperatures.

Chapter 5.

Summary, conclusions, and management options

This work has documented the long-term decline of mountain sucker, a native stream fish in the Black Hills of South Dakota. Historically mountain sucker were present in watersheds across the entire Black Hills in densities ranging from 0.005 to 0.6 fish m^{-2}. Since routine sampling began in the late 1950s, mountain sucker density significantly declined at three nested spatial scales and no significant increases were observed. In addition, the spatial distribution of mountain sucker in the Black Hills has contracted substantially, with populations being extirpated from the majority of the southern Black Hills and substantial portions of the northern Black Hills.

This study used coarse-scale geomorphic, fine-scale sample reach habitat, and fish assemblage variables to model presence of mountain sucker across the Black Hills. The distribution of mountain sucker was best explained by a combination of variables from multiple spatial scales and faunal filters. As the density of trout increased, the presence of mountain sucker approached zero. Periphyton coverage had a strong and positive influence on mountain sucker density. Although Dauwalter and Rahel (2008) provided broad generalizations that could be used to direct future field studies, the incorporation of sample reach habitat variables improved the utility of predictive models and provided more insight into mountain sucker biology. Furthermore, understanding fine-scale habitat and biotic interactions influential to imperiled species (or native assemblages) will be critical to effective conservation.

The thermal tolerance of mountain sucker was intermediate for potentially co-occurring species in the Black Hills, across their range, and when compared to other catostomids. Within the sub-genus *Pantosteus*, the thermal tolerance of mountain sucker was slightly lower than desert sucker *Catostomus clarkii*, however little thermal tolerance data exist for this sub-genus. Overall, results of this study indicate that mountain sucker are currently not limited thermally in the Black Hills, but some areas that are currently suitable for mountain sucker may be lost due to climate change. Of particular conservation interest are the downstream reaches of Whitewood Creek, where mountain sucker are present in some of the highest observed densities. Furthermore, these predictions are highly conservative in that they account for only climatic warming; additional stressors (e.g., riparian land use changes, altered hydrologic patterns, industrial thermal pollution, interactions with invasive species) will likely exacerbate these effects.

Management Implications

These results aid in the understanding of mountain sucker ecology and can be used to proactively address their population trends. Similar to other studies (e.g., Decker and Erman 1992, Giddings et al. 2006, Dauwalter and Rahel 2008), our study documented a negative interaction between mountain sucker and introduced salmonids. Depending on desired outcomes, several management options exist. First, to restore fish assemblages in the Black Hills to pre-European settlement conditions, broad scale removal of introduced species will be required. Some Black Hills streams are impounded, and short of dam removal, will never be returned to their pre-settlement state. Second, if a balance between sport- and native fisheries is desired, broad scale fish

removals would not be necessary but areas of conservation interest could be identified and prioritized, or potentially created through restoration. While the ecological mechanism underlying the interaction between mountain sucker and introduced salmonids is unclear, management actions to conserve mountain sucker would be most effective in areas outside managed trout fisheries. Suitable conservation or translocation areas would contain low densities of introduced trout, conditions supportive of high periphyton production, and would maintain baseflow through periods of drought. A final option would be to take no action. Under this option, the long-term persistence of mountain sucker depends on the interaction between native and introduced fishes and the ability of fishes to disperse throughout the Black Hills.

The results of this study can also be applied more broadly. This study provides further evidence of the potential negative interactions between introduced fishes and native fish assemblages (Crowl et al. 1992). Additionally, understanding multiple-scale habitat and biotic interactions influential to imperiled species (or native assemblages) will be critical to effective native fish conservation and can be used to evaluate the scale that management activities can effectively target.

Research Needs

1) The drought of 2002-2007 impacted the abundance of some sport fishes in the Black Hills, but non-game fish assemblages were not evaluated. Continued monitoring effort throughout the Black Hills is necessary to assess the response of these fishes to the full spectrum of annual hydrologic regimes and identify potential source populations that serve to recolonize stream

reaches throughout the Black Hills following drought. These efforts may also locate areas where mountain sucker have persisted that were not detected during this study.

2) An understanding of the mechanism(s) underlying negative interactions between mountain sucker and introduced trout would aid in the management of sport and native fisheries in the Black Hills, and greatly improve the understanding of the ecology of these species across their overlapping ranges. If the mechanism is predatory in nature, a quantitative assessment of mountain sucker mortality associated with this predation would address numerous knowledge gaps. If the interaction is competition, mediating factors could potentially be identified, further aiding management decisions.
3) Many other benthic grazing fishes respond to periphyton dynamics in streams. An assessment of the movement patterns of mountain sucker could evaluate their response to these dynamic habitat conditions, help explain observed yearly fluctuations in mountain sucker densities, identify potential refugia during drought, and help understand the ecosystem effect(s) of mountain sucker.
4) Although this study documented the thermal tolerance of mountain sucker in the laboratory, an assessment of their field thermal criteria would provide ecologically meaningful insights into observed patterns in their distribution and help further evaluate the consequences of climate change. Of particular interest would be a range-wide assessment of their fundamental and realized

thermal niche (Bettoli 2005, Huff et al. 2005). This information would help identify the degree of thermal overlap between mountain sucker and other species and may help explain observed interactions.

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