Investigating fine-scale movement patterns and comparative swimming performance of the newly identified and threatened Rocky Mountain Sculpin (*Cottus* sp.) across its Canadian distribution

by

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Abstract

Cumulative anthropogenic impacts to the riverscape, including hydrologic alteration, have contributed to an escalated number of freshwater fish species at risk in North America. Species dispersal is an important mechanism underlying many ecological processes. Understanding the scale at which species carry out their life history can inform both conservation actions and recovery potential. Our study used the recently-identified Rocky Mountain Sculpin (*Cottus* sp.), a species federally listed as threatened, to investigate the (1) fine-scale movement potential and (2) comparative swimming ability of adults throughout their restricted Canadian distribution. Rocky Mountain Sculpin are a small-bodied, cryptic benthic species that utilizes interstitial spaces for shelter. To assess the fine-scale movement potential of Rocky Mountain Sculpin, I conducted a mark-recapture study on Lee Creek, Alberta using Passive Integrated Transponder (PIT) and Visible Implant Elastomer (VIE) tags. I assessed the abiotic and biotic factors influencing movement using Boosted Regression Tree models. In this study I found that 89% of sculpins moved less than 30 meters, while a few individuals moved up to 240 meters. Biotic factors indicated sculpins moved from high to low abundances of fish due to intra- and inter- specific competition from congeners and benthic competitors. The most important abiotic factor contributing to movement was abundance of cobble substrate at destination transects. Interestingly, there was a strong interaction between biotic and abiotic components indicating the importance of focusing restoration efforts on both biotic and abiotic factors. To address the second objective, comparative fish swimming performance and recovery potential was assessed in a laboratory on individuals sourced from drastically different hydrologic regimes in Alberta and British Columbia, including the flow augmented, North Milk River. Permutational ANOVAs were used to compare swimming performance between rivers using two aspects of swimming ability: (1) slip velocity, the point at which fish slipped and transitioned into swimming and 2) failure velocity, the point at which fish could no longer hold position against the flow without resting. While we expected swimming ability to be correlated with natal hydrologic regimes, our study found there were no differences in failure or slip velocity between rivers. However, resting oxygen uptake prior to swim tests was significantly higher for fish from the augmented, North Milk River, indicating there may be a physiological response to flow augmentation. Over repeated exercise, fish failure velocity decreased from 7.45 ± 3.10 body lengths per second (BL s^{-1}) in the first test to 6.18 ± 2.56 BL s^{-1} by the third test suggesting the use of anaerobic metabolism to power swimming performance of this small-bodied species. Linear mixed-effects models developed using body characteristics showed caudal morphology to influence both failure and slip velocities, while body height was negatively correlated to slip velocity, demonstrating morphological selection for benthic living. Taken together, these studies suggest that while large-scale flow augmentation may come at an energetic cost to sculpins, fine-scale developments may be equally as detrimental to this dispersal-limited species. Conservation for this species may then require both fine-scale and regional management.

Preface

This thesis is an original work by Marie F. Veillard. Both chapters integrated collaborative efforts from a variety of people. I was responsible for field and laboratory data collection, data analysis, manuscript preparation, and some aspects of designing both studies. Mark Poesch was the primary supervisory author and was involved in study design for both chapters and additionally provided feedback on data analysis and manuscript drafts. Jonathan Ruppert assisted with data analysis and manuscript preparation. Doug Watkinson provided local area knowledge and assisted in the study design and manuscript preparation for Chapter 2. Keith Tierney provided guidance on swim performance study design and gave feedback on the manuscript draft for Chapter 3.

Research for this thesis received ethics approval by the University of Alberta Animal Care and Use Committee under the animal care protocol number: AUP00000759. Field collections were carried out under approved provincial Fish Research Licenses (13-2408 & 14-2415) and federal Species at Risk permits (13-007 & 14-00041) issued under section 73 of the *Species at Risk Act*.

To my sister, Louise ❤

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When the road felt never-ending, my wonderful friends and family kept me company. My friends Alex Bykowski, Kelsey Dokis-Jansen, Jason Davidson, Riley Davidson, Diana Young, Jasmine Lamarre, Danielle Arseneau, and Carleen Etmanski kept me sane by taking my mind off fish every once in a while. The support and love provided by my Mom, Dad and sister, Rae, continually encouraged me to work through challenging times. Finally, I would like to thank Nathan Medinski who became my second set of eyes and personal cheerleader in the past year. Without him in my corner providing words of encouragement this process would been far harder.

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Chapter I: General Introduction

Earth's finite freshwater resources are of paramount importance to both human life and for sustaining biodiversity. Freshwater has become increasingly scarce as water demands intensify with population growth, agricultural irrigation, and industrial activity (Schewe *et al.*, 2014). While technological advances can increase water use efficiency, 80% of humans live in areas with high water security threats (Vörösmarty *et al.*, 2010). This scarcity generates a need for waterway alterations including diversions, dams and water removal to meet human demands (Vörösmarty *et al.*, 2000). While developed nations experience the least threat from water security (Vörösmarty *et al.*, 2010), cumulative effects of human stressors are predicted to reduce water quantity and quality in Canada (Schindler, 2001), resulting in an impending water crisis for the Canadian plains (Schindler and Donahue, 2006).

Humans share aquatic resources with a high number of freshwater organisms (Dudgeon *et al.*, 2006; Abell *et al.*, 2008). Worldwide ichthyofaunal diversity is similarly allocated between freshwater (41% of fish species) and marine (58% of fishes) species despite the fact that freshwater makes up only 0.01% of all water resources on earth (Lundberg *et al.*, 2000). Limited freshwater habitats support an estimated one-third of all vertebrate species and 6% of the total described species on our planet (Dudgeon *et al.*, 2006). Additionally, freshwater habitats support high endemism with new fish species discovered annually (Lundberg *et al.*, 2000).

As expected, water security for humans comes at a cost to freshwater biodiversity and ecosystem integrity (Schindler, 2001; Vörösmarty *et al.*, 2010) resulting in the imperilment of approximately 39% of freshwater fish species in North America (Ricciardi and Rasmussen, 1999; Dudgeon *et al.*, 2006; Jelks *et al.*, 2008). While tropical rainforests and terrestrial systems have dominated the dialogue on biodiversity loss (Ricciardi and Rasmussen, 1999), imperilment of freshwater biodiversity exceeds that of terrestrial systems (Sala *et al.*, 2000; Strayer and Dudgeon, 2010). Acute and chronic anthropogenic changes to the riverscape influence biodiversity loss through flow modification, habitat degradation, overexploitation of fisheries resources, waterway pollution, and species invasions (Dudgeon *et al.*, 2006; Strayer and Dudgeon, 2010). In a review of fish abundance and demography in response to waterway alteration, Poff and Zimmerman (2010) suggest both elevated and reduced flows are detrimental to fish. Impacts to freshwater ecosystems are exacerbated by climate change (Jelks *et al.*, 2008; Chu *et al.*, 2014). In particular, cool- and cold-water fish may be most at risk from the compounding effects of human stressors as thermally suitable habitat decreases (Chu *et al.*, 2005; Buisson *et al.*, 2008; Heino *et al.*, 2009) with increasing water temperatures (Isaak *et al.*, 2012). Species' ability to disperse can buffer the impacts of such changing conditions.

Species dispersal is fundamental in the study of many ecological concepts including population viability (Poos and Jackson, 2012), recolonization potential (Knaepkens *et al.*, 2005), gene flow (Bohonak, 1999) and adaptation to local conditions (Hendry *et al.*, 2007). In the seminal works on island biogeography (MacArthur and Wilson, 1963; 1967) dispersal was described as a key component in emigration and immigration dynamics influencing community composition and species turnover. Expanding on this theory, metapopulation and metacommunity dynamics focused on the migration of individuals between subpopulations (Hanski, 1998; Leibold *et al.*, 2004) and the resultant structure of genetic diversity and gene flow (Wright, 1978; Bohonak, 1999). Eventually, the study of genetic diversity across temporal and spatial scales became known as phylogeography (Avise *et al.*, 1987).

Riverine ecosystems follow a hierarchical dendritic structure setting them apart from terrestrial metapopulation models (Fagan, 2002). Dispersal of individuals through riverscapes relies heavily on connectivity of corridors making fish particularly sensitive to instream barriers (Fagan, 2002; Maitland *et al.*, 2016). While workers such as Gerking (1953; 1959) have suggested fish populations carry out their life history within a restricted range, Gowan *et al.* (1994) disputed this restricted movement paradigm stating bias in movement studies had simply influenced where researchers searched for tagged individuals. Currently, the concept of heterogeneous movement within fish populations suggests that populations are characterized by both sedentary and mobile individuals, resulting in a leptokurtic dispersal distribution (Skalski and Gilliam, 2000; Fraser *et al.*, 2001; Rodriguez, 2002; Radinger and Wolter, 2014). The sedentary component may be most vulnerable to changes at a local scale, while the mobile component is more susceptible to movement barriers at a regional scale. In the absence of barriers, mobile individuals can respond to abiotic and biotic environmental changes to colonize suitable habitat (Gilliam and Fraser, 2001) and re-colonize restored habitat (Lake *et al.*, 2007).

It is important to note the difference between dispersal, movement and locomotion. Dispersal (or migration) can be broadly defined as the displacement "from one spatial unit to another" (Baker, 1978), but is usually reserved for longer-distance movements depending on the study scale and focal species. On the other hand, Baker (1978), defines movement as a "change in position", that may occur within a spatial unit, again, dependent on study scale and species. Finally, locomotion is the force used by an animal to move (Baker, 1978). While not all species are capable of long distance dispersals, both movement and dispersal incorporate locomotion (Baker, 1978).

Some fish species are considered dispersal limited and predominately exhibit movements rather than dispersal events. For example, freshwater sculpins (genus *Cottus*) are a small-bodied, dispersal limited taxa (Breen *et al.*, 2009; Young *et al.*, 2013) moving an average distance of 23 meters in 13 months (Schwalb *et al.*, 2011). Freshwater sculpins occupy a mid-trophic level, feeding on macroinvertebrates, molluscs, fish eggs and larval fishes (Bailey, 1952) and predated upon by larger piscivores (Bailey, 1952; Bond, 1963; Young *et al.*, 2013). Morphometric similarities have resulted in widespread misidentification of sculpins (Peden *et al.*, 1989) leading to unresolved taxonomic clarity. Recent genetic studies have begun to detangle the complex taxonomy of freshwater sculpins (Kinziger *et al.*, 2005; Young *et al.*, 2013) resulting in several newly identified *Cottus* species in recent years (Neely *et al.*, 2007; LeMoine *et al.*, 2014).

One recently identified species is Rocky Mountain Sculpin (*Cottus* sp.) (Neely, 2003 unpublished; COSEWIC, 2005). In Canada, Rocky Mountain Sculpin occupy a restricted distribution found only in southern Alberta and southeastern British Columbia (COSEWIC, 2005). Divided by the Rocky Mountain range, this species is managed as two Designatable Units (DUs) in Canada. The Westslope DU are located in a remote area of British Columbia, and are recommended as special concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) due to low threat risk to populations (COSEWIC, 2010). Alternatively, the Eastslope DU overlaps with an area of extensive waterway management in southern Alberta for agricultural irrigation and has therefore been recommended and listed as threatened in Canada under Schedule 1 of the *Species at Risk Act* (COSEWIC, 2005; Fisheries and Oceans Canada, 2013).

Within the rain shadow of the Rocky Mountains, southern Alberta is among the driest regions in southern Canada (Schindler and Donahue, 2006). To provide stability for local ranchers and agricultural operations, large-scale flow modifications have been erected to distribute water to irrigation districts in southern Alberta (COSEWIC, 2005). In particular, within the range of Rocky Mountain Sculpin, flow modifications both seasonally raise and permanently reduce streamflow magnitude. The St. Mary Canal in Montana was built in 1917 to divert 178 x 10^6 cubic meters of water annually from the St. Mary River to the North Milk River (Bradley and Smith, 1984) drastically increasing peak flows in the North Milk River (Water Survey of Canada, 2015). On the other hand, the construction of the St. Mary Dam in 1951, reduced flows to create the St. Mary Reservoir which feeds a series of irrigation canals (COSEWIC, 2005). Even with flow management, water balance projections for southern Alberta suggest moderate climate warming may result in insufficient flow to sustain irrigation needs (Byrne *et al.*, 1989). While the effects of these modifications on Rocky Mountain Sculpin are largely unknown, dispersal and distribution of freshwater sculpins are known to be impacted by waterway alterations (Roberts, 1988; LeMoine and Bodensteiner, 2014; Maitland *et al.*, 2016).

This thesis aims to investigate the movement ability (Chapter II) and locomotion (Chapter III) of adult Rocky Mountain Sculpin to inform future management of this threatened species. Firstly, to examine movement patterns I used a mark-recapture study conducted on Lee Creek (St. Mary River tributary) to explore how biotic and abiotic components influence movement events of Rocky Mountain Sculpin in the absence of flow modification (Chapter II). Studying factors contributing to “natural” movements can be used as a baseline to understand important components affecting Rocky Mountain Sculpin, while future studies can link movement potential to waterway alterations. In Chapter III I compare the swimming performance and oxygen uptake rates of Rocky Mountain Sculpin sourced from four rivers across the Canadian distribution to assess local adaptations to natal hydrologic systems in an experimental setting. I also used body characteristics and recovery ability from repeated exercise to examine the locomotion capabilities of the species. We anticipate this information to be valuable to fisheries managers working to conserve this dispersal-limited, threatened species facing current and future large-scale flow alterations in its restricted Canadian distribution.

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Chapter II: The importance of incorporating biotic interactions into movement models for dispersal limited species: The threatened Rocky Mountain Sculpin (*Cottus* sp.) as a case study

2.1 Executive Summary

Dispersal is an important mechanism linked with population viability. Increases in species-specific dispersal allows for improved connectivity between habitat patches and populations. However, despite the importance of inter- and intra-specific competition that can influence species-specific behaviour and subsequent movement, the role of these biotic factors are rarely assessed. Here, we seek to understand the role of both biotic and abiotic factors influencing the movement of the recently identified and federally listed as threatened, Rocky Mountain Sculpin (*Cottus* sp.). We conducted a mark-recapture study on Lee Creek in Alberta, Canada using Passive Integrated Transponder and Visible Implant Elastomer tags during the summer of 2013. Boosted Regression Tree models were used to assess movement of 1) all recaptured individuals (global model) and 2) only mobile individuals (movement only model) in response to abiotic and biotic factors. Biotic factors, such as congeners at the destination (8.7%), congeners at the origin (8.0%) and competitors at the origin (7.2%) were the most important variables for predicting movement in the global model. Alternatively, cobble (18.7%) followed by biotic factors including congeners at the origin (9.6%) and competitors at the origin (9.1%) were the most important variables selected in the movement only model. Biotic and abiotic factors showed strong interactions, providing a clear example of the importance of competition in the understanding of movement. Although the vast majority of restoration activities for endangered species are aimed at abiotic (i.e. habitat-related) factors, this study shows how these may be limited without considering biotic interactions, such as the role of inter- and intra-specific competition.

2.2 Introduction

Dispersal is a mechanism underlying many ecological processes. To conserve species, it is imperative we understand movement patterns (Schmetterling and Adams, 2004) that may influence dispersal and the subsequent success of our conservation efforts such as habitat restoration (Radinger and Wolter, 2014). While some fish undertake long distance migrations, many stream fish populations are largely sedentary (Gerking, 1959) with a subset of mobile individuals (Funk, 1957; Rodriguez, 2002). The sedentary portion of the population is often associated with concepts such as home range (Gerking, 1959; Radinger and Wolter, 2014) and territoriality (Gerking, 1953; 1959) resulting in density-dependent movement (Jenkins, 1969). On the other hand, the mobile portion of the population has been suggested to contribute to a host of ecological processes such as range shifts (Hynes, 1970; Radinger and Wolter, 2014), metapopulation dynamics (Hanski, 1998), colonization or recolonization of suitable habitat (Knaepkens *et al.*, 2005) and gene flow (Wright, 1978). The ability to respond to environmental changes may then be influenced by mobile individuals in the population, inter- and intra-species interactions, and changes to suitable habitat, indicating the importance of both biotic and abiotic factors to movement (Gilliam and Fraser, 2001).

Despite the influence of abiotic and biotic factors on stream fish movement, few studies have quantified their importance (Turchin, 1998). Abiotic factors have been more readily incorporated into fish movement studies (Albanese *et al.*, 2004; Petty and Grossman, 2004; Breen *et al.*, 2009), whereas biotic factors such as predation and competition are less frequently used in movement studies despite their importance in structuring fish communities (Jackson *et al.*, 2001). In a movement study conducted by Gilliam and Fraser (2001), they found an interaction between biotic pressures and abiotic physical streambed structure that provided cover to promote movement of the Giant Rivulus (*Rivulus hartii*) in the presence of its predator Trahira (*Hoplias malabaricus*)(Gilliam and Fraser, 2001). However, the role of competitive interactions is less clear for structuring stream fish communities (Jackson *et al.*, 2001). In a study of competitive interactions between the benthic Mottled Sculpin (*Cottus bairdi*) and Fantailed Darter (*Etheostoma flabellare*), Resetarits (1997) found that juveniles from each species under competitive pressure resulted in reduced growth and decreased relative condition, respectively. Additionally, Jenkins (1969) found Brown Trout (*Salmo trutta*) and Rainbow Trout (*Oncorhynchus mykiss*) exhibited movements in relation to inter- and intra-specific agonistic acts resulting in chasing and displacement of individuals.

To investigate movement in relation to both biotic interactions and abiotic environmental factors, freshwater sculpins (Genus *Cottus*) may be an ideal group as they are more sedentary compared to most other species (Radinger and Wolter, 2014). In fact, a review by Schwalb *et al.* (2011) showed that freshwater sculpin species move an average distance of 23 m over an average study duration of 13 months, indicating that as a group they are quite sedentary. This limited movement makes them susceptible to disturbances (McCormick *et al.*, 1994) such as waterway alterations and movement barriers (Maitland *et al.*, 2016). As a sedentary group, they are likely to experience quite variable levels of inter- and intra-species competition that may be related to overall densities of congeners, competitors and predators, as they cannot disperse far to seek out new sources of desired resources (Anderson, 1985; Greenberg, 1991). Further, there are particular tolerances for cool- and cold- water sculpins (Adams and Schmetterling, 2007), that require clean, unembedded cobble to complete their life-history (Bond, 1963; Finger, 1982; Haro and Brusven, 1994). Given this understanding it appears that an investigation into the movement of freshwater sculpins, like many other fish species, needs to incorporate both biotic and abiotic factors to fully comprehend what influences movement.

Several freshwater sculpin species have been identified in recent years (Neely *et al.*, 2007; LeMoine *et al.*, 2014) including the Rocky Mountain Sculpin (*Cottus sp.*) (Neely, 2003 unpublished). Rocky Mountain Sculpin straddles the Continental Divide, where management for the species is separated into a westslope Designatable Unit (DU) in the Flathead River of British Columbia and an eastslope DU for southern Alberta (COSEWIC, 2005). The eastslope DU includes the Milk and St. Mary rivers, which experience threats from drought and waterway alterations (Fisheries and Oceans Canada, 2013), leading to its listing in 2006 as threatened under Canada's *Species at Risk Act* (Fisheries and Oceans Canada, 2012). Local changes to environmental conditions are expected to negatively affect Rocky Mountain Sculpin due to its inferred restricted movement from closely-related sculpin species. It is critical we understand the role of both abiotic and biotic interactions in determining species-specific movement to predict how these changes may impact broader dispersal mediated population and community processes. Using Rocky Mountain Sculpin as a model organism, we use data collected from 884 tagged individuals over the course of the summer and fall seasons of 2013 (July-October), to: 1) evaluate the movement ability of the species and 2) assess abiotic and biotic factors influencing movement. Understanding the factors associated with Rocky Mountain Sculpin movement is paramount for determining sustainability of this range limited species and the broader response to conservation efforts by dispersal limited species.

2.3 Methods

2.3.1 Study Area

Movement patterns of Rocky Mountain Sculpin were monitored on Lee Creek, a tributary to the St. Mary River in Alberta, Canada. Lee Creek is located within the fescue grasslands ecoregion of the Oldman River sub watershed in southern Alberta (Figure 2.1). Flow is predominantly driven by snowmelt and precipitation in this system, with mean lows of 0.2 m^3s^{-1} (November) and highs of 7.5 m^3s^{-1} (June)(Alberta Environment and Parks, 2014). Rocky Mountain Sculpin dominated our catch followed by: Longnose Dace (*Rhinichthys cataractae*), Mountain Sucker (*Catostomus platyrhynchus*), Lake Chub (*Couesius plumbeus*), Burbot (*Lota lota*), Longnose Sucker (*Catostomus catostomus*), White Sucker (*Catostomus commersonii*) and Trout-perch *(Percopsis omiscomaycus*). Catch per unit effort is high within the Canadian range of Rocky Mountain Sculpin, including Lee Creek (16.62 fish min^{-1}) (COSEWIC, 2005). This high density of fish, in consort with a wide range of habitat types found along Lee Creek makes this area an ideal system to study the movement of Rocky Mountain Sculpin and determine biotic and abiotic factors influencing movement of the species.

We conducted a mark-recapture field study within a 400 m stretch of Lee Creek, consisting of an inner 200 m core tagging area with 100 m buffer zones extending upstream and downstream of the core (Figure 2.1c) (Breen *et al.*, 2009). Cross-sectional transects were established every 10 meters throughout the site, totalling 41 transects. The site was chosen to include two main riffle sections connected by runs and pools which characterized a range of optimal, suboptimal and avoided habitat types (Figure 2.1c) (Bailey, 1952). Otherwise natural, historic stream channelization occurred in the upper 150 meters of our study area, creating a straight, uniform stretch.

2.3.2 Fish Tagging and Movement

Fish abundance and abiotic habitat variables were measured over six days during six sampling events, that commenced every 17 ± 1.45 days. To track movement, Passive Integrated Transponder (PIT) and Visible Implant Elastomer (VIE) tags were deployed from 11 July 2013 through to 6 October 2013. Long-lasting remote PIT tagging systems are often used in studies of small-bodied fish (Roussel *et al.*, 2000; Bruyndoncx, 2002; Breen *et al.*, 2009) as an alternative to traditional mark-recapture techniques, such as VIE, that require physical recapture (eg. electrofishing) (Nielsen, 1992).

Utilizing both tagging methods, Rocky Mountain Sculpin were collected and tagged in the core 200 m area containing 21 transects. Fish were collected with a Smith-Root LR-24 backpack electrofisher using a single-pass kick-netting method, allowing shocked individuals to drift into block nets downstream of the anode. Smaller individuals ($45 \geq TL \geq 65$ mm) received only VIE tags (n=661) while large individuals ($TL \geq 65$ mm) were tagged with both VIE and PIT tags (n=223). Cohorts of fish collected on the same day at the same transect were marked with unique VIE tags using a combination of colour and body location. Large fish were anaesthetized in tricaine methanesulfonate (TMS; 0.2 g L^{-1}), and tagged using 12.0 mm x 2.12 mm HDX PIT tags (wt = 0.1 g; Oregon RFID) in the peritoneal cavity (Columbia Basin Fish and Wildlife Authority, 1999; Ruetz *et al.*, 2006). The insertion point was then sealed using 3M Vetbond TM Tissue Adhesive. PIT tagged fish were placed in a recovery bin and allowed a minimum of either 30 minutes to recover or the length of time until they appeared to have regained normal activity levels. Individual fish were released one meter upstream of the transect midpoint, from which they were caught.

PIT tagged individuals were tracked remotely throughout the 400 m study reach using an HDX backpack reader (Oregon RFID). The backpack unit contained a datalogger connected to a copper antenna pole, which generates an electromagnetic field to charge passive tags in the vicinity and store unique numeric codes. Time-stamped detections were sorted into transects and cross-validated with audible detection records from the field. Small individuals marked with VIE tags were tracked and tallied only in the core area during electrofishing events due to the requirement of physical recapture. Throughout the study period we recaptured 182 individuals fitted with PIT tags at least once, and 83 individuals marked with VIE tags. Movement detections gathered from both tagging methods were combined and analyzed together.

2.3.3 Environmental Variables

Movement is known to be influenced by a suite of biotic and abiotic factors as individuals attempt to alleviate stress from competition (Petty and Grossman, 2004) and predation (Owens and Bergstedt, 1994), while optimizing preferred habitat (Tabor *et al.*, 2007). In this study, biotic factors affecting movement were tallied as fish abundances during electrofishing to quantify inter- and intra-specific interactions. Fish abundance was enumerated into 3 groups consisting of: 1) congeners (Rocky Mountain Sculpin), 2) competitors (Longnose Dace, Mountain Sucker, Lake Chub, Longnose Sucker, White Sucker, Trout-perch), and 3) predators (Burbot) in the core area (Table 2.1).

Optimal abiotic habitat for Rocky Mountain Sculpin has been shown to include cobble substrate for shelter and spawning found within riffle habitats (Bailey, 1952). Characterization of pool, riffle, run habitat type can be best determined by a velocity to depth ratio (Jowett, 1993) indicating the importance of these two abiotic factors. To integrate these critical abiotic factors into our movement models, physical habitat variables were measured throughout the 400 m study area, using the Ontario Stream Assessment Protocol (Stanfield, 2010). This protocol has been used as a standardized methodology to collect physical habitat data in a consistent and repeatable manner (Stanfield 2010). Using this protocol six sample points were measured across each established transect at calculated distances based on river width (Stanfield 2010). Abiotic factors used in this study included: depth (cm), velocity (cm s^{-1}) at 40% of the water column from the bottom, point substrate measurements (mm) and largest substrate measurements (mm)(Table 2.1) (Stanfield, 2010). Substrate variables were then classified into fines (< 2 mm), pebble (2-32 mm), gravel (32-64 mm), cobble (64-256 mm), boulder (256-1000 mm), and bedrock (> 1000 mm) using a modified Wentworth Scale (Wentworth, 1922). Abundance of each substrate type was ranked from 0-6 based on its presence or absence in the six point measurements; a substrate class present in all points of a cross-section was given a rank of 6 (Table 2.1). Mean depth and velocity were calculated from the six point measurements taken at each transect; standard deviation was calculated to represent the variability in depth and velocity across each transect (Table 2.1). Field data were summarized into July (period 1-2), August (period 3-4) and September (period 5-6) months, and movement patterns were included if two or more detection events for an individual occurred within the month. This was done to categorize monthly temporal variation for use in the models. Within each sampling period, the last known location for each individual was selected for analysis.

2.3.4 Analysis

We assessed all movements (total, *n*= 363; PIT, *n*= 309; VIE, *n* = 54) using a kernel density smoothing technique for movement events between sampling periods using the *density* function in the R package *stats* (bw= 2.068, adjust= 2, kernel= gaussian) (R Core Team, 2015). Kernel density estimation allows ecologists to make conclusions about populations based on an estimate of the probability density of a sample (Bolker, 2008). Further, to test for differences in upstream and downstream movement distances we used a two-sample t-test assuming equal variances.

To determine what factors influenced movement we used boosted regression tree (BRT) models fitted to minimize a Gaussian loss function (Elith *et al.*, 2008; Hijmans *et al.*, 2012). Distance between unique transect combinations was analyzed in response to abiotic, biotic and temporal variables at the origin and destination transects (Table 2.1). Models were assessed for the core area (Figure 2.1; 200 meters), where data on biotic factors were collected during electrofishing (total, n= 329; PIT, n= 275; VIE, n = 54).

BRT models were fitted using the *gbm.step* function in the *dismo* library in R as described by Elith *et al.* (2008). Due to a small sample size, 10-fold cross-validation was utilized to fit the models rather than splitting the dataset into training and testing data frames for prediction (Elith *et al.*, 2008). We constructed two BRT models: a) a global model with all individuals and b) a movement only model with only individuals that moved, to describe factors affecting movement when zero-movement events were included and excluded, respectively. Final parameters for the global (lr= 0.05) and movement only (lr= 0.05) models were chosen by systematically altering the learning rate to reduce predictive deviance using >1000 trees. A bag fraction of 0.5 and tree complexity of 3, were used following recommendations for small sample sizes by Elith *et al.* (2008). Finally, both models were simplified following Elith *et al.* (2008) to remove redundant variables, thereby increasing parsimony.

2.4 Results

Average recapture rate was higher for PIT tagged individuals (81.6%) than those marked with VIE tags (12.6%). Rocky Mountain Sculpin detections predominantly showed zero movement (Figure 2.2). Of the 363 detections, 244 records (67.2%) indicated no movement at a 10-meter scale. The smoothing kernel illustrated the vast majority (89.3%) of detections to be within 30 meters of the tagging transect (Figure 2.2); the remaining 10.7% of detections were between 30-240 meters with a slight increase at 60 meters (Figure 2.2). The longest movement event from one sample period to the next was 240 meters over 13 days between August 16 and August 29, 2013. There was no significant difference in upstream or downstream movement (t-test, *df= 118, p= 0.79*), so all movements were tallied together.

2.4.1 Global Model: Biotic and abiotic components influencing movement

Biotic factors including: congeners at the destination (8.7% contribution), congeners at the origin (8% contribution), and competitors at the origin (7.2% contribution), were the three most important variables (Figure 2.3a) influencing movement of Rocky Mountain Sculpin using the global model (Deviance Explained = 53.0%, Table 2.2). Movement was best explained by a high abundance of congeners (weighted mean = 16) and competitors (weighted mean = 22) at the origin and a low abundance of congeners at the destination (weighted mean= 6; Figure A2.1; Table A2.1).

The top abiotic factors included variables related to depth and velocity, contributing a total importance of 24.6% and 20.6%, respectively (Figure 2.3a). Modal peak in mean depth shifted from between 15-25 cm at the origin to 30-40 cm at the destination (Figure A2.1, Table A2.1). Standard deviation of depth at the destination showed a bi-modal shape peaking at approximately 5 cm and 20 cm (Figure A2.1). Standard deviation of velocity at the destination most strongly influenced movement at low values of variation (weighted mean= 10.6; Figure A2.1, Table A2.1). Conversely, standard deviation of velocity at origin transects had a bi-modal shape, peaking at variation less than 10 cm s^{-1} and between 20-40 cm s^{-1} (Figure A2.1).

The strongest interaction occurred when standard deviation of velocity was approximately 10 cm s^{-1} at the destination and congener abundance was greater than 25 individuals at the origin (Figure 2.4a, 2.4b). The top four interactions all included congeners or standard deviation of velocity at either the origin or destination transects (Figure 2.4b).

2.4.2 Movement Only Model: Biotic and abiotic components influencing movement

The most important biotic factors in the movement only model (Deviance Explained = 47.03%, Table 2.2) included congeners at the origin (9.6% contribution), competitors at the origin (9.1% contribution), and competitors at the destination (5.6% contribution; Figure 2.3b). Partial plots and weighted means indicated a shift from origin transects with >20 congeners or competitors to destinations with <10 individuals for either biotic group (Table A2.1) demonstrating a strong biotic effect influencing movement.

The variable importance plot (Figure 2.3b) showed cobble at the destination to have a strong modal effect (Figure A2.2) on movement (contributing 18.7%) towards a weighted mean of 6.2 (Table A2.1) signifying the importance of destinations with a high presence of cobble. Additional abiotic factors of importance included velocity and depth variables, with overall importance of 17.8% and 13.1%, respectively (Figure 2.3b). Standard deviation of velocity at the origin showed a similar bi-modal shape as the global model, with peaks at low (< 10 cm s^{-1}) and high (20 cm s^{-1}) variation (Figure A2.2). Likewise, mean velocity at the origin showed two peaks at less than 20 cm s^{-1}, and at approximately 40 cm s^{-1} (Figure A2.2). Standard deviation of depth at the origin peaked between 7-10 cm, while standard deviation of depth at the destination had a weak bimodal shape peaking at approximately 5 cm and 17 cm (Figure A2.2). Substrate variables were more important in the movement only model (40.2% contribution) than in the global model (26.9% contribution).

Three of the four most important interaction terms included the substrate variables cobble and boulder at either the origin or destination (Figure 2.5c) showing a preference for cobble and movement away from boulder. The second most important interaction occurred between the standard deviation of depth and congeners at the origin (Figure 2.5b). For this interaction, Rocky Mountain Sculpin movement was best explained when standard deviation of depth was approximately 7-10 cm and the abundance of congeners at the origin was greater than 25 individuals (Figure 2.5b).

2.5 Discussion

2.5.1 The role of biotic components influencing movement

Inter- and intra- specific competition were among the most important factors explaining Rocky Mountain Sculpin movement. Our study found movement to be clearly influenced by a shift from high to low abundances of Rocky Mountain Sculpin, providing evidence of a density-dependent response. Previous work suggests that high density of congeners can elicit intraspecific interactions between sculpins through both competitive interactions for shelter space (Petty and Grossman, 2004; Grossman *et al.*, 2006) and predatory responses from larger sculpins (Downhower and Brown, 1979; Freeman and Stouder, 1989). Similarly, interspecific competition declined from high to low abundances of small-bodied benthic fishes. Benthic species also compete for the allocation of limited resources such as shelter space (Van Kessel *et al.*, 2011) and food availability (Greenberg, 1991).

The lack of a predator effect was surprising, given the seminal works of Power *et al.* (1985), Matthews *et al.* (1994), and Gilliam and Fraser (2001) who all show predator mediated movement in small bodied fishes. Perhaps the reason for this was that we had a single predator in the system, Burbot, which occurred in relatively low abundances. However, our collection methods targeted small-bodied benthic species and therefore, the community composition and abundance may not accurately represent the fish community in non-target fishes (Mahon, 1980).

The importance of biotic interactions for Rocky Mountain Sculpin movement may make the species vulnerable to non-native species introductions and shifts in community composition. Sculpins have shown adverse responses to introduced competitor species with drastic declines in abundance (Lauer *et al.*, 2004) due, in part, to competition for shelter space (Van Kessel *et al.*, 2011) and nesting sites (Janssen and Jude, 2001). Introduction of non-native predators have also resulted in sharp declines in Cottid abundance as well as a shift in habitat use away from deeper areas towards riffle habitat too shallow for predators (White and Harvey, 2001). In these instances, abundant suitable habitat may buffer the impact of biotic changes up to a certain capacity. Our study suggests sculpins in this system, with high recorded levels of CPUE, may already be experiencing competitive pressure. During the study, food availability in Lee Creek appeared abundant (M. Veillard, personal observation) emphasizing that suitable habitat space may be the limited resource driving inter- and intra-specific competition.

2.5.2 The role of abiotic components influencing movement

The three most important abiotic variables in our study included cobble, velocity and depth. Movement in the movement only model was largely explained by high amounts of cobble at destination transects. While cobble is known to be an important substratum for Rocky

Mountain Sculpin (Bailey, 1952; COSEWIC, 2005), these substrates must also maintain a low degree of embeddedness for microhabitat use by sculpins (Haro and Brusven, 1994; Bateman and Li, 2001). Riffle habitats maintain lower siltation rates and embeddedness (Berkman and Rabeni, 1987) attributable to a high ratio of velocity to depth (Jowett, 1993). The specific relationship between these three abiotic variables maintains interstitial spaces utilized by sculpins for shelter and spawning, lending to the importance of these factors observed in our study. Under competitive pressure, the importance of cobble could be an indication of movement towards riffle margins still containing cobble but where competition may be lower due to slightly slower (Emery *et al.*, 2003) and deeper (Jowett, 1993) water, often resulting in lower benthic invertebrate abundances (Hynes, 1970).

Depth variables suggested a shift from preferred riffle transects at the origin (M. Veillard, personal observation) toward both shallower riffles and deeper waters on the periphery of riffle habitat when cross-validated with field data. Rocky Mountain Sculpin in our study appear to be utilizing a wide range of depths similar to other Cottid species experiencing congener competition (Finger, 1982; Freeman and Stouder, 1989), and interspecific benthic fish competition (Greenberg, 1991). The range of depths at the destination inhabited by Rocky Mountain Sculpin in our study (13.4-61.4 cm; Table 2.1) was slightly higher than previously reported depth ranges (5-42 cm) for the species in southern Alberta (COSEWIC, 2005), potentially due to density-induced movement towards subobtimal habitat.

Consistently, velocity parameters illustrated a density-based movement from preferred riffle habitat represented by the high variation peak (20 cm s^{-2} < sd.vel < 40 cm s^{-2}) towards slightly slower riffle margins (standard deviation of velocity ~ 10 cm s^{-2}). Rocky Mountain Sculpin utilized an assortment of habitats under competitive pressure, demonstrating the adaptive ability of the species to a range of velocities. Bailey (1952) noted Rocky Mountain Sculpin to tolerate a wide spectrum of velocities, only avoiding slow moving reaches where fine particles were deposited on the substrate. In field trials, Facey and Grossman (1992) observed Mottled Sculpin strongly preferring habitats with lower than available river velocities while simultaneously utilizing cover to reduce additional energetic costs of velocity. Similarly, Rocky Mountain Sculpin under competitive pressure in our study area, displayed analogous behaviour to the Mottled Sculpin studied by Facey and Grossman (1992). Rocky Mountain Sculpin exhibited an additional behaviour in our study where individuals occupying pool and run habitats at the origin (standard deviation of velocity < 10 cm s $^{-2}$) moved towards areas with higher variation in velocity, likely representing the margins of riffles. This behaviour may simply represent movement towards more suitable habitat, or could be comparable to findings by White and Harvey (2001) as a response to predator presence in deeper pool areas.

2.5.3 Interactions between abiotic and biotic factors

As a hierarchical tree based method, Boosted Regression Trees models successively split data into increasingly more homogenous groups, inherently assessing interaction terms without having to manually choose important interactions (Elith *et al.*, 2008). The interaction between standard deviation of velocity and congeners was the highest ranked interaction for the global model. For the movement only model, the interaction between standard deviation of depth and congeners was the second highest ranking interaction. These results provide further evidence that movement towards slightly slower velocities at riffle margins and away from depths associated with optimal riffle habitat is linked to congener abundance. In a study on the movement of Mottled Sculpin, Petty and Grossman (2004) concluded that the interaction between stream flow and abundance of conspecifics influenced juvenile movement. Similarly, we found a relationship in both our models between intraspecific competition and velocity and depth variables, which together are a function of stream flow (Hynes, 1970). Additionally, substrate variables were important for interactions in the movement only model, indicating the importance of optimizing physical substrate selection by movement towards cobble and away from boulder. The strong interactions between biotic and abiotic variables further emphasize our need to include both components in movement studies.

2.5.4 Restricted movement of Rocky Mountain Sculpin

Historical studies have been conducted on Rocky Mountain Sculpin in Montana, under the old names *Cottus bairdi punctulatus* (Bailey, 1952) and *Cottus bairdi* Girard (McCleave, 1964) showing the majority of individuals to travel less than 46 to 47 m, respectively. Our study confirms the restricted movement of Rocky Mountain Sculpin using updated tagging and tracking methods since fin clips (McCleave, 1964) and jaw tags (Bailey, 1952; McCleave, 1964). While some individuals ventured longer distances (up to 240 m between recapture events), the majority of our detections (89.3%) were within 30 meters of the original transect lending to the paradigm that fish populations may be comprised of an assortment of stationary and mobile individuals rather than a homogenous population of fish (Rodriguez, 2002). This leptokurtic dispersal pattern has been observed in many freshwater fish families, including: Cottidae, Fundulidae, Percidae, Salmonidae, Esocidae, Cyprinidae, Centrarchidae, Catastomidae and Ictaluridae, as reviewed by Radinger and Wolter (2014). While these families exhibit leptokurtic dispersal, the stationary component does not always indicate zero movement, rather the most common distance moved by individuals (Radinger and Wolter, 2014). For example, Cottidae and Fundulidae are the most dispersal-limited families with the stationary component moving up to a median of 10 m; comparatively the stationary component of Ictalurids, the most mobile family reviewed, moved up to 1000 m (Radinger and Wolter, 2014). Limited movement demonstrated by fish in our study indicates that local river reaches of suitable habitat may be heavily relied upon by the majority of the population to complete their life history.

2.5.5 Implications for conservation

Sedentary movement observed in Cottids suggests limited dispersal, which can reduce connectivity between suitable habitat patches and gene flow. Monitoring changes to freshwater systems is vital as anthropogenic alterations to the riverscape continue to increase dramatically and have led to an increased number of freshwater fish species at risk over the past 20 years (Ricciardi and Rasmussen, 1999; Dudgeon *et al.*, 2006; Jelks *et al.*, 2008). These riverscape alterations lead to increased isolation for freshwater fish populations and can potentially imperil dispersal limited species, such as freshwater sculpin, more so than those with greater dispersal abilities (Maitland *et al.*, 2016). Conservation efforts have primarily focused on abiotic factors including habitat restoration, with little emphasis on biotic interactions. Our study shows that this strategy may be limited without considering the importance of biotic factors in species conservation. The inclusion of these factors into future movement studies can help managers define important parameters of fine scale movement and focus conservation efforts accordingly.

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2.8 Tables

Table 2.1: A summary of raw field data collected from abiotic, biotic and temporal variables included in boosted regression tree movement models.

Variables		Description	Mean (Range)	
Response				
dist		Distance (m) between transects for each movement event	8.43 (0-170)	
Predictors				
Abiotic Factors			Origin	Destination
depth.o	depth.d	Average transect depth (cm)	23.9 (13.4-57.1)	24.46 (13.4-61.4)
sd.depth.o	sd.depth.d	Standard deviation of depth (cm)	9.5 (2.4-22.1)	9.46 (2.8-22.1)
vel.o	vel.d	Average transect velocity (cm/s)	31.39 (4.5-81.5)	27.94 (4.5-81.5)
sd.vel.o	sd.vel.d	Standard deviation of velocity (cm/s)	17.59 (4.8-52.2)	15.55 (4.6-41.2)
fines.o	fines.d	Presence of fine substrate (< 2 mm) at 6 points across each transect	0.56 (0-3)	0.67 (0-3)
peb.o	peb.d	Presence of pebble substrate (2- 32mm) at 6 points across each transect	1.35 (0-4)	1.40 (0-4)
gra.o	gra.d	Presence of gravel substrate (32-64 mm) at 6 points across each transect	2.11 (0-4)	1.90 (0-4)
cob.o	cob.d	Presence of cobble substrate (64-256 mm) at 6 points across each transect	4.53 (1-6)	4.60 (0-6)
bou.o	bou.d	Presence of boulder substrate (256-1000 mm) at 6 points across each transect	0.66 (0-3)	0.68 (0-3)
bed.o	bed.d	Presence of bedrock substrate (>1000 mm) at 6 points across each transect	0.65 (0-5)	0.65 (0-5)
Biotic Factors				
rmsc.o	rmsc.d	Count of congeners at each transect	14.75 (2-30)	14.35 (1-30)
comp.o	comp.d	Count of competitors at each transect	10.50 (0-58)	16.24 (0-60)
pred.o	pred.d	Count of predators at each transect	0.07 (0-1)	0.023 (0-1)
Temporal Factor				
month		Month of recapture event (factor with levels: July, August or September)	-	-

Table 2.2: A summary of boosted regression tree parameters for the final selected global and movement only models.

Parameters and Model Statistics	Global	Movement Only
Sample size (n)	329	100
Number of Trees	4950	1500
Total Deviance	567.47	1859.39
Mean Residual Dev.	0.29	18.61
Estimated Cross-validation Dev.	266.74	984.83
Cross-validation Dev. Standard Error	62.15	164.66
Deviance Explained (%)	53.00	47.03

2.9 Figures

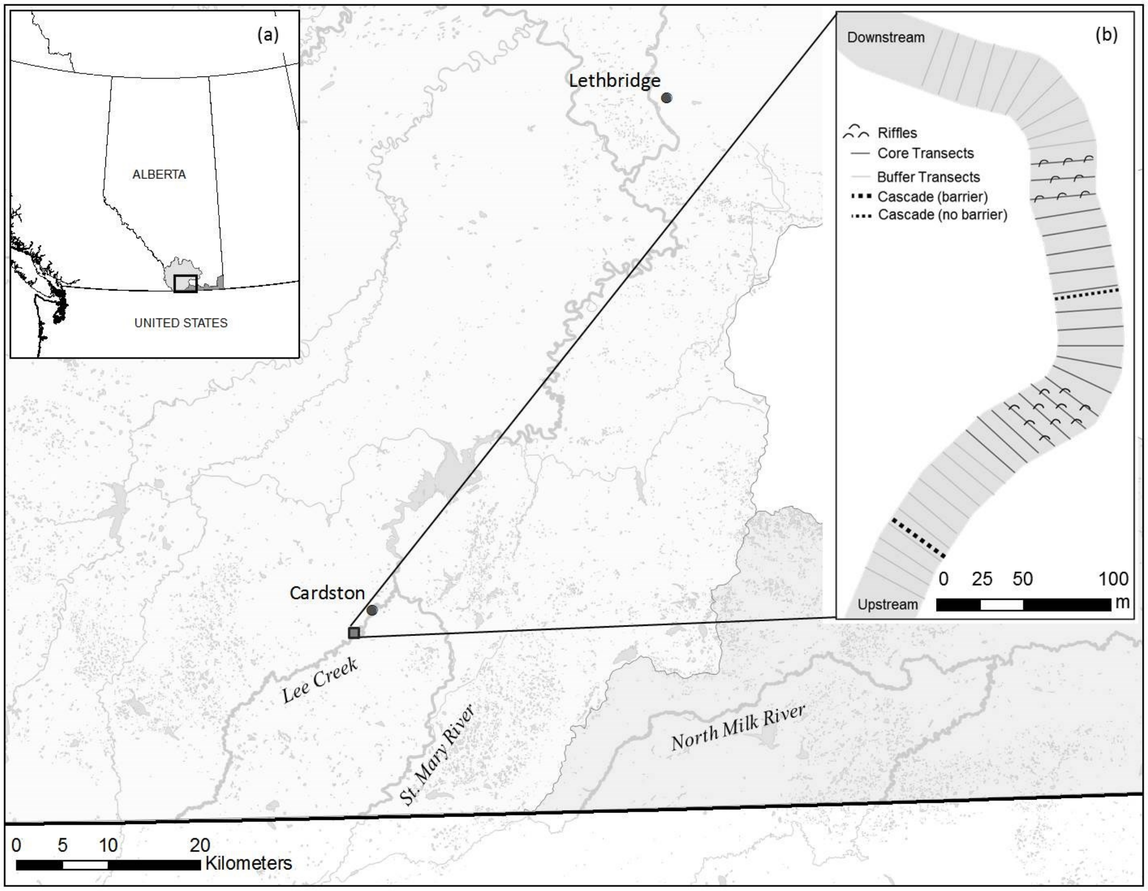


Figure 2.1: Study area in southern Alberta, 5 km southwest of the town of Cardston on Lee Creek. The study area was located near the United States border in southern Alberta (a) within the Oldman River sub watershed (light grey polygon). Fine-scale study design is illustrated in inset (b); core transects (black lines) were electrofished and PIT tagged fish were tracked throughout the entire area including buffer transects (grey lines).

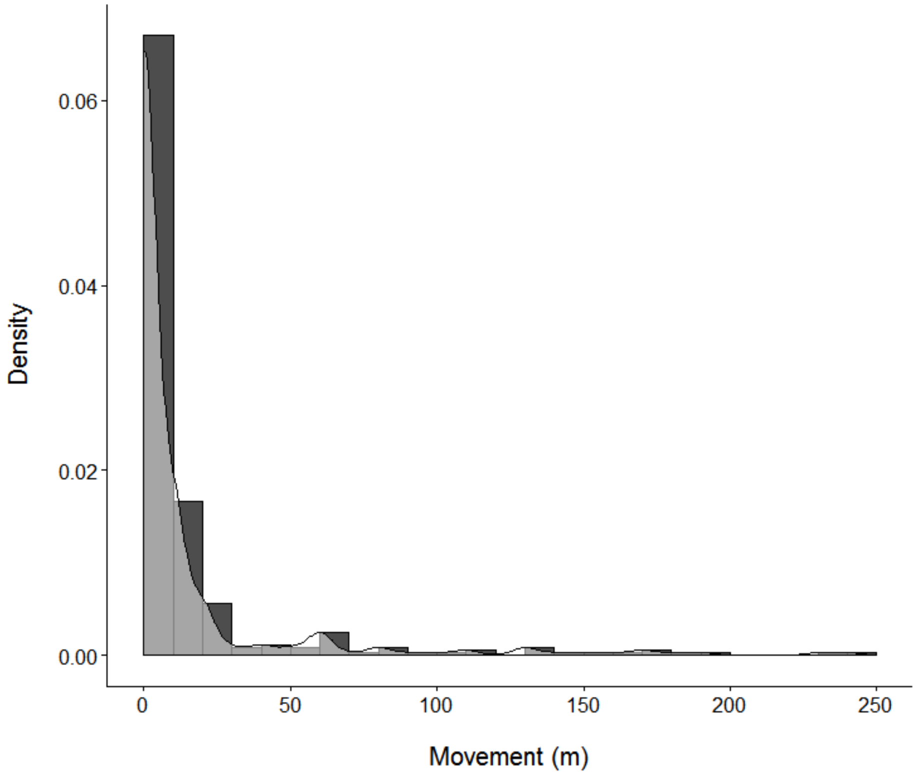


Figure 2.2: Kernel density estimation for movement of Rocky Mountain Sculpin (light grey polygon) is superimposed on top of the raw data (dark grey bars). The kernel density estimation uses a smoothing kernel (adjust=2).

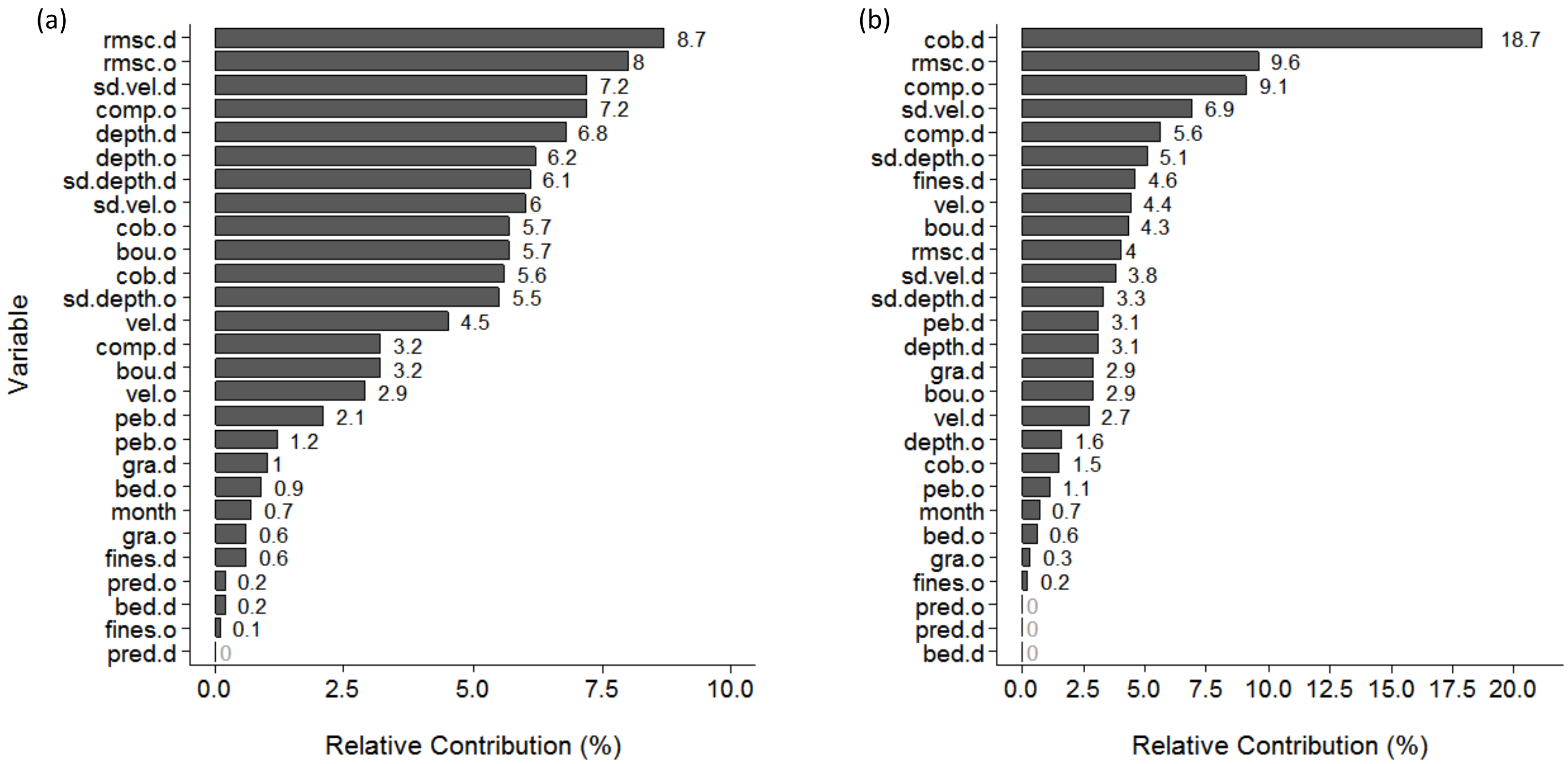
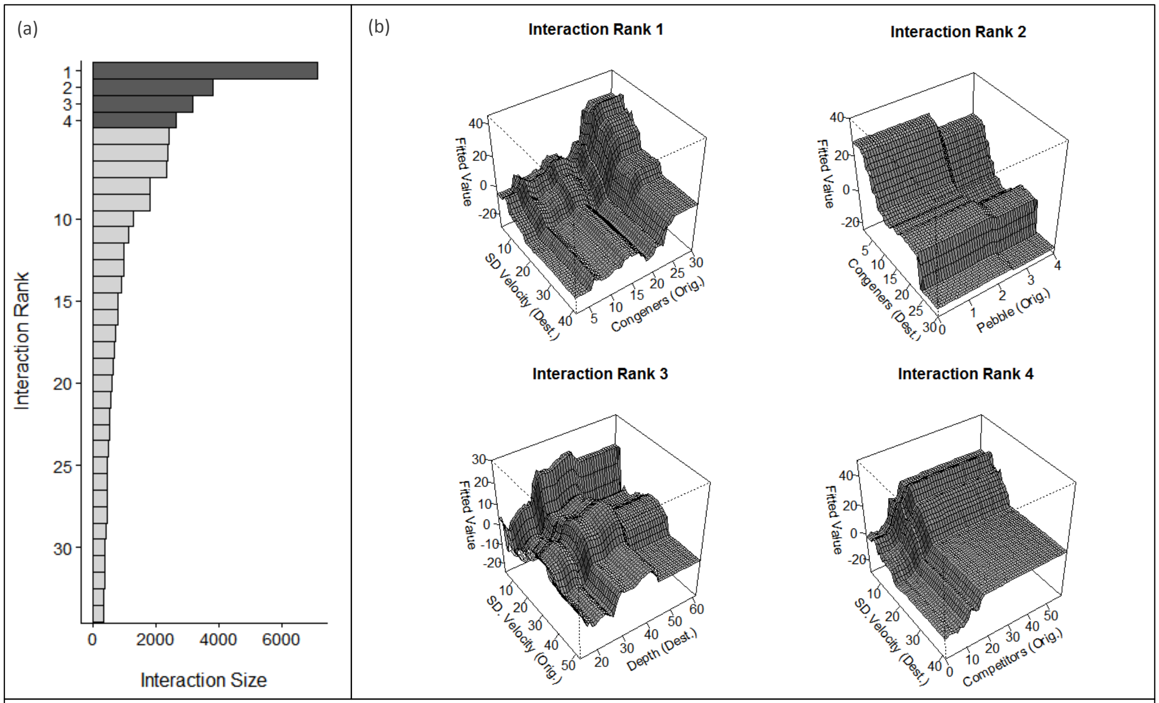


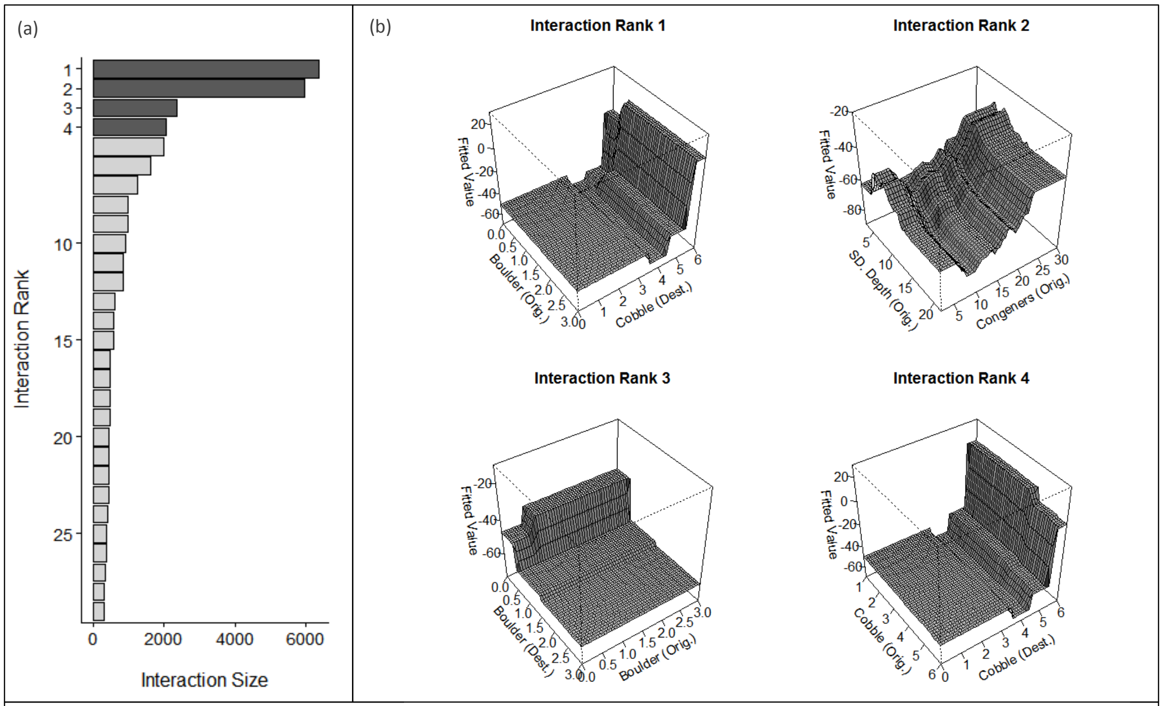
Figure 2.3: Variable importance for the (a) global and (b) movement only models. Numbers at the end of bars represent percent contribution to the model. Bar color indicates if the variable was included in the final model (dark grey) or not (light grey).



(c)

1	rmsc.o	*	sd.vel.d
2	rmsc.d	*	peb.d
3	depth.d	*	sd.vel.o
4	comp.o	*	sd.vel.d
5	cob.d	*	cob.o
6	bou.d	*	cob.o
7	sd.vel.d	*	sd.vel.o
8	sd.depth.d	*	sd.depth.o
9	comp.o	*	depth.d
10	vel.d	*	depth.d
11	cob.d	*	bou.o
12	cob.d	*	sd.depth.o
13	comp.d	*	rmsc.o
14	bou.d	*	sd.vel.o
15	vel.d	*	vel.o
16	rmsc.d	*	rmsc.o
17	rmsc.d	*	bou.o
18	rmsc.o	*	vel.d
19	rmsc.d	*	sd.depth.o
20	rmsc.d	*	depth.o
21	vel.d	*	depth.o
22	rmsc.o	*	depth.o
23	rmsc.o	*	cob.d
24	sd.depth.d	*	sd.vel.o
25	rmsc.d	*	sd.vel.o
26	rmsc.o	*	bou.d
27	cob.d	*	depth.d
28	sd.vel.d	*	cob.o
29	vel.d	*	sd.depth.o
30	depth.d	*	depth.o
31	rmsc.d	*	comp.o
32	comp.o	*	peb.d
33	peb.d	*	cob.o
34	rmsc.o	*	peb.d

Figure 2.4: Global model interaction effects calculated by holding all other variables at their means (Elith and Leathwick 2008). Figure (a) shows interaction rank; dark grey bars indicate the top 4 interaction effects illustrated in figure (b), light grey bars are the remaining interactions. Figure (c) lists the interaction associated with each rank.



(c)

1	cob.d * bou.o	7	bou.d * sd.vel.o	13	rmsc.o * cob.d	19	rmsc.d * sd.vel.o	25	comp.o * gra.d
2	rmsc.o * sd.depth.o	8	gra.d * cob.o	14	cob.d * depth.o	20	fines.d * bou.o	26	cob.d * sd.vel.o
3	bou.d * bou.o	9	fines.d * depth.d	15	cob.d * sd.vel.d	21	fines.d * sd.vel.d	27	bou.d * cob.o
4	cob.d * cob.o	10	fines.d * sd.vel.o	16	cob.d * sd.depth.o	22	fines.d * vel.o	28	comp.o * sd.vel.o
5	rmsc.o * vel.o	11	gra.d * sd.depth.o	17	comp.d * comp.o	23	rmsc.o * month	29	sd.vel.d * sd.depth.o
6	rmsc.o * sd.vel.o	12	cob.d * vel.o	18	sd.depth.d * vel.o	24	rmsc.o * fines.d		

Figure 2.5: Movement only model for all interaction effects calculated by holding all other variables at their means (Elith *et al.*, 2008). Figure (a) shows interaction rank; dark grey bars indicate the top 4 interaction effects illustrated in figure (b), light grey bars are the remaining interactions. Figure (c) lists the interaction associated with each rank.

2.10 Appendices

Appendix 2.1. Partial Dependence Plots

Section 1: Global Model

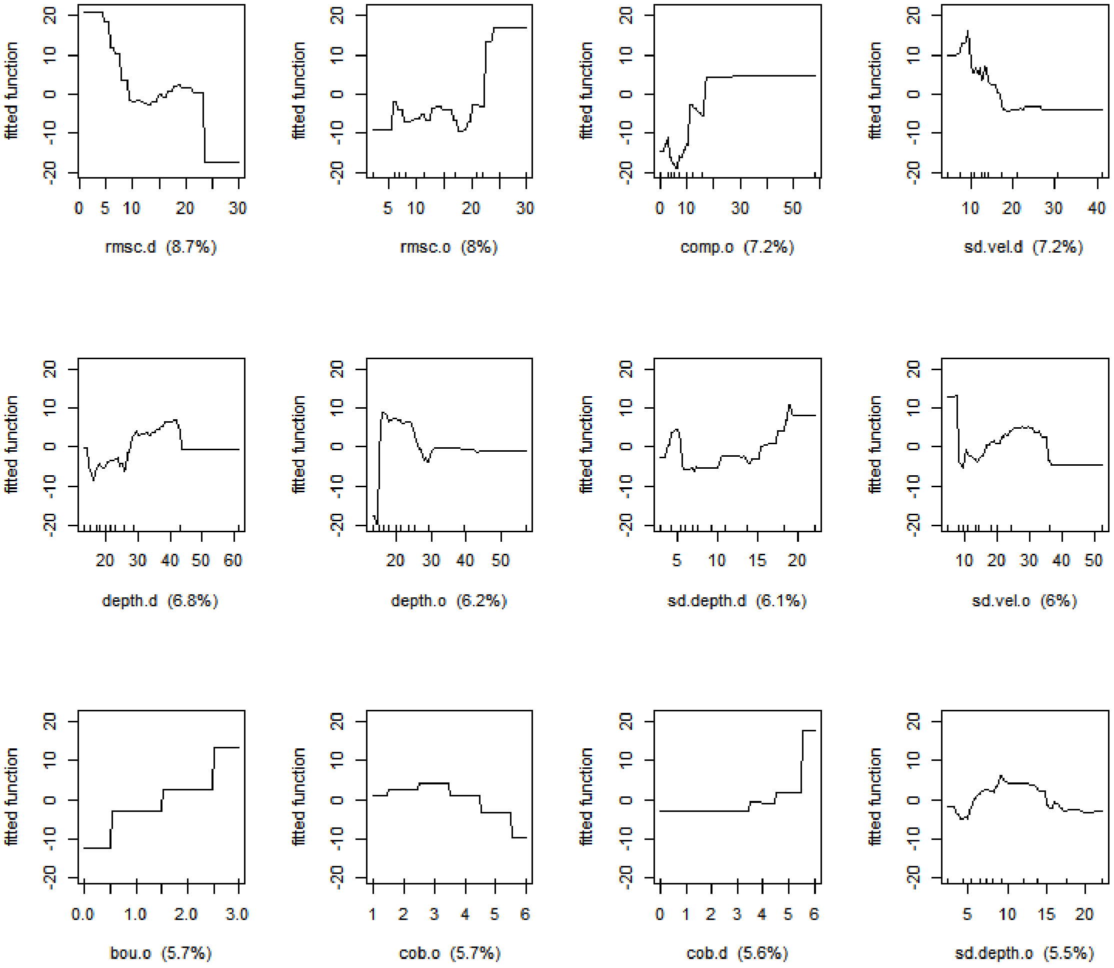


Figure A2.1: Partial dependence plots for the global model. Top 12 variables are plotted for the global model.

Section 2: Movement Only Model

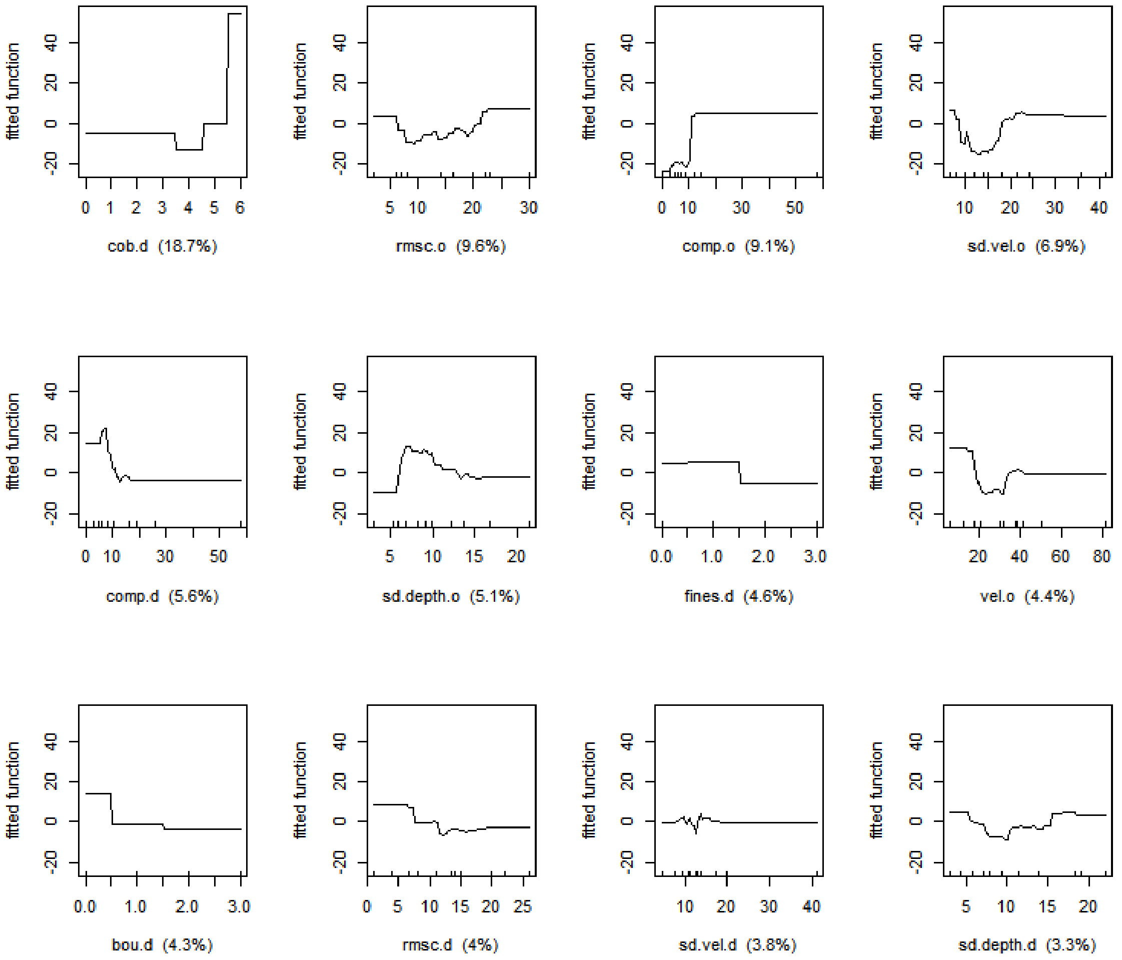


Figure A2.2: Partial dependence plots for the movement only model. Top 12 variables are plotted for the movement only model.

Appendix 2.2. Weighted Means

Table A2.1: Weighted means of each variable at the origin (orig.) and destination (dest.) produced by both models.

	Global		Movement Only	
	Orig.	Dest.	Orig.	Dest.
Abiotic Factors				
Depth (cm)	21.80	24.20	21.30	23.40
SD Depth (cm)	8.80	11.80	8.70	11.00
Velocity (cm/s)	24.10	23.20	25.20	24.40
SD Velocity (cm/s)	15.60	10.60	16.90	10.60
Fines	0.64	1.02	0.58	0.92
Pebble	2.31	2.39	2.21	2.39
Gravel	2.24	1.48	2.28	1.57
Cobble	4.10	6.10	4.10	6.20
Boulder	1.47	-0.04	1.55	-0.04
Bedrock	0.11	0.01	0.12	-
Biotic Factors				
Congeners	16	6	15	6
Competitors	22	6	21	6
Predators	0	-	-	-
Seasonality				
Month	categorical: no weighted mean			

Note: variables removed during model simplification are denoted with a dash (-)

Chapter III: Comparative swimming performance of the threatened Rocky Mountain Sculpin (*Cottus* sp.) from four hydrologically distinct rivers across the Canadian distribution

3.1 Executive Summary

Hydrologic alterations to riverscapes have contributed to an escalation of the number of freshwater fish species becoming at risk in recent years. In particular, complex nesting habitats, limited dispersal, and the need for unembedded substrate for spawning make freshwater sculpins particularly sensitive to large-scale waterway alterations, such as dams. Further, the impact of flow augmentation to hydrologic systems induces selection pressures from high flow in contrast to a reduction in flow, as seen with reservoirs. Our study used the threatened, Rocky Mountain Sculpin (*Cottus* sp.) to compare fish swimming performance over three consecutive tests from individuals that were sourced from drastically different hydrologic regimes in Alberta and British Columbia, including the flow-augmented, North Milk River. Using repeated constant acceleration tests, we found no statistical differences between rivers in the velocity at which fish, 1) slipped and transitioned into swimming (slip velocity) and 2) could no longer hold position against the flow without resting (failure velocity), which could indicate they are equally strong swimmers. However, fish from the augmented North Milk River showed higher oxygen uptake rates during the overnight resting period, suggesting there may be physiological responses to flow augmentation. Overall, failure velocities decreased from 7.45 ± 3.10 body lengths per second (BL s^{-1}) in the first test to 6.18 ± 2.56 BL s^{-1} by the third test suggesting the use of anaerobic metabolism to power swimming performance of this small-bodied species. Individual caudal morphological characteristics influenced both slip and failure velocities, and body height was negatively correlated with slip velocity. Microhabitat selection by sculpins may reduce the impact of broad-scale hydrologic regimes on swimming performance; however, physiological

and morphological plasticity of the species may shape the adaptability of this threatened fish to hydrologic alterations.

3.2 Introduction

Anthropogenic changes to riverscapes, such as habitat degradation through land-use change, flow modification, species invasions, water pollution, and over-exploitation (Dudgeon *et al.*, 2006), have drastically increased the number of freshwater fish species at risk over the past 20 years (Ricciardi and Rasmussen, 1999; Jelks *et al.*, 2008). One of these threatened species is Rocky Mountain Sculpin (*Cottus* sp.), a recently identified benthic fish with a restricted distribution in Canada (COSEWIC, 2005). Freshwater sculpins have been shown to be particularly sensitive to disturbances (Karr *et al.*, 1986; McCormick *et al.*, 1994; Mebane *et al.*, 2003) due to their sedentary nature (Chapter II; Radinger and Wolter, 2014) and requirement for cobble interstices used for spawning and shelter (Bond, 1963; Finger, 1982; Haro and Brusven, 1994). While large-scale flow modifications, such as dams, reduce cottid abundance due to higher levels of sedimentation from reduced flow (Roberts, 1988; Kelly *et al.*, 2016), the effect of flow augmentation on sculpin habitat and fitness is unclear.

Within the range of Rocky Mountain Sculpin, waterway alterations for irrigation have drastically changed habitat and flow regimes in southern Alberta with the construction of the St. Mary Canal in 1917 and the St. Mary Reservoir in 1951 (COSEWIC, 2005). Direct effects of the St. Mary Reservoir on Rocky Mountain Sculpin abundance cannot be quantified due to lack of pre-disturbance data, however, current distribution is limited to the upstream portions of the St. Mary River, indicating that the reservoir appears to be acting as barrier to downstream dispersal by creating poor habitat (COSEWIC, 2005). The St. Mary Canal, on the other hand, annually diverts 178×10^6 cubic meters of water from the St. Mary River to the North Milk River

(Bradley and Smith, 1984) during the irrigation period from May through September. This diversion drastically increases peak flow rates in the North Milk River (3 $m^3 s^{-1}$ to 16 $m^3 s^{-1}$) and maintains an artificially stable discharge throughout the irrigation period (Figure 3.1) (Water Survey of Canada, 2015).

To investigate the effect of such large-scale flow modifications on Rocky Mountain Sculpin, we compared adaptations of swimming ability in individuals from four different rivers that encompass its Canadian distribution. Rocky Mountain Sculpin are found only in the St. Mary and Milk River drainages of southern Alberta and the Flathead basin of southeastern British Columbia (COSEWIC, 2005; 2010). Five-year peak discharge average (2008-2012) differs drastically between the North Milk River (3 $m^3 s^{-1}$ and 16 $m^3 s^{-1}$ for natural and augmented, respectively), Lee Creek (31 $m^3 s^{-1}$; St. Mary River tributary), St. Mary River (80 $m^3 s^{-1}$), and the Flathead River (135 $m^3 s^{-1}$) providing a good study system to test swimming adaptations to flow (Figure 3.1) (Water Survey of Canada, 2015).

Swimming performance reflects morphological (Hynes, 1970; Beamish, 1980; Webster *et al.*, 2011), physiological (Milligan, 1996; Kieffer, 2000; Reidy *et al.*, 2000) and behavioural (Webb, 1989; Carlson and Lauder, 2010) adaptations to reduce energetic costs associated with living in moving water (Vogel, 1994). In lotic systems, pelagic and benthic fishes utilize different techniques to maintain position against a unidirectional current. Pelagic species swim to hold station (Webb *et al.*, 1996) compared to benthic fishes, such as cottids, that interact with the substrate to maintain position (Webb, 1989; Tierney *et al.*, 2011). Depending on locomotor strategy, fishes maintain the capacity for some combination of aerobic, sustained swimming and anaerobic, burst swimming, based on the composition of red and white muscle tissues, respectively (Hammer, 1995; Kieffer, 2000; Lucas *et al.*, 2001). Endurance swimmers, such as salmonids, can have up to 20% red muscle tissue, while burst swimmers, like cottids have as little as 3-5% red muscle mass (Lucas *et al.*, 2001).

Individual variation can influence exhaustive, anaerobic swimming performance in species such as Yellow Perch (*Perca flavenscens*) (Nelson, 1990) and Rainbow Trout (*Oncorhynchus mykiss*) (Kieffer *et al.*, 1994) due to exogenous (eg. water temperature, water quality) and endogenous factors (eg. body size, body condition) (Kieffer, 2000). In particular, anaerobic burst swimming has been linked to predator escape abilities (Webb, 1986; Langerhans *et al.*, 2004), often through morphological adaptations (Hoff and Wassersug, 2000; Dayton *et al.*, 2005). As bursting velocity can influence survivorship of prey species, recovery from anaerobic bursts may then indicate the ability of individuals to respond to repeated stressors.

This study aims to quantify intraspecific variation in Rocky Mountain Sculpin swimming ability and determine if predisposition to natal hydrologic regime influences swimming performance and exercise recovery of this newly identified species. Specifically, our objectives are to (1) quantify differences in swimming performance and oxygen consumption between rivers, (2) determine if previous exercise has an impact on swimming performance, and (3) assess which body characteristics (e.g. caudal length, body height) impact swimming performance for Rocky Mountain Sculpin. Addressing these objectives will provide the first description of Rocky Mountain Sculpin swimming ability and offer valuable insight into the impacts of flow augmentation on this threatened species.

3.3 Methodology

3.3.1 Fish

Rocky Mountain Sculpin were collected throughout their Canadian distribution in Lee Creek (n = 25), St. Mary River (n = 20), North Milk River (n = 25), and the Flathead River (n = 26) using a battery-powered backpack electrofishing unit (Smith-Root, Vancouver, WA, USA). Fish were then transported to the University of Alberta aquatics facility and held in low flow tanks for no less than 3 months until tested. Rocky Mountain Sculpin were fed crushed nutrafin sinking pellets and dissolved invertebrate cubes, five days a week. Water temperature was held at 8°C, using filtered, dechlorinated municipal water on a 0800:2000 light to dark schedule. Shelters were placed in tanks to reduce stress levels for Rocky Mountain Sculpin throughout their time in the aquatics facility.

3.3.2 Respirometry

Twenty-four hours prior to swim tests, experimental fish were isolated from the feeding schedule to reduce the effects of digestion on metabolic rate (Jobling, 1981; Clarke and Johnston, 1999). Up to 12 hours prior to testing, each sculpin was acclimated in one of two Brett-type respirometers (v = 10 L) with freshly flushed 8°C air saturated water, at a velocity of 5 cm s^{-1}. To reduce stress from external movements and stimuli, respirometers were placed behind black curtains and monitored by video. Respirometers were sealed and oxygen levels (mg L^{-1} s^{-1}) were measured to the nearest 0.01 mg L^{-1} overnight using a fiber optic oxygen probe (Loligo Systems, Viborg, Denmark). Fresh water was continually flushed through the outer bath to reduce warming of the inner, sealed test water. Oxygen uptake (mg L^{-1} h^{-1}) was calculated over a 4 hour period, 4-5 hours following introduction into the respirometer to reduce the impact of transportation and handling on metabolic rate (Jobling, 1981; Tierney *et al.*, 2011).

3.3.3 Swimming performance

Swimming performance was tested the following morning through a repeated measures design where each individual was observed in a series of three confined area constant acceleration tests (CATs) to quantify anaerobic burst swimming (U_{burst}) and exercise recovery potential (Reidy *et al.*, 2000). Water velocity in the respirometer started at 5 cm s^{-1} and was programmed to increase by 2.5 cm s^{-1} every 10 seconds until fish reached fatigue. Two measures of swimming performance were recorded during each test: failure velocity and slip velocity. Failure velocity was defined as the point at which Rocky Mountain Sculpin were unable to hold position in the swimming chamber without fully or partially resting on the electrified back plate. To ensure each fish reached a true failure velocity without resting, Rocky Mountain Sculpin were encouraged to move away from the back plate by applying short electrical pulses (0.25 ± 0.03 V) or, if necessary, a temporary reversal of flow direction. Slip velocity was defined as the point at which fish were no longer able to hold station against the current without swimming (Webb *et al.*, 1996). Once fish failed, velocity was returned to 5 cm s^{-1} for a 30 min resting period. Each individual was tested a total of three times (referred to as test number: CAT 1, CAT 2, and CAT 3) to investigate exercise recovery potential following fatigue. After all three tests were completed, sculpins were anaesthetized in tricaine methanesulfonate (TMS, MS-222, 0.2 g L^{-1}) and body characteristics were recorded (Table 3.1). Body characteristics were measured to the nearest 0.01g (weight) and 0.01 mm (total length, body width, body height, caudal peduncle width, caudal peduncle height and caudal length) using a digital scale and digital calipers, respectively (Table 3.1).

3.3.4 Analysis

To account for size differences between fish and number of days held in the aquatics facility, failure and slip velocities were standardized to body lengths per second (BL s^{-1}) and the effect of days held was partialled out using residuals from regression analysis (Appendix 3.1). Permutational analysis of variance (perANOVA) was used to test for differences between treatment groups. PerANOVA has the benefit of comparing groups using a calculated distribution generated from shuffling the data, that does not require normality of the dataset or independent and identical errors, and is therefore superior to standard ANOVAs for ecological data (Anderson, 2001). Post-hoc Tukey tests were used to compare differences in failure and slip velocities between rivers over three exercise tests (Figure 3.2). The same method was used to compare differences in average oxygen uptake between the four rivers (Figure 3.3). All analyses were conducted using the *aovp* function in the *lmPerm* package (Wheeler, 2010) in the R statistical program (R Core Team, 2015).

The effects of body characteristics and repeated tests on failure and slip velocities were assessed using linear mixed-effects models with manual backwards selection (Table 3.2, Table 3.3) (Zuur *et al.*, 2009) in the *gls* and *lme* functions of the *nlme* package (Pinheiro *et al.*, 2015). Mixed-effects models are useful to deal with nested data, such as repeated tests on individuals, by allowing the intercept to vary for each individual (Zuur *et al.*, 2009). Likelihood ratio tests indicated models that were constructed using fish identifying number (FishID) as a random intercept were considerably better than a general linear model estimated with restricted maximum likelihood ($L = 41.70433$, df=1, $p < 0.0001$). FishID was therefore used as a random intercept to account for non-independence of repeated measures. Fixed effects included: test number, weight, caudal length, caudal height, caudal width, body height, body width and river

(Table 3.1) and were found to not be highly correlated using Pearson's correlation coefficients in the *rcorr* function of the *Hmisc* package (Harrell and Dupont, 2015). Likelihood ratio tests were used to select the optimal fixed effects structure of nested models estimated using maximum likelihood (Zuur *et al.*, 2009).

Corrected Akaike's information criterion ($AICc_i$) for small sample sizes (Akaike, 1973; Sugiura, 1978; Bedrick and Tsai, 1994) was used to rank all models created during backwards selection. Models were further compared using Δ_i ($AICc_i - AICc_{min}$) and w_i (akaike weights) to explain the strength of evidence for each model. Models with a $\Delta_i < 2$ were considered similarly fitting models (Burnham and Anderson, 2004) and investigated further (Table 3.4). To control for family-wise error due to multiple comparisons, p-values for fixed effects were adjusted using the Holm-Bonferroni method (Rice, 1989).

3.4 Results

3.4.1 Differences between rivers: Respirometry and swimming performance

Sculpins from the North Milk River had higher rates of oxygen consumption, averaging 0.13 mg L^{-1} h^{-1}, compared to St. Mary River (0.09 mg L^{-1} h^{-1}; df =3, $p = 0.02$), Flathead River (0.09 mg L^{-1} h^{-1}; df =3, $p = 0.002$), and Lee Creek (0.08 mg L^{-1} h^{-1}; df =3, $p = 0.001$) which were not statistically different from each other (df =3, $0.91 < p < 0.99$; Figure 3.3). Fish were standardized for body length and days held in the aquatics facility, and neither failure (df = 3, $0.63 < p < 1.00$) nor slip velocities (df = 3, $0.37 < p < 1.00$) were different between rivers (Figure 3.2). Akaike weights (w_i) for linear mixed-effects models containing the variable *River* were negligible for both failure ($w_i = 0.05$; Table 3.2) and slip velocities ($w_i = 0.01$; Table 3.3). These results indicate that while intraspecific variability in swimming performance was not explained by natal river hydrology, there may be a physiological difference in resting respiration of fish based on their river of origin.

3.4.2 Swimming ability with repeated exercise

Overall, Rocky Mountain Sculpin swam to an average of 6.80 ± 2.90 BL s^{-1} over a duration of 3.21± 1.46 minutes (Table 3.1). Differences in failure velocity between repeated swim tests were observed from CAT 1 (7.45 ± 3.10 BL s^{-1}) to CAT 3 (6.18 ± 2.90 BL s^{-1}; df = 2, $p = 0.008$; Table 3.1; Figure 3.2), but slip velocity showed no differences over repeated tests (df = 2, $0.59 < p < 0.91$; Figure 3.2). Previous exercise was included in the three most supported linear mixed-effects models for failure velocity indicating substantial support that previous exercise is an important variable (Table 3.2). The top three models showed highly significant differences between CAT 1 and CAT 3 ($p < 0.001$) but no differences between CAT 1 and CAT 2 ($p > 0.10$), with negative coefficients showing fish failed at lower velocities in subsequent exercise tests (Table 3.4). There was not enough evidence to suggest that previous exercise influenced slip velocity ($\Delta_i = 3.08$; Table 3.3).

3.4.3 Body characteristics influencing swimming performance

Caudal width was an important variable influencing failure velocity, included in the top three selected models (Table 3.2). Caudal width had a positive relationship with failure velocity signifying fish with wider caudal measurements swam to higher velocities before failing (Table 3.4). Model 1 ($p = 0.16$), Model 2 ($p = 0.07$), and Model 3 ($p = 0.18$) showed caudal width was not significant (Table 3.4). Caudal width was additionally important for explaining slip velocity and was included in both selected models (Table 3.3). Similar to failure velocity models, caudal width had a positive relationship with slip velocity but was not statistically significant in either Model 1 ($p = 0.07$) and Model 2 ($p = 0.08$) (Table 3.4).

Caudal length and caudal height were important for failure and slip velocities, respectively (Table 3.2; Table 3.3) demonstrating the prominence of caudal morphology in swimming performance. Caudal length had a weak positive relationship with failure velocity but was not statistically significant ($p = 0.6$; Table 3.4). Alternatively, caudal height was negatively correlated with slip velocity, but was also not statistically significant ($p = 0.40$; Table 3.4).

Body height was included in both selected slip velocity models (Table 3.2) with negative parameter estimates (Table 3.4). Body height was significant in Model 1 ($p = 0.03$) but not Model 2 ($p = 0.22$) (Table 3.4). Finally, weight was included in the top two failure models (Table 3.2), but was not significant in either Model 1 ($p = 0.09$) or Model 2 ($p = 0.14$; Table 3.4). Parameter estimates indicated a negative relationship between weight and failure velocity in both models (Table 3.4).

3.5 Discussion

3.5.1 Respiratory differences between rivers

Our study indicated oxygen uptake in the augmented, North Milk River was higher (0.13 mg L^{-1} h^{-1}) than in all three other rivers (0.08 – 0.09 mg L^{-1} h^{-1}), suggesting Rocky Mountain Sculpin respiration was, perhaps, influenced by exposure to flow augmentation. Large-scale augmentation in the North Milk River has altered stream channel morphology creating wider channels (Bradley and Smith, 1984) that can lead to insufficient flow when the water ceases at the end of the irrigation period in September (COSEWIC, 2005). This modification, in conjunction with intermittent drought (COSEWIC, 2005), may expose fish from the North Milk River to higher rates of seasonal hypoxia than other rivers. We explain potential tolerance to this flow modification in two ways. First, morphological adaptations to seasonal hypoxia may be responsible for increased respiration efficiency. For example, gill reconstruction is a morphological adaptation that increases respiratory surface area (Sollid *et al.*, 2003; Henriksson *et al.*, 2008) when fish are exposed to hypoxic conditions during the postembryonic development period (Parichy *et al.*, 2009; Harrison *et al.*, 2015). If fish from the North Milk River have adapted to lower oxygen levels, oxygen uptake in normoxic lab conditions may be higher due to increased respiratory efficiency.

Alternatively, lack of adaptation to hypoxic conditions can result in behavioural responses to moderate hypoxia including increased opercular rates and lowered activity levels (Gee *et al.*, 1978). If such is the case, when transferred to lab conditions, a release of hypoxic pressures may result in increased activity levels and subsequent differences in respiration. Throughout the duration of this study, fish from the North Milk River appeared to move outside of shelters more frequently and were more active in holding tanks (personal observation, Veillard, M.). Future morphological, physiological and behavioural studies are required to determine the mechanisms responsible for increased respiration in sculpins from the North Milk River.

3.5.2 Swimming performance difference between rivers

While we found differences in oxygen uptake, swimming performance, as measured by failure and slip velocity, was not significantly different between Rocky Mountain Sculpin from the four rivers despite large differences in discharge. Adaptation to natal hydrologic regimes may be diminished by strong microhabitat selection within these systems. For example, Rocky Mountain Sculpin utilize interstitial spaces created by physical substrate near the stream bed to complete their life history (Bailey, 1952; Finger, 1982; Haro and Brusven, 1994). These microhabitats are found where velocity nears zero, called the boundary layer, as described by the Prandtl-vonKarman velocity equation (Chow, 1959; Hynes, 1970; Gordon *et al.*, 1992; Jowett, 2003). By carrying out their life history in the benthic region of the stream channel, Rocky Mountain Sculpin can evade strong currents by selecting cobble substrate (Bailey, 1952; Finger, 1982) that provides refugias from flow in interstitial spaces (Davis and Barmuta, 1989; Facey and Grossman, 1992). Further, in a study on the energetic costs associated with microhabitat use in relation to velocity, Facey and Grossman (1992) found Mottled Sculpin (*Cottus bairdi*) selected microhabitat with velocities less than 1 BL s^{-1} despite their ability to hold station up to 5.8 BL s^{-1} with little change in respiration (Facey and Grossman, 1990). As a result, microhabitat use of physical stream channel characteristics may shelter Rocky Mountain Sculpins from experiencing the full impact of broad-scale hydrologic regimes, thereby reducing the selection pressure for swimming adaptations.

3.5.3 Swimming ability with repeated exercise

Although interstitial spaces in the stream bed may lessen the impact of flow on Rocky Mountain Sculpin, cottids are known to emerge from cover at night to forage (Greenberg, 1991). When first exposed to flow, our study indicated that Rocky Mountain Sculpin failed at an average velocity of 7.45 BL s^{-1} across all rivers. While no other studies have assessed the swimming performance of Rocky Mountain Sculpin, our findings fall within the range of closely related cottids, such as Slimy Sculpin (*Cottus cognatus*) and Mottled Sculpin that have been found to swim up to velocities of 9.4 BL s^{-1} (Webb, 1978) and 5.8 BL s^{-1} (Facey and Grossman, 1990), respectively.

Additionally, our study indicated that failure velocity in subsequent trials decreased significantly after a thirty minute rest period between tests. Throughout the test duration (average = 3.21 ± 1.46 minutes), Rocky Mountain Sculpin predominantly held station up until the slip velocity, then transitioned into bursting-holding or bursting-coasting techniques until failure, as was noted in the round goby (Tierney *et al.*, 2011). The significant decrease in failure velocity suggests the use of anaerobic metabolism that requires up to twelve hours to recover from exhaustive exercise (Kieffer, 2000) as opposed to aerobic metabolism that can sustain swimming for prolonged periods without the depletion of energy reserves or accumulation of waste products (Hammer, 1995). As bursting ability has been associated with predator evasion (Webb, 1986; Langerhans *et al.*, 2004), reduced failure velocity of Rocky Mountain Sculpin in subsequent tests suggests a hampered ability to repeatedly escape predators and other stressors. Alternatively, slip velocity was not influenced by previous exercise, indicating aerobic respiration may be incorporated into station-holding behaviours associated with foraging.

3.5.4 Body characteristics influencing swimming performance

Morphological characteristics helped explain intraspecific differences in swimming performance at an individual level. While previous studies have linked increases in body size to aerobic swimming performance (Beamish, 1980; Hammer, 1995), burst anaerobic swimming has been shown to be propelled by caudal morphology in Gasterosteids (Webster *et al.*, 2011), Embiotocids (Drucker, 1996), and Anuran tadpoles (Dayton *et al.*, 2005). Consistently, our study demonstrated the importance of caudal characteristics on anaerobic burst swimming performance of Rocky Mountain Sculpin. Fish with wider and longer caudal peduncles were able to hold station against faster velocities resulting in both higher slip and failure velocities for these individuals. Katz *et al.* (1999) showed that increased tail-beat frequency and muscle strain in Milkfish (*Chanos chanos*) were associated with higher swimming velocities during burst swimming. Not only has the caudal region been implicated in burst swimming ability, Carlson and Lauder (2010) found that caudal morphology and position were important for station-holding postures in two species of darter (*Etheostomatinae*). Gait transitions leading into anaerobic burst swimming are often associated with the addition of caudal propulsion (Drucker, 1996; Svendsen *et al.*, 2010; Webster *et al.*, 2011) as the axial skeleton contains more muscle tissue than paired fins (Webb, 1998). In benthic fish, such as sculpins, anaerobic swimming is often preceded by station-holding, rather than steady aerobic swimming (Tierney *et al.*, 2011) indicating a gait transition directly from holding to swimming. For these fish, morphological characteristics associated with anaerobic swimming are, therefore, central to the overall scope of swimming potential. While failure and slip velocities were both associated with caudal morphology, slip velocities additionally suggested that holding behaviour was associated with concepts of hydrodynamic drag (Webb, 1989; Webb *et al.*, 1996).

Slip velocity was negatively influenced by both caudal and body height indicating a selection for dorso-ventrally compressed features (Hynes, 1970; Webb, 1990). To avoid dislodgement from flow, morphological and behavioural characteristics of benthic fishes have been shown to counteract hydrodynamic forces of drag and lift (Webb *et al.*, 1996; Carlson and Lauder, 2010). Studies have indicated that morphological selection pressures from flowing water can reduce body depth of organisms living in the benthos of lotic habitats compared to congeners in lentic systems, thereby reducing drag (Webster *et al.*, 2011; Foster *et al.*, 2015). Additional behaviours, such as the adjustment of angle and position of the pectoral fins, have been shown to create negative lift in benthic species to hold-station against stronger currents (Webb, 1989; Webb *et al.*, 1996; Carlson and Lauder, 2010). Our study indicates the importance of morphological characteristics on station-holding ability of Rocky Mountain Sculpin, while further studies are required to measure body postures related to lift forces.

3.6 Conclusion

This study is the first to describe the swimming ability of Rocky Mountain Sculpin, a newly identified and threatened fish species in Canada. Individual morphological results indicated a selection of characteristics central to burst swimming and benthic life; however, when grouped by broad-scale hydrologic regimes, there was no difference in swimming ability of this species. While it was surprising that flow augmentation may not contribute to differences in swimming performance, resting metabolism may be impacted by seasonal hypoxic conditions in the North Milk River when flows return to natural. Respiration was highest in fish from the augmented North Milk River indicating further study on morphological, physiological and behavioural mechanisms are required to determine the bioenergetic cost of flow augmentation on Rocky Mountain Sculpin.

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3.8 Tables

Table 3.1: Overall body characteristics and raw test results (mean ± 1 st.dev) for Rocky Mountain Sculpin from four rivers.

	Flathead	Lee Creek	North Milk	St. Mary	All Fish
	n = 26	*n* = 25	*n* = 25	*n* = 20	*n* = 96
Body Characteristics					
Weight (g)	6.9 ± 3.8	2.5 ± 0.7	4.2 ± 1.5	3.1 ± 1.6	**4.2 ± 1.9**
Total Length (mm)	85.2 ± 12.6	62.4 ± 4.1	68.5 ± 7.7	64.4 ± 7.8	**70.1 ± 10.4**
Caudal Length (mm)	10.4 ± 2.3	7.8 ± 1	8.7 ± 1.5	7.8 ± 1.8	**8.7 ± 1.2**
Caudal Height (mm)	4.9 ± 0.9	3.8 ± 0.4	4 ± 0.6	4.1 ± 1.1	**4.2 ± 0.5**
Caudal Width (mm)	2.3 ± 0.4	1.8 ± 0.6	2.1 ± 0.5	1.9 ± 0.6	**2.0 ± 0.2**
Body Height (mm)	10.6 ± 2.4	8 ± 1.3	11.2 ± 1.7	9.2 ± 2.4	**9.8 ± 1.4**
Body Width (mm)	10.8 ± 2.6	8.5 ± 1.4	10.9 ± 1.6	9.4 ± 1.9	**9.9 ± 1.2**
Failure Velocity (BL s^{-1})					
CAT 1	8.25 ± 2.42	7.12 ± 3.04	6.73 ± 2.94	7.70 ± 4.00	**7.45 ± 3.10**
CAT 2	7.86 ± 2.63	6.69 ± 3.03	6.09 ± 2.18	6.35 ± 3.61	**6.78 ± 2.90**
CAT 3	7.01 ± 2.22	6.07 ± 2.91	5.51 ± 2.24	6.09 ± 2.74	**6.18 ± 2.56**
All Tests	**7.71 ± 2.46**	**6.63 ± 2.99**	**6.11 ± 2.49**	**6.71 ± 3.50**	**6.80 ± 2.90**
Slip Velocity (BL s^{-1})					
CAT 1	2.48 ± 0.73	4.08 ± 2.20	2.90 ± 1.52	4.11 ± 3.30	**3.21 ± 1.98**
CAT 2	2.71 ± 1.75	3.53 ± 2.09	3.76 ± 2.51	3.33 ± 1.82	**3.24 ± 2.03**
CAT 3	3.15 ± 2.14	3.78 ± 2.92	4.37 ± 2.22	3.37 ± 2.40	**3.61 ± 2.41**
All Tests	**2.76 ± 1.66**	**3.79 ± 2.39**	**3.68 ± 2.16**	**3.59 ± 2.50**	**3.35 ± 2.15**
Test Duration (min)	4.31 ± 1.32	2.75 ± 1.25	2.79 ± 1.16	2.88 ± 1.46	**3.21 ± 1.46**

Table 3.2: Linear mixed-effects model selection for failure velocity using the Akaike information criterion corrected for small sample size ($AICc_i$). Models with a difference (Δ_i) in $AICc_i < 2$ compared to the top model were considered to have substantial evidence and included in further analysis (shown in bold). Akaike weights (w_i) further explain the strength of evidence for each model. Models were assessed for failure velocity using Fish ID as the random intercept and failure velocity (BL s^{-1}) as the dependent variable.

Failure Models	Fixed Effects	Random Effect	Number of parameters (K)	$AICc_i$	Δ_i	w_i
1	**test number, caudal width, weight, caudal length**	**1| FishID**	**5**	**1374.81**	**0.00**	**0.43**
2	**test number, caudal width, weight**	**1| FishID**	**4**	**1375.44**	**0.63**	**0.32**
3	**test number, caudal width**	**1| FishID**	**3**	**1376.71**	**1.90**	**0.17**
4	test number	1| FishID	2	1377.58	2.77	0.11
5	test number, caudal width, weight, caudal length, river	1| FishID	6	1379.20	4.39	0.05
6	test number, caudal width, weight, caudal length, river, body height	1| FishID	7	1380.90	6.09	0.02
7	test number, caudal width, weight, caudal length, river, body height, caudal height	1| FishID	8	1382.62	7.81	0.01
8	test number, caudal width, weight, caudal length, river, body height, caudal height, body width	1| FishID	9	1384.65	9.84	0.00
9	test number, caudal width, weight, caudal length, river, body height, caudal height, body width	-	8	1419.18	44.37	0.00

Table 3.3: Linear mixed-effects model selection for slip velocity using the Akaike information criterion corrected for small sample size ($AICc_i$). Models with a difference (Δ_i) in $AICc_i < 2$ compared to the top model were considered to have substantial evidence and included in further analysis (shown in bold). Akaike weights (w_i) further explain the strength of evidence for each model. Models were assessed for slip velocity using Fish ID as the random intercept and slip velocity (BL s^{-1}) as the dependent variable.

Slip Models	Fixed Effects	Random Effect	Number of parameters (K)	$AICc_i$	Δ_i	w_i
1	**body height, caudal width**	**1| FishID**	**3**	**875.39**	**0.00**	**0.51**
2	**body height, caudal width, caudal height**	**1| FishID**	**4**	**876.25**	**0.87**	**0.33**
3	body height, caudal width, caudal height, test number	1| FishID	5	878.47	3.08	0.11
4	body height, caudal width, caudal height, test number, body width	1| FishID	6	880.04	4.66	0.05
5	body height, caudal width, caudal height, test number, body width, river	1| FishID	7	884.36	8.97	0.01
6	body height, caudal width, caudal height, test number, body width, river, weight	1| FishID	8	885.87	10.48	0.00
7	body height, caudal width, caudal height, test number, body width, river, weight, caudal length	1| FishID	9	888.08	12.70	0.00
8	body height, caudal width, caudal height, test number, body width, river, weight, caudal length	-	8	893.08	17.70	0.00

Table 3.4: Parameter estimates from final linear mixed-effects models explaining failure and slip velocities using body characteristics and repeated exercise tests. Bolded text indicates variable significance at α=0.05 after Holm adjustments.

Response		Fixed Effect	Coefficient	SE	*t* value	*P*
Failure Velocity (BL s^{-1})						
	Model 1	Intercept	-2.32	1.19	-1.95	0.16
		Weight	-0.25	0.10	-2.40	0.09
		Caudal Length	0.24	0.14	1.63	0.16
		Caudal Width	0.96	0.49	1.95	0.16
		CAT 2	-0.66	0.31	-2.14	0.13
		CAT 3	-1.26	0.31	-4.06	**<0.001**
	Model 2	Intercept	-1.02	0.89	-1.15	0.25
		Weight	-0.17	0.09	-1.82	0.14
		Caudal Width	1.16	0.48	2.43	0.07
		CAT 2	-0.66	0.31	-2.14	0.10
		CAT 3	-1.26	0.31	-4.06	**<0.001**
	Model 3	Intercept	-0.81	0.89	-0.90	0.37
		Caudal Width	0.71	0.41	1.71	0.18
		CAT 2	-0.66	0.31	-2.14	0.10
		CAT 3	-1.26	0.31	-4.06	**<0.001**
Slip Velocity (BL s^{-1})						
	Model 1	Intercept	0.81	0.81	1.00	0.32
		Caudal Width	0.83	0.39	2.14	0.07
		Body Height	-0.26	0.10	-2.61	**0.03**
	Model 2	Intercept	1.10	0.85	1.29	0.40
		Caudal Height	-0.28	0.26	-1.09	0.40
		Caudal Width	1.00	0.42	2.40	0.08
		Body Height	-0.20	0.11	-1.81	0.22

3.9 Figures

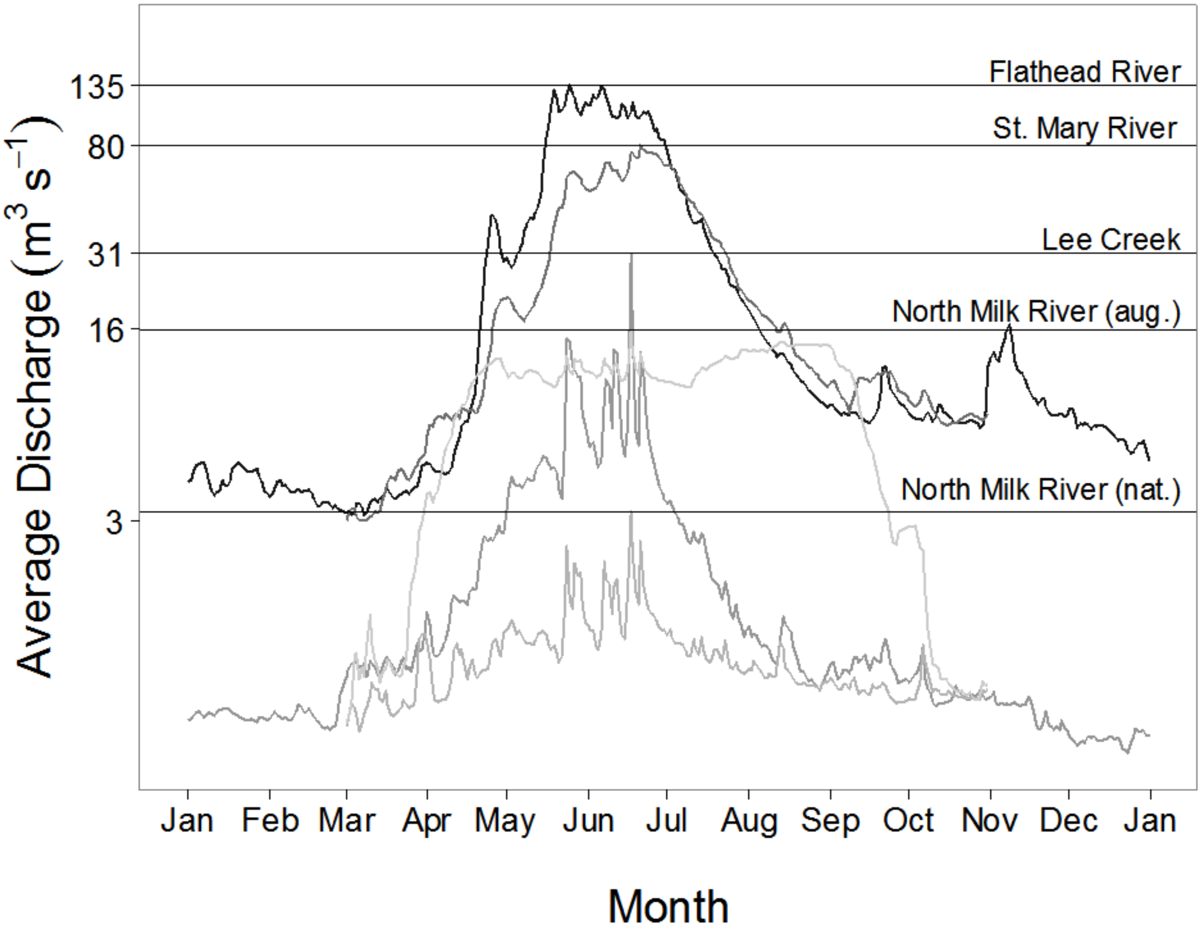

Figure 3.1: Average discharge (m^3 s^{-1}) from 2008-2012 across the Canadian distribution of Rocky Mountain Sculpin taken from five hydrologic stations (Water Survey of Canada, 2015) plotted on a log10 scale. Peak discharge at each station is denoted by horizontal lines. Two stations on the North Milk River were used to illustrate the magnitude of augmentation upstream (nat = natural) and downstream (aug = augmented) of the St. Mary Canal.

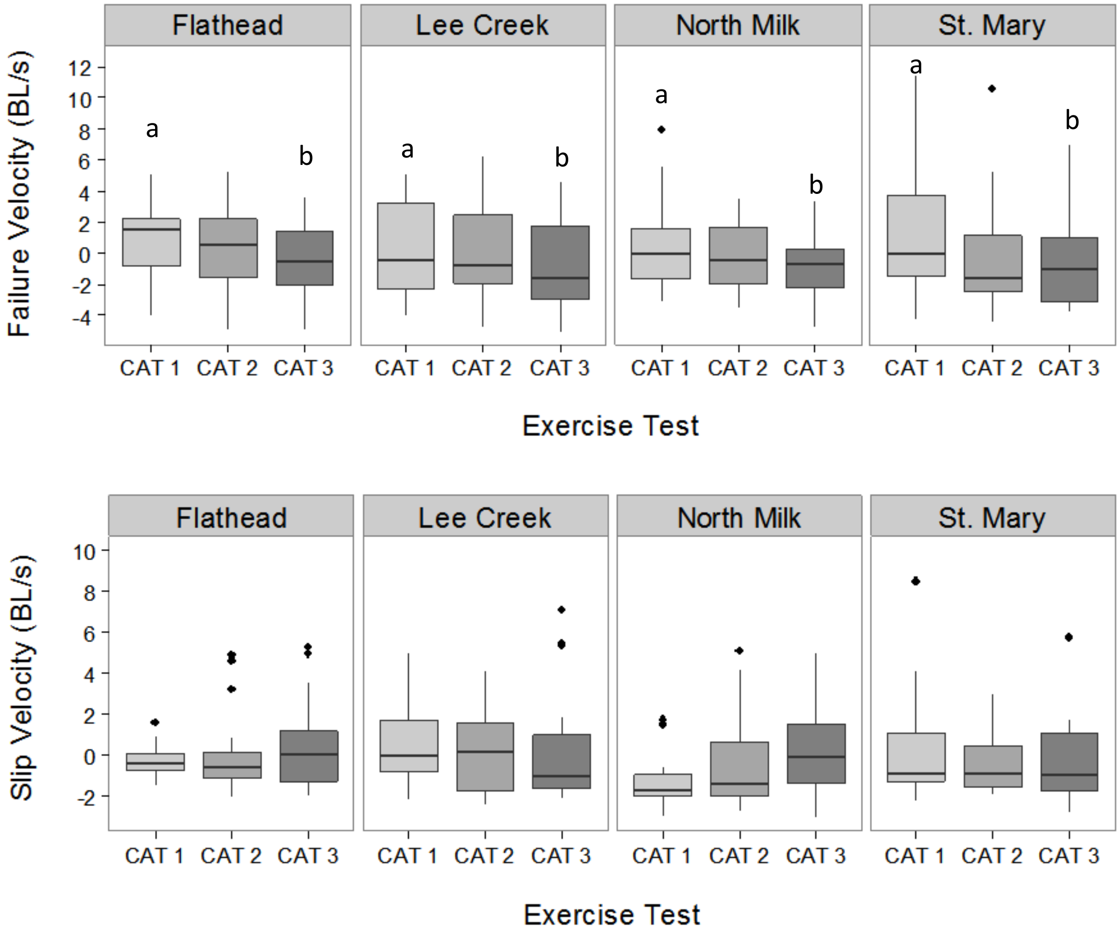

Figure 3.2: Failure and slip velocities in each stream over three exercise tests (constant acceleration test 1, 2 and 3). Significant differences ($p < 0.05$) between exercise tests are denoted with ‘a’ and ‘b’.

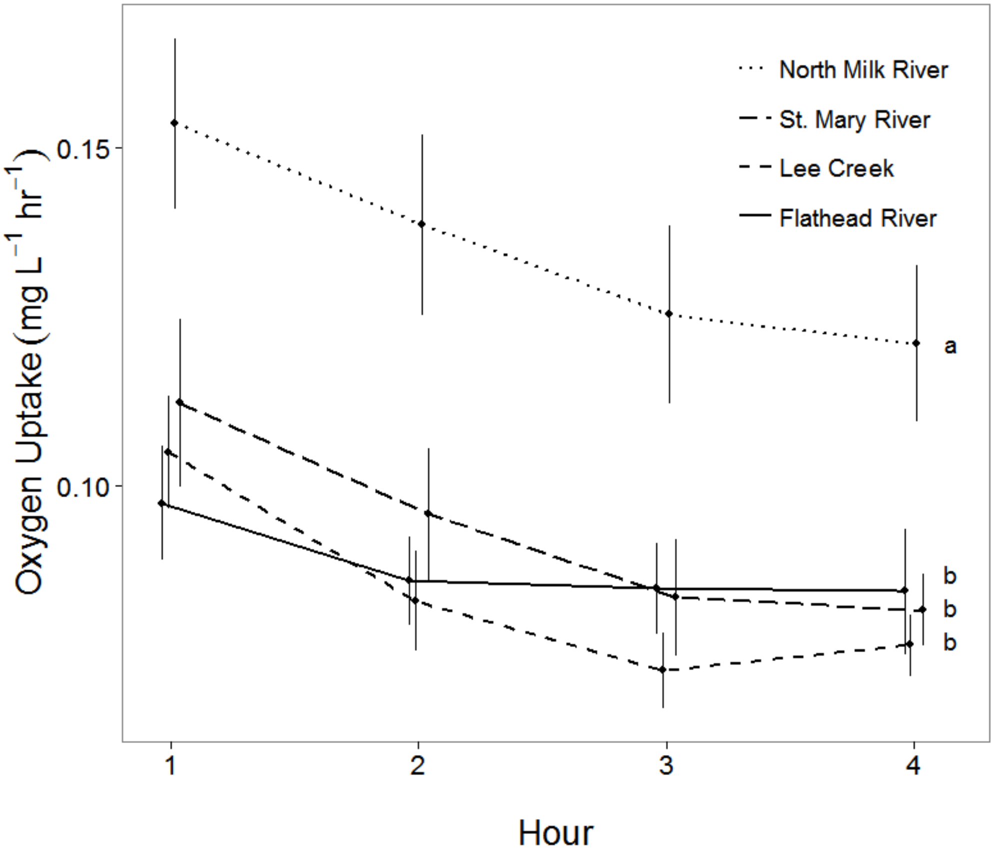

Figure 3.3: Oxygen uptake ± 1 s.e. (mg L^{-1} h^{-1}) of resting, unfed fish from Flathead (n=16), St. Mary (n=9), Lee Creek (n=13), and North Milk (n=13) populations over a 4 hour period, 4-5 hours following introduction into the respirometer. Statistically significant differences in oxygen uptake (perANOVA, α=0.05) between rivers are indicated by letters.

3.10 Appendix

Appendix 3.1: Effect of days held in aquatics facility

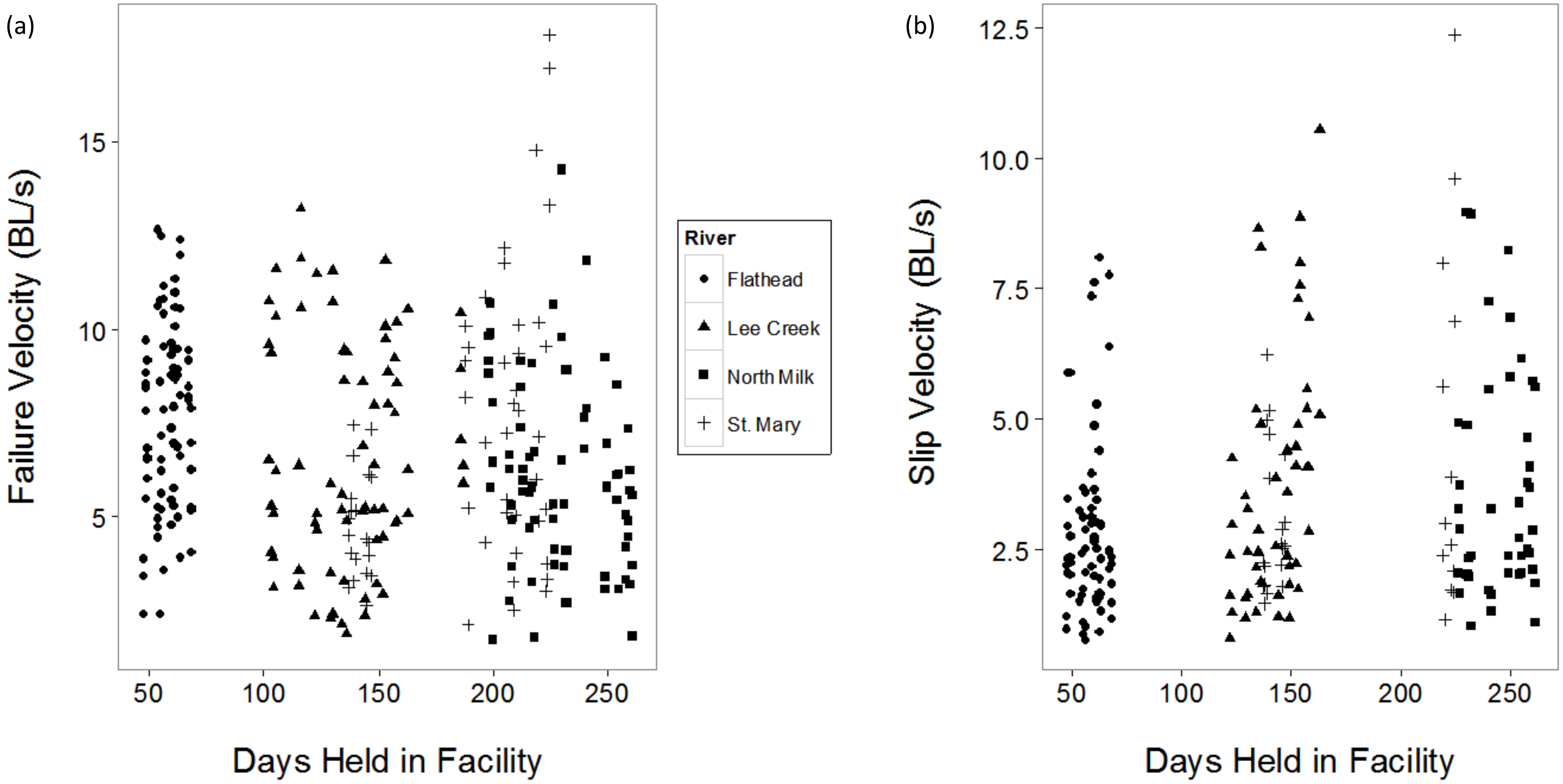

Figure A3.1: Scatterplots showing the effect of number of days held in the aquatics facility on (a) failure velocity and (b) slip velocity.

Chapter IV: General Conclusions

Limited freshwater resources worldwide generates a need for waterway alterations. Global freshwater biodiversity loss emphasizes the need understand how manmade hydrologic alterations impact aquatic organisms. While freshwater organisms respond differently to waterway alteration, conservation management often targets susceptible taxa, such as species at risk. Species dispersal can help to inform decisions pertaining to management scale and the likelihood of response to conservation actions. For poorly understood species like the recently-identified Rocky Mountain Sculpin, filling these biological knowledge gaps can inform recovery and management choices. In this thesis we explored two avenues of sculpin movement through both a field movement study and laboratory swimming performance experiment. These studies suggest two potential stressors for the species: 1) high susceptibility to local abiotic and biotic factors due to restricted movement and 2) potential physiological costs of hypoxic conditions in the North Milk River.

From our field mark-recapture study, we found that sculpins exhibited restricted movement, with the majority of detections less than 30 meters from the marking transect. Some individuals, however, had the capacity to move up to 240 meters. While a 240 meter movement may be substantial for a small-bodied fish, all movement observations encountered in our study would benefit from fine-scale local management. Defining the scale of local management, however, may hinge upon genetic population structure throughout the Canadian distribution of Rocky Mountain Sculpin.

At a fine-scale, these restricted movements were influenced by a variety of biotic and abiotic factors. Most notably, Rocky Mountain Sculpin moved from high to low abundances of both congeners and competitors indicating density-dependent movement. Rocky Mountain

Sculpin may be susceptible to an increased abundance of native and non-native competitors. Currently, concern for introduced species is relatively low throughout the Canadian distribution of Rocky Mountain Sculpin (Fisheries and Oceans Canada, 2012) . The interaction between these biotic variables and abiotic habitat characteristics suggests managers should be cognizant of changes to both the abiotic and biotic conditions facing Rocky Mountain Sculpin. For example, restoration activities to reduce future and current sedimentation in these streams may ultimately relieve competitive pressures on the species by maintaining and creating interstitial spaces used for shelter. Alternatively, point sources of sedimentation are likely to fill interstitial spaces which may result in reduced local abundances and increased density in remaining areas of suitable habitat.

Microhabitat selection for these interstitial spaces may additionally allow fish to inhabit rivers over a wide range of hydrologic regimes as seen throughout the Canadian distribution. In our laboratory study we expected swimming adaptations to be reflective of natal river hydrology. Instead, fish showed no difference in swimming performance across four Canadian rivers, including the augmented North Milk River. We suspect the use of low velocity refugias, such as those created by cobble interstices, as seen in other sculpin species (Facey and Grossman, 1990; Facey and Grossman, 1992), reduces the need for swimming adaptations to high flows. Interestingly, overnight oxygen uptake was higher in fish from the North Milk River, indicating there may be a link between respiration and seasonal hypoxic conditions in the augmented river once the diversion stops. To distinguish the mechanisms behind the elevated oxygen uptake, future studies on the comparative behavior and gill morphology of sculpins from different natal rivers are required. While more research is needed, this study is the first to suggest a potential energetic cost to Rocky Mountain Sculpins living in an augmented system.

Through these studies, it is clear that stressors to adult Rocky Mountain Sculpin may occur from both large-scale flow augmentations and fine-scale environmental conditions. Restricted movement of Rocky Mountain Sculpin makes the species susceptible to fine-scale perturbations in habitat availability and biotic interactions, suggesting targeted conservation activities may have the most impact at a local scale.

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