Improving our ability to assess the impacts of hydrologic alteration on stream fishes: An interdisciplinary approach to assess the Threatened Western Silvery Minnow *Hybognathus argyritis* in Canada

by

Kenton Neufeld

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Abstract

Human induced hydrologic alteration is ubiquitous in North American riverscapes. These alterations have been shown to impact fishes by modifying habitats, influencing movement patterns and driving changes in community structure. Understanding these impacts is an essential first step for the conservation of fish in these systems. We use Western Silvery Minnow *Hybognathus argyritis* and the Milk River of southern Alberta as a model system to develop and apply an interdisciplinary approach to assess the impacts of hydrologic alteration on capture efficiency and habitat suitability of stream fishes. The capture efficiency of sampling gear is a key component of many fish research programs, and understanding the link between hydrology and capture efficiency is critical to accurately assessing the impacts of hydrologic alterations on fish. We measured seine net capture efficiency in the Milk River, and investigated the effects of flow, species, and habitat variables on capture efficiency using mixed effects models. Flow state was an important driver of capture efficiency, which increased ~5 % during augmented flow compared to natural flow. Habitat suitability assessments are commonly used to determine the impacts of hydrologic alteration on fishes, but often rely on poorly understood relationships between fish and their habitat. We used the swimming performance of Western Silvery Minnow to measure the cost of movement between habitat patches in the Milk River and incorporated this cost into a graph theoretic metric of habitat suitability (Equivalent Connected Area). Compared to augmented flow, the proportion of suitable area was ~ 475 % higher during natural flow, the mean cost of movement between habitat patches was ~ 13 % higher and Equivalent Connected Area increased ~ 0.119 (95% C.I. 0.109-0.130). By including flow as a variable in modelling capture efficiency and swimming performance as a mechanism defining habitat suitability, we show the utility and benefits of taking an interdisciplinary approach to assessing the impacts of hydrologic alteration on stream fishes.

Preface

Chapter 2 of this thesis has been published as Neufeld K, Poesch MS, and Watkinson DA, 2015, "The effect of hydrologic alteration on capture efficiency of freshwater fishes in a highly modified prairie stream", *River Research and Applications*, DOI: 10.1002/rra.2913. I was responsible for data collection, analysis, manuscript preparation, and was involved in formulating the objectives and study design. MS Poesch was involved in formulating the objectives and study design as well as providing guidance on data analysis and manuscript preparation. DA Watkinson provided expertise on the study system, support for data collection and guidance on manuscript preparation.

The work contained in this thesis received research ethics approval from the University of Alberta Animal Care and Use Committee (AUP00000759). Field data collection was also authorized by permits 13-008 and 14-00040 issued under section 73 of the Species at Risk Act, Fish Research Licences 13-2408 and 14-2415 issued by the province of Alberta, and Research and Collection Permit No. 13-123 also issued by the province of Alberta.

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1.0 General Introduction

Freshwater systems contain among the highest levels of biodiversity on the planet. Approximately one third of all vertebrate species and almost 6% of all described species inhabit freshwater systems, which only cover 0.8% of the earth's surface (Dudgeon et al, 2006). And still, many new freshwater species continue to be discovered and described by scientists, particularly in tropical areas (Lundberg et al, 2000).

Water scarcity has emerged as a prominent issue globally, and as populations grow, so have the stresses put on water to provide for human needs, as have the impacts from human activities. Vorosmarty et al (2010) found that 80% of the world's population live in areas affected by high water scarcity threats, and while technological advances can mitigate these threats to some extent, that mitigation disproportionately benefits high income nations such as those in western Europe and North America. Developing nations, coincidentally the same nations that often harbour the highest diversity of freshwater species, face growing threats to their water resources that translate into threats to the species inhabiting them.

No region is immune to threats to water security. Canada, a nation with relatively low water security threats and high technological capacity to mitigate those threats (Vorosmarty et al, 2010), is predicted to face growing challenges in the face of changing climate and growing human impacts (Schindler, 2001). Both water quantity and quality are expected to be impacted, with many impacts accentuated in the already arid southern prairies regions of Alberta, Saskatchewan and Manitoba (Schindler and Donahue, 2006). Gan (1998) described decreasing natural streamflow in the summer months and earlier spring runoff events across the prairies region. These shifting conditions will undoubtedly impact aquatic species in the area, including fish of ecologic, economic and social importance.

Threatened aquatic systems are already experiencing large-scale impacts. An average of 7.5 freshwater fish taxa have gone extinct per decade since the 1950s (Burkhead, 2012) and extinction rates have been predicted to increase in the coming century (Ricciardi and Rasmussen, 1999). Approximately 39% of fish species in North America are considered imperiled to some degree, with habitat degradation listed as the number one causal factor (Jelks et al, 2008). Threats contributing to the imperilment of freshwater fishes can be loosely grouped into five categories that overlap and interact: overexploitation, water pollution, habitat degradation, species invasion, and flow modification (Dudgeon et al, 2006). Dams and diversions built for agricultural, industrial and hydroelectric purposes are present on almost all major river systems in North America (Dynesius and Nilsson, 1994; Graf, 1999) and impact fish populations through a number of mechanisms including fragmentation of habitat (Morita and Yamamoto, 2002; Perkin and Gido, 2012), providing a conduit for the introduction of invasive species (Johnson et al, 2008), and altering natural flow regimes (Dudley and Platania, 2007). Altering the natural flow regime of a river often has consequences for the amount, quality and connectivity of habitats, further impacting fish communities.

Altering the flow of a stream can have a strong influence on the availability of various mesohabitat types, potentially eliminating critical habitat types for specialized species (Aadland, 1993). Kehmeier et al (2007) found flat and run habitat significantly increased as flows increased in a sandbed river. In addition to altering the types of habitat present, many flow control structures modify the timing of major discharges, changing the temporal availability of habitat types (Freeman et al, 2001). Natural peak flows are often moderated and extended. Processes that form and shape channels and floodplains can be eliminated, resulting in drastically different stream characteristics (Ward and Stanford, 1995). This can have important consequences for species that are specially adapted to niche habitats or specific flow regimes, as is the case for many fishes in Great Plains rivers.

Flow modification has also been shown to impact fish spawning success and recruitment. Dudley and Platania (2007) showed that changes to the magnitude and timing of water releases from dams, along with the associated habitat alterations could result in increased downstream transport of drifting eggs and embryos of pelagic broadcast spawners. In a highly fragmented landscape, this could transport individuals below barriers and effectively remove them from the population, or result in suffocation in the sediments of reservoirs. Indeed, Perkin and Gido (2011) found that increased fragmentation was associated with declines in pelagic spawning fish in the Great Plains of North America. Freeman et al (2001) found that pulsed water releases from peak-load power generation resulted in unstable shallow water habitats, which negatively impacted small bodied fishes, such as young-of-the-year, that rely upon these areas.

Assessing the impact of flow modification on aquatic systems receives considerable attention and resources from scientists and managers. To do this successfully, fisheries assessment methodologies must be strengthened and in some cases specifically tailored to meet the challenges of hydrologically altered systems. Murchie et al (2008) suggest a number of directions to improve research of river systems with managed flow. Among the suggestions are an increased emphasis on interdisciplinary studies, and more rigorous study design and statistical analysis.

An important factor in the assessment of any fish population is the efficiency of the sampling gear used to capture or sample fish (Arreguin-Sanchez, 1996). Not only does capture efficiency provide the critical link between catch rates and quantitative population estimates, it varies considerably based on numerous parameters, which can confound efforts to compare catch rates between systems and surveys. While numerous factors have been shown to impact capture efficiency for different sampling techniques (Pierce et al, 1990; Bayley and Austen, 2002; Price and Peterson 2010), they are often assessed piecemeal, or assumed to be constant between time and surveys. This can result in misguided confidence in research results. When assessing the effects of hydrologic alteration on fish populations, there is often a high chance of impacts to the population or community and faulty assumptions regarding capture efficiency can lead to misdiagnosis of these impacts. The combined effects of population shifts and an erroneous assessment of those shifts may compound with each other to cause managers to either over or under-react to the actual trend.

Changes in fish habitat are also an important indicator of hydrologic alteration (Bovee, 1986). Relying upon the relationship between habitat and fish, researchers can make inferences about impacts to fish populations based on changes to habitat. An important step in this process is accurately assessing the fish-habitat relationship. To do this, researchers often rely upon habitat suitability indices (HSIs), which mathematically relate habitat parameters to the abundance or presence/absence of a fish species (Rosenfeld, 2003; Ahmadi-Nedushan, 2006). Myriad methods have been used to develop these indices and recently the concept of habitat connectivity has been incorporated using certain graph theory metrics (Pascual-Hortal and Saura, 2006; Saura and Pascual-Hortal, 2007; Saura et al, 2011). Connectivity between habitat patches has been shown to strongly influence the population dynamics (Urban and Keitt, 2001; Söndgerath and Schröder, 2002), and combining information on connectivity and habitat changes could improve assessments of the impacts of hydrologic alterations.

The Milk River of southern Alberta, Canada presents a good system in which to apply and develop techniques for assessing the impacts of hydrologic alteration on fish populations and communities. Since the completion of the St. Mary Canal in Montana in 1917, flow has been diverted from the neighbouring St Mary River to the Milk River, typically from April to late October, and often constituting 1000 -2000 % of the natural flow of the Milk River (International St. Mary – Milk Rivers Administrative Measures Task Force, 2006). The Milk River then flows north into Alberta a few hundred kilometers before turning south once again to return to Montana and eventually enter the Missouri River. This diversion has had a profound impact on the physical structure of the Milk River in Alberta, widening the channel and increasing sediment transport (McLean and Beckstead, 1980). Within this highly modified system, a number of fish species at risk occur, including Western Silvery Minnow (*Hybognathus argyritis*), Rocky Mountain Sculpin (*Cottus sp.*), and Stonecat (*Noturus flavus*) (RL & L Environmental Services Ltd., 2002).

Western Silvery Minnow is a medium-sized cyprinid found in prairie streams in the Missouri and upper Mississippi drainages. While still locally abundant in some areas, it has experienced drastic declines in others (Haslouer et al, 2005; Steffensen et al, 2014). Like many cyprinids, it has been studied only infrequently and there are still gaps in our knowledge of its basic biology and ecology. Most prominent of these gaps are the specie's dispersal patterns and spawning strategy. No previous studies have investigated dispersal and spawning strategy has only been inferred based on that of closely related species, the Plains Minnow (*H. placitus*) and Rio Grande Silvery Minnow (*H. amarus*) (COSEWIC 2008). Both these species are pelagic broadcast spawners, releasing semi-buoyant eggs that suspend in the water column in flowing water (Platania and Altenbach, 1998). Given the pattern of decline in this guild of minnows across the Great Plains (Dudley and Platania, 2007), investigations into the susceptibility of Western Silvery Minnow to effects of hydrologic alteration are needed.

The objective of this thesis is to present two novel advances in assessing fish populations and habitat, which directly contribute to improved understanding of the impacts of hydrologic alteration on stream fishes. Accurately monitoring fish populations relies on a strong understanding of the sampling gear used, how it interacts with the environment and the fish. In chapter 1 I will demonstrate the utility of including flow as a variable influencing capture efficiency of fishes in a hydrologically altered stream. Through better estimates of capture efficiency, researchers and scientists will be better able to detect trends in abundance estimates. When changes in habitat are used as a surrogate for inferring changes to the fish population, it is critical to understand not only the sampling gear, but also the relationship between fish and their habitats. In chapter 2 I will develop a technique for incorporating movement cost into habitat suitability assessments for stream fishes. By using the swimming ability of fish and the water velocity environment they encounter between habitat patches in my movement cost function, I create a more realistic measure of the separation of habitat patches than distance and incorporate this measure into graph theoretic habitat suitability metric. This method is then applied to the Western Silvery Minnow in the Milk River to investigate the impacts of hydrologic alteration on habitat suitability.

2.0 The effect of hydrologic alteration on capture efficiency of freshwater fishes in a highly modified Prairie stream: Implications for bio-monitoring programs

Executive Summary

Hydrology is a defining feature of aquatic ecosystems. Changes in stream hydrology, due to climate change, water use and impoundment, have been shown to negatively affect fish populations. Assessing changes in hydrology and its effect on fish populations and communities remains an important consideration for aquatic monitoring programmes across the globe. In this study, we used the Milk River in southern Alberta as a model system to understand how hydrologic alteration may also affect capture probabilities of fishes and impact instream monitoring programmes. The Milk River receives the majority of its April to October flow via an inter-basin transfer from the St. Mary River, drastically altering the hydrologic regime and instream habitats for fishes during this augmentation period. We estimated species-specific seine net capture probabilities of fishes in the Milk River during augmentation and natural flow periods using depletion surveys in both open and enclosed sites. Using habitat data collected during the seine surveys, linear mixed-effects models were created with capture efficiency as the dependent variable. Models were compared using corrected Akaike's information criterion, and the relative contributions of the different variables to the top models were examined. We found that species and flow characteristics, such as water velocity and the state of augmentation, played a prominent role in many of the top models explaining variation in capture efficiency. These results demonstrate that changes to stream hydrology clearly have the potential to impact gear efficiency and individual species assessments. Stream monitoring programmes, which aim to determine long-term trends in aquatic ecosystem health, need to be mindful that any change to stream hydrology—from climate change, fragmentation or stream alteration—can alter capture efficiency of the sampling gear and inadvertently alter species-specific trends.

Introduction

Freshwater ecosystems are some of the most diverse ecosystems on earth, containing 6% of all described species, yet covering only 0.8% of the surface (Dudgeon et al., 2006). Similarly, fishes are one of the most diverse groups of vertebrates (Helfman et al., 1997), with 40% of fish species inhabiting fresh water (Lundberg et al., 2000) and new freshwater fish species discovered regularly in South America, Africa and tropical Asia (Lundberg et al., 2000). The diversity of freshwater systems, and freshwater fish in particular, is increasingly threatened. An estimated 4.4% of freshwater fish species are threatened globally (Duncan and Lockwood, 2001), and 39% are imperiled in North America (Jelks et al., 2008). Extinction rates have been increasing since 1950 (Burkhead, 2012), with a current rate of 0.4% loss per decade and a predicted increase to 2.4% loss per decade over the next hundred years (Ricciardi and Rasmussen, 1999).

Threats to freshwater biodiversity can be grouped into five main categories: overexploitation, water pollution, flow modification, destruction or degradation of habitat and invasion by exotic species (Dudgeon et al., 2006). Flow modification, or hydrologic alteration, is largely the result of dams built for water storage, diversion and regulation and is prevalent throughout North America (Graf, 1999; Nilsson et al., 2005). Stream fragmentation and hydrologic alteration have been linked to the decline of numerous fish species (Morita and Yamamoto, 2002; Dudley and Platania, 2007). The loss of long, unimpeded sections of river restricts natural movement patterns associated with spawning migrations and egg and larval drift (Perkin and Gido, 2011; 2012), while flow modifications alter physical properties of riverine habitat (Freeman et al., 2001; Murchie et al., 2008). Within this context of declining freshwater fish diversity and increasing threats to fish populations and habitat, accurate assessments of fish populations and communities are essential for effective management. Species supporting commercial, recreational or aboriginal fisheries or those identified as imperiled often receive the majority of researchers' and managers' efforts. Still, managers are often forced to use uncertain results and rely heavily upon professional judgment. When it comes to species not contributing to a fishery or identified as imperiled, there is most often a complete lack of data regarding population status and trends. When such data are collected, it is essential that they be accurate and informative, which requires a thorough understanding of the data collection methods used.

Seine nets are commonly used to sample fish communities in shallow areas of lakes and rivers. There are many factors that impact the effectiveness of seine nets at capturing fish (e.g. water depth, water velocity, substrate type, species targeted, fish size and time of day; Lyons, 1986; Parsley et al., 1989; Pierce et al., 1990; Říha et al., 2008). Failure to recognize any of these impacts may result in inaccurate conclusions and misguided management actions. These factors become especially important when, in addition to impacting capture efficiency, they also affect the fish populations. The result may be an altered fish population or community and hindered attempts to monitor or survey it. Because hydrologic alteration is a known driver of changes in fish communities, it is important to also understand its impact on researchers' ability to monitor those changing communities.

Using the Milk River in Alberta, Canada, as a model system, we aim to investigate the relationship between hydrological alterations and the capture efficiency of freshwater fishes. The majority of the water the Milk River receives is via a diversion from the St. Mary River in Montana, resulting in a relatively constant discharge between 15 and 20 cm/s from April to October (ESRD, 2014). Once augmentation ceases in October, discharge decreases to 1–2cm/s for the duration of winter. This results in two distinct, drastically different flow states. By identifying the impact of the changing flow state on capture efficiency of freshwater fishes, we hope to illustrate the potentially confounding impacts of hydrologic alteration on long-term monitoring programmes.

Methods

The Milk River, located in southern Alberta, Canada, is a medium-sized prairie stream characterized by a low-gradient and sand-dominated substrate in its lower 100 river kilometres (Figure 2-1). The Milk River's cycle of augmented and natural flow states provides a model system to test how common sampling methods used in fisheries research may be affected by changes in hydrology. Sampling of fishes was conducted between 12–20 September 2013 and 3–11 October 2013 during augmentation (flow: 13.4 – 15.9 cm s^{-1}) and after (1.9 – 3.1 cm s^{-1}) (Figure 2-2) (ESRD, 2014). This timing allowed for a before/after contrast while minimizing temporal variability.

Freshwater fishes were enumerated using depletion surveys and mark–recapture techniques to help estimate species specific capture efficiency. Fishes were sampled at 20 sites evenly divided across flow states (augmented and natural) and two reaches, the Ross Ranch and the Pinhorn Ranch (Figure 2-1). Sites were chosen based on our ability to establish an enclosure around the site using block nets, and the likelihood of encountering western silvery minnow (*Hybognathus argyritis*), a threatened species under Canada's Species at Risk Act. This species is typically collected along shallow areas with slow-moving water and silty substrate (COSEWIC, 2008), and consequently, these areas were where most of our sites were situated. Both open and closed survey techniques were used at each site to compare capture efficiencies under contrasting survey conditions. To accomplish this, sampling at each site consisted of three sampling events spaced over 3 days. Before sampling on the first day, the site was enclosed with block nets that were left in place until sampling was completed on Day 2. Block nets had 4.76-mm ace meshing and were dug into the substrate to seal the bottom edge. After surveys were completed on Day 2, block nets were removed, and the site was re-sampled. This resulted in the first two surveys being conducted on a closed system, while the third was on an open system. Each survey type (open or closed) consisted of a removal depletion survey (White et al., 1982) fished with a 9.14 m long × 1.82 m high seine with a 1.82 × 1.82 m bag and 4.76 mm ace meshing throughout. A minimum of three passes were completed for each survey with up to six passes for sites at which the decline in catch between passes was low (Bohrmann and Christman, 2013). After each seine haul, all fishes captured were identified to species and counted. They were released back into the enclosure once all seine passes were complete. Fishes over 60 mm were marked with a visible implant elastomer tag coded specifically to that site.

At each site, mean and maximum water depth and mean water velocity were measured, and substrate composition was estimated to the closest 5 % using a modified Wentworth scale (Cummins, 1962): clay (<0.0039 mm), silt (0.0039– 0.0625 mm), sand (0.0625–2 mm), gravel (2–64 mm), cobble (64–256 mm), boulder (>256 mm) and bedrock. The surface area of each site was estimated from sketches drawn in the field and measurements taken with a laser rangefinder.

Fishes large enough to mark with tags (>60mm) were relatively rare in our samples, comprising only 4.9% of the total catch. Initial review of the data also revealed low recapture rates, with previously marked fish captured in only 16 of 55 surveys. Because of this, we were not able to obtain capture efficiency and abundance estimates from mark– recapture data for most surveys, and mark–recapture data were not used in any of the following analyses. Estimates of species-specific capture efficiency and abundance were obtained for each depletion survey using Carle and Strub's K-pass removal method (Carle and Strub, 1978). The four species groups used for this analysis included the following: (1) flathead chub (*Platygobio gracilis*); (2) longnose dace (*Rhinichthys cataractae*); (3) sucker species [composed of white sucker (*Catostomus commersonii*), longnose sucker (*Catostomus catostomus*) and mountain sucker (*Catostomus* *platyrhynchus*)]; and (4) western silvery minnow. Flathead chub, longnose dace and Catostomus spp. were all encountered in almost every survey, allowing for species-specific comparisons in capture efficiency. Western silvery minnow was included as a species group due to its threatened status and the potential application of the results to other imperiled species.

Factors influencing species-specific capture efficiencies were assessed using linear mixed-effects models fitted by maximum likelihood (Starkweather, 2010). Models were structured with region (Pinhorn or Ross Ranch), site and survey as random effects. Fixed effects included flow state (augmented or natural), species, survey type (open or closed), abundance, mean water depth, water velocity and the interaction between flow state and water velocity. In order to not over-parameterize the number of candidate models, the interaction between flow state and water velocity was the only interaction effect included. Of all the potential interaction effects, this effect was judged to be most relevant to our investigation of the impacts of flow alteration on capture efficiency. All candidate models were ranked using a bias-corrected Akaike's information criterion (AICc) (Akaike, 1973; Sugiura, 1978; Hurvich and Tsai, 1989). In total, 128 candidate models were tested, including all possible combinations of these seven fixed effects plus the null model. Maximum water depth was highly correlated with mean water depth (Pearson's correlation, df = 18, t = 10.6308, p = 3.456e9, R= 0.9288) and excluded from all analyses to reduce redundancy. Substrate was dominated by silt and sand at all sites, and gravel (the only other substrate encountered) was present at only one site, and so we excluded substrate type from the analysis as well.

For each model, $AICc_i$, Δ_i ($AICc_i$ - $AICc_{min}$), and w_i (Akaike weight, the model probability) were calculated as described by Burnham and Anderson (2004). Using $\Delta_i \leq 2$ as indication of a model having considerable support (Burnham and Anderson, 2004), the top models were identified and examined. Presence of a certain fixed effect in the top models was taken as an indication of its importance in determining capture efficiency. Model-averaged predictions of fixed effects were computed as weighted means with model probabilities acting as the weighting factor (Burnham et al., 2011). Factorial analysis of variance (ANOVA) (Crawley, 2012) was also used to assess differences in species-specific capture efficiency for models including flow state and survey type.

Results

Flow state and stream velocity were important factors influencing capture efficiency of freshwater fishes in the Milk River. Of the 128 models tested, eight had $\Delta_i \leq 2$ indicating substantial support for those models from the data (Table 2-1). Species was included as a fixed effect in all of the top eight models, with flow state being the second most frequently occurring fixed effect (present in four models), followed by water velocity (three models), fish abundance (two models), water depth and the interaction between flow state and water velocity (one model each; Table 2-1). The model with the lowest AICc value included only species and flow state as fixed effects. Within this model, western silvery minnow was associated with the highest capture efficiency, followed by Catostomus spp., flathead chub and longnose dace (linear mixed-effects model, df = 3, F = 5.195, p = 0.0022).

The full model including all possible fixed effects was not strongly supported by the data, ranking 64th of the 128 models tested with a Δ_i of 7.8722. Within this model, only species was a significant effect, with capture efficiencies highest for western silvery minnow, followed by Catostomus spp., flathead chub and longnose dace, similar to the highly supported models (Table 2-2). Abundance, mean water depth and water velocity all had a negative impact on capture efficiency. Similar to the other models, capture efficiency was lower during natural flow conditions. Open surveys had higher capture efficiencies than closed surveys; however, survey type did not appear at all in the top eight models. There were relatively high levels of correlation between flow state and mean water depth (R = 0.583), water velocity (R = 0.316) and the interaction between flow state and water velocity (R = 0.448).

In general, the top models agreed on the direction and magnitude of the impact of the fixed effects when they were included in the model. From the top eight models, the model-averaged intercept value is 0.5705, indicating the average capture efficiency if all other fixed effects were zero/null (Table 2-2). Within the species effect, western silvery minnow has the strongest impact on capture efficiency, followed by longnose dace, Catostomus spp. and flathead chub as the null category in that class. The natural flow state had a negative impact on capture efficiency with augmented flow being the null category. Although not included in as many of the top models as other effects, the natural flow state–water velocity interaction and water velocity both had relatively strong negative impacts on capture efficiency. Fish abundance and mean water depth, although included in some of the models, have relatively minor impacts on capture efficiency.

The majority of the random-effect variance was residual (Table 2-2); however, in the top models, the survey effect accounted for almost 43% of the random-effect variance, while site and region accounted for much less. The large amount of variance accounted for by the survey random effect supports the inclusion of at least that random effect in the model, and the use of a linear mixed-effects model in general.

The factorial ANOVA including species and flow state showed that both factors had a significant impact on capture efficiency [species (ANOVA, df = 3, F = 2.913, p = 0.03662) and flow state (ANOVA, df = 1, F = 6.914, p = 0.000951)] (Figure 2-3a). For all species except western silvery minnow, capture efficiency was higher during augmented flow. The ANOVA including species and survey type indicated a significant effect only for species [species (ANOVA, df = 3, F = 3.093, p = 0.0291) (Figure 2-3b). No distinct effect of survey type was readily apparent, with higher capture efficiency in closed surveys for flathead chub and western silvery minnow, lower capture efficiencies in closed surveys for longnose dace and no clear difference for sucker species.

Discussion

Streams are increasingly experiencing modifications to their natural flow regimes due to human activity. Dams and diversion weirs are widespread with the majority of the total river discharge in the northern third of the world regulated for hydroelectric power, reservoir operation, water diversion and irrigation (Dynesius and Nilsson, 1994). In addition, climate change is projected to have significant consequences on the timing and amount of streamflow with earlier spring peaks and lower total discharge (Schindler and Donahue, 2006). With these changing stream conditions and the inevitable changes to the fish communities contained within, researchers run the risk of compounding errors associated with developing trends using long-term monitoring surveys of fish populations. For example, in a review of research performed on fish communities in streams with modified flow regimes, Murchie et al. (2008) found that active sampling methods, such as seine netting, were the most common single sampling method used. When using these methods, a key component that must be understood by the researcher for proper interpretation of the data is the efficiency of the sampling gear, or its capture probability, which provides a link between the sampled population and the actual population (Arreguín-Sánchez, 1996).

We show that stream hydrology, including flow state and water velocity, had a strong influence on the capture probability of freshwater fishes in a hydrologically altered system. Incorporating such knowledge into long-term monitoring programmes is essential to ensure that appropriate trends in aquatic ecosystems are properly enumerated (Poos et al., 2012; Poesch, 2014). Differences in species specific characteristics and their effect on capture probabilities are important reference information for fisheries managers (Poos and Jackson, 2012). For example, the western silvery minnow had higher capture efficiencies under natural flow conditions than during stream augmentation. Population assessments of western silvery minnow, and other imperiled species, may therefore be impacted by the hydrologic conditions during sampling. The effect of habitat on species-specific capture efficiencies is perhaps not surprising given the results of previous studies investigating factors influencing gear efficiency. Capture efficiency of a seine decreases with the increased benthic orientation of a species (Lyons, 1986; Pierce et al., 1990; Poos et al., 2007). This may be a result of more benthic-orientated species evading samplers through the spaces between the seine net and the bed of the water body (Poos et al., 2007) and fish swimming ability. Of the species commonly encountered in our study, longnose dace are benthic specialists, and this was reflected in the lowest capture efficiency of the species considered. Flathead chub had the next lowest capture efficiency, although it was only slightly lower than that of sucker species, and both species probably utilize similar habitats at the juvenile life stage that was most often encountered. The majority of fishes captured were juveniles, and juvenile suckers are known to feed on non-benthic food sources (Nelson and Paetz, 1992), which may make them more susceptible to seine net capture and explain their higher capture efficiency.

The efficiency of sampling gear is reduced when fishes are able to evade capture, with fast-swimming fish being better able to escape an encircling seine net. The swimming ability of a species is often linked to the habitat it occupies, and for stream fish, the water velocity typically encountered (Leavy and Bonner, 2009). Of the species considered in this study, longnose dace is typically associated with the highest-velocity habitat, commonly found in riffle section of streams (Scott and Crossman, 1973). Catostomus spp. and flathead chub are found in a wider range of water velocities but are not usually considered fast-water specialists (Scott and Crossman, 1973; Nelson and Paetz, 1992). Western silvery minnow is usually associated with slow-moving sections of streams (Nelson and Paetz, 1992). Given these habitat use patterns, swimming ability would be expected to be highest and capture efficiency lowest for longnose dace, followed by Catostomus spp. and flathead chub and then western silvery minnow. The observed capture efficiency pattern follows this relationship, indicating that along with benthic orientation, swimming ability may play a role in determining differences in capture efficiency among species. While both swimming ability and benthic orientation of a species may influence capture efficiency, the magnitude and direction of that impact will likely vary for different capture methods. The effect of flow on capture efficiency will likely need to be investigated independently for different capture methods.

With the decrease in discharge from augmented to natural flow states, the physical habitat present in the river changed dramatically. The first obvious change was a reduction of available habitat, with the majority of the previously inundated channel being exposed during natural flows. One expected effect of this would be an increased concentration of fish in the remaining habitat; however, we did not find a strong correlation between flow state and abundance in the full model. This may be because the amount of suitable habitat for the most common species did not change. We were unable to sample large portions of the study reaches during augmented flows because of high water depths and velocity. These deeper, faster areas may be less suitable for the species we commonly encountered and so with the decrease in water levels, there may not have been a significant decrease in available habitat. Another major change between flow states was water clarity. Turbidity measurements were not taken during the augmented period; however, a noticeable increase in water clarity occurred from augmented to natural flow states. The increased flows that occur during augmentation in the Milk River have been linked to increased erosion and sediment transport (AMEC, 2008), accounting for this change. This increased clarity may have contributed to decreased capture efficiency in the natural flow state.

Our choice of seine net as sampling gear excluded much of the river from potential sampling as previously discussed. While capture efficiency was higher during augmented flows at our sample sites, it should be noted that we were also unable to sample a larger portion of the river. This highlights the multiple scales at which flow alteration may influence fish sampling. Considering the entire river, increased flow may reduce the effectiveness of seine nets for representatively sampling the fish community; however, at the local site level, seine nets become more efficient.

Changes to the hydrologic regime of a stream are well documented to impact fish habitat and communities, and the Milk River data provide a good example of this. The increased discharge of the system as a result of augmentation has resulted in a widening of the channel (AMEC, 2008). Increased erosion has increased the silt load in the river during much of the year, increasing turbidity as well as the deposition of sediments in slow-moving portions of the river. Besides changing the amount of water in a system, altering the timing of peak flows can also have significant negative impacts on fish species (Freeman et al., 2001). Many riverine fish species have adapted to specific flow and water temperature regimes, which if altered can have negative consequences for reproduction and young-of-the-year survival (Dudley and Platania, 2007).

Hydrologic alterations impact fish in many direct and indirect ways, and it is often difficult to measure all the indirect habitat parameters that are affected by flow and could potentially influence fish. Similarly, those same habitat parameters that change with flow and affect fish also often influence the efficiency of sampling gear. While much attention has been given to quantifying the impact of various habitat variables on sampling efficiency, the flow state itself (as the driver of many of those habitat conditions) has not often been considered as a quantifiable variable influencing sampling efficiency. We have shown that flow state can play a role in determining capture efficiency of a seine net, independent of some commonly measured habitat variables. We believe that this effect likely translates to other fisheries sampling gear as well. Given the importance of understanding capture efficiency for accurate fisheries assessment, including flow state as a variable in models explaining capture efficiency is strongly recommended. Flow information is often easily accessible and, while not a substitute for other habitat parameters, could help increase researchers' confidence in their sampling results and improve management of increasingly threatened fisheries resources.

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Figures

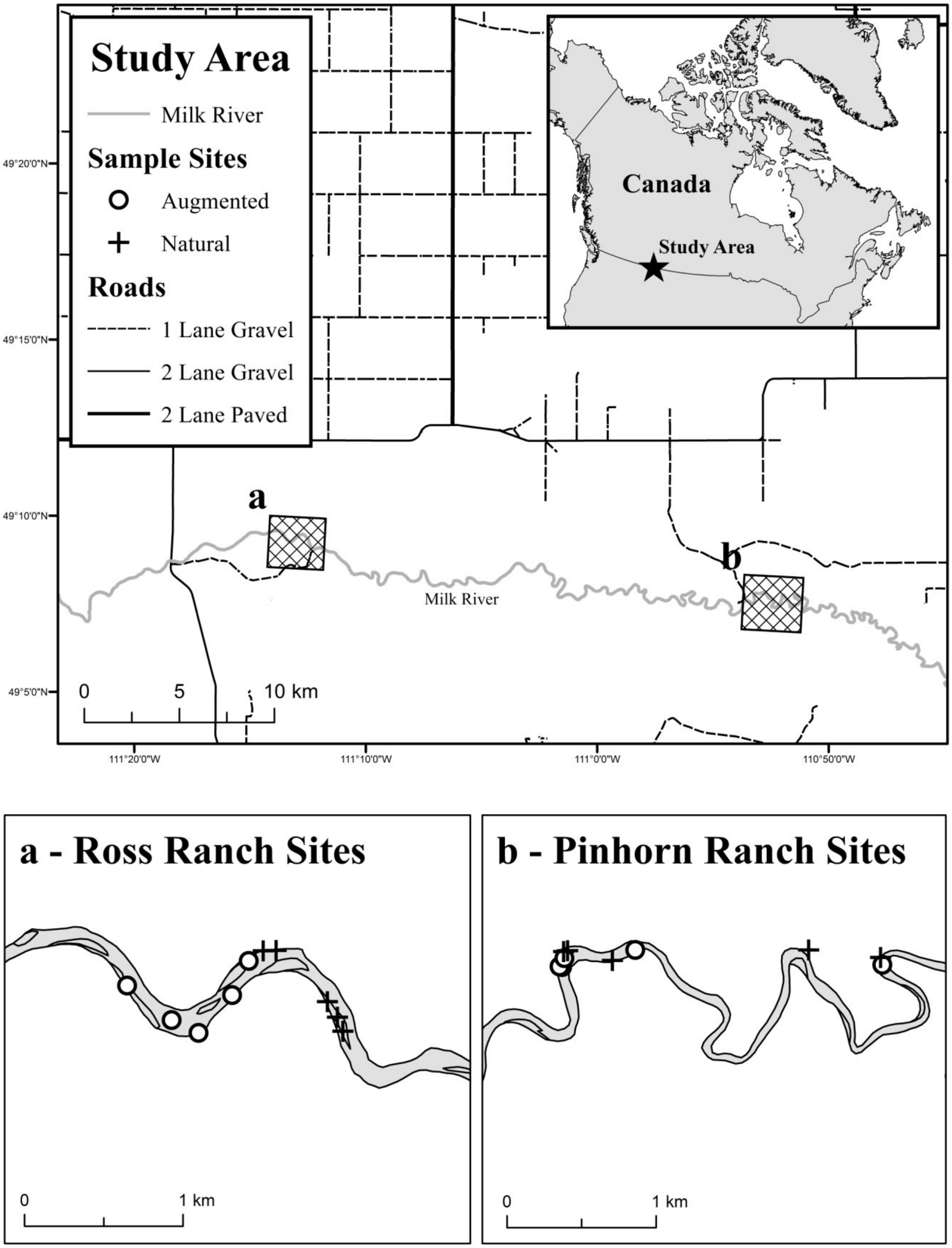

Figure 2-1. Milk River in southern Alberta with sample sites, 2013.

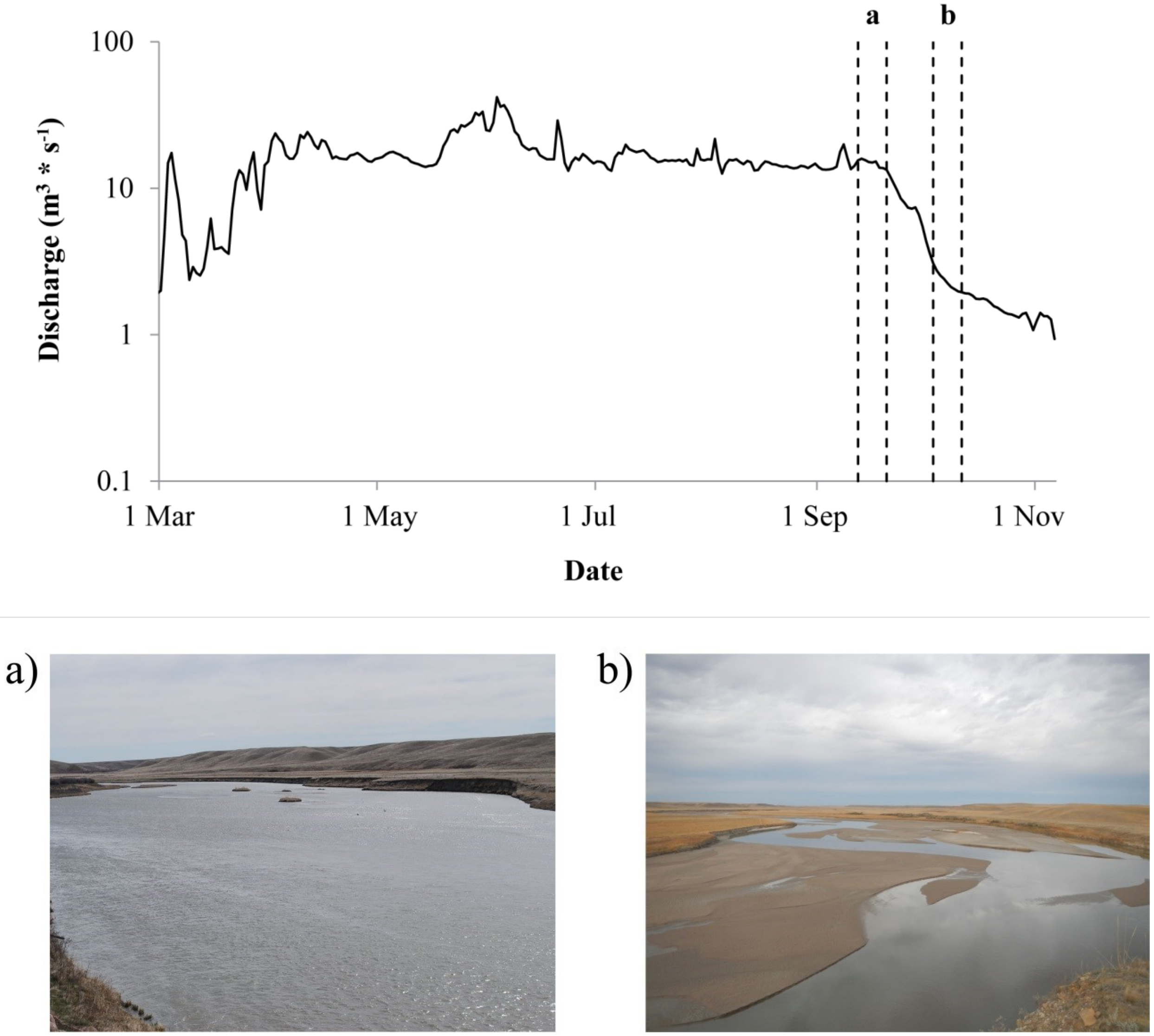

Figure 2-2. Discharge of the Milk River at the eastern international border crossing in 2013. Dashed vertical lines indicate the start and end dates of sampling during the augmented (a) and natural (b) flow periods. Photos show representative conditions during augmented (a) and natural (b) flow periods in the Milk River on the Ross Ranch.

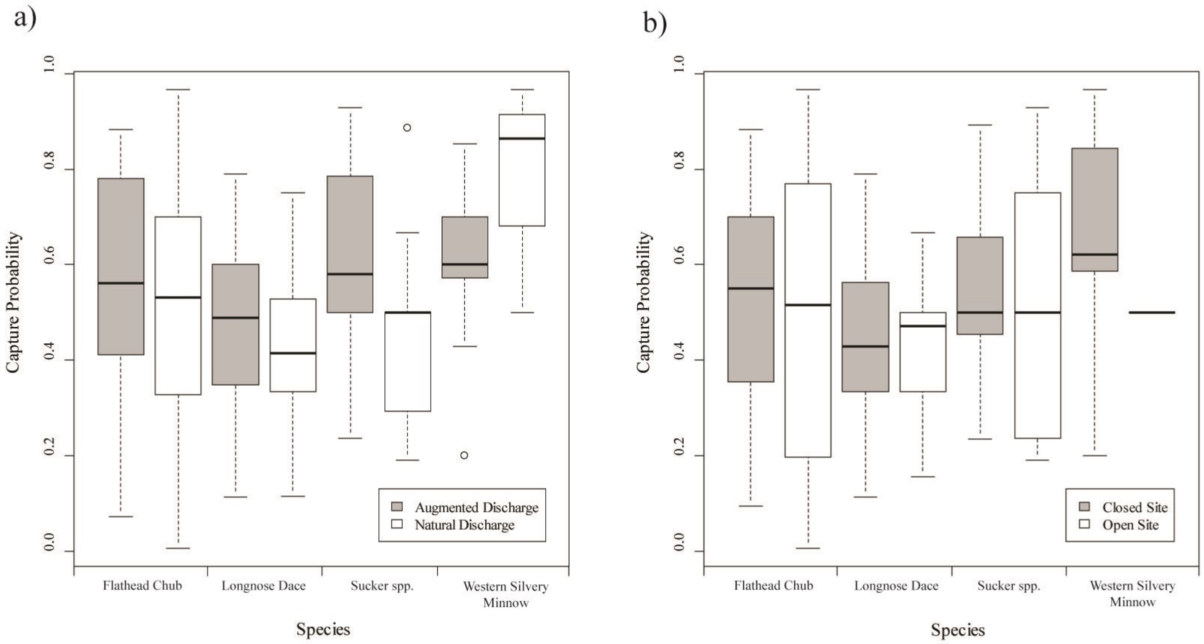

Figure 2-3. Seine net capture probability for flathead chub (*Platygobio gracilis*), longnose dace (*Rhinichthys cataractae*), sucker species and western silvery minnow (*Hybognathus argyritis*), in the Milk River in southern Alberta during augmented and natural flow conditions, and from open and closed surveys, 2013. The dark centre line represents the median; the top and bottom of the box represent the third and first quartiles, respectively; and the top and bottom whiskers represent the maximum and minimum, respectively.

Tables

Table 2-1. Linear mixed effects models with $\Delta_i \leq 2$, with seine net capture efficiency as the dependent variable. 128 candidate models were created using data collected in the Milk River in southern Alberta, 2013. Formula represents only the fixed effect variables included in the model, all models also included region, site and survey as random effects. The bottom model (rank = 64) is the full model, including the entire suite of fixed effects considered for the analysis.

Model Rank	Formula	$AICc_i$	Δ_i	w_i
1	Species + Flow State	-56.7253	0	0.2189
2	Species	-55.9918	0.7335	0.1517
3	Species + Flow State + Abundance	-55.9423	0.7830	0.1480
4	Species + Flow State + Water Velocity	-55.6168	1.1085	0.1258
5	Species + Depth	-55.0858	1.6395	0.0965
6	Species + Water Velocity	-54.9246	1.8007	0.0890
7	Species + Flow State + Abundance + Water Velocity	-54.8857	1.8397	0.0873
8	Species + Flow State * Water Velocity	-54.7815	1.9438	0.0828
64	Species + Flow State + Survey Type + Abundance + Water Velocity + Depth + Flow State * Water Velocity	-48.8531	7.8722	N/A

Table 2-2. Model-averaged values for random and fixed effects from the eight best models and the full model explaining seine net capture efficiency in the Milk River in southern Alberta, 2013. The model-averaged values reported for the random effects are the proportions of the total random effects variance attributed to each random effect. The model-averaged values reported for the fixed effects are the coefficient estimates produced by the models for that effect. Solid dots indicate that the effect was included in the model.

		Top Models									Full Model
		1	2	3	4	5	6	7	8	Model-Averaged	
Random Effects Variance (% of total)	Survey	●	●	●	●	●	●	●	●	0.4298	0.4311
	Site	●	●	●	●	●	●	●	●	0.0229	1.7745E-10
	Region	●	●	●	●	●	●	●	●	2.6502E-11	1.1127E-11
	Residual	●	●	●	●	●	●	●	●	0.5473	0.5689
Fixed Effects Estimates	Intercept	●	●	●	●	●	●	●	●	0.5705	0.6036
	Species - FLCH	●	●	●	●	●	●	●	●	null	null
	Species - LNDC	●	●	●	●	●	●	●	●	-0.0812	-0.0959
	Species - SUCK	●	●	●	●	●	●	●	●	0.0107	0.0008
	Species - WSMN	●	●	●	●	●	●	●	●	0.1113	0.0922
	State - Augmented	●		●	●			●		null	null
	State - Natural	●		●	●			●		-0.0473	-0.0543
	Abundance			●				●		-1.142E-05	-5.122E-05
	Depth					●				-0.0200	-0.0430
	Velocity				●		●	●		-0.2358	-0.2014
	State (Augmented)*Velocity								●	0.0174	null
	State (Natural)*Velocity								●	-0.1306	-1.018
	Survey Type (Closed)									--	null
	Survey Type (Open)									--	0.0045

3.0 Incorporating movement cost with habitat suitability: Using a graph theoretic approach to investigate the impacts of hydrologic alteration on stream fishes

Executive Summary

Hydrologic alterations are widespread in streams worldwide and often detrimentally impact fish populations and communities. Habitat suitability is commonly used to assess these impacts, but frequently relies solely upon observed fish-habitat relationships rather than the mechanistic underpinnings of those relationships. We used laboratory measured swim performance of fishes to develop a movement cost function which was then incorporated into a habitat suitability assessment via a recently developed graph theoretic metric, equivalent connected area (ECA). The movement cost function considered the effects of species specific swim performance as well as the encountered water velocities and provided a more realistic measure of habitat patch separation than Euclidean distance. This technique was then applied to the threatened cyprinid, western silvery minnow *Hybognathus argyritis*, in the Milk River of southern Alberta, Canada to assess the impacts of flow alteration on the species. ECA (as a proportion of the total area), increased ~ 0.119 during natural, low flow rates compared to augmented, high flows indicating potential negative impacts of flow augmentation for this species. Use of the derived movement cost function rather than Euclidean distance as the measure of separation between habitat patches also caused increased estimates of overall habitat suitability, likely due to dispersal assisted by currents. The incorporation of mechanistic principles such as movement cost into habitat suitability assessments will improve our understanding of the effects of hydrologic alterations on stream fishes and increase the effectiveness of monitoring and mitigation efforts.

Introduction

Freshwater fishes are an increasingly imperiled group, with an estimated 0.4 % per decade extinction rate in North America (Ricciardi and Rasmussen, 1999) and 700 taxa listed as vulnerable, threatened or endangered in 2008 (Jelks et al., 2008). Threats to freshwater fishes include over-exploitation, water pollution, habitat degradation, invasive species, and flow modification, all of which can interact with each other (Dudgeon et al., 2006). Hydrologic alterations are widespread in rivers around the world (Dynesius and Nilsson, 1994), with approximately 75,000 dams present in the United States alone, and there are no watersheds > 2000 km^2 in the United States that aren't experiencing some form of hydrologic alteration (Graf, 1999). Dams, diversions and a changing climate all play a role in changing stream flows, impacting the amount and connectivity of suitable fish habitat, affecting some fishes ability to successfully complete all necessary life stages (Bunn and Arthington, 2002; Dudley and Platania, 2007). They also provide a conduit for the introduction of non-native species that may have detrimental effects on native fauna (Johnson et al., 2008).

With the imperiled status of many species and increasing threats, there is a growing need to accurately assess the impacts of hydrologic alteration on fish populations and communities. One method of assessing these impacts is quantifying the effects of hydrologic alterations on aquatic habitats, a technique that relies upon understanding the relationship between a species and its physical environment. The relationships between aquatic habitat and a species' presence or abundance is often quantified in a habitat suitability index (HSI), which is used to identify habitat characteristics or features that are key to the successful persistence of a species (De Kerckhove et al., 2008). An HSI can be modelled in numerous ways, including linear, nonlinear, and logistic regression, principal component analysis, general linear models, general additive models, and artificial neural networks (Ahmadi-Nedushan et al., 2006).

How suitability is defined also plays a large role in the validity and applicability of the HSI. Most commonly, HSI quantifies the observed association between a certain species and particular habitat characteristics (Rosenfeld, 2003). Implicit in this method is the assumption that the habitat occupied by individuals enables them to successfully survive and reproduce. However, it has been shown that individuals do not always occupy the habitat that best meets their needs, and there are factors that can push fish to less than ideal habitats (Van Horne, 1983; Hobbs and Hanley, 1990; Rosenfeld and Boss, 2001). In these instances, using an HSI based on observed habitat associations of a species may be misleading. Another way HSIs commonly define suitability is “preference” (Rosenfeld, 2003). Preference is the selection of certain habitat characteristics over others, and seeks to identify the habitat types that optimize fitness. It is assumed that individual fish will weigh the costs and benefits within their environment and choose the best available habitat. Preference provides a more robust way of estimating suitability, however measuring habitat preferences is often difficult. Isolating the relationship with each habitat parameter, or alternatively, including all habitat parameters in a multifactor model can become complex (Ahmadi-Nedushan et al., 2006). Controlled laboratory or field experiments can help us predict the impacts of individual parameters, and multiple authors have called for the inclusion of this type of empirical data in habitat suitability assessments (Boisclair, 2001; Rosenfeld, 2003; Murchie et al., 2008).

In order to confidently speak to the relationship between fish and their habitat (i.e. truly understand the suitability of a habitat), an understanding of the underlying mechanisms driving the relationship is needed. Mechanisms such as foraging energetics (Mittelbach, 1981), predation and competition (Rosenfeld and Boss, 2011), and physiological constraints such as temperature (Huey, 1991) can all play a role in defining how individuals relate to their environment. Additionally, the ability of individuals to move through their environment (their movement potential) can in a large way define the suitability of habitats (Fagan, 2002) and can also be defined in a very mechanistic way. Factors such as interspecific interactions (eg. predation risk (Fraser et al., 1995)), inhospitable physiological ranges (eg. chemical barriers (Warren et al., 2008)), or physical impediments to movement (eg. dams or culverts (Maitland et al., 2015)) can influence movement potential, restricting or allowing movement to varying degrees. At the population level, movement between habitat patches can often have important implications for persistence, for example source habitat patches providing a source of individuals for sink patches (Dunning et al., 1992).

Assessing the connectivity of environments (and the movement potential of individuals in the environment) provides key insights into its suitability and is commonly done in terrestrial environments (Schadt et al., 2002; LaRue and Nielsen, 2008; Janin et al., 2009; Wang et al., 2009). In aquatic systems, connectivity is most commonly assessed in streams, regarding the environment as a dendritic system with barriers and restrictions to movement corresponding to features such as waterfalls, dams, and culverts (Wofford et al., 2005; Perkin and Gido, 2012). Considering movement potential of fishes in aquatic systems viewed as non-dendritic landscapes is less common, though not completely unheard of (Hoffman et al., 2006; McElroy et al., 2012), and in principle is similar to movement potential in terrestrial environments. Viewing the landscape as a patchwork or grid of different habitats, assigning costs for movement through those habitats and then defining movement potential based on those movement costs is a common technique in terrestrial environments (eg. Schadt et al., 2002; Adriaensen et al., 2003;

LaRue and Nielsen, 2008; Sawyer et al., 2011). A similar concept can be applied to fish in an aquatic system, though the mechanism that defines the cost of movement may be different.

Movement of fish may be restricted by a number of factors, not the least of which is water velocity (Haro et al., 2004). The relationship between water velocity and swimming ability is commonly assessed in laboratory settings for the purposes of evaluating fish passage of potential barriers (Toepfer et al., 1999; Bestgen et al., 2010, Tierney et al., 2011) and the physiological impacts of potential toxicants (Waiwood and Beamish, 1978; Farrell et al., 1998; Jain et al., 1998). Past studies have found that when considering swimming endurance, time to fatigue typically decreases as water velocity increases (Brett, 1964; Brett, 1967; He, 1991; Adams et al., 1999; Cotterell and Wardle, 2004). To address the widespread presence of dams, anthropogenic barriers, and pollutants, the swimming abilities of many different fish species have been assessed (Videler and Wardle, 1991; Hammer, 1995).

There is currently a need for interdisciplinary studies to advance our understanding of the impacts of hydrologic alteration on fishes (Murchie et al., 2008), and incorporating swim performance into estimates of movement potential and subsequently habitat suitability would provide a mechanistic link between physical habitat conditions (water velocity) and habitat suitability. Here, we develop and present a means for incorporating movement potential based on swim performance into habitat suitability models. We consider the consequences of this method for estimating habitat suitability and the impacts of hydrologic alteration on the western silvery minnow (*Hybognathus argyritis*), a threatened species in the Milk River, Canada. By adopting a mechanistic approach, and using swimming ability and water velocity to estimate habitat suitability, we improved our ability to assess the impacts of hydrologic alteration on Western Silvery Minnow in the Milk River.

Methods

Incorporating movement cost into habitat suitability

The study of connectivity and movement potential has a long history in ecology, however terminology has not always been agreed upon (Tischendorf and Fahrig, 2000; Moilanen and Hanski, 2001; Tischendorf and Fahrig, 2001). For the purposes of this study, we use connectivity as a general term describing the permeability of the landscape to movement by organisms. It is a characteristic of the landscape, not the organism. We use movement potential as a general term to describe the ability of an organism to move through their landscape, a characteristic of the organism rather than the landscape. Movement potential can be thought of a landscape scale generalization of the probability of dispersal, referring to the probability that an organism will successfully undertake a movement from one specific location to another. Probability of dispersal is often defined as an exponential decay function of some measure of the separation between two locations (Rodriguez, 2002; Poos and Jackson, 2012). This measure is commonly Euclidean distance, but can be a different measure of movement cost. We define movement cost as a relative value representing the cost of movement from one specific location on the landscape to another.

We incorporate a novel measure of movement cost into Equivalent Connected Area (ECA), a habitat suitability metric based in graph theory. ECA uses characteristics of habitat patches on a landscape (typically the area) and the probability of dispersal between these habitat patches to calculate the equivalent amount of fully connected habitat (Saura et al., 2011). Habitat patches represent the nodes of a graph, while the probability of dispersal gives value to the arcs connecting the nodes. When probability of dispersal between all the patches equals one (all patches are fully connected), ECA equals the sum of the area of all the patches. When the probability of dispersal is zero between all habitat patches, ECA equals the area of the largest single patch. The units of ECA are whatever units were used to describe the habitat patches (eg. square meters when habitat patches are characterized by area), and the ratio of ECA to the total value of the landscape provides a measure of the proportion of the landscape that is suitable.

We incorporate swimming ability into the estimated probability of dispersal between habitat patches, and hence into the estimated ECA. Probability of dispersal defines how easily individuals move from one habitat patch to another and is often defined as an exponential function (Rodriguez, 2002; Equation 1), based on distance and an additional parameter, θ:

$$Probability\ of\ dispersal = e^{-\theta * Distance} \tag{1}$$

Using the water velocity the fish encounters between habitat patches and the swimming ability of the fish, a measure of movement cost was calculated, this was then used instead of distance to calculate the probability of dispersal.

Within lotic systems, water velocity is one of the driving forces that govern fish ecology (Blanchet et al., 2008; Ottaway and Forrest, 1983), and it is reasonable to assume it influences fish dispersal between habitat patches. The ability of fish to move in flowing water (their movement potential) is characterized by their swimming ability, and there is a large field of study dedicated to quantifying swimming ability (Videler and Wardle, 1991; Hammer, 1995; Kieffer, 2000; Nelson et al., 2002). Swimming modes are typically defined as sustained (able to sustain for > 200 min), prolonged (able to sustain for between 20 s and 200 min), and burst (able to sustain < 20 s) (Beamish, 1978). Each mode can be represented by a linear relationship between the log of time to fatigue, and swim speed, though the slopes of the relationships for each mode may not be equal (Videler and Wardle, 1991). While each of these modes could potentially be used in the following calculations, we suggest that prolonged swimming is largely responsible for movement of pelagic species between habitat patches in lotic systems, and as such is most appropriate for calculating movement costs between patches. If a species primarily uses burst swimming to move through its environment (eg. some benthic species such as sculpin) or habitat patches are separated by extremely long distances, then it may be appropriate to consider using burst or sustained swimming modes to calculate movement cost. Time to fatigue is typically related to swim speed by a log-linear equation (He and Wardle, 1988; Peake et al., 1996; Adams et al., 2000; Equation 2):

$$\ln(Time) = a + b\ (Swim\ Speed)\ , \tag{2}$$

where *a* describes the intercept and *b* (typically negative) describes the rate of decline in the relationship. Assuming that the individual fish chooses to swim at a speed that maximizes the ground distance it can cover, the maximum ground distance that can be traversed is expressed as a function of water velocity (Equation 3; Castro-Santos, 2005):

$$Ground\ Distance = -\ \frac{e^{a+b*Water\ Velocity-1}}{b}\ . \tag{3}$$

We use the inverse of this relationship to define the movement cost of individual fish (per meter) as a function of water velocity (Equation 4). This movement cost function is used to create a cost surface, based on water velocity, over which the cost of travel between habitat patches is calculated.

$$Movement\ Cost = -\ \frac{b}{e^{a+b*Water\ Velocity-1}} \tag{4}$$

The relative direction of movement (the absolute difference between the direction of flow and the direction of travel in degrees) is incorporated by multiplying the movement cost by a horizontal factor (*HF*). In constructing the HF, we were unable to find any references to the impact of relative flow direction on movement costs for fish. We adopted the minimum HF of 0.1 when direction of travel equals the direction of flow used by Felicismo et al. (2008) for modeling movement costs for Cory's Shearwaters during transoceanic flights. When the direction of travel is 180 degrees relative to the flow direction, the fish experiences the full cost of movement (*HF* = 1), and the HF declines linearly between 180 and 0 degrees (Equation 5).

$$HF = 0.1 + 0.005 * \mathit{Relative\ direction\ of\ movement} \tag{5}$$

Using least-cost path analysis, the cost surface and the horizontal factor are used to calculate the minimum cost to move from one habitat patch to another, which is then used instead of distance in the probability of dispersal calculation. In this way, the swimming ability of fish, as well as the water velocity environment that they must traverse between habitat patches is incorporated into a measure of overall habitat suitability.

Application to Western Silvery Minnow in an augmented prairie river

The Milk River is a medium sized prairie river that flows through southern Alberta, Canada before joining the Missouri River in Montana (Figure 3-1). It is part of an inter-basin water transfer program that annually diverts flow from the neighbouring St. Mary River into the Milk River (DNRC and Reclamation, 2012). The flow augmentation period in the Milk River typically lasts from April to October and increases discharge in the Milk River by roughly 15 – 20 m^3/s for the duration of the augmentation. Natural flow in the Milk River typically ranges from 1 - 5 m^3/s. Due to the Milk River's connection with the Missouri River drainage, it contains a fish assemblage unique in Alberta as well as several species at risk. Western Silvery Minnow is listed as Threatened in Alberta (Milk River Fish Species at Risk Recovery Team, 2008) and Canada (COSEWIC, 2008) due to its limited distribution as well as the impacts to the population posed by potential changes to ongoing hydrologic alteration (COSEWIC, 2008). Despite its threatened status, little is known about the impacts of the flow augmentation on the Milk River population. We chose this system to apply our new methodology due to the increased interest in the impacts of hydrologic alteration on the habitat suitability and availability for Western Silvery Minnow.

From June to August of 2013, we sampled the fish community in the Milk River in southern Alberta using a seine net. Fish and habitat characteristics including water depth and velocity were sampled at 128 sites. Sites were grouped around 5 main access points, with sampling completed at each access point for 2 days every two weeks during the sample period. Areas with relatively slow moving water were preferentially selected for sampling due to the negative effect of water velocity on seine net capture efficiency (Neufeld et al., 2015). We developed a habitat suitability index (HSI) based on this data using multiple logistic regression, with water depth and velocity as the independent variables and Western Silvery Minnow presence as the dependent variable. Bootstrapping was used to estimate 95 % confidence intervals around the parameter estimates. The model was validated using k-fold cross-validation, with k equal to the number of observations, 128. Area under the receiver operating characteristic curve (AUC) was calculated, and the threshold value that produced the highest accuracy was used as the cut-off for predicting Western Silvery Minnow presence or absence.

In July (augmented flow) and October (natural flow) of 2014, we sampled habitat characteristics at two sites on the Milk River, one approximately 1 km long, the other approximately 2 km long (Figure 3-1). Using an acoustic Doppler current profiler (ADCP) and point measurements taken with a handheld velocity meter, we surveyed water velocity and depth at both sites during both time periods. The density of habitat sample points averaged 0.17 / m^2 over both sites and flow states. Water velocity was averaged through the water column for measurements taken with the ADCP, while handheld velocity measurements were taken at 40% of the depth. Flow direction was also measured using the ADCP. All three metrics (water depth, water velocity, and flow direction) were interpolated across each entire site at a 1 m^2 resolution using an inverse distance weighted function. HSI scores were calculated for each 1 m^2 pixel, and areas with scores higher than the HSI threshold were considered habitat patches. Two-factor ANOVA was used to test for differences in patch size between sites and flow states.

Using data obtained from fixed velocity fatigue tests, we estimated the endurance swimming ability of Western Silvery Minnow (Appendix 1), from which the movement cost function was derived. By applying the movement cost function to the interpolated water velocity data, a movement cost surface was created. A value of one was added to the entire cost surface to represent the baseline cost of traversing the surface. Using least-cost path analysis, we calculated the minimum cost of moving between each pair of habitat patches at both study sites during augmented and natural flow rates. Current direction was incorporated as a horizontal factor, equalling 1 when travel direction was 180 degrees relative to current direction and declining linearly to 0.1 when travel direction equalled current direction. This movement cost was used as a measure of separation instead of Euclidean distance in determining the probability of dispersal between patches. The value of theta (θ) is ideally calibrated against observed or inferred movement data, however that data was not available for this study system. As an alternative, the probability of dispersal between each pair of habitat patches and the resulting ECA values were calculated at a range of θ values: 0, 0.005, 0.01, 0.015, 0.02, 0.025, 0.05, 0.1, 0.2, 0.3, 0.4 and 0.5. The Euclidean distance was also measured between each habitat patch, and the ECA was calculated using that distance measure in the probability of dispersal calculation for the same values of θ.

A mixed effects model fit by maximum likelihood was used to determine the influence of flow state, distance measure, and θ on ECA, with site included as a random variable. Theta was modeled as an exponential by using the natural logarithm of theta in the mixed effects model. We present the coefficient estimates and 95% confidence intervals determined through parametric bootstrapping as an indication of the influence each fixed effect has on ECA. All data analysis was performed in ArcGIS (ESRI, 2012) and R (R Core Team, 2013) with the use of packages minpack.lm (Elzhov et al., 2013), lattice (Sarkar, 2008), ROCR (Sing et al., 2005), boot(Canty and Ripley, 2013), plotrix (Lemon 2006), lme4 (Bates et al., 2014), Rcpp (Eddelbuettel and Francois, 2011), Matrix(Bates and Maechler, 2015), and gplots (Warnes et al., 2015).

Results

Bootstrapped logistic regression used for the creation of the habitat suitability index identified negative coefficients for both water depth (-4.64, 95% CI: -0.42 to -10.48) and water velocity (-3.13, 95% CI: -2.80 to -24.35) and an intercept of 3.91 (95% CI: 2.39 to 6.24). These results indicate a decline in habitat suitability with increasing water depth and velocity (Figure 3-2). The model was most accurate (84%) at a threshold value of 0.68, this was subsequently used as the cut-off for delineating Western Silvery Minnow habitat patches. K-fold cross validation indicated a mean prediction error rate of 0.203.

Average water depth and velocity were lower during natural flow rates than augmentation (Table 3-1). There was also a higher number of suitable habitat patches and a higher proportion of the wetted area that was considered suitable during natural flow (Table 3-1), though patch size did not differ significantly by either site or flow state (Two-factor ANOVA, df = 1,1, $F_{Site} = 1.901$, $F_{Flow} = 1.019$, $p_{Site} = 0.169$, $p_{Flow} = 0.314$). During augmented flow suitable habitat patches were largely confined to the margins of the channel and adjacent to exposed sandbars, particularly in Site 2 (Figure 3-3).

Western Silvery Minnow endurance swimming ability (see Appendix 1), corresponds to a cost function of:

$$Movement\ Cost = \frac{20.53}{e^{17.01-20.53*Water\ Velocity}}, \qquad \text{(Figure 3-4)}$$

following the calculation technique presented above. Mean distance between habitat patches increased during natural flow rates at both sites (Table 3-2). The mean movement cost between habitat patches increased during natural flow at Site 1, and decreased during natural flow at Site 2 (Table 3-2). The mean movement cost between habitat patches was lower than the mean

Euclidean distance for both flow states and both sites. Movement cost was linearly related to Euclidean distance between habitat patches, though each patch pair appeared to fall into one of two distinct linear relationships, corresponding to upstream and downstream movement between patch pairs (Figure 3-5). Distances and movement costs between habitat patches were generally lower for Site 1 than Site 2 as a result of the longer stream length encompassed by Site 2 (Figure 3-6).

Equivalent connected area (ECA) was calculated using both movement cost and Euclidean distance as the measure in the probability of dispersal calculation. When theta was 0, ECA equaled the sum of the areas of all the habitat patches, and as theta increased, ECA declined, asymptotically approaching the area of the largest single habitat patch (Figure 3-7). The logarithm of theta had a negative effect of -0.015 on ECA (Linear mixed effects model, 95% CI = -0.019 - -0.012), as might be expected from the structure of the ECA and probability of dispersal equations. ECA was higher during natural flow than augmented flow (Linear mixed effects model, coefficient = 0.119, 95% CI = 0.109 – 0.130) and lower when calculated using Euclidean distance between habitat patches (Linear mixed effects model, coefficient = -0.017, 95% CI = -0.028 - -0.007). The site random effect accounted for 58.0% of the random effect variance.

Discussion

The incorporation of swim performance into habitat suitability provides a novel technique for assessing the impacts of hydrologic alterations on stream fishes. Compared to the use of Euclidean distance to calculate probability of dispersal, our measure of movement cost was a more realistic indicator of the separation of habitat patches, integrating information about habitat conditions (water velocity) and swimming ability. The use of cost measures other than distance to assess dispersal of organisms has proven a useful tool for describing population structure (Michels et al., 2001; LaRue and Nielsen, 2008; Wang et al., 2009). When equivalent connected area (ECA) was calculated using movement cost instead of distance between habitat patches, the estimates of overall habitat suitability increased. Perhaps more importantly, estimated habitat suitability for Western Silvery Minnow decreased during augmented flow in the Milk River regardless of which measure of separation was used, distance or movement cost.

The increase in estimated habitat suitability when ECA was calculated with movement cost was due to the increased probability of dispersal between habitat patches resulting from a between patch cost which was on average less than the between patch distance. This was the result of the influence of water current and suggests that Western Silvery Minnow may be able to utilize the current to assist movement between habitat patches. Horizontal factors such as water current have been shown to assist movement in other fish species (Arnold et al., 1994; Hinch and Rand, 2000; Kettle and Haines, 2006), though more commonly in birds, insects and plants (Nathan et al., 2002; Gonzalez-Solis et al., 2009; Chapman et al., 2008) using wind to help disperse between habitats. This assistance may be expected for downstream movement, however our results indicate that the cost of between patch movement in the upstream direction was also usually lower than the shortest distance.

The nature of the horizontal factor provides a clear benefit for movement in the downstream direction, with movement costs reduced by up to 90% in the case of movement in the exact same direction as the current (Felicisimo et al., 2008). However, reductions in the full movement cost were still experienced with even small deviations from movement directly against the current. Oblique movements allowed for movement cost to be lower than distance even for movements with a net upstream direction. This result highlights the need for further research into the energetics and costs of downstream and oblique movements by stream fishes. Most research has focused on measuring swimming ability when moving directly against the current, while in natural environments fish can choose to move with, against or at an angle to the water current.

An important consideration when comparing the estimates of habitat suitability calculated using both measures of separation is the question of whether the movement cost values are directly comparable to distance (ie. same units). Movement cost is measured in m^{-1}, and when calculated over the distance between habitat patches, becomes unitless. As such, movement cost as defined here is not a representation of distance, but rather both movement cost and distance are alternate measures of the separation of habitat patches. The question of which measure of separation is more valid in describing the dispersal between habitat patches, should be assessed ideally through validating both models against observed dispersal data, or a surrogate indicator of dispersal (eg. genetic variation (Michels et al., 2001)). Such data is unfortunately not available for this study system and an examination of the underlying assumptions of our movement cost function provides an initial assessment of the validity of the method.

Movement cost as defined here makes several assumptions about fish behaviour and response to water velocity. Least cost path analysis by definition identifies the route between two points that minimizes the cost, and this depends upon having a complete knowledge of the entire landscape

(Adriaensen et al., 2003). With constantly shifting sandbars and high turbidity in the Milk River, Western Silvery Minnow may have limited knowledge of their environment beyond their immediate vicinity. Some studies have shown that despite this, observed animal movements do approximate least cost paths (Janin et al., 2009; McElroy et al., 2012), suggesting that some species are able to select these theoretically ideal pathways. Standen et al. (2004) found Sockeye Salmon *Oncorhynchus nerka* preferentially selected relatively low velocity routes through slow portions of the Seton River, British Columbia. McElroy et al. (2012) showed that Pallid Sturgeon, *Scaphirhynchus albus*, followed routes through the Missouri River that minimized movement cost, suggesting an ability to predict habitat features beyond their immediate perception and select close to optimal routes by fish in a turbid prairie river. These studies suggest least cost path analysis can provide a realistic model of fish movement in rivers.

Our movement modelling also assumes fish are choosing the optimum swim velocity and that the scale of the model is appropriate. Studies have shown that some species, particularly those that undertake large-scale migrations, tend to optimize swim speeds (Hinch and Rand, 2000; Castro-Santos, 2005). Western Silvery Minnow are known to undertake upstream movements of at least 14 km over a short time period (K. Neufeld, unpublished data), which suggests that long migrations may be a component of their life history. If so, optimization of swim speed is a reasonable assumption, though further investigation into this component of their life history is a critical area of future research. The observed long distance movement also supports the scale at which movement was modelled. Study reaches were ~ 1-2 km long, which is well within the range of potential movement for the species. Additionally, the size of cells within the modelled habitat should be smaller than any influential feature in the environment (Adriaensen et al., 2003). While fish have been shown to utilize vortices, nonlinear flow and small pockets of slow moving water to reduce swimming costs (Garner, 1999; Hinch and Rand 2000; Liao et al., 2003), these feature are likely evenly distributed and relatively uncommon due to the uniform substrate and habitat at our study site (AMEC, 2008).

To broaden the applicability of our results, further work should be done to measure the swimming ability of Western Silvery Minnow of different lengths, and at different water temperatures. Our results are based on swim tests run on adult, 85-95 mm Western Silvery Minnow tested at 17 °C for consistency. Body size has been shown to have a large effect on swimming capabilities (Drucker and Jensen, 1996; Peake et al., 1996; Muller et al., 2000), and young of the year individuals would likely have much lower swimming capacities than adults, along with higher movement costs. The effects of augmented flow and the associated higher water velocities would be exacerbated for smaller individuals, with movement potential and habitat suitability further decreased. Water temperature also has a large impact on swim performance (Brett, 1967; Kauffman and Wieser, 1992; Ficke et al., 2011), and the complete range of swimming ability of the species is not represented. Brett (1967) showed that swimming ability of fish peaks, declining both above and below an optimal temperature. Work by Bestgen et al. (2010) on the Rio Grande Silvery Minnow *Hybognathus amarus* and Ficke et al. (2011) on the Brassy Minnow *Hybognathus hankinsoni* suggest that Western Silvery Minnow may have peak endurance capabilities at a temperature greater than 17 °C. During much of the year, water temperatures in the Milk River exceed 17 °C, and movement cost estimates may be reduced for this period if endurance capabilities are higher.

The method described here provides a new tool for those who wish to incorporate powerful movement modelling capabilities with habitat suitability assessments. Modelling the movement of fish in stream systems has been given a boost by the advent of easy to use GIS interfaces and the applicability of these systems has been demonstrated by others (eg. Le Pichon et al., 2006; McElroy et al., 2012). Still, there is abundant opportunity for further development and refinement of these modelling techniques. Circuit theory offers an alternative to graph theory for modelling connectivity of habitat patches that could incorporate the effects of alternate pathways (McRae et al., 2008). Movement functions may be based on concepts other than swimming ability, such as drag (McElroy et al., 2012) or energetics (eg. unified foraging theory (Railsback et al., 1999)). Dispersal could also be described as a leptokurtic distribution (Skalski and Gilliam, 2000), rather than a normal distribution, which may match well with described alternate swim behaviours in fish (i.e. non-performers in swim tests; Adams et al., 2000; Parsons and Smiley, 2003). While numerous options exist for further refinement, we feel that the movement cost function described here provides a strong basis on which to build.

The results of this study indicate that during augmented flow, habitat suitability for Western Silvery Minnow is reduced. Consistently across all three metrics, HSI, ECA calculated using distance, and ECA calculated using movement cost, the amount of available suitable habitat was lower during augmented flow in July 2014 than natural flow in October, 2014. This may have important implications in the event of further alterations to flow in the Milk River, with additional augmentation unlikely to provide additional suitable habitat. Spawning and overwintering habitats must also be considered when predicting the impacts of hydrologic alteration on the species. The spawning requirements of Western Silvery Minnow are not currently well understood, with closely related species utilizing pelagic broadcast spawning (Plains Minnow *Hybognathus placitus* [Ree et al., 2005]; Rio Grande Silvery Minnow *Hybognathus amarus* [Platania and Altenbach, 1998]). If it is a pelagic broadcast spawner, low flows and the associated lower water velocities may be detrimental to egg survival and recruitment (Platania and Altenbach, 1988). Overwintering habitat is a potentially limiting factor for the species, especially in the Milk River where drought has at times reduced winter flows to nil and caused large die-offs when isolated pools dry up or freeze (RL&L Environmental Services Ltd., 2002). In these instances, increased flow in winter months may ensure that adequate overwintering habitat exists, and prevent increased mortality. As more information becomes available on spawning and overwintering habitat requirements, that data can be compiled with the information presented here to provide a more complete picture of the impacts of hydrologic alteration on Western Silvery Minnow.

We have described a method for incorporating movement cost into habitat suitability assessments for freshwater fishes. Our movement cost function, while strongly correlated with distance, provides an alternate method for estimating probability of dispersal that includes the mechanistic influences of swimming ability and water velocity. While we have demonstrated the utility of this method, validation against observed dispersal data is needed to determine its accuracy. We have also shown that flow augmentation in the Milk River of southern Alberta is likely reducing the amount of suitable habitat for Threatened Western Silvery Minnow and increasing the cost of movement between habitat patches. Movement in the Milk River at the scale assessed is likely critical to the ability of Western Silvery Minnow to recolonize dewatered reaches and for the continued persistence of the species. Any inhibition of this movement may have detrimental effects on the species.

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Figures

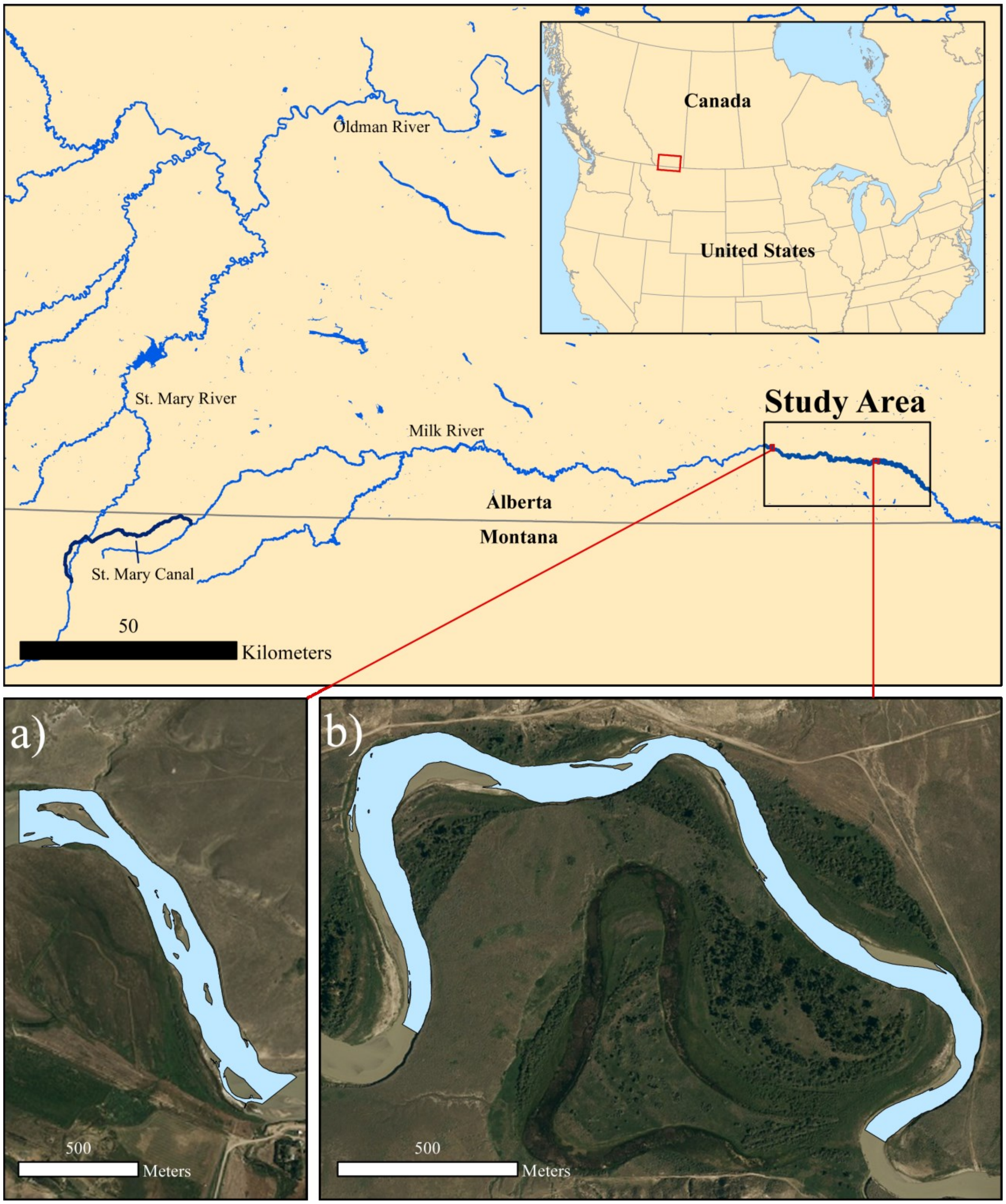

Figure 3-1.The Milk River of southern Alberta, Canada. The study area indicates the extent of the Western Silvery Minnow sampling in 2013 that was used to create the habitat suitability index. Site 1 (a), and Site 2 (b) indicate the extent of water depth and velocity sampling in July and October of 2014.

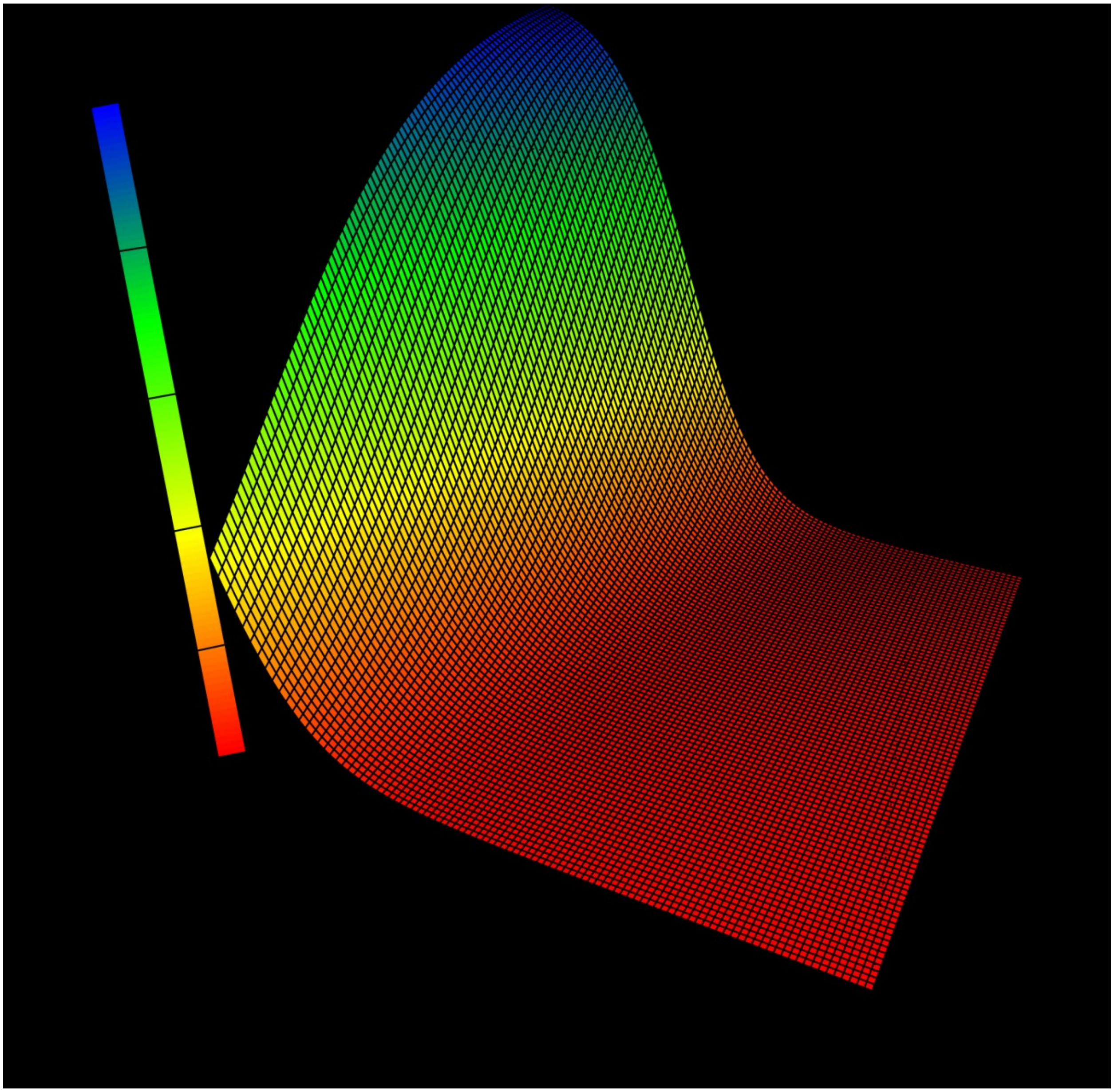

Figure 3-2. Habitat suitability index based on water depth and velocity for Western Silvery Minnow in the Milk River of southern Alberta. Based on multiple logistic regression with a coefficient for water depth of -4.64 (95% CI: -0.42 to -10.48) and water velocity -13.13 (95% CI: -2.80 to -24.345) and an intercept of 3.91 (95% CI: 2.39 to 6.24).

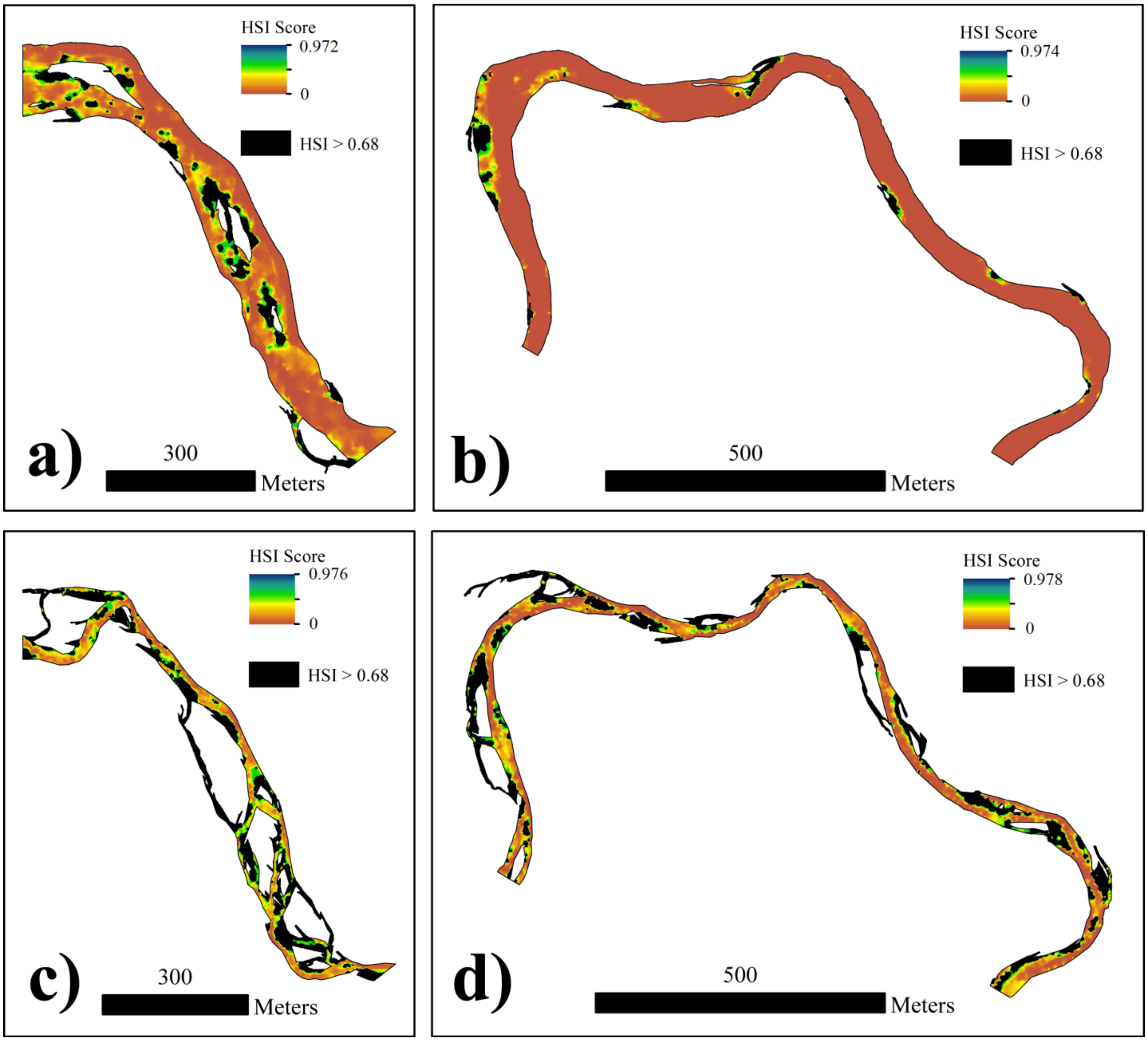

Figure 3-3. Geographical representation of the Western Silvery Minnow habitat suitability index for a) Site 1 during augmented flow, b) Site 2 during augmented flow, c) Site 1 during natural flow, and d) Site 2 during natural flow. Black areas indicate patches of suitable habitat with a HSI score > 0.68.

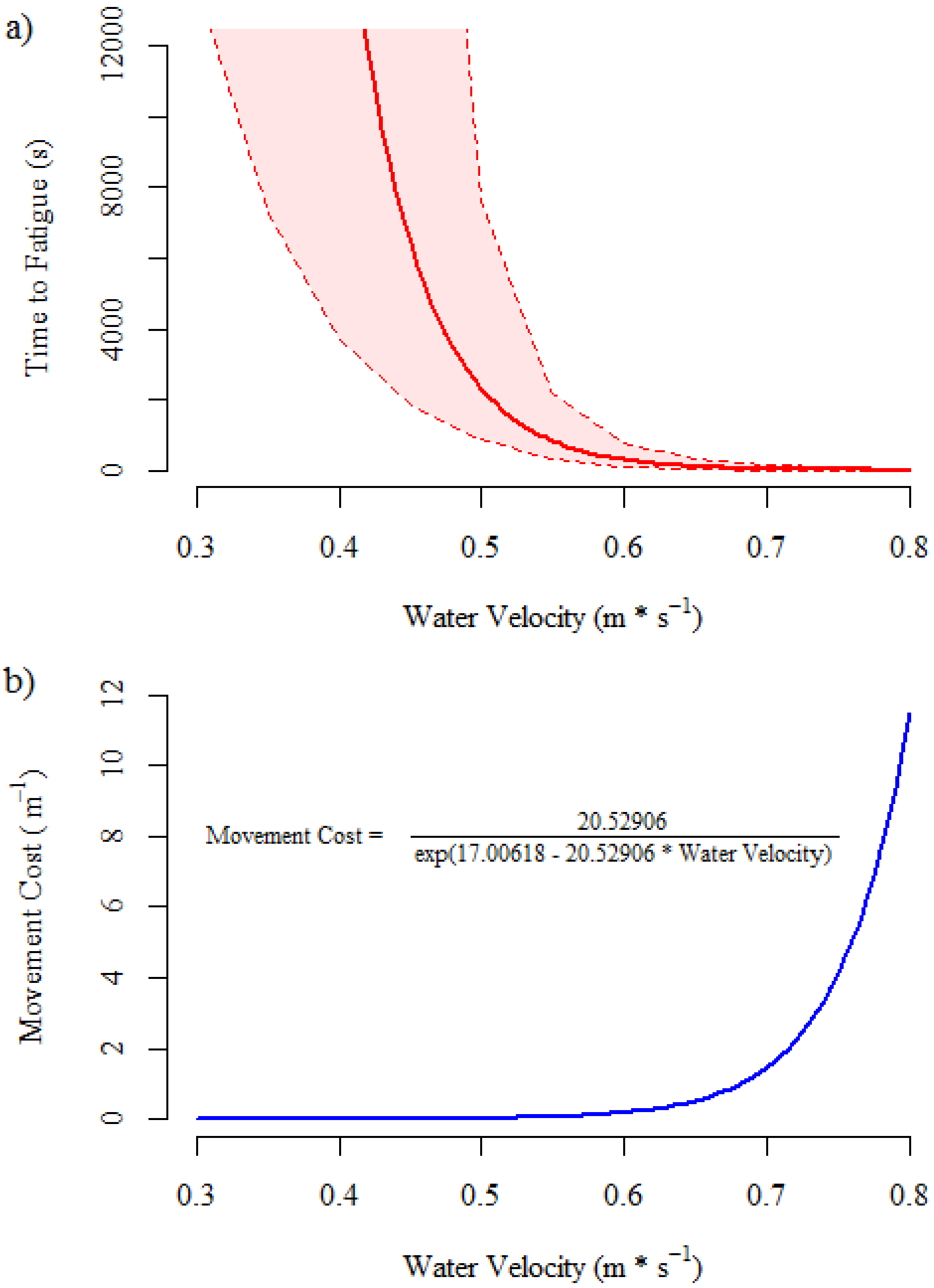

Figure 3-4. The endurance – water velocity relationship for 85-95 mm (fork length) Western Silvery Minnow (a), with 95% confidence intervals shaded in light red. The associated movement cost function is shown in panel b).

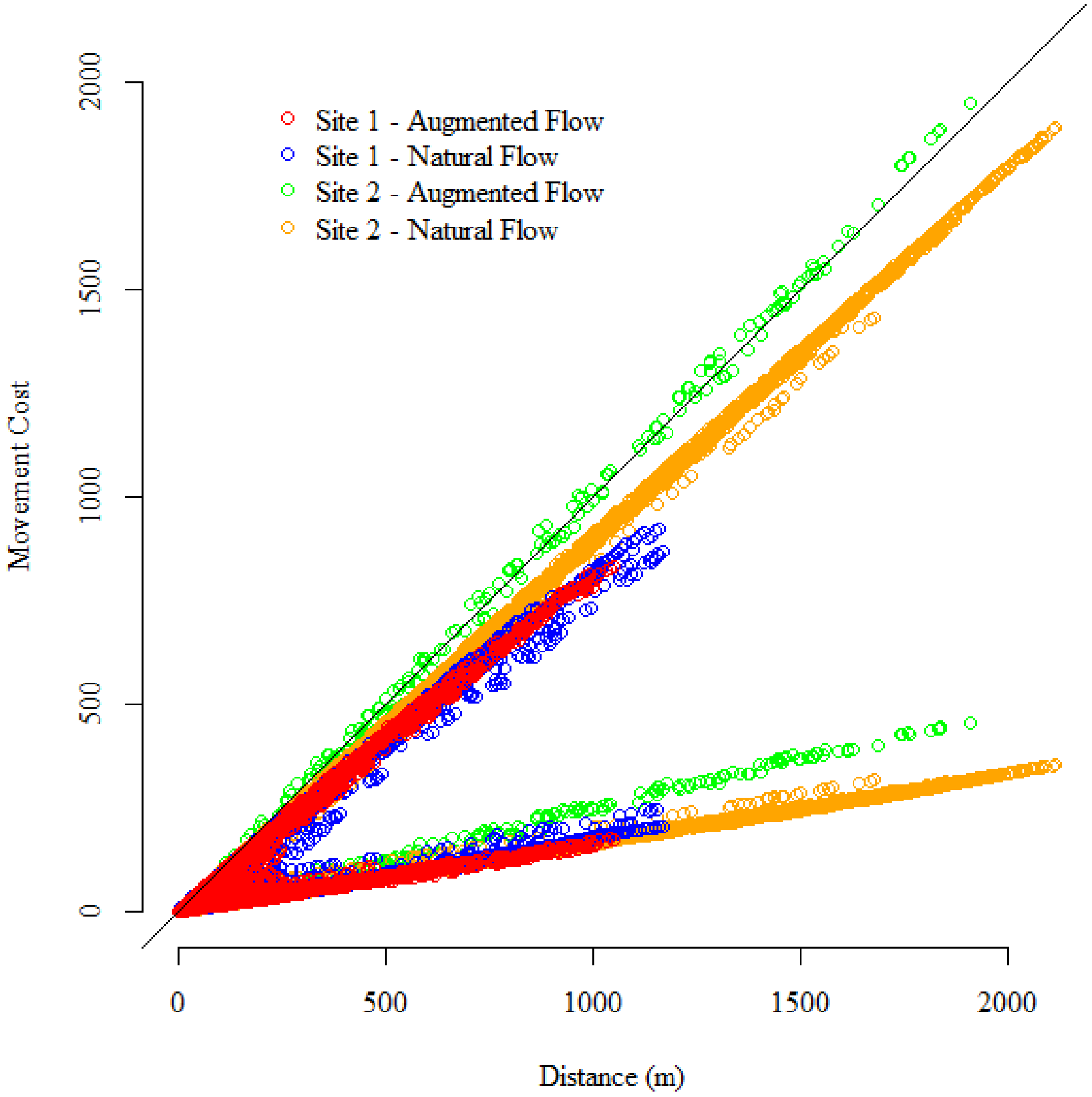

Figure 3-5. Movement cost vs. Euclidean distance between all habitat patch pairs for both sites during augmented and natural flows. The black line represents a 1:1 relationship.

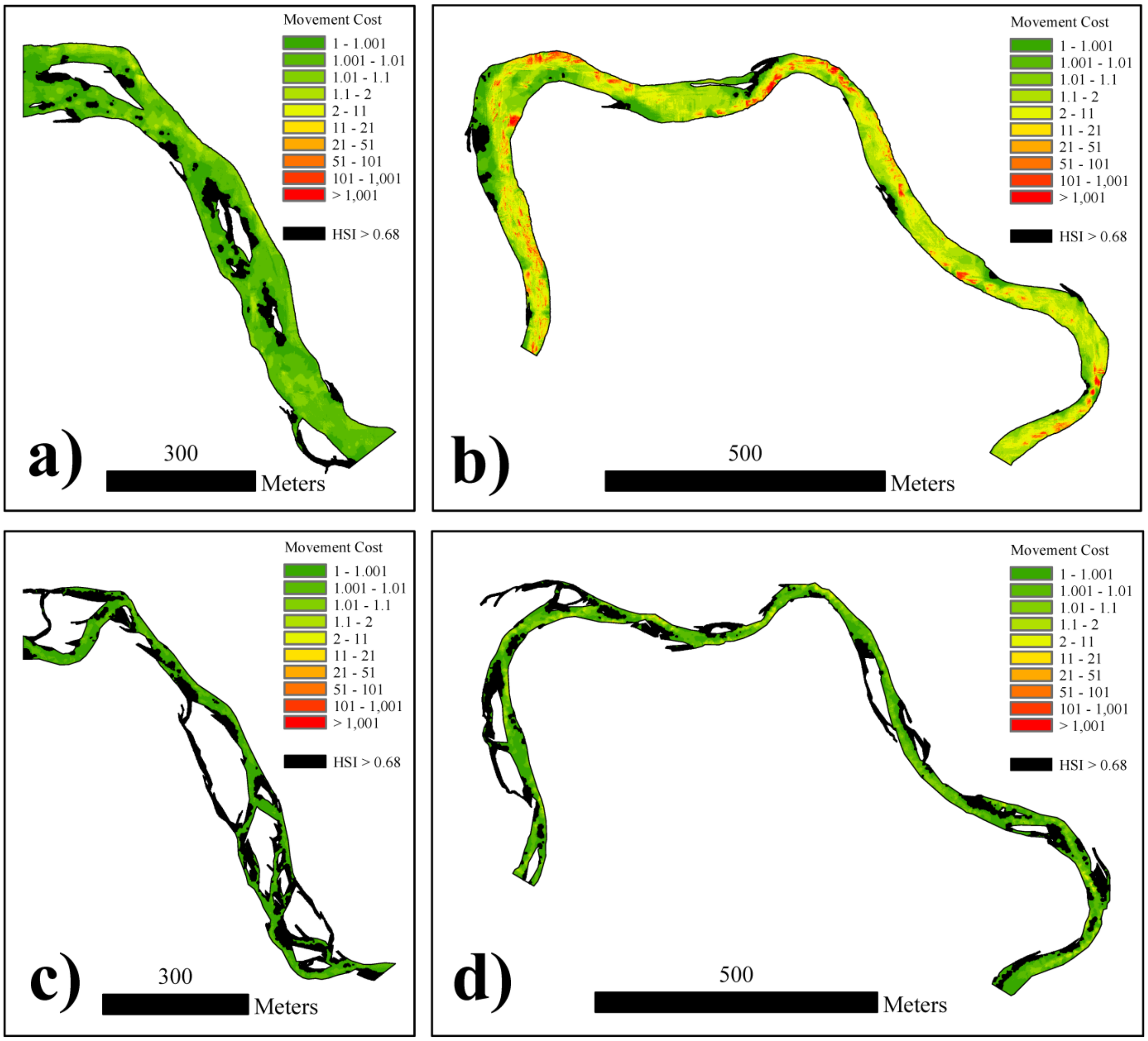

Figure 3-6. Geographical representation of movement cost based on water velocity for a) Site 1 during augmented flow, b) Site 2 during augmented flow, c) Site 1 during natural flow, and d) Site 2 during natural flow. Black areas represent suitable habitat patches with a HSI score > 0.68.

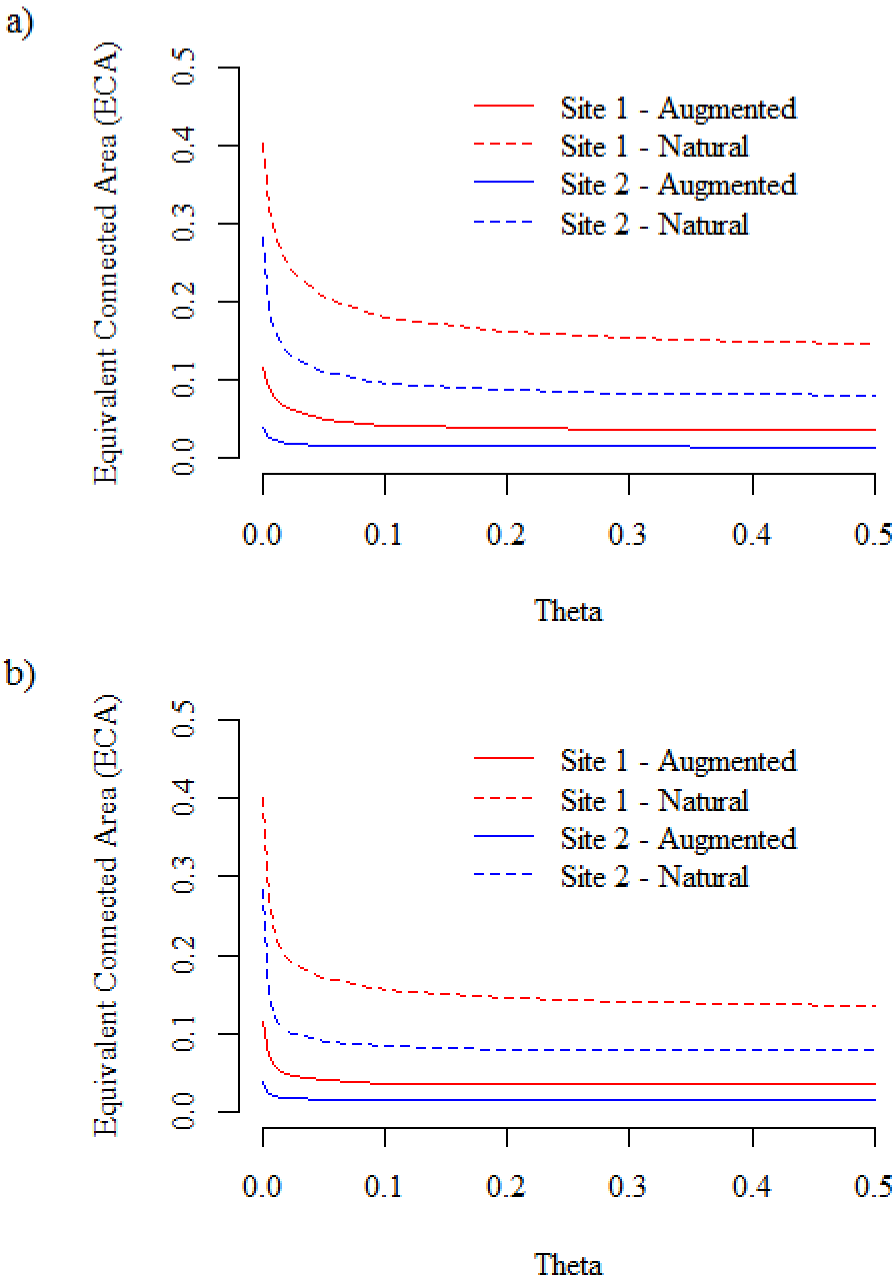

Figure 3-7. Equivalent connected area (ECA) over theta values from 0 to 0.5, calculated using movement cost (a) and Euclidean distance (b) as the measure of separation in the probability of dispersal calculation.

Tables

Table 3-1. Physical habitat and habitat suitability measurements for Sites 1 and 2 during augmented and natural flows.

Site	Flow State	Total Wetted Area (m^2)	Mean Water Depth (m)	Mean Water Velocity (m/s)	Number of Suitable Habitat Patches	Total Suitable Area (m^2)	Suitable Area as Proportion of Wetted Area	Mean Patch Size (m^2)
1	Augmented	107446	0.33	0.35	35	10260	0.095	293.1
1	Natural	53848	0.20	0.21	57	21628	0.402	379.4
2	Augmented	103383	0.55	0.60	23	4002	0.039	174
2	Natural	63064	0.24	0.29	81	17853	0.283	220.4

Table 3-2. Euclidean distance and movement cost measurements for Sites 1 and 2 during augmented and natural flows.

Site	Flow State	Minimum Between Patch Distance (m)	Maximum Between Patch Distance (m)	Mean Between Patch Distance (m)	Minimum Between Patch Cost	Maximum Between Patch Cost	Mean Between Patch Cost
1	Augmented	2.83	1051.52	352.38	0.44	831.53	176.08
1	Natural	3	1167.84	414.52	0.57	923.45	205.08
2	Augmented	4	1908.25	714.19	0.55	1950.63	445.41
2	Natural	3	2114.04	764.54	0.49	1890.15	405.43

Appendices

Appendix 1. Endurance Swimming Ability of Western Silvery Minnow Hybognathus argyritis

Forty adult Western Silvery Minnow, 85-95 mm long (fork length), were captured in the Milk River on October 24-26, 2013 and transported to the University of Alberta in Edmonton, Alberta to undergo endurance swim testing. Fish were housed in 2 120 L aerated tanks held at 17 °C, and fed a mixture of size 0 trout pellets (BioVita starter from Bio-Oregon®) and spirulina flakes (Nutrafin Max Spirulina Flakes®) once a day. Fixed velocity fatigue swim tests were run from May 5, 2014 to September 12, 2014. Due to some mortality not all 40 Western Silvery Minnow were put through the swim test: twenty one individuals were tested twice, and 7 individuals were tested once for a total of 49 tests completed.

The swim tests followed protocols for fixed velocity tests described by previous authors (Brett,1967; Videler and Wardle, 1991; Hammer 1995). Individuals were transferred from their holding tanks to a 10 L Loligo® swim tunnel respirometer filled with fresh 17 °C water. After 30 minutes of acclimation at 0.05 m/s, water velocity was slowly increased at a rate of 0.05 m/s per minute until a predetermined target velocity was reached. Eleven evenly distributed target velocities were determined based on preliminary testing: 0.31, 0.35, 0.39, 0.43, 0.47, 0.52, 0.56, 0.61, 0.65, 0.70, and 0.75 m/s. Once the fish reached the target velocity, the time to fatigue was noted, with fatigue defined as the point in time at which fish could no longer maintain their position without being pushed against the back grate. If the fish failed to reach the target velocity, time to fatigue was recorded as zero. All tests were stopped at 200 minutes if the fish were still swimming. Water velocity was assumed to be equal to swim speed for the duration of the tests.

Logistic regression was used to calculate the water velocity at time to 50 % fatigue for a series of time to fatigue thresholds (Brett 1967). The relationship between time to 50% fatigue and water velocity was fit to a log-linear curve using linear regression in R (R Core Team, 2013). This two step process was bootstrapped 10,000 times to generate confidence intervals around parameter estimates and confidence bands around the predicted relationship.

Western Silvery Minnow endurance swimming ability, when fit to a log-linear curve as described above was represented by:

$$Time = \ e^{a+b(Swim\ Speed)}$$

where a $= 18.01$ (95% CI $= \ 12.29 - 25.17$), and b $= \ -20.53$ (95% CI $= \ -32.98 - -10.51$) (Figure A-1).

In order to assess the suitability of the analysis technique used, we compared the performance of the technique to that of simple linear regression using simulated data with known parameter values and error structure. We simulated time to fatigue data at the eleven water velocities tested above based on the endurance relationship:

$$Time\ to\ Fatigue = e^{18-21\,*\,Water\ Velocity}$$

with a log-normal error distribution. Time to fatigue values greater than 12000 seconds were truncated to 12000 seconds, as in actual experimental data. Both the method described by Brett (1967) and linear regression were used to estimate parameter values based on the simulated data. We simulated data with total sample sizes of 11, 33, 55, 110, 220, and 550, and standard deviations of 1, 10, 100, 1000, and 10000 seconds. For each combination of sample size and simulated standard deviation, we created 1000 simulated datasets and analyzed each dataset using both methods. The estimated mean parameter values were compared to the known parameter values of the simulated data, and the standard deviation of the estimated parameter values were compared between analysis methods.

The method proposed by Brett (1967) and used in this appendix produced parameter estimates that were much less biased than linear regression (Figure A-2). Bias for both parameters was low by a sample size of ~50 for all levels of standard deviation in the simulated data. Linear regression produced increasing bias as standard deviation in the simulated data increased, with no effect of sample size.

There was lower variation in the parameter estimates from linear regression, as indicated by standard deviation (Figure A-3). This pattern was consistent across all sample sizes and standard deviations of simulated data. For both methods, variation in the parameter estimates declined as sample size increased and as the standard deviation of the simulated data decreased.

The method proposed by Brett (1967) and used in this appendix produces less biased parameter estimates for endurance swim test data, though the variation in those parameter estimates is greater. A potential bias is more detrimental to the interpretation of our data than high uncertainty, especially when the uncertainty is quantifiable. Consequently, the use of linear regression should be avoided for interpretting truncated endurance swim test data in favour of the method proposed by Brett (1967).

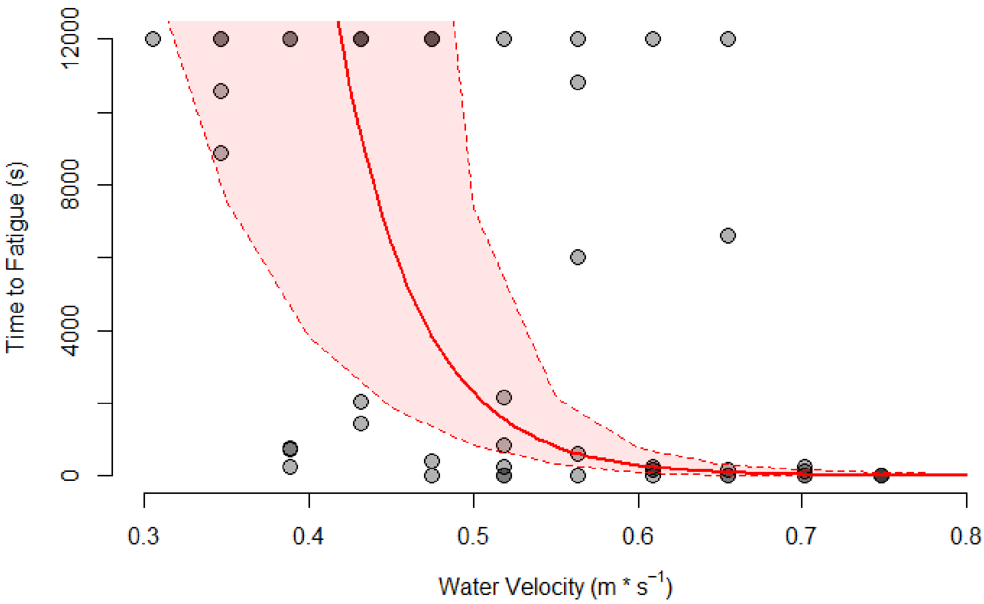

Figure A-1. Raw Western Silvery Minnow swim test data with log-linear curve (solid red line). Dashed lines and shaded area represent 95% prediction intervals for the relationship.

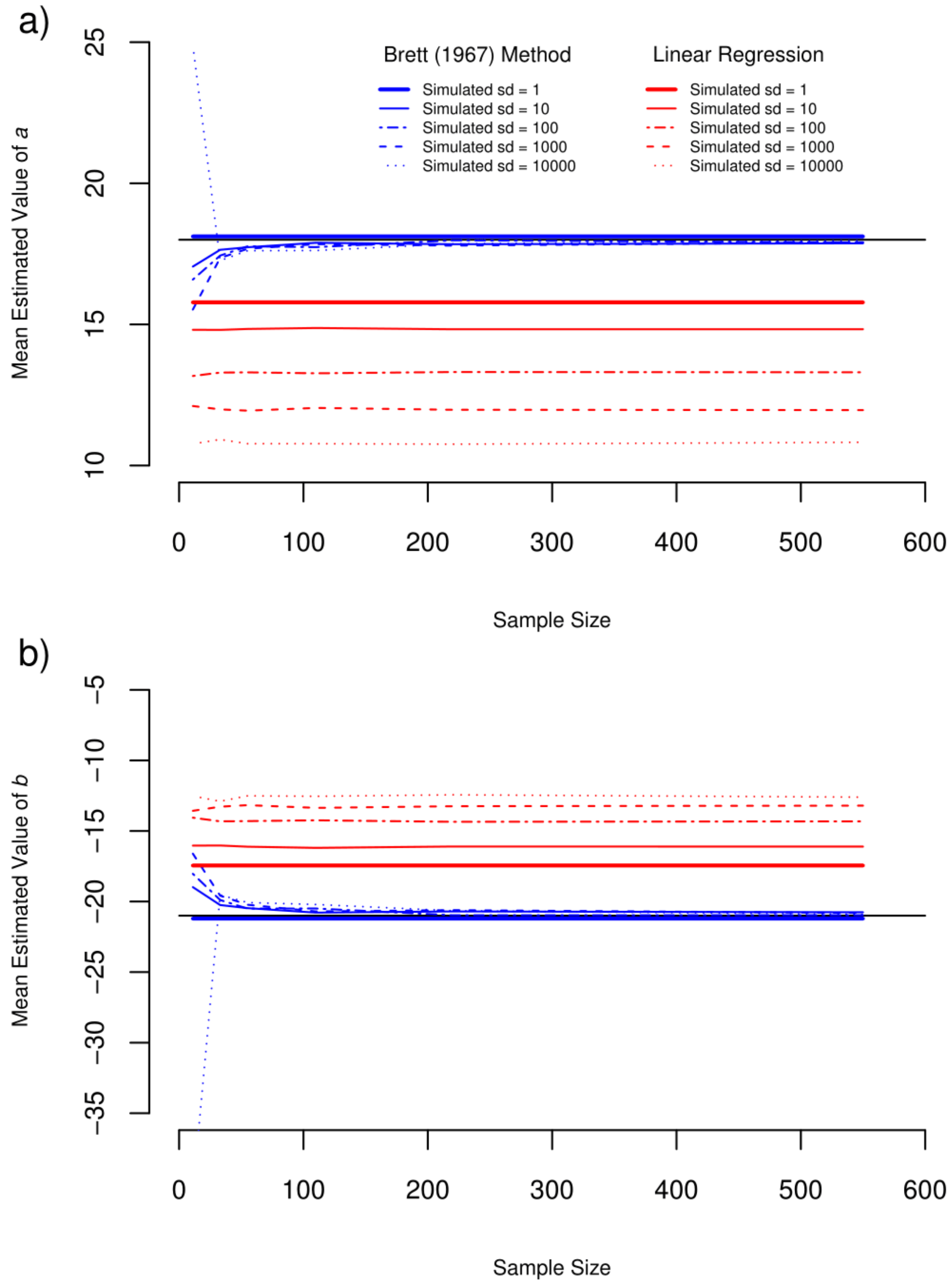

Figure A-2. Mean estimated parameter values for the log-linear relationship describing endurance from simulated data. Parameter estimates made using linear regression and the method described by Brett (1967) are both shown. Panel a shows parameter estimates for a from Log(Time to Fatigue) = a + b*(Water Velocity). Panel b shows parameter estimates for b from Log(Time to Fatigue) = a + b*(Water Velocity).

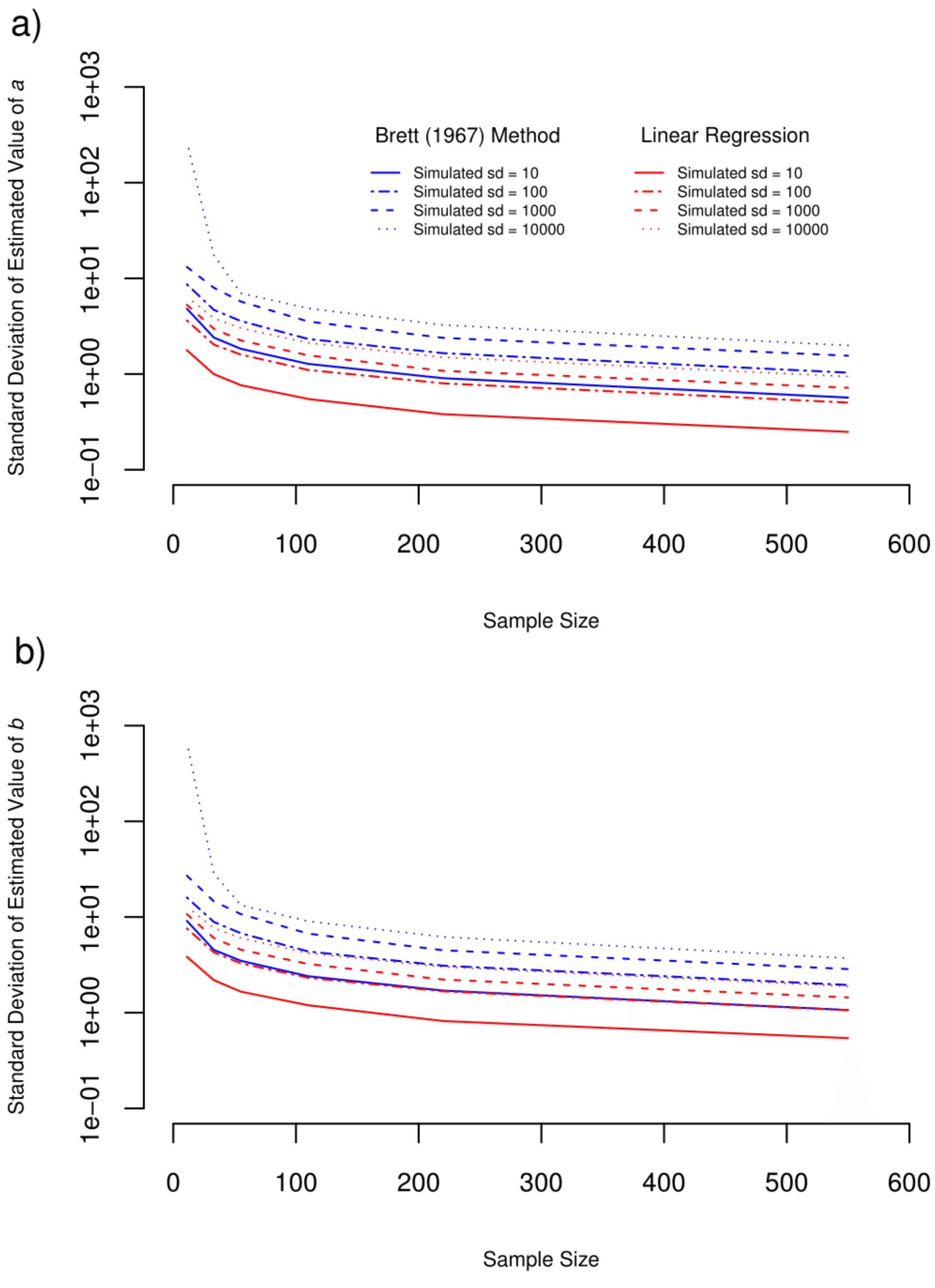

Figure A-3. Standard deviation of estimated parameter values for the log-linear relationship describing endurance from simulated data. Parameter estimates made using linear regression and the method described by Brett (1967) are both shown. Panel a shows standard deviation of parameter estimates for a from Log(Time to Fatigue) = a + b*(Water Velocity). Panel b shows standard deviation of parameter estimates for b from Log(Time to Fatigue) = a + b*(Water Velocity).

4.0 General Conclusions

With rapidly changing stream fish communities and habitats worldwide, researchers must adapt and develop techniques that are able to effectively assess these changes. An interdisciplinary approach incorporates aspects from fields of study that may be traditionally underutilized by many fish scientists, but nonetheless have a large impact on structuring fish communities and populations. Acknowledging that hydrology not only impacts fish directly, but also the methodologies we use to monitor them opens the door to developing more robust techniques. To ignore these impacts could confound our efforts to monitor populations that are already experiencing multiple stressors. We investigated two separate, but related examples of adopting an interdisciplinary approach to assessing fish populations: the effects of incorporating flow state into estimates of capture efficiency and incorporating swim performance into habitat suitability assessments.

The incorporation of unique parameters with analysis and modeling techniques used for assessing the impacts of hydrologic alteration on fishes improved our understanding of these impacts. In the case of capture efficiency, acknowledging flow as a factor influencing our ability to monitor fish populations improved our ability to estimate capture efficiency. Including swim performance of fishes as a mechanism contributing to the suitability of habitat enables us to move beyond basic assumptions about the probability of dispersal between habitat patches and presents a more accurate picture of the overall suitability of a riverscape. Both these examples demonstrate the utility and benefits of considering concepts from various disciplines.

The direct connection between capture efficiency of fish sampling gear and flow rate has not been previously investigated (to our knowledge) and this advancement provides a clear advantage for those who rely upon capture efficiency estimates to assess fish population metrics.

Capture efficiency of fish sampling gear has been commonly linked to various physical habitat, and fish characteristic variables (Parslet et al., 1989; Bayley and Herendeen, 2000) and any further reduction in uncertainty in population assessments will allow scientists and managers to better manage and protect populations from the many threats they currently face. It highlights the need for researchers to look beyond traditionally acknowledged effects to quantify capture efficiency in a changing hydrologic environment. With the numerous other types of sampling gear used to monitor fish in streams and rivers, there is an urgent need to assess the impacts of flow on their capture efficiency as well. Electrofishing, various types of netting, visual surveys, and tag detection systems may all be linked to flow.

The use of hydraulic modelling and habitat suitability curves has been increasingly used to assess the impacts of flow on fishes (Katopodis, 2003; Mouton et al., 2007; Garcia et al., 2011). Concurrently, movement cost functions have been developed to model dispersal and habitat connectivity in aquatic systems (Michels et al., 2001). The combination of habitat suitability and connectivity measures in recently developed graph theory metrics (Saura and Pascual-Horton, 2007) is an important step towards integrating multiple fields, however it does not address shortcomings in the methods used to define suitability or connectivity. An interdisciplinary approach is needed to provide a mechanistic foundation for the metrics that define these base features. By including fish swim performance in our habitat suitability assessment, we introduced a mechanistic approach for defining connectivity. It is important to note that other mechanisms can and should be investigated as potentially informative. Other ecological, behavioural and physiological constraints may drive connectivity of landscapes and methods of incorporating them into connectivity measures could be explored. Fish movement may be driven to some extent by interspecific interactions, physiological constraints, and other physical habitat variables. Additionally, while we were unable to evaluate the movement cost function developed in Chapter 3 with empirical data, such evaluations should be the goal as new cost measures are created. The collection of actual movement data, or a surrogate such as genetic information could add value to studies developing these cost metrics.

Our findings suggest that the hydrologic alteration in the Milk River is having an impact on the Western Silvery Minnow population. The number of suitable habitat patches was reduced during augmented flow, along with the overall amount of suitable habitat. The response in movement costs between habitat patches to change in flow was not as consistent, with costs increasing at one site and decreasing at another. Overall, flow augmentation currently seems to be having a detrimental effect in the Milk River. The increased capture efficiency of seine nets during augmented flow provides a good example of the potentially confounding effects of inaccurate assessments methodologies. While increased flow may be detrimental to populations, seining may be more effective at capturing fish during augmented flow. If population assessments rely upon comparisons between seine net catch rates that occurred at different flow rates, estimates of relative population size at high flows may be artificially inflated, indicating the opposite of the actual effect.

The unique augmentation situation in the Milk River limits the potential discharges at which sampling can be done. Generally, there is only augmented and natural flow, both of which are relatively constant, and the intermediate discharges only occur for short periods as diversion ramps up or draws down. This means that a complete assessment of effects at intermediate flows cannot easily be directly measured. An important next step in determining the full impacts of hydrologic alteration on the Western Silvery Minnow would be hydrologic modelling of physical habitat at intermediate discharges. Programs such as River 2D (Steffler and Blackburn, 2002) provide these capabilities and further research into applying programs such as this are needed.

An assessment of the spawning strategy of Western Silvery Minnow and the implications of flow rate on recruitment is also needed. While our results indicate that greater flows reduce available habitat, previous studies have found that pelagic broadcast spawning fish require extended sections of flowing water for persistence (Dudley and Platania, 2007). This information incorporated with overwintering habitat requirements would provide a much clearer picture of the impacts of hydrologic alteration. Any program designed to monitor Western Silvery Minnow populations in these changing flows should also incorporate flow as a potentially confounding variable in estimates of capture efficiency.

This work has shown the inherent benefits of taking a interdisciplinary approach to the assessment of hydrologic alteration on stream fishes. With the critical threats facing many fish populations, it is more essential than ever for scientists and managers to be able to accurately describe the populations and communities they work with. With hydrologic alteration impacting fish directly as well as their required habitats, methods for assessing both these components should incorporate mechanistic principles that reduce uncertainty and add predicting power to the results. As climate continues to change and human induced stressors continue to grow, scientists must continue to adapt and develop new techniques to answer questions that will decide the fates of stream fishes around the globe.

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