Incorporating asymmetric movement costs into measures of habitat connectivity to assess impacts of hydrologic alteration to stream fishes

Kenton Neufeld1 | Douglas A. Watkinson2 | Keith Tierney3 | Mark S. Poesch1

1Department of Renewable Resources, University of Alberta, Edmonton, AB, Canada
2Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, Canada
3Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada

Correspondence
Mark S. Poesch, Department of Renewable Resources, University of Alberta, Edmonton, AB, Canada.
Email: poesch@ualberta.ca

Funding information
Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: RES0017085; Alberta Conservation Association; Fisheries and Oceans Canada

Abstract

Aim: Hydrologic alterations are widespread in freshwater ecosystems worldwide and often detrimentally impact fish populations. Habitat suitability models are commonly used to assess these impacts, but these models frequently rely upon observed fish–habitat relationships rather than more mechanistic underpinnings. The aim of this study was to demonstrate how to incorporate swim performance into a measure of habitat connectivity at a fine scale, providing a method for assessing the availability of suitable habitat for stream fishes.

Location: We applied this technique to an endangered species, the Western Silvery Minnow Hybognathus argyritis, in the Milk River of southern Alberta, Canada. The Milk River is an augmented system, where a diversion in nearby St. Mary River augments flow by a factor >3 × (from 1–5 m3/s to 15–20 m3/s).

Methods: We used laboratory measured swim performance of Western Silvery Minnow to develop a movement cost function that was used in conjunction with a habitat suitability model to assess habitat availability via a recently developed graph-theoretic metric, equivalent connected area (ECA).

Results: Stream augmentation altered not only habitat suitability but also habitat connectivity for this species. During augmentation, suitable habitat area declined by 81.3%. Changes in habitat connectivity were site dependent. Movement costs between habitat patches were lower during augmentation due to current-assisted dispersal and increased distance to patches during natural flows from dried streambeds. When movement costs were incorporated into ECA, ECA decreased by 78.0% during augmentation.

Main conclusions: With changing climate and increasing anthropogenic impacts on aquatic ecosystems, understanding how freshwater fishes relate to their habitat is critical for appropriate management. In many cases, such as the Western Silvery Minnow, mitigating habitat suitability may not be sufficient, as species are unable to reach suitable habitat. The incorporation of swim performance into habitat connectivity assessments, as carried out here, can be easily adapted to other species and situations and can improve the understanding of impacts to stream fishes and increase the effectiveness of mitigation efforts.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2018 The Authors. Diversity and Distributions Published by John Wiley & Sons Ltd.
INTRODUCTION

Freshwater fishes are an increasingly imperilled group, with an estimated extinction rate of 0.4% per decade in North America (Ricciardi & Rasmussen, 1999) and 700 taxa listed as vulnerable, threatened or endangered (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 & Nilsson, 1994). With approximately 75,000 dams present in the United States alone, there are no watersheds >2,000 km² in the United States that are not 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 and affecting some fishes ability to successfully complete all necessary life stages (Bunn & Arthington, 2002; Dudley & Platania, 2007). Dams and other stream structures also provide a conduit for the introduction of non-native species that may have detrimental effects on native fauna (Johnson, Olden, & Vander Zanden, 2008).

There is a growing need to accurately assess the impacts of hydrologic alteration on fish populations and communities given the imperilled status of many lotic species and increasing threats. Quantifying the effects of hydrologic alterations on aquatic habitats relies upon understanding the relationship between a species and its physical environment. The relationships between aquatic habitat and a species’ presence or abundance are often quantified using a habitat suitability index (HSI), which is used to identify habitat characteristics or features that are key to the successful persistence of a species (Barry & Elith, 2006; Guisan & Thuiller, 2005). A 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 determines the validity and applicability of the HSI. Most commonly, HSIs quantify the observed association between a species and 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, individuals do not always occupy habitat that best meets their needs, and there are factors that can limit fish to less than ideal habitats (Guisan & Thuiller, 2005; Rosenfeld & Boss, 2001; Van Horne, 1983). In these instances, using a 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 individuals 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 predict the impacts of individual parameters, and there has been a widespread call for the inclusion of mechanistic-empirical data into habitat suitability assessments (Boisclair, 2001; Murchie et al., 2008; Rosenfeld, 2003).

Determining the relationship between species and their habitat requires not only an understanding of habitat suitability, but also habitat connectivity, that is the permeability of an environment to movement by individuals (Fagan, 2002). In terrestrial systems, movement potential of individuals is often determined at a landscape scale, where movement potential is defined using the cost of moving through a patchwork or grid of different habitats (Adriaensen et al., 2003; LaRue & Nielsen, 2008; Sawyer, Epps, & Brashears, 2011). Movement potential of fishes in river systems is less commonly assessed (Hoffman et al., 2006; McElroy, Delonay, & Jacobson, 2012), although in principle is similar to movement potential in terrestrial environments. To date, most assessments of river systems have defined habitat connectivity based on barriers and restrictions to movement corresponding to features such as waterfalls, dams and culverts (Perkin & Gido, 2012; Wofford, Gresswell, & Banks, 2005). However, new habitat connectivity measures, and their application to dendritic networks, have helped move these assessments to a riverscape scale (Erös, Olden, Schick, Schmera, & Fortin, 2012; McKay, Schramski, Comyngham, & Fischenich, 2013; Peterson et al., 2013).

Movement of lotic fish may be restricted by a number of factors, not the least of which is water velocity (Haró, Castro-Santos, Noreika, & Odeh, 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 (Bestgen, Mefford, Bundy, Walford, & Compton, 2010; Tierney, Kasurak, Zielinski, & Higgs, 2011; Toepfer, Fisher, & Haubelt, 1999) and the physiological impacts of potential toxicants (Farrell, Gamperl, & Birtwell, 1998; Jain, Birtwell, & Farrell, 1998; Tierney, Casselman, Takeda, Farrell, & Kennedy, 2007; Walwood & Beamish, 1978). Swimming endurance typically decreases with increased water velocity which has important implications for the designs of dam and water control structures, and as a result, the swimming ability of many different species has been assessed (Hammer, 1995; Videler & Wardle, 1991).

Incorporating swim performance into estimates of habitat connectivity would provide a mechanistic link between physical habitat
conditions (water velocity) and the availability of suitable habitat. Here, we present a new method for assessing habitat connectivity using swim performance as an indicator of movement cost. We then combine habitat connectivity and habitat suitability using equivalent connected area (ECA; Saura, Estreguil, Mouton, & Rodriguez-Freire, 2011) to investigate the utility of this method for estimating habitat availability and the impacts of hydrologic alteration on the Western Silvery Minnow (Hybognathus argyritis), an endangered species in the Milk River, Canada.

2 | METHODS

2.1 | Incorporating movement cost into habitat availability

The study of connectivity and movement potential has a long history in ecology; however, terminology has not always been agreed upon (Moilanen & Hanski, 2001; Tischendorf & Fahrig, 2000, 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 as 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 (Poos & Jackson, 2012; Rodriguez, 2002). This measure is commonly Euclidean distance, but can be a different measure of movement cost. We define movement cost as a relative value, specific to a species swimming ability and the flow at a given site, representing the cost of movement from one specific location on the landscape to another.

We incorporate a novel measure of movement cost into ECA, a habitat availability metric based on graph theory (Saura et al., 2011). 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 (e.g., square metres 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 individuals move from one habitat patch to another and is often defined as a declining exponential function (Rodriguez, 2002; Equation 1), based on distance and an additional parameter, $\theta$:

$$
\text{Probability of dispersal} = e^{-\theta \times \text{Distance}}.
$$

(1)

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

Within lotic systems, water velocity is one of the driving forces that govern fish ecology (Blanchett, Loot, & Dodson, 2008; Ottaway & Forrest, 1983), and it is reasonable to assume it influences fish dispersal between habitat patches. The ability of fish to move in flowing water is characterized by their swimming ability, and there is a large field of study dedicated to quantifying swimming ability (Hammer, 1995; Kieffer, 2000, 2010; Nelson, Gotwalt, Reidy, & Webber, 2002; Videler & Wardle, 1991). 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 & 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, like some benthic species such as sculpin (Veillard et al. 2017), 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. Experimental data have shown that time to fatigue is typically related to swim speed by a log-linear equation (Adams, Hoover, & Killgore, 2000; He & Wardle, 1988; Peake, Beamish, McKinley, Scruton, & Katopodis, 1996) (Equation 2):

$$
\ln (\text{Time}) = a + b \times \text{Swim speed},
$$

(2)

where $a$ describes the intercept and $b$ (typically negative) describes the rate of decline in the relationship. Castro-Santos (2005) found that fish ascending flumes were able to select swim speeds that maximized the ground distance covered when water velocities corresponded to prolonged swim speeds. When fish assume this optimizing behaviour, the maximum ground distance that can be traversed can be expressed as a function of water velocity (Equation 3; Castro-Santos, 2005):

$$
\text{Ground distance} = \frac{e^{a+b \times \text{Water velocity}} - 1}{b}.
$$

(3)

We use the inverse of this relationship to define the movement cost of individual fish (per metre) 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.

\[
\text{Movement cost} = \frac{b}{e^{ad + b \times \text{Water velocity}} - 1}.
\] (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). We adopted the minimum HF of 0.1 when direction of travel equals the direction of flow. This value was previously used for modeling movement costs for Cory’s Shearwaters during transoceanic flights (Felicisimo, Munoz, & Gonzalez-Solis, 2008). When the direction of travel is 180° relative to the flow direction, the fish experiences the full cost of movement (HF = 1), and the HF declines linearly between 180 and 0° (Equation 5).

\[
\text{HF} = 0.1 + 0.005 \times \text{Relative direction of movement}.
\] (5)

Using least-cost path analysis, the cost surface and the HF 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 availability.

2.2 | Application to hydrologic alteration and the Western Silvery Minnow

The Milk River is a medium-sized prairie river that flows through southern Alberta, Canada, before joining the Missouri River in Montana (Figure 1). It is part of an interbasin water transfer programme that annually diverts flow from the neighbouring St. Mary River in the United States into the Milk River for enhanced irrigation throughout the mid-western Prairies (DNRC, 2012). Natural flow in the Milk River typically ranges from 1 to 5 m³/s. During flow augmentation (April to October), flow more than triples to a range between 15 and 20 m³/s. Due to the Milk River’s connection with the Missouri River drainage, it contains a fish assemblage unique in Canada as well as multiple species at risk. Western Silvery Minnow is listed as Endangered by the Committee on the Status of Endangered Wildlife in Canada due to its limited distribution as
well as the impacts to the population posed by potential changes to ongoing hydrologic alteration (COSEWIC, 2008). We chose this system to apply our new methodology due to the magnitude of hydrologic alteration and its possible impact on the habitat suitability and availability for Western Silvery Minnow.

We developed a HSI for Western Silvery Minnow based on water depth and velocity, which was used to identify habitat conditions that would constitute a habitat patch (Appendix S1). Using data obtained from fixed velocity fatigue tests, we estimated the endurance swimming ability of Western Silvery Minnow, and from this, the movement cost function was derived (Appendix S2). 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 and the other approximately 2 km long (Figure 1). Using an Acoustic Doppler Current Profiler (ADCP) and 1 m² point measurements taken with a handheld velocity meter, we surveyed water velocity and depth at both sites during both natural and augmented flow periods. The density of habitat sample points averaged 0.17/m² 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 site at a 1 m² resolution using an inverse-distance-weighted function. HSI scores were calculated for each 1 m² 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.

By applying the movement cost function to the interpolated water velocity and direction data, a movement cost surface was created. 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. 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) in the probability of dispersal equation is ideally calibrated against observed or inferred movement data; however, that data were not available for this study system. As an alternative, the probability of dispersal between each pair of habitat patches and the resulting ECA values was calculated at a range of θ values: 0, .005, .01, .015, .02, .025, .05, .1, .2, .3, .4 and .5. The Euclidean distance was also measured between each habitat patch, and the ECA was calculated using Euclidean distance 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, and distance measure on ECA, with theta and site included as random variables. 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, Mullen, Spiess, & Bolker, 2013), lattice (Sarkar, 2008), rOCR (Sing, Sander, Beerenwinkel, & Lengauer, 2005), boot (Canty & Ripley, 2013), plotrix (Lemon, 2006), lme4 (Bates et al., 2014), Rcpp

| Site | Flow state | Total wetted area (m²) | Mean water depth (m) | Mean water velocity (m/s) | Number of suitable habitat patches | Total suitable area (m²) | Suitable area as proportion of wetted area | Mean patch size (m²) |
|------|------------|------------------------|----------------------|--------------------------|-----------------------------------|-------------------------|-------------------------------------------|----------------------|
| 1    | Augmented  | 107,446                | 0.33                 | 0.35                     | 35                                | 10,260                  | 0.095                                      | 293.1                |
| 1    | Natural    | 53,848                 | 0.20                 | 0.21                     | 57                                | 21,628                  | 0.402                                      | 379.4                |
| 2    | Augmented  | 103,383                | 0.55                 | 0.60                     | 23                                | 4,002                   | 0.039                                      | 174.4                |
| 2    | Natural    | 63,064                 | 0.24                 | 0.29                     | 81                                | 17,683                  | 0.298                                      | 200.4                |
(Eddelbuettel & Francois, 2011), MAtRiX (Bates & Maechler, 2015) and GplotS (Warnes et al., 2015).

3 | RESULTS

3.1 | Habitat suitability

The HSI 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; intercept of 3.91 [95% CI: 2.39–6.24]). These results indicate a decline in habitat suitability with increasing water depth and velocity (Figure S1). The model was most accurate (84%) at a threshold value of 0.68, and 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.

Stream augmentation altered habitat suitability for the endangered Western Silvery Minnow in the Milk River (Table 1, Figure 2). During augmentation, mean suitable habitat declined (as a portion of wetted area) by 81.3%, from 34.3% to 6.7% (Table 1). On average, the number of suitable habitat patches declined during augmented flow by 55.1% with the mean patch size also declining by 21.9%. These differences were largely due to differences in water velocity between the flow states, with velocity almost doubled during augmentation (mean increase = 1.87× natural rate; Table 1). The sites had similar wetted areas, even though site 2 covered nearly twice the stream length of site 1. Site 1 was generally shallower, with lower velocity water and had a higher proportion of suitable habitat.

3.2 | Movement costs and distances between habitat patches

Mean distance between habitat patches significantly increased during natural flow (two-factor ANOVA, df = 1,1, F_{Flow} = 37.65, p_{site} ≤ .0001). This was due to an increase in dried area during low-flow events (Figures 2 and 3). On the contrary, movement costs for Western Silvery Minnow were site dependent. The mean movement cost between habitat patches increased during natural flow at site 1 and decreased during natural flow at site 2 (Table 2). There was no significant difference in between patch cost at the two flow states (two-factor ANOVA, df = 1,1, F_{Flow} = 2.909, p_{site} = .088).

High movement costs were typically associated with areas of high water velocity (Figure 3). Site 2 during augmented flow exhibited relatively large areas of high movement cost while both sites during natural flow levels had low movement costs throughout most of their area. Most of site 1 during augmented flow had low movement costs as well. Small areas of high movement cost during natural flow and at site 1 during augmented flow were found where the channel constricted and water velocities increased.

When comparing measures of separation for habitat patches, Euclidean distance was consistently higher than estimated movement costs derived from swim performance tests and field-based water velocity measurements. 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 4). This linear relationship was most evident when considered over a large
scale and less evident when only patches in close proximity (<10 m) were considered. 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 4).

### 3.3 Impacts of hydrologic alteration on habitat availability

Equivalent connected area was higher during natural flows than augmented flows (linear mixed-effect model, coefficient = .132, 95% CI = 0.118–0.145) (Figure 5). This was true for every value of theta, at each site, and when calculated using both movement cost and Euclidean distance as the measure of separation.

When theta was 0, ECA equalled 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 5). ECA was lower when calculated with Euclidean distance than movement cost (linear mixed-effects model, coefficient = −.016, 95% CI = −0.030 to −0.002), though the effect size was small (Figure 5). Theta explained 41% of the remaining variation not already explained by the fixed variables in the model, while the site explained 29%.

### 4 DISCUSSION

Habitat suitability for stream fish is often assessed apart from connectivity, even though connectivity can play a major role in the availability of specific habitats (Isaak et al., 2007). We have described a new method for incorporating swim performance into a measure of habitat availability using a graph-theoretic approach. Graph theory provides a flexible, easy to use framework for incorporating habitat connectivity and is increasingly being used for assessing aquatic environments (Saunders et al., 2016). A strength of graph analysis is that it is less onerous for data requirements than some other techniques (Minor &
Graphs are constructed of only two components, nodes and edges, which can both represent habitat patches and connections between those patches. This basic structure can be enhanced by adding qualities to the nodes and edges which may represent patch quality or size, or dispersal probability through a barrier. This simple yet flexible structure allows for a wide variety of applications. Dendritic networks have been analysed with edges representing stream lengths and nodes representing any breaks or potential barriers in the network (McKay et al., 2013); however, a more common method is to represent habitat patches as nodes and edges as the connectivity between them (Perkin et al., 2015). There are many ways of measuring connectivity (Calabrese & Fagan, 2004), with a common method defining probability of dispersal based on distance between patches (Schick & Lindley, 2007). Our analysis utilized two methods for estimating the probability of dispersal and highlighted the flexibility of the method.

Careful consideration of the modelled dispersal process is necessary for this technique to produce meaningful results. Individual behaviour can vary between active “dispersers,” and “stayers” that tend to have more limited dispersal (Fraser et al., 2001). As both endurance swimming and least-cost path analysis would be most appropriate for active dispersers, this technique may not be appropriate to use for individuals that use different dispersal techniques, such as passive transport or a random walk. Similarly, the mode of movement impacts the way in which swim performance is converted to movement cost. Benthic fish that inhabit swift flowing streams may use burst swimming to move short distances between small habitat patches (Veillard et al., 2017). In these instances, the equation used here for translating swim performance to movement cost may not be appropriate and further work to quantify this relationship would be necessary.

Assessing habitat connectivity can aid in the conservation of species by identifying potential bottlenecks, where species are unable to disperse to different habitats and thus are more prone to stochastic events and over-harvest. In some cases, bottlenecks may be easy to identify. For example, Lake Sturgeon (Acipenser fluvescens) show highly restricted movement and habitat use during over-winter periods dispersal (Thayer et al., 2017). However, in many cases, bottlenecks may not be obvious. Here, we have shown that with increased flow, overall habitat availability for Western Silvery Minnow decreases dramatically in the Milk River. This was evident through decreases in both the per cent of suitable area measured with a HSI and with ECA. While changes in the amount of suitable habitat are routinely measured, here the connectivity of that suitable habitat was demonstrated to be an important bottleneck. Most previous habitat suitability assessments for the species have not considered connectivity of habitat at the scale considered here, and this additional information allows for a more complete understanding of the species’ interaction with its modified environment and improves conservation efforts.

Two major limitations to our analysis exist that need to be acknowledged when interpreting the results. The first is the length of time that the Western Silvery Minnow were held in captivity prior to undergoing swim performance testing. Individuals were held between ~6 and 11 months prior to testing, and the effect of this length of captivity

![Graph showing movement cost vs. distance for different scales of habitat patches.](image-url)
Incorporating movement potential into habitat suitability has the potential to contribute to our understanding of the impacts of climate change and human-induced habitat alterations on stream fish populations. Climate change is projected to have significant impacts on stream hydrology in many areas (Schindler, 2001; Schindler & Donahue, 2006), and the impacts of these changes on fish movement potential and habitat suitability are an important topic of future research. Managing species at risk in these changing riverscapes will present unique challenges to scientists and managers. The physical habitat data necessary for an analysis, such as the one we have described, are commonly collected and analysed in programs such as PHABSIM (Milhous & Waddle, 2012) and Blue Kenue (NRCC, 2015). The remaining data requirement, swim performance, is often available from the literature. The reasonable data requirements and easy to interpret output make this a valuable addition to researcher’s toolsets (see Appendix S3 for analysis flow chart).

**CONCLUSION**

With changing climate and increasing anthropogenic impacts on aquatic ecosystems, understanding how freshwater fishes relate to their habitat is critical for predicting and mitigating shifts in fish communities. While traditionally habitat was viewed as the physical characteristics of a specific location, there is an increasing acknowledgement of the importance of connectivity in structuring aquatic communities. The ability of individual fish to move from one location to another can be measured in different ways, but incorporating the underlying mechanisms controlling fish movement into habitat availability assessments provides an important advancement in evaluating habitat for fishes. We demonstrated a method of incorporating the swimming ability of fish into a measure of movement cost and subsequently habitat availability through least-cost path analysis and graph theory. This revealed that flow augmentation dramatically impacted the availability of suitable habitat for the endangered Western Silvery Minnow. This technique can be readily applied to other systems and species, where asymmetrical movement costs occur (e.g., birds), and on swim performance is unknown. Bestgen et al. (2010) measured the endurance swim performance of wild captured Rio Grande Silvery Minnow (*Hybognathus amarus*) after 4 days acclimation and found similar swimming capabilities, which suggests that our long holding period had little effect. Still, future studies should shorten the holding period if possible to confirm our results. Secondly, we averaged water velocity throughout the entire water column. Fish can take advantage of vortices in turbulent flow to aid movement (Liao et al. 2003) and the area of turbulent flow along the bottom of the stream channel could provide a zone of lower velocity water to reduce movement costs for fishes. Our analysis simplified the complexity of turbulent flow to allow for analysis with common GIS programmes and eliminate the need for 3D considerations. While a more complex analysis could be performed, there is likely a strong correlation between mean water velocity in a water column and minimum velocity in a water column, and the pattern of results incorporating 3D considerations would likely be similar to those with velocity averaged through the water column.

In addition to presenting a new methodology for linking fish behaviour and physiology with habitat availability, this research emphasizes the critical role that scale plays in spatial analyses of habitat suitability and availability. It highlights the question: what is the appropriate scale at which to consider habitat connectivity for fishes? Previous research investigating fish habitat connectivity has often focused on the macroscale, looking at factors at the scale of the stream (Perkin & Gido, 2011), watershed (Perkin & Gido, 2012) or ocean (Treml et al. 2008). But individual fish have a limited range of perception and factors within their immediate zone of perception undoubtedly influence their behaviour. It is the accumulation of these numerous small decisions that help form the large-scale patterns of movement and dispersal that are so ecologically relevant in aquatic ecosystems. The results of our analysis have shown that environmental factors at a fine scale (in our case water velocity measured at the 1 m$^2$ resolution) can have a large impact on the ability of an organism to access its habitat and move through its environment. Wang et al. (2009) measured the gene flow of Tiger Salamanders (*Ambystoma californiense*) between ponds to estimate the relative costs of different habitat types at the 1 m$^2$ resolution to overland salamander movement. Rather than work from a measure of dispersal (gene flow) as Wang et al. (2009) did, we started from physiological (swim performance) data to come to the same general conclusion that fine-scale habitat features can have an important role in the movement of organisms.
ACKNOWLEDGEMENTS

Funding for this project was provided by a grant from Alberta Conservation Association, Fisheries and Oceans Canada Species at Risk Fund and NSERC Discovery Grant to MP. This work was conducted under an approved animal care permit (AUP001001), and sampling was conducted under an approved Species at Risk Permit (SARA C&A 13-008) and Alberta Fish Research Licence (13-2408 FR). Terry Clayton provided expert advice on the biology and ecology of Western Silvery Minnow. Troy Adams and Marie Veillard assisted with field collections and accommodations were provided by Alberta Parks. We also thank the anonymous reviewers for suggestions which considerably improved the manuscript.

ORCID

Mark S. Poesch http://orcid.org/0000-0001-7452-8180

REFERENCES

Adams, S. R., Hoover, J. J., & Killgore, K. J. (2000). Swimming performance of the Topeka Shiner (Notropis topeka) and endangered Midwestern minnow. The American Midland Naturalist, 144, 178–186. https://doi.org/10.1674/0003-0031(2000)144[0178:SPOTSTS]2.0.CO;2
Adriaensen, F., Chardon, J. P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., & Matthysen, E. (2003). The application of ‘least-cost’ modelling as a functional landscape model. Landscape and Urban Planning, 64, 233–247. https://doi.org/10.1016/S0169-2046(02)00242-6
Ahmadi-Nedushan, B., St-Hilaire, A., Bérubé, M., Robichaud, É., Théîmonge, N., & Bobée, B. (2006). A review of statistical methods for the evaluation of aquatic habitat suitability for instream flow assessment. River Research and Applications, 22, 503–523. https://doi.org/10.1002/ (ISSN)1535-1467
Barry, S., & Elith, J. (2006). Error and uncertainty in habitat models. Journal of Applied Ecology, 43, 413–423. https://doi. org/10.1111/j.1365-2664.2006.01136.x
Bates, D., & Maechler, M. (2015). Matrix: Sparse and dense matrix classes and methods. R package version: 1.2-0. https://cran.r-project.org/web/packages/Matrix/Matrix.pdf
Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version: 1.1-7. https://cran.r-project.org/web/packages/lme4/lme4.pdf
Beamish, F. W. H. (1978). Swimming capacity. In W. S. Hoar, & D. J. Randall (Eds.), Fish Physiology VII: Locomotion (pp. 101–188). New York, NY: Academic Press.
Bestgen, K. R., Mefford, B., Bundy, J. M., Walford, C. D., & Compton, R. I. (2010). Swimming performance and fishway model passage success of Rio Grande Silvery Minnow. Transactions of the American Fisheries Society, 139, 433–448. https://doi.org/10.1577/T09-085.1
Blanchett, S., Lott, G., & Dodson, J. J. (2008). Competition, predation and flow rate as mediators of direct and indirect effects in a stream food chain. Oecologia, 157, 93–104. https://doi.org/10.1007/s00442-008-1044-8
Boisclair, D. (2001). Fish habitat modeling: From conceptual framework to functional tools. Canadian Journal of Fisheries and Aquatic Sciences, 58, 1–9. https://doi.org/10.1139/f00-251
Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management, 30, 492–507. https://doi.org/10.1007/s00267-002-2737-0
Calabrese, J. M., & Fagan, W. F. (2004). A comparison-shopper’s guide to connectivity metrics. Frontiers in Ecology and the Environment, 2, 529–536. https://doi.org/10.1890/1540-9295(2004)002[0529:ACGTCM]2.0.CO;2
Carty, A., & Ripley, B. (2013). boot: Bootstrap R (S-Plus) functions. R package version 1.3-9. http://ftp.auckland.ac.nz/software/CRAN/src/contrib/Descriptions/boot.html
Castro-Santos, T. (2005). Optimal swim speeds for traversing velocity barriers: An analysis of volitional high-speed swimming behavior of migratory fishes. Journal of Experimental Biology, 208, 421–432. https://doi. org/10.1242/jeb.01380
COSEWIC (2008). COSEWIC assessment and update status report on the western silvery minnow Hybognathus argyritis in Canada (pp. vii + 38). Committee on the Status of Endangered Wildlife in Canada, Ottawa, ON, Canada.
DNRC (2012). St. Mary river and milk river basins study summary report (p. 46). U.S. Department of the Interior, Bureau of Reclamation.
Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Lévêque, C., … Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats and conservation challenges. Biological Reviews, 81, 163–182. https://doi.org/10.1017/S1464793105006950
Dudley, R. K., & Platania, S. P. (2007). Flow regulation and fragmentation imperil pelagic-spawning riverine fishes. Ecological Applications, 17, 2074–2086. https://doi.org/10.1890/06-1252.1
Dynesius, M., & Nilsson, C. (1994). Regulation of river systems in the northern third of the world. Science, 266, 753–762. https://doi.org/10.1126/science.266.5186.753
Eddelbuettel, D., & Francois, R. (2011). Rcpp: Seamless R and C++ integration. Journal of Statistical Software, 40, 1–18.
Elzhov, T. V., Mullen, K. M., Spiess, A., & Bolker, B. (2013). minpack.lm: R interface to the Levenberg-Marquardt nonlinear least-squares algorithm found in MINPACK, plus support for bounds. R Package version 1.1-8. https://cran.r-project.org/web/packages/minpack.lm/minpack.lm.pdf
Erös, T., Olden, J. D., Schick, R. S., Schmera, D., & Fortin, M. J. (2012). Characterizing connectivity relationships in freshwaters using patch-based graphs. Landscape Ecology, 27, 303–317. https://doi.org/10.1007/s10189-011-9659-2
ESRI (2012). ArcGIS desktop: Version 10.1. Redlands, CA: Environmental Systems Research Institute.
Fagan, W. F. (2002). Connectivity, fragmentation, and extinction risk in dendritic metapopulations. Ecology, 83, 3243–3249. https://doi.org/10.1890/0012-9658(2002)083[3243:CFEARI]2.0.CO;2
Farrell, A. P., Gamperl, A. K., & Birtwell, I. K. (1998). Prolonged swimming, recovery and repeat swimming performance of mature sockeye salmon Oncorhynchus nerka exposed to moderate hypoxia and pentachlorophenol. Journal of Experimental Biology, 201, 2183–2193.
Felicesimo, A. M., Munoz, J., & Gonzalez-Solis, J. (2008). Ocean surface winds drive dynamics of transoceanic aerial movements. PLoS One, 3, e2928. https://doi.org/10.1371/journal.pone.0002928
Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N., & Skalski, G. T. (2001). Explaining leptoikuritic movement distributions: Intrapopulation variation in boldness and exploration. The American Naturalist, 158, 124–135. https://doi.org/10.1086/321307
Graf, W. L. (1999). Dam nation: A geographic census of American dams and their large-scale hydrologic impacts. Water Resources Research, 35, 1305–1311. https://doi.org/10.1029/1999WR900016
Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. Ecology Letters, 8, 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Neufeld et al.
Schick, R. S., & Lindley, S. T. (2007). Directed connectivity among fish populations in a riverine network. *Journal of Applied Ecology, 44*, 1116–1126. https://doi.org/10.1111/j.1365-2664.2007.01383.x

Schindler, D. W. (2001). The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. *Canadian Journal of Fisheries and Aquatic Sciences, 58*, 18–29. https://doi.org/10.1139/f00-179

Schindler, D. W., & Donahue, W. F. (2006). An impending water crisis in Canada’s western prairie provinces. *Proceedings of the National Academy of Sciences, 103*, 7210–7216. https://doi.org/10.1073/pnas.0601568103

Sing, T., Sander, O., Beerenwinkel, N., & Lengauer, T. (2005). ROCR: Visualizing the classifier performance in R. *Bioinformatics, 21*, 7881.

Thayer, D., Ruppert, J. L. W., Watkinson, D. A., Clayton, T. A., & Poesch, M. S. (2017). Identifying temporal bottlenecks for the conservation of large-bodied fishes: Lake Sturgeon (*Acipenser fulvescens*) show highly restricted movement and habitat-use overwinter. *Global Ecology and Conservation, 10*, 194–205. https://doi.org/10.1016/j.geco.2017.03.008

Tierney, K. B., Casselman, M., Takeda, S., Farrell, T., & Kennedy, C. (2007). The relationship between cholinesterase inhibition and two types of swimming performance in chlorpyrifos-exposed coho salmon (*Oncorhynchus kisutch*). *Environmental Toxicology and Chemistry, 26*, 998–1004. https://doi.org/10.1897/06-459R.1

Tierney, K. B., Kasurak, A. V., Zielinski, B. S., & Higgs, D. M. (2011). Swimming performance and invasion potential of the round goby. *Environmental Biology of Fishes, 92*, 491–502. https://doi.org/10.1007/s10641-011-9867-2

Tischendorf, L., & Fahrig, L. (2000). On the usage and measurement of landscape connectivity. *Oikos, 90*, 7–19. https://doi.org/10.1034/j.1600-0706.2000.900102.x

Tischendorf, L., & Fahrig, L. (2001). On the use of connectivity measures in spatial ecology. A reply. *Oikos, 95*, 152–155. https://doi.org/10.1034/j.1600-0706.2001.950117.x

Treml, E. A., Halpin, P. N., Urban, D. L., & Pratson, L. F. (2008). Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. *Landscape Ecology, 23*, 19–36. https://doi.org/10.1007/s10641-007-9138-y

Toepfer, C. S., Fisher, W. L., & Haubelt, J. A. (1999). Swimming performance of the threatened leopard darter in relation to road culverts. *Transactions of the American Fisheries Society, 128*, 155–161. https://doi.org/10.1577/1548-8659(1999)128<0155:SPOTTL>2.0.CO;2

Van Horne, B. (1983). Density as a misleading indicator of habitat quality. *The Journal of Wildlife Management, 47*, 893–901. https://doi.org/10.2307/3808148

Veillard, M. F., Ruppert, J. L. W., Tierney, K., Watkinson, D., & Poesch, M. S. (2017). Comparative swimming and station-holding ability of the threatened Rocky Mountain Sculpin (*Cottus sp.*) from four hydrologically distinct rivers. *Conservation Physiology, 5*, 1–12.

Videler, J. J., & Wardle, C. S. (1991). Fish swimming stride by stride: Speed limits and endurance. *Reviews in Fish Biology and Fisheries, 1*, 23–40. https://doi.org/10.1007/BF000042660

Waiwood, K. G., & Beamish, F. W. H. (1978). Effects of copper, pH and hardness on the critical swimming performance of rainbow trout (*Salmo gairdneri Richardson*). *Water Research, 12*, 611–619. https://doi.org/10.1016/0043-1354(78)90141-0

Wang, I. J., Savage, W. K., & Shaffer, H. B. (2009). Landscape genetics and least-cost path analysis reveal unexpected dispersal routes in the *California tiger salamander* (*Ambystoma californiense*). *Molecular Ecology, 18*, 1365–1374. https://doi.org/10.1111/j.1365-294X.2009.04122.x

Warnes, G. R., Bolker, B., Bonebakker, L., Gentleman, R., Liaw, W. H. A., Lumley, T., … Venables, B. (2015). gplots: Various R programming tools for plotting data. R package version: 2.16.0. https://cran.r-project.org/web/packages/gplots/index.html

Wofford, J. E. B., Gresswell, R. E., & Banks, M. A. (2005). Influence of barriers to movement on within-watershed genetic variation of coastal cutthroat trout. *Ecological Applications, 15*, 628–637.

**BIOSKETCHES**

This research was conducted in the Fisheries and Aquatic Conservation Laboratory (FACL) at the University of Alberta (UofA). Kenton Neufeld was a graduate student in FACL and is currently a fisheries biologist with the Province of Alberta.

Doug Watkinson is a Research Biologist at Fisheries and Oceans Canada, specializing on species at risk. Keith Tierney is an Associate Professor at UofA, specializing in fish physiology.

Mark Poesch is an Assistant Professor at UofA and principle investigator of the FACL, with a research focus on understanding impacts to declining or at-risk species and improving assessment and restoration methods for such species.

Author contributions: K.N. led the data collection, analysis and writing; D.W. contributed to the concept development, data collection and writing; K.T. contributed to data collection (swim performance) and writing; and M.P. led concept development and contributed to data analysis and writing.

**SUPPORTING INFORMATION**

Additional Supporting Information may be found online in the supporting information tab for this article.

**How to cite this article:** Neufeld K, Watkinson DA, Tierney K, Poesch MS. Incorporating asymmetric movement costs into measures of habitat connectivity to assess impacts of hydrologic alteration to stream fishes. *Divers Distrib.* 2018;24:593–604. https://doi.org/10.1111/ddi.12713