

**WHAT COMES DOWN MUST GO UP: ASSESSING THE VALIDITY OF
STREAM CONNECTIVITY TECHNIQUES WITH THE USE OF *IN SITU* FISH
MOVEMENT AND STREAM COMMUNITY METRICS**

by

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ABSTRACT

Stream fragmentation is considered an important factor in the persistence of many aquatic species. My research is focused on validating local and riverscape metrics of connectivity to help assist in evaluating their efficacy. I used *in situ* brook trout (*Salvelinus fontinalis*) movements in Terra Nova National Park, Newfoundland, to determine the accuracy of local scale fish passability metrics and I used community assemblages in southern Ontario to evaluate a structural index used to measure the connectedness of a system. I found that local scales of passability were conservative in predicting brook trout passage and failed to consistently predict fish movement. Furthermore, I found that riverscape scale structural indices have power in explaining both community structure, species presence/absence and abundance. The results from my research will provide researchers future areas of study along with confidence in structural indices for the evaluation of watershed level connectivity metrics.

Keywords: FishXing, brook trout, Dendritic Connectivity Index, passability, community structure, structural indices,

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List of Abbreviations and Symbols

Δ AIC – Change in Akiake’s Information Criteria

AIC – Akiake’s Information Criteria

BNN – Bayesian belief networks

BS – Burst speed

BUAP – Build-up area pervious

BUIP – Build-up area impervious

CF – Continuous forest

CR – Cropland

db-RDA – Distance based redundancy analysis

DCI – Dendritic Connectivity Index

DCId – Diadromous Dendritic Connectivity Index

DCIp – Potamodrmous Dendritic Connectivity Index

DCIs – Site Dendritic Connectivity Index

DEM – Digital elevation model

DF – Deciduous forest

DFO – Department of Fisheries and Oceans

ELE – Elevation

GIS – Graphical Information System

GLMM – Generalized mixed effects model

IQR – Inter-quartile range

MCMC – Markov Chain Monte Carlo

MF – Mixed forest

PAF – Pasture and Abandoned Fields

PC – Parks Canada

PIT – Passive integrated transponder

OMNR – Ontario Ministry of Natural Resources

SE – Standard error

SOLRIS – Southern Ontario Land Resource Information System

SS – Sustained speed

SW – Stream width

TNNP – Terra Nova National Park

UCC – Upstream cell count

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CHAPTER 1. INTRODUCTION AND OVERVIEW

1.1 Connectivity in the Aquatic Environment

Connectivity is “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993, p. 571). It is necessary for populations to move freely between habitat patches, such as feeding areas, refugia, and reproductive habitat, throughout their life. Consequently, it is thought that a decrease in connectivity is a major factor in the loss and decline of many species (Tischendorf and Fahrig 2000). Both anthropogenic (e.g., roads) and natural barriers (e.g., rivers) have the ability to reduce the connectedness of a landscape which can lead to declines in species abundance (Bennett 1998), fitness (Baguette and Van Dyck 2007), gene flow (Sork and Smouse 2006) and implications for recolonization.

Historically, landscape studies were primarily focused on terrestrial environments and considered aquatic environments as elements of the landscape mosaic (Wiens 2002). However, riverscape ecology (Ward 1998, page 269) has gained traction (Schick and Lindley 2007, Cote et al. 2009, Fullerton et al. 2010, O’Hanley 2011) and many of the basic principles of landscape ecology can be applied to lotic ecosystems (Fausch et al. 2002, Ward et al. 2002, Wiens 2002). Like terrestrial landscape connectivity, movement between aquatic habitats is a critical component in the persistence of freshwater biota.

The relationship between structural and functional connectivity is an important aspect in riverscape (Fausch et al. 2002) and landscape ecology (Kindlmann and Burel 2008, Kupfer 2012) and understanding this relationship will allow us to identify areas of degradation and formulate appropriate management actions. Although a wide range of

structural models are available to help characterize functional connectivity, ecological relationships remain elusive (Turner 2005, Kupfer 2012). Thus, when we consider the vast resources that are required to reconnect aquatic habitats (Bernhardt et al. 2005), it is imperative to use structural indices that have been shown to have ecological relevance so as to maximize our efforts to mitigate the anthropogenic influences on biotic communities.

1.2 Barriers and the Importance of Passability

Barriers can impede upstream migrations of obligate aquatic species to critical habitats (Roni et al. 2002). The use of riverscape theory has shifted the focus of studies from a local scale (e.g., stream reach) to broader extents (e.g., watershed) to help determine the effects of stream features (e.g., cumulative effects of barriers) and to understand their influences on different biotic and abiotic processes (Fausch et al. 2002). However, our understanding of broad scale effects is often dependent on an adequate characterization of fine scale processes.

One example of a fine scale processes is the effect of barrier passability. Barrier passability is simply the ability of an individual to navigate past an obstacle (e.g., dam or waterfall). Characterizing passability is complex in that it is dependent on the species and their behavior, size, and the environmental conditions present when passage occurs (Cahoon et al. 2007). As passability is a key factor in assessing watershed connectivity, any variations in its calculation is carried forward through watershed scale assessments (Bourne et al. 2011).

Several analytical tools are available to determine the passage of a barrier and how confounding factors influence passage (for a recent review see Kemp and O'Hanley 2010). Although direct observations are thought to be more accurate, simpler barrier summarizations are widely used because of their affordability (e.g., flow charts; Kemp and O'Hanley 2010), ability to analyze numerous barriers quickly (Bourne et al. 2011), and their applicability across scales (Kemp and O'Hanley 2010). However some drawbacks do exist with barrier summarizations. For instance, it is thought that barrier summarizations may not be applicable across species (McLaughlin et al. 2006), may use inaccurate parameters to determine passability (Castro-Santos 2006, Peake and Farrell 2006, Bourne et al. 2011), and are too simple, often missing intermediate levels of passability (Burford et al. 2009, Poplar-Jeffers et al. 2009, Anderson et al. 2012). While some standard tools exist to assess passability, limited empirical evidence is available to validate passability models which are central to calculations of connectivity across broader scales.

1.3 Structural Connectivity Indices

Structural connectivity indices are a general category of tools used to 1) identify the overall fragmentation of a system (Cote et al. 2009, Padgham and Webb 2010) and/or 2) to prioritize management objectives to mitigate potential impacts of fragmentation (Cote et al. 2009, O'Hanley 2011). These include score and ranking methods (Pess et al. 1998, Poplar-Jeffers et al. 2009), optimization models (Kemp and O'Hanley 2010, O'Hanley 2011), patched-based graphs (Schick and Lindley 2007, Erős et al. 2011, Erős et al. 2012), and connectivity indices (Cote et al. 2009, Padgham and Webb 2010).

Structural indices offer a wide range of flexibility to help define and quantify connectivity based on model inputs and many of the recent structural indices are conceptually simple and are based on readily available riverscape structures (Cote et al. 2009, O’Hanley 2011). These offer an attractive and valuable tool to meet management goals.

To date, the validity of structural indices is based on speculation that a relationship exists between structure and function. This promotes the selection of structural indices that are based on their computational convenience rather than their ecological relevance (Li and Wu 2004, Kupfer 2012). It is therefore necessary to understand the limitations of these methods (both statistical and ecological) so that they can be used to define and shape management decisions (Kupfer 2012).

1.4 Thesis Overview

My thesis links work to quantify methods of structural and functional connectivity and how individual species and stream community composition relate to measures of connectivity. Often structural connectivity indices are used to describe functional connectivity to help identify management actions. Despite the prevalence of work focusing on improving connectivity (Schick and Lindley 2007, Cote et al. 2009, Bourne et al. 2011, O’Hanley 2011, Perkin and Gido 2012), and the expense required to do this work (Bernhardt et al. 2005), there remains little understanding of how structural indices reflect function connectivity (Kupfer 2012).

For example, FishXing is a commonly used local scale (i.e., at the level of a single barrier) model which assesses fish passage at stream culverts (Furniss et al. 2006).

FishXing incorporates swimming metrics of a species and hydrological metrics of a culvert to calculate a range of flows that a particular species is able to pass. Furthermore, recent work has improved flow predictions through on site calibration (Bourne et al. 2011) but it remains unknown if fish movements are accurately predicted with improved hydrological modeling. Without rigorous testing of common passability metrics we may be making management decisions that have little impact on improving functional connectivity. I tracked *in-situ* movements of brook trout (*Salvelinus fontinalis*) across 4 culverts around Terra Nova National Park, Canada. The use of passive integrated transponder (PIT) tags to study fish movement allows me to 1) analyze, under natural flow conditions, whether culverts alter fish movement compared to reference sites and 2) test the efficacy of FishXing to predict brook trout movement through culverts (Chapter 2).

Determining how structural indices relate to the biotic community is a critical step towards understanding the relationship between structural and functional connectivity of riverscapes and our ability to predict those relationships. One structural index that calculates a connectivity metric of a watershed based on the probability of an individual being able to move from a single point in a stream to any other random point in the stream network is the Dendritic Connectivity Index (DCI; Cote et al. 2009). To date, the DCI has largely only been tested in simulated systems (Cote et al. 2009) using modeled passabilities (Bourne et al. 2011). Although the DCI was found to significantly explain community structure in small segments of riverine systems (Perkin and Gido 2012) it is unknown whether the relationship will persist at broader spatial extents where

confounding effects may play a larger role in community structure. Using fish community assemblages from 5 watersheds in southern Ontario, I analyzed the biological relevance of the DCI by determining whether a change in structural connectivity is representative of a change in fish community composition while controlling for confounding environmental variables. I also used a modified, site-specific version of the DCI to a) determine the relationship between changes in single species presence and abundances and changes in connectivity and b) determine the relationship between changes in species richness and changes in habitat (Chapter 3).

In the final chapter (Chapter 4), I discuss the implications of the work and how structural connectivity relates to functional connectivity at both local scales and at larger spatial extents. Specifically, my work will help bridge the gap between the relationships of structural and functional connectivity. This has broad implications not only across riverscapes in defining the efficacy of local and regional structural indices but also in landscape connectivity where describing these relationships are rare and difficult to define.

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Co-authorship Statement

The following two manuscript chapters (chapters 2 and 3 of this thesis) were co-authored with Dr. Dave Cote, Mr. Dan Kehler, and Dr. Yolanda Wiersma. In addition, Mr. Keith Clark was a co-author on Chapter 2, and Mr. Les Stanfield on Chapter 3. I was the principal contributor to the design, proposal, data analyses, and manuscript preparation for all chapters of the thesis. Dr. Cote and Mr. Clarke contributed to the design and data collection for Chapter 2 and Mr. Stanfield contributed catch data and partial barrier locations for Chapter 3. Dr. Cote, Dr. Wiersma, and Mr. Kehler provided critical guidance and feedback from the initial study design through manuscript preparation for both manuscript chapters.

Chapters 2 and 3 are written for the submission to journals with only minor modifications. Thus, it was necessary to repeat some information from Chapter 1 in the study scope and objectives in both Chapters 2 and 3 and formats between the two chapters may differ slightly to conform to target journal guidelines. Also, Chapter 3 includes community analysis of biomass which is not included in the manuscript version. Chapter 2 was accepted at the *Transactions of the American Fisheries Society* on 2 July 2013 and Chapter 3 will be submitted simultaneously to *Canadian Journal of Fisheries and Aquatic Sciences* with completion of the thesis manuscript.

CHAPTER 2. EVALUATING THE BARRIER ASSESSMENT TECHNIQUE FishXing AND THE UPSTREAM MOVEMENT OF BROOK TROUT THROUGH ROAD CULVERTS

2.1 Introduction

The re-establishment of natural processes is a critical step in restoring and maintaining diverse biological communities (Roni et al. 2002, Palmer et al. 2005). Aquatic connectivity is increasingly recognized as an important characteristic of aquatic ecosystems and has gained considerable attention in recent years (Fullerton et al. 2010, Olden et al. 2010). Unlike terrestrial landscapes that may have multiple pathways between habitat patches, riverscapes have a single movement corridor among habitat patches for obligate aquatic species. Consequently, the obstruction of these pathways by culverts, dams, and other barriers can alter community assemblages, impede the completion of life history stages, and limit the dispersal of aquatic species within meta-communities (Fagan 2002, Fahrig 2003, Schick and Lindley 2007, Fullerton et al. 2010, Perkin and Gido 2012). Recent advancements in connectivity models have developed riverscape approaches to measure the fragmentation of dendritic ecosystems (Cote et al. 2009, Padgham and Webb 2010, O’Hanley 2011) since terrestrial metrics of fragmentation (e.g., Kindlmann and Burel 2008) are of limited utility in riverine systems.

Barrier location and passability are two components routinely used in assessing the degree of fragmentation in watersheds. The first component helps determine the maximum amount of total habitat that could be gained by restoring or removing a single barrier (Cote et al. 2009, O’Hanley 2011). For the second component, determining how a

focal species navigates past a barrier can indicate the degree to which an obstacle impedes stream movement for an aquatic species. This is often difficult to resolve because of the complex and dynamic nature of passability (Cote et al. 2009, Padgham and Webb 2010, Bourne et al. 2011). Furthermore, accurate measures of connectivity are sensitive to barrier assessment methods (Bourne et al. 2011) and thus it is critical to know whether barrier assessment methods are representative of fish movements.

Various methods exist to analyze the passability of barriers (Kemp and O'Hanley 2010). Common methods used to calculate culvert passability include flow charts (Taylor and Love 2003, Clarkin et al. 2005, Coffman 2005) and computer simulations (Hotchkiss et al. 2008). These barrier assessment methods are particularly appealing because of their simplicity and affordability to gather and process the required information. However, hydrological data needed to assess barriers are often missing or the data can be difficult to obtain (Kemp and O'Hanley 2010) and only a few studies have examined the accuracy of barrier assessment methods using *in-situ* field experiments (Coffman 2005, Burford et al. 2009).

FishXing is one commonly used method that was originally designed to assist in the evaluation and design of culverts to promote upstream fish passage (Furniss et al. 2006). By incorporating species-specific metrics (e.g., species length and swimming capabilities) and hydrologic properties of the culvert (e.g., culvert slope, length, and roughness), FishXing is able to estimate the stream flow that a particular individual is able to pass. In theory, this should lead to a more accurate passability estimates than simpler, rule-of-thumb type assessments. FishXing has been used extensively to model

culverts for fish passage (Flanders and Cariello 2000, Taylor and Love 2003, Standage 2007, Davis and Davis 2008, Hendrickson et al. 2008). However, remarkably few studies have analyzed the effectiveness of FishXing as a barrier assessment tool (Burford et al. 2009), despite the widespread perception that FishXing produces conservative outputs (Poplar-Jeffers et al. 2009, Bourne et al. 2011).

Poplar-Jeffers et al. (2009) found that outputs from FishXing appear to categorize most barriers as completely impassible, when in reality some form of intermediate passability may be more appropriate (Anderson et al. 2012). Potentially, default swim speeds in FishXing are underestimated since they are calculated in laboratory settings through forced swim performance methods (Castro-Santos 2006, Peake and Farrell 2006). Furthermore, culvert hydrological properties, used for FishXing, are modeled after maximum stream flow characteristics within the culvert (Burford et al. 2009, Bourne et al. 2011), which have been shown to overestimate the severity of a barrier (Lang et al. 2004). In reality, culverts rarely exhibit the flows that are predicted by FishXing default parameters. Several studies have focused on the accurate calculation of hydrological properties in hopes of improving predictions of fish movement. For instance, Burford et al. (2009), following the approach of Karl (2005), adjusted the roughness coefficient but found only modest changes in their error rate between observed and actual flow depths. Moreover, Bourne et al. (2011) did extensive culvert modeling using methods from Straub and Morris (1950a, b) to adjust the roughness coefficients of barriers. Although they could not always predict water flow through culverts, the use of the more precise entrance loss and roughness coefficients improved the accuracy of the stream flow

predictions (Bourne et al. 2011). However, even with the increased precision of the hydrological modeling by Bourne et al. (2011) it is still unknown if the stream flows predicted by FishXing as passable are representative of what fish can navigate under natural conditions.

We monitored Brook Trout *Salvelinus fontinalis* upstream passage across four culverts over three years in the Terra Nova National Park area of Newfoundland, Canada, using passive integrated transponder (PIT) tags. The use of PIT tags to study fish movement allows an opportunity to analyze, under natural flow conditions, whether culverts alter fish movement and if so, to test if the predictions of a commonly used barrier assessment technique are accurate. We first evaluated whether there were differences between upstream fish passage in culverts compared to reference sites. If culverts influence the movement of Brook Trout we expect to see a wider range of stream flows that Brook Trout are able to pass in reference sites when compared to culverts. We also determined the accuracy of FishXing estimates with the use of *in-situ* fish movements. Verifying the accuracy of FishXing with *in-situ* Brook Trout movements will provide direct empirical support for the efficacy of FishXing for use in barrier assessments.

2.2 Methods

2.2.1. Study Area

The study was conducted in the boreal stream systems of the Terra Nova National Park area (TNNP) of Newfoundland, Canada. TNNP is a low productivity system with

low species richness dominated by salmonids (Cote 2007). Native Brook Trout exhibit both anadromous and diadromous life histories in the study area.

2.2.2. Field Data Collection

We used a portable Smith Root Inc. electroshocker (model 12-B) to capture fish for tagging at the 4 study sites (~150 meters upstream and downstream of the culverts of interest). Sampling intervals occurred yearly in May and June from 2009 to 2011 after the installation of fish tracking arrays. We attempted to tag sea run brook trout in some systems but these were not well represented in our study area. As a result we focused on juveniles. All fish were measured (fork length; mm) and weighed (wet mass; g). Fish greater than 95 mm were implanted with PIT tags (model RI-TRP-WRHP; Texas Instruments Inc.; 23.1 mm in length and 3.9 mm in diameter, mass in air of 0.6 g; tag-to-fish ratio: 0.9–5.7%) through a small ventral incision made anterior to the pelvic girdle. One suture (4-0 SoftSild TM) was used to close the incision and the fish were then placed in flow-through holding pens within the capture area to recover for 24 hours before release.

Fish passage was monitored using detection arrays (Oregon RFID, www.oregonrfid.biz) placed near culverts and reference sites (unaltered areas of the stream) from May to November during the sampling years. At culvert locations, arrays were established across the stream with 2 antennae deployed upstream of the culvert (at the culvert entrance and 2-3 m upstream) and 2 deployed downstream (at the culvert outlet and 2-3 m downstream; see Figure 2.1). The order of detection on the antennae allowed the direction of movement to be determined and the success or failure of an

upstream passage attempt. We considered a pass attempt successful if a fish registered at one of the downstream antennae followed by a detection at either upstream antennae. Conversely, it was considered a failed attempt if the individual moved upstream past the two downstream antennae, did not register at either of the upstream antennae prior to being recorded a second time at the furthest downstream antennae. Reference sites were established with detection arrays in unaltered adjacent areas of the stream approximately 50 m from the culvert and in a manner that mimicked culvert lengths. The reference sites for culverts A, B, and C were located downstream of the culvert while the reference site for culvert D was located upstream due to the proximity of culvert D to the ocean. Discharge was derived from water level loggers (Solinst Levellogger Gold) deployed in each study stream to record hourly water temperature and depth during the study period. Each site was visited across a broad range of discharges to establish a rating curve with which discharge could be modeled on an hourly basis based on water depth (Riggs 1985). To determine the temporal availability of suitable stream flow we calculated the cumulative frequency of stream discharge for each culvert.

We chose three partial barriers (culverts A, B, and C) based on a previous assessment in conjunction with a cost-benefit analysis of all barriers in TNNP that suggested improving passage at these locations would provide the most ecological benefit. Culvert D was an opportunistic addition to the study after Hurricane Igor washed it out in 2010. We used culvert measurements collected from various sources (Table 2.1). Detailed characteristics of culverts A, B, and C were summarized in Bourne (2013) and culvert D was resurveyed after it was replaced.

2.2.3. *Analysis*

We used FishXing to predict the stream flows for each culvert that 50 to 250 mm Brook Trout would be able to pass. We used sustained and burst speeds for Brook Trout defined by Peake et al. (1997; Table 2.2). Minimum depths were based on 2/5 body length. This is less than earlier studies that used minimum depths between 9 to 24 cm (Bates et al. 2003, Burford et al. 2009, Bourne 2013). Previous work in TNNP used a value of 3/4 body length (Bourne et al. 2011), which was considered conservative given prior field observations of fish movements within the study area. We therefore selected a lower value of 2/5 body length. Lastly, jumping height was based on 2 times the length of the Brook Trout (Bourne 2013). Using methods outlined by Bourne et al. (2011), we calculated K_e values from Straub and Morris (1950a, b) and back calculated the Manning's roughness coefficient (n) using data from the culvert surveys. Finally we modeled tail-water depth using the channel cross section method outlined by the FishXing User Manual (Furniss et al. 2006). For a given range of water flow values, FishXing predicts the range at which a fish will experience i) passable flows, ii) a depth barrier (insufficient water depth for fish to navigate), iii) a leap barrier (perched culvert elevation too high), or iv) a velocity barrier (water velocity is too great for an individual to pass).

Fish movements in unaltered systems are temporally variable. For example, it might be expected that fish movement rates would be impacted by discharge and/or seasonal life history demands (Gowan and Fausch 1996, Klemetsen et al. 2003). To isolate the effects of culverts on fish movement, reference sites were monitored to

compare fish movement in relation to stream discharge in the absence of anthropogenic barriers. We compared the range of discharges associated with successful passage across culverts and reference sites. To limit the influence of outliers, passage range was defined as the 25th percentile minus 1.5 times the inter-quartile range (IQR) and the 75th percentile plus 1.5 times the IQR. A permutation test was used to determine significance. Specifically, we randomly re-assigned the stream discharges associated with passage events to either reference or culvert locations and recalculated the range for the permuted reference and culverts sites (10,000 permutations). The distribution of permuted values was compared to the observed value to evaluate whether there were significant differences in the discharge range where Brook Trout passability occurred ($\alpha = 0.05$).

We also tested to see if observed fish movement was consistent with predicted movement as calculated with FishXing, by using a generalized linear mixed effects model (GLMM) with a binomial distribution (Bates et al. 2011, R Development Core Team 2012) as follows:

$$\text{Event}_{ijk} = \text{intercept} + \text{individual}_i + \text{site}_k + \text{predicted}_{ijk}$$

where Event_{ijk} was binary (successful passage / failed passage) for individual i at site k . We included individual_i and site_k as random effects to account for variation associated with repeated observations at the same levels of these variables. The final term, predicted_{ijk} variable, was also a binary event (successful passage / failed passage) that represented the FishXing prediction, given the associated culvert and flow parameters. To

test the significance of the fixed effect, we used a likelihood ratio test ($\alpha = 0.05$). All statistical analyses were carried out with the program R (version 2.15.2; R Development Core Team 2012).

2.3 Results

We captured and tagged 462 Brook Trout across the four culverts in the study. Seventy of these trout were later observed in the culvert and reference arrays, which generated a total of 415 upstream passage attempts in culverts (69% success rate) and 1,123 passage attempts at reference sites (56% success rate). Furthermore, 26 of the 70 individuals were observed in both reference and culvert sites. Brook Trout that successfully moved through the culvert and reference sites did not differ significantly in size when compared to the population of Brook Trout caught and tagged ($\chi^2 = 0.9576$, $df = 1$, $p\text{-value} = 0.33$). Moreover, lengths of successful Brook Trout migrants did not significantly differ ($\chi^2 = 0.1312$, $df = 1$, $p\text{-value} = 0.72$) between culvert and reference sites. Timing of the passage events occurred throughout the day with peaks in the early morning and afternoon. Three of the four culverts were predicted by FishXing to have passable stream flows (grey zones Figure 2.2). Only culvert D was predicted to be an impassable barrier by FishXing. Predicted passable stream flows increased with increases in Brook Trout size (grey zones in Figure 2.2). Stream flows that were considered barriers were classified by FishXing as either depth or velocity barriers with depth barriers observed during low flows and velocity barriers observed during high flow periods. No jump barriers were observed across the four culverts in this study regardless of stream flows.

Comparing the range of passable flows between reference sites and stream culverts indicate a decreased range of passable flows through culverts. Permutation tests showed that culverts A, B, and C had a significantly smaller range of passable flows compared to their respective reference stream sections (Figure 2.3). However, culvert D had a significantly higher range of passable flows compared to its reference stream site (Figure 2.3). The decreased range of passable flows in culverts A, B, and C support the presence of a velocity barrier. Failed attempts were more frequent at lower flows but often corresponded to at least one successful passage at similar flows (Figure 2.2).

The prediction from FishXing regarding whether the fish would pass was not a significant explanatory variable in observed passage events. We were unable to accurately predict fish passage with FishXing across the four culverts ($\chi^2 = 0.9192$, $df = 415$, $P = 0.338$; Figure 2.2). In each culvert, with the exception of culvert A, fish were able to pass stream discharges that exceeded two or three times the upper discharge threshold predicted using FishXing. We also observed fish passage at flows that were considered depth barriers to Brook Trout movement (Figure 2.2A). To identify the minimum water depth and maximum water velocity that Brook Trout successfully passed, we used FishXing to calculate hydraulic characteristics at observed flows. Brook Trout were recorded successfully passing estimated water depths as low as 3 cm (135 mm Brook Trout in culvert A at 0.009 cms^{-1}) and a maximum water velocity of 1.56 ms^{-1} (135 mm Brook Trout in culvert D at 0.628 cms^{-1}) which were respectively predicted as depth and velocity barriers to Brook Trout movement.

2.4 Discussion

The frequency of fish movement is temporally variable and fluctuates according to season, environmental factors, and life history stages (Riley et al. 1992, Gowan and Fausch 1996, Klemetsen et al. 2003). It is therefore important to assess fish passage through barriers within the context of when fish are moving under natural conditions. The use of reference sites allowed us to isolate the effects of culverts from other confounding influences. Comparison of movements of PIT tagged Brook Trout in reference sites and culverts indicated that culverts impair fish passage. Because stream discharge is the same in paired reference and culvert sites, disparities in fish movement indicate that barriers exist in culverts due to low water depth or increased velocities (Cote et al. 2005). This supports previous studies which found barriers impaired movement of Brook Trout through culverts when compared to reference sites (Belford and Gould 1989, Thompson and Rahel 1998, Burford et al. 2009). It is therefore important to recognize that non-perched culverts can also be problematic and create conditions that limit the upstream movement of fish (see also MacPherson et al. 2012). This underscores the complexity of connectivity in many systems as barriers may not always be easily characterized as fully passable or impassable (e.g., Park et al. 2008, Burford et al. 2009, O'Hanley 2011).

We were unable to accurately predict the movement of fish passage through culverts using FishXing. With increased effort to improve hydrological modeling of culverts, it was expected that FishXing predictions would be useful in determining fish passage. Unfortunately, FishXing is a complex model that incorporates physiological information of the species and hydrological information associated with the culvert. While qualitative assessments of barriers from FishXing remain useful (they were

accurate for three of the four barriers), the severity of a barrier is an important element for quantifying connectivity or prioritizing restoration.

Beyond refining hydrologic parameters, the predictive shortcomings of FishXing might be associated with an incomplete knowledge of fish physiology and/or behavior. The underestimation of fish swimming abilities can account for the conservative estimates by FishXing. Past studies that have derived swim speeds from forced swimming methodologies have been criticized because they do not reflect conditions in natural systems (Castro-Santos 2006, Peake and Farrell 2006). Haro et al. (2004) analyzed swim speeds of several species of fish exhibiting anadromous, amphidromous and potamodromous life histories using an open channel flume. In that study, fish were allowed to transverse the flume under their own volition, which is different from past studies that used forced swim speeds. They found that by allowing fish to mimic their natural tendencies (multiple pass attempts, movement under own volition) to navigate the flume, they were able to record speeds that were well above those previously observed. However, Haro et al. (2004) used a smooth channeled flume with relatively constant flow regimes and recommended that these swim speeds should be used in situations that mimic these flow profiles (e.g., box culverts). Such improvements in understanding species swim performance would enhance fish passage methods like FishXing that rely on swimming performances.

Many obstacles to fish movement, both natural and anthropogenic, incorporate non-uniform flow characteristics with areas of velocity refugia consisting of lower velocity flow patterns (e.g., culvert boundary layers). For instance, in this study, fish

were observed idly resting in the boundary layers of culverts (low velocity zones near the edge of the culvert) with little or no effort to maintain their position. Clearly, laboratory settings that replicate the turbulent conditions found in nature would be useful in understanding of how fish optimize passage (Haro et al. 2004, Castro-Santos 2006, Neary 2012) and will benefit future assessments and restoration practices by allowing us to focus on velocity zones that are critical to fish passage.

Behavior plays an important role in how fish move past barriers. Minimum depth is a biological parameter incorporated into FishXing that determines whether individuals are able to successfully navigate a culvert at low stream flows. Water depth remains an important aspect of culvert passage as predictions of depth barriers can be common in studies using FishXing (Gibson et al. 2005). However, Burford et al. (2009) indicated that this parameter had very little influence on determining the upstream movement of fish. Inconsistencies with FishXing predictions from previous work (Bourne 2013) and field observations of fish movements led us to reduce the models minimum depth measurement. Our results indicate that this threshold remains conservative. We defined the minimum depth as $\frac{2}{5}$ the body length (minimum depth from 4 to 8 cm) of an individual which was more liberal than the 9.1 cm used by Burford et al. (2009). Both the values in this study and in Burford et al. (2009) are considerably lower than recommended minimum depth values (Bates et al. 2003). However, we found that using $\frac{2}{5}$ body length was accurate in three of the culverts in this study (only culvert A was considered a depth barrier). Unfortunately, we were unable to capture *in-situ* measurements of culvert hydrologic characteristics to calculate minimum depth, and thus

we used FishXing outputs to derive minimum depth for culvert A. While it is useful to know at what depth fish are able to pass, it is unclear whether the precision of FishXing is accurate enough to back calculate such parameters. Therefore, further work is needed to continue to refine how depth influences fish movements and how individuals interact with anthropogenic structures in low flow situations.

The installation and replacement of stream crossings is an expensive endeavor (Bernhardt et al. 2005) and using inaccurate barrier assessment methods to prioritize culvert restoration could unnecessarily burden limited financial resources when no action is needed to promote fish passage. However, the conservative outputs of FishXing, when predicting fish movement, may be advantageous as a precautionary tool. FishXing was created to help in the design of culverts to promote fish passage, and within this framework, a precautionary approach is beneficial. Designing culverts in excess of what is needed for fish passage will ensure fish movement throughout the range of flows encountered by fish. However, at what point does designing culverts for fish passage based on a conservative FishXing output become too costly when a less conservative design can have the same effects on the aquatic community? Continued advancements in the understanding of fish passage should lead to a balance that will promote effective culvert designs without accruing unneeded expenditures.

An alternate approach to FishXing would be to focus on identifying specific physical thresholds that create a pass/no pass scenario and would continue to capitalize on the simplicity and affordability of commonly used barriers assessment methods. Past methods such as flow chart methods, have calculated culvert passabilities but few have

been rigorously tested as to whether these predictions match actual fish movement (Kemp and O'Hanley 2010). In spite of this, one flow chart model developed by Coffman (2005) uses several easy-to-calculate measurements based on culvert slope, length, and tail-water area to calculate the passability of a culvert. Although the methods used by Coffman (mark recapture using fin clips; 2005) likely produce conservative results, it is still appealing in that model estimates were based on observations of fish movement to determine thresholds. The benefit of using a model like that of Coffman (2005) is that it allows the user to quickly and easily assess a culvert and assign a passability value to it with an associated degree of confidence. However, Anderson et al. (2012) postulated that binary responses likely over-simplify culvert passage of many fish species. Using Bayesian belief networks (BBN), Anderson et al. (2012) concluded that the inclusion of two and three levels of criteria would distinguish partial barriers that were previously labeled as complete barriers with a pass/no pass analysis. But not unlike other barrier assessment methods, the use of BBNs to calculate probabilities of culvert passage is still dependent on accurately defining thresholds, a trait shared by other culvert assessment techniques (Haro et al. 2004, Coffman 2005, Furniss et al. 2006, Kondratieff and Myrick 2006, Kemp and O'Hanley 2010, Anderson et al. 2012).

Barrier assessments are an integral part of understanding and maintaining riverscape connectivity. Passability metrics are one measurement that can be difficult to assess but which have been shown to influence connectivity models (Bourne et al. 2011). Our results isolate the effects of culvert impacts on fish movements and provide support to previous studies that speculated on the conservative nature of FishXing (Burford et al.

2009, Bourne et al. 2011) and highlight the need to continue to validate the effectiveness of common barrier assessment models and how fish interact with barriers. The implications of using inaccurate barrier assessment techniques could lead to misidentifying barriers as impassable and result in costly management actions that have little or no ecological impact on the focal species.

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Table 2.1. FishXing hydrologic input parameters used for each culvert in TNNP. Culvert roughness was back calculated using the entrance loss coefficients of Straub and Morris (1950a, b).

Measurement	Culvert A	Culvert B ^a	Culvert C	Culvert D ^a
Shape (unit less)	Circular	Circular	Circular	Circular
Diameter (cm)	87	75	78	240
Material (unit less)	CMP ^b	CMP ^b	Concrete	CMP ^b
Entrance type (unit less)	Projecting	Projecting	Projecting	Projecting
Entrance loss (K _e)	0.7	0.9	0.9	0.9
Culvert roughness (n)	0.01	0.024	0.16	0.015
Length (m)	14	12	6.2	36
Inlet bottom elevation (m)	147.32	67.18	98.6	10.10
Slope (%)	2.29	1.50	1.77	1.83
Outlet bottom elevation (m)	147	67	98.6	9.44
Water surface elevation (m)	147.07	67.22	99.05	9.64
Velocity reduction factors inlet/barrel/outlet (unit less)	0.8/0.6/0.8	0.8/0.6/0.8	0.8/0.6/0.8	0.8/0.6/0.8
Channel bottom slope (%)	3.4	4.6	3.1	2.1
Outlet pool bottom elevation (m)	146.75	67.146	98.66	9.3
Tail-water roughness (unit less)	0.2	0.05	0.46	0.04
Tail-water cross section station (elevation) (m)	0.00 (146.95)	0.00 (67.57)	1.0 (98.96)	1.50 (10.33)
	1.70 (146.82)	0.45 (67.53)	2.0 (98.73)	1.95 (9.83)
	1.90 (146.78)	1.05 (67.15)	3.0 (98.77)	3.80 (9.82)
	1.95 (146.82)	1.40 (67.22)	4.0 (98.80)	5.25 (9.69)
	2.10 (146.75)	1.80 (67.20)	5.0 (98.86)	6.00 (9.45)
	2.40 (146.75)	2.15 (67.20)	6.0 (98.73)	6.30 (9.40)
	2.70 (146.80)	2.45 (67.23)	7.0 (98.78)	6.60 (9.30)
	2.80 (146.77)	2.70 (67.29)	8.0 (98.77)	7.20 (9.30)
	3.05 (146.79)	3.66 (67.75)	9.0 (98.83)	7.50 (9.36)
	3.50 (146.77)	4.45 (67.69)	10.0 (99.0)	7.80 (9.43)
	4.20 (147.02)			8.30 (9.64)
				9.10 (9.75)
				9.90 (9.98)
				10.70 (9.92)
				12.00 (10.33)

a Culverts A and D had secondary overflow culverts that were not modeled in FishXing. b Corrugated Metal Pipe

Table 2.2. Brook Trout *Salvelinus fontinalis* biological parameters used for FishXing. Burst (maintaining swim speeds for 20 s; BS) and sustained (maintaining speeds for 600 s; SS) swim speeds for Brook Trout based on Brook Trout swim speed models by Peake et al. (1997). Minimum depth was calculated as 2/5 the size of the Brook Trout. Jump Height was calculated as 2 times the length of the Brook Trout.

Length (mm)	BS(m/s)	SS (m/s)	Min depth (m)	Jump height (m)
50	0.374	0.266	0.02	0.1
100	0.599	0.491	0.04	0.2
150	0.824	0.716	0.06	0.3
200	1.049	0.941	0.08	0.4
250	1.274	1.166	0.1	0.5

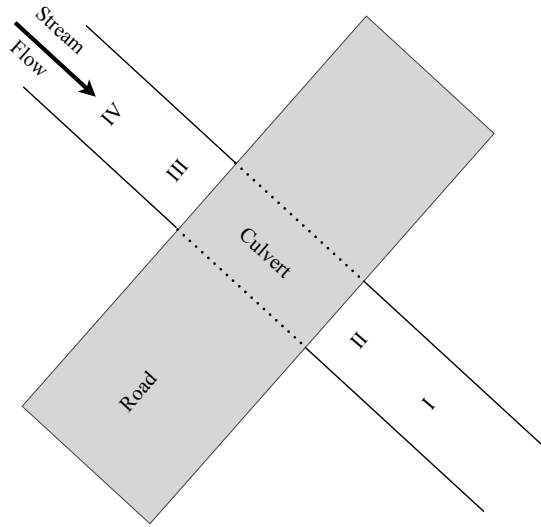


Figure 2.1. Antennae setup for all culvert sites. Antennae II and III are on the inlet and outlet of the culvert respectively. Antennae I and IV are located at the outlet and inlet pools approximately 2 to 3 meters from the culvert respectively.

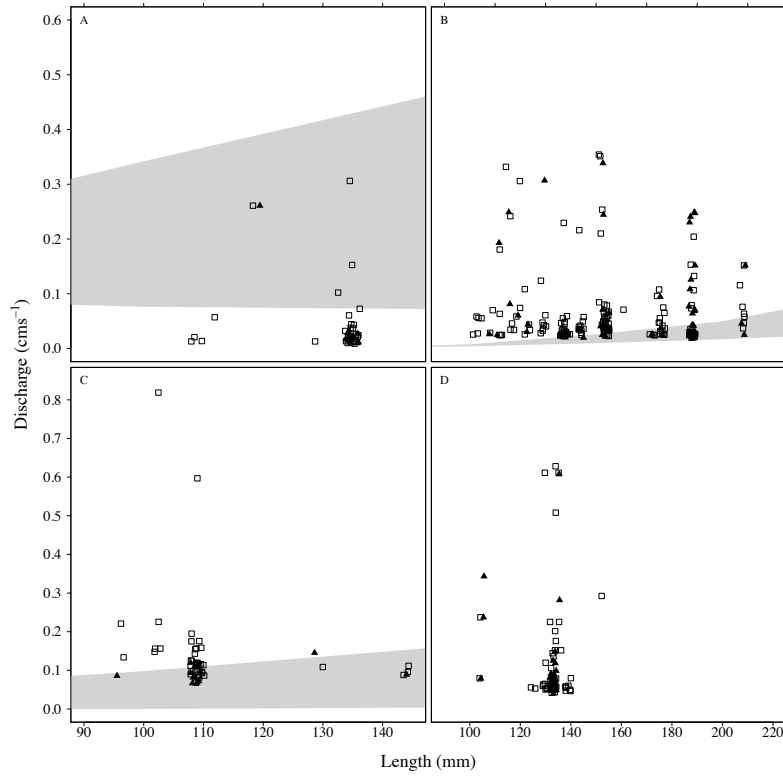


Figure 2.2. Successful and failed passage of Brook Trout based on length and discharge at the time of the pass attempt. Grey zones indicated the conditions under which Brook Trout are predicted to be able to pass at each culvert based on FishXing. Open squares represent successful pass attempts and black triangles represent unsuccessful pass attempts by Brook Trout. Panels A-D correspond to data from the 4 culverts, and culvert parameters (A-D) are given in Table 2.2.

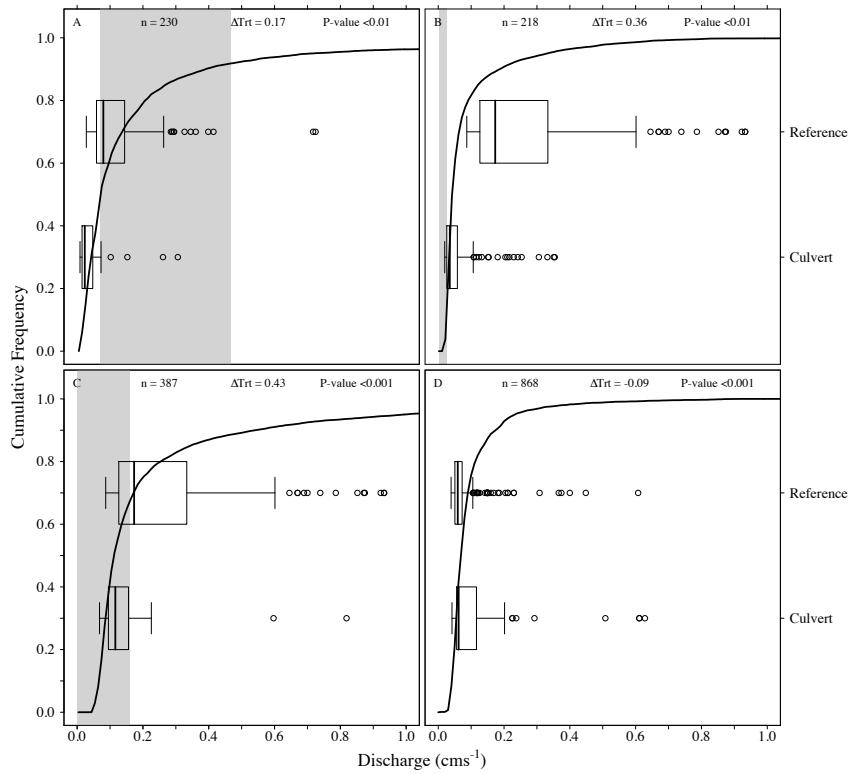


Figure 2.3. Timing of Brook Trout passage relative to the cumulative distribution of stream discharge (black line), observed culvert and reference site passage (box plots), and predicted passage as determined by FishXing (grey zone). Predicted passage was based on FishXing passable flows outputs for 100 to 150 mm Brook Trout. The boxes represent the inter-quartile range (IQR), solid dark line is the median, whiskers are 1.5 times the IQR. Outliers are represented by open circles. Sample size (n) is the total number of successful pass events for a given site, which consists of a reference and culvert telemetry array. ΔTrt is the difference of the range (represented by the whiskers) of passable flows between the reference site and culvert site. Positive numbers indicate that culverts had a smaller range of passable discharges compared to reference sites.

CHAPTER 3. ASSESSING THE BIOLOGICAL VALIDITY OF AQUATIC CONNECTIVITY INDICES USING STREAM FISH COMMUNITIES DATA

3.1 Introduction

The increased awareness of the effects of anthropogenic barriers on aquatic ecosystems has prompted new research to understand, quantify, and mitigate these impacts (Fullerton et al. 2010). Previous work has focused on individual barriers and how they influence the aquatic communities (Warren and Pardew 1998, Coffman 2005, Mahlum et al. *no date*). However, recent efforts have extended the spatial scope to consider the cumulative effects of multiple barriers (Schick and Lindley 2007, Cote et al. 2009, Padgham and Webb 2010, Bourne et al. 2011, O’Hanley 2011), including the importance of incorporating smaller dams and culverts (Januchowski-Hartley et al. 2013). It is thought that assessing cumulative impacts of multiple barriers is a critical aspect required to determine the connectivity of aquatic systems and how barriers influence stream communities at various spatial extents.

Landscape metrics of connectivity have been well studied over the last 30 years, with aquatic environments simply being regarded as a habitat feature embedded within the terrestrial landscape (Wiens 2002). Increasingly, basic principles from terrestrial landscape ecology have been tailored for river ecosystems (Ward 1998, Fausch et al. 2002, Ward et al. 2002, Wiens 2002). Following this foundational work, several research efforts have developed structural indices of connectivity appropriate for the dendritic nature of aquatic systems. These include score and ranking methods (Pess et al. 1998, WDFW 2000, Taylor and Love 2003, Poplar-Jeffers et al. 2009), optimization techniques

(Kemp and O'Hanley 2010, O'Hanley 2011), patch-based graphs (Schick and Lindley 2007, Erős et al. 2011, Erős et al. 2012), and connectivity indices (Cote et al. 2009, Padgham and Webb 2010). These indices are particularly accommodating to help prioritize restoration efforts, as reconnecting aquatic habitats can be quite expensive (Bernhardt et al. 2005, Januchowski-Hartley et al. 2013). However, the use of structural indices are predicated on efficiently improving ecological integrity by maximizing *potential* biological gains through increasing structural connectivity (Schick and Lindley 2007, Cote et al. 2009, Padgham and Webb 2010, O'Hanley 2011) by the removal or restoration of particular barriers. Although these indices provide conceptually simple methods to systematically improve theoretical connectivity, it is poorly understood whether the recommendations yield biologically meaningful results (see Perkin and Gido 2012 for an exception). It is therefore necessary to understand the limitations (both statistical and ecological) of structural indices and their ecological response in aquatic communities (Kupfer 2012).

One method to assess the ecological relevance of structural indices is to test for relationships between a given structural index and biological community patterns across stream systems with variable degrees of fragmentation. For instance, Perkin and Gido (2012) found a strong relationship between fish community structure within second and third order stream units and a structural connectivity index. Understanding the response of structural indices at small spatial extents is an important development, yet it remains unknown whether these relationships will continue to be present at larger spatial extents where confounding variables may have an increased influence on aquatic communities.

For example, Branco et al. (2011) found that environmental and human pressures, but not the presence of barriers, were the dominant driver of the distribution of several potamodromous and resident fish species. However, Branco et al. (2011) acknowledged that they used a relatively simple index of connectivity and called for a more thorough assessment of connectivity at broader spatial extents.

We analyzed the relationship between structural connectivity and patterns in fish community structure using data from five southern Ontario, Canada watersheds which have a high degree of biodiversity. The focus of this study was to determine if a relatively simple structural index, the Dendritic Connectivity Index (DCI), has biological relevance. Although we expect multiple confounding variables (e.g., elevation, watershed land use, stream network topology) to contribute to the explanation of patterns in community structure; we predict changes in fish community data in response to variation in the DCI. Furthermore, increases in connectivity result in increases in patch size and available habitat which could support a broader range of stream biota (Bain and Wine 2009). Therefore, it is expected that we would see increases in species richness with increases in the value of the DCI. We also tested the importance of the DCI for individual fish species for both presence and abundance data. At an individual species level, we expect to see an increase in species presence and abundance as connectivity increases across sites. Primarily, it is anticipated that individual species that have life histories that require broad scale movements (e.g., salmonids) will be affected by losses in connectivity more than species that may not require the same broad scale movements (e.g., cyprinids).

3.2 Methods

3.2.1 Study Area

Southern Ontario exhibits a high degree of freshwater fish biodiversity (Chu et al. 2003). The diversity is attributed to a combination of postglacial dispersal and the anthropogenic introduction of non-native species (Dextrase and Mandrak 2006). The study was conducted in the watersheds of Wilmot, Oshawa, Ganaraska, Cobourg, and Duffins in southern Ontario, just east of the metropolitan area of Toronto (Figure 3.1). The five watersheds studied here are dominated by developed urban areas at their confluence with Lake Ontario, agricultural landscape in the mid reaches and a mixture of forest and low intensity agriculture in the headwaters. They range in watershed size of 98 km² for Wilmot to 283 km² for Ganaraska.

3.2.2 Data Layers

Fish community data, structural index, and habitat variables were incorporated into the analysis (Table 3.1). Fish sampling was conducted from 1997 to 2009 by various agencies as part of a collaborative monitoring program (TRCA, 2010) using the Ontario Stream Assessment Protocol (Stanfield 2010). Sampled sites consisted of those with single and multiple sampling visits, of which the latter were averaged across sampling periods to eliminate pseudo-replication. Sites were a minimum length of 40 m and were bounded by “crossovers” (where the thalweg crossed to the opposite side of the stream) to ensure adequate sampling of all habitat types (Stanfield 2010). Single-pass electrofishing was used to capture fish at a targeted effort of 7 to 15 s/m². All fish were measured, weighed, and identified to species with the exception of lampreys

(*Petromyzontidae*), which were identified to family due to inconsistencies in identification to the species level.

3.2.3 Connectivity index

To measure the structural connectivity across the 5 watersheds, we employed the Dendritic Connectivity Index (Cote et al. 2009). The DCI is a structural connectivity index that is calculated based on the probability that an individual can move freely between two random points in a dendritic network. This takes into consideration the amount of potential habitat between barriers along with a measure of passability for each barrier. Furthermore, the DCI is flexible in that it can be modified to address the natural connectivity of a stream based on both potamodromous (DCI_p) and diadromous (DCI_d) life histories. The DCI_p applies to life histories that typically live in riverine systems and do not require the movement to and from larger water bodies. DCI_p is defined as:

$$DCI_p = \sum_{i=1}^n \sum_{j=1}^n c_{ij} \frac{l_i}{L} \frac{l_j}{L} * 100$$

where l is the length of the segment i and j , c_{ij} is the connectivity between segments i and j , and L is the total stream length of all stream segments. The DCI_d applies to all life histories that migrate between a fixed point (e.g., estuary) and all upstream areas within a riverine system. DCI_d is calculated as:

$$DCI_d = \sum_{i=1}^n c_{ij} \frac{l_i}{L} * 100$$

where L is the total length of the stream sections, l_i is the length of section i , c_{ij} is the connectivity between segments i and j . While the DCI_p and DCI_d measure the overall

connectedness of a system, it could be beneficial to apply a structural connectivity metric at finer spatial scales (e.g., stream reach) to control for local pressures of connectivity on the biotic community. As noted in Cote et al. (2009), the DCI_d can be applied to measure the connectivity from any stream segment to the rest of the watershed. We denote this value as DCI_s , and used this in models for data collected at the scale of the stream segment. We used the Fish Passage Extension (FIPEX v2.2.1) for ArcGIS (v9.3.1) using a hydrological stream network provided by OMNR to calculate connectivity indices described above.

3.2.4 Determining barrier passability

Identifying all barriers in a system is imperative in order to accurately assess connectivity (Cote et al. 2009, O’Hanley 2011, Januchowski-Hartley et al. 2013). A partial list of barrier locations was provided by OMNR which consisted of 298 barriers across the 5 watersheds used in this study (Table 3.2). We also used the National Hydro Network obtained via GeoBase (<http://www.geobase.ca/>) to identify dams not in the OMNR dataset (Table 3.2). Furthermore, road culverts are thought to outnumber dams by up to 38 times, with as many as two-thirds of them being designated as complete or partial barriers to fish movement (Januchowski-Hartley et al. 2013). Therefore, to help identify potential barriers, we used ArcGIS to identify intersections between streams and roads (stream/road intersections) that would indicate a potential barrier and help create an inclusive barrier database to calculate the DCI (Table 3.2). All sources of barrier locations were cross checked to prevent multiple occurrences of the same barrier in the dataset. We calculated and analyzed the DCI with regards to community structure and

species richness with only known barriers and then again with the inclusion of potential barriers identified through GIS (stream/road intersections). This will provide insight into GIS derived barrier locations and the potential benefits of modeling all potential barrier locations.

Determining passability values for potential barriers in these watersheds was challenging due to their vast number and the limited information available for them. This limitation is not unique to this study and underscores some of the common obstacles to riverscape-scale analyses in larger watersheds (for an example see Meixler et al. 2009). Passabilities (0 = impassable and 1 = passable) of zero were first assigned to all dams and perched culverts (jumping height of the barrier exceeded the threshold of most species encountered within the system; Table 3.2). The remaining 75% of potential barriers lacked a passability score (Table 3.2). Several studies have found a relationship between culvert passabilities and channel slope (McCleary and Hassan 2008, Poplar-Jeffers et al. 2009), and we followed this approach to infer passability values for barriers with unknown passability. We used an available data set ($n = 18$) from Terra Nova National Park (TNNP), Newfoundland, Canada that contained both passability scores and channel slopes. Passabilities in TNNP were calculated using FishXing (Furniss et al. 2006) and were based on the percent of time stream flows were within a passable range for brook trout (*Salvelinus fontinalis*). We calculated channel slope for culverts in Newfoundland and Ontario using a 10-m digital elevation model (DEM) by creating a 100 m diameter buffer around the barrier and taking the difference in elevation between the furthestmost

upstream and downstream points and then dividing by the stream length between those points. Finally, we used a nonlinear regression,

$$\log\left(\frac{p_i}{1-p_i}\right) = 1 + \beta_1 x_i + \varepsilon_i$$

where $i = 1$ to number of culverts (N), p is passability, x is channel slope, and $\varepsilon_i \sim N(0, \delta^2)$, to estimate the relationship between culvert passability and channel slope in TNNP and then applied that relationship to the channel slopes measured to potential barriers in southern Ontario that lacked a passability metric.

3.2.5 *Accounting for confounding variables*

It is thought that stream process and patterns are continually changing along the longitudinal gradient of the stream (Vannote et al. 1980) and these changes can significantly affect the biotic community (Fausch et al. 2002). Some of these influences can be segregated into habitat variables (e.g., elevation and stream width) and landscape use (e.g., urban and farmland). Several factors were incorporated into our analysis to control for confounding effects that have been shown to influence community structure (see Table 3.1). These included elevation (ELE; Rahel and Hubert 1991, Stanfield and Kilgour 2006), land cover (Allan et al. 1997, Allan 2004, Stanfield and Kilgour 2006), stream network topology (Hitt and Angermeier 2008b, Betz et al. 2010), and stream width (SW; Stanfield and Kilgour 2006, Cote 2007). We extracted elevation for each sampling site from a 10-m DEM obtained from OMNR. Land cover was quantified using the Southern Ontario Land Resource Information System (SOLRIS; Ontario Ministry of Natural Resources 2006) by determining the percentage of the watershed in each land

cover type. We selected different land covers variables that are thought to influence stream biota (Table 3.1). To measure stream network topology, we calculated the Upstream Cell Count (UCC) following guidelines described in Betz et al. (2010). Lastly, stream width (SW) was measured during biological sampling by taking an average of 10 transects measuring SW throughout the sampling site (Stanfield 2010).

3.2.6 *Analysis*

A multivariate distance-based redundancy analysis (db-RDA) was used to determine how connectivity affects community structure (Legendre and Anderson 1999). Specifically, we analyzed how community similarities of abundance and biomass changed with structural connectivity as determined by the DCI_s , DCI_p , and DCI_d . We chose to use db-RDA because 1) db-RDA can accommodate the non-Euclidean distance measures used in community similarity metrics, 2) it can control for confounding variables, and 3) db-RDA uses nonparametric permutation methods which freed us from the assumption of normality (Legendre and Anderson 1999). For the multivariate analysis, a fourth root transformation on the fish community data was employed to emphasize diversity (Clarke and Warwick 2001). Finally, we used the Bray-Curtis Index (Bray and Curtis 1957) as a similarity measure because of its robustness and appropriateness for ecological community data (Faith et al. 1987, Clarke and Warwick 2001). A correction factor was not incorporated for the negative-eigenvalues to correct for Type 1 errors based on McArdle and Anderson (2001). Significance was determined by a pseudo-F statistic at $\alpha = 0.05$.

To select co-variables (Table 3.1) for the inclusion in our analysis, we used Akaike's Information Criteria (Akaike 1973, Burnham and Anderson 2002, Oksanen 2007, Oksanen et al. 2012). Before we identified candidate models, we removed collinear variables (Spearman's rank correlations > 0.7). Next using variables identified in Table 3.1, *a-priori* candidate models were created for abundance and biomass ranging from simple (single variable) to more complex (maximum 9 variables in our global model). To assess how well co-variables contributed to explaining the data, we calculated the ΔAIC (difference in AIC values from the model with the smallest AIC value) and AIC weights (the amount of support that a given model is the best). Only models that were within $\Delta AIC < 2$ of the top model were considered for the inclusion in the analysis (Burnham and Anderson 2002). To maintain consistency between the different analyses throughout the study, we incorporated variables identified through the model selected procedure for all levels of analysis .

We used generalized linear mixed model (GLMM) approach to test the effects of connectivity on species richness, as this allowed us to account for the potential pseudo-replication within watersheds (Bates et al. 2011). Species richness was quantified by calculating the total number of fish species at each site. Using the GLMM, we analyzed the relationship between the DCI_s and the species richness of a site while controlling for confounding variables previously identified. Significance was determined by a z-statistic at $\alpha = 0.05$.

We also tested to see how connectivity, calculated with known barriers and potential barriers, affected the presence and abundance of individual species. Seven

relatively abundant species across three families were selected to represent a wide range of life history characteristics (e.g., diadromous) and that were also relatively abundant across sites (Table 3.3 and 3.4). Once the species were selected, we used a GLMM to analyze the presence of a selected species with a binomial distribution (Bates et al. 2011) versus the DCI_s while controlling for confounding variables identified in the model selection procedures. Then, to analyze species abundances we continued to use a GLMM. However, to account for overdispersion and to test for the significance of the fixed effects, we used a Markov Chain Monte Carlo (MCMC) approach ($\alpha = 0.05$) with 10,000 iterations (Hadfield 2010). All statistical analysis was carried out with the statistical program R (v. 2.15.2, R Development Core Team 2012).

3.3 Results

A total of 273 stream sites were selected across 5 watersheds (range of 27 to 70 sites per watershed). We used the selected sites for all levels of analysis within this study. A total of 38 species were sampled across the study sites with a mean of 25.4 species per watershed (range = 21 to 28). In addition to the 298 barriers identified by OMNR, we identified an additional 85 dams and 1,041 stream/road intersections (Table 3.2). The relationship between stream slope and passability obtained from barriers in Terra Nova National Park was reasonably strong ($r^2 = 0.68$; Figure 3.2). When applied to southern Ontario stream/road intersections, the predicted passabilities of un-surveyed barriers ranged from 0.0 to 0.99 (Figure 3.3). Calculated connectivity scores for our study area in southern Ontario ranged from 0.0 to 41.1 for DCI_s at the site scale and, 14.9 to 22.6 for the DCI_p, and 0.3 to 31.2 for the DCI_d, both at the watershed scale (Table 3.5).

Twenty-two different models of community similarities were analyzed each for abundance and biomass (Table 3.6). Results of the Spearman's correlation matrix indicated that SW and UCC were highly correlated ($r = 0.8$). As a result, we did not include SW and UCC in the same model. The top model for abundance ($\Delta AIC < 2$) included ELE, SW, and built-up area-pervious (BUAP; areas of urban development). The top model for biomass included ELE, SW, and BUAP. All other additional confounding variables did not adequately explain community structure given the dataset and were represented in models that had $\Delta AIC > 2$. The top model for abundance and biomass both had 80 and 83 percent of evidence in support of the top model respectively, and to maintain consistency between the different analyses, we elected to use ELE, SW, and BUAP to control for confounding effects in our facets of our analysis.

The db-RDA models used to analyze the relationships between the DCI_s , DCI_p , and DCI_d , calculated based on known barriers, and community structure for abundance data, with the co-variables of ELE, SW, and BUAP, explained 21.1, 21.4, and 24.4 percent of the total variation in species composition respectively. We used a type III sum of squares and found all three co-variables significantly related to community structure in all three models (Models 1-3; Table 3.7). The DCI_s , DCI_p , and DCI_d was significantly related to community structure as well ($F = 3.67$, $df = 1$, $p < 0.01$; $F = 4.74$, $df = 1$, $p < 0.005$; $F = 15.64$, $df = 1$, $p < 0.005$ respectively). A positive correlation was also seen for the DCI_s ($r = 0.65$) and DCI_d ($r = 0.48$) for axis 1 and a negative correlation was seen for the DCI_p with axis 2 ($r = -0.67$).

The db-RDA models used to analyze the relationships between the DCI_s, DCI_p, and DCI_d, calculated with known barriers and potential barriers, and community structure for abundance data, with the co-variables of ELE, SW, and BUAP, explained 21.9, 22.2, and 24.4 percent of the total variation in species composition respectively (Models 4-6; Table 3.7 and Figure 3.4). Using additional barrier information derived from GIS data improved our models and the amount of variation explained with our connectivity metric. Following the trends with the models which used only known barriers (models 1-3), we found that all confounding variables for models 4-6 significantly explained community structure (Table 3.7). The DCI_s, DCI_p, and DCI_d were significantly related to community structure as well ($F = 6.37$, $df = 1$, $p < 0.005$; $F = 7.64$, $df = 1$, $p < 0.005$; $F = 15.52$, $df = 1$, $p < 0.005$ respectively). Axis 1 of the db-RDA is negatively correlated with ELE for model 4 and 6 and positively correlated with ELE for model 5 (Table 3.7). Stream width has a positive correlation with axis 1 for model 4 and 6 and a negative correlation with axis 1 for model 5 (Table 3.7). Axis 2 of the db-RDA had a positive correlation with BUAP for models 4 and 5 and a negative correlation with model 6 (Table 3.7). A positive correlation was also seen for the DCI_s ($r = 0.65$) and DCI_d ($r = 0.48$) with axis 1 and a negative correlation was seen for the DCI_p with axis 2 ($r = -0.67$).

The db-RDA models analyzing the relationship between the DCI_s, DCI_p, and DCI_d, calculated with known barriers and potential barriers, and community structure for biomass, with the co-variables of elevation ELE, SW, and BUAP, explained 21.6, 22.3, and 24.1 percent of the total variation in species composition respectively (Models 7-9; Table 3.7 and Figure 3.5). Following the trends seen for abundance, we found that all

three co-variables for each biomass models were significantly related to community structure (Table 3.7). The DCI_s , DCI_p , and DCI_d were significantly related to community structure as well ($F = 4.87$, $df = 1$, $p < 0.005$; $F = 7.1$, $df = 1$, $p < 0.005$; $F = 16.21$, $df = 1$, $p < 0.005$ respectively). Axis 1 of the db-RDA was positively correlated with ELE for biomass models 1 and 3 and negatively correlated with model 2. Axis 1 was positively correlated with SW for model 2 and negatively correlated with models 1 and 3. Axis 2 had a positive correlation with BUAP for biomass models 1 and 3 but a negative correlation with BUAP for biomass model 2 (Table 3.7). Finally, the DCI_s and DCI_d was negatively correlated with axis 1 ($r = -0.61$ and $r = -0.46$) and the DCI_p had a positive correlation with axis 2 ($r = 0.42$).

To analyze how species richness changes with connectivity with only known barriers, we failed to explain increases in species richness with increases in connectivity (DCI_s ; $z = 0.001$, $n = 273$, $p\text{-value} = 0.307$; Figure 3.6a). However, when we included potential barriers into the DCI calculation, species richness was significantly affected by the DCI_s ($z = 0.004$, $n = 273$, $p\text{-value} = 0.02$; Figure 3.6b). Furthermore, ELE and SW was a significant determinate of changes in species richness ($z = -0.002$, $n = 273$, $p\text{-value} < 0.001$; $z = 0.07$, $n = 273$, $p\text{-value} < 0.001$ respectively). However, the land cover variable used (BUAP) did not show a significant relationship with species richness ($z = 0.016$, $n = 273$, $p\text{-value} = 0.719$).

For the species-level presence analyses, we found only two species had a significant relationship with the DCI_s : rainbow trout (*Oncorhynchus mykiss*) and mottled sculpin (*Cottus bairdii*; $z = 0.07$, $n = 273$, $p\text{-value} = <0.001$ and $z = 0.017$, $n = 273$, $p\text{-value} = 0.001$ respectively).

value = <0.001 respectively; Table 3.3). Furthermore, abundance data for rainbow trout (mean = 0.07, n = 273, p-value = 0.001), mottled sculpin (mean = 0.09, n = 273, p-value = 0.001), and longnose dace (mean = 0.05, n = 273, p-value = 0.014; *Rhinichthys cataractae*) were found to have a significant relationship with the DCI_s (Table 3.4; Figure 3.7). At least one confounding variable had a significant relationship in the individual species analysis with ELE the dominant predictor variable most commonly seen between the species.

3.4 Discussion

Structural indices have been increasingly used to determine the degree of connectivity across watersheds but interpretation of these results are hampered by the lack of demonstrations of biological relevance to aquatic ecosystems. Understanding these relationships is important to provide context into the appropriateness and limitations of simple structural indices, such as the DCI, and their use in aquatic ecosystems. We demonstrated that the DCI has some biological relevance with regards to understanding fish communities and individual species distribution and abundance, even in the presence of confounding variables such as elevation, stream width, and land cover. This conclusion is consistent with findings by Perkin and Gido (2012) who found a significant relationship between the same connectivity index analyzed here and community structure within relatively small study units consisting of second and third order streams. The finer spatial extents examined in that study likely minimized confounding variables and showed an even stronger relationship between connectivity and fish communities ($r^2 = 0.66$). Since the importance of environmental factors to

stream biota is often scale-dependent (Wiens 1989, Poff 1997, Labbe and Fausch 2000, Fausch et al. 2002, Wiens 2002, Hitt and Angermeier 2008a, Hitt and Angermeier 2008b, Stanfield and Kilgour 2012), it remains unknown whether links between structural connectivity and communities will persist at spatial extents larger than the present study. However, it has been shown that increases in interpatch distance significantly decreases the landscape connectivity (Goodwin and Fahrig 2003) and it could be expected that the same trends would persist in aquatic environments.

The biology of the various species likely impacted the sensitivity of fish communities to structural connectivity. This study found relationships between the DCI_s and the abundance of several species. As expected, we found species that require extensive movements (e.g., rainbow trout) during their life history were significantly influenced by a lack of longitudinal connectivity. In contrast, other species (mottled sculpin and longnose dace), less known for extensive migration (Johnston 2003), were also influenced by the presence of anthropogenic barriers. Past studies have found local scale effects of barriers on small stream fishes (Warren and Pardew 1998, Coffman 2005, Norman et al. 2009) and in support of Meixler et al. (2009), it appears that local scale effects of barriers translate into community wide impacts on the persistence of at least some small stream fishes. Furthermore, some of our species-specific predictions with regards to connectivity did not bear out. For example, we expected brook trout, a native species to the study area, would be more affected by losses in connectivity than other species because they require a variety of habitats throughout their life cycle, which often result in long migrations. However, the presence of anthropogenic barriers did not seem

to have a significant relationship with brook trout abundance. This may be attributed to low species abundances or confounding circumstances not modeled in this study. For instance, brown trout (*Salmo trutta*) have been shown to impact brook trout through competition of important habitat (e.g., spawning habitat and refugia) and predation (Fausch and White 1981). Furthermore, we found a strong elevation influence for these two species which might further indicate that brook trout are being pushed into the headwaters where they are still competitive (Stanfield et al. 2006). Although fragmentation may be a factor in the eventual recovery of brook trout and other salmonids, it appears that other confounding variables currently have a greater impact on the persistence of this species. Understanding how fragmentation specifically plays in species distributions will assist managers in the recovery of imperiled species and how to mitigate the effects of anthropogenic disturbances.

In the absence of anthropogenic alterations to the landscape (e.g., barriers), alternate pressures can influence ecological processes and patterns (Hargis et al. 1999, Fagan 2002). In addition to the effects seen with the DCI, environmental variables had a strong relationship with community structure as well as with individual species (also seen in Stanfield et al. 2006). This supports previous connectivity studies that found environmental factors affected metapopulations (e.g., land cover and water quality; Meixler et al. 2009, Branco et al. 2011). Confounding variables such as the ones modeled here are an important aspect associated with stream communities and controlling for these environmental metrics will help assist in determining how structural indices influence stream biota.

Presenting connectivity at watershed scales is useful to estimate watershed integrity or to prioritize restoration actions, but can be limiting at local scales or linking structural connectivity to locally sampled fish communities. We modified this watershed scale index into a local habitat variable and matched it to corresponding biotic information. We consider this a useful addition to typical quantification methods of connectivity that either focused primarily on barrier prioritization (Poplar-Jeffers et al. 2009, Kemp and O'Hanley 2010, O'Hanley 2011) or are overly simplistic (e.g., count of the number of barriers; Branco et al. 2011), and that miss important aspects of fragmentation (for a review see Kindlmann and Burel 2008, Padgham and Webb 2010). Measuring connectivity at a common scale to other local aquatic community variables will expand the understanding of how connectivity processes relate to biota and will be useful in theoretical and management applications.

Identifying barrier locations is an important aspect in the management of aquatic systems. The failure to account for all barriers may result in costly management actions that produce negligible ecological results (Bernhardt et al. 2005, Januchowski-Hartley et al. 2013). Although minimal barrier information (known barriers) significantly explained community structure, we saw an improvement with the inclusion of potential barriers (stream/road intersections) both in explaining community structure and species richness. This is useful information that lends support to Januchowski-Hartley (2013) who advocate for the incorporation of all stream/river intersections into current barrier databases.

We had relatively low explanatory power to explain community structure and we were unable to predict abundance of multiple species with aquatic connectivity. One explanation could be our methodology to calculate passability. Identifying the passability of barriers was the largest obstacle in assessing connectivity over the relatively large study area. The use of GIS allowed us to identify potential barriers based on locations where streams and roadways intersected. However, assigning passability values required estimates based on known relationships with channel slope in another well studied area. Furthermore, passabilities were based on brook trout movements in Newfoundland streams. This is not appropriate for all species and likely overestimates passage for many species (e.g., *Cyprinidae*; Coffman 2005, McLaughlin et al. 2006). While the relationship between channel slope and passability was not perfect, and FishXing is known to be conservative (Burford et al. 2009, Mahlum et al. *in press*), fish community metrics still showed significant effects using this approach.

It is reasonable that thresholds of connectivity exist and are associated with the biology of the focal organism or community. Determining scale dependent thresholds of biotic communities to structural indices is important to the persistence of species (Monkkonen and Reunanen 1999). Despite the relatively large study area, only the lower end of the connectivity spectrum was captured in this study and critical thresholds may exist outside the range studied here. Capturing the full spectrum of connectivity scores at similar scales may be difficult as pristine and highly fragmented stream systems will likely differ from one another in many other ways. However, identifying thresholds to

help set management goals remains an important aspect in the recovery of focal species and the application of current structural indices (Perkin et al. 2013).

Structural connectivity indices can incorporate functionality (e.g., habitat quality, observed fish movement across barriers) that consider the perceptions an organism has of its landscape, as well as more straightforward physical parameters (e.g., stream length, barrier properties) that may not have biological relevance (Tischendorf and Fahrig 2000, Kindlmann and Burel 2008). It remains necessary to incorporate functionality into structural indices to achieve meaningful measures of connectivity (Kindlmann and Burel 2008), but doing so comes with tradeoffs such as increased data requirements, computational complexity, and decreased ease of interpretation (Kupfer 2012). Yet, incorporating more functional metrics without understanding their limitations may not necessarily increase their validity (Kupfer 2012). Recent work by Bourne (2013) found that incorporating a more functional habitat variable into structural indices influenced the magnitude of fragmentation of a system but not necessarily the qualitative conclusions (i.e., prioritization of the restoration action) when compared to physical properties of habitat. This indicates that, at least in some cases, simple physical measurements may be appropriate, and can save considerable time and resources.

Numerous structural indices are available to aid management efforts to reconnect stream movement corridors. It is important that the predicted relationships between such indices and biological communities are compared and validated. Our results here show that structural connectivity can relate to community structure at relatively broad riverscape scales.

3.5 References

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Table 3.1. Categories of variables used in the analysis with the associated symbol used within the text. Predictions for each abundance and biomass are included in the table with (+) indicating a predicted change in community structure and (-) indicating no predicted change in community structure.

Category	Variable	Symbol	Units	Abundance	Biomass
Dependent variables					
Fish Community	Abundance	A	Count	NA	NA
	Biomass	B	Kg	NA	NA
Independent variables					
Structural Index	DCI _d	DCI _d	Percentage of natural connectivity	+	+
	DCI _p	DCI _p	Percentage of natural connectivity	+	+
	DCI _s	DCI _s	Percentage of natural connectivity	+	+
Stream Position	Up-Stream Cell Count	UCC	Count	+	+
	Elevation	ELE	Meters	+	+
	Stream Width	SW	Meters	+	+
Land Cover	Build-up area Pervious	BUAP	Proportion watershed	of +	+
	Build-up area Impervious	BUAI	Proportion watershed	of +	+
	Cropland	CR	Proportion watershed	of +	+
	Pasture and Abandoned Fields	PAF	Proportion watershed	of +	+
	Mixed forest	MF	Proportion watershed	of +	+
	Deciduous forest	DF	Proportion watershed	of +	+

Table 3.2. Summary of barriers used to calculate the Dendritic Connectivity Index.

Source/type of barrier	Number
Ontario Ministry of Natural Resources	
Perched Culverts	108
Dams	10
Natural Barriers	13
Unclassified Barriers	167
Geobase	
Dams	85
Stream/Road Intersects	1041

Table 3.3. The results of the single species presence/absence analysis. Predictions (Pred) represent the expected relationship between the species and variable. Positive values indicate that species presence is predicted to increase with increases in the corresponding variable while negative values indicate that species presence is predicted to decrease with increases in the corresponding variable. The sample size (n) is based on the number of sites across all 5 watersheds. The estimate is analogous to the slope, standard error (SE), and p-value of the generalized mixed model were determined by the z statistic. Asterisks indicate significance at $\alpha = 0.05$.

Species	Pred	Variable	n	Estimate	SE	z-value	p-value
<i>Oncorhynchus mykiss</i>	+	ELE	273	-0.018	0.004	-4.417	< 0.001*
	-	BUAP		-0.518	0.467	-1.111	0.267
	+	SW		0.111	0.057	1.936	0.053
	+	DCI _s		0.058	0.016	3.757	< 0.001*
<i>Salmo trutta</i>	+	ELE	273	0.003	0.004	0.718	0.473
	-	BUAP		-0.837	0.217	-3.854	< 0.001*
	+	SW		0.349	0.062	5.641	< 0.001*
	+	DCI _s		0.020	0.016	1.255	0.209
<i>Salvelinus fontinalis</i>	+	ELE	273	0.030	0.005	6.471	< 0.001*
	-	BUAP		-0.674	0.308	-2.191	0.028*
	+	SW		0.109	0.063	1.723	0.085
	+	DCI _s		0.002	0.016	0.121	0.903
<i>Rhinichthys obtusus</i>	-	ELE	273	-0.018	0.004	-4.485	< 0.001*
	-	BUAP		0.557	0.282	1.977	0.048*
	-	SW		0.014	0.063	0.214	0.830
	+	DCI _s		-0.019	0.015	-1.253	0.210
<i>Rhinichthys cataractae</i>	-	ELE	273	-0.018	0.005	-3.721	< 0.001*
	-	BUAP		0.375	0.538	0.696	0.486
	-	SW		0.760	0.112	6.758	< 0.001*
	+	DCI _s		0.019	0.021	0.883	0.377
<i>Semotilus atromaculatus</i>	-	ELE	273	-0.013	0.003	-4.070	< 0.001*
	-	BUAP		0.531	0.210	2.531	0.011*
	-	SW		-0.051	0.051	-0.990	0.322
	+	DCI _s		0.008	0.013	0.639	0.523
<i>Cottus bairdii</i>	-	ELE	273	-0.005	0.004	-1.310	0.190
	-	BUAP		0.021	0.560	0.037	0.971
	+	SW		0.196	0.059	3.289	0.001*
	+	DCI _s		0.081	0.017	4.917	< 0.001*

Table 3.4. The results of the single species abundance analysis. Predictions represent the expected relationship between the species and variable. Positive values indicate that species abundance is predicted to increase with increases in the corresponding variable while negative values indicate that species abundance is predicted to decrease with increases in the corresponding variable. The sample size (n) is based on the number of sites the across all 5 watersheds. The mean is the analogous to the slope, standard error (SE), and p-value of the generalized mixed model where the results are based on a Markov Chain Monte Carlo permutation test (10,000 iterations). Asterisks indicate significance at $\alpha = 0.05$.

Species	Prediction	Variable	n	Mean	SE	p-value
<i>Oncorhynchus mykiss</i>	+	ELE	273	-0.02	0.00	0.001*
	-	BUAP		-0.50	0.02	0.310
	+	SW		0.16	0.00	0.001*
	+	DCIs		0.07	0.00	0.001*
<i>Salmo trutta</i>	+	ELE	273	0.02	0.00	0.001*
	-	BUAP		-0.96	0.02	0.082
	+	SW		0.42	0.00	0.001*
	+	DCIs		0.02	0.00	0.126
<i>Salvelinus fontinalis</i>	+	ELE	273	0.03	0.00	0.001*
	-	BUAP		-0.62	0.02	0.084
	+	SW		0.02	0.00	0.792
	+	DCIs		-0.01	0.00	0.722
<i>Rhinichthys obtusus</i>	-	ELE	273	-0.02	0.00	0.001*
	-	BUAP		0.58	0.02	0.154
	-	SW		-0.07	0.00	0.212
	+	DCIs		0.00	0.00	0.756
<i>Rhinichthys cataractae</i>	-	ELE	273	-0.02	0.00	0.001*
	-	BUAP		0.06	0.04	0.920
	-	SW		0.65	0.00	0.001*
	+	DCIs		0.05	0.00	0.014*
<i>Semotilus atromaculatus</i>	-	ELE	273	-0.02	0.00	0.001*
	-	BUAP		0.74	0.03	0.262
	-	SW		-0.18	0.00	0.004*
	+	DCIs		0.00	0.00	0.898
<i>Cottus bairdii</i>	-	ELE	273	-0.01	0.00	0.060
	-	BUAP		0.08	0.06	0.978
	+	SW		0.18	0.00	0.001*
	+	DCIs		0.09	0.00	0.001*

Table 3.5. The results of the connectivity analysis with included for each watershed as measured by the Dendritic Connectivity Index (Cote et al. 2009). For each watershed a connectivity measurement was calculated with known barriers and known barriers plus stream/river intersects for potamodromous life histories (DCI_p), diadromous life histories (DCI_d), and a site connectivity measures (DCI_s). A site is defined by the stream area between the upstream and downstream barriers. DCI values range from 0-100, with values of 100 indicating a watershed that is fully connected, and values approaching 0 indicating a high degree of fragmentation.

Watershed	Known Barriers			Known Barriers with Stream/River Intersects		
	DCI _p	DCI _d	DCI _s Range	DCI _p	DCI _d	DCI _s Range
Duffins	35.4	2.3	0.0 - 58.52	16.1	1.7	0.0 - 35.0
Oshawa	24.2	42.0	0.0 - 46.63	16.8	24.8	0.4 - 33.7
Cobourg	20.4	32.4	0.0 - 32.35	14.9	22.1	0.0 - 26.2
Ganaraska	24.4	0.4	0.0 - 46.63	18.4	0.3	0.5 - 39.1
Wilmot	51.3	67.0	0.0 - 67.02	22.6	31.2	14.9 - 41.1

Table 3.6. The results of co-variable selection based on the Akaike's Information Criterion (Burnham and Anderson 2002). We analyzed 22 models for each biomass and abundance. Model parameters are given in Table 3.1. K is defined by the number of parameters in the model plus 1, the ΔAIC is calculated by the difference between the smallest AIC value (the top model) and the AIC value of each subsequent model. The weight of the model is a calculation on the amount support for the top model is the best model relative to all models given the data.

Model	K	AIC	ΔAIC	Exp	Weight
Abundance:					
A ~ ELE + SW + BUAP	4	1181.69	0.00	1.000	0.805
A ~ ELE + UCC + BUAP	4	1184.79	3.09	0.213	0.171
A ~ ELE + SW + BUAI	4	1189.69	8.00	0.018	0.015
A ~ ELE + UCC + BUAI	4	1192.71	11.01	0.004	0.003
A ~ ELE + SW + PAF	4	1194.27	12.58	0.002	0.001
A ~ ELE + SW + FAP	4	1194.27	12.58	0.002	0.001
A ~ ELE + SW + MF	4	1194.54	12.85	0.002	0.001
A ~ ELE + SW + DF	4	1197.75	16.05	0.000	0.000
A ~ ELE + UCC + PAF	4	1197.76	16.06	0.000	0.000
A ~ ELE + UCC + FAP	4	1197.76	16.06	0.000	0.000
A ~ ELE + SW + CR	4	1197.90	16.21	0.000	0.000
A ~ ELE + SW + CR	4	1197.90	16.21	0.000	0.000
A ~ ELE + UCC + MF	4	1198.08	16.39	0.000	0.000
A ~ ELE + UCC + MF	4	1198.08	16.39	0.000	0.000
A ~ ELE + SW	3	1201.23	19.54	0.000	0.000
A ~ ELE + UCC + DF	4	1201.56	19.87	0.000	0.000
A ~ ELE + UCC + CR	4	1202.14	20.44	0.000	0.000
A ~ ELE + UCC	3	1205.64	23.95	0.000	0.000
A ~ ELE	2	1211.63	29.93	0.000	0.000
A ~ SW	2	1216.68	34.98	0.000	0.000
A ~ UCC	2	1219.02	37.32	0.000	0.000
^a A ~ ELE + UCC + SW + BUAP + BUAI + CR + PAF + MF + DF	8	1226.36	44.66	0.000	0.000
Biomass:					
B ~ ELE + SW + BUAP	4	1072.62	0.00	1.000	0.831
B ~ ELE + UCC + BUAP	4	1076.66	4.05	0.132	0.110
B ~ ELE + SW + BUAI	4	1079.37	6.76	0.034	0.028
B ~ ELE + SW + MF	4	1081.52	8.90	0.012	0.010
B ~ ELE + SW + PAF	4	1082.69	10.07	0.007	0.005
B ~ ELE + SW + FAP	4	1082.69	10.07	0.007	0.005
B ~ ELE + UCC + BUAI	4	1083.77	11.16	0.004	0.003
B ~ ELE + SW + DF	4	1084.73	12.11	0.002	0.002
B ~ ELE + UCC + MF	4	1085.94	13.32	0.001	0.001
B ~ ELE + UCC + MF	4	1085.94	13.32	0.001	0.001
B ~ ELE + SW + CR	4	1086.04	13.43	0.001	0.001
B ~ ELE + SW + CR	4	1086.04	13.43	0.001	0.001
B ~ ELE + UCC + PAF	4	1087.59	14.98	0.001	0.000
B ~ ELE + UCC + FAP	4	1087.59	14.98	0.001	0.000

B ~ ELE + SW	3	1088.51	15.90	0.000	0.000
B ~ ELE + UCC + DF	4	1089.80	17.18	0.000	0.000
B ~ ELE + UCC + CR	4	1091.39	18.78	0.000	0.000
B ~ ELE + UCC	3	1094.21	21.60	0.000	0.000
B ~ ELE	2	1099.53	26.91	0.000	0.000
B ~ SW	2	1102.19	29.57	0.000	0.000
B ~ UCC	2	1106.10	33.49	0.000	0.000
^a B ~ ELE + UCC + SW + BUAP + BUAI + CR + PAF + MF + DF	8	1120.22	47.60	0.000	0.000

^a Represents the global model (model that includes all variables) used in the model selection.

Table 3.7. The output of 9 different models for abundance and biomass to determine the relationship between longitudinal connectivity as measured by the Dendritic Connectivity Index (Cote et al. 2009) and community structure. Abundance 1 models used DCI values calculated with only known barriers whereas Abundance 2 models used DCI values calculated with known barriers and stream/river intersections. The percent of variation explained is based on the total variation available in the model. The pseudo-F statistic is a permutation based estimate of the F statistic to calculate the p-value. Due to permutation based estimates, significance was calculated to 0.005. We calculated the correlation for axis 1 and 2 for the multivariate analysis for each variable.

Model	df	% Variation Explained	Pseudo-F	p-value	Axis 1	Axis 2
Abundance 1:						
Full Model 1	4	21.1	17.93	0.005		
ELE	1	8	17.83	0.005	0.91	-0.16
BUIP	1	8.7	21.79	0.005	0.11	0.88
SW	1	3.8	12.6	0.005	-0.77	-0.28
DCIs	1	1.2	3.76	0.01	-0.49	-0.14
Residuals	268	78.3				
Full Model 2	4	21.4	18.23	0.005		
ELE	1	9.5	20.06	0.005	-0.92	0.17
BUIP	1	6.5	17.11	0.005	-0.13	-0.87
SW	1	3.9	12.82	0.005	0.79	0.25
DCIp	1	1	4.74	0.005	0.31	0.46
Residuals	268	79				
Full Model 3	4	24.4	21.64	0.005		
ELE	1	9.4	20.6	0.005	-0.77	0.54
BUIP	1	6.5	18.01	0.005	-0.43	-0.68
SW	1	4.3	13.65	0.005	0.74	-0.19
DCId	1	5.4	15.64	0.005	0.54	0.41
Residuals	268	74.4				
Abundance 2:						
Full Model 4	4	21.9	18.74	0.005		
ELE	1	7.1	16.63	0.005	-0.88	-0.28
BUIP	1	8.4	21.33	0.005	-0.2	0.85
SW	1	3.6	12.39	0.005	0.77	-0.16
DCIs	1	2.7	6.37	0.005	0.65	-0.16
Residuals	268	78.1				
Full Model 5	4	22.2	19.14	0.005		
ELE	1	9.8	20.69	0.005	0.93	-0.16
BUIP	1	4.4	12.35	0.005	0.13	0.86
SW	1	4	13.01	0.005	-0.79	-0.23
DCIp	1	2.3	7.64	0.005	-0.22	-0.67
Residuals	268	79.6				

Full Model 6	4	24.4	21.6	0.005		
ELE	1	9.3	20.64	0.005	-0.78	0.52
BUIP	1	7.5	20.24	0.005	-0.41	-0.69
SW	1	4.4	13.66	0.005	0.75	-0.17
DCId	1	5.4	15.52	0.005	0.48	0.37
Residuals	268	73.4				
Biomass:						
Full Model 7	4	21.6	16.97	0.005		
ELE	1	6.7	15.33	0.005	0.81	-0.43
BUAP	1	7.9	18.66	0.005	0.28	0.77
SW	1	5.2	14.72	0.005	-0.84	-0.12
DCI _s	1	2.1	4.87	0.005	-0.61	0.02
Residuals	246	78.1				
Full Model 8	4	22.3	17.67	0.005	NA	NA
ELE	1	8.8	18.4	0.005	-0.84	0.4
BUAP	1	5.3	13.66	0.005	-0.26	-0.78
SW	1	5.8	15.58	0.005	0.87	0.14
DCI _p	1	2	7.1	0.005	0.25	0.42
Residuals	246	78.2				
Full Model 9	4	24.1	19.57	0.005		
ELE	1	8.4	18.2	0.005	0.7	-0.61
BUAP	1	7.5	18.48	0.005	0.43	0.67
SW	1	6.1	16.21	0.005	-0.79	0.15
DCI _d	1	4.5	13.17	0.005	-0.46	-0.18
Residuals	246	73.5				

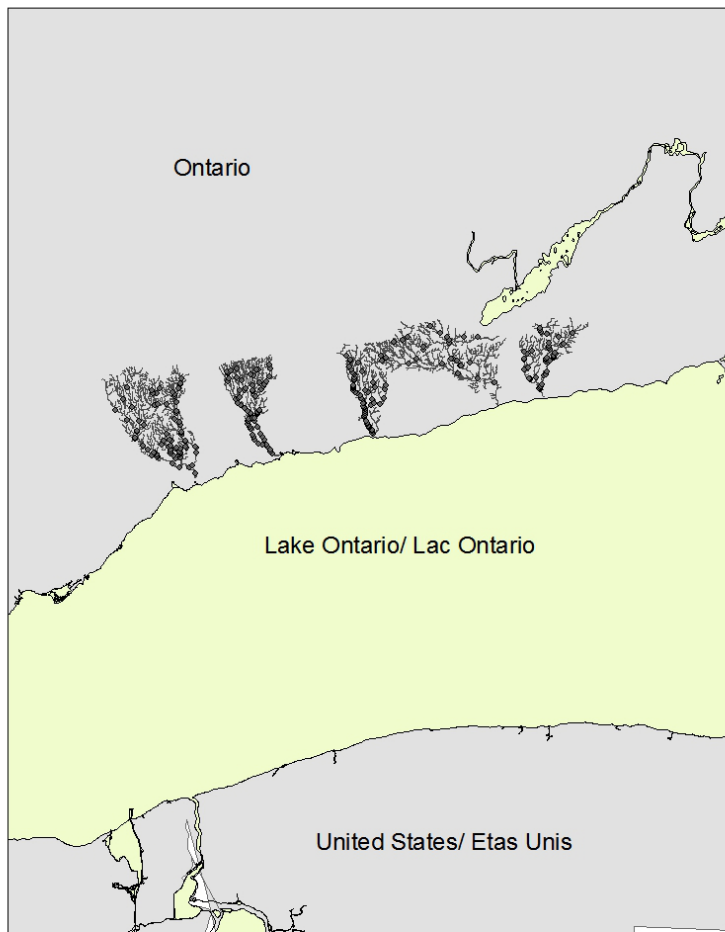


Figure 3.1. The study area in southern Ontario with the sampling sites.

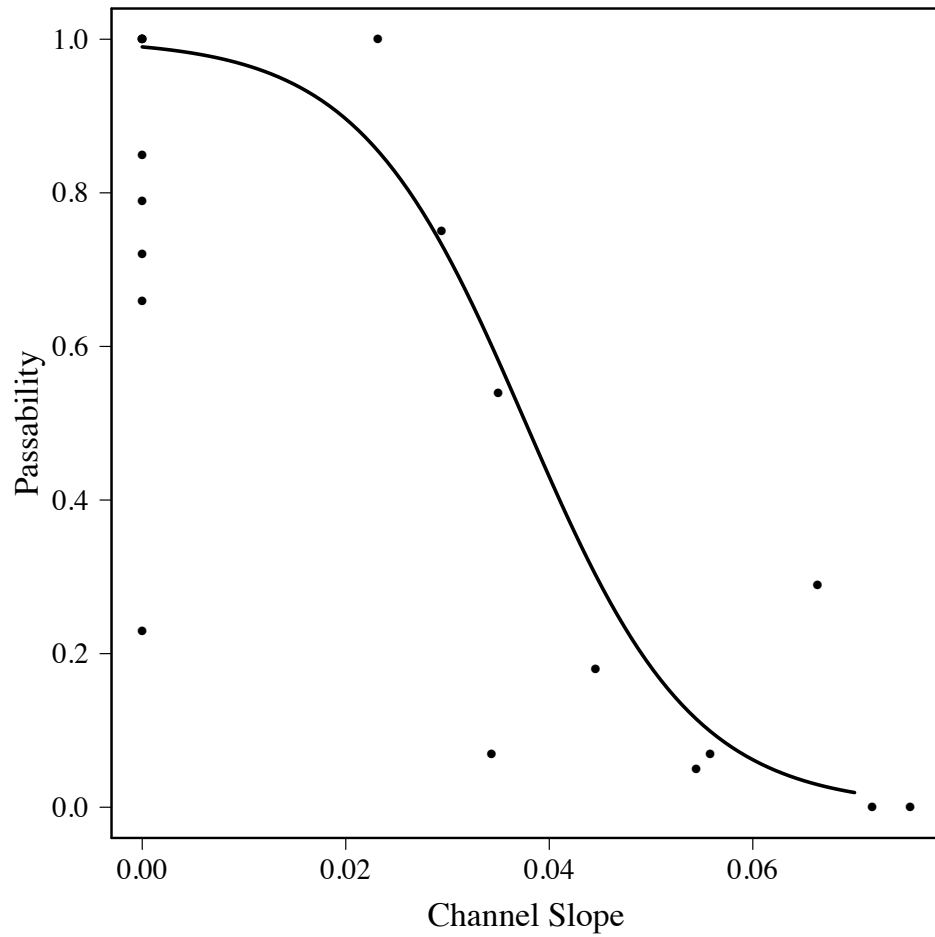


Figure 3.2. Relationship between channel slope and passability in Terra Nova National Park, Newfoundland and Labrador, Canada. We applied this relationship to barriers in Southern Ontario to determine the passability of unidentified barriers.

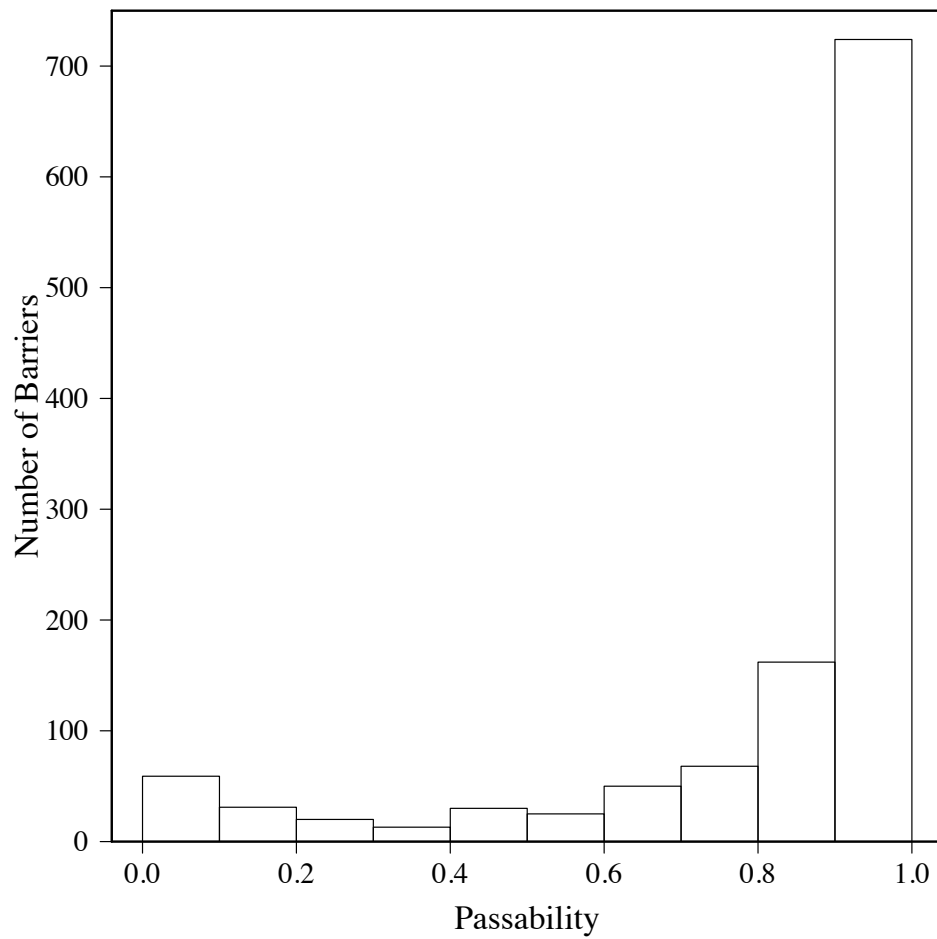


Figure 3.3. Histogram of barrier passabilities in the study watersheds based on the relationship between channel slope and culvert passability in Terra Nova National Park, Newfoundland and Labrador, Canada.

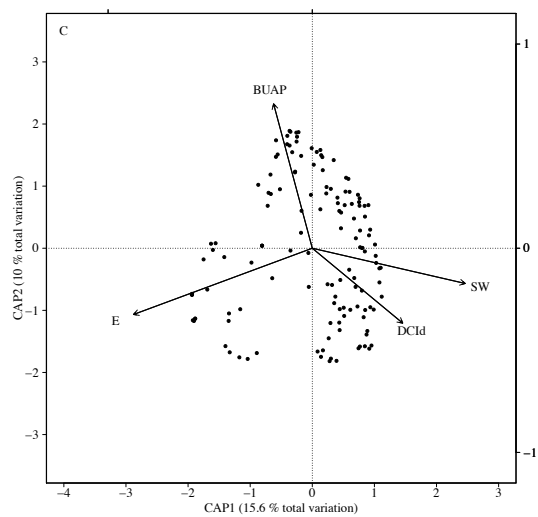
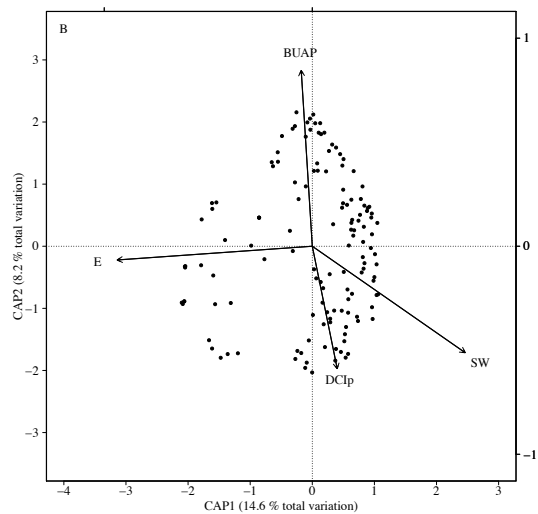
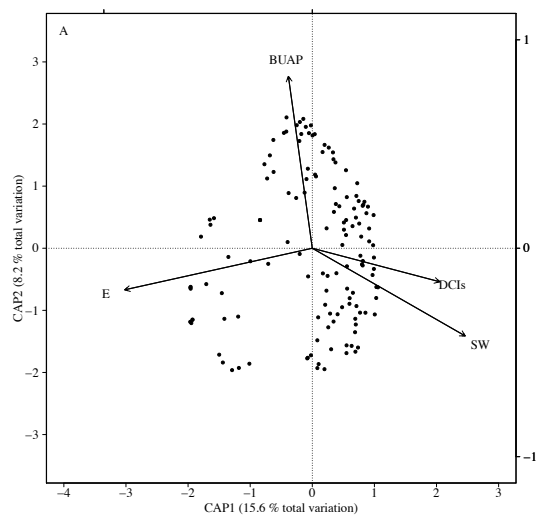


Figure 3.4. The distance based redundancy analysis comparing the DCI_s , DCI_p and DCI_d (calculated with known barriers and stream/road intersections; plot A, B, and C respectively) and associated co-variables (ELE = Elevation, SW = Stream Width, and BUAP = Built-up area-pervious) for fish abundance data in southern Ontario. Variable significance and axis correlations can be found in Table 3.7.

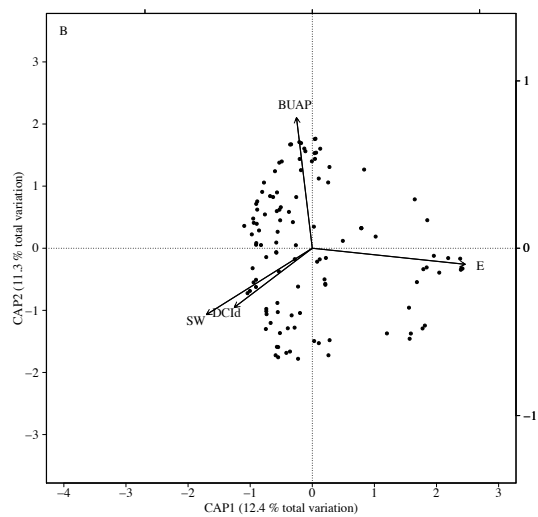
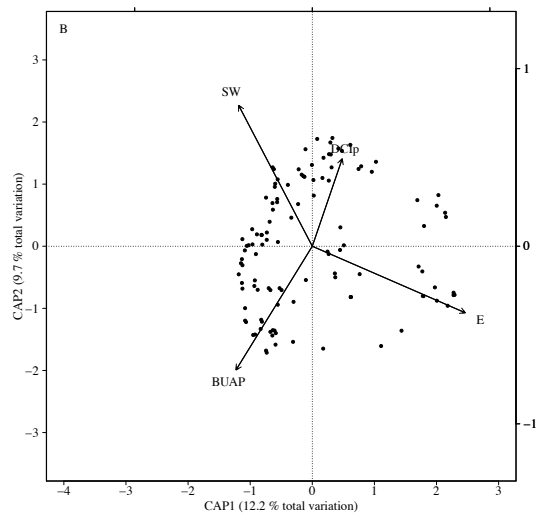
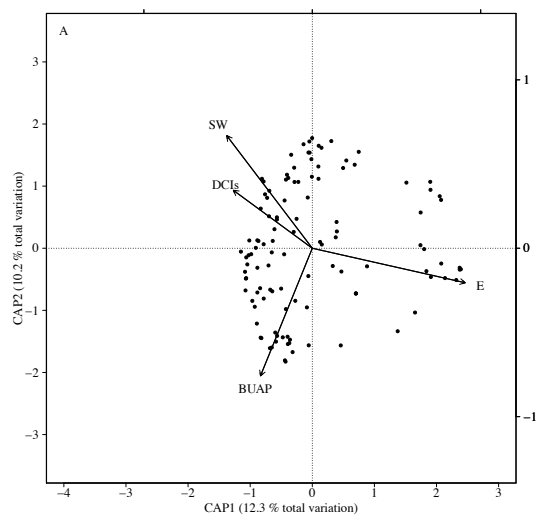


Figure 3.5. The distance based redundancy analysis comparing the DCI_s, DCI_p and DCI_d (plot A, B, and C respectively) and associated co-variables (ELE = Elevation, SW = Stream Width, and BUAP = Built-up area-pervious) for fish biomass data in southern Ontario. Variable significance and axis correlations can be found in Table 3.7.

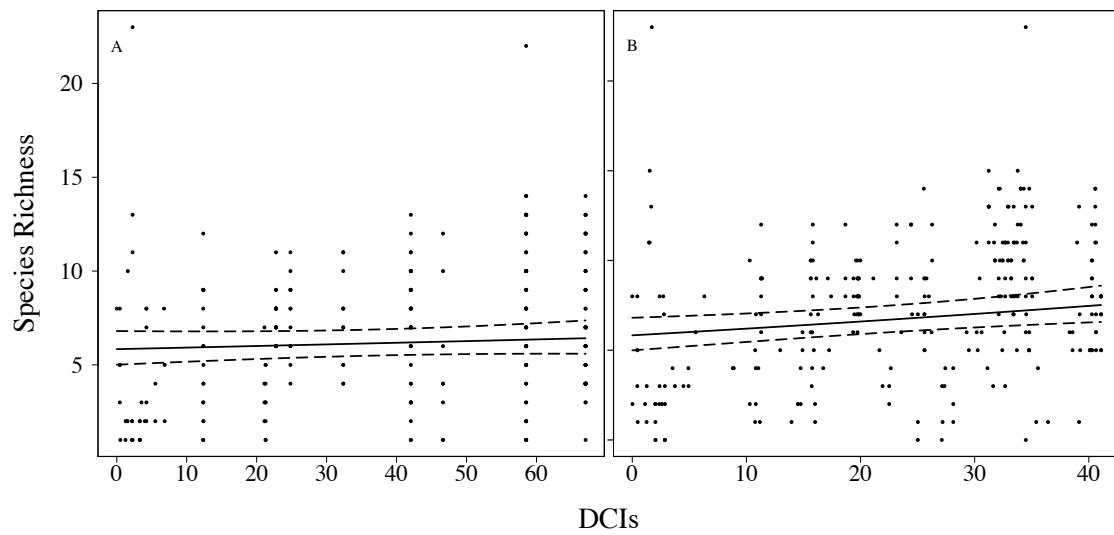


Figure 3.6. Relationship between species richness and the DCI_s in 5 southern Ontario streams while controlling for elevation, stream width, and built-up area-pervious. The DCI for A is calculated using only known barriers and the DCI for B is calculated using known barriers and stream/road intersections. Circles indicate species richness at individual sites while dashed lines indicating 95 percent confidence intervals.

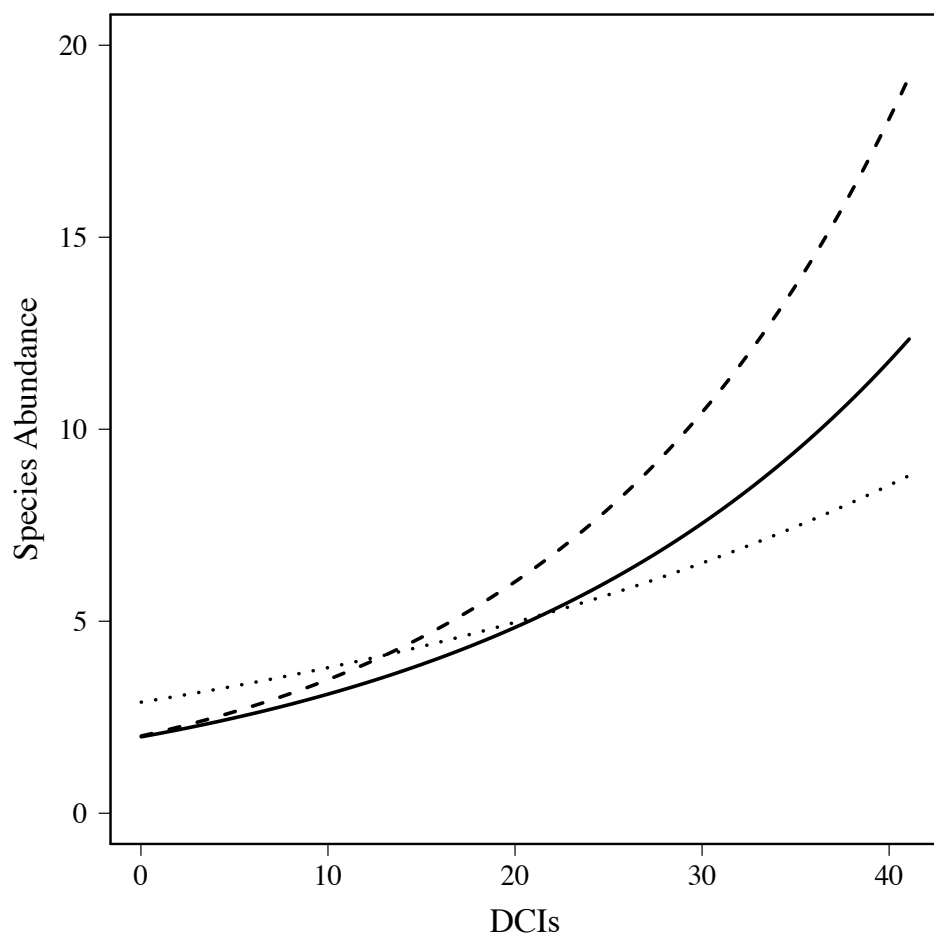


Figure 3.7. Relationship of the DCI and species abundances for rainbow trout (dashed line), longnose dace (solid line), and mottled sculpin (dotted line).

CHAPTER 4: SUMMARY AND CONCLUSIONS

4.1 Summary and Conclusions

My research addresses the relationship between structure and function and the efficacy of structural connectivity indices (Chapter 3) and their components (e.g., passability; Chapter 2). Specifically, I found that FishXing, a metric used to evaluate culvert passage based on culvert hydraulics and fish swimming metrics, had negligible explanatory power when predicting fish movements through culverts (Chapter 2). At broader spatial extents, we found a significant relationship between the Dendritic Connectivity Index (DCI), and community composition along with a significant relationship between site specific measurements of connectivity and species presence and abundance (Chapter 3).

It is thought that incorporating functionality into structural indices is an important aspect required to derive meaningful relationships between structural and functional connectivity (Kindlmann and Burel 2008). However, including functionality does not necessarily create ecologically relevant metrics (Kupfer 2012). For instance, passability was a critical aspect in Chapters 2 and 3 of this thesis which allows the incorporation of functionality into the DCI. As concluded in Chapter 2, I found FishXing was ineffective in explaining brook trout passage across 4 culverts after using more precise culvert modeling procedures (Bourne et al. 2011). This supports a common perception (Poplar-Jeffers et al. 2009, Bourne et al. 2011) and a previous study (Burford et al. 2009) as to the conservative nature of the fish passage assessment program FishXing. Although FishXing was not perfect, it was able to qualitatively measure barrier passage by

accurately predicting binary fish passage at three of the four culverts. This was further supported in Chapter 3 where I used a correlation between stream channel slope and passability as calculated by FishXing. Using this relationship to determine passability contributed to the significant explanation of various ecological metrics and the DCI. This could indicate that even though FishXing is unable to directly predict fish passage, a relative relationship between barrier passage may exist with FishXing outputs.

The binary accuracy of FishXing is comparable to simpler flow charts (Kemp and O'Hanley 2010). However, I observed that fish passage is not binary and that intermediate levels of passability occur (Chapter 2). Thus it is necessary to account and identify these barriers with current passability metrics (Anderson et al. 2012). The inability to accurately identify intermediate levels of passability can result in mislabeling barriers which can lead to management actions with minimal impacts. It is important to improve our understanding of fish swimming metrics such as swim speeds (Haro et al. 2004), navigation of non-uniform flows patterns (Neary 2012), and behavioral aspects of culvert passage (Kondratieff and Myrick 2006, Burford et al. 2009, Russon and Kemp 2011) so that managers have the ability to incorporate information into current passability models and therefore improve the predictive power of barrier passage. To understand the limitations of connectivity metrics, it is essential that future research continues to analyze how including functionality into structural indices relates to ecological communities.

Another aspect of passability that is often overlooked is how barriers influence downstream passage. Passability metrics primarily consider upstream passage and how

barriers affects those interactions with little regard to the impact on fish movement to downstream movement past barriers (Warren and Pardew 1998, Burford et al. 2009). However, it has been shown that barriers can influence the downstream passage for various fish species (Peake et al. 1997, Arnekleiv et al. 2007, Russon and Kemp 2011). For instance, Arnekleiv et al (2007) found that downstream movement of brown trout (*Salmo trutta*) smolts and kelts depended on the surface release of water at a hydroelectric dam in Norway. Even though a fishway entrance was included for upstream passage, Arnekleiv et al (2007) found that few individuals used this for downstream movement. Fish also encounter other potential challenges to downstream movements such as mortality due to hydropower turbines or increased predation due to delayed downstream migration at the barrier (Peake et al. 1997, Vélez-Espino et al. 2011). Furthermore, behavioral responses of fish to changes in velocity regimes may deter them from attempting downstream passage of a culvert (Russon and Kemp 2011). It is advantageous to continue to understand not only upstream movements but also downstream movements of fish. This will allow researchers to incorporate accurate bi-directional passabilities of barriers into current structural indices, potentially improving the relationship between structural indices and functional connectivity.

Although my thesis takes important steps to improve our understanding of how structure relates to function, several critical aspects of structural connectivity remain. For example, measuring at an appropriate spatial scales is a key aspect of structural connectivity indices and can be difficult to determine (Kupfer 2012). Which scale is most important to measure at is dependent on multiple factors along with the objectives of

various stakeholders. For instance, small spatial scales are appropriate when considering small stream fishes that do not require large home ranges throughout their life history (Johnston 2003, Perkin and Guido 2012). Conversely, dispersal is an important characteristic of many aquatic species that allows fish to maintain genetic movement between metapopulations, repopulate habitat patches after extirpation events, or emigrate to new habitats (Hudman and Guido 2013). To capture connectivity relationships between such scenarios, it might be necessary to incorporate relevant spatial scales that determine the connectivity between multiple watersheds. Although I found a significant relationship with regards to connectivity at the watershed scale, it is unknown whether this relationship will persist at larger extents (e.g., between two watersheds). It is therefore necessary that future research continues to analyze the efficacy of structural connectivity indices at different spatial extents to determine the appropriate scales for the different ecological metrics and questions encountered.

The use of structural connectivity indices to quantify the fragmentation of a system is important. However, equally important is the ability to determine appropriate management goals and objectives (Roni et al. 2002, Palmer et al. 2005). Identifying scale dependent thresholds of connectivity is one tool that can assist stakeholders in setting ecological relevant targets which could otherwise lead to un-realistic expectations (Monkkonen and Reunanen 1999). Unfortunately, I was unable to identify such a relationship due to the small range of connectivity scores within this study area. Identifying thresholds can be particularly difficult to determine due to the lack of comparable systems exhibiting the range of connectivity scores and the confounding

effects that are often associated at broader spatial extents (Labbe and Fausch 2000, Branco et al. 2011). The ability to identify thresholds to help set management goals remains an important aspect in the recovery of focal species and our capacity to maximize resources to improve functional connectivity with structural connectivity indices.

The tradeoff of isolation versus colonization has only recently become a concern for stakeholders (Fausch et al. 2009). Longitudinal connectivity has primarily focused on identifying barriers to remove or modify in order to reconnect habitat patches (Fullerton et al. 2010). However, the prevalence of invasive species across the landscape and their ability to displace native fauna is another concern facing managers today (Rahel 2013). It has been shown that intentionally incorporating barriers to isolate species may prevent the spread of invasive species thereby protecting the native fauna that are often at a competitive disadvantage or at risk of genetic hybridization (Novinger and Rahel 2003, Fausch et al. 2009). Utilizing ecologically relevant structural indices can be instrumental in determining potential areas to isolate and thereby protect native species.

It is not only important to continue to analyze the ecological relevance of structural indices but it is also necessary to determine how their parts relate to function. The use of valid structural metrics and indices should improve the efficacy of connectivity analysis and assist to accurately identify critical areas of fragmentation. My research represents an important step to detect useful metrics to assess connectivity and potential areas to focus future research to help improve our inferences of structural and functional connectivity.

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