HOW TO QUANTIFY AQUATIC CONNECTIVITY? VERIFIYING THE EFFECTIVENESS OF THE DENDRITIC CONNECTIVITY INDEX AS A TOOL FOR ASSESSING STREAM FRAGMENTATION

by

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A Thesis submitted to the

School of Graduate Studies

in partial fulfillment of the requirements for the degree of

Master of Science

Biology

Memorial University of Newfoundland

April 2013

St. John's Newfoundland and Labrador

Abstract

In recent decades the study of landscape ecology has moved beyond its terrestrial roots to explore the impacts of habitat fragmentation in aquatic systems, where populations of freshwater fish are declining at an alarming rate worldwide. Quantifying fragmentation within these habitats has been a challenge for ecologists, as the spatial arrangement of stream networks influences the distribution of both organisms and habitat features. I used the Dendritic Connectivity Index (DCI) to evaluate aquatic connectivity in Terra Nova National Park, Newfoundland, and Prince Edward Island National Park, testing the impacts of barrier assessment methods and inclusion of biological data in the index to evaluate functional connectivity. I found that while the passability values of individual barriers (road culverts) can vary widely with assessment method, connectivity estimates provided by the DCI for entire catchments did not show the same degree of variability and overall assessment results did not change when using different methods. When a functional parameter (biomass) was substituted for a structural one in the DCI, connectivity values for catchments changed, but not significantly. These simulations demonstrated that the DCI is a robust tool for evaluating stream connectivity which can provide meaningful results to managers, even when resources and data are limited.

Acknowledgements

First and foremost I would like to thank my supervisor, Dr. Yolanda Wiersma, who took me on as her first graduate student and helped to make my graduate school experience an extremely educational and positive one. Yolanda has been a wonderful mentor, encouraging me to try new things, keeping me motivated and always finding time to meet – even if it meant in her own home.

I also want to acknowledge Parks Canada for providing funding, access to data, field support and so much more as I completed my research. In particular, I would like to sincerely thank my committee members, Dr. Dave Cote and Dan Kehler of Parks Canada, both of whom contributed so much to this project. Dave's knowledge of fish ecology and perspective as a park biologist was invaluable, as were Dan's statistical skills and insight into the technical aspects of the DCI.

In addition to my committee members, all the other staff members at Parks Canada who were involved with this project were always helpful and supportive. The technical staff of both parks were invaluable in the field, particularly Tracey Harvey, Mervin Langdon and Ross Collier of Terra Nova National Park. I would also like to acknowledge the cadets of the Royal Military College who assisted with culvert surveys in 2008.

I also want to thank my fellow LESA lab mates who made my time in the lab a rewarding and fun experience – especially Julie Anderson, Stacey Camus, Randy Skinner, Patricia Howse and our 'honorary' lab member Erin Carruthers. A special thank you needs to go to Tony McCue who not only completed his own thesis with me, but also

became a great friend as we learned to use GIS, planned our respective weddings, found jobs and even trained our dogs alongside one another! I would also like to thank Shad Mahlum for taking an interest in continuing the work I started and being so helpful with sharing his experience and thoughts as he completed his own graduate work.

And finally I need to thank my friends and family for supporting me throughout my master's program. In particular my husband Jim Pelley for encouraging me and understanding the late nights and hours spent writing, and my mom for being my always dependable proof-reader! I also want to thank Dr. Ian Jones for encouraging me to pursue graduate studies in biology and introducing me to Yolanda and her work in landscape ecology.

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CHAPTER 1: INTRODUCTION AND OVERVIEW

1.1 Landscape ecology and stream fragmentation

The technological developments of the last century led to major advances in every discipline of science, including ecology. Where in the past ecologists were limited to viewing the world at a relatively small spatial scale, focusing on single habitats and the organisms within them, the advent of aerial photography and satellite imagery made it possible to view large areas and observe the heterogeneity, complexity and underlying pattern of natural features within landscapes. When presented with these larger views, ecologists began to ask questions about the interactions of different habitat types and their effects on entire landscapes and ecosystems – questions that led to the advent of landscape ecology in the mid twentieth century; a sub-discipline of ecology which combines theory and practice from geography and biology to examine the effects of large scale pattern on ecological processes (Turner et al. 2001).

Since its inception, the discipline of landscape ecology has grown rapidly and various theories and models have been developed to explain the interactions between spatial patterns and biological processes within landscapes (Turner 2005). In particular, the concept of fragmentation –the breaking up of large connected habitats into smaller patches – has received a great deal of attention (e.g., Fagan 2002; Hilty et al. 2006), largely due to the widespread habitat destruction and alteration caused by humans worldwide and its potential impact on ecological integrity (e.g. community structure, species composition). These studies have traditionally been focused on terrestrial habitats, where heterogeneity and fragmentation are often obvious (e.g., clear cut forests, agricultural development). In contrast, aquatic systems were historically viewed as features of the landscape (Weins 2002), largely homogeneous and unchanging. However in more recent years ecologists have come to recognize the fact that aquatic systems are in fact heterogeneous landscapes in and of themselves (Schlosser 1991; Poole 2002; Benda et al. 2004) and, as with terrestrial landscapes, are also impacted by fragmentation (Pringle 2003; Kondolf et al. 2006).

Humans have had numerous negative impacts on aquatic habitats worldwide; some, such as heavy pollution or damming, can be obvious, others are more subtle. The latter is often the case with aquatic fragmentation, which might not be visually apparent but nonetheless may have serious impacts on stream dwelling species – including fish population decline and extinction (Sheldon 1988; Dunham et al. 1997; Morita and Yamamoto 2002; O'Hanley and Tomberlin 2005; Musil et al. 2012). A major cause of fragmentation in stream networks is the creation of physical movement barriers for native species, often done through the construction of roads (Jones et al. 2000; Trombulak and Frissell 2000) and installation of road culverts – structures which are typically the most cost-effective option (compared to bridges or weirs), but also the most detrimental to fish populations, especially when installed improperly or without consideration to native fish populations (e.g., Kemp and Williams 2008; Park et al. 2008; Doehring et al. 2011).

Barriers within aquatic networks can isolate stream segments, effectively creating habitat patches (Cote et al. 2009). While there may be a very short distance separating two patches (i.e., the length of a culvert or width of a dam), movement between them by aquatic organisms is often impaired. Unlike terrestrial systems, where organisms can often move between patches by crossing a matrix of inhospitable habitat, a barrier within a stream network can completely isolate aquatic organisms from all other patches regardless of the linear distance between them (Fagan 2002). In addition, the directionality of water flow within stream networks provides a further challenge to animals attempting to move between patches, as the velocity and resulting force of the water itself may create a movement barrier (Castro-Santos 2004). Thus, both the longitudinal and dendritic nature of stream networks makes the spatial relationships between patches quite different from those in terrestrial landscapes, and this has presented challenges when studying and attempting to model aquatic connectivity (Poole 2002; Grant et al. 2007; Cote et al. 2009; Fullerton et al. 2010).

1.2 Measuring aquatic connectivity

Understanding the impacts of movement barriers on stream networks and the associated loss in aquatic connectivity is important, as freshwater fish populations are experiencing serious declines worldwide (Pringle 2003; Olden et al. 2010). In Canada, a priority of the national parks is to maintain and restore the ecological integrity of habitats within their boundaries. Thus, Parks Canada has taken an interest in the issue of stream fragmentation; most national parks are transected by roadways, and so the potential for negative anthropogenic impacts on native freshwater species within them is high. In order to understand, quantify and mitigate these potential impacts, ecologists and managers working in the parks – and in freshwater ecosystems worldwide, need tools to help with the quantification and assessment of stream fragmentation.

While ecologists' initial approach to mitigating barriers in aquatic systems was to focus on individual structures (Roni et al. 2002), by removing or replacing obvious barriers in hopes that impacted fish populations would recover, it was soon recognized that spatial context was an important factor when considering aquatic connectivity (Weins 2002; Lowe et al. 2006). Stream networks are large and complex; processes occurring upstream at headwaters can have cascading impacts downstream (Vannote et al. 1980; Poole 2002), habitat features can vary from reach to reach (Benda et al. 2004; Lowe et al. 2006), and the migration and dispersal patterns of fishes can be heavily influenced by the heterogeneity and spatial features of the entire network (Schlosser 1991; Fausch et al. 2002; Baguette and Van dyck 2007; Flitcroft et al. 2012). These factors led ecologists to take a larger, landscape approach when assessing aquatic fragmentation; taking not just individual stream reaches and barriers into consideration, but rather looking at the entire stream network. This approach helps to ensure that the limited resources which are allocated to projects (i.e., removal of individual barriers) will provide the greatest benefits to stream systems as a whole (Roni et al. 2002; O'Hanley and Tomberlin 2005; Poplar-Jeffers et al. 2008; Cote et al. 2009).

Landscape ecology has historically been focused on the impacts of terrestrial fragmentation, with various metrics having been developed to quantify connectivity based on parameters such as patch area, perimeter, richness and proximity to other patches (Turner et al. 2001). These metrics, however, are generally not applicable to the study of fish within stream fragmented networks, due to the unique dendritic structure of the habitat and the physical limitations of the study species (Fagan 2002; Grant et al. 2007; Fullerton et al. 2010). Movement between patches in aquatic systems is restricted by the longitudinal nature of the networks, where fish generally only have the ability to move either up or downstream; crossing the matrix of dry land to move from stream segment to segment is rarely an option (Weins 2002; Olden et al. 2010). In addition, the distribution of barriers within stream networks can have significant effects on connectivity (Cote et al. 2009; Rolls 2011). A single barrier at the mouth of a stream may be extremely detrimental for fish that must migrate upstream from the ocean to spawn (diadromous), but may have little impact on species that move only within the freshwater network (potamodromous). Multiple barriers may have compounding effects, each adding to the severity of the fragmentation of the system (Kemp and O'Hanley 2010; Rolls 2011; Musil et al. 2012). To further complicate matters, some barriers may be partially passable while others are completely impassable – and the measure of that passability will vary with assessment method (Blank et al. 2005; Meixler et al. 2009; Bourne et al. 2011). Creating a model that can take all of these factors into account has been a challenge for aquatic ecologists.

In addition to the spatial considerations and barrier parameters, the ecology of the stream network and its associated species can also play an important role in the impacts of connectivity loss. The physical, chemical and biological features of a stream network can vary widely from headwaters to mouth (Ward 1989), and each species has its own habitat preferences (e.g., Bult 1998; Cote 2007; Isaac et al. 2007). This preferred habitat can also vary according to the season, life stage or species composition of the native fish assemblages (e.g., Schlosser 1991; Robertson et al. 2003). Models of fragmentation therefore need to be capable of accounting for factors such as temporal variability, patterns of fish dispersal and habitat use.

Various approaches have been taken to model the structural complexity of stream networks and their associated barriers in order to assess fragmentation, these range from simple field-based methods (e.g., Joy and Death 2000; Park et al. 2008) to sophisticated applications of mathematical formulas and graph theory (e.g., Schick and Lindley 2007; Eros et al. 2012). One model which has shown potential for aquatic fragmentation assessment is the Dendritic Connectivity Index (DCI), which was developed by Cote et al. (2009) as a tool for quantitatively evaluating the cumulative impacts of multiple barriers on entire stream networks. Cote et al. (2009) used the DCI to assess connectivity of simulated stream networks, as well as one actual system in Terra Nova National Park, Newfoundland, Canada. Their simulations demonstrated that the first few barriers added to a stream system generally have the highest impacts on structural connectivity; diadromous fish were most impacted by downstream barriers and were more negatively affected by fragmentation than potamodromous fish; and that incremental improvements to barriers with some passability may provide greater gains in connectivity than improvements to those with lower passability levels. These results suggested that the DCI could be a valuable tool for understanding and assessing fragmentation in stream systems and for prioritizing barrier replacement. However, Cote et al. (2009) did not address in detail how the DCI would be applied using actual field data. The simulations were done using uniform passability values for all barriers, and the authors did not provide recommendations as to how users of the index could obtain these values for a specific setting (i.e. species, time of year, riverscape, etc.) based on field data – an essential and potentially challenging step when applying the DCI to real world systems.

The DCI, as presented in Cote et al. (2009) is a simple index of structural aquatic connectivity, focusing on the spatial arrangement of stream segments and barriers, and the effects they have on fish movement within the network. While modeling the structural features of dendritic networks does provide a significant challenge for ecologists and has been the focus of the majority of existing aquatic connectivity models (Fulerton et al. 2010), there is also a functional aspect to connectivity which should not be overlooked. As with aquatic systems, studies of connectivity in terrestrial habitats also began with a heavy focus on the spatial aspects of the landscapes and patches within them (Turner et al. 2001). However, as the science of landscape ecology evolved it was recognized that connectivity is the result not only of the structural features of habitats, but also the response of native organisms to that structure and changes within it (Belisle 2005, Baguette & Van Dyck 2007). This recognition led to the incorporation of more ecological, functional data into terrestrial connectivity models (Tischendorf & Fahrig 2000; Turner 2005; Hilty et al. 2006), a crucial step in understanding the effects of fragmentation on ecosystems and the species within them. It has been recommended that aquatic ecologists attempt to follow the example of terrestrial connectivity studies and also include functional aspects in their models (Sheer & Steele 2006; Fullerton et al. 2010; Kemp & O'Hanley 2010), as the dispersal of fish throughout stream networks can be highly influenced by factors such as habitat quality (e.g. Spens 2007; Dunbar et al. 2011), which are not typically included in structural indices.

1.3 Thesis Overview

In chapter 2 of this thesis, I took the DCI beyond the simplified simulations done by et al. (2009) by evaluating the sensitivity of the index to various barrier assessment methods. I compared connectivity estimates provided for multiple stream networks in Terra Nova National Park, Newfoundland and Prince Edward Island National Park by the DCI. Specifically, I compared the barrier passability values and resulting stream connectivity estimates obtained by using rapid field-based culvert assessments versus those derived from FishXing software (Furniss et al. 2006), in order to determine whether using the more resource intensive computerized method would provide significantly different, and potentially more informative, results. In addition, I evaluated the difference in connectivity values provided by the DCI for stream networks when passability was modeled for two different species, temporal periods and with natural barriers in order to demonstrate the potential impacts of input parameters on the DCI's assessment of connectivity.

In the third chapter, I went on to test the effects of including functional data in the DCI. Functional data includes metrics which can help account for biological and ecological process in the network, aside from purely structural features. I did this by using habitat quality as a predictor of fish biomass in stream networks in Terra Nova National Park, including both stream segments and ponds, and weighting habitat patches using those biomass estimates. I compared the results obtained from the structural and functional scenarios for all stream segments within the park to demonstrate the potential impacts and improvements in connectivity estimates that could ensue when functional data were included in DCI calculations.

1.4 Co-Authorship Statement

Chapter 2 of this thesis was co-authored by Dan G. Kehler, Yolanda F. Wiersma and Dave Cote. I was the principal contributor to data collection and analysis, and manuscript preparation. Mr. Kehler and Dr. Cote contributed to project design and statistical analysis, Dr. Wiersma provided expertise in the fields of landscape ecology, GIS analysis and statistical modeling.

I was the principal author of chapter 3, having completed all data collection, analysis and manuscript preparation. Mr. Kehler and Dr. Cote also contributed to this chapter through providing professional input and advice. Dr. Wiersma provided critical support in the form of research guidance throughout the process from initial project design to manuscript preparation, as was also the case for the previous chapter.

Both chapter 2 and 3 have been written for submission for peer-reviewed publication. Chapter 2 has been published in *Aquatic Ecology* (Bourne et al. 2011) with some revisions, notably the exclusion of Prince Edward Island National Park data. Chapter 3 will be submitted to *Transactions of the American Fisheries Society*. There has therefore been some repetition of information between chapters and there is some slight variation in formatting of each chapter to conform to the individual journal standards.

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CHAPTER 2: BARRIERS TO FISH PASSAGE AND BARRIERS TO FISH PASSAGE ASSESSMENTS: THE IMPACT OF ASSESSMENT METHODS AND ASSUMPTIONS ON BARRIER IDENTIFICATION AND QUANTIFICATION OF STREAM NETWORK CONNECTIVITY

2.1 Abstract

Barriers (e.g. culverts and dams) can impede fish passage and affect the overall habitat connectivity of stream networks. However, a challenge lies in how to conceptualize and adequately measure passability at barriers. We hypothesized that estimates of barrier and catchment connectivity are dependent on assumptions about the nature of passability, and how it is measured. Specifically, we compared passability estimates in Terra Nova National Park and Prince Edward Island National Park, Canada for individual barrier assessment methods (a rapid field-based assessment and one based on FishXing software), two salmonid species and two temporal periods with varying hydrological conditions. Catchment connectivity was calculated using the Dendritic Connectivity Index (DCI). Lastly, we tested to see what the impact of the various factors was on the practical goal: prioritizing barriers for restoration. Our results show that barrier passability estimates can vary drastically for some barriers (0-100%). In general, the rapid assessment tended to give more conservative estimates of passability than those based on FishXing. Estimates of catchment connectivity were not as sensitive to the assumptions and methods used (DCI: 40-83). Importantly, variation in DCI had little impact on the restoration priorities. The same barrier was retained as the top priority >96% of the time. Thus, managers wishing to assess barriers for restoration need to

carefully consider how passability is to be measured, but can reduce the impact of these decisions by considering barriers in the catchment context using a connectivity index such as the DCI.

2.2 Introduction

Fragmentation of many of the world's stream networks has been recognized as a serious threat to the population diversity, abundance and persistence of a variety of aquatic species (e.g. Sheldon 1988; Dunham et al. 1997; Khan and Colbo 2008; Olden et al. 2010). Human activities are largely to blame for these connectivity losses, often through the installation of physical barriers (such as dams and culverts) to movement (e.g., Morita and Yamamoto 2002; Park et al. 2008; Doehring et al. 2011; Hall et al. 2011; Rolls 2011). While many of these barriers can be eliminated or mitigated by modification, such as by the construction of fishways or instillation of culvert baffles, the process is typically expensive and budgetary constraints restrict the amount of restoration that can occur (Gibson et al. 2005; Poplar-Jeffers et al. 2008; Kibler et al. 2011). Thus, a solid understanding of the ecological impacts of potential barriers on entire stream networks is essential to prioritize restoration efforts and maximize returns on limited funding.

While natural stream features such as high bottom gradients and waterfalls can create barriers to fish movement (e.g., Spens et al. 2007), anthropogenic disturbances are responsible for the majority of stream fragmentation (Pringle 2003). Road culverts, in particular, have been identified as widespread movement barriers. These structures are frequently used at road crossings due to their affordability; however, poor culvert design and installation often leads to deleterious alteration of natural stream features through things like the creation of high outflow drops and areas of increased water velocity (e.g., Warren and Pardew 1998; Kemp and Williams 2008; Park et al. 2008). In addition, culverts can become barriers over time as they rust, collapse, accumulate debris, or alter downstream reaches through scour and/or sedimentation (Broadfoot and Murphy 2002; Lachance et al. 2008).

Although in simplest terms, we know that barriers impact the passage of fish, quantifying this impact is challenging because barrier passability is difficult to define and measure. Many definitions and methods for estimating passability exist (see Kemp and O'Hanley 2010 for a recent summary). Common methods include measuring or modeling the physical characteristics of a barrier and comparing it to known fish physiological parameters (e.g. FishXing (Furniss et al. 2006)), through mark-recapture (e.g. Helfrich et al. 1999; Porto et al. 1999 for dams; Blank et al. 2005 for culverts), analysis of genetic structure of the population (Neraas and Spruell 2001; Kemp and O'Hanley 2010), or by tracking individual fish attempting to navigate the barrier (Bjornn and Peery 1992; Steig et al. 2005; Cahoon et al. 2007). Passability is also challenging to quantify because it is dynamic. Fish physiological capacity varies by species, size, amongst individuals and across environmental conditions, while the physical characteristics of barriers also vary temporally due to variations in stream flow (see Bjornn and Peery 1992; Rolls 2011). Such physiological and environmental variability makes the task of defining passability at a population or landscape scale challenging.

A second factor important to understanding barrier impacts is the need to consider the context in which a barrier is found (Cote et al. 2009; Rolls 2011). Previous studies of aquatic barriers were based largely on the effects that the barriers had on nearby portions of stream systems (Roni et al. 2002). More recently, concepts from landscape ecology, such as fragmentation and patch dynamics, have been applied to aquatic systems to investigate the impacts of barriers on entire stream networks and catchments (Park et al. 2008; Cote et al. 2009; Fullerton et al. 2010; Flitcroft et al. 2012; Musli et al. 2012). This broad view is crucial to understanding and mitigating the ecological consequences of stream fragmentation, as the effects of even a single barrier may have large impacts on entire stream networks, and multiple barriers may lead to cumulative impacts (Kemp and O'Hanley 2010; Rolls 2011; however, see Padgham and Webb 2010 for a model which suggests that multiple impacts are simply equal to the sum of the parts).

One method for quantitatively evaluating the cumulative impacts of barriers on entire stream networks is the Dendritic Connectivity Index (DCI; Cote et al. 2009), which could be a valuable tool for assessing fragmentation in stream systems and for prioritizing barrier restoration. The DCI requires two key data inputs: spatial location of barriers (both artificial and natural) within a stream or river network and a passability value for each individual barrier. While spatial data for the barriers are relatively simple to acquire, useful barrier passability estimates are not. In this paper, we examine how different barrier assessment methods and definitions of passability affect (1) estimates of connectivity at both the barrier and the landscape scale, as measured by the DCI, as well as (2) the prioritization of restoration efforts.

Cote et al. (2009) suggested passability could be quantified in several different ways and noted that decisions on how to define and measure passability would be important to interpret and evaluate catchment connectivity. Interpretations that capture the variability in fish physiology within and amongst species (e.g. assigning a passability of 0.5 to a barrier that is passable to 50% of the target population) may be insensitive to temporal environmental variation, while definitions that account for temporal variation of physical characteristics (e.g. the barrier is passable 50% of the time to fish with a defined physiological capacity) may not account for variation amongst individual fish. Furthermore, once defined, subsequent passability values will reflect decisions regarding the time period of the assessment (i.e. stream discharge), the species being modeled and the accuracy of the swim speeds estimates. Unfortunately, the sensitivity of barrier passability estimates, and subsequent catchment connectivity estimates to these decisions is unknown. If these measures are highly sensitive to variation in fish physiology or environmental conditions at barriers, then the utility and general applicability of catchment connectivity estimates will be reduced, and managers wishing to use them will have to be very careful about how data are collected.

We used multiple stream networks in Terra Nova National Park (TNNP), Newfoundland and Labrador and in Prince Edward Island National Park (PEINP) as a case study to examine the sensitivity of passability estimates and resulting river connectivity (catchment and park-wide) to three aspects of barrier passability: (1) the fish species of interest; (2) barrier assessment methodology; and (3) temporal variability in stream flow. The results of these simulation scenarios are also evaluated in terms of their effects on restoration priorities in the tested catchment, and for the effects of including natural barriers in assessments. The simulations are interpreted with respect to the effect on individual barrier assessments and on the catchment connectivity using the DCI.

We predicted that if the DCI is a robust method of quantifying fragmentation, it would behave consistently across a range of spatial and temporal scales. Stream systems vary in their size and spatial arrangement, which in turn, leads to variations in connectivity depending largely on the placement of barriers (Cote et al. 2009; Rolls 2011). We predicted that the connectivity values produced by the DCI would reflect these differences accurately across the range of stream systems evaluated, and that the values produced would not be dependent on the overall catchment area or stream length of those systems, but rather on the spatial arrangement of their segments and barriers as found in their simulated systems (Cote et al. 2009). We also expected that stream connectivity would vary with species, reflecting the differences in their physical abilities to pass barriers. Due to their larger size and faster swimming speeds, we expected barrier passability on average to be higher for Atlantic salmon (*Salmo salar*) than brook trout (*Salvelinus fontinalis*). Because connectivity is largely determined by barrier passability values, we predicted that passabilities obtained using differing methods would in turn provide different DCI values – particularly when comparing those obtained using simple assessments versus computer modeling.

2.3 Methods

2.3.1 Calculating the DCI

The barrier passability values used in DCI calculations range from 0 to 1, with 0 being impassable (a complete barrier), 1 fully passable and values in between considered partially passable. We obtained connectivity values for potamodromous (DCI_P) and diadromous (DCI_D) fish life histories for all park catchments using fish size/swim speed and stream flow parameters. Diadromous life history refers to fish that move between ocean and freshwater (in either direction) during their life cycle. The species examined in this study exhibit anadromy; a form of diadromy where spawning occurs in freshwater and adults spend part of their life at sea, but the form of diadromy is irrelevant for this analysis. The formula for calculating potamodromous connectivity (in both upstream and downstream directions) is taken from Cote et al. (2009) and requires dividing the catchment into segments, where segments are separated by barriers. The formula is:

$$DCI_P = \sum_{i=1}^{n} \sum_{j=1}^{n} c_{ij} \frac{l_i}{L} \frac{l_j}{L} \tag{1}$$

where *l* is the length of segment *i* and *j*, c_{ij} is the connectivity between segments *i* and *j*, and *L* is the total stream length. Diadromous connectivity applies to both anadromous and catadromous (migrating from ocean to freshwater) cases and is calculated as follows from Cote et al. (2009):

$$DCI_D = \sum_{i=1}^{n} \frac{l_i}{L} \left(\prod_{m=1}^{M} p_m^u p_m^d \right) * 100 \tag{2}$$

where l_i is the length of segment *i*, *p* (u and d) upstream and downstream passabilities of the *m*th barrier ($m = 1 \ldots M$) between the river mouth and section *i*, and *L* is the total stream length. Maximum DCI value is 100, which indicates a fully connected catchment, with connectivity decreasing as DCI values decrease from 100.

We used the DCI_P and DCI_D values to calculate ‘percent natural connectivity,’ which represented the proportion of natural connectivity remaining after human alterations (barrier construction/installation). In addition, we calculated DCI values for both single catchments and the parks as a whole, which was intended to give a broader picture of connectivity for managers. To prioritize culvert replacement based on the greatest potential gains to connectivity, we calculated DCI values for each park under a scenario where each individual culvert was restored to full passability. In addition, we generated prioritization lists for parks using square root transformed passability values. In doing this we intended to effectively weight the value of each culvert based on the proportion of time for which it was impassible (i.e., its passability value), to determine if gains in connectivity were proportional as culvert passability increased. This was meant to potentially demonstrate that replacing culverts with the poorest passability values may not always be the best approach – as a culvert with a moderately high passability value might provide larger gains to overall network connectivity when fully passable.

2.3.2 Fish species of interest

Barrier assessments were conducted for two different salmonid species which are native to both parks: brook trout and the larger Atlantic salmon. These species have well-studied physiology, are widely distributed in the study areas and are culturally and recreationally important (Scott and Crossman 1973). Though brook trout and Atlantic salmon are of the same family, Atlantic salmon has superior swimming capabilities (Peake et al. 1997) and diadromous individuals can attain larger sizes than those of brook trout. We based our Atlantic salmon assessments on the physiology of a 50 cm (fork length; FL) individual and the physiology of a 15 cm (FL) individual for brook trout assessments. These lengths were chosen to represent fish within the size range found in TNNP and PEINP, and also the range that had been used in past studies to determine swim speed velocities (Peake 2007).

2.3.3 Mapping stream networks and catchments

To determine the aquatic connectivity of stream networks in TNNP and PEINP, we first created maps of both study sites to measure the spatial parameters required for DCI calculations. We did this using Geographic Information System (GIS) shapefiles obtained from park staff to make maps using ArcGIS software (ESRI, ArcInfo v.9.2) (Fig. 2.1 and 2.2). The stream shapefile from TNNP did not show all of the smaller tributaries (stream segments) associated with stream systems, and as a result some barriers were not located on mapped streams. We used Arc Hydro software (terrain preprocessing tools, V 1.1 beta) and a digital elevation model (DEM) obtained from park staff, to delineate all smaller streams in TNNP, setting a threshold drainage area of 1000 cells, or $10km^2$ – meaning that for a raster cell on the DEM to be considered part of a stream, at least 1000 other cells needed to drain into it. Threshold values are subjective and influence parameters of total stream length (Rumman et al. 2005); we chose this value because it produced streams at all barrier locations. We also used Arc Hydro to delineate new, finer-scale catchments (areas of land where surface water drain into a single stream system) in TNNP based on the DEM, as not all of the barriers and small tributaries were contained within the catchments mapped using the data we had received.

2.3.4 Barrier evaluation

Anthropogenic barriers within the stream systems of both parks were all road culverts (n=43 in TNNP, n=21 in PEINP). Site information for each culvert was recorded, including the reaches directly up and downstream, and the tailwater control – the area directly downstream of the culvert outlet pool (see Appendix A for details of survey procedures). We completed initial surveys in TNNP in May and June 2007, with the assistance of park technicians. We carried out further surveys of the Big Brook stream system in May 2008, along with engineering officer cadets from the Royal Military College. All culvert field surveys in PEINP were done by park staff in October 2007.

Natural barriers in TNNP (*n*=13) were located and surveyed by park staff in November and December 2008; only stream systems with anthropogenic barriers were surveyed. All natural barriers identified consisted of regions of stream that were designated as completely impassable due to high jumps (>30 cm) or extended steep reaches of cascading water with very shallow or no plunge pools. Because these surveys were done in winter, ice cover made evaluations difficult; however, all barriers were familiar to park staff and believed to be completely impassable for the study species. No natural barriers were identified in PEINP.

We used two methods to evaluate passability of park culverts; rapid field assessments (which examine culvert passabilities during a single visit), and more detailed field data coupled with modeling software (that integrates variation in stream flow in the evaluation of culvert passabilities). Field assessments consisted of a screening process for barriers, based on a set of criteria (Fig. 2.3) adapted from previous culvert inventories (Clarkin et al. 2005). More detailed assessments were conducted using FishXing, a widely used freeware that creates hydrological models of culverts based on data collected in the field (culvert shape, length (m), material, slope, installation type) together with flow equations and fish movement parameters. While FishXing can model culverts using minimal field data, more detailed data can be included such as the cross-section topography of the tailwater control area and discharge rates for the study stream. FishXing also identifies which of three mechanisms impede the passage of fish: insufficient water depth in the culvert (depth barrier), excessive height for fish to jump into the culvert (height barrier) and excessive water flow for fish passage (velocity barrier).

The data collection for the rapid assessment surveys took from 5 to 15 min per culvert, whereas for the FishXing assessments, surveys in the field took from 20 to 40 min per culvert with an additional time of 5-10 min per culvert for computer simulations (and more when default values proved problematic—see below for details).

We collected additional parameters (e.g. water depth and water velocity in culvert) to ground-truth FishXing results, and three culverts were revisited to improve congruence between field and FishXing outputs. Using the FishXing software also requires additional inputs of fish limitations for burst and sustained swimming speed, minimum water depth and maximum outflow drop (Table 2.1). These values were obtained for our species from Peake et al. (1997) and from Peake (unpublished data).

We encountered some challenges when assessing culverts using FishXing. Specifically, the default values provided by the software (Table 2.2) for the culvert entrance loss coefficient (K_e) and the culvert and tailwater control roughness coefficients (n)—parameters used to model water flow in open channels (Brater and King 1976)—did not provide accurate approximations of field conditions (Table 2.3). Thus, at a given discharge rate, modeled values of culvert water depth and velocity were often very different from the actual values measured in the field at that discharge rate—leading us to suspect that the modeled values provided by FishXing at other discharge rates were also inaccurate. This issue has been observed in other evaluations using FishXing (Blank et al. 2005; Poplar-Jeffers et al. 2008) and likely occurs because the software uses K_e values which are derived from culverts under full water and roughness coefficients which are often derived from large streams and generalized to all streams without considering details such as the presence of debris, inconsistencies in substrate across a small area or rapid changes in slope or wetted width (R. Gubernick, FishXing design team, pers. comm.; see also Mangin et al. 2010). To more accurately model the study sites, we obtained new K_e values for partially full culverts from Straub and Morris (1950a, b) and back-calculated new roughness coefficient values (n) using field data from original culvert surveys and from the three culverts which were revisited for ground-truthing (see Appendix B for details of calculations). Though the culvert parameters provided by FishXing did not always match field values exactly, our modifications to the n and K_e values did improve the precision of all culvert models (Table 2.3).

2.3.5 Temporal variability in stream flow

We investigated the effect of temporal period and flow variability for catchments in TNNP by calculating the DCI_P and DCI_D for two time periods: when fish are migrating, and the whole year, using daily discharge data averaged over a 20-year period from the Southwest Brook gauging station (station 02YS003) located in the park. We did not calculate yearly simulations for PEINP because many of the structures were difficult to model (e.g., immediately downstream from ponds) or lacking tailwater control data. Due to these limitations, most of the culverts in PEINP were designated as completely passable or impassable ($p = 1$ or 0) regardless of assessment techniques; therefore comparing DCI values obtained using a variety of barrier evaluation methods for this park may not be as informative as for TNNP. Instead, passability values for PEINP were calculated based on the migration period only, using data from the Winter River (near Suffolk, station 01CC002) and Bear River (station 01CD005) gauging stations, located near park catchments.

2.4 Results

We calculated passability, DCI_P, and DCI_D with variations in fish species, barrier assessment method, and stream flow period, as described above. Here, we report how estimated passability varied at the barrier, and DCI at the catchment and park scales.

2.4.1 Barrier passability

The definition and method of measuring passability affected the passability estimate for individual barriers in both parks (see Appendix C for detailed culvert passability values). In PEINP, only two scenarios were tested – passability for a 15 cm brook trout versus a 50 cm salmon, both during the migration period. Of the 21 culverts in the park, 8 were full barriers, 6 were partial barriers and 7 were fully passable for both species. There were some differences in the passability of partially passable barriers between assessment methods but not between species; the majority of barriers (81%) remained the same regardless of assessment method. Modeling these culverts was challenging as 16 of them did not have detailed tailwater control data due to poor field conditions or a lack of tailwater region (culverts drained directly into ponds), potentially creating over simplified models of fish passage. While the issues encountered in PEINP do provide valuable information on potential problems with assessments, the lack of variation in the results, and the issues with modeling the park's barriers led to the decision to largely focus this study on the impacts of assessment methods on TNNP, as was also the approach taken in the primary publication of these results (Bourne et al. 2011).

In TNNP (Fig. 2.4) passability results differed considerably amongst culverts. Twenty-two of 43 culverts were impervious to any change in methodology and definition of passability, with 20 being completely impassable in all scenarios and 2 fully passable. For the remaining culverts, passability values consistently increased when assessed for a full year versus the migration period. The majority (86%) of partially passable culverts had higher passability values for brook trout than they did for salmon.

2.4.2 Single catchment scale

For the DCI_P in PEINP the range of values encountered was 20-100, and for the DCI_D 38-100 (see Appendix D for a full table of DCI values). DCI_D values were higher than DCI_P values in 3 catchments for trout, and 2 for salmon, with differences ranging from 1-14%. One catchment had full connectivity (100) as it contained only one barrier which was fully passable; in the remaining 4 catchments, connectivity values were lower for salmon than brook trout (Fig. 2.5).

The range of DCI_P values encountered in TNNP was 40–70, and for the DCI_D the range of values encountered was 42–83 with values differing among all 4 evaluation methods (Fig 2.6). In 11 of 15 TNNP catchments, DCI_P values for both species during the migration period were identical or differed slightly (less than 8%). However, for 3 catchments DCI_P values for trout were 30-40% greater than those of salmon, and for 1 catchment the value for salmon was 43% higher than that of trout. For simulations done for the entire year, DCI_P values remained the same as they were for the migration period or showed slight increases (from 1-6%).

DCI_D results for TNNP catchments showed similar trends to those for DCI_P evaluations (Fig 2.6b). For 8 catchments, connectivity values for trout and salmon were the same or within 5% of one another. Values for trout were higher for 6 catchments (6 to 76%), and for 1 catchment the DCI_D value for salmon was 60% greater than that of trout. For most catchments the yearly connectivity values were the same or slightly higher (up to 8%) for both species. However, for 2 catchments for trout and 1 for salmon, the DCI_D values increased by approximately 15%.

2.4.3 National Park scale

Across all catchments within TNNP connectivity values varied differently depending on whether the rapid field-based assessment or field assessment plus modeling in FishXing was used to estimate barrier passability (Fig. 2.6 and 2.7). DCI values were lower for most catchments when the field assessment alone was used, although the difference was not as dramatic for the diadromous case as the potamodromous one. In the potamodromous case, 6 catchments (40%) had DCI values between 0 and 40 when the field assessments were used, while all catchments had DCI of 41 or higher when passability estimates from FishXing were used (Fig. 2.6). In the diadromous case, only 5 catchments (33%) dropped to a lower DCI category with the field assessment (Fig. 2.7). DCI values across park catchments were also quite variable depending on whether passability was calculated based on an annual flow period, or restricted to flow during fish migration period. For example, more catchments were in a lower category of DCI (<50) when passability was calculated during trout migration period than for the whole year (Fig. 2.6).

2.4.4 Natural connectivity

Of the 15 catchments containing culverts in TNNP, 8 had no natural barriers (natural connectivity of 100) making their percent natural connectivity values equal the ('absolute') DCI values discussed above. For the remaining 7 catchments the ratio of absolute to natural DCI values was used to obtain percent natural connectivity values for brook trout during the migration period. For all 7 catchments, the percent natural potamodromous connectivity values were quite high (all above 90%). The percent natural diadromous connectivity showed greater variation, with 3 catchments having values below 50% (Table 2.4).

The absolute potamodromous connectivity of PEINP was 86.37 and diadromous connectivity was 84.21 for brook trout during their migration period. Since there were no natural barriers in the park, the percent natural connectivity values were the same as these absolute values (Table 2.5). For TNNP, the percent natural connectivity values for brook trout during the migration period were 81.1% for the potamodromous case and 74.0% for the diadromous simulations, based on the park-wide absolute and natural connectivity values (Table 2.5). The DCI values for Atlantic salmon were within 1% of brook trout.

2.4.5 Barrier prioritization

Park catchments which had only single barriers (2 in PEINP, 6 in TNNP) became fully connected (absolute DCI = 100) when those barriers were restored. In each of the remaining catchments there was a single 'key culvert' that provided the greatest gains to absolute connectivity for both the potamodromous and diadromous case when restored to fully passable, a trend seen with both species. In PEINP all of these key culverts had passabilities of 0 before restoration (Table 2.6). In TNNP the key culverts were not always the barriers with the lowest passabilities in the catchments before restoration (Table 2.7); however key culverts were all located next to the largest stream segments in the system.

When the same passability values were square root transformed to investigate the potential effects of weighting values by the amount of time they were passable, the values of culverts in 7 of the 15 park catchments changed – the remaining 8 catchments had culverts with passabilities of 0 or 1, so transformation had no effect. Of the 7 catchments with new passability values, the key culvert changed in the prioritization tables of 2 catchments (Table 2.8).

2.4.6 Effects of catchment size and barrier position

The area of catchments containing barriers in both parks (n = 20) ranged from 0.02 to 7.43 ha, with each catchment having from 1 to 11 barriers. A comparison between the area of these catchments and their associated connectivity (for brook trout during their migration period) showed no trend for either DCI_P or DCI_D (Fig. 2.8). It did appear that the number of barriers present in a catchment increased with area (r^2=0.25, p=0.02); the number also had a possible relationship with DCI_P but no relationship to DCI_D (Fig. 2.9). The placement and passability of barriers did appear to have an effect on DCI values. Diadromous connectivity was clearly negatively influenced by barriers located near stream outlets, which was the case for 8 catchments in TNNP and 2 in PEINP, all of which had DCI_D values which were lower than their DCI_P (Fig. 2.5, 2.6, 2.7). In comparison, potamodromous connectivity was negatively impacted by more centrally located barriers, for example, catchments H, J, K and M in TNNP and A in PEINP (Fig. 2.5, 2.6, 2.7). Four catchments in TNNP had high potamodromous as well as diadromous connectivity values. The culverts in these catchments were all either highly passable or located at the extremities of stream systems, but not near outlets (Fig. 2.7).

2.5 Discussion

The preservation and restoration of aquatic connectivity has been recognized as a major conservation goal in stream systems (Pringle 2003); and new methods have been developed to measure the alteration of connectivity in dendritic systems. Common to all methods is the difficulty in assessing barrier passability—the dynamic component of connectivity. Our results demonstrate how passability varies by species and hydrological conditions (see also Poplar-Jeffers et al. 2008; Meizler et al. 2009; Kemp and O'Hanley 2010; Rolls 2011) and managers will often be forced to select a target demographic and/or target conditions when evaluating barrier passability. In this study, we showed the implications of making such decisions (i.e. differences associated with picking a particular method or a particular target species) as well as the error that may be related to parameter estimates on passability and connectivity at the catchment scale.

Through these evaluations we found that catchment connectivity results can vary with barrier assessment methods—making the choice of method a crucial and influential step in connectivity assessment. For most culverts, using a simple set of criteria to do barrier field assessments produced passability values that were more conservative than those calculated by computer modeling (FishXing) for fish of the same size and species, which in turn led to reduced connectivity values (Figs. 2.4, 2.6). It remains likely that the simple field assessments were too conservative when compared to those provided by FishXing. Because the rapid field-based assessments have been developed as general installation/assessment guidelines (Fig. 2.3; see also Clarkin et al. 2005), they do not account for the variable nature of passability. Hence, they are necessarily precautionary and less accurate. Though the simplified field assessments did give very different estimates of passability in this study, with modified criteria and further evaluations of partial barriers using FishXing, they could be used more efficiently as tools to save time during culvert surveys by 'screening' obvious barriers—a practice which has been implemented in other studies and surveys (e.g. Clarkin et al. 2005). The modeling approach has an advantage in that it can account for variability in passability through time and for different species. Unfortunately, specific biological data (i.e. fish telemetry data) were not available to directly assess the accuracy of culvert passability estimates in this study. Such information would enable researchers to assess key assumptions in fish passage, but this remains a common data gap in passability assessments (see Mahlum et al. (in review) for validation of passability in TNNP).

While it is a useful tool, FishXing, is not without issues and limitations. As others have noted (Blank et al. 2005; Poplar-Jeffers 2008; R. Gubernick pers. comm.), FishXing uses conservative modeling which does not account for all variables and, as with any model, must be used with caution. Though we were able to improve the results provided by the software by obtaining outputs that were more similar to field conditions than those provided when program default parameter values were used, it was still difficult to simulate passage for some culverts. This was especially the case for culverts in PEINP where tailwater data were often lacking and we encountered environmental conditions that were not possible to model using FishXing (e.g., ponds directly up or downstream of culverts). The passability values generated for PEINP by FishXing, as a result, were likely less accurate than those provided by the software for TNNP, where a greater amount of field data could be input into the program.

In this study, the assessment period (i.e. full year vs. migration period) did not have a substantial impact on catchment connectivity in TNNP due to the fact that stream hydrology during the migration period for the two species assessed was representative of the entire year (i.e. both including floods and low water events). Thus, in similar systems to TNNP, catchment connectivity estimates based on a shorter hydrological time period might be reliable – given that the time period chosen captures most of the variation in the system hydrology. These results are specific to the Terra Nova situation, but are likely relevant to catchments in elsewhere. For example, in an examination of fish community assemblages above and below low-head dams in Kansas, Gillette et al. (2005) found seasonal effects. Similarly, Rolls (2011) examined catchments with and without barriers in Australia and found a significant effect of migratory period on barrier passage for some species. Both of these studies (Gillette et al. 2005; Rolls 2011) did not consider overall catchment connectivity, but at the barrier scale the patterns observed were similar to ours in Terra Nova, suggesting that some of our overall conclusions and recommendations on assessment methods may be worth considering in other systems. However, the relatively minimal impact of temporal scale observed here may not be the case in systems where species have more restricted discharge-dependent migration periods (e.g. Pacific salmon and see Rolls 2011 for an example of variation in connectivity depending on migration strategy), or in seasonally arid landscapes where streambeds go dry for months at a time (Eby et al. 2003). Nonetheless, our assessment clearly demonstrates that field assessments that evaluate barriers based on conditions for only a single day (the rapid assessment method, Fig. 2.3) give very different values for connectivity than those that use more dynamic assessment methods to evaluate passability. Thus, barrier assessments need to be considered in the context of ecological conditions at a particular study site, and researchers should choose appropriate assessment methods based on the local species and hydrology.

Barrier assessments done for two different salmonid species demonstrated the variation in passability values that can be associated with both species and size class. Though brook trout and Atlantic salmon are physically similar species, their swimming capabilities differ—with Atlantic salmon being able to attain higher swimming speeds (Peake et al. 1997) and larger sizes than brook trout. The predominantly lower passability values obtained for salmon were therefore surprising, as we expected they would be able to pass a larger range of flows and outflow drops than the smaller, weaker brook trout. However, we had set the minimum culvert water depth for both species at 75% of their body length, giving depth values of 11.25 cm for brook trout and 37.5 cm for salmon. Many of the culverts in our study areas do not have water exceeding 30 cm deep. These evaluations were likely conservative, as large Atlantic salmon have been observed moving upstream in water less than 30 cm deep in TNNP (D. Cote, pers. obs.). This example demonstrates the importance in choosing parameters for barrier evaluations that are accurate for the study species, and if applicable, the subset of the population being targeted. There is a general requirement for better information on fish swimming capacity and behaviour, particularly for non-salmonids (Kemp and O'Hanley 2010).

We demonstrate a means to calculate an integrated stream connectivity value that accounts for variation in hydrology, fish size and species variation. As such, it presents a useful approach for ecosystem-based management of aquatic systems. When conducting assessments, choosing a 'target' species or sizes could cause difficulty in determining a generalized connectivity value, particularly in systems with higher diversity and more varied species. Wiens (2002) suggested that it could be useful to group similar species in order to obtain fewer connectivity values per system. However, recent research on fish passage has shown that taxonomic and physical similarities may not be adequate predictors of barrier sensitivity (McLaughlin et al. 2006). Nonetheless, in many cases, assessing catchment connectivity for a specific target species of management interest may be very useful and appropriate.

The DCI preformed consistently across a range of spatial scales, showing no relationship between catchment area and connectivity. This was expected as the degree of fragmentation in a given stream system is determined by the placement and passability of barriers and the spatial arrangement of habitat patches, not the physical size of the system (Fagan 2002; Poole 2002; Saura and Pascual-Hortal 2007; Cote et al. 2009). We did observe a possible relationship between catchment size and the number of barriers, which was not surprising; if barriers are distributed consistently across a landscape then larger areas would contain proportionately more barriers. It might be expected that this increased number of barriers in large systems would produce lower connectivity values, a trend which was not apparent in this study. However, the simulations done by Cote et al. (2009) showed that connectivity did not decrease linearly with the number of barriers – the greatest losses occurred with the addition of the first few barriers. In contrast, Padgham and Webb (2010) asserted that the effects of multiple modifications to stream networks generally approximated the sum of the impacts of each individual modification. We were not able to confirm either of these hypotheses using field data, as the majority of the catchments in our study sites contained very low numbers of barriers which did not provide adequate data to reveal significant relationships regarding barrier number.

Barrier prioritization was done using the approach of systematically simulating the restoration of one culvert at a time and assessing the effect on the DCI results. Connectivity in this case is based on the extent of catchment (in km) that becomes available when a barrier is removed, without any consideration of habitat quality (although incorporation of habitat quality is possible with these methods). This approach has the benefit of examining all possible scenarios of which culvert to restore to assess the net gain in connectivity with each. This facilitates a cost-benefit analysis; if the next-to-optimal culvert is significantly cheaper to restore than the most optimal, then this may be the most pragmatic solution. Alternative approaches have been proposed and include using integer-based programming to optimize decisions (O'Hanley and Tomberlin 2005; Kemp and O'Hanley 2010) as well as an experimental approach to assessing restoration effects (Kibler et al. 2010). Consistently during these simulations, the culvert which provided the greatest gains to connectivity when restored was adjacent to the largest segment in the stream system, thus expanding the size of the catchment's largest habitat patch upon restoration. These 'key culverts' were often not those with the lowest passability values, once again demonstrating the importance of barrier location over barrier passability. For example, a completely impassable culvert located near a stream extremity would not be expected to have large impacts on potamodromous connectivity, and thus would not provide large improvements if removed or restored – whereas a barrier in a more central location, but with higher passability value would provide greater overall gains.

Though barrier placement does play a major role in the impacts they will have on a stream system, passability is still an important aspect of connectivity and is used in DCI barrier replacement prioritization calculations. We transformed passability data in order to investigate whether prioritization would change when culverts with lower passability were weighted more than those with higher values. This could be a useful approach for stocks that require less than 100% recruitment. For example, a stock which requires 60%

recruitment would theoretically maintain its population size with barriers which had passability values of 0.6 or higher. In such a case, it would be a higher priority to replace culverts with passabilities below 0.6, but without transforming the data the DCI would not reflect that priority. We did see a change in the key culvert for two of the largest catchments when using transformed data for prioritizations, with both the "new" key culverts having lower passabilities than those designated in the initial prioritizations. Most of the other catchments in the park had small numbers of culverts, or multiple barriers that were all completely impassible, so data transformation had no impact. It is likely that in large, complex systems, transformation of passability values could provide very different and potentially informative results.

It is assumed that features which create natural barriers were historically part of the stream system, and that native fish populations have colonized and adapted to their presence. Maintaining or restoring natural connectivity, even if it was never very high, is the usual goal of managers (Kondolf et al. 2006). For this reason, we calculated percent natural connectivity to express the relative impacts of anthropogenic barriers on stream systems. In the majority of park catchments, the percent natural connectivity was quite high, largely because the natural barriers were either located in stream extremities or in close proximity to impassable culverts, which meant that the culverts had negligible impacts on the natural state of the system. The absolute connectivity values used to obtain percent connectivity considered the impacts of both types of barriers when looking at stream fragmentation. Though the effects of natural barriers are not typically considered when evaluating stream fragmentation, absolute connectivity values could be useful in systems where managers wish to make previously inaccessible habitat available for colonization by sensitive populations through the removal natural barriers – effectively increasing the natural connectivity of systems.

An examination of barrier properties across TNNP suggests some modifications to the preliminary screening process, based on physical characteristics of the culverts and the degree to which passability was compromised based on our assessments with FishXing. For the field screening method used for brook trout and salmon in our study areas, we recommend altering both the maximum outflow drop height and slope in the evaluation flowchart (Fig. 2.3). Based on the FishXing simulations and field data collected on multiple dates at the same sites in TNNP, we observed that outflow drop heights can vary with changes in discharge and that culverts which were partially or fully passable at times had outflow drops exceeding 30cm – the maximum drop on the flowchart.. Therefore, the maximum outflow drop height could be changed from 30 to 40 cm (for 15 cm salmonids) to compensate for these potential fluctuation in drops with discharge. For field assessments, we also recommend that the slope used to automatically designate a barrier as impassable be increased from 1.5 to 4.0%, based again on the FishXing results and field data which showed that culverts with slopes exceeding 1.5% were often partially passable. Though 4.0% is steeper than most culvert assessment guides recommend, the further evaluation of culverts using FishXing would be expected to identify barriers that were missed by the initial field assessment and this increase would prevent the potential of screening out passable or partially passable culverts during assessments. Finally, we recommend caution when determining whether culverts are backwatered as some appeared to be passable at low flows, but were actually barriers at higher discharges. Drop height and slope have been shown to be the limiting factors for juvenile fish in a field experiment (Doehring et al. 2011), so we believe these parameters should be the primary focus of assessments.

When considering modifications to culvert structure to enhance restoration, it should be noted that the type of barrier (velocity, depth or jump) varies based on discharge rates. If fish migration/dispersal periods coincide with periods of high or low flow, than culvert modifications should be prioritized to address the main barrier type. For example, at low-flow rates, most culverts in TNNP were depth barriers for adult/50 cm salmon. Since periods of low stream flow coincide with salmon migration, then modifications should aim to increase water depth within the culvert. Conversely, for brook trout, most barriers at high-flow rates (and some barriers for salmon) are velocity barriers; thus, modifications should be carried out to reduce water velocity in culverts (for example, though the use of flow baffles). These modifications are applicable to the system in TNNP; similar modifications to a flowchart-based assessment for systems in other parts of the world would have to be based on *in situ* assessments of local condition and species. However, our findings illustrate that coupling field-based assessments with modeling can help to customize the field-based assessments to better assess culvert passability.

This first test of the DCI using field data showed its potential as a valuable tool in aquatic connectivity assessment. The index is a fairly simple one to calculate, modify and interpret, and provides one of the first methods for quantifying stream fragmentation. The most problematic aspect of DCI application was obtaining appropriate passability values. When choosing barrier assessment methods, managers need to consider a range of factors, such as resource availability (time, equipment, etc.), the number of barriers requiring surveys, variations in hydrological conditions, and the ecology of the system and species of interest. It is likely that in most scenarios, the evaluation of potential barriers will have to be done with the exclusion of some details; otherwise the process would become too complex – particularly in large systems with a high number of barriers. This uncertainty must be considered when connectivity values are reported. In addition, the connectivity values themselves can be calculated based on single stream systems, catchments, or as in this example, collections of catchments – all giving different values. These variations make it essential that anyone who uses the DCI implements it and interprets its results in conjunction with knowledge and data from other sources to make informed decisions.

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Table 2.1: Swim speeds and culvert water parameters[a] input into FishXing to model passage for 15 cm brook trout and 50 cm Atlantic salmon

Species	Burst swim speed (m/s)[d]	Prolonged swim speed (m/s)[e]	Minimum culvert water depth (m)	Maximum culvert outlet drop (m)
Brook trout[b]	1.19	0.94	0.1125	0.3
Atlantic salmon[c]	3.24	2.02	0.375	1

a. provided by Steve Peake (unpublished report 2007)
b. derived from multiple regression equation from Peake et al. (1997)
c. taken from results of Colavecchia et al. (1998)
d. capable of being maintained for 20 s
e. capable of being maintained for 600s

Table 2.2: Hydraulic parameters used to model water flow and fish passage in FishXing software

Parameter	Description
Culvert Roughness (n)	Manning's roughness coefficient for open-channel flow; used in the Manning's equation to account for friction applied to the flow by the channel. n values, which fall between 0 and 1, can be found in hydraulic engineering tables for common surfaces or they can be back calculated using field measurements of water velocity and slope in the channel.
Entrance Loss (K_e)	Known as the inlet head loss coefficient, K_e is a constant in the entrance loss equation. It denotes how much energy is lost as water enters a culvert. The value, between 0 and 1, is dependent on the geometry of the inlet edge. It measures the efficiency of the inlet to smoothly transition flow from the stream to the culvert.

Table 2.3: Comparison of field measurements of 5 culvert parameters to values estimated by FishXing using i) program defaults and ii) manually adjusted culvert entrance loss coefficients (K_e) and culvert and tailwater roughness coefficients (n), for 3 culverts in Terra Nova National Park

Culvert	**Culvert Parameters**	**Field values**	**FishXing defaults**	**Adjusted K_e and n values**
A	Avg. culvert water depth (m)	0.08	0.08	0.12
	Headwater depth (m)	0.35	0.14	0.28
	Tailwater depth (m)	0.15	-0.07	0.16
	Outlet drop (m)	0	0.15	0
	Avg. culvert velocity (m/s)	0.39	0.86	0.45
B	Avg. culvert water depth (m)	0.10	0.10	0.14
	Headwater depth (m)	0.20	0.20	0.19
	Tailwater depth (m)	0.16	-0.03	0.16
	Outlet drop (m)	0	0.13	0
	Avg. culvert velocity (m/s)	0.67	1.21	0.78
C	Avg. culvert water depth (m)	0.25	0.13	0.30
	Headwater depth (m)	0.11	0.25	0.30
	Tailwater depth (m)	0.38	0.25	0.30
	Outlet drop (m)	0	0	0
	Avg. culvert velocity (m/s)	0.20	1.19	0.28

Table 2.4: Absolute, natural and percent natural connectivity values obtained for Terra Nova National Park, based on 15 cm brook trout during the migration period of May to December

catchment	**DCI$_p$**			**DCI$_D$**		
	absolute	*natural*	*% natural*	*absolute*	*natural*	*% natural*
E	86.1	86.4	99.8	2.5	7.3	34.2
F	90.8	90.9	99.9	1.2	4.8	25.1
G	84.9	85.1	99.8	6.9	8.1	85.2
H	47.6	49.2	96.8	27.3	29.9	91.2
I	51.5	55.2	93.3	31.7	66.2	47.9
N	56.3	56.9	99.1	30.4	31.5	96.5
O	91.0	94.1	96.7	95.2	97.0	98.2

Table 2.5: Absolute, natural and percent natural connectivity values obtained for Terra Nova and Prince Edward Island National Parks, based on 15 cm brook trout during the migration period of May to December using the DCI. Park level connectivity was calculated by taking a weighted average of the individual connectivity values for all catchments within the park.

Park	**DCI$_p$**			**DCI$_D$**		
	absolute	*natural*	*% natural*	*absolute*	*natural*	*% natural*
Terra Nova	69.5	92.0	81.1	63.6	85.9	74.0
Prince Edward Island	86.37	100	86.37	84.21	100	84.21

Table 2.6: Changes in catchment connectivity associated with culvert restorations within Prince Edward Island National Park. Culverts in bold represent those which would provide the greatest gains to connectivity when passability is restored to 1 (fully passable). The third column shows passability scores of the individual culverts prior to restoration.

catchment	restored culvert (pass = 1)	passability without restoration	DCI_p	DCI_D
A	none		26.4	42.3
	a	0.95	26.7	43.3
	b	1	26.4	42.3
	c	1	26.4	42.3
	d	0	29.7	46.0
	e	0	27.2	42.3
	f	0.98	26.4	42.3
	g	**0**	**39.3**	**56.8**
	h	1	26.4	42.3
	i	0.70	26.6	42.3
	j	1	26.4	42.3
	k	0.03	31.6	42.3
	l	0	28.6	42.3
B	none		56.5	68.0
	m	**0**	**100.0**	**100.0**
	n	1	56.5	68.0
	o	1	56.5	68.0
D	none		91.5	95.6
	q	1	91.5	95.6
	r	**0**	**97.0**	**98.5**
	s	0.66	91.3	95.7
	t	0	93.7	96.8
	u	0.50	91.5	95.6

Table 2.7: Changes in DCI values for 15 cm brook trout during the migration period associated with culvert restorations within four Terra Nova National Park catchments. Culverts in bold represent those which would provide the greatest gains to connectivity when passability is restored to 1 (fully passable). The third column shows passability scores of the individual culverts prior to restoration

catchment	restored culvert (pass = 1)	passability without restoration	DCI_p	DCI_D
A	none		57.1	57.8
	a	**0.22**	**70.8**	**81.9**
	b	0.08	60.9	62.3
C	none		85.2	2.4
	d	0	85.9	16.9
	e	**0**	**87.2**	**85.5**
J	none		46.5	58.4
	t	0.29	46.5	58.4
	u	0	46.7	58.4
	v	0.06	47.1	58.8
	w	1	46.5	58.4
	x	0	57.7	68.3
	y	0	48.1	59.8
	z	0	49.8	61.3
	ag	**0.14**	**46.5**	**58.4**
K	none		81.2	89.5
	ah	0.18	82.3	90.1
	ai	0.15	81.5	89.7
	aj	0.54	83.0	90.5
	ak	0	81.7	89.8
	al	**.79**	**86.3**	**92.9**
	am	1	81.2	89.5
	an	0	81.3	89.6
	ao	.85	81.9	89.9
	ap	.33	85.6	92.2
	aq	.25	81.4	89.5

Table 2.8: Changes in barrier prioritizations for 2 catchments in TNNP when passability values were square root transformed. Culverts in bold represent those which would provide the greatest gains to connectivity for each simulation

catchment	restored culvert (pass=1)	DCI_p	DCI_D	sq transformed DCI_p	sq transformed DCI_D
H	none	47.6	27.3	53.2	31.4
	k	**48.5**	**28.9**	53.7	32.7
	l	48.1	28.2	**94.4**	**97.1**
	m	47.7	27.3	54.1	32.9
K	none	81.2	89.5	87.2	90.1
	ah	82.3	90.1	88.6	93.8
	ai	81.5	89.7	87.5	93.2
	aj	83.0	90.5	88.3	93.6
	ak	81.7	89.8	88.1	93.5
	al	**86.3**	**92.9**	90.0	94.9
	am	81.2	89.5	87.2	93.1
	an	81.3	89.6	87.3	93.3
	ao	81.9	89.9	87.6	93.1
	ap	85.6	92.2	**90.5**	**95.0**
	aq	81.4	89.5	87.4	93.0

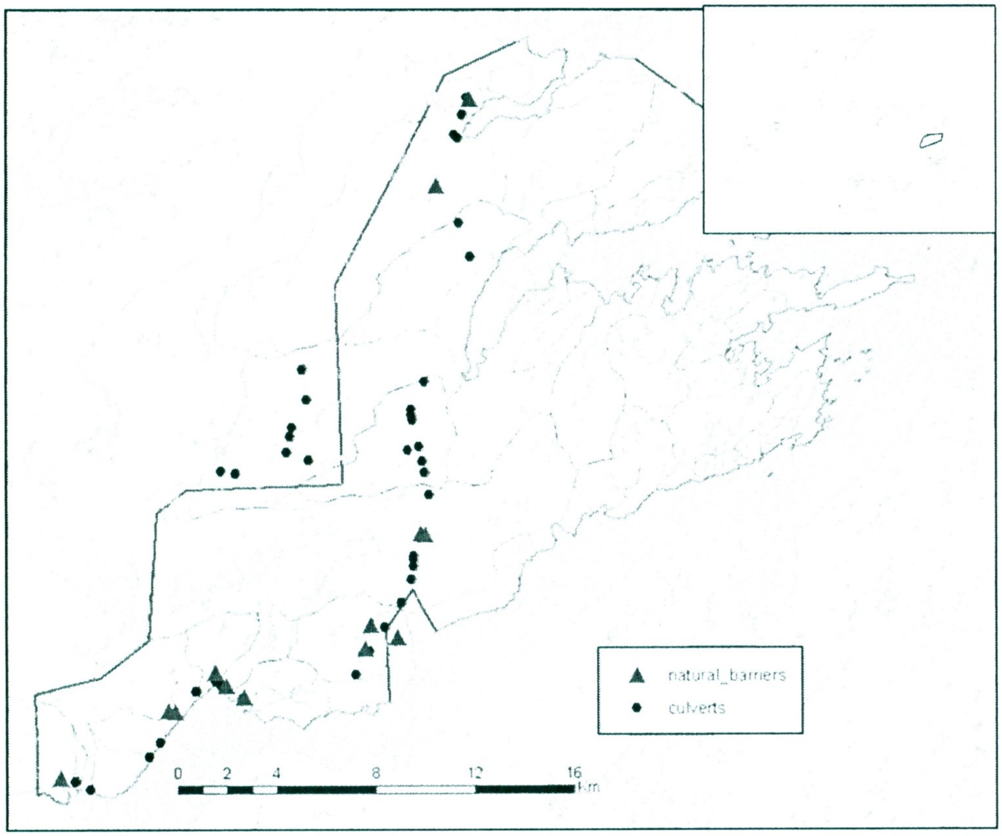

Figure 2.1: Locations of stream networks, catchments (thin grey lines), culverts (hexagons) and natural barriers (triangles) of Terra Nova National Park (thick grey line is the park boundary), Newfoundland. Inset map shows park location in Newfoundland

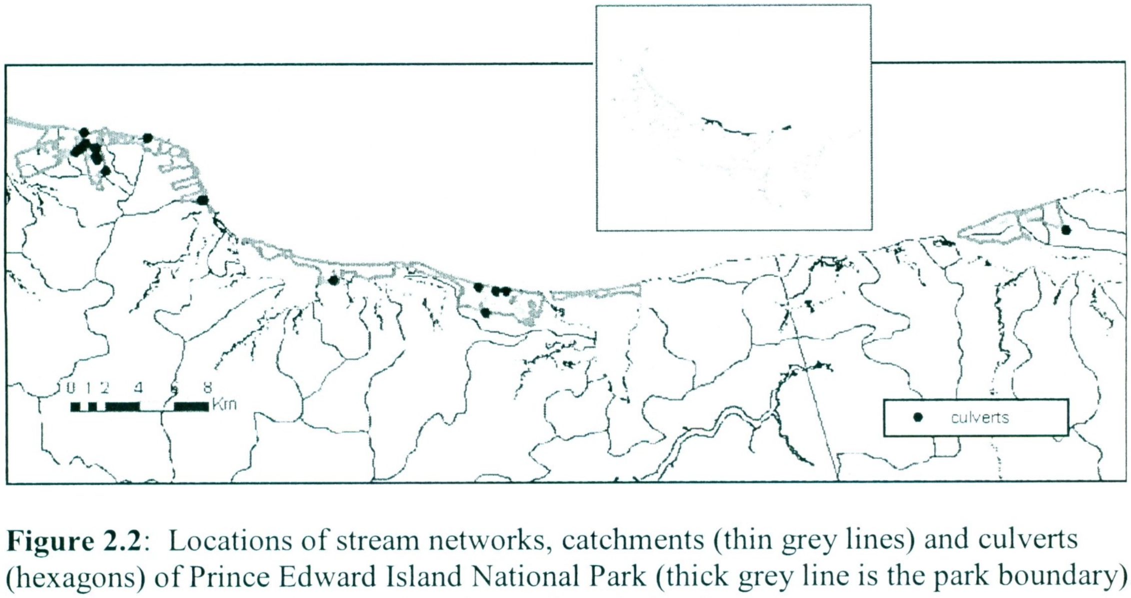

Figure 2.2: Locations of stream networks, catchments (thin grey lines) and culverts (hexagons) of Prince Edward Island National Park (thick grey line is the park boundary). Inset map shows park location in Prince Edward Island

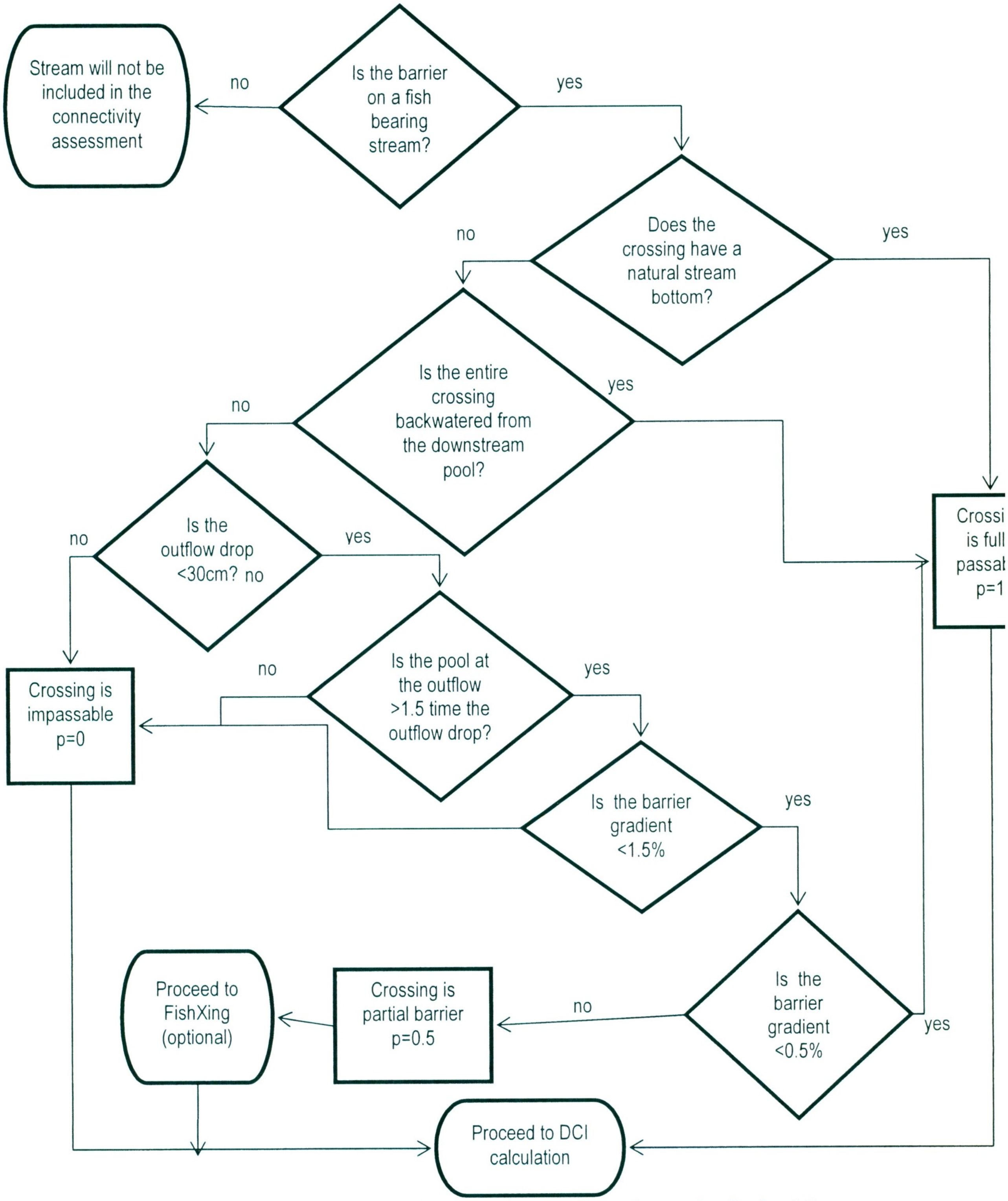

Figure 2.3: Flowchart for preliminary culvert evaluation based on criteria for 15 cm salmonid, developed by Dave Cote, Terra Nova National Park (adapted from Clarkin et al. 2005)

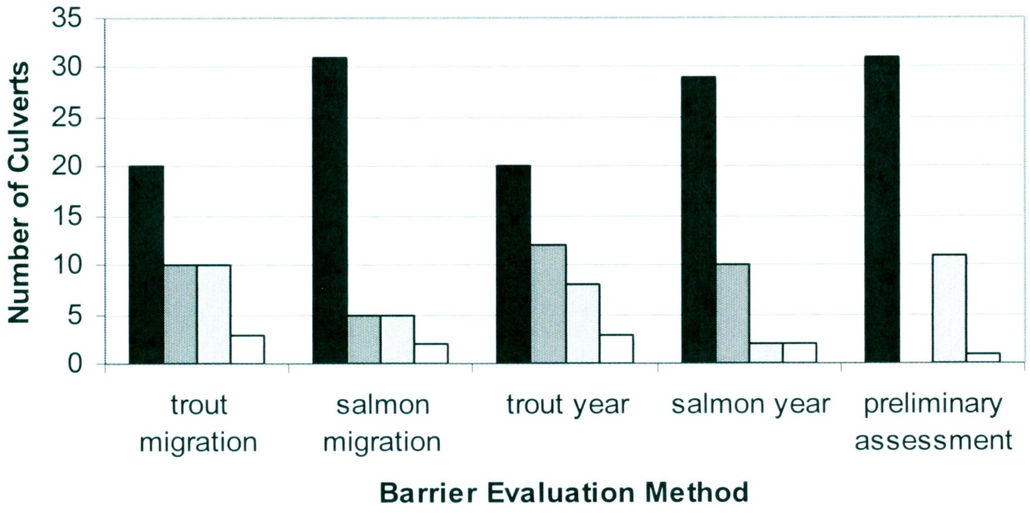

Figure 2.4: Number of culverts (*n*=43) in Terra Nova National Park with complete (1.0 – white bars), good (0.5-0.99 – light grey bars), poor (0.01-0.49 – dark grey bars) and no (0.0 – black bars) passability based on calculations completed using FishXing during fish migration period and across the entire year for both brook trout and salmon, as well as based on a rapid assessment of passability using only the preliminary assessment

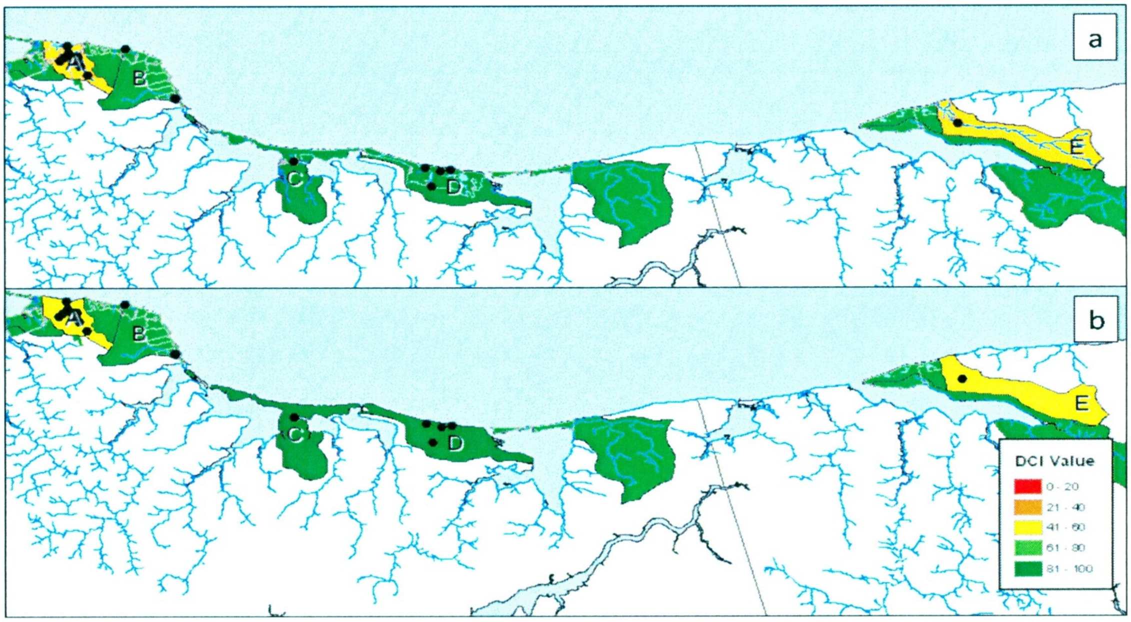

Figure 2.5: Diadromous DCI values of catchments in Prince Edward Island National Park for **a** 15 cm brook trout and **b** 50cm Atlantic salmon during their migration period, with black points indicating culvert locations

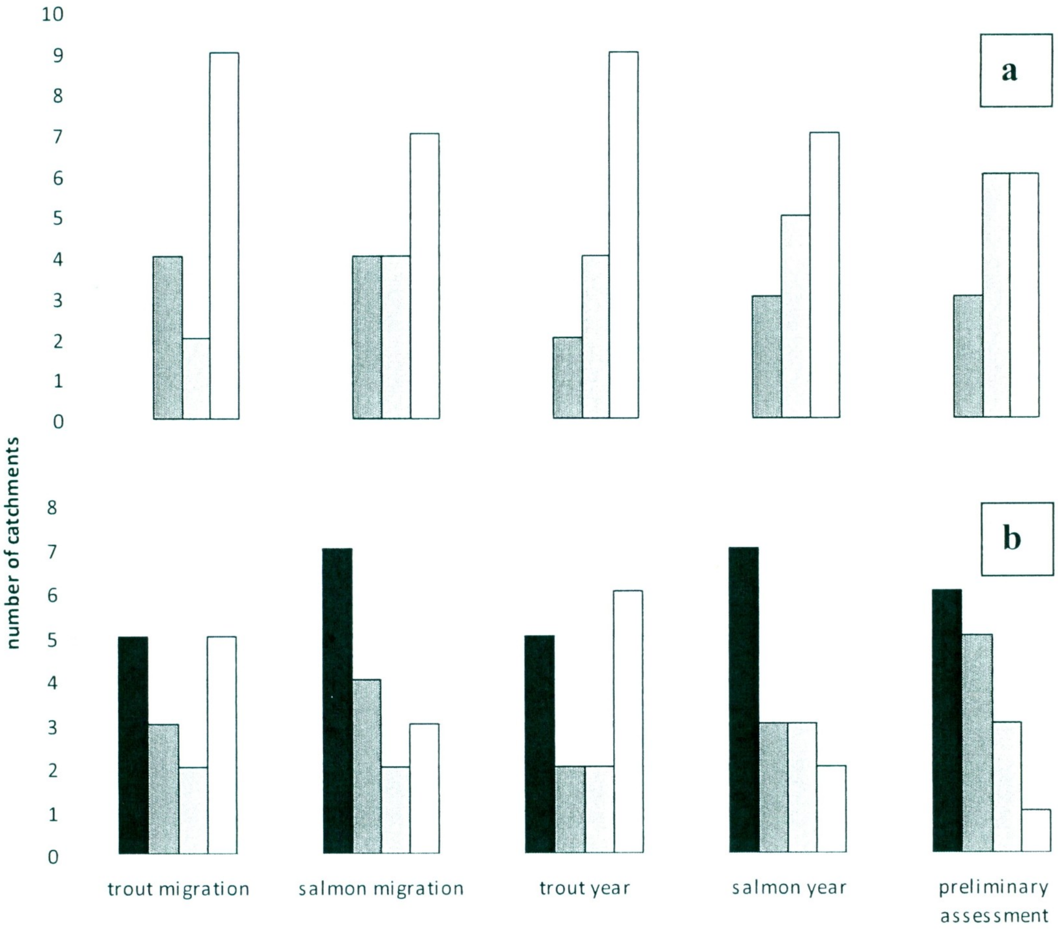

Figure 2.6: Comparison of variability in DCI as a result of using different seasons, species and methods to examine passability. Figure shows the number of catchments containing culverts (*n*=15) in Terra Nova National Park with high (76-100 – white bars), moderate (51-75 – light grey bars) and low (26-50 – dark grey bars) and very low (0-25 – black bars) connectivity measured using the DCI in the **a** potamodromous case and **b** diadromous case. DCI values are based on calculating passability with FishXing during fish migration period and across the entire year for both brook trout and salmon, as well as based on a rapid assessment of passability using only the preliminary assessment

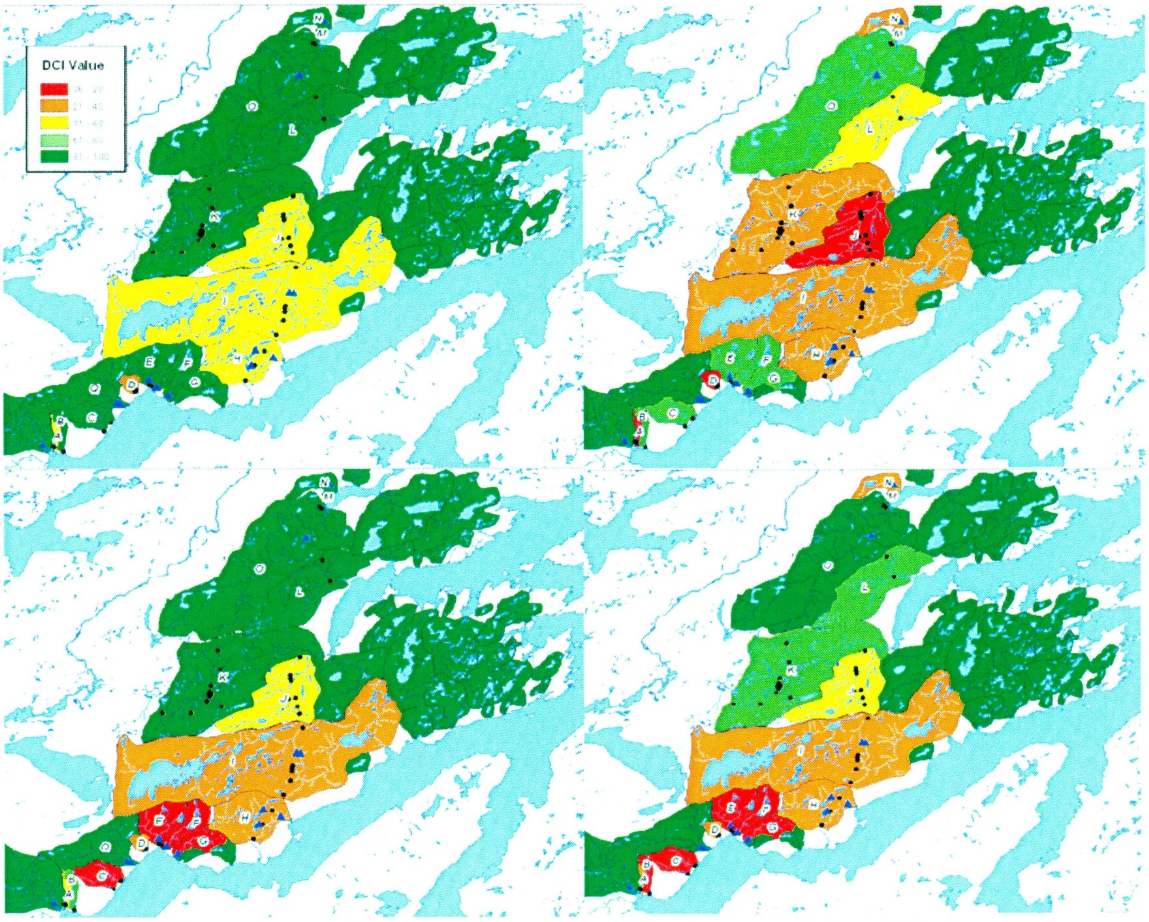

Figure 2.7: Comparison of absolute potamodromous (top panels) and diadromous (bottom panels) DCI of catchments in Terra Nova National Park obtained using computer modeling (left hand panels) and field evaluations (right hand panels) of culverts based on 15 cm brook trout during the migration period

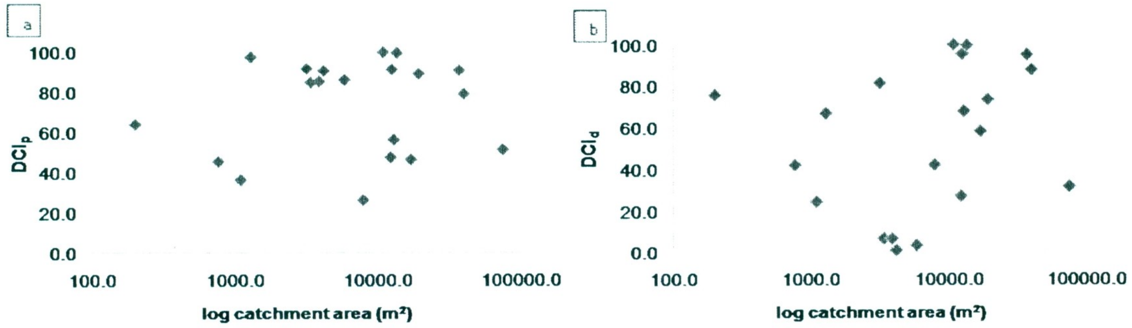

Figure 2.8: The effect of the total area of catchments containing barriers in Terra Nova and Prince Edward Island national parks on **a** potadramous (r^2=0.005, p=0.75) and **b** diadromous connectivity (r^2=0.333, p=0.44)

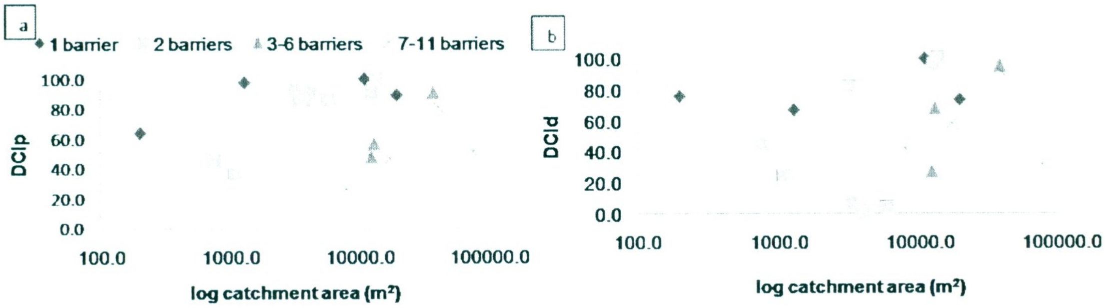

Figure 2.9: The effect of area and number of culverts in catchments in Terra Nova and Prince Edward Island national parks on **a** potadramous (r^2=0.38, p=0.003) and **b** diadromous connectivity (r^2=0.006, p=0.73)

CHAPTER 3: INCORPORATING HABITAT QUALITY INTO THE DENDRITIC CONNECITIVTY INDEX: MOVING BEYOND A PURELY STRUCTURAL APPROACH

3.1 Abstract

Habitat fragmentation has become a serious issue in many stream networks worldwide, contributing to the decline and extinction of numerous freshwater fish species. While various models have been developed to help aquatic ecologists assess the structural fragmentation of stream networks, few take functional fragmentation – the role of ecological attributes in habitat connectivity, into account. I predicted that the addition of ecological data to the Dendritic Connectivity Index (DCI) would produce large changes in connectivity estimates for stream networks, particularly in scenarios where the value of habitat quality was disproportionate to stream segment length (i.e. patch size), reflecting the importance of habitat quality on the distribution of fish within stream networks. Specifically, I used brook trout (*Salvelinus fontinalis*) habitat indices to derive trout biomass estimates for stream segments and ponds within Terra Nova National Park, Canada and incorporated those biomass estimates into the DCI calculations to create a functional version of the index which would reflect habitat quality. My results showed that when stream segment biomass estimates for brook trout were included in the DCI, connectivity values differed for both potamodromous and diadromous simulations when compared to the structural estimates. In general, diadromous connectivity values were higher (6 to 60%) while potamodromous were more variable (-24 to 60%) The addition of pond trout biomass data to the functional DCI caused even further discrepancy from structural connectivity estimates, with values decreasing for most catchments in the

diadromous simulations by 50% or more, and increasing for the potamodromous (2-76%). However, despite the changes observed in connectivity values between the structural and functional versions of the DCI, there was still a significant correlation between the values for each catchment, demonstrating that in this case study the DCI was a robust index which provided meaningful connectivity estimates, even in the absence of functional data.

3.2 Introduction

In recent years, with populations of freshwater fish experiencing worldwide declines (Olden et al. 2010), ecologists have recognized the serious threats posed to aquatic ecosystems through habitat fragmentation – a concept that was historically applied to terrestrial landscapes (Weins 2002; Pringle 2003). Aquatic fragmentation most often occurs through the construction of dams and roadways, which create barriers to fish movement and lead to issues such as population isolation, declines, and even extinction (e.g., Sheldon 1988; Trombulak & Fissell 2000; Dunham et al. 2002; Fagan 2002; Gillette et al. 2005; Morita and Yamamoto 2002; Olden et al. 2010; Musil et al. 2012). While some barriers may be obvious, such as dams that impede all water flow, others are not. Road culverts, for example, are designed to efficiently move water through a crossing, and appear to be a modified continuum of the stream. In reality, these structures often partially or completely inhibit fish passage (e.g., Blank et al. 2005; Bourne et al. 2011; Doehring et al. 2011). The severity, spatial arrangement and number of these barriers within a stream network can play an important role in the overall connectivity of the system, and to accurately assess and mitigate aquatic fragmentation, a landscape level approach needs to be taken (Lowe et al. 2006; Sheer and Steel 2006; Cote et al. 2009; Bourne et al. 2011; Rolls 2011; Flitcroft et al. 2012). Developing tools and methods to conduct these large scale assessments has been a challenge for ecologists, largely due to the complex structural and ecological attributes of stream networks.

The Dendritic Connectivity Index (DCI) is a tool which was developed to help ecologists model the complexity of aquatic systems and quantitatively measure riverscape connectivity (Cote et al. 2009). The DCI uses the parameters of total stream network length (L), stream segment length (l) – (where a segment is a habitat patch created by movement barriers), and barrier passability (p) – which is measured on a scale from 0 to 1 and can be determined using different methods (chapter 2; Bourne et al. 2011). This index assesses the dendritic structure of stream networks, as well as the effects of barrier locations within them, to provide an overall connectivity value and a prioritized list of barriers for replacement (based on the potential connectivity gains from removing individual barriers). In addition the DCI also accounts for different dispersal/life history strategies by modeling both potamodromous and diadromous connectivity, where potamodromous simulations calculate connectivity for a fish moving from any one segment to any other, versus diadromous connectivity that looks at movement from outlets to headwaters (upstream only). This comprehensive evaluation makes the DCI a powerful tool for real world applications and fragmentation assessments (Bourne et al. 2011; Mahlum et al. (in review); Perkin and Gido (in press)). However, as the study of connectivity dynamics in terrestrial landscape ecology has demonstrated (Hilty et al. 2006), patch size (segment length in the DCI) is not the only driver of connectivity.

Since their inception, landscape ecology models of terrestrial connectivity have grown increasingly sophisticated, moving beyond a purely structural approach (i.e., measuring patch size and other physical attributes) to incorporate functional aspects of species' ecology and behavior, such as dispersion patterns, responses to patches of varying habitat quality, and other biological characteristics (Tischendorf and Fahrig 2000; Turner et al. 2002; Turner 2005; Hilty et al. 2006). Models which include aspects of functional connectivity are thought to be more informative than those which do not, as they account not only for the structure of a landscape, but also the response of organisms to that structure (e.g., Belisle 2005; Baguette and Van Dyck 2007). However, despite the often extensive dispersal and migration of fish within stream networks, most models of aquatic fragmentation lack data regarding functional connectivity (Fullerton et al. 2010). This is likely attributable to the relative novelty of aquatic connectivity as a field of study, but may also be due to the costs of incorporating detailed biological data into models, with increasing complexity that can potentially limit application to very specific scenarios and require significantly more resources to obtain model parameters (Calabrese and Fagan 2004).

As with terrestrial landscapes, if the connectivity of aquatic networks is assessed without including functional data, the results obtained may not provide the most informative evaluation of fragmentation for the ecosystem and/or species in question (Sheer and Steel 2006; Fullerton et al. 2010; Kemp and O'Hanley 2010). The DCI, for example, assumes that all stream segments of the same length are of equal value to fish when modeling connectivity. It is reasonable to expect, however, that patch quality differs throughout stream networks, given that the physical, chemical and biological attributes of stream segments can vary from headwaters to outlet (Vannote et al. 1980; Benda et al. 2004; Fausch et al. 2002; Poole 2002; Lowe et al. 2006; Thorp et al. 2006).

Such heterogeneity is reflected in the distribution and movement patterns of stream fish during different phases of their migration and life cycles (Schlosser 1991; Padgham and Webb 2010). While structural approaches may be adequate for assessing fragmentation effects on localized, non-migratory species (O'Hanley 2011),they may not be providing the most ecologically accurate assessments of connectivity for migratory species such as salmonids which aggregate and disperse largely based on habitat quality (Sheer and Steel 2006).

Aquatic ecologists have long recognized the influence of habitat quality on the distribution of fish within stream networks, and consequently have used these relationships to build predictive distribution models for many species (e.g., Joy and Death 2000; Kennard et al. 2006; Spens et al. 2007; Perkin and Gido (in press)). These models can be crucial for conducting population assessments, evaluating habitat loss impacts and studying species distributions in large systems where field surveys can be expensive and logistically difficult (Joy and Death 2000; Olden et al. 2002; McCleary and Hassan 2008). However, until the recent recognition of aquatic fragmentation as a serious risk to aquatic species and the subsequent development of connectivity metrics for stream networks, measures of connectivity were not generally included in habitat models (Gillette et al. 2005).

A metric often used in predictive habitat models of fish occurrence is biomass – the total weight of fish present in a given area, population or stock of interest (e.g., Cote 2007; Warren et al. 2010). Cote (2007) developed a habitat model which predicted the biomass of salmonids in stream networks in Newfoundland, Canada – the same systems where initial simulations of the DCI were conducted (Cote et al. 2009; Bourne et al.

2011). While Cote's (2007) stream habitat model accounts for the associations of salmonids with various structural habitat characteristics, it includes no measure of connectivity within stream networks – a parameter that could improve predictive power by more accurately modeling the dispersal of fish within the system by accounting for movement barriers (Spens et al. 2007; Dunbar et al. 2011; Flitcroft et al. 2012). I predict that adding the parameter of connectivity, obtained from the DCI, will improve the predictive power of Cote's (2007) habitat model of biomass by accounting for stream network connectivity when modeling fish distribution.

To observe the effects of converting the DCI from its initial form as a structural index (hereafter the DCI-s) to a functional one (DCI-f), I modified the index's connectivity equations to include a measure of habitat quality for adult fish; specifically, biomass estimates derived from Cote's habitat model (2007) for brook trout (*Salvelinus fontinalis*), one of the study species used in the previous DCI simulations (Cote et al. 2009; Bourne et al. 2011). I predict that connectivity values produced by the DCI-s and DCI-f will differ, as stream segments in the functional scenario are represented in the index not simply by their length, but also by their estimated biomass, a parameter which varies according to habitat quality and can be different for stream segments of the same length.

The DCI-s did not account for the increased habitat availability associated with small ponds located within the stream networks because these were represented by a simple length measurement (a line drawn through the pond connecting its associated stream segments). Yet these ponds ranged from less than 900 to more than 120,000 m^2 in surface area, potentially representing a significant amount of habitat for native fish. As highlighted by Eros et al. (2011), small water bodies such as these are often closely associated with stream networks or, as is the case in TNNP, are embedded within them (i.e. streams flowing in and/or out of the pond). For this study, including the habitat represented by these ponds in the DCI is important as brook trout in the study area utilize ponds (O'Connell and Dempson 1996; Cote et al. 2011) as important rearing areas (O'Connell and Dempson 1995). To incorporate the ecological value of ponds, I used a lacustrine habitat model that was based on surface area (Cote et al. 2011). I predict that DCI-f values, obtained when pond biomass estimates are included in stream network connectivity calculations will differ greatly from both the DCI-s and the DCI-f values produced without pond data, as the size of ponds (surface area) was not represented in the previous models and thus the value of ponds as habitat for the study species may have been greatly underestimated.

Though habitat features do play a role in salmonid dispersal and influence in-stream movement, it is likely that patch size is the most important parameter in assessments as it may dictate the likelihood of a fish being in that patch (given that other, smaller patches are equally accessible) and is a determinant of dispersal distance (Isaak et al. 2007; Hitt and Angermeier 2008; O'Hanley 2011). Therefore in stream networks, segment length (*l*) may be the ultimate determinant of connectivity as each segment represents a habitat patch which is isolated from the entire network by barriers and terrestrial features on either side. Segment length is still included in DCI-f calculations (when determining biomass) but potentially provides more informative results. I predict that while the connectivity values produced by the DCI-s and the DCI-f will differ within the study area, the results of the two will be correlated and display the same overall trends.

3.3 Methods

3.3.1 Study area and species

To test the effect of adding the functional component of biomass to the DCI, I applied the DCI-f to 8 stream networks in TNNP. Within the park's 400 km^2 area there are over 40 catchments of varying size, all composed of stream networks and small, shallow ponds which are characterized by low primary productivity and species diversity (Cote et al. 2011). Typical of the boreal ecosystem in which they are found (Eros et al. 2012), these ponds are largely embedded in their associated stream networks. Of the 40 catchments, 15 contain road culverts and have previously been evaluated using the DCI (Cote et al. 2009; Bourne et al. 2011) and 8 of these have also been surveyed using electrofishing in the past 10 years (catchments E, H-L and N-O, Fig 3.1). I mapped these stream networks using methods outlined in chapter 2. I focused on development of the DCI-f in these 8 catchments since the biomass equations used had been derived directly from field data measured in these stream networks. In addition, these catchments represented a range of sizes and spatial complexities in terms of the number of barriers, and size and distribution of ponds. Brook trout were used as a model species due to their prevalence in the area and the availability of predictive habitat models for this species (Cote 2007; Cote et al. 2011).

3.3.2 Estimating brook trout biomass of stream segments

Stream (wetted) width is a simple but strong predictor of brook trout biomass per unit area in the streams of my study area (D. Cote 2007 To determine the wetted width of stream segments, something which would be labor intensive and impractical in the field, I used a dataset of 55 wetted width measurements obtained during park culvert surveys in 2007 and 2008 (detailed in chapter 2; Bourne et al. 2011), as well as measurements taken by park staff during electrofishing surveys in 2006 and 2007. I plotted the coordinates of each measurement on the park map and visually determined stream order, resulting in a set of two variables for each data point (stream order and wetted width). I then ran an ANOVA analysis using R statistical software (v.2.7.1) and found a significant relationship (p=<0.001) between stream order and wetted width.

Using these stream data, I estimated the mean wetted width of first, second and third order streams in my study area (Table 3.1). Because stream order could easily be determined by viewing the map, I was able to assign a wetted width value to any stream segment in my study area which had not been directly measured in the field. Once this was done, I estimated brook trout biomass for all segments by first multiplying segment length by average wetted width to obtain a surface area estimate (m^2), and then multiplying that value by the estimated biomass (g/m^2) – providing a total brook trout biomass estimate for the segment (total weight in g). Biomass estimates were taken from Coté (2007) who used an allometric approach (Randall 2002) to account for size varioan in production-to-biomass ratios.

3.3.3 Estimating brook trout biomass of ponds

Cote et al. (2011) found that both the surface area of Newfoundland ponds and the Basin Permanence Index (BPI) - the ratio of basin volume to shoreline length, are significant predictors of brook trout biomass (r^2 = 0.53 and 0.51 respectively). To calculate the brook trout biomass of ponds within my study area for inclusion in the DCI-f, I applied Cote et al.'s (2011) model, using surface area as the independent variable ($B = -0.54*SA + 2.71$, where B is brook trout biomass and SA surface area). I chose to use surface area rather than BPI as it could easily be measured using GIS, where BPI requires depth data that was unavailable for all water bodies.

3.3.4 Model selection

I tested whether adding connectivity would improve Cote's (2007) model for predicting stream segment biomass using an information theoretic approach. I computed multiple general linear models (GLMs) with R statistical software (v. 2.7.1) that combined the parameters of stream network dendritic connectivity (DCI_D) for diadromous fish, segment stream order (SO), and wetted width (WW) in every possible combination (Table 3.2), with measured biomass values as the independent variable. These biomass measurements were obtained from Cote 2007, who conducted electrofishing surveys of park stream segments in 2003 and 2005. Though DCI values are computed for entire stream networks, I felt that using DCI_D would be a good model parameter for this analysis as the electrofishing points where biomass measurements were obtained for these segments were located below barriers (Fig. 3.1) – in the first stream segment, where DCI_D is calculated from, thus making them comparable across systems. The data was found to have overdispersion, differing from the expected Poission distribution, possibly due to the aggregation of fish. To compensate I compared models using $QAIC_c$ which accounts for overdispersion present in the data.

3.3.5 Calculating functional DCI values

Previously, the DCI equations (Saura and Pascual-Hortal 2007; Cote et al. 2009) had been calculated using the structural parameters of stream network length (L), stream segment lengths (*l*), and barrier passabilities (*p*). To calculate a more functional, ecologically relevant DCI, I replaced *L* with total estimated stream network biomass (*B)*, and *l* with the estimated stream segment biomass (*b*). Estimates of barrier passability had been previously calculated using various methods (chapter 2; Bourne et al. 2011) in order to investigate the effects of culvert assessment method. For this analysis I used passability values which I had obtained using FishXing software (V.3 beta), which were thought to have given the most accurate results (see Chapter 2. The values were based on a 15 cm brook trout during the migration period of May to December, which corresponded with the time period of electrofishing surveys from which biomass data were taken.

Values of both potamodromous connectivity (based on a fish moving between all segments in the system) and diadromous connectivity (based on a fish moving from the most downstream segment to any upstream segment) were calculated for all stream segments twice – once using biomass estimates of stream segments only, and a second time with biomass estimates for ponds included in stream segment biomass estimates. A prioritized list was also produced for each stream network which provided DCI values for the system when individual barriers were restored to fully passable. I compared the results of the DCI-s to the DCI-f using a Spearman's rank correlation coefficient for both potamodromous and diadromous simulations.

3.4 Results

3.4.1 Biomass predictions

Based on the $QAIC_c$ scores, the biomass model results showed that of the models compared (Table 3.2), the one which included wetted width, stream order and a interaction between the two as variables was the best predictor of biomass (QAIC weight 0.351) – which was not surprising given the correlation between stream order and wetted width. This was followed by the model which included wetted width, stream order and DCI ($\Delta_{t}QAIC_{c} = 0.195$ QAIC weight 0.319) and then stream order alone ($\Delta_{t}QAIC_{c}$ 0.482; weight 0.276).

After calculating the biomass of all stream segments, I added estimated pond biomass. This increased the total biomass estimates by more than 80% in 7 catchments, with one (catchment I) increasing by 175%. The only catchment which showed little change (an increase of 2%) was catchment L, which only has 3 very small ponds within its stream network.

3.4.2 DCI-f assessments

The diadromous connectivity values for 7 of 8 evaluated catchments in TNNP increased (ranging from 6 to 60%) when stream segment biomass was substituted for segment length; the connectivity of the remaining catchment (O) decreased by 11% (Fig. 3.2, Table 3.3). Potamodromous connectivity values increased for 3 catchments (ranging from 1 to 24%) when calculated using DCI-f versus DCI-s, where the other 5 catchments showed decreases ranging from 7 to 24% (Fig. 3.2, Table 3.3).

When pond trout biomass was also included in the DCI-f calculations the diadromous connectivity, compared to DCI-s values, decreased for 6 catchments, 5 of which had decreases of 50% or more. Two catchments showed increases, but these were less than 4% (Fig. 3.2, Table 3.3). In contrast, the potamodromous connectivity increased for most catchments when pond brook trout biomass was included in the DCI-f model, with 7 of 8 catchments showing increases ranging from 2 to 76%. In the single catchment where connectivity decreased, the difference was only 3% (Fig. 3.2, Table 3.3).

Spearman's rank correlations between DCI-f and DCI-s values showed both indices to be highly correlated in all scenarios (Table 3.4).

3.4.3 Culvert restoration prioritizations

For 7 of 8 catchments, the same culvert provided the largest gains to connectivity when made fully passable for all three DCI scenarios (structural, functional with and without ponds). In addition, for these 7 catchments, the gains provided were all of the same magnitude (within 2% of DCI value with no restorations). In one catchment (K) the 'key culvert' which provided the greatest connectivity gains was the same for the DCI-s and the DCI-f without ponds, but was different for the DCI-f with ponds (Table 3.5).

3.4.4 Effects of pond size and position

When the total biomass of ponds per catchment was compared to the change in DCI (structural to functional, and functional without ponds to with ponds), no significant relationship was found (r^2=0.09, p=0.47 without ponds and $r^{2=}$0.02 p= 0.39 with ponds) (Fig. 3.3). In catchments where DCI$_D$ decreased by more than 50% from the structural model to functional with ponds, there were either multiple small-medium sized ponds, or a few comparatively large ponds upstream of barriers (Fig.3.4). For those catchments where only slight DCI$_D$ decreases were observed with the addition of ponds, ponds upstream of barriers were small or ponds were also found downstream from barriers. In the cases where DCI$_D$ increased with the addition of ponds, the ponds were quite small and in the case of catchment O, upstream of a barrier with high passability (passability = 0.75). In the case of potamodromous connectivity, all catchments that saw an increase in

DCI (from structural to functional with ponds) of 25% or more had multiple or large ponds located in their largest segments. For catchments that saw increases in DCI less than 25%, ponds were smaller and more widely distributed among segments. In catchment L where the DCI value decreased slightly, there were only a few very small ponds in the largest segment (Fig. 3.4).

3.5 Discussion

As with earlier studies of fragmentation in terrestrial landscape ecology, most initial models of aquatic connectivity have been focused on structural habitat features (Fullerton et al. 2010). However, purely structural models may not adequately account for the influences that stream features can have on the dispersal and distribution of aquatic organisms (e.g., Lowe et al. 2006, Grant et al. 2007), thus potentially limiting their ability to provide meaningful ecological assessments of fragmentation impacts. The DCI is an example of an aquatic connectivity model which, while effectively accounting for the placement of barriers and the dendritic nature of stream networks (Cote et al. 2009), bases its assessments on structural features alone. By combining the DCI with a habitat model for Newfoundland brook trout, I was able to verify my prediction that the model's estimates of biomass would be improved with the addition of connectivity estimates. In addition, by including estimates of biomass in the DCI, I was able to add a functional component to measures of aquatic connectivity.

My results supported my prediction that the DCI-f would give different connectivity values from the DCI-s. Through this analysis I also confirmed that the inclusion of ponds would further alter the results of the DCI-f, as these water bodies can at times greatly increase the biomass estimates of stream segments within the model. This inclusion of ponds is important as we know that in Newfoundland freshwater species often utilize both pond and stream habitat throughout their life cycles (Gibson et al. 1993; Hutchings 1986); thus including ponds in DCI-f estimates may be essential to obtaining relevant connectivity estimates. Also as predicted, all three versions of the DCI showed the same overall trends in connectivity for the study area and, in most cases, the prioritization of barriers for removal did not change. This demonstrated that in this study area, though the inclusion of functional data did change connectivity estimates, the overall trends and management recommendations generally remained the same regardless of input parameters. This is particularly important when it comes to the allocation of funding and resources for the restoration of connectivity, as the structural index requires less intensive surveys. Though it is always advisable to take an approach which incorporates as much ecological data as possible, the results from TNNP indicate that in this specific case the structural index alone may still provide an informative assessment of stream fragmentation in the absence of functional data. However, it should be noted that there was a potential limitation with the calculation of the DCI-f for TNNP in that stream segment biomass estimates were highly proportional to the stream segment length values used in the DCI-s. Had the biomass model been formulated with different metrics, or another habitat feature used to create a functional index, larger discrepancies may have been observed between the DCI-s and the DCI-f. This is further exemplified by the larger differences observed when pond biomass was added to the DCI-f, a parameter which was not derived from those used in the DCI-s.

Using an information theoretic approach, I was able to demonstrate that the inclusion of DCI-derived connectivity values in the brook trout biomass model developed by Cote (2007) helped to improve its predictive power, as the model including DCI values was one of the most highly weighted in the analysis. This was expected, as including a measure of fragmentation added another aspect of habitat suitability, providing further detail in the model regarding the structure of the stream network and accessibility of preferred habitat patches for a fish species that disperses throughout steam networks. The potential improvement to predictive habitat models through the addition of connectivity measures has been increasingly recognized by aquatic ecologists, as the issue of fragmentation comes to the forefront (e.g., Spens et al. 2007; Perkin and Gido (in press)). These results also demonstrate a need for caution on the part of aquatic ecologists when using habitat models that were derived in the absence of connectivity data, in particular if those models are being applied to fragmented stream networks, as they may not provide the most accurate model of fish distribution.

The inclusion of brook trout biomass in the DCI provided a functional aspect to the index, allowing for connectivity modeling that accounted not only for the potential movement of fish upstream (in the diadromous case) and throughout the network (potamodromous case) as was done with the DCI-s, but also the distribution of the study species within stream networks based on habitat preference. An advantage to using Cote's (2007) habitat model to derive a functional parameter (biomass) was that the parameters required for the model could be easily obtained or derived from stream network maps using GIS – a strategy which has been used in other studies of aquatic connectivity (e.g., Hitt and Angermeier 2008; McCleary and Hassan 2008; Poplar-Jeffers et al. 2008; Flitcroft et al. 2012) and requires substantially less time and effort than conducting field surveys of entire stream networks to measure habitat parameters in individual stream segments.

There were some issues with Cote's (2007) brook trout model which may have affected the accuracy of my stream segment biomass estimates. Specifically, most of the study systems were fragmented by road culverts at the time when electofishing was done, meaning that the model provided biomass estimates for the networks in the fragmented (versus natural) state, when fish dispersal was potentially limited by movement barriers. The DCI is meant to provide estimates of connectivity and assessments of fragmentation impacts based on the dispersal of fish through a fully connected stream system without barriers, so using biomass estimates that came from a network where fragmentation had already occurred likely did not give accurate estimates of fish presence in a natural system to compare with the current fragmented state. To more accurately model functional connectivity based on habitat associations and dispersal, efforts should be made to derive some estimate of fish distribution in the absence of barriers and fragmentation. A recommended approach to doing this is to survey reference networks which are structurally and ecologically similar to study sites, but absent of barriers (i.e., fully connected), for comparison purposes (Joy and Death 2000; Kennard et al. 2006). However, such pristine systems are rare and the cost involved in surveying them may be uneconomical, in practice it would be more reasonable for ecologists to instead apply the DCI while considering the potential bias involved when working on fragmented networks.

A second issue with the biomass estimation was that the majority of electofishing sites used to derive the stream habitat model were in the segments nearest outlets, often below barriers. Alternatively, habitat downstream may have been more or less preferable than headwaters, due to natural heterogeneity in stream reaches (Bult et al. 1998; Lowe et al. 2006; Hitt and Angermeier 2008) or changes caused to physical and biological stream elements by the culverts themselves (e.g., Roni et al. 2002; Lachance et al. 2008; Doehring et al. 2011). If this was the case, the assumption that the observed habitat relationships were applicable across the entire stream network may not have been correct. Ideally samples should have been taken from first, second and third order stream segments throughout the network to give a more comprehensive representation of biomass and habitat associations (Mahlum in review.). In addition, the biomass estimations did not account for the size or life stage of the fish, which plays a role in habitat selection and distribution (Gibson et al. 1993). However, for the purposes of this simulation the biomass estimates were adequate to demonstrate the functionality of the index, as the purpose of this study was not to quantify fish abundance but rather demonstrate the potential improvements to structural connectivity measures by adding a functional parameter.

As predicted, DCI-f values differed from those calculated using the DCI-s, as the weight of habitat patches (stream segments) in the model was now not only determined by length, but also by estimated brook trout biomass, via stream order. In the case of diadromous connectivity, the DCI-f value of all but one catchment was higher than that of the DCI-s, reflecting the structure of the stream networks and distribution of habitat above and below barriers in the study area. All of the catchments in the study site were bisected by a major highway with most crossings consisting of road culverts – potential movement barriers for brook trout. Although the catchments had differing sizes and spatial arrangements of segments, the location of the highway meant the majority of stream networks had at least one culvert in their lower reaches. This meant that in those networks diadromous brook trout may have been unable to move upstream and access the majority of most suitable habitat. This was reflected in the DCI_D values which were generally low in both the functional and structural scenario, as the DCI_D is based on the potential movement of a fish from the furthest downstream segment to all those above it. Had the highway been located further from the coastline and bisected the networks nearer the headwaters, the DCI_D would have likely produced much higher connectivity values to reflect the fact that the majority of habitat was readily accessible from downstream.

The increases observed in DCI_D values for the functional scenario illustrate the effect that accounting for habitat associations can have on connectivity assessments. Though the majority of habitat was upstream of barriers in most catchments in the study area, the downstream portions were typically highly branched with a large proportion of first and second order segments, which were, according to the habitat model (Cote 2007), of the highest value to brook trout (Cote 2007). When segments in the DCI are weighted by stream order, the downstream segments became proportionately more valuable to diadromous fish than they were in the DCI-s when only length was considered. In ecological terms, the functional index accounts for the fact that primary habitat is not always evenly distributed throughout stream networks (i.e., they are heterogeneous) and that reaching the furthest upstream reaches may not be as important to diadromous brook trout in this system as is assumed in the DCI-s.

One catchment did differ from the others when the DCI-f was applied, with its connectivity value decreasing rather than increasing as it had in the rest of the study area.

This catchment differed structurally from the others in that its only barrier was located on a side branch, rather than the main reach, and thus it did not prevent access to the majority of the upstream habitat. When this catchment was assessed using the functional index, the value of that side branch received a comparatively lower score than it had in the structural case, meaning that the small portion of inaccessible stream had even less value to brook trout in the functional scenario. This catchment highlights the fact that the results of the DCI, and connectivity assessments in general, are highly dependent on the spatial arrangement of stream segments, the relative habitat quality of these segments, and the location of barriers within them (Fagan 2002; Cote et al. 2009; Fullerton et al. 2010).

Unlike the diadromous simulations, adding a functional parameter to the potamodromous DCI did not produce a clear trend when compared to results obtained using the structural DCI. Potamodromous connectivity assessment is based on the ability of fish to move between any two segments in the stream network, not exclusively upstream as was the case for diadromous simulations. This means that when evaluated using the DCI-s, the potamodromous connectivity of stream networks increases with the size (total length) of the largest segment; i.e., the larger the proportion of the stream network that is fully connected, the higher the connectivity value, regardless of whether that large patch is up or downstream of barriers in relation to the stream outlet. In the catchments where increases were observed, the largest connected habitat patches were highly branched with large proportions of first order segments – the more preferable brook trout habitat in the stream habitat model. For the remaining catchments, the most highly branched segments were separated from the largest patches by barriers, thus decreasing DCI values and reflecting the inability of the fish to access areas of potentially high value habitat.

When conducting assessments for the purpose of barrier removal and mitigation with a limited budget, it may still be advisable to always aim for increasing the size of the largest patch to make more habitat available to potamodromous fish (Cote et al. 2009; O'Hanley 2011), as it has been suggested that patch size is the most important determinant of connectivity, not habitat quality (Isaac et al. 2007). However, as with heterogeneous terrestrial habitats, stream networks are not always easily divided into habitat patches. For this evaluation I am referring to the area between barriers as a habitat patch, but in reality one large area such as this could contain multiple smaller patches (Eros et al. 2012) – for example, a collection of first and second order segments, or patches within those segments consisting of areas with differing physical and chemical properties. This emphasizes the need to consider both the scale and the habitat utilization of the target species during assessments, as generalizing could lead to incorrect assumptions about the definition of a patch and the effects of fragmentation.

In previous simulations of the DCI (Cote et al. 2009, Bourne et al. 2011), the presence of ponds within stream networks was largely unaccounted for, despite their importance as brook trout habitat (O'Connell and Dempson 1996), their influence on process within the stream network (Gibson 2002), and the fact that in some catchments they compose a large proportion of the habitat by both water volume and surface area. By including the brook trout biomass estimates of ponds in the DCI-f, I was able to account for their influence on fish distribution and add to the relevance of connectivity scores by including all available habitat in the model proportionately (versus in the past simulations where ponds were merely represented by a centerline drawn through them and included in stream segments). The inclusion of ponds in the model changed connectivity values for all catchments, as predicted, with values differing from both the DCI-s and DCI-f scenario when pond biomass was not included.

As with stream segments and barriers, the spatial arrangement of ponds within catchments had a large impact on connectivity scores. No significant relationship was found between the total biomass of ponds in each catchment and the change in DCI resulting from their addition, showing that the observed changes were not simply attributable to the increased habitat size that resulted from using pond surface area to calculate connectivity. Rather, the changes observed were a result of the combination of the location, number, and size of ponds. The changes in DCI-f with the addition of ponds is of particular interest in TNNP systems as the pond biomass model (Cote et al. 2011), unlike that for stream segments (Cote 2007), did not use a parameter already included in the DCI-s and thus added biological information that had not in any way been present in the DCI-s.

For the diadromous simulations, connectivity values dropped considerably from the values obtained using both the DCI-s and the DCI-f (with only stream biomass) for more than half of the catchments when pond biomass was included in the model. In these cases, all or most of the ponds associated with the stream network were upstream of barriers and some of the largest ponds in the study area were found within these catchments. This increased the overall biomass estimates upstream of barriers, giving the segments more weight in the model and driving the DCI_D value down as fish migrating upstream could not access these potentially valuable habitat patches. In the remaining catchments where decreases in connectivity were less significant, the ponds were fewer, smaller and well dispersed throughout the catchment; so though the entire biomass estimate for the catchment increased, the relative values for the up and downstream areas remained about the same and caused only slight changes in connectivity. Again, the only catchment that differed from the others was the one in which the only barrier present blocked access to a small side branch. In this scenario, the connectivity increased when pond biomass was added and the value was the highest of the three obtained due to the fact that most of the ponds were located in the large, accessible segment and the relative value of that habitat patch was much higher than that of the small disconnected side branch.

When pond biomass was incorporated into the DCI_P calculations, an overall trend of increased connectivity was observed. In catchments where there were significant increases, most or all of the ponds in the stream system were located within the one large segment and the ponds made up a comparatively large amount of habitat in relation to stream segment lengths. In those catchments where connectivity increases were not as large, ponds tended to be fairly small and widely distributed throughout the stream segments, minimizing their impact on overall biomass estimates for the segments and thus not shifting the connectivity values as the segments were still comparatively similar in terms of habitat value for brook trout. However, it should be noted that ponds and streams may each be required at different life stages depending on the species (e.g., Gibson et al. 1993; O'Connell and Dempson 1996), something that should be considered when calculating DCI values.

Despite the changes observed in connectivity values for all 8 catchments when functional data were added to the DCI, the prioritization of barriers for removal only changed in one case. In this catchment, the same barriers were ranked as first and second priority for the DCI-s and the DCI-f without ponds, but when pond biomass was added the two switched position on the prioritization list. This was likely because there was a large pond directly upstream of the barrier which gave its upstream segment a much larger value than it had had based on length alone, thus increasing its value in the model. The catchment in which these barriers were located was the largest and most complex in the study system, with multiple barriers of varying passability. These results give the overall suggestion that adding functional data to the DCI may not have a large impact on management decisions in regards to barrier replacement, as in most cases the 'key culvert' which would provide the greatest gains in connectivity when restored did not change between scenarios. However, the fact that a change in prioritization was observed in the largest and most complex catchment may demonstrate that in systems with a high degree of spatial heterogeneity (in terms of both habitat and barriers), changes in DCI input parameters may have greater effects when compared to smaller, simpler systems. This is a possibility that will require further testing using larger and more diverse stream networks. In addition, the DCI-f (both with and without ponds) has biomass information derived from a model which produces results which are derived from structural data, as discussed above. Applying a version of the DCI-f derived from different habitat indices and models may produce more widely varying results in terms of culvert prioritization.

The correlation between the different DCI models (structural, compared to functional both with and without ponds) was confirmed for both the potamodromous and diadromous case using the Spearman's rank coefficient. This test showed that the closest correlation was between DCI results obtained using the structural model and stream biomass as would be expected, given the model parameters. The coefficient was slightly lower when ponds were added to the segment values – but still significant. This demonstrated that the overall results for TNNP stream networks in terms of connectivity values obtained using the DCI were similar regardless of which DCI model was used. This supports the idea that while functional data may help improve the DCI, the structural index will still provide meaningful results for managers and ecologists.

As with any habitat, stream networks can be extremely complex, both structurally and functionally. Each species within the system is impacted by processes occurring from headwaters to outlets, and alteration of that habitat at any point in the stream network may have far reaching impacts (Bult et al. 1998; Lowe et al. 2006; Cote et al. 2009; Flitcroft et al. 2012). In addition, many aquatic species have diverse life histories, migrating and dispersing throughout catchments based on ecological, temporal and physiological factors (Faush et al. 2002; Hitt and Angermeier 2008). The recognition of this complexity has led to the suggestion that stream connectivity models should attempt include both the network structure of the habitat and aspects of species and habitat ecology (Sheer and Steel 2006; Fullerton et al. 2010). While this study demonstrated the potential to improve aquatic connectivity estimates produced from the DCI through including functional data that takes habitat quality into consideration, it also showed that the structural DCI may provide meaningful assessments of stream fragmentation and barrier prioritizations based on structural data alone in some cases. While it is always the best practice when modeling ecological processes to include as much significant data as possible, when managers and ecologists are faced with limited resources, taking a more simplified, structural approach, while applying the DCI may still provide meaningful results, when interpreted using ecological knowledge.

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Table 3.1: Mean wetted width and estimated brook trout biomass (from Cote 2007) for 1st, 2nd and 3rd order streams in Terra Nova National Park, Newfoundland, based on ANOVA analysis 55 park stream segments

Stream order	Mean Wetted Width (m)	Std. Deviation	Estimated Brook Trout Biomass (g/m^2)	Std. Deviation
1	1.28	0.6	4.22	1.1
2	2.5	1.0	2.05	0.8
3	4.57	1.5	1.05	0.4

Table 3.2: $QAIC_c$ values for multiple general linear models to predict brook trout biomass in Terra Nova Park streams using wetted width (WW), stream order (SO), and dendritic connectivity index values (DCI) as model parameters

Model	**c**	**loglik/c**	**K**	**$QAIC_C$**	**delta-i**	**exp(delta-i)**	**wei**
WW+SO+WW*SO	3.64	-8.87	3	24.95	0.000	1.00	0.3
WW+SO+DCI	3.477	-8.97	3	25.14	0.195	0.91	0.3
SO	3.22	-11.62	1	25.43	0.482	0.79	0.2
WW+DCI	2.6	-12.10	2	28.77	3.830	0.15	0.0
WW+SO	2.15	-15.34	2	35.26	10.313	0.01	0.0
WW+SO+DCI+WW*DCI+SO*DCI	2.4	-12.80	5	38.93	13.984	0.00	0.0
SO+DCI	2	-18.64	2	41.85	16.902	0.00	0.0
DCI	1.98	-20.18	1	42.54	17.591	0.00	0.0
WW+SO+DCI+WW*SO+WW*DCI+SO*DCI	2.11	-14.07	6	45.08	20.137	0.00	0.0
WW+SO+DCI+WW*SO+WW*DCI	1.655	-18.66	5	50.66	25.710	0.00	0.0
WW+DCI+WW*DCI	1.322	-23.62	3	54.44	29.494	0.00	0.0
WW	1.26	-26.56	1	55.31	30.365	0.00	0.0
SO+DCI+SO*DCI	1.45	-25.16	3	57.53	32.581	0.00	0.0
WW+SO+DCI+WW*DCI	1.22	-25.40	4	60.90	35.953	0.00	0.0
						2.85	1

Table 3.3: Percent change in DCI connectivity estimates associated with the addition of functional data (brook trout biomass) for stream segments and ponds for 8 catchments in Terra Nova National Park

	Potamodromous case		Diadromous case	
Catchment	Percent change from DCI-s when stream biomass included	Percent change from DCI-s when stream and pond biomass included	Percent change from DCI-s when stream biomass included	Percent change from DCI-s when stream and pond biomass included
E	0.7	15.5	44.0	-94.4
H	-24.1	64.1	15.0	-82.3
I	-11.2	65.3	59.2	-74.2
J	24.3	76.2	29.8	-58.2
K	14.9	2.6	11.4	-3.4
L	-7.5	-3.5	6.1	2.4
N	-12.9	51.4	24.3	-87.9
O	-18.5	6.6	-11.4	3.0

Table 3.4: Spearman's rank correlation results for comparisons between connectivity values produced for TNNP catchments using the DCI-s and DCI-f (with and without ponds) for the diadromous and potamodromous scenarios

DCI models compared	Spearman's rank correlation coefficient	P value
$\mathrm{DCI_D}$-s and $\mathrm{DCI_D}$-f (no ponds)	0.976	<0.001
$\mathrm{DCI_P}$-s and $\mathrm{DCI_P}$-f (no ponds)	0.88	0.007
$\mathrm{DCI_D}$-s and $\mathrm{DCI_D}$-f (with ponds)	0.92	0.002
$\mathrm{DCI_P}$-s and $\mathrm{DCI_P}$-f (with ponds)	0.83	0.015

Table 3.5: Projected changes in connectivity in catchment K for the DCI-s and DCI-f (with and without ponds) associated with culvert restorations. Shaded values represent those provided by the culvert which would create the greatest gains to connectivity in each scenario when removed or restored to fully passable (passability = 1)

	DCI-s		DCI-f no ponds		DCI-f with ponds	
restored culvert (pass=1)	DCI_P	DCI_D	DCI_P	DCI_D	DCI_P	DCI_D
none	**57.0**	**71.3**	**65.5**	**79.5**	**58.5**	**68.9**
ah	82.6	89.9	72.5	83.9	63.1	76.4
ai	79.6	88.2	67.3	80.4	58.8	69.1
aj	81.1	89.1	68.0	81.0	58.9	69.2
ak	80.8	88.9	68.6	81.4	59.1	69.3
al	89.9	94.8	75.4	86.5	60.5	70.4
am	79.3	88.0	65.5	79.5	58.5	68.9
an	79.4	88.1	71.5	83.2	59.6	69.7
ao	81.3	89.2	65.8	79.6	58.5	68.9

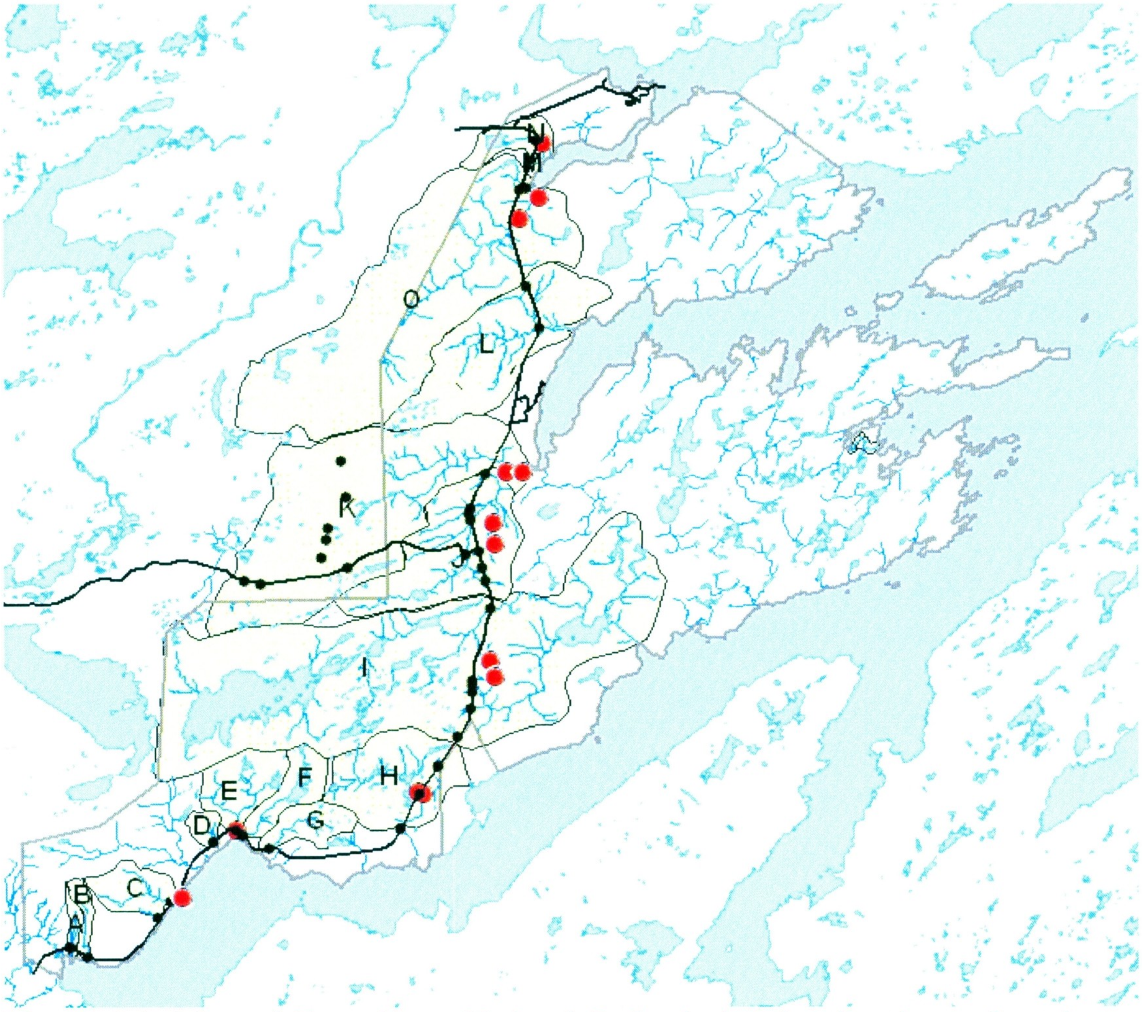

Figure 3.1: Map of Terra Nova National Park, depicturing locations of catchments (denoted by letters A to N), stream networks, ponds, major roads (black lines), culverts (black points) and electrofishing locations used in model analysis (red circles).

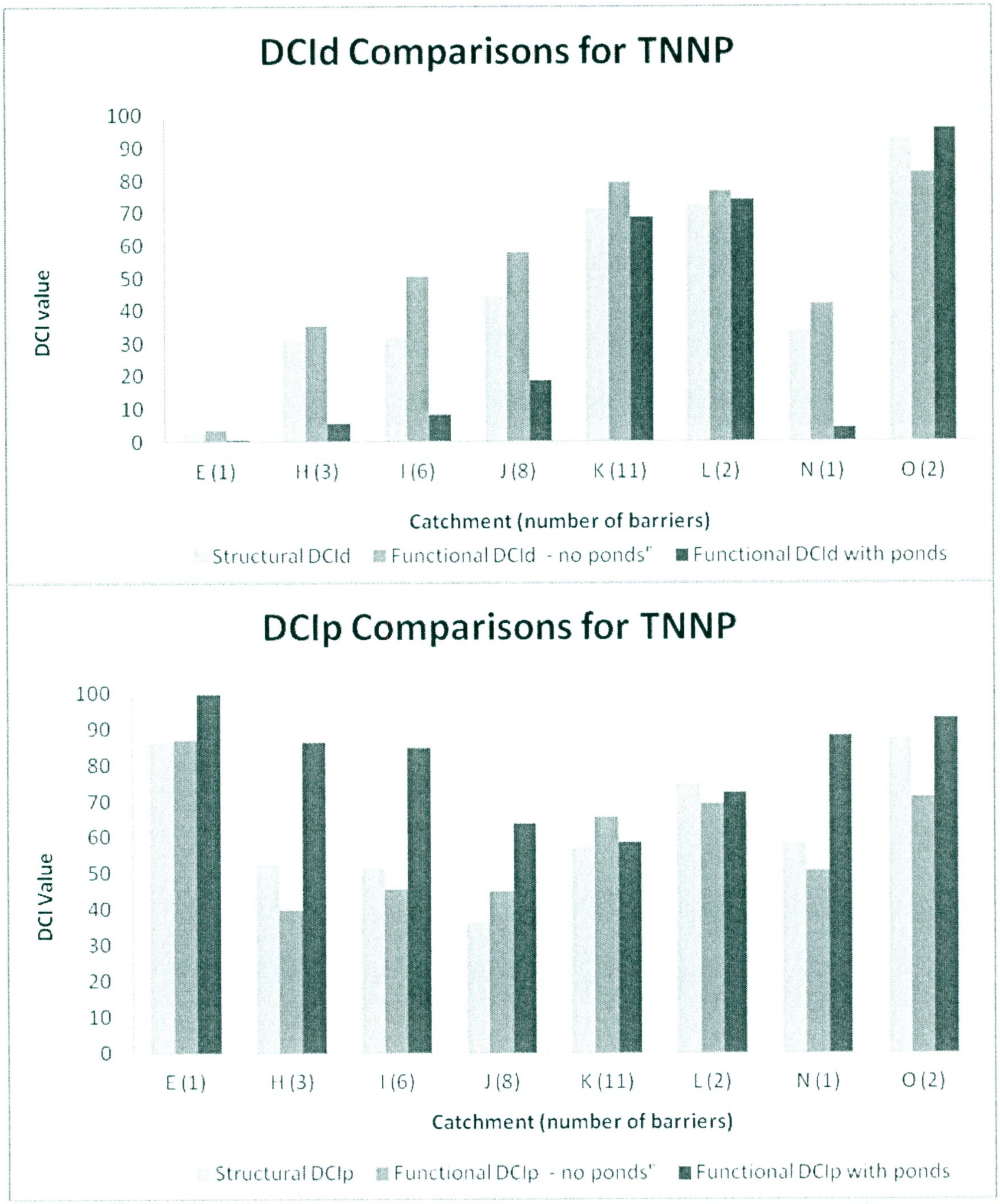

Figure 3.2: Comparisons of connectivity values (diadromous above, potamodromous below) for 8 TNNP catchments, calculated using DCI-s and DCI-f (with and without ponds)

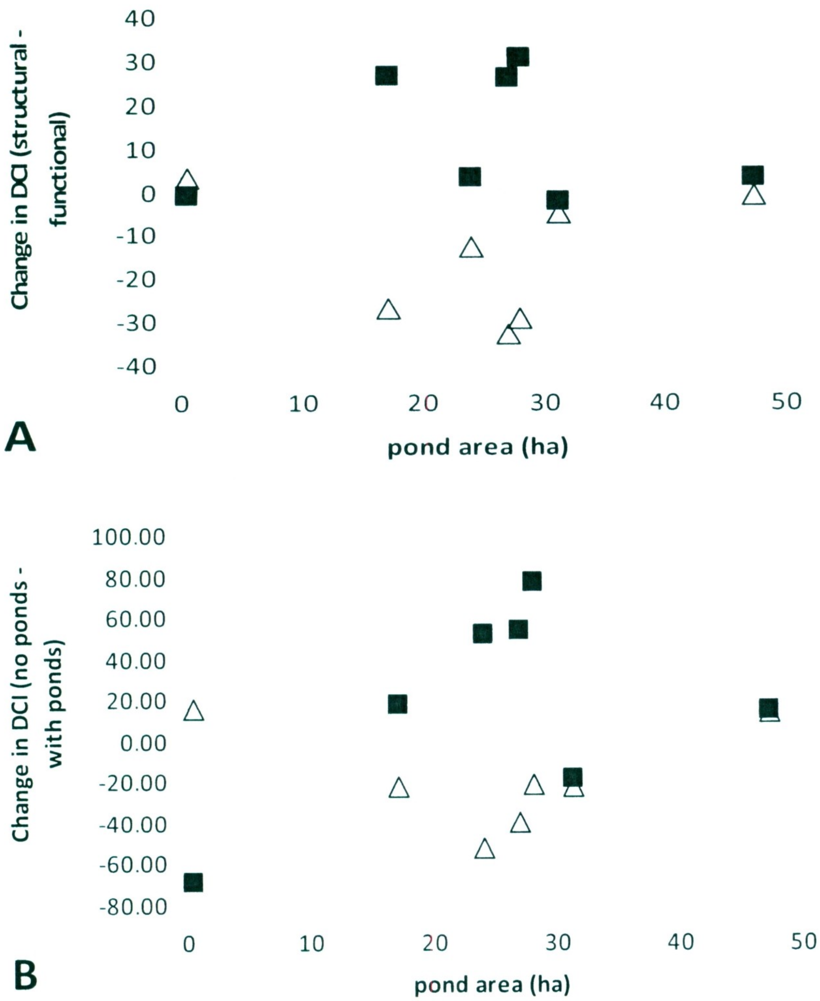

Figure 3.3: The effect of total pond surface area on the change in catchment DCI values between structural and functional models (Panel A; r^2=0.09, *p*=0.47) and functional with and without ponds (Panel B; r^2=0.02, *p*=0.39). Closed squares are potamodromous DCI, open triangles diadromous

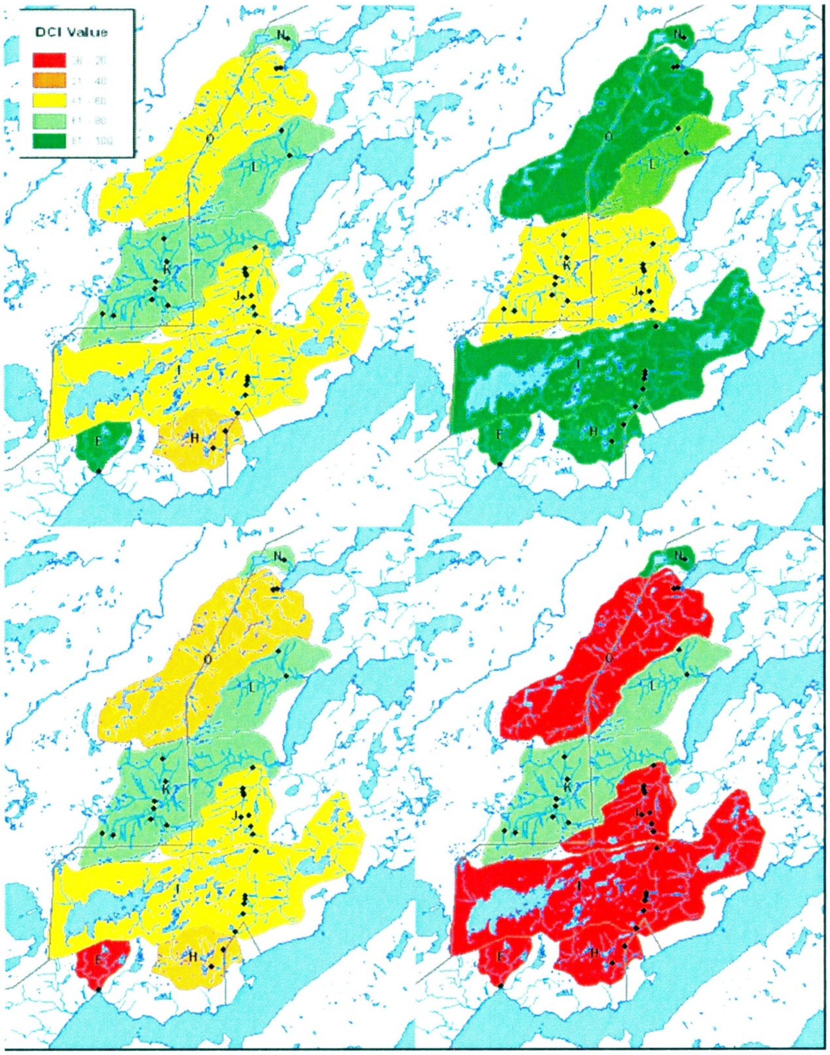

Figure 3.4: Comparison of potamodromous (top panels) and diadromous (bottom panels) functional DCI of catchments in Terra Nova National Park including stream segment biomass (left hand panels) and pond biomass (right hand panels) based on 15 cm brook trout during the migration period. Black dots represent culverts, letters correspond to catchments.

CHAPTER 4: SUMMARY AND CONCLUSIONS

4.1 Summary

Since its development in the early twentieth century, landscape ecology has been focused largely on studying the impacts of fragmentation on terrestrial systems (Fagan 2002; Turner 2005; Hilty et al. 2006). The need to understand this issue has only grown more urgent with time, as habitat alteration and destruction caused by humans has become the major cause of species declines and extinctions worldwide (Pringle 2003; Butchart et al. 2010). Recently ecologists have come to recognize that habitat fragmentation is not just a terrestrial issue and that, although not as visually obvious as on dry land, our aquatic ecosystems are also suffering connectivity losses as human development and encroachment progressively alter the natural conditions within them (Weins 2002; Pringle 2003; Fullerton et al. 2010). It has been suggested that due to the linear nature of stream networks and the restrictions that their ecological and spatial attributes place on organisms within them, that the impacts of fragmentation on aquatic systems may be more severe than they are on land where animals often have fewer dispersal limitations (Fagan 2002; Olden et al. 2010). There have certainly been cases where negative population impacts have been observed in aquatic species due to levels of habitat fragmentation (i.e., number of habitat patches) that would not be considered extremely high in terrestrial systems (e.g., Dunham et al. 1997; Morita and Yamaoto 2002; McLaughlin et al. 2006). The unique spatial features of stream networks have also presented challenges for ecologists when attempting to assess aquatic fragmentation, as most existing models of connectivity and theories regarding patch dynamics were developed for terrestrial systems, not the spatial arrangement of stream networks (Fagan 2002; Grant et al. 2007; Fullterton et al. 2010).

The Dendritic Connectivity Index (DCI) (Cote et al. 2009) was developed as a tool to quantitatively measure connectivity within stream networks, by accounting for the potential movement of fish, passability of barriers and the spatial arrangement of stream segments within complex networks. In this thesis I have attempted to demonstrate the versatility and effectiveness of this index through conducting assessments of stream network connectivity in Terra Nova and Prince Edward Island National Parks using the DCI. Specifically, I have demonstrated how, despite the wide range of input parameters that can be chosen by the user to evaluate stream fragmentation using the DCI, it consistently provides reliable estimates of connectivity and useful information regarding barrier impacts on entire systems, thus making it a robust tool for conducting assessments.

4.2 Assessment of movement barriers

One of the major contributors to stream fragmentation is the improper installation of road culverts (e.g., Gibson et al. 2005; Doehring et al. 2011). These structures may allow water to pass, but they often dramatically alter the flow of the stream (e.g., Peake 2004; Kemp and Williams 2008) or create conditions such as large outflow drops which make it extremely difficult or impossible for fish to pass (e.g., Park et al. 2008). Given that a single stream network can be crossed by several roads and thus have dozens of culverts located along its reaches, it is extremely important that ecologists and managers can efficiently and effectively survey and quantify fish passage through culverts. Formulating these methods can be challenging, as various factors influence culvert passability, including stream flow (which varies temporally), the dimensions of the culvert itself, and the physiology and life history of the species in question (Baker and Votapka 1990). In addition, resources such as time, staff and equipment are often limiting factors in both assessments and mitigation of barriers (Gibson et al. 2005; O'Hanley and Tomberlin 2005; Poplar-Jeffers 2008; Kibler et al. 2011).

In chapter two of this thesis, I tested the effects of various barrier assessment methods on the outcome of DCI results in both parks (Bourne et al. 2011). I found that the passability estimates of barriers can vary, drastically at times, with assessment method. Rule-based based methods tended to give more conservative estimates than those conducted using FixhXing (software that models fish passage through culverts). However, despite greater potential accuracy, FishXing was not without issues, as other studies have found (Poplar-Jeffers et al. 2008; Perkin and Gido (in press)). In particular, it could not account for atypical field conditions for many culverts in Prince Edward Island National Park, and some parameters provided by the program needed to be recalculated for culverts in both parks to better reproduce field conditions.

Despite the differences in results provided by barrier assessment methods, the estimates of catchment connectivity did not show as much variation and in most cases barrier restoration priorities did not change. This demonstrated the robustness of the DCI, as it provided the same overall results for managers when examining catchments as a whole, even when limited field data were used to evaluate culverts. The results of this chapter also highlighted the importance of validation of assessment results through field testing, as estimates provided by both field surveys and FishXing were potentially conservative, and did not necessarily provide accurate representations of field conditions across a range of discharge levels. This will be of particular importance to assessments conducted in areas of environmental extremes, where flows within a culvert can fluctuate widely with season.

4.3 Functional connectivity

In addition to barrier passability values, the parameters of stream segment and network length in the DCI can also be changed by the user based on the available data and the specific needs of the assessment being conducted. As with most other quantitative models of aquatic connectivity which have been developed (Fullerton et al. 2010), the DCI focuses largely on modeling a challenging spatial feature of stream networks – the arrangement of stream segments and barriers. However, there is also a functional aspect to connectivity which should not be ignored when conducting assessments (Fausch et al. 2002; Calabrese and Fagan 2004; Sheer and Steel 2006; Meixler et al. 2009; Musil et al. 2012). Most organisms show some level of dispersal within their habitats, to forage, reproduce, complete various life stages and overwinter. These movements are often closely linked to habitat preferences and influenced by the spatial arrangement of habitat patches (Belisle 2005; Baguette and Van dyck 2007). Freshwater fish are no exception, with salmonids in particular displaying strong habitat associations (Dunbar et al. 2011). While the DCI does account for some ecological traits by modeling the movement of diadromous and potamodromous fish, it does not consider functional parameters such as habitat quality which may play an important role in the impacts of individual barriers on fish populations (Roni et al. 2002; Lowe et al. 2006; Sheer and Steel 2006).

In the third chapter of this thesis, I modified the DCI from a structural to a functional index by replacing the parameter of stream segment length with brook trout biomass, which had been derived from models of habitat preference (Cote 2007; Cote et al. 2011). In doing so I was able to model the dispersal of fish throughout stream networks in TNNP based on habitat quality, by effectively weighting each stream segment by an estimate of its value to the study species. Based on my results, adding functional data to the DCI can potentially improve connectivity assessments, particularly when ponds are accounted for. However, despite differences for individual segments inputs the overall results for catchments and the park as a whole did not differ significantly, though a number of caveats still remain and results may be somewhat site-specific to TNNP.

These findings support the assertion that the DCI is a robust index, capable of providing meaningful results even in the absence of functional data in the study area. While it is typically preferable to include functional data when modeling ecological systems in order to accurately model process and relationships within them (Calabrese and Fagan 2004; Baguette and Van dyck 2007), there will always be situations when this is not possible due to limited resources, data and knowledge. This may be the case particularly in large, complex systems where detailed field surveys of barriers and habitat would be too labor intensive, or in systems with a high species diversity where modeling the habitat associations of all species of interest would be extremely difficult – particularly if they were not well studied. For these situations, the DCI can likely still provide meaningful estimates of catchment connectivity and prioritized barrier replacement lists.

Other studies have suggested that habitat quality may not be the most informative parameter for measuring fragmentation effects on stream fish and that, as was the case with the potamodromous DCI, the focus should primarily be on the maximizing the size of stream segments, or habitat patches (Isaac et al. 2007;Cote et al. 2009; O'Hanley 2011). This may be the case in largely homogeneous stream networks, where conditions show relatively little variation throughout their reaches; or when the largest stream segment happens to be in the area of the network which contains the highest proportion of suitable habitat. However, if functional data are available it would always be advisable to include it in the connectivity measure as the dispersal of many fish species, particularly diadromous salmonids, can be heavily influenced by habitat features (Fausch et al. 2002; Dunbar et al. 2011) and in turn, populations can be severely impacted by barrier placement in relation to sites of high habitat quality (Roni et al. 2002; Cote et al. 2009; Olden et al. 2010; Rolls 2011).

4.3 Conclusions and further work

This thesis represents the results of the first application of the DCI using field derived data and, as with any ecological model, further testing and most importantly, validation, is required to better understand its behavior in varied systems and confirm the accuracy of its results (Olden et al. 2002; Turner 2005). Field testing of the DCI is needed to investigate the effects of varying parameter inputs and barrier assessment methods on the overall results in various conditions. In particular, it would be advantageous to apply the DCI to much larger, more complex systems where greater spatial and ecological heterogeneity exists to see if the trends observed in TNNP and PEINP are applicable in other areas and with different species. In addition, results of DCI assessments should be confirmed whenever possible by surveying fish populations above and below barriers, monitoring fish passage through culverts and conducting comparative surveys in similar, but non-fragmented streams (Joy and Death 2000; Kennard et al. 2006). The assessment of connectivity in PEINP highlighted some of the challenges in barrier assessment which may be encountered when working in the field and served as a reminder that models, while useful, may not always be the best option for real world situations. The results presented in this thesis have confirmed the potential utility of the DCI for managers and ecologists, while also providing insights into potential modifications and applications of the index in ecologically and spatially varied systems.

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Appendix A: Detailed culvert survey procedures for FishXing analysis used in Terra Nova and Prince Edward Island National Park (from D. Cote, Terra Nova National Park)

Section 1: Site Info

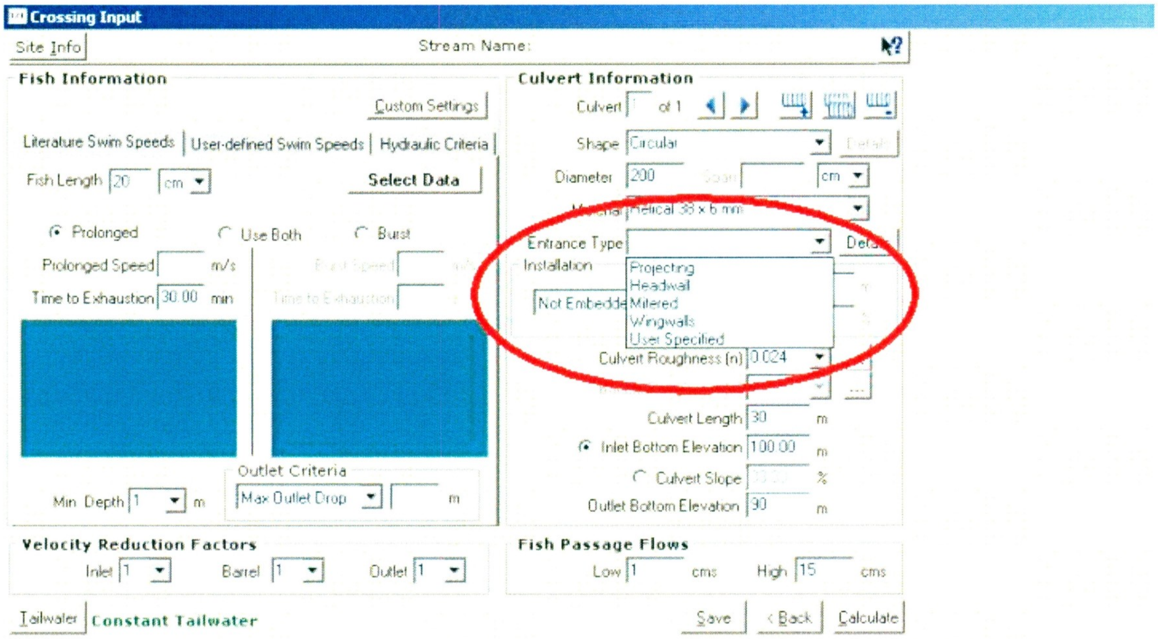
1) Date: The date on which the culvert survey was conducted.
2) Lat/Long: The precise location of the crossing as determined by GPS.
3) Crossing Name: Each crossing should be given a unique identifying name. In Terra Nova NP each culvert was named according to its distance, in km's, from the park's east boundary.
4) Road: The roadway on which the crossing is located.
5) Photographs: Digital photographs should be taken of the inlet and the outlet. In FishXing 3, these photos can be linked to the survey information.

Section 2: Culvert Info

1) Culvert Shape (A): Note the shape of the culvert being surveyed. Is it circular? An arch? You can find a list of all the culvert types that can be entered into FishXing in the FishXing help files.
2) Culvert Diameter (B): Measure the distance across the culvert outlet, at its widest point.
3) Culvert Material (C): Culvert material is an important feature when predicting water velocities, as more complex bottoms impede efficient flow of water. Make note of the texture of the bottom of the culvert. Is it smooth (e.g. concrete)? If it's a corrugated metal culvert, how deep are its corrugations and how far apart are the corrugations (top of one corrugation to top next one)?

Are there rocks and boulders lining the culvert bottom? Or is the culvert embedded in the substrate with a natural bottom? FishXing allows you to choose from a list of possible bottom types and provides the corresponding roughness coefficient for each. If the culvert has a natural stream bottom, choose one of the roughness coefficients from Appendix C. If it's a non-natural bottom just note the material.

4) Entrance type (D): The type of culvert entrance affects flow velocity and depth near the inflow. There are 4 types of entrance options that FishXing allows: Projecting: when the culvert tube projects beyond the bank; Headwall: when the culvert inlet appears as a hole in a vertical wall of concrete-shaped like a "T"; Mitred: when the barrel of the culvert is cut off at the angle of the bank; Wingwalls: the water is funneled into the culvert by adjacent walls – shaped like a "Y". Make note of the entrance type.



Fish Length 20 cm

● Prolonged ○ Use Both ○ Burst

Prolonged Speed m/s

Time to Exhaustion 30.00 min

Min. Depth 1 m

Outlet Criteria: Max Outlet Drop m

Inlet 1 Barrel 1 Outlet 1

Culvert of 1

Shape Circular

Diameter 200 cm

Material Helical 38 x 6 mm

Not Embedded

Culvert Roughness (n) 0.024

Culvert Length 30 m

● Inlet Bottom Elevation 100.00 m

○ Culvert Slope %

Outlet Bottom Elevation 90 m

Low 1 cms High 15 cms

5) *Wetted width (E): *Optional*. Using a measuring tape, measure the width across the culvert at the water's surface. This element is not necessary to predict stream flow but can document the difference between culvert condition and adjacent habitat conditions (culverts typically constrict flows more than adjacent habitats).

6) *High Water Mark (F): *Optional*. Measure the depth across the culvert at the point that marks the highest level at which water flows through. This point is often identified by a rust mark or discoloration on the culvert walls. Once again, this element is not necessary for model predictions but could provide a means to ground-truth stream discharge inferences.

7) *Water depth (G): *Optional*. Using a meter stick, measure the current water depth in the culvert at the outlet, inlet and, if possible (if the culvert is large enough to walk through), the middle. This information, while not necessary for making predictions, can be used to ground truth them as FishXing provides water depth estimates within culverts along its length.

8) *Water Velocity (H): *Optional*. Using a velocity meter, measure the water velocity, in m/s, at the culvert outlet, inlet and, if possible, in the middle of the culvert. Water velocity measurements should always be taken at 60% of the way from the water level to the bottom. For example, in a stream that is 100cm deep, the water velocity should be measured at 60 cm down from the surface. This information, while not necessary for making predictions, can be used to ground truth them as FishXing provides water velocity estimates within culverts along its length. It will also provide an in-field measurement that can be used to roughly evaluate passability for that discharge (based on known swimming limits of brook trout).

9) Culvert Length (I): In large culverts the length can simply be determined by walking though the culvert with a tape measure. In smaller culverts a piece of string, attached to a small float of some sort, can be sent through the culvert and the length of string can be measured afterwards.

10) Culvert Gradient (J): Determine the slope of the culvert (slope = rise/run*100). Two people are required for this measurement to operate the survey instrument and the range pole (Fig. 4). The person operating the survey instrument sets up their tripod in a spot where they will be able to see

the range pole at both ends of the culvert. The other person first holds the range pole at the lowest point of the culvert at the inflow and the relative height of the survey instrument is recorded. Then the range pole is moved to the outflow and the step is repeated. The difference between the two values provides the "rise" of the culvert. The length of the culvert can be used for the "run".

11) Culvert Bottom Elevation (K): FishXing requires that all information be entered in elevation. Absolute elevation is difficult to measure accurately with the tools we have. Fortunately, relative elevation is all this is required for assessment purposes. To circumvent this problem, we estimate the absolute elevation of one point (the culvert bottom elevation) with GPS and relate all other features to that using relative elevation measured with survey instruments. All these relative measures have to be converted back to absolute elevation before entering them into FishXing. This is a common omission for first time users.

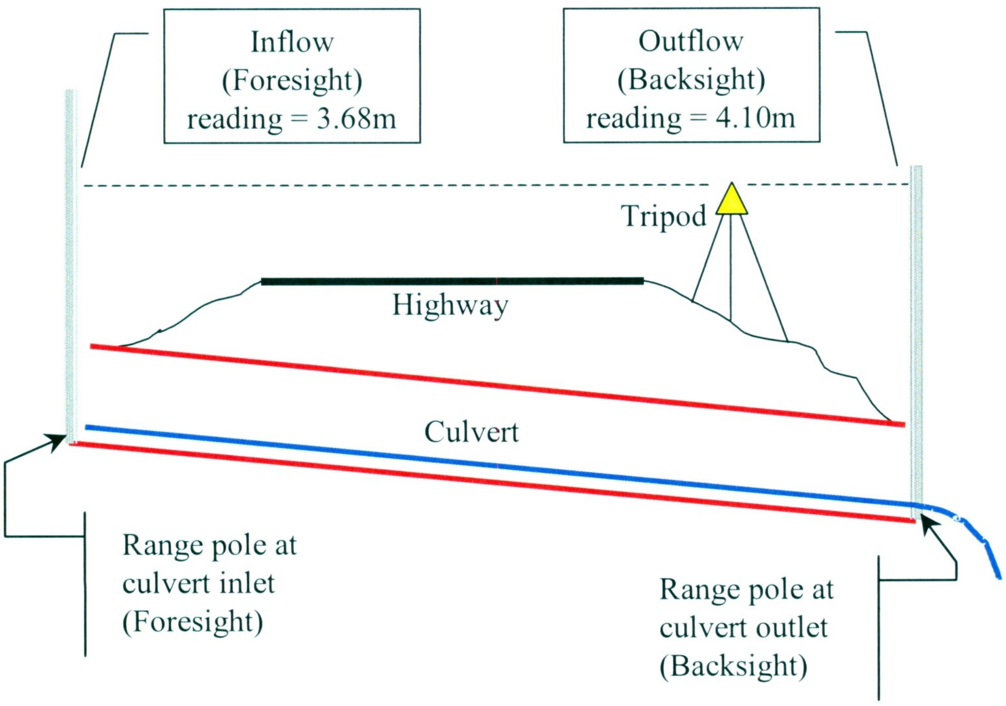


Figure 4: Survey method to determine culvert gradient.

Section 3: Stream Characterization (optional)

These measurements will enable us to characterize hydrological conditions in the natural environment beyond the culvert. It is best to collect this data beyond the outflow pools (which are usually a by-product of the culvert). To avoid duplication of effort, it is advisable to collect the downstream depth/velocity data at the tailwater control (see section 4). Note: All stream measurements are to be taken downstream of the culvert.

1) *Wetted Width (L): *Optional.* Measure the width of the stream at the point that the water meets the river banks. Try and choose a section of stream that is representative of the stream. *While this is not used in hydrologic prediction it*

can be used with culvert wetted widths (if they were collected) to assess channel constriction.

2) *Bankfull Width (M): *Optional.* Measure the width of the stream at the high water mark. This can be identified as the point on the stream bank above which flood waters will spill into the flood plain. In most cases it will be represented by a distinct edge to the stream channel. In some cases, where distinct edges are not apparent, the character of the vegetation can be used to estimate the bank edge. *While this is not used in hydrologic prediction it can be used evaluate the reliability of discharge predictions inferred from other gauging stations.*

3) *Water Depth (N): *Optional.* Using a meter stick, take 5 measurements of the stream channel depth at equal increments across the stream. These measurements will be used to determine the average stream depth at that cross section. Hint: to find the width increments divide the wetted width by 6. *While this is not used in hydrologic prediction it can be used (with water velocity below) to calculate a point discharge and evaluate the reliability of discharge predictions inferred from other gauging stations.*

4) *Water Velocity (O): *Optional.* Using a velocity meter, measure the velocity of the stream at the same points you measured the channel depth (these measurements are best collected as you are collecting depths (see above)). Use these measurements to determine the average water velocity in the stream at

this cross section. Remember to measure the velocities at 0.6 of the water depth from the surface. *While this is not used in hydrologic prediction it can be used (with water depth above) to calculate a point discharge and evaluate the reliability of discharge predictions inferred from other gauging stations. Water velocities can also be used to compare to those in the culvert to assess whether culvert velocities are typical of that in the stream. Note: discharge is the product of wetted width, average depth and average velocity.*

5) *Stream Gradient (P): *Optional.* Determine the gradient of the water surface from the downstream end of the outflow pool to a point 5 m downstream. Use the survey gear and the same approach used to find the slope of the culvert. *This is required if the dynamic tailwater control option is being used in FishXing. This information may also be useful for assessing future restoration options.*

Section 4: Tailwater Control

The tailwater control is the downstream feature that affects the depth of water in the pool below the culvert. It is easily located as the first riffle after the downstream pool. Measurement of the tailwater control allows us to be able to account for changes in the outflow drop associated with changing water levels. If there is no downstream pool, the culvert may not have a tailwater control and only items 1 and 2 (see below) are required. All of the following measurements will be entered in FishXing under the "tailwater control" section. In FishXing, there are three options available for modeling outflow drop and pool depth. The first is "constant tailwater", which assumes that the outflow drop and pool depth does not change with discharge. Using the constant tailwater feature only requires information on pool depth and pool surface elevation. While this is less realistic, it may be functional since at high flows, when outflow drop is reduced, velocities in the culvert are more likely to impede passage. The second option is to account for the dynamic nature of the tailwater. While additional measurements are needed (tailwater depth and velocity cross section), this approach accounts for changes in the outflow drop and pool when assessing fish passage.

All elevations that are measured in this section are taken relative to the culvert bottom elevation, determined in section 2. For example, if the culvert bottom elevation was determined to be 100m above sea level and the pool surface elevation was measured as 40cm below the culvert bottom, you would enter the pool surface elevation in FishXing as 99.6m. It may be easier to write the relative elevations on your field sheet (40cm) and do the absolute calculations back in the office. Follow the same procedure for all measurements in this section.

Note: Since FishXing does not accept negative values (because it won't allow points to be below sea level), we have to ensure all elevations are positive. Failure to do so will result in an error message. Should your GPS elevation result in some values being less than zero, the reference elevation (culvert bottom) may need to be adjusted accordingly.

1) Pool Depth (Q): Use the survey equipment to measure the depth of the outflow pool where the water plunges in (Fig. 5).

2) Pool Surface Elevation (outflow drop) (R): Use the same procedure to determine the elevation of the pool's surface from the culvert bottom (Fig. 5).

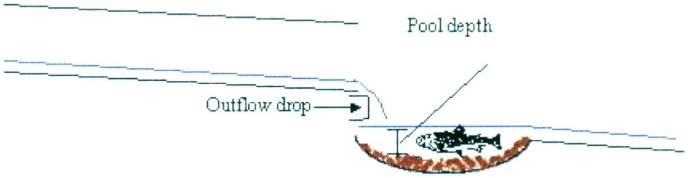


Figure 5: Measurement locations of pool depth and outflow drop.

3) *Channel Cross Section (S): *Optional*. Here you will be creating a cross-sectional profile of the stream at its tailwater control. The Tailwater Control is defined by FishXing as the channel feature that determines the water surface elevation immediately downstream of the culvert outlet. The location controlling the tailwater elevation is often at the riffle crest immediately below the outlet pool. In order to create a stream profile simply set up a

transect across the bankfull width of this section of stream. Using the survey equipment, measure the elevation (T) at each key change in topography in the cross-section (Fig. 6). Make note of the distance across the stream at which each measurement is taken (S or station on the data sheet), and the roughness coefficient of the stream bottom (U). FishXing provides a list of roughness coefficient values for different types of streams (these roughness values are used to estimate the turbulence and associated velocity reductions in the stream). Use this list to find a description that best matches your study area. *These methods are only required if you are utilizing the dynamic tailwater control option.*

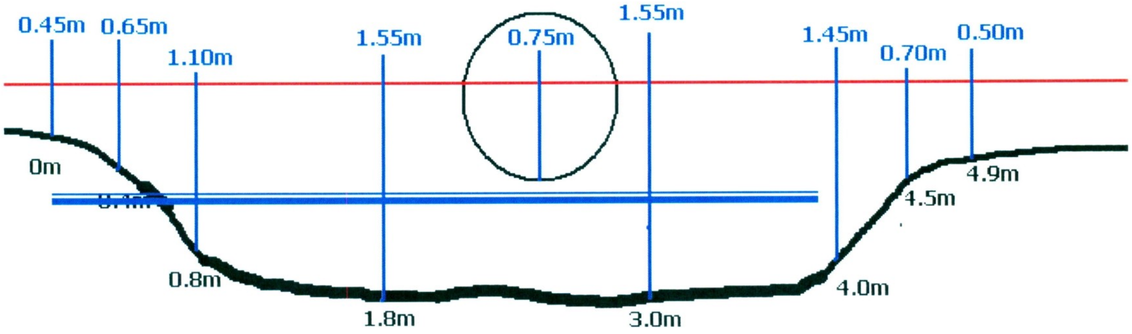


Figure 6: Cross Channel Section. Note: red line represents survey level height (and range pole measurements), doubled blue line represents water level, the black circle is the culvert outlet.

In the example above, the culvert bottom could have an absolute elevation of 100 m. Using the survey equipment, a reading of 75cm was measured on the survey stick. Other measurements are taken from the stick as it is moved around to the key features. In the office these measurements can be converted to relative elevations and then to absolute elevations for entry into FishXing (see table below):

Distance along transect	Reading on survey range pole	Relative elevation (subtract reference elevation 0.75)	Absolute elevation (sum relative elevation to absolute elevation of culvert bottom)
0m	0.45m	0.35m	100.35m
0.4m	0.65m	0.10m	100.10m
0.8m	1.10m	-0.35m	99.65m
1.8m	1.55m	-0.80m	99.20m
3.0m	1.55m	-0.80m	99.20m
4.0m	1.45m	-0.70m	99.30m
4.5m	0.70m	0.05m	100.05m
4.9m	0.75m	0.25m	100.25m

Appendix B: Procedure for back calculation of Manning's Roughness coefficients of culverts using field data

FishXing provides default values for these coefficients which are often derived from large streams and generalized without much information (Gubernick, pers. comm.). To obtain values which were more appropriate to individual culverts, I back calculated new values based on field data, using the Manning's equation for open channel flow (1).

(1) $$V = \frac{R_h^{2/3} s^{1/2}}{n}$$

where V is the average channel velocity in meters per second, R_h is the hydraulic radius in meters and s is the channel slope in drop in meters over length in meters (a unitless value).

For culverts V and s were determined directly from field observations, with the average culvert velocity being used for V. The formula used to calculate R_h was

(2) $$R_h = A/P$$

in which A is the area of flow (or wetted area) of the channel in square meters, and P is the wetted perimeter in meters. For circular culverts, the calculation of both these parameters required knowing the central angle (θ) of the water from the center of the culvert (Fig. 1).

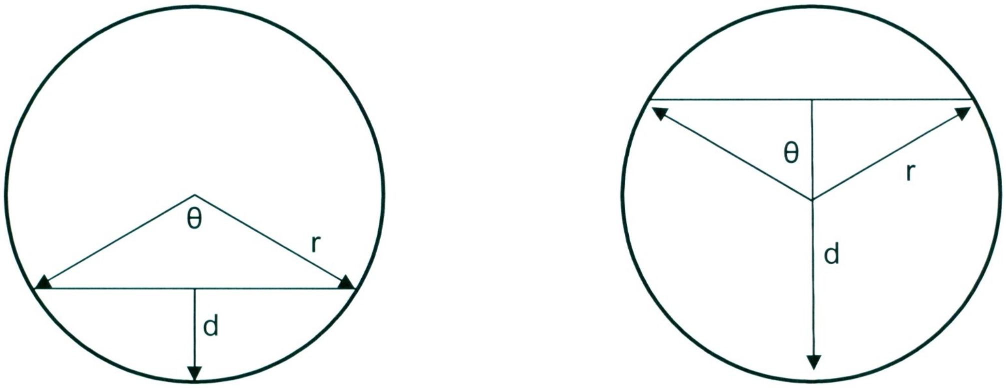


Figure 1: Central angle (θ) of a culvert that is less than half full (left), more than half full (right)

The formula for the central angle of a circular culvert is

(3) $$\theta = 2\arccos(r\text{-}d/r)$$

where r is the radius of the culvert and d is the average depth of the water inside the culvert, both of which were obtained by field measurements. The formula used to calculate A and P for culverts that were less than half full were

(4) $A = \frac{r^2 (\theta - \sin\theta)}{2}$

(5) $P = r\,\theta$

and for culverts greater than half full

(6) $A = \pi r^2 - \frac{r^2 (\theta - \sin\theta)}{2}$

(7) $P = 2\pi r - r\,\theta$

The resulting values of P and A were then used to solve equation 2, the result of which was used in turn to solve equation 1 and obtain a field derived roughness coefficient. After completing these calculations, I input this new n value directly into FishXing. Though some numbers were much higher than those listed for culverts in hydraulic tables, they were used as a means of ensuring that the culvert profiles provided by FishXing matched the field observations as closely as possible.

I also recalculated the roughness coefficients for the tailwater control. To do this I used equations 1 and.2, as with the culverts, but because stream channels are not circular, equations 3 through 7 were not applicable. To determine the area of flow and wetted perimeter I used equations derived for parabolic open channels – which often approximate natural stream beds (Brater & King, 1976).

The equation for the area of flow in a parabolic cross section is

(8) $A = \frac{2D^2}{3x^{1/2}}$

where D is the maximum depth and x is D divided by the wetted width (W) of the stream. The equation for the wetted perimeter of the stream section is

(9) $P = \left[(16x^2 + 1)^{1/2} + \frac{1}{4x} \ln (16x^2 + 1 + 4x)\right] \frac{D}{2x}$

I substituted P and A into equation 2 and used this to solve equation 1 to obtain the tailwater n coefficient. If this n value did not provide results which matched the field data I had to adjust the tailwater n value manually until the outflow drop and tailwater depth matched or closely approximated field values. It should be noted that this had to be done for the majority of cases and it would likely be easier to use a 'guess and check' method for estimating the tailwater n value rather than back calculating it. These larger discrepancies were likely due to the wide range of conditions that occur in streambeds that are not reflected by the input parameters, such as debris, substrate, vegetation, etc.

Appendix C: Passabilities for culverts surveyed in Terra Nova National Park using various methods of barrier assessment (trout and salmon for an entire year using FishXing software, trout and salmon for the May-Dec migration period using FishXing, and a simple field-based method using a flowchart of criteria).

culvert	trout migration	salmon migration	trout year	salmon year	flowchart
a	21.7	0	33.1	0	0
b	7.7	0	18.9	0	0
c	65.7	0.01	80.9	0.06	0
d	0	0	0	0	0
e	0	0	0	0	0
f	0	0	0	0	0
g	0	0	0	0	0
h	0	0	0	0	0
i	0	0	0	0	0
j	0	0	0	0	0
k	6.5	0	18.6	0	0
l	0	0	0	0	0
m	5.4	0	17	0	0
n	0	0	0	0	0
o	0	0.02	0	0.02	0
p	0	0	0	0	0
q	0	0	0	0	0
r	0	0.14	0	0.21	0
s	0	0.57	0	0.4	0
t	28.5	0	42.1	0.01	0
u	0	0	0	0	0
v	6.2	0	18.1	0	50
w	100	100	100	100	50
x	0	0	0	0	0
y	0	0	0	0	0
z	0	0	0	0	0
aa	99.5	0.06	90.3	0.39	50
ab	100	100	100	100	50
ac	83.8	0.53	89.6	0.6	100
ad	74.7	0.62	90.9	0.74	50
ae	5.5	0	17.2	0	0
af	84.2	0.08	94.9	0.17	0
ag	13.5	0	16	0	0
ah	18	0	31.4	0.01	50

ai	15.2	0	30	0	50
aj	53.5	0	67.2	0.03	50
ak	0	0	0	0	0
culvert	**trout migration**	**50 cm salmon migration**	**trout year**	**50 cm salmon year**	**flowchart**
al	78.5	0.52	90	0.7	50
am	100	0.01	100	0.11	50
an	0	0	0	0	0
ao	84.7	0.66	89.5	0.85	50
ap	33	0.01	36.5	0.1	0
aq	25.3	0	30.5	0	0

Appendix D: Dendritic Connectivity Index (DCI) values for potamodromous (DCIp) and diadromous (DCI_D) fish in catchments in Terra Nova National Park using various assessment methods (trout and salmon for an entire year using FishXing software, trout and salmon for the May-Dec migration period using FishXing, and a simple field-based method using a flowchart of criteria).

	DCIp					DCId				
Catchment	trout migration	salmon migration	trout year	salmon year	flowchart	trout migration	salmon migration	trout year	salmon year	flowchart
A	45.4	37.43	51.3	37.43	37.4	44.2	32.35	52.0	32.35	35.4
B	97.6	93.09	98.7	93.72	93.0	67.0	4.58	81.6	13.26	3.6
C	85.2	85.22	85.2	85.22	85.2	2.4	2.42	2.4	2.42	2.4
D	36.4	36.38	36.4	36.38	36.4	24.6	24.57	24.6	24.57	24.6
E	86.4	95.04	86.4	95.04	86.4	2.5	0	2.5	0	2.5
F	90.8	90.8	90.8	90.8	90.8	1.2	1.2	1.2	1.2	1.2
G	84.9	84.9	84.9	84.9	84.9	6.9	6.9	6.9	6.9	6.9
H	47.6	52.59	53.0	52.59	52.6	27.3	30.47	30.7	30.47	30.7
	51.3	94.46	51.3	93.82	51.3	31.7	97.17	31.7	96.84	31.7
J	46.5	42.2	47.4	42.2	36.1	58.4	54.17	59.2	54.17	44.5
K	81.2	43.75	85.3	50.56	57.0	89.5	60.81	92.0	66.65	71.3
L	99.8	53.74	95.2	69.98	74.7	99.7	47.1	94.5	65.67	71.4
M	64.0	61.92	68.5	61.92	61.9	75.8	0	78.8	0	74.4
N	91.9	58.77	97.7	62.8	58.2	81.6	39.19	96.6	45.14	33.9
O	91.0	100	98.8	100	87.2	95.2	100	99.4	100	93.2