The ecology of fish movement in six Lake Ontario tributaries

Ivan J. Dolinsek

A thesis

in

The Department

of

Biology

Presented in partial fulfillment of the requirements

for the Degree of Doctor of Philosophy at

Concordia University,

Montreal, Quebec, Canada

November 2011

CONCORDIA UNIVERSITY
SCHOOL OF GRADUATE STUDIES

This is to certify that the thesis prepared

By: **Ivan J. Dolinsek**

Entitled: **The ecology of fish movement in six Lake Ontario tributaries**

and submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY (Biology)

complies with the regulations of the University and meets the accepted standards with respect to originality and quality.

Signed by the final examining committee:

Dr. Paul Joyce	**Chair**
Dr. Michael Fox	**External Examiner**
Dr. Jochen Jaeger	**External to Program**
Dr. Pascale Biron	**Examiner**
Dr. Grant Brown	**Examiner**
Dr. James Grant	**Thesis Co-Supervisor**
Dr. Robert McLaughlin	**Thesis Co-Supervisor**

Approved by ____
Chair of Department or Graduate Program Director

November 17, 2011 ________________________________
Dean of Faculty of Arts and Science

Abstract

The ecology of fish movement in six Lake Ontario tributaries

Ivan J. Dolinsek, Ph.D.

Concordia University, 2011.

Despite a rich literature on the ecology of freshwater fishes, the movement behaviour of many stream fish remains poorly understood, yet is expected to be important for key ecological and micro-evolutionary processes. The main purpose of my thesis was to improve our understanding of fish movements by evaluating the movement of multiple species across multiple streams and entire watersheds. I undertook three steps to achieve this: 1) a comparative study addressing whether information in natural history accounts provide reliable information for predicting the behaviour of other populations of stream fishes (Chapter 1); 2) adapted, tested and extended existing theory on sex-biased arrival by conducting a broad test of four hypotheses on stream fishes at spawning sites (Chapter 2); and 3) to extend and contribute to a management concern of broad interest regarding invasive species control by examining the degree to which fishes move between adjacent streams (Chapter 3). Comparisons between my data and those from the literature demonstrated a strong correlation regarding key biological indices, suggesting that natural history information is a reliable source of information and can be used in most management decisions regarding freshwater stream fishes. My detailed data set also revealed novel findings unknown to the natural history literature: juveniles moved into the streams along with spawning adults; and species with known "anadromous-like" life histories spend more time in the streams than previously thought. Secondly, my data suggested that the most common form of sex-biased timing is males arriving before females, consistent with hypotheses that males are better able to cope with the prevailing conditions at the spawning sites, as well as to increase their reproductive success by encountering more females. However, there was considerable variation within and among species of fishes. Finally, my thesis suggested that the fish assemblages in these Lake Ontario catchments are dynamic, exchanging individuals at rates and spatial extents likely to be important for metapopulation dynamics and gene flow. Understanding the movement behaviour of fishes, a critical aspect of their life histories, will be important in developing proper conservation plans. Knowledge gained from this study will serve to improve our understanding of how concepts such as metapopulations, habitat fragmentation, and movement apply to stream fishes and to efforts to control invasive fish species.

Acknowledgements

I would like to express my sincerest gratitude to my two co-supervisors, Robert L. McLaughlin and James W.A. Grant for their guidance, support, and especially their patience over the years. I am grateful to James Grant for his dedication as a mentor, his advice, encouragement, and most importantly, his friendship. I am also grateful to Robert McLaughlin for introducing me to the world of fish movement and PIT-tagging, and for his continued support and encouragement. I will never forget his dedication in making sure I was always OK, and for helping push a wheel-barrel with 6 car batteries 2 kilometres over a muddy field in the rain to a study site. Words cannot express my gratitude to the both of you.

My advisory committee members, P. Biron and G. Brown have always been accessible and helpful. Their advice and comments on this thesis are greatly appreciated. I am also grateful to Dr.'s Michael Fox and Jochen Jaeger for their helpful comments on improving this thesis.

I am greatly appreciative of the students I've had a chance to share a lab with, for their company and friendship over the years, and who made this experience all the more fulfilling. These people are among others, Jae-Woo Kim, Nathalie Brodeur, Lia Clark, Jacquelyn Wood, and Amanda Lindeman. Trust me when I say the office is not the same without you guys! I thank my assistants, Jenny Adams, Debbie DePasquale, Michelle Farwell, Celina and Sylvia Gadzinski, Bill Harford, Lindzie O'Reilly, Cameron Redsell, Trevor Shore, and Katie Stammler for their hard work and dedication in the field at various times during the study.

I thank Lisa O'Connor and Tom Pratt for their input, advice, and encouragement during the project, and Greg Elliott and Bill Gardner for showing me how to set up the

antennae arrays during the first year of the study. Finally, I am grateful to the various property owners who graciously allowed us access to the field sites, and the Ontario Ministry of Natural Resources for providing us with a license to catch fish for scientific purposes.

During the research and writing of this thesis, I was supported by the Natural Sciences and Engineering Research Council of Canada post-graduate doctoral scholarship (NSERC), the Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT) postgraduate scholarship, a Concordia Graduate Fellowship, the Bourse d'études Hydro Quebec award, and a Doctoral Thesis Completion Award from Concordia University. In addition, I was supported from research grants to R.L. McLaughlin from the Great Lakes Fishery Commission, Sea Lamprey Research Program, Canada Foundation for Innovation, and Ontario Innovation Trust, as well as J.W.A Grant from the Natural Sciences and Engineering Research Council of Canada.

Finally, I have received a lot of loving support and encouragement from my family, and especially my wife, Sylvia, and my adorable daughter Katryna. I dedicate this thesis to them.

Table of Contents

List of Figures

List of Tables

Contribution of Authors

The chapters of this thesis were prepared as manuscripts for submission to peer-reviewed journals. I contributed to the planning, collection of data, data analyses, and writing of all manuscripts. Dr. J.W.A. Grant and Dr. R.L. McLaughlin contributed to the planning, data analysis, and editing of all manuscripts. Dr. T.C. Pratt and L.M. O'Connor contributed to the planning and data collection of all manuscripts.

Chapter 1 was submitted to the Journal of Fish Biology as:

Dolinsek, I.J., McLaughlin, R.L., and Grant, J.W.A., O'Connor, L.M., and Pratt, T.C. How well do historical natural history data predict the movement ecology of stream fishes?

Chapter 2 will be submitted to a behaviour or ecology journal as:

Dolinsek, I.J., McLaughlin, R.L., and Grant, J.W.A., O'Connor, L.M., and Pratt, T.C. Mechanisms influencing the sex-biased arrival of fishes at spawning sites in Lake Ontario streams.

Chapter 3 will be submitted to a fisheries journal as:

Dolinsek, I.J., McLaughlin, R.L., and Grant, J.W.A., O'Connor, L.M., and Pratt, T.C. Inter-stream movements of fishes in Lake Ontario tributaries: Insights into rates of homing and straying in freshwater fish.

General introduction

The movement of individuals between habitats is important for key ecological and micro-evolutionary processes, such as metapopulation dynamics, and the degree of gene flow and local adaptation (McDowall 1988; Metcalfe et al. 2002; Wilson et al. 2004; Knaepkens et al. 2005). Typically, a single habitat is not optimal for all activities, so individuals or populations move from one well-defined area (or habitat) to another for reproduction, feeding, or to seek refuge (Northcote 1997; Lucas and Baras 2001). Furthermore, the movement of individuals between spatially separated local populations can affect the dynamics of local populations, including local rates of recruitment, persistence, and extinction (Wilson et al. 2004), as well as for re-colonizing unoccupied habitats and maintaining the dynamics and stability of the regional meta-population (Hanski and Gilpin 1997). Understanding such movements is particularly important in species of management or conservation interest. For instance, due to their small population size, species at risk have reduced gene flow, reduced number of colonizers, and are susceptible to habitat fragmentation and loss.

There is a wide diversity of movement types in animal species. The most well known, migration, is the cyclical movement of individuals or populations from one habitat to another (McDowall 1988; Metcalfe et al. 2002). Migration is both spatially and temporally predictable, and brings individuals to habitats offering food and mates (Gross 1987, Hendry et al. 2004a). The most spectacular and best known migrations are those that occur on a large scale, *i.e*. the wildebeest (*Connochaetes taurinus*) of the Serengeti Plains of East Africa, and herds of caribou (*Rangifer tarandus*) in Canada. However, migration does not always imply a return to the habitat where an individual was born. The movement of individuals can take on two distinct forms: individuals returning to their place of birth (homing); and the movement of individuals away from their place of birth to a new habitat in search of food or mates (dispersal) (Hendry et al. 2004b). Homing has several benefits, including: increasing the chances of finding a suitable habitat or mate; increasing familiarity with local environmental conditions; returning individuals to habitats to which they are locally adapted; and, avoiding the movement costs associated with dispersing to a new habitat through unknown environments (Hendry et al. 2004b). Probably the best known example of homing is observed in the Atlantic salmon (*Salmo salar*), where juveniles leave their natal streams in the spring and can migrate up to thousands of kilometres to ocean feeding grounds, only to return to these same streams several years later to spawn (McCormick et al. 1998). Conversely, dispersal helps to buffer against temporal variation in environmental conditions, allows the (re)colonization of habitats, reduces inbreeding depression, and reduces competition between kin (Hendry et al. 2004b).

Despite its importance in ecology, information on the movement behaviour of many species is limited, unavailable, or lacks quantitative evidence (Abell 2002; Mandrak et al. 2003; Poos et al. 2008), particularly for species with little or no commercial value (Northcote 1998; Lucas and Baras 2001; Knaepkens et al. 2004; Smith and Jones 2007). But measuring the movement of species poses challenges to researchers and scientists. Ideally, investigators would like to track individuals over a lifetime; however, they are often limited to snippets over a short period of time and small spatial scales, mostly because of restricted sampling (Smith and Jones 2007). For example, short-term field studies could miss individuals/species that use a specific habitat on a seasonal basis, whereas information derived from multiple sources is often incomplete because of spatial and temporal gaps (Smith and Jones 2007). Additionally, non-standardized sampling protocols between studies (*i.e.* sampling effort, gear used, spatial extent of the study, number of years and seasons sampled) can further compound the issue (Smith and Jones 2007).

This thesis developed from a large scale study using PIT-tags to track multiple Lake Ontario stream fishes over six adjacent streams over three years. Specifically, the original study was designed to assess the inter-stream movements of sea lampreys (*Petromyzon marinus*) and selected non-target fishes in response to sea lamprey barriers. The normal movement of fishes can be impeded by in-stream structures, both natural (*i.e.* waterfalls) and anthropogenic (*i.e.* barriers, dams). These structures deny access to potential spawning habitats and isolate upstream populations genetically and demographically (Morita et al. 2000), possibly affecting biodiversity, population dynamics, and species interactions (Northcote 1998; Fahrig 2003). In the Laurentian Great Lakes, low-head barriers have been used as a valuable tool for restricting the movement and reproduction of invasive species, such as the sea lamprey (Porto et al. 1999; Baxter et al. 2003). However, these barriers may also block the migration of native species by removing potential spawning habitats (Porto et al. 1999). Evidence at the stream and eco-region scale suggests that in-stream barriers can influence the movements, numbers, and kinds of non-target fishes in stream sections above a barrier (Porto et al.1999; Morita et al. 2000; Dodd et al. 2003; Harford and McLaughlin 2007), but no studies have yet investigated their impact at the meta-population scale. This work is important as it will help researchers understand if, and how frequently, sea lampreys denied access to their first choice of streams will move to other streams, as well as assess the effect of barriers on other non-target species denied access.

I quickly recognized that studies like this could provide much broader and valuable insights into the movement behaviour and life histories of stream fishes than what the study was originally proposed to do. First, unlike earlier studies, this research offers a unique opportunity to study the movement behaviour of multiple species within a single watershed. Second, although many freshwater fish are assumed to be sedentary or exhibiting restricted movement, mainly due to the limited number of studies and biased sampling designs of past studies (Gerking 1959; Rodriguez 2002), recent studies suggest that movement in many populations of stream fishes is more common than previously thought (Lucas and Baras 2001; Rodriguez 2002; Mandrak et al. 2003). I used stream fishes to examine movement behaviour because: 1) the linear nature of streams makes it relatively simple to track individuals using strategically placed nets or detection antennae; 2) the great taxonomic and biological diversity of stream fishes, particularly in the Laurentian Great Lakes (~145 native species), makes them ideal subjects to examine the movement of multiple species at the level of multiple streams and entire watersheds (Blanckenhorn 2005; Fairbairn 2007); and 3) the life span of the majority of Canadian freshwater fishes, typically between 4 – 9 years (Wootton 1984), makes it possible to follow individuals over multiple reproductive seasons.

Advances in tracking technologies are also providing an opportunity to address the challenges of properly understanding and describing the movement behaviour of freshwater species (Roussel et al. 2000). PIT-tags were used in this study because they have several advantages over other tagging systems that make them attractive in the study of movement behaviour in freshwater fishes:1) they are not restricted by climatic conditions that limit the use of traps, snorkelling surveys, or electrofishing (Zydlewski et al. 2001); 2) their small size (12 – 32mm) allows the study of smaller-bodied and juvenile life-stages of fishes, unlike larger radiotransmitters (Roussel et al. 2000; Fischer et al. 2001); 3) their relatively low cost compared to radiotransmitters makes larger-scale sampling and mark-recapture studies feasible (Castro-Santos et al. 1996); 4) PIT-tagging procedures are less invasive than other radiotelemetry methods (Skalski et al. 2001); 5) fish are detected automatically without the need to recapture or track individuals, unlike other radiotransmitters (Fischer et al. 2001; Bateman and Gresswell 2006); and 6) the longer life-span of PIT-tags compared to radiotransmitters allows for long-term studies on the movement behaviour of individuals (Ombredane et al. 1998; Roussel et al. 2000).

I used the movement behaviour of fishes for three different purposes in this study. First, I conducted a comparative study addressing whether information provided in natural history accounts could be applied to other populations of stream fishes. Successful conservation and recovery plans often rely upon the available knowledge regarding the movement behaviour of a species (Abell 2002; Poos et al. 2008). Unfortunately, this information is often limited or missing for many freshwater species (Abell 2002; Mandrak et al. 2003; Poos et al. 2008). Comparing my detailed quantitative data to the more qualitative information available in the literature can demonstrate the potential of using this latter source of information as a basis for management. Second, I used the arrival times of 17 species of stream fishes to conduct a broad test of four hypotheses for the sex-biased arrival of fishes at spawning sites, particularly the arrival of males before females at breeding areas (*i.e.* protandry) (Morbey and Ydenberg 2001). Because these hypotheses have been developed primarily for birds and mammals, my goal was to adapt, test and extend this theory to a complete community of freshwater fishes. Quantifying the incidence of, and the mechanisms for, the sex-biased timing of reproductive movements will allow the identification of general patterns and provide insights into the selection pressures affecting fishes during the mating season (Morbey 2000). Third, I assessed the management application for which the study was originally designed by examining the degree to which fishes move between adjacent streams. The rates of movement out of and between streams is likely important for understanding key ecological and micro-evolutionary processes, such as metapopulation dynamics, and the degree of gene flow and local adaptation, which will be useful for predicting the effects of dams and other barriers to movement. Hence, my thesis will: 1) provide an evaluation and advancement of existing natural history literature needed for successful conservation and recovery plans (Chapter 1); 2) extend existing theory on arrival timing to new taxa (Chapter 2) on a broad spatial and temporal scale; and 3) extend and contribute to a management concern of broad interest regarding invasive species control (Chapter 3).

Chapter 1: How well do historical natural history data predict the movement ecology of stream fishes?

Introduction

Human impacts on the biosphere are placing an increasing demand on scientists to provide information and solutions to help conserve native biodiversity and ecosystem services (Venter et al. 2006; Smith and Jones 2007). To date, most of the focus has been on the decline of species in terrestrial habitats, particularly those in the tropical forests, because these ecosystems are perceived to be in greater peril (Ricciardi and Rasmussen 1999). However, recent studies have suggested that freshwater fauna are more threatened than terrestrial species (Richter et al. 1997; Ricciardi and Rasmussen 1999). For example, North American freshwater biodiversity is decreasing at a rate of 1-8% of species per decade (Ricciardi and Rasmussen 1999), and the future extinction rates for freshwater fishes are projected to be several times greater than for terrestrial and marine fauna (Richter et al. 1997; Ricciardi and Rasmussen 1999). Twenty-one percent (n = 1851) of freshwater fishes that have been evaluated by the International Union for Conservation of Nature (IUCN) are considered to be threatened globally (IUCN 2010), and 30% of the freshwater and diadromous fishes in Canada have been assessed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as being at risk throughout all or parts of their ranges (Hutchings and Festa-Blanchet 2009; COSEWIC 2010).

Successful conservation and recovery plans rely upon the best available knowledge regarding the biology, ecology, and the life history of a species (Abell 2002; Poos et al.

2008). Unfortunately, detailed information on the population structure and life histories of many freshwater species, including many fishes, is often limited, anecdotal, or unavailable (Abell 2002; Mandrak et al. 2003; Poos et al. 2008). Decision makers are therefore faced with the decision of relying on existing natural history data, at the potential risk of inappropriate management or conservation actions should the existing data be incomplete or inaccurate (Smith and Jones 2007), or finding additional funding, resources, and time to collect the needed information (Smith and Jones 2007).

Understanding the movement behaviour and habitat use of fishes, including the degree of movement between streams, could be valuable for conservation and recovery plans. Many freshwater fishes require specific habitats to complete the different stages of their lifecycles (Lucas and Baras 2001). These habitats are often spatially separated, so individuals may move long distances, and between different tributaries or across bodies of water, to reach suitable habitats to meet their needs. These movements can affect reproductive fitness and help maintain metapopulation dynamics and stabilize fragmented populations via the rescue effect (Wilson et al. 2004; Primack 2008). However, until recently many freshwater fishes were assumed to be sedentary or exhibit restricted movement (Gerking 1959; Rodriguez 2002), due to imprecise and limited sampling. Results from more recent tracking studies have indicated that movement in many populations of stream fishes is more common, and more variable among populations and species, than previously thought (Lucas and Baras 2001; Rodriguez 2002; Mandrak et al. 2003). Some studies have reported partial migration, with individuals adopting migration or residency as alternative life-history strategies (Morinville and Rasmussen 2003).

New tracking technologies, such as PIT-tags, are affording opportunities to track the movements of small fishes more quantitatively, widely, and affordably (Roussel et al. 2000). This technology has been an effective and valuable tool in movement studies at the scale of single streams. When combined with strategically placed antennas, it can facilitate the collection of data on the movement behaviour and habitat use by individuals of different size and life-stage (Ombredane et al. 1998). Each tag has a unique identification code, making it possible to assign the data to a specific individual of known species, sex, length, weight, and sexual state, as well as its original stream of capture, allowing biologists to gather vital information on movement behaviour, habitat use, and growth of individuals. PIT tags have been used successfully to determine habitat use and movement behaviour in Atlantic salmon (*Salmo salar*), burbot (*Lota lota)*, brown trout (*Salmo trutta*), cutthroat trout (*Onchorhynchus clarkii clarkii*), and mottled sculpin (*Cottus bairdii*) (Nunnalle et al. 1998; Ombredane et al. 1998; Greenberg and Giller 2000; Fischer et al. 2001; Zydlewski et al. 2001; Breen et al. 2009; Zydlewski et al. 2009).

Information on the movement behaviour of many species is often limited, unavailable, or lacks quantitative evidence (Abell 2002; Mandrak et al. 2003; Poos et al. 2008). Most studies on freshwater fishes have focussed on species with commercial or recreational value (*i.e.* walleye, perch, and salmonids) (Northcote 1998; Lucas and Baras 2001; Knaepkens et al. 2004), invasive species (*i.e.* sea lamprey) (Bjerselius et al. 2000; Li et al. 1995), and model species for toxicology and monitoring (*i.e.* fathead minnow) (Russom et al. 1997; Ankley and Villeneuve 2006). Furthermore, relatively few studies focus on entire fish communities (Poos et al. 2008), scarce species, or those with low perceived importance (Northcote 1998; Lucas and Baras 2001; Knaepkens et al. 2004) despite their potential importance to food webs, biodiversity, and ecosystem services. The great diversity of freshwater fishes in the Laurentian Great Lakes offers a unique opportunity to study the ecology of movement and habitat use of multiple species. Approximately 145 species are native to the Great Lakes, with 108 of these co-occurring in Lake Ontario (Coon 1999).

This chapter uses data from a multi-species study of fish movements to assess the adequacy of qualitative literature information available for the habitat use and movement behaviour of stream fishes. My movement data for fishes were collected over three years from six adjacent tributaries of Lake Ontario. I captured over 15,000 individuals from 37 species, including more than 4,500 PIT-tagged individuals from 26 species. My assessment consisted of 4 steps. First, I tested whether arrival times in streams for the fish I tracked were related to water temperature, and then tested whether water temperature upon arrival in my study streams matched estimates of water temperature for arrival in literature accounts. Second, I recorded stage (juvenile/adult) and sex of individuals sampled in my study to infer which individuals were moving into the streams. Literature sources typically cite spawning as the reason for migration. However, large numbers of immature individuals entering streams would indicate that movements into the streams also occur for reasons other than reproduction. To test this, I also compared the water temperatures in the five main study streams with that of Lake Ontario to examine the possibility that differences in water temperature between the two bodies of water might influence why and when juveniles would enter the streams. Third, I compared stream residence times estimated for migrants in my study area with coarse estimates of residence times provided in the literature. Fourth, I compared the proportions of individuals using lake and stream habitats versus those using only stream habitats in my study with similar estimates based on literature reports indicating whether the species moved between lakes and rivers, within rivers, or were sedentary. Many species thought to be sedentary are classified as uncertain in the literature, so I treated these studies as though movements were only within rivers. While my comparisons do not consider all aspects of movement behaviour, they provide a reasonable test of the utility of some of the literature data on the movement behaviour of fishes that managers might acquire from the literature to inform their decisions.

Materials and Methods

Study sites

My study was conducted using fishes collected and tracked from late March to late June of 2005-2007 in six adjacent tributaries of Lake Ontario: Cobourg Brook (43° 57' 40" N 78° 10' 39" W), Covert Creek (43° 57' 35" N 78° 6' 25" W), Grafton Creek (43° 58' 3" N 78° 3' 20" W), Shelter Valley Creek (43° 57' 58" N 77° 59' 58" W), Colborne Creek (43° 58' 49" N 77° 54' 1" W), and Salem Creek (43° 59' 58" N 77° 49' 53" W) (Figure 1.1). Tributaries were 4.3 – 8.3 km apart (mean = 5.8 km) when measured from mouth to mouth. All tributaries had in-stream barriers located within 0.4 – 2.1 km (mean = 0.97 km) of the tributary mouth, which is common for tributaries in southern Ontario. Cobourg Brook, Grafton, Shelter Valley, and Colborne Creeks have low-head dams (~1.0 - 1.7 m in height) used to restrict the reproductive movements of invasive sea lamprey (*Petromyzon marinus*) (Porto et al. 1999; Baxter et al. 2003). Covert Creek has an elevated culvert ~ 1.0 m above the stream bed with no fishway. Salem Creek has an elevated culvert ~ 2.0 m above the stream bed with no fishway. Physical and hydraulic characteristics of the five main study streams are summarized in Appendix I.

Quantification of timing, size, and sex

Arrival of individuals from various species in each tributary was quantified using nets and monitoring stations for PIT-tags. Netting involved daily operation of hoop or trap nets in each tributary except Cobourg Brook. Hoop nets (Murphy and Willis 1996) were placed 80 – 685 m (mean = 300 m) from the stream mouth and used to sample the entire stream width in Covert (stretched mesh size 2.5 mm), Grafton (stretched mesh size 4 mm), and Salem Creeks (stretched mesh size 15 mm), and about 50% and 75% of Colborne (stretched mesh size 4 mm) and Shelter Valley Creeks (stretched mesh size 15 mm), respectively. Trap nets (Murphy and Willis 1996) (stretched mesh size 12.5 mm) were located 150 m (Shelter Valley Creek) and 170 m (Colborne Creek) from the stream mouth and used in Shelter Valley and Colborne Creeks in 2005 to supplement the hoop nets. Differences in mesh sizes are unlikely to have biased our results because even the largest mesh size used was able to catch some immature individuals of the smallest species. Nets were placed as close to the mouth of the tributary as possible. However, at Grafton, Shelter Valley, and Colborne, the nets could not be placed right at the mouth because the water was pond-like and too deep for effective netting, whereas at Covert, the stream mouth was difficult to access. Cobourg Brook was not sampled using nets, but was included in the study because a PIT-tag detection station from an earlier study (Pratt et al 2009) detected some of my PIT-tagged fish.

Each day, captured fish were identified to species, state of reproductive maturity, sex, scanned for the presence of a PIT-tag using a portable PIT-tag reader (Allflex RFID Portable

Reader), and measured for fork length to the nearest mm. The state of maturity and sex of an individual was determined by first squeezing its abdomen for the presence of eggs or milt and then by examining for the presence of conspicuous secondary sexual traits (Appendix II), using sexually dimorphic traits described in the literature (Scott and Crossman 1998; Holm et al. 2009). Individuals were classified as unknown gender if they lacked identifiable sexual attributes, but were assessed to be large enough to mature later in the spawning season based on size at maturity estimates from the literature (Scott and Crossman 1998). Males, females, and individuals of unknown gender were also referred to as adult individuals in some analyses. Individuals were classified as juveniles if they were smaller than the normal size at maturity and consistently displayed no evidence of being reproductive.

PIT-tagging

Unmarked individuals of all species greater than 100 mm in fork length were PIT-tagged. Individuals were anesthetised in a bath of 0.2 ml/L clove oil until loss of equilibrium. A surgical incision was made in the ventral cavity, 4-5 mm off of the midline and just anterior of the pelvic girdle (for teleost fishes; Adams et al. 1998), or 1-2 mm off the midline anterior of the gills slits, where the first dorsal fin begins (for sea lamprey). A half-duplex PIT-tag (23 X 4 mm) (Oregon RFID) was then inserted into the body cavity. The incision was closed using external tissue adhesive (3M™ Vetbond™ Tissue Adhesive, 3M, St. Paul, MN). The individual was allowed to recover in a 68 L container filled with fresh stream water and released several metres upstream of the capture point. Loss or shedding of PIT-tags was not measured; however, only 15 of 564 (2.7%) individuals recaptured over the course of the three-year project had an obvious scar at the incision point, but no detectable

PIT-tag. Tagging mortality was ~1.4%, with 62 dead individuals recovered within 5 days following tagging, comparable to other studies using similar techniques(Sigourney et al. 2005; Bateman and Gresswell 2006). Only one individual died during the ~20-30 minute recovery period prior to being released in the streams.

Quantification of movement

Movement of PIT-tagged fishes into, within, and between the study streams was monitored from March to late-June of 2005 – 2007 using two PIT-tag detection arrays per stream. Each array consisted of two antennae placed 2.3 – 17.4 m apart (mean = 6.7 m), spanning the width of the stream (details of operation in Appendix I). For each stream, the downstream array was positioned 21 – 240 m from the stream mouth (mean = 110 m). Downstream arrays were positioned as close to the mouths of the streams as possible given the constraints on accessibility and the effects stream width and depth can have on the efficiency of the antennae. The upstream array was positioned just downstream of the first in-stream barrier to fish movement, 370 – 2030 m from the stream mouth (mean = 970 m). Additionally, in 2006 and 2007, a third antenna was placed above the barrier, approximately 10 m from the barrier at Grafton, Shelter Valley, and Colborne creeks, to detect fish passing over the barrier. Arrays recorded the PIT-tag number, date, and time a tagged fish was detected passing an antenna. Details of antenna efficiency are discussed in the Appendix section of this thesis.

All arrays were powered by deep cycle marine batteries. Batteries were exchanged every 7 days, on average. At that time, the data were downloaded and a test tag was passed within the loop of both antennae at the array, over the entire length of the antenna located in the stream, to ensure that the antennae were properly detecting PIT-tags. If needed, the antennae were calibrated to ensure maximum tag detection.

Stream and lake water temperature

Water temperature was measured in 2007 for each of the five main study streams from 23 April to 27 June and for Lake Ontario close to the mouths of the streams from 6 May – 25 June. Stream water temperatures were recorded using a HOBO Pendant Temperature/Alarm Data Logger model UA-001-08 (Onset Computer Corporation, Bourne, MA). Each logger was secured within a 15cm piece of polyvinyl chloride (PVC) piping, attached to the upstream antennae in flowing water, and set to record water temperature at 15 minute intervals. Data were downloaded when the antennae were removed at the end of the field season. Lake water temperature was recorded using generic min/max submersible water thermometers. Each thermometer was attached to a 20cm × 20cm × 41cm cinder block using a 1m long nylon rope, and placed 10-20m from shore at locations close to the mouths of the five main study streams, at a depth of ~1.2m. Lake water temperature was recorded daily and the thermometer reset.

Data analysis

Water temperatures at the time of arrival (step 1)

I tested whether arrival times in streams for the fish I tracked were related to spawning migrations cited in the literature. However, spawning times reported in the literature usually covered an extended period (*e.g.* May – June), or were imprecise (*e.g.* late-spring), so I used water temperatures reported in the literature for spawning as a surrogate for arrival time. This analysis was addressed in two parts. I first tested whether arrival times were related to water temperature and then related water temperatures observed in my study with those reported in the broader literature. Arrival date was estimated as the median arrival time of all adult-sized individuals for a species from the telemetry and net-capture data. Next, I determined the water temperature for each yearly sample that corresponded to the overall median arrival time of the species. The stream water temperature of all yearly samples with adult-sized individuals was used to account for variance in water temperature among streams. Mean water temperature was then calculated as the average of all yearly samples for a species. I included only species with a total of 10 adult-sized individuals in each year of the study. I chose 10 individuals in each year to provide a reasonable estimate of water temperature for each species and yet to maximize the sample size. In total, 11415 adult-sized individuals from 18 species were included in the analysis. The relationship between median arrival time and mean water temperature from this study were compared by two-tailed Pearson correlation.

Second, I related the mean water temperature at arrival for the fishes in this study and compared those values with temperatures from the literature to determine if movements into the streams correspond to spawning migrations. Mean water temperatures at arrival for species in this study were determined from the above analysis. Water temperature when a species typically arrives at the streams from the literature was obtained from Portt et al. (1988) and Scott and Crossman (1998). These studies typically report the water temperature at which a species first moves to spawning sites; hence they are a good approximation of relative arrival time given that water temperatures typically increase over the spring and early-summer. Whenever possible, the exact value cited in the literature was used. When a range was given, I used the mid-point of the range. The two data sets were then compared by two-tailed Pearson correlation.

Biological reasons for using stream habitat (step 2)

I used the information collected on reproductive status, sex, and size relative to size at maturity to infer whether individuals were moving into the streams for reproductive or non-reproductive purposes. Non-reproductive purposes, such as foraging or seeking refuge, was suggested by the presence of juvenile sized fish that were not producing milt or eggs. For these fish, I had no way of determining the specific purpose for movement into the streams. Only species with a minimum of 10 adult-sized individuals were included in the analysis to provide a reasonable estimate for each species and yet maximize the sample size. A total of 11442 individuals from 28 species were used in the final analysis.

Next, I compared the water temperatures in the five main study streams with that of Lake Ontario to examine the possibility that differences in water temperature might influence why and when individuals would enter the streams. Warmer waters typically have greater primary productivity and hence higher growth potential (Kishi et al. 2005). I hypothesized that fish, particularly juveniles, would move towards warmer stream habitats in the spring, and move back to the lake over the course of the summer when stream water temperatures likely approached the thermal tolerance limits of the species (Kishi et al. 2005). I used the maximum water temperature recorded by the stream loggers in a 24hr period and the maximum lake-water temperature recorded by the min-max thermometer for each study location for that day to compare between lake and stream habitats. Water temperature data were presented for only four of the five study streams because of a loss of equipment in

Shelter Valley Creek. I used one-way ANOVA to determine if water temperature differed between habitats, with habitat (lake vs. stream) as a fixed factor, study stream as a random factor, and water temperature as my dependant variable. Stream was included as a random factor because, although there might be differences in water temperature between streams, I was particularly interested in differences in water temperature between the streams and the lake.

Time spent in the streams (step 3)

The time spent in the streams was quantified only for individuals detected leaving a stream, as the difference between an individual's arrival and departure dates. These values were then aggregated and used to calculate the mean time spent in the streams for each species. Only species with minimum of 10 individuals detected leaving the streams over the three years were used to provide a reasonable estimate of time spent in the streams for each species and yet to maximize the sample size. A total 1279 adult-sized individuals from 12 species were used in the final analysis. Although the analyses of time spent in the streams ignored fish departing after the field season and individuals that remained in the streams, which likely underestimated duration times, my goal was to estimate the time spent in stream habitats for each species. I used 2-way ANOVA without replication (Sokal and Rohlf 1969) to determine if the time spent in the streams differed between species and between years, with species and year as fixed factors, and mean duration time as the dependant variable.

Literature accounts for time spent in the streams for most species were obtained from Scott and Crossman (1998). Additional information was obtained for lake chub (Brown et al. 1970), pumpkinseed (Danylchuk and Fox 1996), rock bass (Gross and Nowell 1980), and smallmouth bass (Brown et al. 2009). Whenever possible, the exact value cited in the literature was used. When a range was provided, I used the mid-point of the range.

I compared the mean time spent in the streams of adult-sized individuals from this study to literature data for each species to determine if the time adult-sized individuals spent in the streams was related to spawning. The mean time spent in the streams for each individual in this study was calculated using the procedures described in the previous section. Rainbow trout were excluded from this comparison because many adults had already arrived in the streams prior to net placement and were not tagged, and would have likely biased the results. Also, brook charr were excluded from the analysis because this species spawns in the fall, and estimates on time spent in the streams from the literature are typically given for the spawning season. To be included in the analysis, each yearly sample consisted of a minimum of 10 adult-sized individuals to provide a reasonable estimate of time spent in the streams for each species and yet to maximize the sample size. The two data sets were then compared by two-tailed Pearson correlation. Overall, 1121 adult-sized individuals from 9 species were analysed.

Relative use of stream and lake habitats (step 4)

Telemetry data from the antennae arrays were used to determine a species relative use of stream and lake habitats. To determine the relative habitat use of species, PIT-tagged individuals were assigned to one of four categories based on their tracking histories. Individual fish were categorized as: (1) never detected after tagging (fish with unknown histories); (2) detected only in their original stream of capture (by either the upstream or downstream arrays), or recaptured in the nets operated in their original stream of capture and tagging (residents); (3) detected by both antennae in the lower array in the correct temporal order, or detected on only the downstream antenna of the lower array and never detected or recaptured afterwards (emigrants); and (4) detected or recaptured in another stream (inter-stream migrants). Categories were then aggregated for each species to identify individuals that only used the stream habitat (categories 1 and 2) or used both stream and lake habitat (categories 3 and 4) and then used to estimate the proportion of individuals that used the lake. Individuals from category 1 were treated as stream residents that did not move far enough to be detected by the arrays or be recaptured in the nets, or possibly died shortly after tagging. A study of stream fish combining similar tagging and tracking techniques with electrofishing surveys and stable isotope analysis determined that individuals with unknown histories were stream residents (Coppaway 2011). Individuals from categories 3 and 4 were combined because they likely, and definitely, left the streams for Lake Ontario, respectively. Only species with a minimum of 10 individuals (total of adult-sized individuals and juveniles) were ranked for the propensity of a species' relative use of stream or lake habitat to provide a reasonable estimate for each species and yet to maximize the sample size. Overall, 4864 individuals from 18 species were used in the analysis.

Literature estimates of habitat use were made using information provided from the Fish Migration and Passage Knowledgebase (http://fishmap.uoguelph.ca/). Species were classified as moving between lakes and rivers (*i.e.* use of lake habitat), moving within rivers (*i.e.* use of stream habitat), or as having their movement behaviour described as uncertain (Mandrak et al. 2003). A species was listed as uncertain when there was no information provided to indicate the species moved significant distances over its life span. However, many species classified as uncertain are also thought to be stream resident, but there was inadequate data to support this conclusion (Mandrak et al. 2003); nonetheless I treated these as if they were stream resident for this analysis. These studies were then added to the studies reporting movement within rivers. Relative use of lake habitat for species in the literature was calculated as the number of studies reporting movements between lakes and rivers divided by the sum of all studies.

For my comparison, one species (round goby) was removed because measures of habitat use from the database are lacking and the species is still invading part of the Great Lakes and hence not at equilibrium in terms of habitat occurrence. Sea lamprey were also excluded from the analysis because this species is semelparous with adults dying after spawning, and results regarding the relative use of lake habitat from this study might not be comparable with those from the literature. Relative habitat use from this study were then compared to those estimated from the literature. In addition, four species considered in the analysis are known to move between lakes and rivers in an "anadromous-like" life cycle (*i.e.* lake chub, rainbow smelt, rainbow trout, and white sucker). Therefore I also estimated habitat use for these species as though all individuals were detected emigrating from the streams (*i.e.* 100% use of lake habitat rather than actual values from this study) to test if these species move more extensively or not. The two measures of habitat use were compared using two-tailed Pearson correlation. It is important to note that although the calculated relative use of lake habitat between the two data sets were collected from different sources, my intention was to compare the relative use of different habitats in this study compared to the literature. All analyses were done using SPSS v12.0.1, with a critical level of significance set at 0.05.

Results

Overall, 15,375 individuals from 37 species were caught during the study, including 5143 females, 3811 males, 2538 adult sized individuals of unknown sex, and 3883 juveniles (Appendix III). Of these, 4586 individuals from 26 species were PIT tagged, consisting of 1174 females, 1031 males, 827 individuals of unknown sex, and 1554 juveniles.

Water temperature at the time of arrival

Median arrival times of adult-sized individuals for the 18 species analysed was positively correlated with the mean stream water temperatures in this study (two-tailed Pearson correlation, $r = 0.83$, $n = 18$, $p < 0.001$), with earlier arrival corresponding to lower stream water temperatures (Figure 1.2a). When only spring spawning species were considered, there was again a significant positive correlation between median arrival date and stream water temperatures in this study (two-tailed Pearson correlation, $r = 0.75$, $n = 16$, $p = 0.001$).

Stream-water temperatures at arrival in this study were positively correlated with those cited in the literature for spawning. For the 18 species with a minimum of 10 individuals in each year of the study, mean stream-water temperature at arrival in this study was highly correlated with values of water temperatures cited in the literature for spawning (two-tailed Pearson correlation, $r = 0.59$, $n = 18$, $p = 0.01$) (Figure 1.2b). Similarly, when only spring spawning species were considered, there was again a significant positive correlation between stream water temperature at arrival in this study and stream water temperatures cited in the literature for spawning (two-tailed Pearson correlation, $r = 0.55$, $n = 16$, $p = 0.029$). Nonetheless, when examining the slope (0.25) and intercept (12.48) of the relationship, the slope differed from 1 (95% CI = 0.07 - 0.42), and the intercept differed from 0 (95% CI = 9.60 - 15.35). However, because of error in the estimation of the X variable, I also calculated the slope (0.41) using model II regression (Sokal and Rolff 1969); however, the resulting slope still differed from 1 (95% CI = 0.23 - 0.59).

Biological reasons for using stream habitats

Many individuals from a variety of species were moving for reasons other than reproduction. A total of 7547 of 15375 individuals (49.1%) entering the streams were in spawning condition. When only adult-sized individuals were considered (males, females, and individuals of unknown gender), 65.8% of individuals entered the streams in spawning condition, and this number increased to 84.3% when only males and females were considered. Of the 28 species with at least 10 adult-sized individuals captured, 27 spawn during the spring, whereas only one species, brook charr, spawn during the fall. Only 2 of the 27 spring spawning species had no individuals in spawning condition, whereas 15 of the 27 had more than 50% in spawning condition (Table 1.1). All individuals of the fall-spawning species were not in spawning condition (Figure 1.3, Appendix IV).

Individuals in non-spawning condition (unknown sex, adult-sized immature and juveniles) represented half of all individuals captured (50.1%) for spring-spawning species. Juveniles alone made up ~25% of all individuals captured (*n* = 3909) and the proportion of individuals in non-spawning condition varied considerably among species. The proportion of individuals in non-spawning condition was high (64.4 – 96.8%) in rainbow trout, brown bullhead, round goby, yellow perch, emerald shiner, mottled sculpin, rock bass, and pumpkinseed, and low (0.80 – 37.9%) for sea lamprey, rainbow smelt, longnose dace, northern redbelly dace, bluntnose minnow, common shiner, golden shiner, blacknose dace, and fathead minnow (Table 1.1).

I also compared the water temperature between the streams and lake because differences between the two habitats might influence why individuals in non-spawning condition, particularly juveniles, entered the streams. Water temperature differed significantly between the streams and the lake (Randomized block by stream, one-way ANOVA, habitat effect: $F_{[1, 198]} = 46.12$, $p = 0.006$), with mean water temperatures consistently higher in the streams (16.72 ±SD 2.7°C) than in the lake (12.18 ±SD 2.0°C) (Figure 1.4). On average, all four streams were warmer than the lake: Colborne Creek (mean difference = 6.3°C); Covert Creek (4.8°C); Grafton Creek (4.2°C); and Salem Creek (3.0°C). No comparison was possible for Shelter Valley Creek because of a loss of equipment.

Time spent in the tributaries

Mean time that individuals spent in the streams differed significantly among the 12 species analysed (2-way ANOVA, species effect: $F_{[11, 22]} = 2.33$, $p = 0.044$). On average, adult-sized individuals of all species spent 9.3 days in the streams. Durations ranged from 1.3 days for brook charr to 23.0 days for smallmouth bass (Table 1.2). Time spent in the streams also did not differ significantly among years (2-way ANOVA, year effect: $F_{[2, 22]} = 2.77$, $p = 0.084$).

I also tested if the mean time spent in the streams was related to the median arrival date of a species, since the estimated length of time an individual could spend in the stream is likely dependent on the length of time between when an individual was tagged and when the antennae were removed (henceforth referred to as “time at large”). For the 12 species with at least 10 adult-sized individuals, there was no significant correlation between median arrival date and the mean time spent in the streams (two-tailed Pearson correlation, $r = 0.12$, $n = 12$, $p = 0.70$), suggesting that the time spent in the stream did not differ between individuals tagged shortly before the removal of the antennae compared to individuals tagged early in the season.

Estimated times spent in the streams of adult-sized individuals (rainbow trout and brook charr were excluded) corresponded reasonably well with estimates provided in the literature (two-tailed Pearson correlation, $r = 0.79$, $n = 9$, $p = 0.012$) (Figure 1.5). Time spent in the stream was noticeably underestimated in three species; common shiner, brown bullhead, and pumpkinseed; the latter two species were some of the last to arrive at the streams. Furthermore, when examining the slope (0.88) and intercept (-1.50) of the relationship, the slope did not differ from 1 (95% CI = 0.27 - 1.5), and the intercept did not differ from 0 (95% CI = -10.85 - 7.84). However, because of error in the estimation of the X variable, I also calculated the slope (1.12) using model II regression (Sokal and Rolff 1969). The resulting slope also did not differ from 1 (95% CI = 0.50 - 1.73).

Relative use of lake and stream habitats

For the 18 species with at least 10 individuals of all age classes ($n = 4864$), there was considerable variation in their relative use of lake habitat, as indicated by the differences in proportion of individuals leaving a stream (categories 3 + 4) versus remaining in the stream (G-test: $G = 2354.42$, df = 17, $p < 0.001$) (Table 1.3; Figure 1.6). Species on the stream-resident end of the spectrum included creek chub (9.1% using the lake), brook charr (12.3%), longnose dace (17.0%), brown trout (19.2%), logperch (30.0%), largemouth bass (30.0%), and common shiner (31.9%) (Figure 1.6). Species more toward the lake end of the spectrum included brown bullhead (42.4%), pumpkinseed (43.3%), rock bass (49.6%), yellow perch (52.6%), and smallmouth bass (75.0%).

The relative use of stream habitat differed significantly in species known to undertake “anadromous-like” spawning migrations (*i.e.* moving between lakes and streams) (*G*-test: $G = 866.59$, df = 5, $p < 0.001$). For example, rainbow smelt (10.5% use of lake habitat), sea lamprey (32.6%), and rainbow trout (35.5%) were on the stream-resident end of the continuum, whereas lake chub (73.7%) were detected more often leaving for the lake. White sucker were observed to use both stream and lake habitat almost equally (47.6%). Differences between the relative habitat use estimated in this study compared to the expected based on life-history could possibly indicate that these populations exhibit partial migration.

I compared the relative use of lake habitat in the literature (Table 1.4) to those reported in this study (*i.e.* categories 3 + 4). Percent use of lake habitat in my study did not correlate with that reported in the literature (two-tailed Pearson correlation, $r = 0.04$, $n = 16$, $p = 0.89$), nor when known "anadromous" species were removed from the analysis (two-tailed Pearson correlation, $r = 0.05$, $n = 12$, $p = 0.88$) (Table 1.4; Figure 1.7a). However, when known "anadromous" species were assumed to have 100% use of lake habitat (excluding sea lamprey), there was a significant positive correlation between the habitat use in this study compared to that reported in the literature (two-tailed Pearson correlation, $r = 0.69$ $n = 16$, $p = 0.003$) (Figure 1.7b).

Discussion

My assessment suggests that natural history information from the literature coarsely captures some of the movement ecology of stream fishes, but is also inadequate in some respects. Based on the significant correlations, literature data on the timing of arrival at the streams, water temperature at arrival, and the time spent in the streams were good predictors of the patterns in my data, whereas the relative use of the lake was not. Furthermore, an analysis of the stage classes moving revealed a novel finding: in many species juveniles were also moving into streams. However, when the slope and intercept of the relationship were analysed against a 1:1 line, time spent in the streams waswell predicted by the literature data but temperature was not. The results of the model II regression illustrated important quantitative differences between the two data sets regarding the water temperature at arrival. While I cannot provide an explanation for all outliers, I can speculate on some. For example, brook charr spawn in the fall, and hence water temperatures reported in this study are likely not representative of the spawning temperatures cited in the literature (Figure 1.2b). Similarly, the movements observed for brown bullhead are not likely for spawning purposes - this species is known to provide parental care (Scott and Crossman 1998), and yet individuals were detected leaving significantly earlier than cited in the literature (Figure 1.5). This might also explain the lower than predicted water temperature at arrival observed for this species (Figure 1.2b). Finally, adult rainbow trout had likely arrived in the streams prior to net placement, which could explain the warmer temperatures at arrival than cited in the literature (Figure 1.2b). As such, fishery managers can use natural history information to gain coarse insights into the movement ecology of fishes, but should also recognize that this information remains incomplete in important ways.

Natural history information from the literature adequately captured some key aspects regarding the movement ecology of stream fishes. The biological reasons commonly provided for fish moving into the streams are reproduction, foraging, and seeking refuge from predators or less hospitable environmental conditions (Northcote 1997; Lucas and Baras 2001). Comparisons between data from this study and the natural history literature regarding the timing of arrival, water temperature at arrival, and the time spent in the streams suggests that adult individuals were likely moving into the streams to reproduce, with a large proportion of the fish moving into streams in spawning condition. This timing was also consistent across years, illustrating the seasonal and temporal predictability of these movements into the streams for these species (Hendry et al. 2004a). The fact that there was good similarity with the natural history literature regarding these aspects of the movement ecology of stream fishes has important implications for conservation and management plans, since these plans are often made based on available existing (historical) data because comprehensive and rigorous field surveys are often expensive or time consuming (Smith and Jones 2007). For example, information regarding the timing of arrival to streams has implications for the timing of construction activities, so as to minimize the impact these activities might have on stream fish populations, particularly during the spawning run. Results from this study suggest that in such cases, available natural history information from the literature regarding the movement behaviour of a species can be used with some confidence in decisions regarding freshwater stream fishes when recent studies are not available.

Natural history information from the literature did not adequately capture the use of stream or lake habitat of species in this study; however this was most likely because of differences in sampling design between my study and the literature. Natural history literature are often compared with current surveys to assess, for example, changes in the biological community, as well as to identify areas of high endemism and biodiversity, which can introduce biases and lead to inappropriate management or conservation actions, particularly when different sampling protocols are used (Smith and Jones 2007). For example, information on habitat use from the literature is often based on studies reporting the occurrence of a species (Smith and Jones 2007), whereas data from this study on the relative use of lake habitat were based on the proportion of individuals leaving the streams for the lake. The relative use of lake habitat for the sea lamprey provide a perfect example of this bias, with proportionately more studies citing the use of lake habitat from the literature (0.90) than from this study (0.33). This is not surprising given that juveniles of this species are known to leave streams for the lake to grow before returning to the streams to spawn (literature accounts of occurrence), while adults die shortly after spawning; hence few adult individuals would be expected to leave the streams (this study) (Beamish 1980). However, fisheries managers should not dismiss biological information simply because of possible uncertainties (Peterman 2004), but the limitations and biases of comparing natural history data to field studies should be made clear, illustrating the need to interpret such comparisons with caution (Smith and Jones 2007).

The occurrence of juveniles moving into streams suggests that there were also individuals moving into the streams for reasons other than reproduction. However, most studies make no reference to juvenile life-stages, limiting the information available regarding movement and habitat use in the natural history literature. Streams are particularly important for the juvenile age-classes, as they provide habitats where individuals could maximize growth during specific parts of the season, as well as areas where individuals can seek refuge (Northcote 1997; Lucas and Baras 2001; Salas and Snyder 2010). Foraging and refuge habitats are often similar in terms of spatial location and habitat characteristics, particularly in stream fishes (Lucas and Baras 2001). Juveniles could have entered stream habitats to escape predators in the lake because the lake tends to be predator-rich environment compared to the small streams (Jepsen et al. 1998; Olsson and Greenberg 2004). The warmer water temperatures in the streams relative to the lake during spring could also provide a thermal refuge for juveniles (Power et al. 1999; Torgersen et al. 1999), with juveniles moving back to the lake later in summer when stream water temperatures increase toward the thermal tolerance limits of each species (Kishi et. al. 2005). The streams could have also served as foraging habitats for juvenile fish, either due to the higher productivity of warmer stream waters compared to the lake in the spring (Mallet et al. 1999; Morin et al. 1999, Kishi et al. 2005; Bal et al. 2011), or as an opportunity by juveniles to feed on the eggs of their own or other species (Scott and Crossman 1998). Finally, juveniles might move into streams to acquire information spawning locations and behaviour that they will use later in life (Dodson 1988; Lucas and Baras, 2001). Whatever the reason for juveniles entering the streams, their presence was apparent in my field study, is rarely mentioned in the natural history accounts, and could be a topic important to ecological assessments and worthy of additional research.

Movements between lakes and its tributaries may be more common than previously thought based on the numbers of individuals detected emigrating from the streams in this study. Traditionally, stream fishes were viewed as exhibiting restricted movement, remaining in a specific area for a large portion of their lives (Gerking 1959; Gowan et al. 1994; Smithson and Johnston 1999; Lucas and Baras 2001; Rodriguez 2002). Recent studies, however, have suggested that stream fishes move more often and farther than previously thought (Gowan and Fausch 1996; Lucas and Baras 2001; Rodriguez 2002; Mandrak et al. 2003), and individuals within populations exhibit considerable variability in movement behaviour (Gowan and Fausch 1996; Young 1996; Hutchings and Gerber 2002). Furthermore, studies have also identified populations demonstrating partial migration, a phenomenon commonly observed in salmonids, with individuals adopting migration or residency as a life-history strategy (Finlay et al. 2002; Morinville and Rasmussen 2003; Swanson et al. 2010). It is possible that this strategy might also be more common in other freshwater fishes thought to be stream resident. With advances in tagging and tracking technologies (*i.e.* PIT-tags) combined with improved study designs, the opportunity now exists for future studies to measure the movement behaviour of stream fishes with more precision, comprehensiveness, and rigour.

Although the natural history data on timing and nature of movements are representative for larger species, they remain to be assessed for small bodied fishes. Few field studies have examined the movement behaviour and use of habitat in small-bodied freshwater fishes (Bruyndoncx et al. 2002; Cookingham and Ruetz 2008; Breen et al. 2009), with most studies focusing on species with commercial or recreational importance (*i.e.* salmonids; Ombredane et al. 1998; Roussel et al. 2000; Zydlewski et al. 2001; Letcher et al. 2002; Sigourney et al. 2005; Bateman and Gresswell 2006). Studies on smaller-bodied fishes often precludes the use of electronic tags (*i.e*. PIT-tags), which can adversely affect tagging mortality in smaller individuals (Roussell et al. 2000), limiting both the types and numbers of fish that could be followed. Indeed, of all fishes categorized as small-bodied, I was able to gather information on the habitat use and movement behaviour of only one species, the longnose dace (Table 1.4). Improvements in tagging technologies, as well as the recognition of the importance of smaller-bodied fishes to biodiversity and ecosystem services, could potentially increase the number and type of fishes that could be tracked, and provide novel insights regarding the movement behaviour and use of habitat in these smaller-bodied freshwater fishes (Roussel et al. 2000; Fischer et al. 2001).

Scientists believe that the quality of conservation or recovery plans can be improved by the addition of more biological information (Abell 2002; Poos et al. 2008). However, the ability to implement and the success of these plans can be limited if information regarding life history and movement behaviour is anecdotal, qualitative, or simply unavailable (Mandrak et al. 2003; Smith and Jones 2007). Despite this, conservation and management plans are often made based on available existing (historical) data because comprehensive and rigorous field surveys are often expensive or time consuming (Smith and Jones 2007). Results from this study suggest that in such cases, available natural history information from the literature regarding the movement behaviour of a species can be used when recent studies are not available. However, these data also include limitations and biases due to differences in sampling protocols, sampling efforts, incomplete sampling, and limited tracking ability of existing datasets (Smith and Jones 2007).

Table 1.1: Inferred reasons for movements into the streams based on the proportion of adult-sized individuals in spawning condition captured in streams for each of 30 species (with a minimum of 10 total individuals), and the proportion of juveniles for each species.

Species	Total	Proportion of adult-sized individuals in spawning condition	Use of streams[1]	Proportion juveniles
banded killifish	17	0.00	non-reproductive	0.00
blacknose dace	1252	0.67	reproductive	0.04
bluntnose minnow	695	0.73	reproductive	0.00
brook charr	116	0.00	non-reproductive	0.20
brook stickleback	354	0.55	reproductive	0.07
brown bullhead	175	0.06	non-reproductive	0.34
brown trout	78	0.00	non-reproductive	0.94
chinook salmon[2]	230	—	non-reproductive	1.00
common shiner	314	0.72	reproductive	0.09
creek chub	1717	0.69	reproductive	0.18
emerald shiner	275	0.18	non-reproductive	0.09
fathead minnow	832	0.64	reproductive	0.03
golden shiner	119	0.68	reproductive	0.05
Johnny darter	216	0.53	reproductive	0.11
lake chub	105	0.45	non-reproductive	0.00
largemouth bass	11	0.10	non-reproductive	0.09
logperch	14	0.85	reproductive	0.07
longnose dace	2030	0.79	reproductive	0.00
mottled sculpin	55	0.27	non-reproductive	0.13
northern redbelly dace	1388	0.77	reproductive	0.01

pumpkinseed	208	0.42	non-reproductive	0.15
rainbow smelt	30	0.87	reproductive	0.00
rainbow trout	2141	0.65	reproductive	0.95
rock bass	389	0.29	non-reproductive	0.13
round goby	400	0.34	non-reproductive	0.87
sea lamprey	490	0.99	reproductive	0.00
smallmouth bass	13	0.31	non-reproductive	0.00
three-spine stickleback	14	0.00	non-reproductive	0.00
white sucker	1497	0.64	reproductive	0.35
yellow perch	179	0.05	non-reproductive	0.02

Note: [1]use of streams for reproduction if > 50% of adult-sized individuals were sexually mature; [2]no adults were captured for this species.

Table 1.2: Median date of arrival at, departure from, and duration (time spent) in the study streams by adult-sized (males, females, and individuals of unknown gender) individuals summarized by species and year, in order of median arrival date, as well as the overall median arrival date, departure date, and duration of all adult-sized individuals and juveniles (juv.) for each species.

	Arrival date					**Departure date**					**Duration (days)**	
	Year			**Overall median**		**Year**			**Overall median**		**Overall mean**	
Species	**2005**	**2006**	**2007**	**Adults**	**Juv.**	**2005**	**2006**	**2007**	**Adults**	**Juv.**	**Adults**	**Juv.**
white sucker	138.4	108.5	116.9	121.5	143.7	171.9	128.1	120.0	143.3	170.2	13.3	10.6
rainbow trout	136.4	110.7	123.5	121.6	139.5	148.9	120.1	136.0	130.9	150.9	3.4	4.1
emerald shiner	157.0	147.4	140.6	141.8	156.7							
sea lamprey	160.2	137.5	154.0	146.7		167.8	141.7	158.0	147.7		2.5	
yellow perch	161.5	145.5	161.6	149.7	172.4	178.9	135.9	145.7	165.2		8.5	
bluntnose minnow	156.7	152.4	149.4	150.4	142.6							
brook charr	153.8	135.4	151.6	151.1	153.5	163.2	134.4	157.0	156.1	154.2	1.3	0.3
creek chub	149.5	153.6	153.5	152.5	157.6	161.6	158.9	153.8	156.6		10.0	
longnose dace	160.6	151.4	142.6	153.5	150.1							
fathead minnow	139.0	146.4	155.5	153.6	170.5							
Johnny darter	153.9	150.4	161.0	154.4	149.6							
common shiner	155.5	155.4	154.7	155.4	157.4	165.0	168.9	164.9	166.0		7.9	

lake chub	159.7	152.3	151.0	156.5		160.9	157.1	158.4	160.4	5.0	
rock bass	160.5	151.4	153.4	157.7	131.6	177.1	186.2	173.9	177.9	20.1	
northern redbelly dace	157.6	167.4	154.6	158.5	157.6						
brown bullhead	160.7	150.0	141.5	159.5		164.9	173.7	160.9	164.9	6.2	27.0
blacknose dace	155.6	165.4	161.5	160.6	132.5						
brook stickleback	154.4	154.1	172.4	160.6	156.5						
pumpkinseed	171.5	167.7	170.6	169.7	170.6	170.7	180.4	189.3	177.6	10.0	
smallmouth bass*						159.1	157.1	181.3	168.6	23.0	

Note: *Smallmouth bass were not included in the analysis of arrival times because fewer than 10 individuals were captured in each year of the study, but were included in the analyses of time spent in the streams (duration) because more than 10 individuals were detected leaving the streams.

Table 1.3: The movement behaviour of all PIT-tagged individuals (n = 4888) including individuals detected on the antennae in subsequent years, summarized by species, gender, where they were detected, and the percentage of all individuals detected leaving the streams. Percentage of fish leaving a stream was calculated only for species with at least 10 individuals. Detection categories were: 1 = never detected after tagging; 2 = detected only in stream of capture; 3 = detected leaving a stream; and 4 = moved to another stream.

	Gender																
	Adult-sized individuals												**Juveniles**				
	Female				**Male**				**Unknown**								
	Detection																
Species	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**Left stream**
blacknose dace									1		1						—
brook charr					1	3			11	66	7	5	4	8		1	12.3%
brown bullhead		1	5	1					47	19	44	4	13	19	18	1	42.4%
brown trout										4	3		17	21	7		19.2%
central stoneroller	1																—
chinook salmon													5	2	1		—
common shiner	1	3	2	2	17	28	15	4									31.9%
creek chub	233	202	31	1	70	120	31			1							9.1%
emerald shiner							1				2						—
golden shiner			2							1	2						—
hornyhead chub					1												—
lake chub	9	5	30	2	2	9	38										73.7%
largemouth bass		1								6	3						30.0%

logperch	2	1	2		2	1				1	1						30.0%
longnose dace	14	17	6	1	2	3	1		2	1							17.0%
mottled sculpin										1							—
northern pike										1	1		1				—
pumpkinseed	4	3	3			3	8	4	22	6	9	5					43.3%
rainbow smelt	7				6		2		4								10.5%
rainbow trout	5	3	9	1	9	13	25	3	8	4	8	2	429	359	381	28	35.5%
rock bass	5	28	41	4	4	12	22	5	65	97	128	8					49.6%
round goby	1	4	2			1				2							20.0%
sea lamprey	55	76	61	3	71	123	83	11	3		1						32.6%
smallmouth bass		1	1			1	1		1	2	3	10					75.0%
white sucker	108	80	156	35	79	84	139	25	50	66	160	3	135	60	82	2	47.6%
yellow perch							4	1	10	8	15						52.6%
Total	445	425	351	50	264	401	370	53	224	286	388	37	604	469	489	32	36.2%

Table 1.4: The number of studies reporting on the movement behaviour of fishes between lakes and rivers (use of lake habitat), within rivers only (use of stream habitat), and where movement behaviour was uncertain, the percentage of studies categorizing movement behaviour as uncertain (% uncertain) (Migration and Passage Knowledge Database; Mandrak et al. 2003), for species with at least 10 individuals in this study, the proportion of literature studies citing the use of lake habitat and the proportion of individuals detected leaving the streams from this study (Categories 3 + 4).

	Movement behaviour					
Common Name	between lakes and rivers	within rivers	Uncertain[1]	% uncertain	Lake use (literature)	Lake use (this study)
alewife	15	0	0	0	—	—
American brook lamprey[2]	3	2	2	29	—	—
banded killifish[2]	0	0	6	100	—	—
blacknose dace[2]	0	4	3	43	—	—
bluntnose minnow[2]	2	1	4	57	—	—
brook stickleback[2]	1	4	3	38	—	—
brook charr	4	5	1	10	0.40	0.13
brown bullhead	3	0	5	63	0.38	0.43
brown trout	3	1	2	33	0.50	0.19
central stoneroller	0	3	3	50	—	—
chinook salmon	12	1	1	7	—	—
coho salmon	9	0	0	0	—	—
common shiner	0	5	3	38	0.00	0.32
creek chub	1	5	3	33	0.11	0.09
emerald shiner[2]	1	2	3	50	—	—

fantailed darter[2]	0	4	3	43	—	—
fathead minnow[2]	1	3	5	56	—	—
golden shiner[2]	3	0	6	67	—	—
hornyhead chub	0	1	4	80	—	—
Johnny darter[2]	0	2	5	71	—	—
lake chub	3	0	2	40	0.60	0.74
largemouth bass	2	0	4	67	0.33	0.30
logperch	0	1	4	80	0.00	0.30
longnose dace[2]	2	1	3	50	0.33	0.19
mottled sculpin[2]	0	2	3	60	—	—
northern pike	5	0	2	29	—	—
northern redbelly dace[2]	0	0	3	100	—	—
pumpkinseed	0	2	6	75	0.00	0.43
rainbow smelt	7	0	0	0	1.00	0.11
rainbow trout	10	1	1	8	0.83	0.36
rock bass	1	3	4	50	0.13	0.50
round goby[3]	—	—	—	—	na	0.20
sea lamprey	9	1	0	0	0.90	0.33
smallmouth bass	3	5	3	27	0.27	0.75
threespine stickleback3	3	0	2	40	—	—
white sucker	11	5	1	6	0.65	0.48
yellow perch	4	1	4	44	0.44	0.53

Note: [1]Studies were categorized as uncertain if there was ambiguity regarding the movement behaviour of a species (Mandrak et al. 2003). [2]Species categorized as small-bodied, with mean fork length of all individuals < 75mm. [3]No studies were available for the round goby in the database.

Figure 1.1: Map indicating the locations of the study streams and the positions of the first upstream barrier within each stream (black rectangle). Asterisks (*) represent the approximate locations where sea lamprey were released (see Chapter 3). Inset map shows the location of the study area (outlined) in relation to the Laurentian Great Lakes.

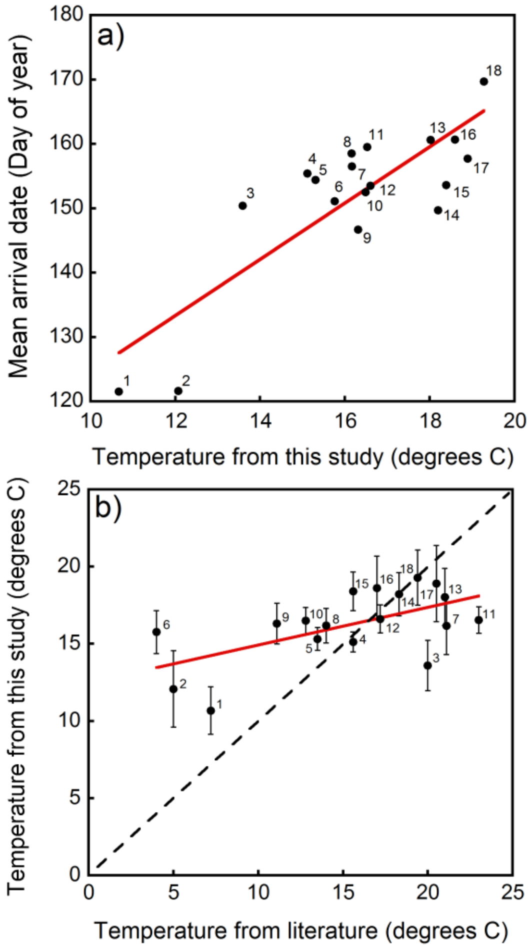

Figure 1.2: Relationship between the mean stream-water temperatures at arrival in this study (with 95% CI for figure b) and a) median date of arrival of species with a minimum of 10 individuals in each year of the study (*n* = 18), and b) mean spawning temperatures reported in the literature. Solid line represents least squares line. Dashed line represents a 1:1 line. Species are: 1) white sucker; 2) rainbow trout; 3) bluntnose minnow; 4) common shiner; 5) Johnny darter; 6) brook charr; 7) Northern redbelly dace; 8) lake chub; 9) sea lamprey; 10) creek chub; 11) brown bullhead; 12) longnose dace; 13) blacknose dace; 14) yellow perch; 15) fathead minnow; 16) brook stickleback; 17) rock bass; 18) pumpkinseed.

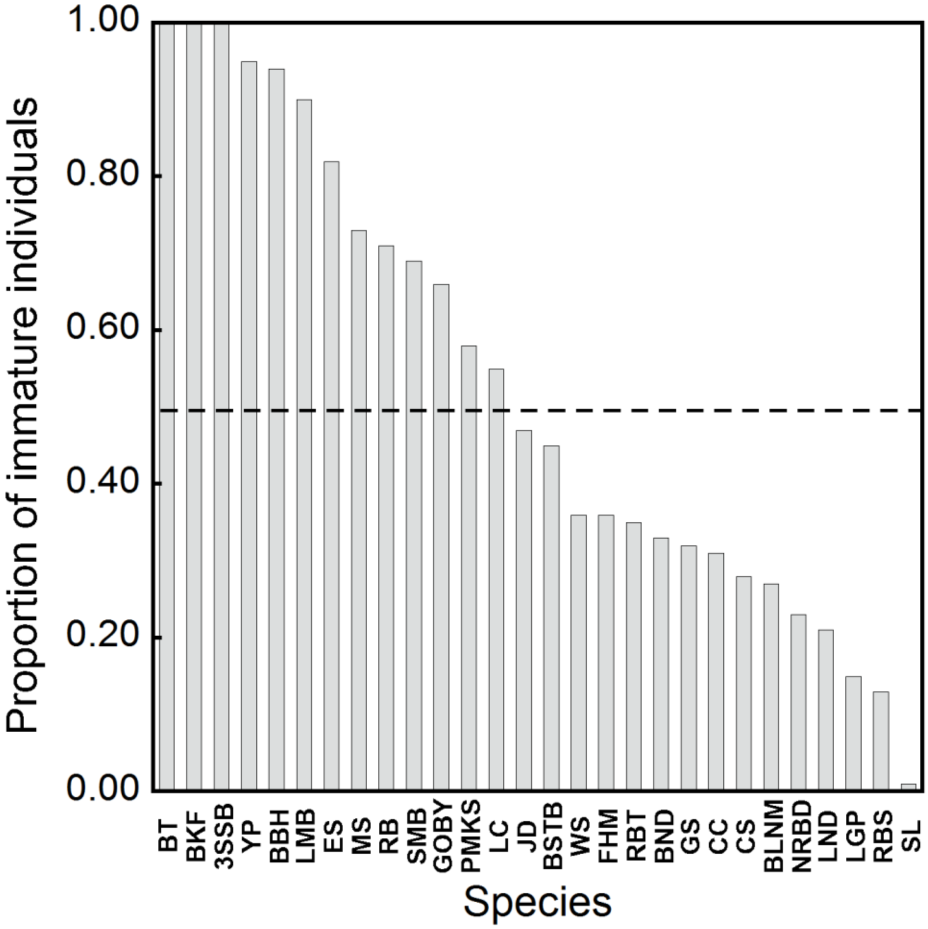

Figure 1.3: Proportion of immature adult-sized individuals, summarized by species with a minimum of 10 adult-sized individuals. The dashed line represents an equal proportion (0.50) of mature and immature individuals. Species are: brook charr (BT), banded killifish (BKF), three-spine stickleback (3SSB), yellow perch (YP), brown bullhead (BBH), largemouth bass (LMB), emerald shiner (ES), mottled sculpin (MS), rock bass (RB), smallmouth bass (SMB), round goby (GOBY), pumpkinseed (PMKS), lake chub (LC), Johnny darter (JD), brook stickleback (BSTB), white sucker (WS), fathead minnow (FTM), rainbow trout (RBT), blacknose dace (BND), golden shiner (GS), creek chub (CC), common shiner (CS), bluntnose minnow (BLNM), northern redbelly dace (NRBD), longnose dace (LND), logperch (LGP), rainbow smelt (RBS), and sea lamprey (SL).

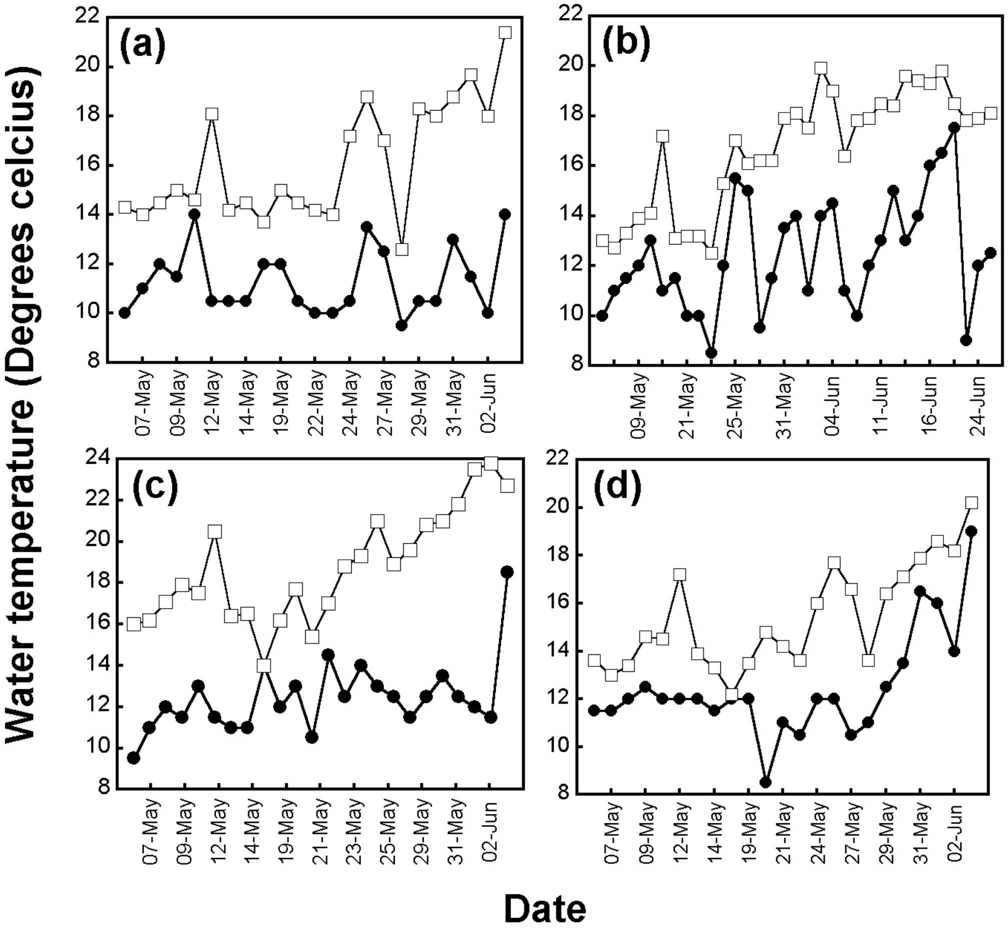

Figure 1.4: Daily maximum water temperatures from data loggers in the study streams (open boxes), and that from Lake Ontario (solid circles) taken at locations close to the mouths of the study streams, for (a) Covert Creek, (b) Grafton Creek, (c) Colborne Creek, and (d) Salem Creek.

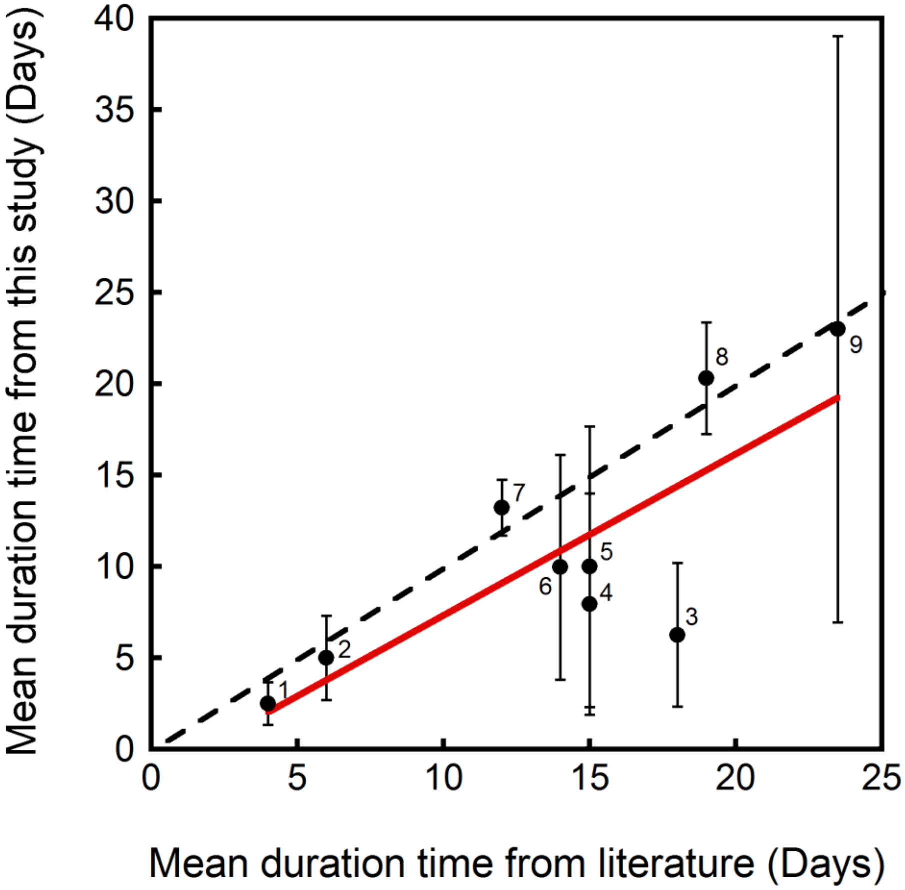

Figure 1.5: Relationship between the time spent in the streams reported in the literature against the time spent in the streams estimated in this study for species (*n* = 9) with a minimum of 10 individuals detected leaving the streams (with 95% CI). Solid line represents least squares line. Dashed line represents a 1:1 line. Species are: 1) sea lamprey; 2) lake chub; 3) brown bullhead; 4) common shiner; 5)pumpkinseed ; 6) creek chub; 7) white sucker; 8) rock bass; 9) smallmouth bass.

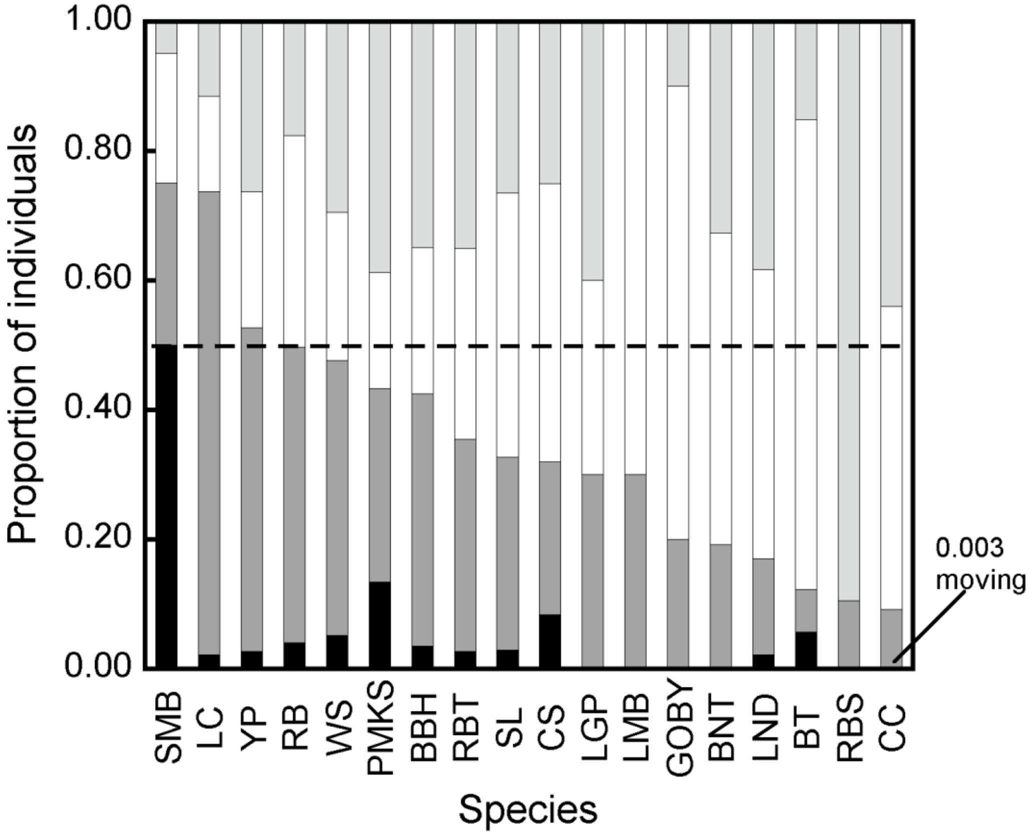

Figure 1.6: Proportion of PIT-tagged individuals never detected (light grey), detected only in their original stream of capture (open bar), detected leaving a stream (dark grey), and detected moving to another stream (black bar), summarized by species with at least 10 individuals. The dashed line represents an equal proportion (0.50) of individuals detected in the stream only and detected entering the lake. Species are: smallmouth bass (SMB), lake chub (LC), yellow perch (YP), rock bass (RB), white sucker (WS), pumpkinseed (PMKS), brown bullhead (BBH), rainbow trout (RBT), sea lamprey (SL), common shiner (CS), logperch (LP), largemouth bass (LMB), round goby (GOBY), brown trout (BNT), longnose dace (LND), brook charr (BT), rainbow smelt (RBS), and creek chub (CC).

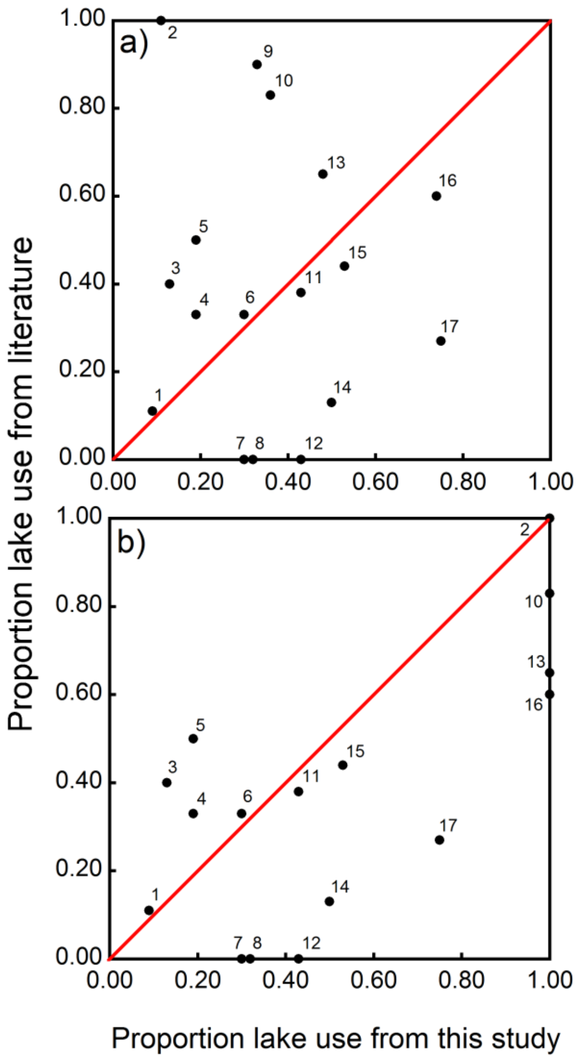

Figure 1.7: Relationship between the proportion of individuals using lake habitat reported in the literature versus a) the actual values of habitat use reported in this study (*n* = 17), and b) assuming anadromous species all left the streams (*n* = 16; excluding sea lamprey). Solid line represents a 1:1 line. Species are: 1) creek chub; 2) rainbow smelt; 3) brook charr; 4) longnose dace; 5) brown trout; 6) largemouth bass; 7) logperch; 8) common shiner; 9) sea lamprey; 10) rainbow trout; 11) brown bullhead; 12) pumpkinseed; 13) white sucker; 14) rock bass; 15) yellow perch; 16) lake chub; and 17) smallmouth bass.

Chapter 2: Patterns and mechanisms of sex-biased arrival of fishes at spawning sites in Lake Ontario streams

Introduction

Sexual selection can lead to the evolution of conspicuous secondary sexual characteristics, typically in males of a species (Andersson 1994; Blanckenhorn 2005), but also in females (Clutton-Brock 2007). Differences between males and females are commonly exhibited in behaviour, body size, weaponry, and colouration (Andersson 1994; Savalli 2001; Quinn et al. 2001; Fairbairn 2007; Clutton-Brock 2009), but this sexual dimorphism can also be expressed in the sex-biased timing of arrival at breeding sites. Sex-biased arrival at breeding areas is observed in many animal taxa, including mammals (Michener 1983), birds (Møller 1994; Kokko 1999; Mills 2005), insects (Wedell 1992; Carvalho et al. 1998), amphibians (Semlitsch 1985), and reptiles (Olsson and Madsen 1996; Olsson et al. 1999), and has been reported in some fishes, mainly salmonids (Morbey 2000; Seamons et al. 2004; Yamamoto and Edo 2006). Arrival of males before females at breeding areas (protandry) is the most common form of sex-biased timing (Morbey and Ydenberg 2001). Arrival of females before males at breeding sites (protogyny) is less common, but has been observed in some bird species (Morbey and Ydenberg 2001), and in some fishes, such as Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* (Dahl et al. 2004). In terms of effects on reproductive success, these behavioural differences in arrival can be comparable in magnitude to those associated with differences in morphology (Dickerson et al. 2002; Dickerson et al. 2005).

Quantifying the incidence of, and the mechanisms for, the sex-biased timing of reproductive movements can provide insights into the selection pressures that males and females face during the mating season (Morbey 2000). Fish are ideal subjects to test mechanisms proposed to explain the incidence of sex-biased reproductive timing for several reasons. First, the great variation among species in size, sexual size dimorphism, timing of reproduction, and mating behaviour (Blanckenhorn 2005; Fairbairn 2007) allows the testing of multiple hypotheses proposed for sex-biased reproductive timing. Second, earlier success in testing for sex-biased timing in fishes, mainly Pacific salmonids (Morbey 2000, 2002, 2003; Seamons et al. 2004; Yamamoto and Edo 2006), demonstrated the potential for using fishes to identify broad patterns of selection on timing. Third, the life span of the majority of Canadian freshwater fishes is typically between 4 – 9 years (Wootton 1984), so it is possible to follow individuals over multiple reproductive seasons, and to test several hypotheses across years to identify trends. Fourth, given that streams are linear habitats, the use of strategically placed nets or detection antennae provides a good indication of arrival time. Finally, testing hypotheses for sex-biased timing across a wide variety of fishes that reproduce under similar environmental conditions in the same set of streams over the same set of years provides insights into the specific selection pressures a particular species faces during the mating season.

Seven hypotheses have been proposed to explain sex-biased timing in animals *i.e.* protandry and protogyny (for a review, see Morbey and Ydenberg 2001). In this chapter, I test four of these hypotheses: the susceptibility, rank-advantage, mate-opportunity, and waiting-cost hypotheses. The susceptibility hypothesis supposes that environmental conditions on the breeding grounds early in the reproductive season are adverse and that the sexes are differentially susceptible (Morbey and Ydenberg 2001). For example, males of a species may be larger than females, and thus better able to cope with the prevailing conditions than females, thereby selecting for males to arrive at the breeding sites earlier than females (Morbey and Ydenberg 2001). In fishes, as with birds (Ketterson and Nolan 1983; Francis and Cooke 1986; Møller 1994), susceptibility to adverse conditions can be related to body size, leading to the predictions that larger individuals of both sexes should arrive earlier than smaller individuals (P1 and P2). By extension, it is also predicted that the frequency of larger individuals arriving earlier would be higher in protandrous than non-protandrous populations in both sexes (P3 and P4). Furthermore, the differences between male and female arrival times should increase as the degree of sexual dimorphism in size increases (P5) because in species with a high degree of male-biased sexual size dimorphism, even the smallest males would potentially be larger than the largest females, and hence less susceptible to environmental conditions (Table 2.1).

The rank-advantage hypothesis supposes that one sex, typically males, compete for reproductive territories. Territories can differ in quality creating selection pressure on males to arrive early to acquire the best territories and gain knowledge about the environment, which could provide a prior-residency advantage over individuals arriving later (Francis and Cooke 1986; O'Connor et al. 2000). When there is intense interference competition for territories, sexual selection will further favour males of larger size (Singer 1982), because larger males gain an advantage over smaller males in competition for resources, such as territories (Parker 1992; Yamamoto and Edo 2006). This hypothesis predicts that in territorial species, larger males will arrive before smaller males in order to acquire the best territories (P1), and that the incidence of larger males arriving first will be higher when protandry is exhibited versus not (P3). This hypothesis also predicts that the degree of protandry will increase as the degree of sexual dimorphism in size increases (P5), especially if males are less susceptible to adverse environmental conditions earlier in the breeding season as stated by the susceptibility hypothesis, and that the degree of protandry will be greater in territorial than non-territorial species (P6) (Table 2.1).

The mate-opportunity hypothesis supposes that males arriving earlier will encounter more females, and increase their reproductive success compared to late-arriving males (Singer 1982; Wedell 1992; Carvalho et al. 1998; Morbey and Ydenberg 2001; Mills 2005). This effect will be strengthened when females preferentially mate with early- versus late-arriving males (Wedell 1992). In addition to predictions P1-P4, this hypothesis also predicts that the degree of protandry will increase as the ratio of sexually mature males to females in a population increases (P7) (Table 2.1), because the variance in reproductive success among males is expected to increase as the sex ratio becomes more male-biased, with fewer males able to mate (Emlen and Oring 1977; Morbey 2002).

The waiting-cost hypothesis supposes that males require time to secure territories or establish dominance hierarchies and build nests, before they are ready to mate (Morbey and Ydenberg 2001). Under such conditions, females may gain fitness benefits by delaying their arrival to the breeding sites to avoid exposure to male conflict, predators, and adverse environmental conditions at future spawning sites (Wedell 1992). This hypothesis therefore predicts that the degree of protandry will be greater in territorial compared to non-territorial species (P6), because males in species with a territorial mating system must arrive before females to establish a territory prior to mating (Table 2.1).

Lake Ontario provides a unique opportunity to test these hypotheses for two reasons. First, Lake Ontario is the 12th largest freshwater lake in the world, which offers a rich diversity of freshwater fish (108 species; Coon 1999) and multiple species to test hypotheses on sex-biased timing. Second, large lakes produce a large range of prey sizes and types, which often induce stream-resident fish to adopt an "anadromous" style of life history. Hence, I expect to encounter a large number of species moving into the tributaries to spawn.

The relative timing of males and females is an important component of any mating system (Morbey 2000). Although sex-biased timing is known to exist in salmon, the magnitude and frequency of sex-biased timing have not been documented in a great many freshwater stream fishes. This study had two primary objectives: 1) to quantify the incidence and magnitude of sex-biased reproductive movements for 17 fish species in six tributaries of Lake Ontario; and 2) to test predictions of the four hypotheses proposed to explain the occurrence of sex-biased timing (Table 2.1).

Materials and Methods

See Chapter 1 for Materials and Methods.

Data Analysis

Quantifying the degree of protandry entailed four steps: 1) transforming all dates of capture or detection to day of the year, 2) estimating when each individual first arrived in a tributary, 3) estimating the mean and median arrival dates for males and females within a species for each yearly sample (*i.e.* population) at a tributary, and 4) calculating the differences between the mean and median arrival dates of each gender to calculate the degree of protandry for each yearly sample. I first estimated the arrival times of all individuals using the first instance that a fish was captured in a net in 2005 because this was the initial year of the study and no fishes had previously been tagged. For individuals that were (re)captured in 2006 and 2007, I estimated arrival times using the earlier of the initial catch date or the first antenna recording for that particular year. Data acquired for each species in each stream in each year for each gender were initially treated as independent replicates (*i.e.* male creek chub, Covert Creek, 2005; henceforth referred to as a yearly sample) because of significant interactions in arrival times between tributaries and years for most species. The degree of protandry was then calculated as the difference between male and female mean and median arrival times for each yearly sample (Morbey 2000). Most predictions were tested at the yearly sample level. For example, sex ratio varies at the population level (Kvarnemo and Ahnesjo 1996), so I treated each yearly sample (*i.e.* population) as a replicate in the analysis. However, some variables, such as mating system and sexual size dimorphism, are believed to be species specific traits (Breder and Rosen 1966; Balon 1975; Lovich and Gibbons 1992), hence predictions regarding these variables would be appropriately tested at the species level. Nonetheless, for consistency across analyses, and because differences may also exist between tributaries and populations, I tested all hypotheses at both the yearly sample and species level.

Sex-biased arrival

A grand total of 11 104 individuals from 34 species were captured over the course of the study, representing 298 yearly samples. Of these, 4565 were female, 3424 were male, 1801 individuals of unknown sex, and 1314 were juvenile. I decided that a yearly sample must consist of a minimum of five males and five females in order to provide a reasonable estimate of arrival timing for each gender and yet maximize the sample size. Seventeen of 34 species had sufficient data to be included in the analysis (see Appendix II for names and scientific names). Rainbow trout were not included in the analysis because many individuals had already entered the streams prior to net placement. Additionally, yearly samples where more than 25% of adult-sized individuals could not be identified to sex were also not included in the final analyses to increase the certainty that sexes were properly classified and improve my estimate of arrival timing. Based on these criteria, 69 yearly samples from 17 species were analysed for sex-biased timing, totalling 7891 individuals, including 3955 females, 3045 males, 276 individuals of unknown sex, and 617 juveniles (Appendix V).

To examine sex-biased differences in arrival timing within a species, arrival times in the streams of all individuals were analysed using nested ANOVA, with gender as a fixed factor, and stream and year within stream as random factors. To examine if sex-biased arrival timing differed between species, overall differences between male and female arrival times (*i.e.* degree of protandry) for each yearly sample were analysed using a nested analysis of variance (ANOVA), with species and stream within species as random factors. In both analyses, my intention was to determine whether sex-biased arrival differed within and between species, and was not directly related to the predictions.

Test of predictions

P1 and P2: Larger fish arrive earlier in both males and females

The prediction that larger individuals arrive earlier than smaller individuals in males and females was first tested by regressing arrival date against body length of each gender for each species and yearly sample. The slope of all yearly samples were then analysed using a Wilcoxon Sign Ranked test to determine if larger individuals arrived earlier than smaller individuals in both males (P1) and females (P2).

To test this prediction at the species level, I first regressed the arrival date of each individual against body length for males and females of each species in each year sampled. The mean weighted slopes for each species were then analysed using a Wilcoxon Sign Ranked test to determine if larger individuals arrived earlier than smaller individuals in both males (P1) and females (P2) at the species level. Next, to determine if larger individuals arrived before smaller individuals within a species, an analysis of covariance (ANCOVA) was used to detect any significant differences in the slopes of each yearly sample for both males and females. When the interaction (yearly sample x length) was not significant, data were analysed with ANCOVA without replication, with arrival date as the dependent variable, yearly sample as the factor, and length as the covariate (Sokal and Rohlf 1969) to determine if arrival time differed with length for a given species. The slope and 95% confidence interval were determined for each species, for both males and females. In species with significant differences in the slopes among yearly samples, a separate regression (body size versus arrival date) was calculated for each yearly sample by species and gender. The weighted mean slope and 95% confidence interval for a species were then used to judge whether, in general, larger males and females arrived earlier at the breeding sites within a species.

P3 – P4: Sex-biased arrival and the size of individuals in protandrous versus non-protandrous yearly samples and species

The prediction that larger males and females arrive earlier than smaller individuals was also tested using only those yearly samples with a significant difference in arrival times. *t*- tests were first used to compare the mean slopes in significantly protandrous yearly samples to those in significantly protogynous yearly samples, for both males (P3) and females (P4). Two-tailed Pearson correlation was then performed using the slope of the relationship between length and arrival time and the degree of protandry of each yearly sample to determine if the incidence of larger individuals arriving earlier would differ with the degree of protandry.

To test this prediction at the species level, *t*- tests were first used to compare the weighted mean slopes of protandrous to non-protandrous species used in the analysis, for both males and females. As was the case with the yearly sample analysis, two-tailed Pearson correlation was then performed using weighted means of the slopes of relationship between length and arrival time and the mean degree of protandry of all yearly samples for each species, to determine if the incidence of larger individuals arriving earlier would differ with the degree of protandry.

P5: Sex biased arrival and the degree of sexual size dimorphism

The prediction that the degree of protandry would be greater when the degree of male-biased sexual size dimorphism was higher was tested by regressing the index of size dimorphism (SDI) against the difference in the arrival times between males and females. SDI was calculated for each yearly sample by dividing the mean size of all individuals of the larger sex by the mean size of all individuals of the smaller sex, and subtracting the value one (Lovich and Gibbons 1992). The value was then made positive when males were larger than females and negative when females were larger than males. This index has been used widely in studies on sexual size dimorphism (Fairbairn 2007) and is preferred over other indices because the same degree of male- and female-biased dimorphism will provide values symmetrical about a value of zero and values of the index are continuous and can be analyzed using correlation and parametric analyses (Lovich and Gibbons 1992; Fairbairn 2007). While this index ignores age and growth rate, the susceptibility hypothesis makes predictions about absolute size rather than about relative size (i.e. growth rate).

I first explored whether sexual size dimorphism differed between and within species. For differences in sexual size dimorphism between species, each yearly sample was analysed by a nested analysis of variance (ANOVA), with SDI as the dependent variable, and species and stream within species as random factors. The degree of sexual size dimorphism within a species was also quantified by a nested ANOVA using all males and females of a species, with length as the dependent variable, and gender, stream, and year within stream as random factors. In both analyses, I was simply interested in the degree of sexual size dimorphism between and within species.

To test the prediction that protandry would be greater when the degree of male-biased sexual size dimorphism was higher at the yearly sample level, differences between male and female arrival times were regressed against the SDI for each yearly sample using two-tailed Pearson correlation analysis (P5). Because the degree of sexual dimorphism tends to be a species-specific trait, species means were used to examine whether the degree of protandry would be greater when the size differences between males and females was greater by regressing the differences in arrival times against SDI of each species using two-tailed Pearson correlation analysis.

P6: Sex biased arrival and mating behaviour

The prediction that protandry is greater in species with a territorial mating system than in species with non-territorial mating systems (P6) was tested by comparing the degree of protandry between the two groups. Species were first classified as territorial or non-territorial based on literature accounts of their reproductive behaviour (Breder and Rosen 1966; Scott and Crossman 1998; Holm et al 2009). Species were classified as territorial if males defend reproductive territories prior to mating, and/or defended eggs or offspring. Territorial species included: blacknose dace, bluntnose minnow, brook stickleback, creek chub, common shiner, fathead minnow, Johnny darter, longnose dace, pumpkinseed, rock bass, round goby, and sea lamprey. Non-territorial species included: golden shiner, lake chub, northern redbelly dace, rainbow smelt, and white sucker. For the analysis at the yearly sample level, overall differences in arrival times between territorial and non-territorial species were analysed by a nested analysis of variance (ANOVA), with the median degree of protandry for each yearly sample as the dependent variable, and mating strategy and species within mating strategy as random factors. An analysis at the species level was also conducted because the mating system is a species-specific trait. I first calculated the species mean degree of protandry from all yearly samples, and compared these values to the species mating system using a t-test.

P7: Sex biased arrival timing and operational sex ratio

The prediction that the degree of protandry would be greater when the ratio of reproductively active males to females is greater (P7) (Morbey 2002) was tested by comparing the total number of sexually mature individuals between males and females. Sex ratio was quantified as the ratio of sexually mature males to the total number of males and females (Kvarnemo and Ahnesjo 1996) for each yearly sample. Differences between male and female median arrival times were then regressed against the sex ratio for each yearly sample to determine if arrival timing varied by sex ratio (P7) using two-tailed Pearson correlation analysis. I also repeated this analysis using species means for the degree of protandry and sex ratio. The mean difference in median arrival times of all yearly samples was then regressed against the mean sex ratio for each species using two-tailed Pearson correlation analysis to determine if arrival timing varied by sex ratio at the species level All analyses were done using SPSS v12.0.1, with a critical level of significance set at 0.05.

Results

Sex-biased differences in arrival

In general, males tended to arrive earlier in tributaries than females (40 of 69 yearly samples; Wilcoxon Sign Rank, Z = -2.46, $p = 0.014$) (Figure 2.1). While differences between male and female arrival times were statistically significant (2-sample t-tests, p values <0.05) in just 20 of the 69 yearly samples, males arrived earlier than females in 15 of these 20 samples (Wilcoxon Sign Rank, Z = -1.93, $p = 0.053$).

The degree of protandry did not differ significantly among species (nested ANOVA, species effect: $F_{[16, 30]} = 1.35$, $p = 0.23$) (Figure 2.2), and strong evidence of protandry was observed in only four of the 17 species (Figure 2.2). Males arrived before females in all nine yearly samples for creek chub (nested ANOVA, gender effect: $F_{[1, 1107]} = 82.14$, $p < 0.001$), six of seven yearly samples for blacknose dace ($F_{[1, 652]} = 32.08$, $p < 0.001$), all five yearly samples for common shiner ($F_{[1, 193]} = 8.18$, $p = 0.005$), and all five yearly samples for fathead minnow ($F_{[1, 590]} = 7.69$, $p = 0.006$). Strong evidence of protogyny was observed only for the bluntnose minnow, with females arriving earlier than males in all three samples ($F_{[1, 604]} = 10.76$, $p = 0.001$). Evidence of consistent sex-biased timing of arrival was lacking for the remaining 13 species. For example, male white suckers arrived before females in only six of 11 samples ($F_{[1, 803]} = 0.374$, $p = 0.54$). Similar lack of consistency was observed for brook stickleback, golden shiner, Johnny darter, lake chub, longnose dace, northern redbelly dace, pumpkinseed, rainbow smelt, rock bass, round goby, and sea lamprey.

P1 and P2: Sex biased arrival and the size of individuals

The prediction that larger individuals would arrive earlier in streams than smaller individuals for males (P1) and females (P2) was supported. At the yearly sample level, larger individuals arrived earlier than smaller individuals in 53 of 69 yearly samples of males (P1) (Wilcoxon Sign Rank, Z = -4.45, $p < 0.001$) and 46 of 68 yearly samples of females (P2) (Wilcoxon Sign Rank, Z = -2.91, $p = 0.004$) (Table 2.2). Of the significant correlations, 15 of 19 were negative for females (Wilcoxon Sign Rank, Z = -2.52, $p = 0.012$) and 15 of 16 were negative for males (Wilcoxon Sign Rank, Z = -3.50, $p < 0.001$), indicating that larger individuals arrived before smaller individuals. The weighted mean slope of the relationship, however, did not differ between the sexes for all samples (paired *t*-test, $t = 1.40$, df = 67, $p = 0.17$), or for those with significant correlations (paired *t*-test, $t = 0.74$, df = 29, $p = 0.47$).

The prediction that larger individuals would arrive earlier than smaller individuals was also supported when analyzed at the species level. Larger females arrived before smaller females in 15 of 17 species (Wilcoxon Sign Rank, Z = -3.15, $p = 0.002$), with significant differences in eight of the 17 species (Table 2.2; Figure 2.3a). Larger females arrived earlier than smaller females in the common shiner (ANCOVA, length effect: $F_{[1, 140]} = 15.36$, $p < 0.001$), rock bass ($F_{[1, 36]} = 4.88$, $p = 0.034$) and the sea lamprey ($F_{[1, 155]} = 5.90$, $p = 0.016$), but not in the brook stickleback, golden shiner, Johnny darter, lake chub, pumpkinseed, rainbow smelt, and round goby (Figure 2.3a). For species in which the slopes differed significantly between yearly samples, separate regression analyses showed that larger females tended to arrive earlier in the bluntnose minnow, blacknose dace, creek chub, fathead minnow, and white sucker (Table 2.2; Figure 2.3a). No significant trend was observed in female longnose dace or northern redbelly dace (Table 2.2; Figure 2.3a).

In males, larger individuals arrived to the streams before smaller males in 14 of the 17 species analysed (Wilcoxon Sign Rank, Z = -2.67, $p = 0.008$), but only four of the 17 regressions were significant (Table 2.2; Figure 2.3b). Larger individuals arrived earlier than smaller fish in the creek chub (two-way ANCOVA, length effect: $F_{[1, 195]} = 8.84$, $p = 0.003$) and fathead minnow ($F_{[1, 214]} = 9.32$, $p = 0.003$), but not in the brook stickleback, common shiner, golden shiner, Johnny darter, lake chub, northern redbelly dace, pumpkinseed, rainbow smelt, rock bass, and round goby (Figure 2.3b). In species where the slopes differed significantly among yearly samples, separate regression analyses showed that larger males arrived earlier in sea lamprey and white sucker, but not in the bluntnose minnow, blacknose dace, and longnose dace (Table 2.2; Figure 2.3b).

P3 and P4: Sex biased arrival and the size of individuals in protandrous versus non-protandrous yearly samples

The prediction that in populations exhibiting protandry, larger individuals would arrive before smaller individuals was partially supported at the yearly sample level. When comparing between only the 20 yearly samples with a significant difference between male and female arrival, larger males (P3) arrived earlier at the spawning sites in protandrous than protogynous populations, as indicated by a significant difference in the mean slopes of the relationship (*t*-test, $t = 3.17$, df = 18, $p = 0.005$), but not in females (P4) (*t*-test, $t = 0.40$, df = 17, $p = 0.70$). However, regression analysis revealed that the incidence of larger individuals arriving earlier did not differ with the degree of protandry in males (two-tailed Pearson correlation, $r = -0.23$, $n = 20$, $p = 0.34$) or females (two-tailed Pearson correlation, $r = -0.14$, $n = 20$, $p = 0.58$) at the yearly sample level. Furthermore, when the 20 yearly samples with a significant difference in arrival time between males and females are compared with the remaining 49 yearly samples in which there was no significant difference, the mean slopes of the relationship did not differ in males (*t*-test, $t = 1.10$, df = 67, $p = 0.28$) or females (*t*-test, $t = 0.66$, df = 66, $p = 0.52$), nor when the 15 protandrous yearly samples are compared with the remaining 54 non-protandrous yearly samples for males (*t*-test, $t = 0.05$, df = 67, $p = 0.96$) or females (*t*-test, $t = 0.78$, df = 66, $p = 0.44$).

The prediction that larger individuals would arrive before smaller individuals in populations exhibiting protandry was not supported at the species level. The mean slope of the relationship did not differ between the four protandrous species and the remaining 13 species, for either males (P3) (*t*-test, $t = 1.59$, df = 15, $p = 0.13$) or females (P4) (*t*-test, $t = 1.69$, df = 15, $p = 0.11$). Furthermore, regression analysis revealed that the incidence of larger individuals arriving earlier did not differ with the degree of protandry in males (two-tailed Pearson correlation, $r = -0.028$, $n = 17$, $p = 0.92$) or females (two-tailed Pearson correlation, $r = 0.042$, $n = 17$, $p = 0.87$) at the species level.

P5: Sex biased arrival and the degree of sexual size dimorphism

Species varied considerably in the degree of sexual size dimorphism (nested ANOVA, species effect: $F_{[16, 29]} = 14.25$, $p < 0.001$) (Figure 2.4, Figure 2.5). Males were significantly larger than females in the creek chub (nested ANOVA, gender effect: $F_{[1, 1094]} = 1068.21$, $p < 0.001$), bluntnose minnow ($F_{[1, 601]} = 655.24$, $p < 0.001$), fathead minnow ($F_{[1, 587]} = 347.08$, $p < 0.001$), common shiner ($F_{[1, 191]} = 234.62$, $p < 0.001$), blacknose dace ($F_{[1, 651]} = 88.15$, $p < 0.001$) and Johnny darter ($F_{[1, 19]} = 7.70$, $p = 0.012$), whereas females were significantly larger than males in the longnose dace ($F_{[1, 1362]} = 181.31$, $p < 0.001$), white sucker ($F_{[1, 552]} = 164.66$, $p < 0.001$), lake chub ($F_{[1, 95]} = 81.89$, $p < 0.001$), northern redbelly dace ($F_{[1, 924]} = 69.62$, $p < 0.001$), golden shiner ($F_{[1, 18]} = 15.03$, $p = 0.001$), round goby ($F_{[1, 18]} = 8.02$, $p = 0.011$), and brook stickleback ($F_{[1, 26]} = 6.90$, $p = 0.014$) (Figure 2.5). There was no statistical evidence for sexual size dimorphism in the pumpkinseed, rainbow smelt, rock bass, or the sea lamprey.

The prediction that the degree of protandry would be greater when the degree of sexual size dimorphism was male-biased was strongly supported. As predicted, the degree of protandry increased as male size relative to female size increased at the yearly sample level (two-tailed Pearson correlation, $r = 0.56$, $n = 68$, $p < 0.0001$; Figure 2.6a) and species level ($r = 0.58$, $n = 17$, $p = 0.008$; Figure 2.6b).

P6: Sex biased arrival and mating behaviour

The prediction that the degree of protandry is greater in territorial species than in non-territorial species was not supported. At the yearly sample level, there was no statistically significant difference in the degree of protandry between territorial and non-territorial species (nested ANOVA, mating strategy effect: $F_{[1, 52]} = 0.45$, $p = 0.51$) even though the mean degree of protandry estimated for territorial species (2.45 ± SE 2.06 days) was greater than the mean degree of protandry estimated for non-territorial mating systems (-0.35 ± SE 3.39 days). At the species level, males again arrived on the spawning areas earlier than females in species with territorial mating systems (species mean degree of protandry = 2.45 ± SE 1.99 days), whereas females arrived earlier than males in species with a scramble mating system (species mean degree of protandry = -0.35 ± SE 0.45 days), but the difference in arrival times between mating strategies was just barely not statistically significant (Independent-samples *t*-test, $t_{15} = 4.21$, $p = 0.058$).

P7: Sex biased arrival timing and operational sex ratio

The prediction that the degree of protandry would be greater with a male-biased than a females-biased sex ratio was not supported. Contrary to our prediction, the difference in arrival times was negatively correlated with the ratio of reproductive males to females for both yearly samples (two-tailed Pearson correlation, $r = -0.42$, $n = 69$, $p < 0.001$) (Figure 2.7a) and species ($r = -0.79$, $n = 17$, $p < 0.001$; Figure 2.7b).

Discussion

My analysis of the variation in sex-biased arrival times suggests this behaviour is both interesting and potentially important ecologically. This conclusion is supported by two lines of evidence. First, the wide variety of fishes considered here exhibited great variation in sex-biased timing despite reproducing under similar environmental conditions in the same set of streams over the same set of years. Second, species, and populations within species, tended to be protandrous, on average, suggesting that the variation was not due to chance. Some degree of protandry was observed in 40 of 69 yearly samples, as well as significant differences in 15 of 20 yearly samples and 4 of 4 species.

The degree of sex-biased arrival at spawning sites was similar to that found in other species of fishes. The degree of protandry described in this study (median = 6.93 days; range 0.01 – 44.13 days) was comparable to that found in Pacific salmonids, where males typically arrive 0-5 days earlier than females (Morbey 2000; Seamons et al. 2004). While these differences are not large, a male need only arrive slightly before a female to maximize their chances of breeding, to establish a territory, to learn about its environment, or to wait to intercept females on their upstream migration (Seamons et al. 2004). Males arriving before and close to the median date of female arrival typically have greater mating opportunities (Carvalho et al. 1998). Indeed, 80% of female steelhead trout *Oncorhynchus mykiss* mated with males already at the breeding sites rather than with males that arrived at the same time or after the females (Seamons et al. 2004). Early arriving male pink salmon *Oncorhynchus gorbuscha* had significantly more offspring than late arriving males (Dickerson et al. 2005). The offspring of early-arriving male Coho salmon *Oncorhynchus kisutch* were larger at a common date than offspring from males that arrived later, which can provide a possible mechanism linking arrival timing to offspring viability (Anderson et al. 2010). The benefits of arriving earlier are also observed in other organisms. For example in birds, early arriving American redstart *Setophaga ruticilla* settled on higher quality territories and had higher reproductive success than later arrivals (Smith and Moore 2005). However, arriving too far in advance of females might cause males to increase their energy required for mating (Morbey and Ydenberg 2001; Seamons et al. 2004), increase an individual's risk of predation because of the longer time spent at the spawning sites (Quinn et al. 2001; Quinn et al. 2003), and the duration of time exposed to adverse environmental conditions (Møller et al. 2009).

For example, predation on sockeye salmon *Oncorhynchus nerka* by brown bears *Ursus arctos* was higher early and late in the season when fish densities were low (Quinn et al. 2003). Hence, it is likely that stabilizing selection acts on male arrival date in order to maximize mating success, and that selection has driven populations to equilibrium (Dickerson et al. 2005; Møller et al. 2009).

To my knowledge, this is the first study to examine multiple possible mechanisms for the incidence of sex-biased timing across a broad range of fish species, and over several reproductive seasons. My data provided strong support for four of five predictions of the susceptibility hypothesis (Table 2.1). Furthermore, my data tended to support the fourth prediction (P4), larger females arrive earlier in protandrous species than in other, but the difference was not significant. Only two of four predictions of the rank advantage hypothesis were supported by our data. My data also tended to support the predictions that larger males arrive earlier in protandrous species than in others, and the degree of protandry is greater in territorial than non-territorial species, but the differences were not significant. While two of five predictions of the mate opportunity hypothesis were supported by my data, one result falsified the hypothesis: the degree of protandry decreased significantly with the male/female sex ratio. There was no support for the waiting cost hypothesis. While no single hypothesis provided a satisfactory explanation for all my data, the susceptibility hypothesis was the best overall predictor of the patterns observed in this study.

Strong support for the susceptibility hypothesis suggests that body size plays an important role in determining arrival timing in teleost fishes. How body size and arrival timing affect reproductive success in males and females of many species is, however, not known. For example, while arriving early allows an individual to acquire a higher quality territory (rank advantage) or monopolize a resource (Harwood et al. 2003), larger size is also a major factor in successfully competing for territories in fishes (Cutts et al. 1999; Johnsson et al. 1999; Prenter et al. 2008), and in withstanding adverse environmental conditions because of greater energy stores (Roff 1988). Both in turn can result in more mating opportunities if territory quality or early arrival in males is important to female choice (mate-opportunity). That larger individuals within each sex arrive at the breeding grounds earlier suggests that size plays an important part in influencing arrival timing, and deserves more attention in future studies.

Although my results provide strong support for the susceptibility hypothesis, the incidence of protandry in a particular population could be entirely incidental. First, protandry could be a side effect of selection for female-biased sexual size dimorphism (SSD) (Wiklund and Solbreck 1982; Morbey 2000). Females may mature and arrive at the spawning sites later than males (Wedell 1992) because larger females may need a longer time to mature in the spring because the production of eggs production requires more resources than sperm (Francis and Cooke 1986; Matsuura 2006). However, this explanation is not likely causing the incidence of protandry observed in this study for three reasons: (i) the average body size of both sexes was larger early in the reproductive season, (ii) males in protandrous species were generally larger than females, and (iii) the added growth an individual would gain by delaying entry into a stream would probably be negligible within a spawning season (Morbey 2000), particularly for spring spawning fish.

Second, early arrival of larger fish at the breeding sites may simply be a function of better swimming speed and endurance in larger individuals (Ojanguren and Brana 2003). In addition, in iteroparous species with overlapping generations, larger, older individuals may also be better at finding spawning sites and avoiding predators (Tallman et al. 2002). Therefore, one might expect larger individuals to arrive at the spawning grounds earlier than smaller individuals. However, this hypothesis alone cannot explain the incidence of protandry observed in this study, otherwise protogyny would be observed more frequently in species where females are larger than males, such as in the white sucker. Nonetheless, in both cases, protandry may be a side effect of other selective forces acting differently on the sexes, making it difficult to distinguish from direct sexual selection for protandry itself (Matsuura 2006).

Table 2.1: The four hypotheses tested explaining the incidence of protandry, their corresponding predictions, and the observed relationships.

		Hypothesis				Observed	
Predictions	Prediction #	Susceptibility	Rank advantage	Mate opportunity	Waiting cost	Yearly sample level	Species level
Larger fish arrive earlier for:							
MALES	P1	Y	Y	Y	—	Y*	Y*
FEMALES	P2	Y	—	Y	—	Y*	Y*
Larger fish arrive earlier in protandrous than non-protandrous:							
MALES	P3	Y	Y	Y	—	Y*	Y^{ns}
FEMALES	P4	Y	—	Y	—	Y^{ns}	Y^{ns}
The degree of protandry is positively correlated with the degree of sexual dimorphism in size	P5	Y	Y	—	—	Y*	Y*
The degree of protandry is greater in territorial than non-territorial species	P6	—	Y	—	Y	Y^{ns}	Y^{ns}
The degree of protandry increases when the sex ratio is male biased	P7	—	—	Y	—	N*	N*

Note: Y indicates that the prediction is expected for a given hypothesis, N indicates that the result is opposite of the prediction, whereas a dash (—) indicates that no prediction is made for a given hypothesis. * indicates the relationship was significant ($p < 0.05$), whereas ns indicates $p > 0.05$.

Table 2.2: Relationship between mean arrival time and body size analysed by separate regressions for each sample within species, summarized by gender. Data show the number of yearly samples (*n*), samples with a negative slope (# neg), samples with significantly negative slopes ($p < 0.05$) within brackets, mean slope ($\bar{X}$ slope), and the lower and upper 95% CL.

	Females					Males				
Species	*n*	# neg[1]	$\bar{X}$ slope[2]	Lower bound	Upper bound	*n*	# neg[1]	$\bar{X}$ slope[2]	Lower bound	Upper bound
bluntnose minnow	3	2(1)	-0.33	-0.65	-0.01	3	1(1)	-0.08	-0.38	0.23
blacknose dace	7	5(2)	-0.33	-0.46	-0.19	7	5(1)	-0.17	-0.41	0.08
brook stickleback	1	1	-0.15[a]	-2.01	1.70	1	1	-0.12[a]	-0.44	0.19
common shiner	5	4	-0.30[a]	-0.45	-0.15	5	4	-0.12[a]	-0.28	0.05
creek chub	9	8(4)	-0.14	-0.19	-0.09	9	8	-0.14[a]	-0.24	-0.05
fathead minnow	5	3(1)	-0.58	-0.92	-0.24	5	3(1)	-0.69[a]	-1.13	-0.24
golden shiner	1	1	-0.02[a]	-0.08	0.05	1	—	0.26[a]	-0.39	0.91
Johnny darter	1	—	0.84[a]	-0.34	2.01	1	—	0.27[a]	-1.17	1.70
lake chub	2	1	-0.09[a]	-0.34	0.15	2	2	-0.12[a]	-0.53	0.30
longnose dace	7	4(1)	-0.08	-0.17	0.01	7	5(3)	-0.07	-0.19	0.05
northern redbelly dace	7	3(2)	0.07	-0.04	0.17	7	6	-0.07[a]	-0.28	0.14
pumpkinseed	1	—	0.000[a]	-1.12	1.12	1	1	-0.06[a]	-0.87	0.76

rainbow smelt	1	—	0.002[a]	-0.001	0.004	1	1	-0.09[a]	-0.86	0.69
rock bass	2	1	-0.34[a]	-0.64	-0.04	2	2	-0.08[a]	-0.27	0.11
round goby	1	1	-0.44[a]	-1.06	0.19	1	1	-0.09[a]	-0.33	0.16
sea lamprey	5	4	-0.07[a]	-0.12	-0.01	5	5(3)	-0.09	-0.13	-0.05
white sucker	11	8(4)	-0.06	-0.09	-0.02	11	8(6)	-0.12	-0.15	-0.10

[1] Negative slope indicates that larger fish arrive earlier. [2] Test of a significant difference from an ANCOVA[a] or by the weighted mean slope (± 95% CL) of all yearly samples for a species.

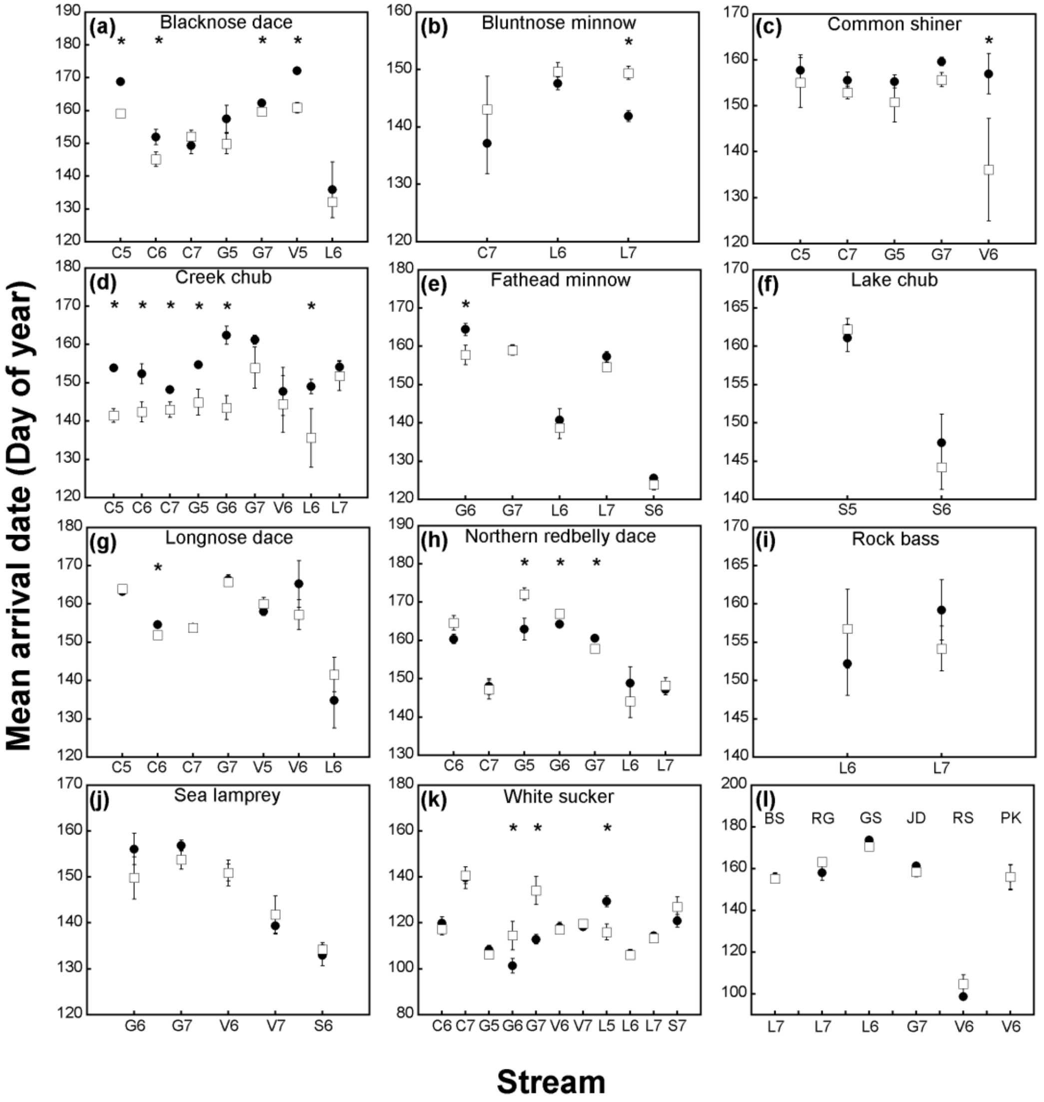

Figure 2.1: Mean date of arrival (±SE) of males (□) and females (●) for each yearly sample; the first character denotes the stream (C = Covert; G = Grafton; L = Colborne; S = Salem; and V = Shelter Valley) and the second denotes the year (5 = 2005; 6 = 2006; and 7 = 2007). * denotes significant differences between male and female arrival times (*t* test, $p < 0.05$). For box (L), species are: BS = brook stickleback, RG = round goby, GS = golden shiner, JD = Johnny darter, RS = rainbow smelt, and PK = pumpkinseed.

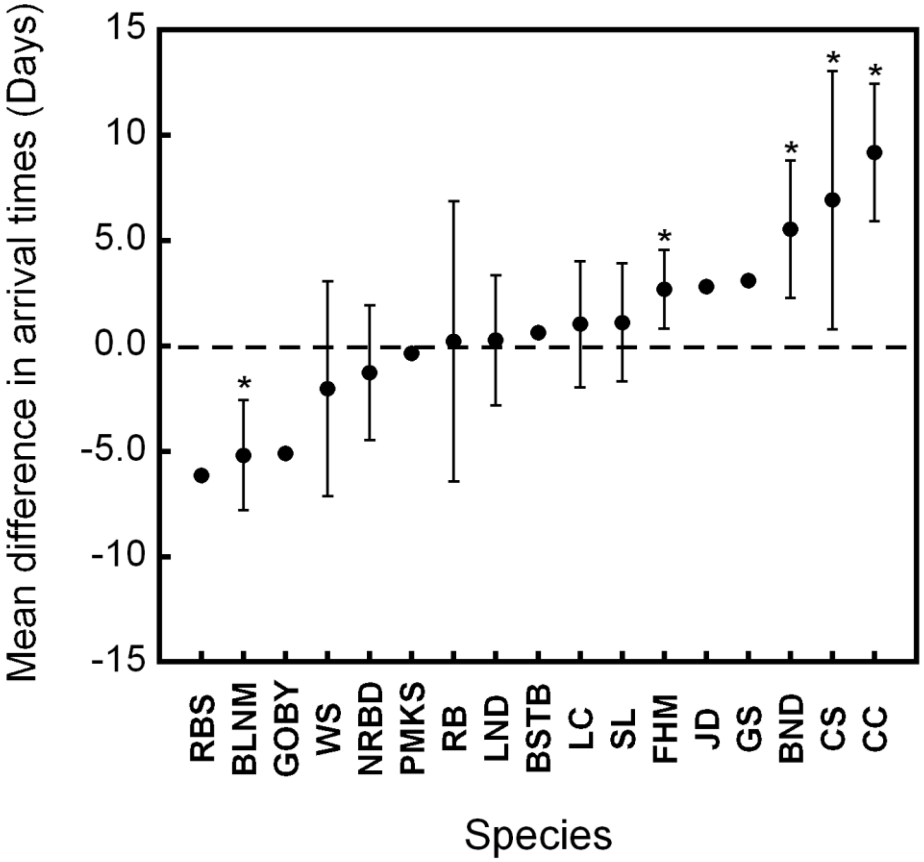

Figure 2.2: Mean difference in arrival times between males and females summarized by species. Positive values for differences in arrival times indicate that males arrived first. * indicates a significant differences between male and female arrival times. Species are: rainbow smelt (RBS), bluntnose minnow (BLNM), round goby (GOBY), white sucker (WS), northern redbelly dace (NRBD), pumpkinseed (PMKS), rock bass (RB), longnose dace (LND), brook stickleback (BSTB), lake chub (LC), sea lamprey (SL), fathead minnow (FHM), Johnny darter (JD), golden shiner (GS), blacknose dace (BND), common shiner (CS), and creek chub (CC).

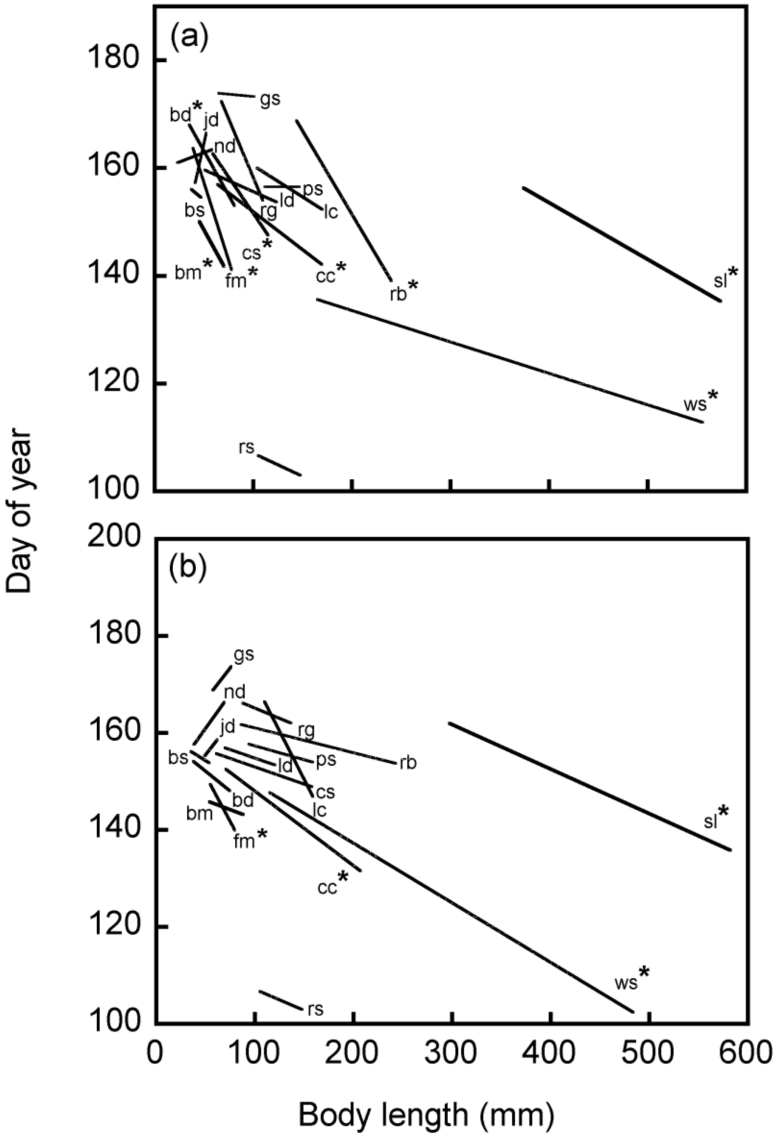

Figure 2.3: The relationship between mean arrival day and body length for (a) females and (b) males, summarized by species. Species are: bd = blacknose dace; bm = bluntnose minnow; bs = brook stickleback; cc = creek chub; cs = common shiner; fm = fathead minnow; gs = golden shiner; jd = Johnny darter; lc = lake chub; ld = longnose dace; nd = Northern redbelly dace; ps = pumpkinseed; rb = rock bass; rg = round goby; rs = rainbow smelt; sl = sea lamprey; and ws = white sucker). * indicates significance at $p < 0.05$.

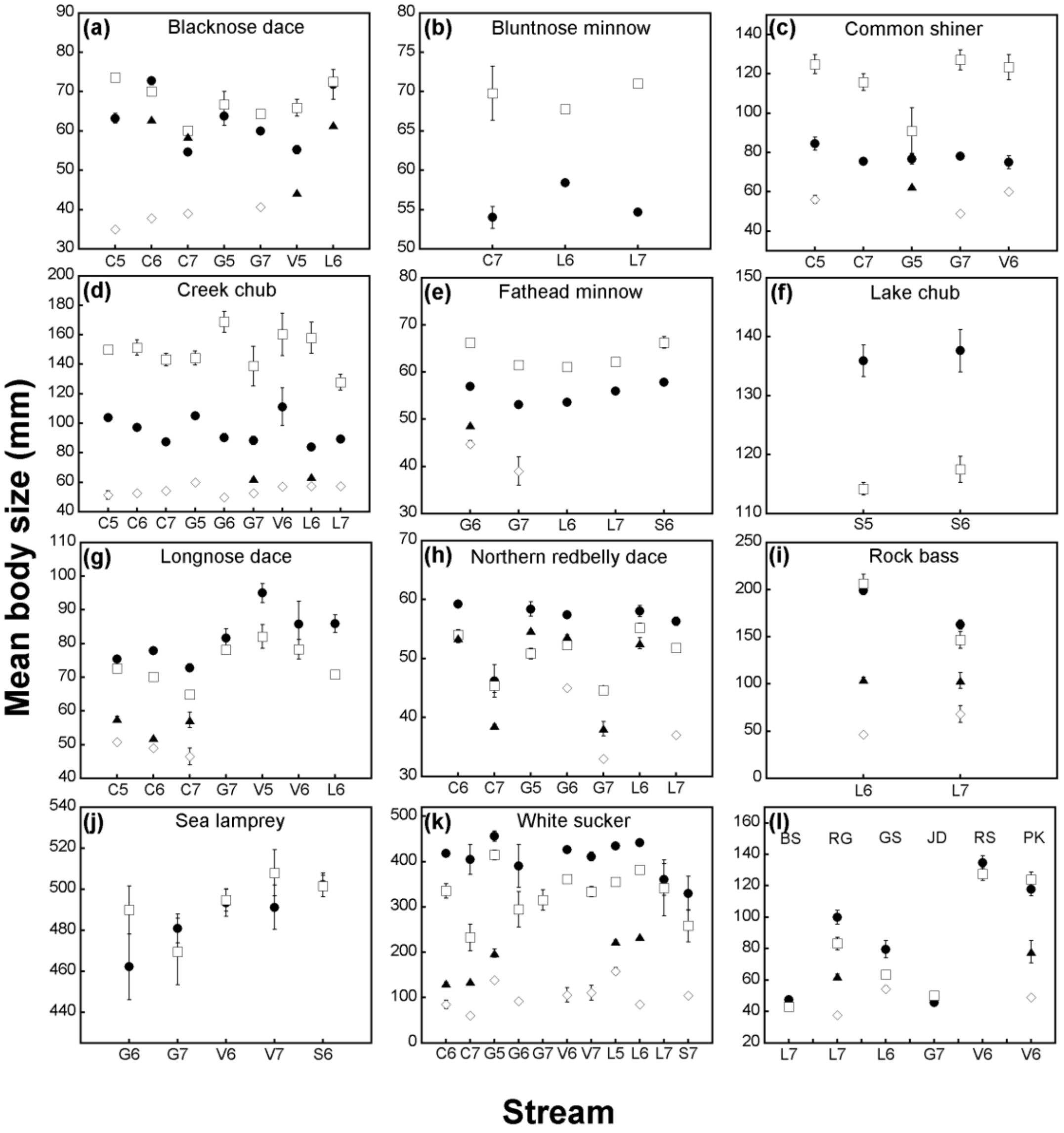

Figure 2.4: Mean body size (mm ±SE) of males (□), females (●), individuals of unknown sex (▲), and juveniles (◊) summarized by yearly sample for each species. For each yearly sample, the first character denotes the stream (C = Covert; G = Grafton; L = Colborne; S = Salem; and V = Shelter Valley) and the second denotes the year (5 = 2005; 6 = 2006; and 7 = 2007). For box (L), species are: BS = brook stickleback, RG = round goby, GS = golden shiner, JD = Johnny darter, RS = rainbow smelt, and PK = pumpkinseed.

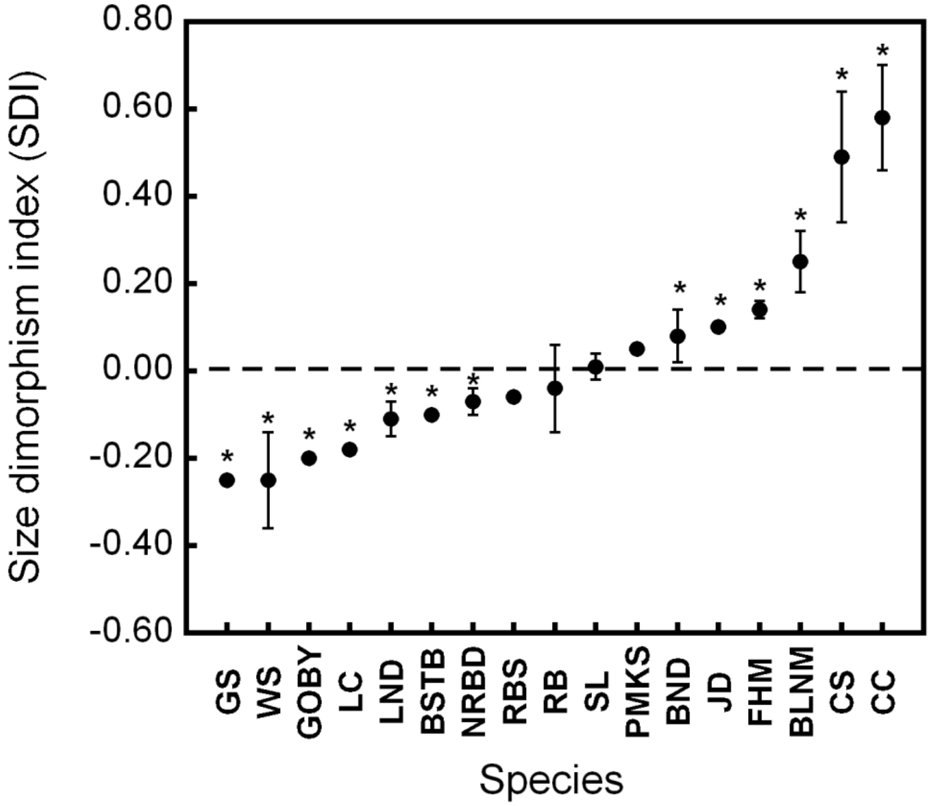

Figure 2.5: The mean degree of sexual size dimorphism between males and females summarized by species. Positive values for sexual size dimorphism indicate that males are larger. * indicated a significant differences in sexual size dimorphism. Species are: golden shiner (GS), white sucker (WS), round goby (GOBY), lake chub (LC), brook stickleback (BSTB), longnose dace (LND), northern redbelly dace (NRBD), rainbow smelt (RBS), rock bass (RB), sea lamprey (SL), pumpkinseed (PMKS), blacknose dace (BND), Johnny darter (JD), fathead minnow (FTM), bluntnose minnow (BLNM), common shiner (CS), and creek chub (CC).

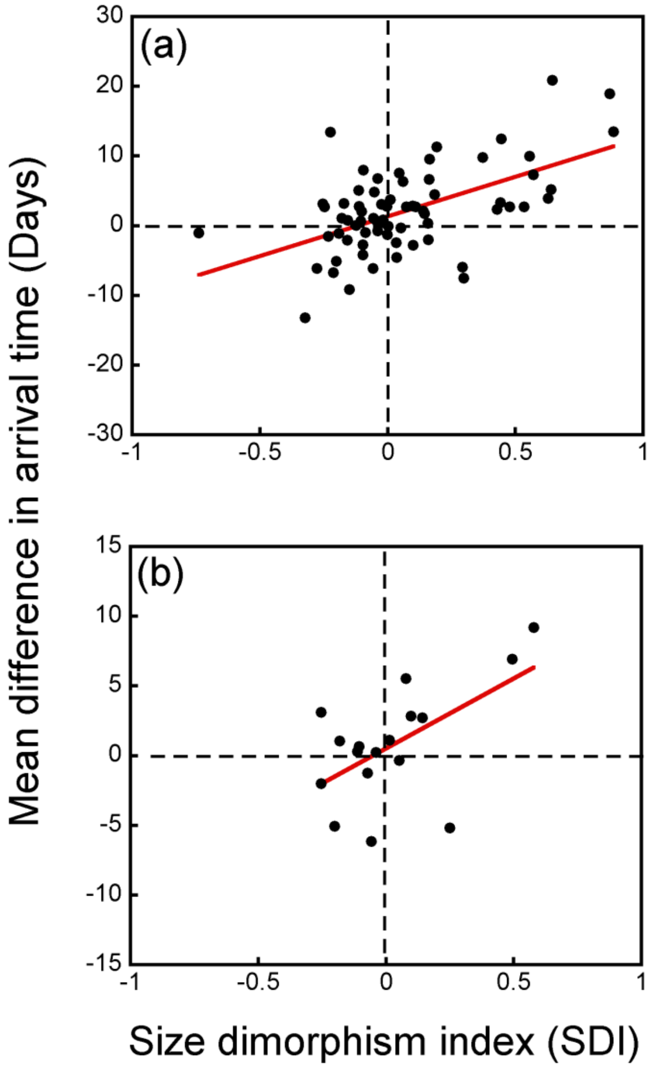

Figure 2.6: Differences in mean arrival times of males versus females in relation to the degree of sexual size dimorphism analyzed by (a) yearly sample (*n* = 69) and (b) species (*n* = 17). Positive values for differences in arrival times indicate that males arrived first, whereas positive values for the degree of sexual dimorphism indicate that males are larger than females.

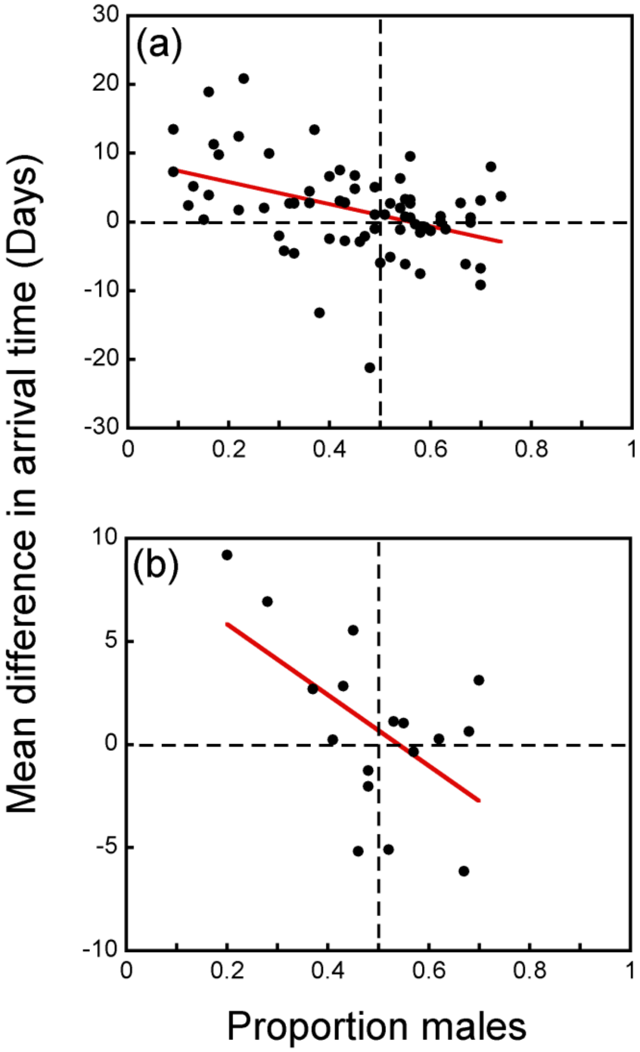

Figure 2.7: Differences in mean arrival times of males versus females in relation to the proportion of males when analyzed by (a) yearly sample (*n* = 69) and (b) species (*n* = 17). Positive values for differences in arrival times indicate that males arrived first.

Chapter 3: Inter-stream movement of fishes in Lake Ontario tributaries: Insights into rates of homing and straying in freshwater fishes

Introduction

Freshwater fishes exhibit a variety of movement behaviour over a wide range of spatial and temporal scales (Schlosser 1995; Young 1996; McCormick et al. 1998). This variety includes daily movement to and from foraging stations, habitats, or refuges, to seasonal movement between foraging, spawning, and over-wintering habitats, to long-distance movement between rivers, lakes, oceans, and adjacent local populations (e.g. a metapopulation) (Schlosser 1995; Young 1996; McCormick et al. 1998; Lucas and Baras 2001). Much of the existing literature on fish movement has focused on the long-distance migrations of anadromous and oceanodromous species, largely overlooking the potential significance of the "short-distance" movements of freshwater fishes (Northcote 1998; Lucas and Baras 2001).

Despite a rich literature on the ecology of freshwater fishes, the movement behaviour of many of these fishes remains poorly understood (Northcote 1998). Traditionally, stream fishes were viewed as exhibiting restricted movement, remaining in a specific area of stream for a considerable period of time, even years, *i.e.* the restricted movement paradigm (RMP) (Gerking 1959; Gowan et al. 1994; Smithson and Johnston 1999; Lucas and Baras 2001; Rodriguez 2002). Recent studies, however, suggest that stream fishes move more often and farther than previously thought (Gowan and Fausch

1996; Lucas and Baras 2001; Rodriguez 2002; Mandrak et al. 2003). In addition, many populations exhibit considerable inter-individual variability in movement behaviour, from metres to several kilometres within a reproductive season (Gowan and Fausch 1996; Young 1996; Hutchings and Gerber 2002).

There is growing evidence that the movement by stream fishes can be important to the persistence and short-term microevolution of many stream fish populations and metapopulations (Knaepkens et al. 2005). A metapopulation exists as a population of sub-populations interacting via the movements of individuals between subpopulations (Hanski 1998). Movement between spatially separated local populations can affect the dynamics of local populations, including local rates of recruitment, persistence, and extinction (Wilson et al. 2004). Long-distance movements made by a few individuals, over challenging or inhospitable habitats, and between distant locations and sub-populations can be important for re-colonizing unoccupied habitats and maintaining the dynamics and stability of the regional metapopulation (Hanski and Gilpin 1997). For example, surplus individuals from highly productive source habitats may immigrate into less productive sink habitats (Pulliam and Danielson 1991), stabilizing the sink populations via the rescue effect (Ingvarsson 2001; Gotelli 2008; Primack 2008), and possibly contributing to and maintaining genetic diversity within a subpopulation (Lucas and Baras 2001). Nonetheless, too much movement between populations can lead to a loss of local adaptation (Hendry et al. 2004a).

Rates of homing and straying have important implications for studies on movement at the watershed scale. However, much of what is known about the movements of stream fishes has been developed from extensive research on the movement of salmonids, due to their recreational and commercial importance (Kahler et al. 2001). Even for salmonids, the degree to which individuals move between neighbouring populations or sub-populations, or neighbouring catchments, remains uncertain, as do the characteristics of individuals that are most likely to move (Northcote 1998; Schrank and Rahel 2006). Rates of reproductive homing, the inverse of straying for anadromous salmonids, typically range from 90 – 100% (Lucas and Baras 2001). The few studies reporting homing rates for non-salmonid species indicate that homing rates are lower than for salmonids (e.g. white sucker 85%, Lucas and Baras 2001; smallmouth bass 14 - 41%, Pflug and Pauley 1983; Hodgson et al. 1998) because the olfactory system in these species is typically not as well developed as in salmon (Werner and Lannoo 1994). Homing increases the likelihood of finding a suitable habitat or mate, increases familiarity with local breeding conditions, returns locally adapted individuals to appropriate habitats, improves access to parental resources, and also avoids costs associated with moving to an unknown habitat (Hendry et al. 2004a). Straying, on the other hand, is beneficial when the natal spawning habitat is unsuitable at the time of migration and has benefits at the population level (the colonization of new environments, reduces inbreeding depression) and at the level of the individual (reducing competition between kin) (Hendry et al. 2004a).

A more comprehensive understanding of the large-scale patterns of fish movement is particularly important in the context of the use of in-stream barriers as a tool for ecosystem management. In my study area, 4 of the 6 study stream have low-head barriers (~0.4–2.0 m in height) designed to restrict the movement and reproduction of invasive species, such as the sea lamprey (*Petromyzon marinus*), thereby protecting native species and ecosystems (Porto et al. 1999; Lavis et al. 2003; Baxter et al. 2003; McLaughlin et al. 2007). Conversely, such barriers can be a source of concern when they restrict the movement of native, non-target fishes in ways that alter their population dynamics and reduce the persistence of non-target populations (Porto et al. 1999; McLaughlin et al. 2006; Harford and McLaughlin 2007). There are two uncertainties regarding the long distance movement of fishes that are important to understanding the effect of barriers for sea lamprey control and their effects on non-target species. First, large-scale inter-stream movement by sea lamprey could be a concern if spawning fish respond to a barrier by moving out of a barrier stream and into an adjacent stream (e.g., Kelso and Gardner 2000), possibly one that lacks a barrier or other forms of control (e.g., lampricides). Second, inter-stream movement by large numbers of non-target fishes could help stabilize remnant populations of native species downstream of barriers. Therefore, sea lamprey barriers can be used as a general model for long-term responses to fragmentation.

This study had three main objectives. First, because the movement of many freshwater stream fishes is poorly understood, I quantified the degree to which fish move between adjacent streams within and between reproductive seasons. Second, because little is known regarding which individuals are more likely to move between streams, I tested whether gender, size, and body condition of fish exhibiting inter-stream movement differed from fish that did not exhibit inter-stream movement. Finally, because the rates of homing and straying in many non-salmonid species has received little attention, I conducted two separate experiments: (i) a release experiment where naïve, tagged sea lamprey were released off the mouths of study streams to determine whether naïve sea lamprey would exhibit greater inter-stream (sampling) movement than sea lamprey caught, tagged, and released in their stream of capture; and (ii) a translocation experiment to test whether individuals unfamiliar with their stream would move more than non-translocated, stream caught fish (henceforth referred to as reference fish) in an attempt to return to their original stream of capture (i.e. homing).

Materials and Methods

For details on the study sites, quantification of arrival, size, and sex of individuals, PIT tagging protocols, and quantification of movement, see the Materials and Methods section of Chapter 1.

Release and translocation experiments

Two experiments were conducted in 2006 to provide experimental data on the rates of homing and straying. First, in a release experiment, I quantified the movement of sea lamprey, which were trapped by the Toronto Conservation Authority at the Humber River (~10 km west of Toronto, ON) and Duffins Creek (~35 km east of Toronto, ON), and then transported and released at locations close to the mouths of the streams. I then compared these movements with those of sea lamprey netted, marked, and released in their stream of capture. Because these were naïve individuals likely unfamiliar with the study area, I expected translocated individuals to exhibit greater inter-stream (sampling) movement than sea lamprey caught and released in their stream of capture. A total of 605 sea lamprey (485 females, 120 males) were obtained from the Fisheries and Oceans

Canada holding facility at the Ganaraska Region Conservation Authority (Port Hope, ON) which were caught as part of the normal trapping operations. Sea lamprey were transported ~180 km in an aerated container by truck to the Hagan Aqualab at the University of Guelph, and held in holding tanks for 48 h. Individuals were then (i) anesthetised, (ii) measured for fork length, weight, and sex, (iii) implanted with a PIT tag, (iv) marked externally with a plastic streamer tag and with a V-notch in the second dorsal fin, and (v) returned to the holding tank with fresh flowing water to recover for an additional 48 h. The additional V-notch was to aid trap operators in identifying my tagged sea lamprey to get a more accurate assessment of the movement behaviour of these individuals. Tagged sea lamprey were transported ~200 km to the study area and 121 randomly selected individuals were released in the lake at a depth of ~1.0m, off the mouths of the five main study streams (except Cobourg Brook) (mean distance from stream mouth = 425m; range = 40 – 985m), 15-20m from the shore (see Chap. 1, Figure 1.1). Movements into and out of streams were tracked using the PIT-tag antenna arrays.

In the translocation experiment, I used a sub-sample of teleost species captured in nets during our daily sampling effort to assess whether translocated fish would “home” to their chosen spawning stream. A sub-sample of 680 sexually mature fish from 6 species were tagged during the fish collection operations between early April and mid-June 2006 and assigned to this experiment. Sexually mature fish were chosen with the notion that sexually mature individuals would be more inclined to return to their initial stream of capture. A total of 183 individuals from 6 species were assigned to a translocation treatment and 497 to a reference treatment. I only used a sub-sample of individuals captured in the streams for the translocation experiment because my objective for the study was to examine the inter-stream movement behaviour of stream-caught fishes. Of these, 168 translocated individuals were sexed (87 females, 81 males). Overall, 7 creek chub (2 females, 5 males), 4 lake chub (1 females, 3 males), 6 pumpkinseed, 19 rock bass (14 females, 5 males), 144 white sucker (70 females, 68 males), and 3 yellow perch were used in the translocation experiments. Fish in the translocation treatment were tagged according to the protocols described above. After completely regaining their equilibrium, which took about 10-15 minutes, fish assigned to the translocated treatment were immediately transported in aerated 68 L containers to a randomly assigned study stream, their PIT tag number recorded, and released in groups of 3-5 individuals at locations between the upstream and downstream antenna arrays. Fish in the reference treatment were allowed to recover following tagging and released in the stream of capture as described in Chapter 1.

Data Analysis

The frequency of inter-stream movement of fishes, both within and between reproductive seasons, were inferred from the telemetry data collected by the antenna stations, and calculated for each species. Telemetry data were also used to estimate site fidelity and straying rates (*i.e.* the proportion of individuals that moved to another stream) within and between reproductive seasons. The probability of inter-stream movement within and between reproductive seasons was calculated as the total number of fish moving between streams divided by the total number of individuals captured (within years), and detected or recaptured (between years) in the streams. Because fish moved between streams infrequently (see below), only species with at least 10 tagged individuals or one individual detected moving between streams within reproductive seasons were included in the analysis to provide a reasonable estimate of inter-stream movement, yet maximize the sample size. I included species with a minimum of 10 individuals to account for species where individuals were detected on the antennae, but no inter-stream movement was observed. Furthermore, any species with at least one individual moving between streams were included because I was primarily interested in inter-stream movement. Based on this criterion, 2830 individuals from 15 species were included in the within-year analysis. For the between-year analysis, because fewer individuals were detected, I relaxed my assumptions, and included those species with at least 5 individuals detected or one individual detected moving between streams to maximize sample size. As with the within-year analysis, I included species with a minimum of 5 individuals to account for species where no inter-stream movement was detected. Any species with at least one individual moving between streams were again included because I was primarily interested in inter-stream movement. For the between years analysis, 480 individuals from 11 species were included.

To compare the rates of inter-stream movement within and between years, I included only those species that met the requirements above *i.e.* at least 10 tagged individuals or one individual detected moving between streams within reproductive seasons, and at least 5 individuals detected or one individual detected moving between streams between reproductive seasons. My objective was to examine if inter-stream movements differ within and between reproductive seasons. The rates of inter-stream movements within and between reproductive seasons for each species were then ranked and correlated using a two-tailed Spearman rank correlation. To determine if this trend was also observed at the species level, the mean rates of inter-stream movements within and between reproductive seasons for each species were then compared using a paired *t*-test.

I also tested if the proportion of fish detected moving between streams (see categories 4 from Chapter 1) was related to the median arrival date, since my ability to detect a fish moving between streams could be dependent on the length of time between when an individual was tagging and when the antennae were pulled (i.e. time at large). However, some species might not have any individuals moving between streams, so I included all individuals detected leaving a stream (categories 3 & 4 from Chapter 1) for this analysis. I hypothesized that fish tagged later in the season had less time to leave a stream than fish marked earlier in the season, so the proportion of individuals detected leaving the streams for a species should correlate with median arrival time.

I also calculated the number of migrants per generation, since studies suggest that one migrant per generation between populations is sufficient gene flow to offset genetic deterioration within subpopulations (Mills and Allendorf 1996; Vucetich and Waite 2000; Wang 2004). The generation time for each species was determined as the average age of males and females at the time of maximum egg production (Froese and Binohlan 2000) and obtained from http://www.fishbase.org. No values of generation time were available for the Great Lakes region; therefore the values used in this calculation represent the mean generation time of the species in general, and were used to calculate the number of individuals moving per generation. For each species, the number of individuals moving per generation was calculated as the total number of individuals moving both within and between years multiplied by the generation time, divided by the number of years of the study (3) and the number of streams (5 or 6) (Hill et al. 2002). The movement of juvenile or larval size classes are not considered using this method; therefore my estimate of the number of migrants per generation is likely an underestimate.

I examined whether individuals exhibiting inter-stream movements differed in size and body condition from fish that did not move. I hypothesized that there may be size-related constraints on inter-stream movement, *i.e.* smaller individuals may simply not have the energy resources to undertake long-distance, inter-stream movements (Roff 1988). Because of sexual size dimorphism within many species, each species was analysed separately by gender, both within and between years. For fish moving between reproductive seasons that were only detected on the antenna and never recaptured, I used the length from the previous year for all analyses. For body condition, an individual fish's body condition relative to its own population was estimated using the residuals from the regression of $\log_{10}$ (weight) against $\log_{10}$ (length) (Ricker 1975). I then examined each species for differences in slopes between years using an ANCOVA, with yearly sample as the fixed factor, $\log_{10}$ (length) as the covariate, and $\log_{10}$ (weight) as the dependent variable. Because of significant differences in the slopes of these regressions between years for most species, a separate regression analysis was done for each year for each species. For individuals moving between years that were only detected on the antennae and never recaptured, I used body condition from the previous year for all analyses. The residual for each individual of a species was then used to determine if there were differences in body condition between fish that moved between streams compared to those individuals that did not. Differences between movers and non-movers for both males and females of each species were then analysed by one-way ANOVA, with movement behaviour as the fixed factor, and $\log_{10}$ (length) and body condition as the dependent variables, using all individuals of the species. All analyses were done using SPSS v12.0.1, with a critical level of significance set at 0.05. To address the issue of multiple comparisons, analyses were Bonferoni corrected for both length ($n = 25$, $\alpha = 0.002$) and body condition ($n = 15$, $\alpha = 0.0033$).

Results

Sampling and tagging effort

Excluding those used in the release and translocation experiments, 4403 individuals from 26 species were PIT-tagged: 2686 fish in 2005, 1304 in 2006, and 412 in 2007 (Table 3.1). Differences in the number of fish tagged between years were due, in part, to differences in collection effort and method (Appendix II). Five species (creek chub, rock bass, rainbow trout, sea lamprey, and white suckers) accounted for 84% of all tagged individuals.

Inter-stream movement

Inter-stream movement by fishes occurred infrequently within reproductive seasons. Of the 4403 individuals PIT-tagged during the study, 2861 (65.0%) were detected on an antennae, of which 2754 (96.3%) were detected only in the stream where they were originally captured (Table 3.2). A total of 107 individuals (3.7%) moved between streams during a reproductive season: 54 in 2005, 43 in 2006, and 10 in 2007. Proportions of individuals moving between streams did not differ significantly among years (*G*-test: $G = 5.71$; df = 2; $p = 0.058$), although this result was just barely non-significant.

The frequency of inter-stream movement between reproductive seasons was also low (Table 3.3). Overall, 484 individuals tagged in a previous year were detected or recaptured returning to the study streams in a subsequent reproductive season. Eighty-one percent of individuals (n = 392) were detected returning to their original stream of capture/tagging, whereas 19% (n = 92) moved to another tributary. As was the case within reproductive seasons, the proportion of individuals moving between streams did not differ significantly between years (*G*-test: $G = 1.72$; df = 1; $p = 0.19$). However, the proportion of individuals moving was significantly higher between than within reproductive seasons (*G*-test: $G = 173.09$; df = 1; $p < 0.001$) (Tables 3.2, 3.3).

Fish that where tagged later in the season were just as likely to be detected leaving the streams as fish tagged earlier in the season. There was no significant correlation between median arrival time and the proportion of individuals detected leaving the streams (one-tailed Pearson correlation, $r = 0.23$, $n = 18$, $p = 0.18$).

Inter-stream movement between species

For species with at least 10 individuals detected on the antennae or one individual moving between streams, the propensity for inter-stream movement differed between species within reproductive seasons (*G*-test: $G = 147.65$; df = 14; $p < 0.001$), and ranged from 0% for brown trout and largemouth bass to 41.7% for smallmouth bass (Table 3.2).

For species with at least 5 individuals detected on the antennae or one individual moving between streams, the propensity for inter-stream movement also differed significantly among species between reproductive seasons (*G*-test: $G = 155.28$; df = 10; $p < 0.001$). Overall, inter-stream movement varied from 0% for creek chub to 100% for common shiner (Table 3.3). However, it is important to note that only one common shiner that was marked was detected.

When the rates of inter-stream movement of the 11 species included from both analyses were compared within and between reproductive seasons, a strong, positive correlation was evident (two-tailed Spearman correlation, $r_s = 0.76$, $n = 11$, $p = 0.006$, Figure 3.1). Nonetheless, the mean rate of inter-stream movement of these 11 species was higher between than within reproductive seasons (paired *t*-test: $t = -3.55$, df = 10, $p = 0.005$) (Figure 3.1).

Dispersal of inter-stream movers

The inter-stream movement of fishes was generally into an adjacent stream within reproductive seasons (Figure 3.2a). Overall, 59.8% (64/107) of all fish moved to an adjacent stream, whereas 16.8, 17.8, and 5.6% of the tagged individuals were detected moving 2, 3, and 4 streams from their original tagging location, respectively (Figure 3.2a). Similarly, between reproductive seasons, 70.7% (65/92) of observed movement was to an adjacent stream, whereas 14.1, 4.3, 8.7, and 2.2% of tagged individuals were detected moving 2, 3, 4, and 5 streams from their original tagging location, respectively (Figure 3.2b). The proportion of individuals dispersing a given distance differed significantly within compared to between reproductive years (*G*-test: $G = 33.17$; df = 4; $p < 0.001$), with proportionately more individuals dispersing to an adjacent stream between years, and proportionately more individuals dispersing a greater distance within years (Figure 3.2).

However, the arrangement of my streams could potentially bias the results, with more individuals likely to move shorter distances based on the study design. For example, with 6 study streams, there are 9 different ways that a fish can move 1 stream (see Figure 1.1). However, there are only 7, 5, 3 and 1 ways that a fish can move 2, 3, 4, or 5 streams, respectively. I corrected for this bias by calculating the expected number of fish that would be recaptured after moving 1-5 streams, assuming that fish are equally likely of being captured in any of the streams. For example, a fish from either extreme of my study area (i.e. Salem or Cobourg) would have only 1 possible choice of moving 1, 2, 3, 4, or 5 streams, respectively. Hence, all fish from Salem and Cobourg were assigned an equal probability (0.2) of moving 1, 2, 3, 4, or 5 streams. However, a fish from Shelter Valley, for example, would have 2 possible choices for moving 1 and 2 streams, and 1 choice for moving 3 streams. Hence, all fish from Shelter Valley were assigned a probability of 0.4 of moving 1 or 2 streams, 0.2 of moving 3 streams and no chance of moving 4 or 5 streams. The expected number of fish moving 1-5 streams was then calculated for each stream of origin using the total number of fish that were recaptured in another stream multiplied by the probability of moving a given number of streams. The observed number of fish moving 1 to 5 streams was then compared to the expected number for all streams, both within and between reproductive seasons. Dispersal distance, in terms of the number of streams moved, was shorter than expected by chance based on the study design (Chi-square: $\chi^2 = 25.43$; df = 4; $p < 0.001$) (Figure 3.2a).

Similarly, individuals moved a shorter distance than expected ($\chi^2 = 48.08$; df = 4; $p < 0.001$) (Figure 3.2b) between reproductive seasons.

Eight of the 15 species tagged with at least 10 individuals detected had at least one individual moving between streams per generation. Furthermore, only white sucker had > 10 individuals moving per generation (Table 3.4). Five species had < 1 individual moving per generation, whereas 2 species (brown trout and largemouth bass) had no individuals moving between streams (Table 3.4).

Size and body condition of movers and non-movers

No consistent differences in gender, total length (size), or body condition were observed between fish that did or did not exhibit inter-stream movement within a reproductive season. Of the 107 individuals moving between streams, 52 were sexually mature (females: n = 22; males: n = 30), whereas 19 were of unknown sex and 36 were juveniles. The proportion of individuals moving between streams for each gender/maturity category did not differ from the overall proportion of individuals PIT-tagged and categorized as female, male, unknown sex, or juvenile (*G*-test: $G = 2.86$; df = 3; $p = 0.41$). No differences in length were observed between movers and non-movers for any of the 13 species when analysed by gender (one-way ANOVA's, all *p*-values > 0.05; all *p*-values > 0.002 Bonferroni corrected, or sequential Bonferroni corrected). Only male sea lamprey differed in body condition (one-way ANOVA: $F_{[1,213]} = 6.88$, $p = 0.009$), with individuals that moved between streams in better condition than non-movers.

No consistent differences in gender, length, or body condition were observed between reproductive seasons between fish that did or did not exhibit inter-stream movement. Of the 92 individuals detected moving, 59 were sexually mature (females: n = 32; males: n = 27), whereas 23 were of unknown sex and 10 were juveniles. The proportion of individuals moving between streams for each gender/maturity category did not differ from the overall proportion of individuals PIT-tagged and categorized as female, male, unknown sex, or juvenile detected in subsequent years (*G*-test: $G = 0.60$; df = 3; $p = 0.90$). Only the length of male rock bass differed between movers and non-movers. Male rock bass that moved between streams were significantly smaller than non-movers (one-way ANOVA: $F_{[1,12]} = 22.53$, $p < 0.001$). No differences were observed for body condition between movers and non-movers for any of the 10 species (one-way ANOVA's, all *p*-values > 0.05; all *p*-values > 0.0033 Bonferoni corrected, or sequential Bonferroni corrected).

Sea lamprey release experiment

More reference sea lamprey (226 of 312; 72.4%), which were tagged and released within their stream of capture, were detected on the antennae than naïve sea lamprey that were released close to the mouths of the five study streams (254 of 605; 42.0%) (2006 data; *G*-test: $G = 49.64$, df = 1, $p < 0.001$).

Of the 254 released sea lamprey detected on the antennae or captured in the nets, only 122 individuals (48.0%) entered the stream closest to where they were released. Once a released sea lamprey was detected in a stream, however, its behaviour was similar to those tagged and released in their stream of capture. For a released sea lamprey to be scored as having moved, it had to be detected entering one stream and then detected in a second stream. The frequency of inter-stream movements did not differ significantly between released (2.8% of 254) and reference (5.3% of 226) sea lamprey in 2006 (*G*-test: $G = 2.09$, df = 1, $p = 0.15$).

Translocation experiment

The behaviour of translocated fish differed from reference fish. Overall, translocated fish were significantly more likely to be detected on the antenna arrays (164 of 183) than reference fish (351 of 497) (*G*-test: $G = 11.13$, df = 1, $p < 0.001$). Within a reproductive season, the frequency of inter-stream movements was higher for translocated fish (32 of 164; 19.5%) compared to reference fish (15 of 351; 4.3%) (*G*-test: $G = 36.63$, df = 1, $p < 0.0001$). Of the 32 translocated individuals exhibiting inter-stream movement, 28 were white suckers, 3 were rock bass, and 1 was a lake chub. When fish exhibited inter-stream movements, 24 of 32 individuals (75.0%) returned to their original stream of capture. Overall, 20 of 28 white suckers (71.4%), 3 of 3 (100%) rock bass, as well as the lone lake chub, returned to their original stream of capture following translocation. No individual creek chub, pumpkinseed, and yellow perch had individuals moving between streams.

Between reproductive seasons, the frequency of inter-stream movements was higher for translocated (moving from their translocated stream) (57 of 63; 90.5%) than for reference (20 of 117; 17.1%) fish (*G*-test: $G = 69.02$, df = 1, $p < 0.0001$). However, the degree of homing, defined here as a fish returning to its original stream of capture, did not differ significantly between groups (*G*-test: $G = 1.51$, df = 1, $p = 0.22$), with 97 reference fish (82.9%) compared to 39 translocated fish (61.9%) homing back to their original stream of capture. Only 6 translocated individuals (5 white suckers and 1 pumpkinseed), returned to their translocated stream.

Discussion

The frequency of inter-stream movements reported in this study does not support the notion that fishes respond to an in-stream barrier by moving *en masse* to a new spawning location in a different stream. This finding is valuable because how fishes respond behaviourally to in-stream barriers remains poorly understood (McLaughlin et al. 2007). In-stream barriers used to control sea lamprey might be viewed less favourably, in terms of sea lamprey control, if sea lamprey responded by moving out of the barrier tributary and into another tributary, especially a tributary that was not controlled regularly via other means. Conversely, in-stream barriers might be viewed more favourably, in terms of non-target effects (Porto et al. 1999; Dodd et al. 2003), if native fishes responded by moving to spawning location in a neighbouring tributary, rather than being delayed below or remaining within a restricted downstream portion of the barrier tributary (Schilt 2007). Although spawning habitat below the barriers was likely available, increased competition for space may drive some individuals to move to another stream. Nonetheless, one possibility for the low rates of inter-stream movement is that even in these barrier streams, suitable spawning habitat was not a limiting factor. A second possibility for the low rates of inter-stream movements is that the fish occupying these streams may have already either adapted evolutionarily or demographically to the presence of these barriers. The barriers in Colborne, Shelter Valley, and Grafton Creeks, and Cobourg Brook, were installed in 1984, 1985, 1987, and 1996, respectively (Lavis et al. 2003). Given the life history of fishes in these streams, individuals that would normally avoid barriers may have already left these streams since the barriers were installed. Finally, species in these populations might also be displaying partial migration, with individuals adopting migration or residency as a life-history strategy (Morinville and Rasmussen 2003). These findings further reinforce the need for research to develop fishways designed to pass a greater range of species, while still preventing the upstream migration of sea lamprey (McLaughlin et al. 2007).

The frequency of inter-stream movements made by stream fishes is probably inadequate to support metapopulation dynamics and the colonization of new habitats. However, this study also focused on the exchange of larger individuals that could be tagged and did not consider possible dispersal by smaller juvenile stages. Nonetheless, even small immigration rates can have important consequences for metapopulation persistence (Hill et al. 2002). In a simulation using Pacific salmon (*Oncorhynchus* spp) as a model species, a straying rate of $\delta = 0.1$ (10% of the intrinsic growth rate) resulted in a doubling of the time to extinction compared to a population with no straying (Hill et al. 2002). In this study, δ varied from 0.004 for creek chub to 0.56 for smallmouth bass, and other than smallmouth bass, only the white sucker had a $\delta \geq 0.10$ (Table 3.4). Additionally, 7 of 13 species had $\delta < 0.05$ (Table 3.4); these species may be more susceptible to environmental degradation, fragmentation, and loss of habitat since proportionately fewer individuals are likely to move to colonize new habitats. Although some species had few individuals that dispersed in general, the distance that individuals move can be just as important in maintaining metapopulation dynamics (Nachman 1991).

Of the individuals exhibiting inter-stream movements, 40.2% (43/107 from 10 species) and 29.4% (27/92 from 6 species) also moved at least two streams over from their original capture location, within and between reproductive seasons, respectively, or a minimum of 11.4 km on average, a remarkable distance considering many stream fishes are thought to be sedentary. These long-distance movers are of particular interest because they can help re-colonize unoccupied habitats and help stabilize smaller populations via the rescue effect (Ingvarsson 2001). Understanding how individuals exhibiting inter-stream movements affect the persistence of neighbouring populations (Hill et al. 2002) was not examined here and remains an important subject for future research.

The frequency of inter-stream movements made by stream fishes was probably adequate for gene flow between populations. A common rule of thumb holds that one migrant per generation between populations is sufficient gene flow to offset genetic deterioration within subpopulations (Mills and Allendorf 1996; Vucetich and Waite 2000; Wang 2004). This estimate is best considered a desirable minimum for natural populations and may be inadequate for resource management (Vucetich and Waite 2000). Some experts have suggested 1 - 10 migrants per generation would be an appropriate general rule of thumb (Mills and Allendorf 1996), whereas others have suggested >10 immigrants per generation are needed to avoid a substantial loss of genetic diversity, particularly in highly fluctuating populations (Vucetich and Waite 2000). In this study, only 8 of the 15 species tagged had at least one individual moving between streams per generation, and only white sucker had > 10 individuals moving per generation (Table 3.4). Five species had < 1 individual moving per generation, while 2 species had no individuals moving between streams (Table 3.4). These low rates of movement between streams might eventually lead to the reproductive isolation of these populations (Hendry et al. 2004a). However, given that juvenile and larval size classes were not considered, the number of migrants per generation is most likely an underestimate. The recommended level of connectivity between populations has become a central issue in conservation biology in the face of habitat fragmentation and isolation (Mills and Allendorf 1996), and is particularly relevant to in-stream barriers (e.g. low-head sea lamprey barriers), which can influence the movements, numbers, and kinds of non-target fishes in stream sections above a barrier (Porto et al.1999; Morita et al. 2000; Dodd et al. 2003; Harford and McLaughlin 2007). Understanding how individuals exhibiting inter-stream movements affect the level of gene flow realized between neighbouring populations was also not quantified here and remains an important subject for future research.

Individuals in this study moved shorter distances than expected by chance alone, both within and between reproductive seasons (Figure 3.2). However, the null model used to predict the expected distribution was not intended to account for other potential aspects of movement behaviour. First, because this study was limited to 6 streams, fish could potentially move outside the study area, which I was unable to detect. Hence, the rates of movement reported here are possibly an underestimate. Furthermore, fish can also potentially move into my study streams from outside the study area, but again I cannot detect this as movement from another stream. Two streams of comparable size are located within 4.0 km east of Salem Creek, while 4 comparable streams, including the Ganaraska River, are located within 10.0 km west of Cobourg Brook. However, based on the distribution of distances moved within my study area (see Figure 3.2), movement into and out of my study area was possible, but was likely to be rare. Second, the distances between streams might also influence which species are more likely to be detected moving, given that some distances might be too great for smaller species. Although I didn't specifically consider how the distance between streams might influence the likelihood of movement, even given the bias in detecting fish moving to neighbouring streams, which is included in the expected values, more than expected fish moved to neighbouring streams. The distribution of number of streams moved (i.e. Figure 3.2) suggests that most fish move along the shoreline of Lake Ontario. Hence, when they do move between streams they tend to enter the first available stream encountered. If fish tended to move far out into Lake Ontario and then returned to the study streams, then the distribution would probably look more like the expected distribution. Accounting for these boundary effects in future models can potentially improve our understanding regarding the inter-stream movements of fishes.

Explaining which species and individuals are likely to exhibit inter-stream movements presents a complex challenge. At the species level, there was some consistency in the taxa exhibiting inter-stream movements, illustrated by the strong, positive correlation in the movement rates of species within and between reproductive seasons (Figure 3.2). Several studies have reported that mobile individuals of species were longer, but in poorer condition than their non-mobile counterparts in Arctic char *Salvelinus alpinus* (Naslund et al. 1993), cutthroat trout *Oncorhynchus clarkii* (Hilderbrand and Kershner 2004), and brook charr *Salvelinus fontinalis* (Gowan and Fausch 1996). Hence, some individuals may simply not have the energy reserves to undertake these long-distance, inter-stream movements (Roff 1988), suggesting that there may be size-related constraints on inter-stream movement. My data, however, did not support this hypothesis at the individual level as gender, body length, and body condition were not strong predictors of which individuals move. A clearer understanding of what physiological characters influence inter-stream movements in species requires further study.

Comparing the inter-stream movements exhibited by translocated and reference (not translocated) fishes can help delineate some of the mechanisms influencing inter-stream movements (Lucas and Baras 2001). For sea lamprey, the selection of streams by the spawning individuals is not determined by homing (Applegate and Smith 1951; Smith and Elliott 1953; Bergstedt and Seelye 1995; Kelso and Gardner 2000). However, based on results from this study, it would seem that sea lampreys also do not select streams indiscriminately. In the sea lamprey release experiment, individuals entered the closest stream to their release point only 42% of the time. However, once the released sea lamprey entered a stream, the frequency of inter-stream movements was low and comparable to that observed for sea lamprey tagged and released in their stream of capture. Rates of inter-stream movement for both groups were generally lower than the rate of 10-50% reported by Kelso and Gardner (2000) for released sea lamprey, although their individuals were released within a tributary, rather than in a lake, as in this experiment. Future studies at this spatial scale will need to incorporate the influence that other factors, including stream size and the sea lamprey migration pheromone (Bjerselius et al. 2000; Sorensen et al. 2003; Fine and Sorensen 2005) have on stream selection by spawning-run sea lamprey.

Similarly, translocated teleost fishes were capable of moving between streams and exhibited spawning site fidelity and reproductive homing. At least some translocated fishes moved between streams to return to their original stream of capture, indicating they likely had the sensory and physiological abilities required to make inter-stream movements and that inter-stream movements may be infrequent, due in part, to site fidelity and reproductive homing. Numerous studies examining the movement of translocated North American freshwater fishes have reported that between 14 – 100% of individuals return to their initial stream of capture (Gerking 1959; Werner 1979; Halvorsen and Stabell 1990; Ridgway and Shuter 1996; Hodgson et al. 1998; Lucas and Baras 2001), potentially limiting mixing between populations (Lucas and Baras 2001; Hendry et al. 2004a). However, in this study, 59% of translocated white suckers homed back to their original stream of capture, compared to 83% of reference individuals and the 85% reported in the literature (Lucas and Baras 2001), suggesting that this species' ability to home may not be as developed as in salmonids (Werner and Lannoo 1994). In the future, translocation of individuals to areas outside of their presumed home ranges and comparisons of moving and resident fish will provide insightful opportunities to further delineate mechanisms determining the degree of inter-stream movement, particularly for non-salmonid fishes.

Species in this study displayed the ability to home to their original stream of capture, ranging from 0 – 100%. Rates of homing and straying have important implications for the local adaptability of populations (Hendry et al. 2004a), as well as the susceptibility of a population to stream fragmentation. Common shiner, smallmouth bass, and brown bullhead exhibited low rates of homing, ranging from 0 – 20%. Although these species may be less adapted to their local environment due to the higher rates of dispersal, they may also be less susceptible to stream fragmentation because individuals would be capable of responding to such fragmentation by moving to another stream. At the other extreme, white sucker, rock bass, lake chub, and creek chub exhibited a high degree of homing, ranging from 81 – 100%, allowing individuals to adapt to their local environments. However, these species may be more susceptible to stream fragmentation due to barriers to movement. These in-stream barriers may decrease available reproductive habitat, causing a decrease in recruitment since it is likely that individuals will continue to return to the same streams. However, given that there has been ~200 years of dam building in the Great Lakes (Regier and Hartman 1973), many species that would be susceptible to fragmentation might have already been extirpated. Nonetheless, not only will results from this study add to the limited information on homing and straying in non-salmonid species (see Lucas and Baras 2001), but may also help to identify species that are more susceptible to habitat fragmentation by new or planned barriers.

The homing of individuals to their original stream brings individuals back to an environment known to be suitable for reproduction, as well as timing their arrival with that of other sexually mature fish (Wootton 1990; Lucas and Barras 2001; Hendry et al. 2004a). However, the rate of homing and straying in many freshwater fishes remains unknown. Rates of homing are generally higher for salmonid than non-salmonid species, and typically range from 90 – 100% (Lucas and Baras 2001). Both adult-sized (males, females, and individuals of unknown sex) and juvenile rainbow trout in this homed at a rate of only 75%, lower than the 94% reported in the literature for this species (Lucas and Baras 2001). One possibility for the low homing rates is that rainbow trout populations in this area may consist of more individuals with a “straying genotype”, *i.e.,* more prone to stray from their “home” stream. All rainbow trout in the Great Lakes have their origins from several strains of hatchery stocks dating back to the late-1800 – early-1900’s (MacCrimmon and Gots 1972), which may have come from populations exhibiting more straying in their natural environments. Given how quickly the species had naturalized in the Great Lakes, the movement of individuals beyond their initial planting areas may still be an ongoing process, with individuals (re)colonizing new habitats.

This study has uniquely demonstrated that the fish assemblages in these Lake Ontario catchments are dynamic, exchanging individuals at rates and spatial extents likely to be important for key ecological and micro-evolutionary processes, such as metapopulation dynamics and gene flow. For sea lamprey, however, rates of inter-stream movement were not high enough to support the hypothesis that spawning-run individuals respond to in-stream barriers by moving *en masse* to adjacent streams, which would potentially reduce the benefits of a sea lamprey barrier. Similarly, for native teleost fishes, the rates of inter-stream movement were also not high enough to lessen concern about the potential effects sea lamprey barriers can have on stream fishes via habitat fragmentation. The dynamic nature of adjacent fish assemblages suggest consideration of larger scale movement needs to be considered in assessing the effects of decisions involving sea lamprey barriers, in terms of both the effectiveness of sea lamprey control and the effects on native fishes. The low frequency of inter-stream movement in response to barriers also reinforces the value of providing selective and effective fish passage at barriers.

Table 3.1: Number of individuals implanted with a Passive Integrated Transponder (PIT) tag summarized by species andyear.

Species		Year			
Common name	**Scientific name**	**2005**	**2006**	**2007**	**Total**
blacknose dace	*Rhinichthys atratulus*	2			2
brook trout	*Salvelinus fontinalis*	66	17	20	103
brown bullhead	*Ameiurus nebulosus*	126	19	22	167
brown trout	*Salmo trutta*	41	5	3	49
central stoneroller	*Campostoma anomalum*		1		1
chinook salmon	*Oncorhynchus tshawytscha*	4	3	1	8
common shiner	*Luxilus cornutus*	21	20	30	71
creek chub	*Semotilus atromaculatus*	437	109	126	672
emerald shiner	*Notropis atherinoides*	1	2		3
golden shiner	*Notemigonus crysoleucas*		5		5
hornyhead chub	*Nocomis biguttatus*		1		1
lake chub	*Couesius plumbeus*	60	17	1	78
largemouth bass	*Micropterus salmoides*		3	7	10
logperch	*Percina caprodes*	6		4	10
longnose dace	*Rhinichthys cataractae*	21	15	6	42
mottled sculpin	*Cottus bairdii*	1			1
northern pike	*Esox lucius*	2	1		3
pumpkinseed	*Lepomis gibbosus*	36	23	1	60
rainbow smelt	*Osmerus mordax mordax*	4	15		19
rainbow trout	*Oncorhynchus mykiss*	834	385	20	1239
rock bass	*Ambloplites rupestris*	243	29	31	303
round goby	*Neogobius melanostomus*		3	6	9
sea lamprey	*Petromyzon marinus*	80	311	96	487

smallmouth bass	*Micropterus dolomieu*	8	1	4	13
white sucker	*Catostomus commersoni*	670	312	27	1009
yellow perch	*Perca flavescens*	24	7	7	38
Covert Creek		585	141	107	833
Grafton Creek		416	186	104	706
Shelter Valley Creek		604	366	96	1066
Colborne Creek		416	253	86	755
Salem Creek		666	358	19	1043
Grand Total		**2687**	**1304**	**412**	**4403**

Table 3.2: Number of fish detected by the antennae arrays, summarized by species and whether individuals remained in their stream of capture (0) or moved 1 to 4 streams from their original stream within a reproductive season. The percent of individuals moving was calculated only for species with at least 10 individuals detected or 1 individual moving between streams.

	Streams moved					
Species	0	1	2	3	4	% moving
blacknose dace	1	0	0	0	0	—
brook trout	82	2	1	0	2	5.7
brown bullhead	104	3	0	0	0	2.8
brown trout	32	0	0	0	0	0
central stoneroller						—
chinook salmon	3	0	0	0	0	—
common shiner	48	5	0	0	0	9.4
creek chub	367	0	0	1	1	0.5
emerald shiner	3	0	0	0	0	—
golden shiner	5	0	0	0	0	—
hornyhead chub						—
lake chub	66	0	1	0	0	1.5
largemouth bass	10	0	0	0	0	0
logperch	6	0	0	0	0	—
longnose dace	24	0	0	1	0	4.0
mottled sculpin	1	0	0	0	0	—
northern pike	2	0	0	0	0	—
pumpkinseed	27	5	2	0	0	20.6
rainbow smelt	2	0	0	0	0	—
rainbow trout	753	21	3	12	0	4.6
rock bass	220	2	1	1	1	2.2
round goby	8	0	0	0	0	—
sea lamprey	343	5	8	1	1	4.2
smallmouth bass	7	4	0	1	0	41.7
white sucker	613	16	2	2	1	3.3
yellow perch	27	1	0	0	0	3.6
Grand total	2754	64	18	19	6	3.7

Table 3.3: Number of fish detected by the antennae arrays, summarized by species and whether individuals remained in their stream of capture (0) or moved 1 to 5 streams from their original stream between reproductive seasons. The percentage of individuals straying was calculated for species with at least 5 individuals detected or 1 individual moving between streams.

	Streams moved						
Species	0	1	2	3	4	5	% straying
brook trout	1	2	0	0	0	0	66.7
brown bullhead	1	3	1	0	0	0	80.0
brown trout	3	0	0	0	0	0	—
common shiner	0	1	0	0	0	0	100
creek chub	16	0	0	0	0	0	0
lake chub	16	1	0	0	0	0	5.9
longnose dace	3	0	0	1	1	0	40.0
pumpkinseed	5	1	1	0	0	0	28.6
rainbow trout	36	9	3	0	0	0	25.0
rock bass	102	12	1	0	1	0	12.1
round goby	1	0	0	0	0	0	—
smallmouth bass	1	6	0	0	0	0	85.7
white sucker	207	30	7	3	6	2	18.8
Grand total	392	65	13	4	8	2	19.0

Table 3.4: Number of fish detected by the antennae arrays within and between reproductive seasons, and the total number of movers, summarized by species. The proportion of movers, generation time, overall number of fish moving per generation, intrinsic growth rate, and the straying rate (δ) was calculated only for species with at least 10 individuals detected.

Species	# detected	# moved	Prop. movers	Generation time[1]	Movers per generation[2]	Intrinsic growth rate[1]	Straying rate (δ)[3]
blacknose dace	1	0	—	—	—	—	—
brook charr	90	7	0.078	3.2	1.2	1.04	0.075
brown bullhead	112	7	0.063	2.1	1.0	2.02	0.031
brown trout	35	0	0.000	5.0	0.0	0.80	0.000
central stoneroller	0	0	—	—	—	—	—
chinook salmon	3	0	—	—	—	—	—
common shiner	54	6	0.111	1.3	0.5	3.40	0.033
creek chub	385	2	0.005	3.4	0.4	1.38	0.004
emerald shiner	3	0	—	—	—	—	—
golden shiner	5	0	—	—	—	—	—
hornyhead chub	0	0	—	—	—	—	—
lake chub	84	2	0.024	3.1	0.4	2.74	0.009
largemouth bass	10	0	0.000	3.3	0.0	1.30	0.000
logperch	6	0	—	—	—	—	—
longnose dace	30	3	0.100	3.0	0.6	1.50	0.067
mottled sculpin	1	0	—	—	—	—	—
northern pike	2	0	—	—	—	—	—
pumpkinseed	41	9	0.220	5.2	3.1	2.78	0.079
rainbow smelt	2	0	—	—	—	—	—

rainbow trout	837	48	0.057	1.6	4.3	2.34	0.025
rock bass	341	19	0.056	3.1	3.3	1.78	0.031
round goby	9	0	—	—	—	—	—
sea lamprey	358	15	0.042	10.6	8.8	0.48	0.087
smallmouth bass	19	11	0.579	4.4	2.7	1.04	0.557
white sucker	889	69	0.078	5.9	22.6	0.78	0.100
yellow perch	28	1	0.036	2.2	0.1	1.92	0.019

[1] Generation time and intrinsic growth rate for each species was taken from the Key facts summary page at http://www.fishbase.org. [2] Number of individuals per generation was calculated as the total number of fish moving both within and between years for each species / 3 years / 5 streams (brown bullhead, common shiner, lake chub, longnose dace, pumpkinseed, and yellow perch) or 6 streams (brook charr, creek chub, rainbow trout, rock bass, sea lamprey, smallmouth bass, and white sucker). [3] Straying rate (δ) was calculated as the proportion of individuals moving between streams both within and between years / intrinsic growth rate for each species.

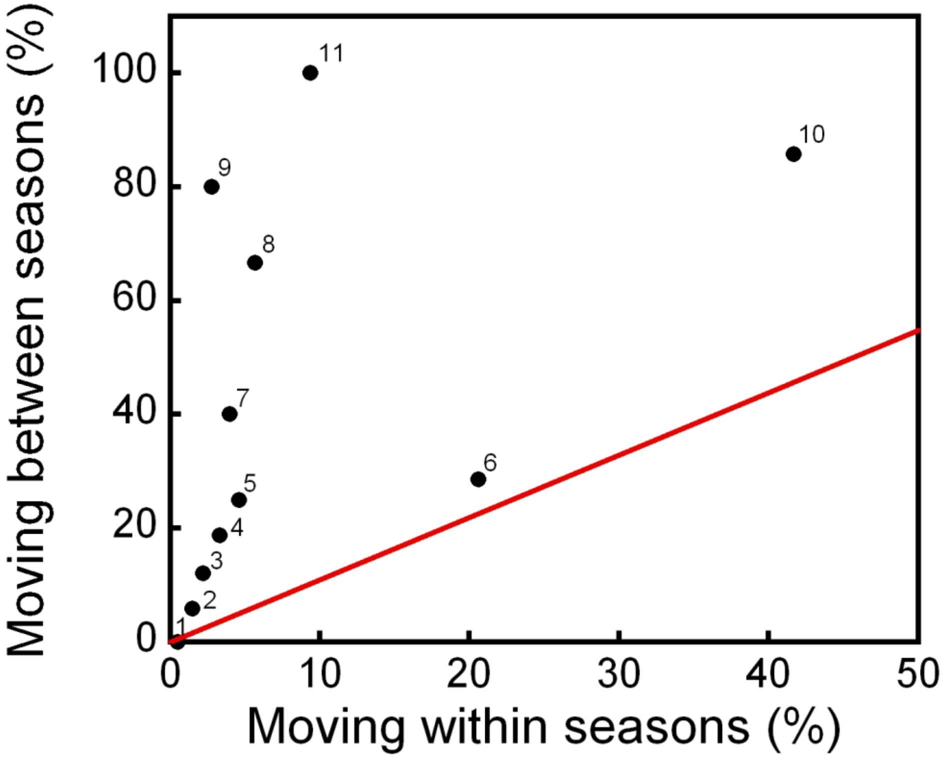

Figure 3.1: Relationship between the rate of inter-stream movement of species (n = 11) within and between reproductive years. Solid line represents a 1:1 line. Species are: 1) creek chub; 2) lake chub; 3) rock bass; 4) white sucker; 5) rainbow trout; 6) pumpkinseed; 7) longnose dace 8); brook charr; 9) brown bullhead; 10) smallmouth bass; and 11) common shiner.

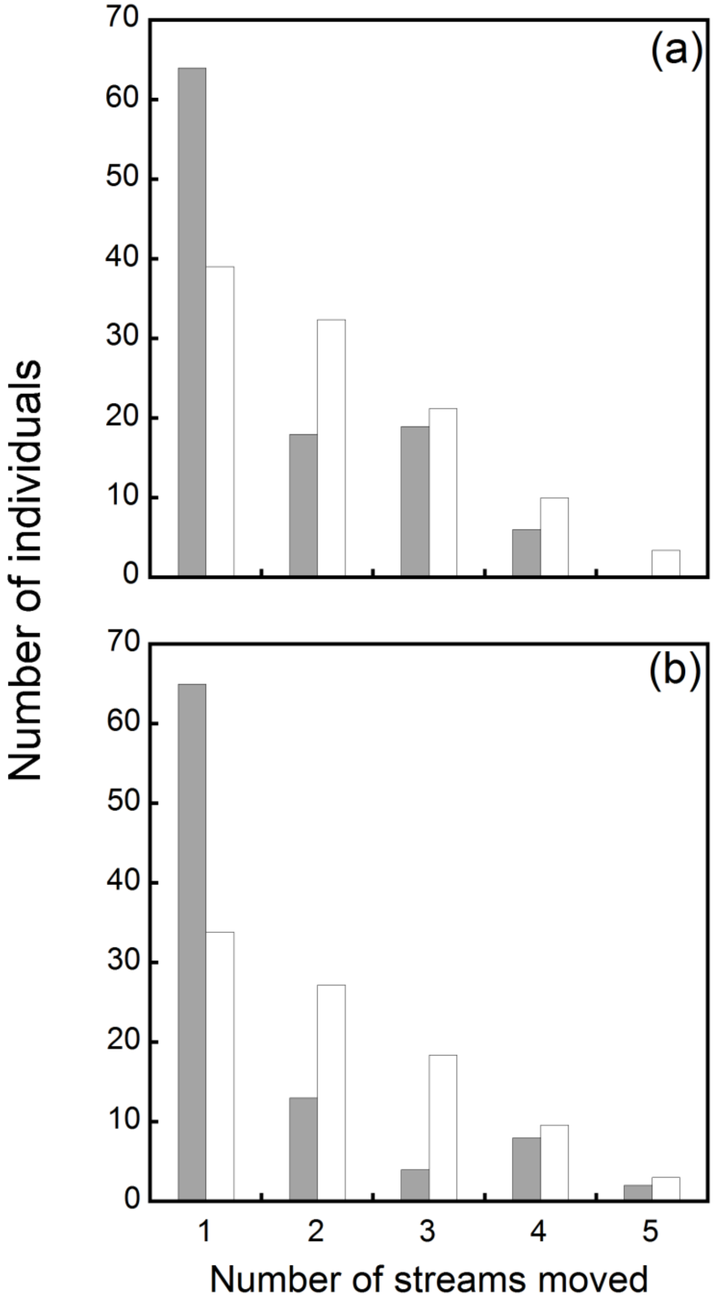

Figure 3.2: The observed (dark grey bar) and expected (open bar) number of fish in relation to the number of streams moved from the original stream of capture (a) within, and (b) between reproductive seasons.

General Discussion

The main purpose of my thesis was to improve our understanding of fish movements by evaluating the movement of multiple species across multiple streams and entire watersheds. My thesis has provided three important contributions to the advancement of knowledge regarding the movement behaviour of stream fishes. First, it provided an evaluation and advancement of existing natural history literature needed for successful conservation and recovery plans (Chapter 1). Comparisons between my data and those from the literature demonstrated a strong correlation regarding key biological indices, providing instances where natural history information can be used with some confidence in decisions regarding freshwater stream fishes. But my data also provided novel findings, suggesting that juveniles are moving into the streams along with adults, and that species with known "anadromous-like" life histories spend more time in the streams before leaving for the lake than previously thought. Secondly, my thesis successfully adapted, tested and extended existing theory on sex-biased arrival timing developed for birds and mammals to stream fishes, suggesting that the wide variety of fishes considered exhibited great variation in sex-biased timing, with males arriving before females in the majority of species and populations (Chapter 2). Finally, my thesis extended and contributed to a management concern of broad interest regarding invasive species control, suggesting that the fish assemblages in these Lake Ontario catchments are dynamic, exchanging individuals at rates and spatial extents likely to be important for key ecological and micro-evolutionary processes, such as meta-population dynamics and gene flow (Chapter 3). However, my results also suggest that the low rates of inter-stream movement exhibited by some species needs to be considered with regard to the potential effects in-stream barriers can have on stream fishes via habitat fragmentation.

Results from this thesis are interesting and reveal some novel insights into the movement behaviour of stream fishes, but they also highlight the need for future studies to address aspects on the movement behaviour of freshwater fishes not covered by this study. For example, while my study spanned three years, it did not explicitly examine the costs and benefits of movement. Future studies examining the costs and benefits of movement would need to span the life-time of a tagged individual, typically 4-9 years for Canadian freshwater fishes (Wootton 1984). Longer-term studies quantifying the survival (costs) and year to year growth (benefits) of tagged individuals from the juvenile until the reproductive stage (ideally until death) would greatly improve our understanding of movement behaviour in stream fishes by linking the life history of individuals to population dynamics (Ombredane et al. 1998; Roussel et al. 2000). These studies would also provide valuable information regarding additional management applications, such as the timing of movements relative to the timing of construction activities in order to minimize the impact these activities might have on stream fish populations.

Future studies should also focus on juveniles to determine why they are moving into the streams with adults. Results from this study suggest that juveniles moved into the streams with the arrival of adults; however I was only able to speculate as to the reason(s) for their arrival. Streams are particularly important for the juvenile age-classes, providing refuge, as well as providing habitats to maximize growth (Northcote 1997; Lucas and Baras 2001; Salas and Snyder 2010). However, their presence is rarely mentioned in the natural history accounts regarding the movement behaviour of freshwater fishes, with most studies focusing on adults. Although past tagging techniques precluded the study of small-bodied fishes due to increased tagging mortality (Roussell et al. 2000), advances in PIT tagging and tracking technology, such as smaller tags (i.e. half-duplex 12mm tags) can provide novel insights into the movement behaviour and use of habitat in these juvenile life stages (Roussel et al. 2000; Fischer et al. 2001).

Although my study was able to adapt, test and extend existing theory on sex-biased arrival timing developed for birds and mammals to stream fishes, further refinements of these hypotheses are necessary to better understand the selection pressures male and female fishes face during the breeding season and how these pressures shape their behaviour and ecology. For example, one of the key assumptions regarding sex-biased timing is that individuals that arrive earlier have greater reproductive potential (Morbey and Ydenberg 2001), which was not tested in this study. Advances in genetic analysis, such as the use of microsatellites, can be used to analyze both adults entering the streams and juveniles leaving the streams to determine if earlier arrival results in greater reproductive potential. This technique has been effective at discriminating between kin and non-kin progeny in past studies (Brodeur et al. 2008); hence reproductive success and its relationship with sex-biased arrival timing can be determined by assigning the progeny back to their parents.

New quantitative methods can potentially further refine questions concerning the movement behaviour of freshwater fishes. In populations where individuals adopt an anadromous (migrant) or nonanadromous (resident) life-history strategy (*i.e.* partial migration), stable isotope analysis has shown that residents and migrants differ in their stable isotope signatures, making it possible to distinguish between the two forms (Finlay et al. 2002; Morinville and Rasmussen 2003; Swanson et al. 2010). Although this is phenomenon is commonly observed in salmonids (Finlay et al. 2002; Morinville and Rasmussen 2003; Swanson et al. 2010), it is possible that this strategy might also be more common in other freshwater fishes thought to be stream resident.

Advances in electronic-tagging technology may also improve our understanding of the movement behaviour of freshwater fishes. The results from this thesis suggest that individuals of many species use both lake and stream habitat; however this assumption is based solely on the detection of individuals on the antennae or their recapture during the netting activities, but ignores movements outside my study streams. But movement of individuals beyond the study area cannot be ascertained using this technique, although long-distance movements of 30-90 km from their original tagging locations have been reported in some species (Young 1996; Brenkman and Corbett 2005). Pop-up satellite archival tags (PSATs), for example, are able to track an individual's movement over the life of the tag without the need of recapture or detection by antennae. PSATs are programmed to measure and record depth, water temperature, as well geographic location, and are designed to detach from the fish at a pre-programmed date, floating to the surface to transmit stored data via the Argos satellite system (Hoolihan et al. 2011). At the moment, however, their use in most freshwater systems is not feasible because their large size (~160mm X 40mm; 65g) and cost (~$US 3000 per tag) (Hoolihan et al. 2011) makes them both unusable on smaller-bodied fishes and in large-scale tagging studies.

Results from this study are both interesting and encouraging, and provide additional information to the limited knowledge on the movement behaviour of stream fishes. However, given the uniqueness of the study, these results might not be replicable in other, smaller lakes for several reasons. First, the size of Lake Ontario may influence the movement behaviour of fishes. Lake Ontario is the 12th largest freshwater lake in the world, with an area of almost 20,000 km^2, roughly 6 orders of magnitude larger than the global average size of lakes (~0.01km; Downing et al. 2006). Typically, larger lakes have higher primary productivity than smaller lakes (Guildford et al. 1994; Dodson et al. 2000). Hence, movement out of the streams towards the lake to grow might be more common in fishes found in these habitats than in other, smaller lakes. Secondly, because species richness is related to the size of a lake (Barbour and Brown 1974; Eadie et al. 1986), it would be particularly difficult to find small lakes with such species. Finally, the number of streams in this study (6) would be difficult to replicate in smaller lakes. It seems likely that the number of tributaries for a given lake might be a function of lake surface area.

As with any study, ours has some important limitations. Acknowledging these can ensure our results are interpreted appropriately and identify areas where future research will be beneficial. Our findings were potentially biased, to unknown degrees, by tag loss, inefficiencies of tag detection by the antennas, small sample sizes for rarer species, the proper identification of sexes, and any effects the handling and PIT tagging of fishes might have on their health, survival and reproduction (Sigourney et al. 2005; Bateman and Gresswell 2006). We did take steps to address some of these issues. We found little evidence of tag loss, at least within a season. Our estimate of loss (~ 2.7%) was similar to earlier studies demonstrating that PIT tag retention was high: brown trout (*Salmo trutta*) (54-129 mm) 96.6% tag retention (Ombredane et al. 1998); Atlantic salmon parr (>90 mm) tag retention exceeded 99.0% (Zydlewski et al. 2001), Atlantic salmon parr (64-94 mm) without sutures 84.8% tag retention (Roussel et al. 2000); and 97.0% tag retention in rainbow trout (Bateman and Gresswell 2006). In addition, we routinely checked the antennae for areas of poor detection, and constructed and tuned the antennae to maximize detection efficiency. Also, the minimum size of individuals selected for PIT-tagging in our study (100 mm) was considerably larger than reported in studies by Sigourney et al. (2005) (~ 62 mm) and Bateman and Gresswell 2006 (73-97 mm) using the same sized tag, and was well above the size suggested to have strong effects on survival and growth of small individuals (<80 mm) (Sigourney et al. 2005). Nevertheless, the stress of handling and tagging could have influenced the overall rates of movement by the study fishes. The number of streams monitored in this study (6) was also far greater than that in any previous study examining movements in fishes (which are typically limited to a single stream). Despite this consideration, the number of streams might not have been sufficient to detect extremely long-distance movements outside of the study area. My results suggested that such movements are possible. The maximum distance between streams was ~29.0 km (from the mouths of Cobourg Brook to Salem Creek) and several studies of stream fishes have reported movements of fish on the order of 30-90 km from their original tagging locations (Young 1996, see references therein; Brenkman and Corbett 2005). As such, estimates of the rate and distance of inter-stream movement are likely underestimates, and developing a practical and economical design to overcome these limitations will be a significant challenge for future studies. Nonetheless, my rate of antenna detection efficiency was high (91.6%, see Appendix section), hence interpolation of the rates of inter-stream movement presented herein are robust.

General Conclusion

In-stream barriers are a potentially valuable tool for controlling the movement and reproduction of invasive species; however, they may also represent an important environmental concern if they fragment populations or meta-populations of stream fishes (Porto et al. 1999; McLaughlin et al. 2006; Harford and McLaughlin 2007). Since many aquatic vertebrates have highly complex life histories, with each stage in their life history requiring a different habitat type that might be separated from the other (Schlosser 1995), the importance of understanding the impact of these barriers on fish movement becomes paramount. In addition, if sea lampreys move between streams after encountering a barrier, then the use of barriers as a management tool for invasive species control may need to be re-evaluated. In contrast, inter-stream movement of non-target species after encountering a barrier could be desirable, especially if these fishes move and reproduce elsewhere.

Clearly, there is still much to be learned regarding the movement behaviour of fishes. However, potomodromy seems to be more prevalent than commonly thought, with many more species than expected detected leaving the streams in this study. It is clear that movement represents an important component of the ecology of many stream fish populations (Knaepkens et al. 2005). Understanding the movement behaviour of fishes is critical in developing proper conservation plans, as well as gaining a better understanding on their particular life histories (Knaepkens et al. 2004). Knowledge gained from this study will serve as a vehicle to improving our understanding of how concepts such as meta-populations, habitat fragmentation, and movement apply to stream fishes and to efforts to control invasive fish species.

References

Abell, R. (2002). Conservation biology for the biodiversity crisis: A freshwater follow-up. Conservation Biology **16**: 1435-1437.

Achord, S., Matthews, G. M., Johnson, O. W., and Marsh, D. M. (1996). Use of passive integrated transponder (PIT) tags to monitor migration timing of Snake River chinook salmon smolts. North American Journal of Fisheries Management **16**: 302-313.

Adams, N. S., Rondorf, D. W., Evans, S. D., Kelly, J. E., and Perry, R. W. (1998). Effects of surgically and gastrically implanted radio transmitters on swimming performance and predator avoidance of juvenile chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences **55**: 781-787.

Anderson, J. H., Faulds, P. L., Atlas, W. I., Pess, G. R., and Quinn, T. P. (2010). Selection on breeding date and body size in colonizing coho salmon, *Oncorhynchus kisutch*. Molecular Ecology **19**: 2562-2573.

Andersson, M. (1994). Sexual selection. Princeton University Press. Princeton, New Jersey.

Ankley, G. T. and Villeneuve, D. L. (2006). The fathead minnow in aquatic toxicology: Past, present and future. Aquatic Toxicology **78**: 91-102.

Applegate, V. C. and Smith, B. R. (1951). Movement and dispersion of a blocked spawning run of sea lampreys in the Great Lakes. Transactions of the North American Wildlife and Natural Resources Conference **16**: 243-251.

Armstrong, J. D., Braithwaite, V. A., and Rycroft, P. (1996). A flat-bed passive integrated transponder antenna array for monitoring behaviour of Atlantic salmon parr and other fish. Journal of Fish Biology **48**: 539-541.

Axel, G. A., Prentice, E. F., and Sandford, B. P. (2005). PIT-tag detection system for large-diameter juvenile fish bypass pipes at Columbia River basin hydroelectric dams. North American Journal of Fisheries Management **25**: 646-651.

Aymes, J. C. and Rives, J. (2009). Detection efficiency of multiplexed Passive Integrated Transponder antennas is influenced by environmental conditions and fish swimming behaviour. Ecology of Freshwater Fish **18**: 507-513.

Bal, G., Rivot, E., Prevost, E., Piou, C., and Bagliniere, J. L. (2011). Effect of water temperature and density of juvenile salmonids on growth of young-of-the-year Atlantic Salmon *Salmo salar*. Journal of Fish Biology **78**: 1002-1022.

Balon. E.K. (1975). Reproductive guilds of fishes: a proposal and definition. Journal of the Fisheries Research Board of Canada **32**: 821-864.

Barbour, C. D. and Brown, J. H. (1974). Fish species diversity in lakes. American Naturalist **108**: 473-489.

Bateman, D. S. and Gresswell, R. E. (2006). Survival and growth of age-0 steelhead after surgical implantation of 23-mm passive integrated transponders. North American Journal of Fisheries Management **26**: 545-550.

Baxter, J. S., Birch, G. J., and Olmsted, W. R. (2003). Assessment of a constructed fish migration barrier using radio telemetry and floy tagging. North American Journal of Fisheries Management **23**: 1030-1035.

Beamish, F. W. H. (1980). Biology of the North American anadromous Sea Lamprey, *Petromyzon marinus*. Canadian Journal of Fisheries and Aquatic Sciences **37**: 1924-1943.

Bergstedt, R. A. and Seelye, J. G. (1995). Evidence for a lack of homing by sea lampreys. Transactions of the American Fisheries Society **124**: 235-239.

Bjerselius, R., Li, W. M., Teeter, J. H., Seelye, J. G., Johnsen, P. B., Maniak, P. J., Grant, G. C., Polkinghorne, C. N., and Sorensen, P. W. (2000). Direct behavioral evidence that unique bile acids released by larval sea lamprey (*Petromyzon marinus*) function as a migratory pheromone. Canadian Journal of Fisheries and Aquatic Sciences **57**: 557-569.

Blanckenhorn, W. U. (2005). Behavioral causes and consequences of sexual size dimorphism. Ethology **111**: 977-1016.

Breder, C. M. and Rosen, D. E. (1966). Modes of reproduction in fishes. T.F.H. Publications, Neptune City, New Jersey.

Breen, M. J., Ruetz, C. R., Thompson, K. J., and Kohler, S. L. (2009). Movements of mottled sculpins (*Cottus bairdii*) in a Michigan stream: How restricted are they? Canadian Journal of Fisheries and Aquatic Sciences **66**: 31-41.

Brenkman, S. J. and Corbett, S. C. (2005). Extent of anadromy in bull trout and implications for conservation of a threatened species. North American Journal of Fisheries Management **25**: 1073-1081.

Brodeur, N. N., Noel, M. V., Venter, O., Bernatchez, L., Dayanandan, S., and Grant, J. W. A. (2008). No evidence of kin bias in dispersion of young-of-the-year Atlantic salmon *Salmo salar* L. in a natural stream. Journal of Fish Biology **73**: 2361-2370.

Brown, J. H., Hammer, U. T., and Koshinsky, G. D. (1970). Breeding biology of the Lake Chub, *Couesius plumbeus*, at Lac la Ronge, Saskatchewan. Journal of the Fisheries Research Board of Canada **27**: 1005-1015.

Brown, T. G., Runciman B., Pollard, S., Grant, A. D. A., and Bradford, M. J. (2009). Biological synopsis of smallmouth bass (*Micropterus dolomieu*). Canadian Manuscript Report of Fisheries and Aquatic Sciences **2887**: 58 pp.

Bruyndoncx, L., Knaepkens, G., Meeus, W., Bervoets, L., and Eens, M. (2002). The evaluation of passive integrated transponder (PIT) tags and visible implant elastomer (VIE) marks as new marking techniques for the bullhead. Journal of Fish Biology **60**: 260-262.

Carvalho, M. C., Queiroz, P. C. D., and Ruszczyk, A. (1998). Protandry and female size-fecundity variation in the tropical butterfly *Brassolis sophorae*. Oecologia **116**: 98-102.

Castro-Santos, T., Haro, A., and Walk, S. (1996). A passive integrated transponder (PIT) tag system for monitoring fishways. Fisheries Research **28**: 253-261.

Clutton-Brock, T. (2007). Sexual selection in males and females. Science **318**: 1882-1885.

Clutton-Brock, T. (2009). Sexual selection in females. Animal Behaviour **77**: 3-11.

Connolly, P. J., Jezorek, I. G., Martens, K. D., and Prentice, E. F. (2008). Measuring the performance of two stationary interrogation systems for detecting downstream and upstream movement of PIT-tagged salmonids. North American Journal of Fisheries Management **28**: 402-417.

Cookingham, M. N. and Ruetz, C. R. (2008). Evaluating passive integrated transponder tags for tracking movements of round gobies. Ecology of Freshwater Fish **17**: 303-311.

Coon, T. G. (1999). Ichthyofauna of the Great Lakes basin, pp. 55-71 *in* W.W. Taylor and C. Paola Ferreri [eds.], Great Lakes Fisheries Policy and Management: A Binational Perspective. Michigan State University Press, East Lansing, MI.

Coppaway, C. W. (2004). Dynamics of residency for Brook charr (*Salvelinus fontinalis*) in Lake Superior tributaries. Master's thesis, University of Guelph, Guelph, Ontario, Canada.

Cutts, C. J., Metcalfe, N. B., and Taylor, A. C. (1999). Competitive asymmetries in territorial juvenile Atlantic salmon, *Salmo salar*. Oikos **86**: 479-486.

Dahl, J., Dannewitz, J., Karlsson, L., Petersson, E., Lof, A., and Ragnarsson, B. (2004). The timing of spawning migration: implications of environmental variation, life history, and sex. Canadian Journal of Zoology **82**: 1864-1870.

Danylchuk, A. J. and Fox, M. G. (1996). Size and age-related variation in the seasonal timing of nesting activity, nest characteristics, and female choice of parental male pumpkinseed sunfish (*Lepomis gibbosus*). Canadian Journal of Zoology **74**: 1834-1840.

Dickerson, B. R., Quinn, T. P., and Willson, M. F. (2002). Body size, arrival date, and reproductive success of pink salmon, *Oncorhynchus gorbuscha*. Ethology Ecology & Evolution **14**: 29-44.

Dickerson, B. R., Brinck, K. W., Willson, M. F., Bentzen, P., and Quinn, T. P. (2005). Relative importance of salmon body size and arrival time at breeding grounds to reproductive success. Ecology **86**: 347-352.

Dodd, H. R., Hayes, D. B., Baylis, J. R., Carl, L. M., Goldstein, J. D., Mclaughlin, R. L., Noakes, D. L. G., Porto, L. M., and Jones, M. L. (2003). Low-head sea lamprey barrier effects on stream habitat and fish communities in the Great Lakes basin. Journal of Great Lakes Research **29**: 386-402.

Dodson, J. J. (1988). The nature and role of learning in the orientation and migratory behavior of fishes. Environmental Biology of Fishes **23**: 161-182.

Dodson, S. I., Arnott, S. E., and Cottingham, K. L. (2000). The relationship in lake communities between primary productivity and species richness. Ecology **81**: 2662-2679.

Downing, J. A., Prairie, Y. T., Cole, J. J., Duarte, C. M., Tranvik, L. J., Striegl, R. G., Mcdowell, W. H., Kortelainen, P., Caraco, N. F., Melack, J. M., and Middelburg, J. J. (2006). The global abundance and size distribution of lakes, ponds, and impoundments. Limnology and Oceanography**51**: 2388-2397.

Eadie, J. M., Hurly, T. A., Montgomerie, R. D., and Teather, K. L. (1986). Lakes and rivers are islands - species-area relationships in the fish faunas of Ontario. Environmental Biology of Fishes **15**: 81-89.

Emlen, S. T. and Oring, L. W. (1977). Ecology, sexual selection and the evolution of mating systems. Science **197**: 215-223.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. Annual Review of Ecology Evolution and Systematics **34**: 487-515.

Fairbairn, D. J. (2007). Introduction: the enigma of sexual selection, pp. 1-10 *in* Sex, size, and gender roles: Evolutionary studies of sexual size dimorphism. *Edited by* D.J. Fairbairn, W.U. Blackenhorn, and T. Székely. Oxford University Press, New York.

Fine, J. M. and Sorensen, P. W. (2005). Biologically relevant concentrations of petromyzonol sulfate, a component of the sea lamprey migratory pheromone, measured in streamwater. Journal of Chemical Ecology **31**: 2205-2210.

Finlay, J. C., Khandwala, S., and Power, M. E. (2002). Spatial scales of carbon flow in a river food web. Ecology **83**: 1845-1859.

Fischer, P., Kautz, H., Weber, H., and Obergfell, W. (2001). The use of passive integrated transponder systems (PIT) triggered by infrared-gates for behavioural studies in nocturnal, bottom-dwelling fish species. Journal of Fish Biology **58**: 295-298.

Francis, C. M. and Cooke, F. (1986). Differential timing of spring migration in Wood warblers (Parulinae). Auk **103**: 548-556.

Froese, R. and Binohlan, C. (2000). Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. Journal of Fish Biology **56**: 758-773.

Gerking, S. D. (1959). The restricted movement of fish populations. Biological Reviews, **34**: 221-242.

Gotelli, N. J. (2008). A primer of ecology, 4th edition. Sinauer Associates Inc., Sunderland, MA.

Gowan, C. and Fausch, K. D. (1996). Mobile brook trout in two high-elevation Colorado streams: Re-evaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences **53**: 1370-1381.

Gowan, C., Young, M. K., Fausch, K. D., and Riley, S. C. (1994). Restricted movement in resident stream salmonids - a paradigm lost. Canadian Journal of Fisheries and Aquatic Sciences **51**: 2626-2637.

Greenberg, L. A. and Giller, P. S. (2000). The potential of flat-bed passive integrated transponder antennae for studying habitat use by stream fishes. Ecology of Freshwater Fish **9**: 74-80.

Gries, G. and Letcher, B. H. (2002). Tag retention and survival of age-0 Atlantic salmon following surgical implantation with passive integrated transponder tags. North American Journal of Fisheries Management **22**: 219-222.

Gross, M. R. (1987). Evolution of diadromy in fishes. American Fisheries Society Symposium **1**: 14-25.

Gross, M. R. and Nowell, W. A. (1980). The reproductive biology of rock bass, *Ambloplites rupestris* (Centrarchidae), in Lake Opinicon, Ontario. Copeia **1980**: 482-494.

Guildford, S. J., Hendzel, L. L., Kling, H. J., Fee, E. J., Robinson, G. G. C., Hecky, R. E., and Kasian, S. E. M. (1994). Effects of lake size on phytoplankoton nutrient status. Canadian Journal of Fisheries and Aquatic Sciences **51**: 2769-2783.

Halvorsen, M. and Stabell, O. B. (1990). Homing behaviour of displaced stream-dwelling brown trout. Animal Behaviour **39**: 1089-1097.

Hanski, I. (1998). Metapopulation dynamics. Nature **396**: 41-49.

Hanski, I. and Gilpin, M. E. eds. (1997). Metapopulation biology: Ecology, genetics, and evolution. Academic Press, San Diego.

Harford, W. J. and Mclaughlin, R. L. (2007). Understanding uncertainty in the effect of low-head dams on fishes of Great Lakes tributaries. Ecological Applications **17**: 1783-1796.

Harwood, A. J., Griffiths, S. W., Metcalfe, N. B., and Armstrong, J. D. (2003). The relative influence of prior residency and dominance on the early feeding behaviour of juvenile Atlantic salmon. Animal Behaviour **65**: 1141-1149.

Hendry, A. P., Bohlin, T., Jonsson, B., and Berg, O. K. (2004a). To sea or not to sea? Anadromy vs. non-anadromy in salmonids, pp. 92-125 *in* A. P. Hendry and S. C. Sterns [eds.], Evolution illuminated: salmon and their relatives. Oxford University Press, New York, NY.

Hendry, A. P., Castric, V., Kinnison, M. T., and Quinn, T. P. (2004b). The evolution of philopatry and dispersal: Homing versus straying in salmonids, pp. 52-91 *in* A. P. Hendry and S. C. Sterns [eds.], Evolution illuminated: salmon and their relatives. Oxford University Press, New York, NY.

Hilderbrand, R. H. and Kershner, J. L. (2004). Are there differences in growth and condition between mobile and resident cutthroat trout? Transactions of the American Fisheries Society **133**: 1042-1046.

Hill, M. F., Hastings, A., and Botsford, L. W. (2002). The effects of small dispersal rates on extinction times in structured metapopulation models. American Naturalist **160**: 389-402.

Hodgson, J. R., Schindler, D. E., and He, X. (1998). Homing tendency of three piscivorous fishes in a north temperate lake. Transactions of the American Fisheries Society **127**: 1078-1081.

Holm, E., Mandrak, N., and Burridge, M. (2009). The ROM field guide to freshwater fishes of Ontario. Royal Ontario Museum, Toronto.

Hoolihan, J. P., Luo, J. G., Abascal, F. J., Campana, S. E., De Metrio, G., Dewar, H., Domeier, M. L., Howey, L. A., Lutcavage, M. E., Musyl, M. K., Neilson, J. D., Orbesen, E. S., Prince, E. D., and Rooker, J. R. (2011). Evaluating post-release behaviour modification in large pelagic fish deployed with pop-up satellite archival tags. Ices Journal of Marine Science **68**: 880-889.

Hutchings, J. A. and Gerber, L. (2002). Sex-biased dispersal in a salmonid fish. Proceedings of the Royal Society of London Series B-Biological Sciences **269**: 2487-2493.

Hutchings, J. A. and Festa-Bianchet, M. (2009). Canadian species at risk (2006-2008), with particular emphasis on fishes. Environmental Reviews **17**: 53-65.

Ingvarsson, P. K. (2001). Restoration of genetic variation lost - The genetic rescue hypothesis. Trends in Ecology & Evolution **16**: 62-63.

Jepsen, N., Aarestrup, K., Okland, F., and Rasmussen, G. (1998). Survival of radio-tagged Atlantic salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.) smolts passing a reservoir during seaward migration. Hydrobiologia **372**: 347-353.

Johnsson, J. I., Nobbelin, F., and Bohlin, T. (1999). Territorial competition among wild brown trout fry: effects of ownership and body size. Journal of Fish Biology **54**: 469-472.

Kahler, T. H., Roni, P., and Quinn, T. P. (2001). Summer movement and growth of juvenile anadromous salmonids in small western Washington streams. Canadian Journal of Fisheries and Aquatic Sciences **58**: 1947-1956.

Kelso, J. R. M. and Gardner, W. M. (2000). Emigration, upstream movement, and habitat use by sterile and fertile sea lampreys in three Lake Superior tributaries. North American Journal of Fisheries Management **20**: 144-153.

Ketterson, E. D. and Nolan V. Jr. (1983). The evolution of differential bird migration, pp. 357-402 *in* Current Ornithology: Volume 1. Edited by RF Johnston. Plenum Press, New York.

Kishi, D., Murakami, M., Nakano, S., and Maekawa, K. (2005). Water temperature determines strength of top-down control in a stream food web. Freshwater Biology **50**: 1315-1322.

Knaepkens, G., Bruyndoncx, L., and Eens, M. (2004). Assessment of residency and movement of the endangered bullhead (*Cottus gobio*) in two Flemish rivers. Ecology of Freshwater Fish **13**: 317-322.

Knaepkens, G., Baekelandt, K., and Eens, A. (2005). Assessment of the movement behaviour of the bullhead (*Cottus gobio*), an endangered European freshwater fish. Animal Biology **55**: 219-226.

Kokko, H. (1999). Competition for early arrival in migratory birds. Journal of Animal Ecology **68**: 940-950.

Kvarnemo, C. and Ahnesjo, I. (1996). The dynamics of operational sex ratios and competition for mates. Trends in Ecology & Evolution **11**: 404-408.

Lavis, D. S., Hallett, A., Koon, E. M., and Mcauley, T. C. (2003). History of and advances in barriers as an alternative method to suppress sea lampreys in the Great Lakes. Journal of Great Lakes Research **29**: 362-372.

Letcher, B. H., Gries, G., and Juanes, F. (2002). Survival of stream-dwelling Atlantic salmon: Effects of life history variation, season, and age. Transactions of the American Fisheries Society **131**: 838-854.

Li, W. M., Sorensen, P. W., and Gallaher, D. D. (1995). The olfactory system of migratory adult sea lamprey (*Petromyzon marinus*) is specifically and acutely sensitive to unique bile-acids released by conspecific larvae. Journal of General Physiology **105**: 569-587.

Lovich, J. E. and Gibbons, J. W. (1992). A review of techniques for quantifying sexual size dimorphism. Growth Development and Aging **56**: 269-281.

Lucas, M. C. and Baras, E. (2001). Migration of freshwater fishes. Blackwell Science.

MacCrimmon, H. R. and Gots, B. L. (1972). Rainbow trout in the Great Lakes. Ontario Ministry of Natural Resources.

Mallet, J. P., Charles, S., Persat, H., and Auger, P. (1999). Growth modelling in accordance with daily water temperature in European grayling (*Thymallus thymallus* L.). Canadian Journal of Fisheries and Aquatic Sciences **56**: 994-1000.

Mandrak, N. E., Jones, M. L., and McLaughlin, R. L. (2003). Evaluation of the Great Lakes fishery commission interim policy on barrier placement. Great Lakes Fishery Commission Final Report.

Matsuura, K. (2006). Early emergence of males in the termite *Reticulitermes speratus* (Isoptera : Rhinotermitidae): Protandry as a side effect of sexual size dimorphism. Annals of the Entomological Society of America **99**: 625-628.

McCormick, S. D., Hansen, L. P., Quinn, T. P., and Saunders, R. L. (1998). Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences **55**: 77-92.

McDowall, R. M. (1988). Diadromy in fishes: migrations between freshwater and marine environments. Cambridge University Press.

Mclaughlin, R. L., Hallett, A., Pratt, T. C., O'Connor, L. M., and McDonald, D. G. (2007). Research to guide use of barriers, traps, and fishways to control sea lamprey. Journal of Great Lakes Research **33**: 7-19.

Mclaughlin, R. L., Porto, L., Noakes, D. L. G., Baylis, J. R., Carl, L. M., Dodd, H. R., Goldstein, J. D., Hayes, D. B., and Randall, R. G. (2006). Effects of low-head barriers on stream fishes: taxonomic affiliations and morphological correlates of sensitive species. Canadian Journal of Fisheries and Aquatic Sciences **63**: 766-779.

Metcalfe, J., Arnold, G., and McDowall, R. (2002). Migration, pp175-199 *in* P. J. B. Hart and J. D. Reynolds [eds.], Handbook of fish biology and fisheries: Volume 1. Blackwell Publishing.

Michener, G. R. (1983). Spring emergence schedules and vernal behavior of Richardson's ground squirrels: why do males emerge from hibernation before females? Behavioral Ecology and Sociobiology **14**: 29-38.

Mills, A. M. (2005). Protogyny in autumn migration: Do male birds "play chicken"? Auk **122**: 71-81.

Mills, L. S. and Allendorf, F. W. (1996). The one-migrant-per-generation rule in conservation and management. Conservation Biology **10**: 1509-1518.

Møller, A. P. (1994). Phenotype-dependent arrival time and its consequences in a migratory bird . Behavioral Ecology and Sociobiology **35**: 115-122.

Møller, A. P., Balbontin, J., Cuervo, J. J., Hermosell, I. G., and De Lope, F. (2009). Individual differences in protandry, sexual selection, and fitness. Behavioral Ecology **20**: 433-440.

Morbey, Y. (2000). Protandry in Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences **57**: 1252-1257.

Morbey, Y. E. (2002). Protandry models and their application to salmon. Behavioral Ecology **13**: 337-343.

Morbey, Y. E. (2003). Pair formation, pre-spawning waiting, and protandry in kokanee, *Oncorhynchus nerka*. Behavioral Ecology and Sociobiology **54**: 127-135.

Morbey, Y. E. and Ydenberg, R. C. (2001). Protandrous arrival timing to breeding areas: a review. Ecology Letters **4**: 663-673.

Morin, A., Lamoureux, W., and Busnarda, J. (1999). Empirical models predicting primary productivity from chlorophyll a and water temperature for stream periphyton and lake and ocean phytoplankton. Journal of the North American Benthological Society **18**: 299-307.

Morinville, G. R. and Rasmussen, J. B. (2003). Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences **60**: 401-410.

Morita, K., Yamamoto, S., and Hoshino, N. (2000). Extreme life history change of white-spotted char (*Salvelinus leucomaenis*) after damming. Canadian Journal of Fisheries and Aquatic Sciences **57**: 1300-1306.

Murphy, B. R. and Willis, D. W. (1996). Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, MD.

Nachman, G. (1991). An acarine predator-prey metapopulation system inhabiting greenhouse cucumbers. Biological Journal of the Linnean Society **42**: 285-303.

Naslund, I., Milbrink, G., Eriksson, L. O., and Holmgren, S. (1993). Importance of habitat productivity differences, competition, and predation for the migratory behavior of Arctic charr. Oikos **66**: 538-546.

Northcote, T. G. (1997). Potamodromy in Salmonidae - Living and moving in the fast lane. North American Journal of Fisheries Management **17**: 1029-1045.

Northcote, T. G. (1998). Migratory behaviour of fish and its significance to movement through riverine fish passage facilities, pp. 3-18 *in* M. Jungwirth, S. Schmutz, S. Weiss [eds.], Fish migration and fish bypass. Blackwell Science.

Nunnallee, E. P., Prentice, E. F., Jonasson, B. F., and Patten, W. (1998). Evaluation of a flat-plate PIT tag interrogation system at Bonneville Dam. Aquacultural Engineering **17**: 261-272.

O'connor, K. I., Metcalfe, N. B., and Taylor, A. C. (2000). The effects of prior residence on behavior and growth rates in juvenile Atlantic salmon (*Salmo salar*). Behavioral Ecology **11**: 13-18.

Ojanguren, A. F. and Brana, F. (2003). Effects of size and morphology on swimming performance in juvenile brown trout (*Salmo trutta* L.). Ecology of Freshwater Fish **12**: 241-246.

Olsson, I. C. and Greenberg, L. A. (2004). Partial migration in a landlocked brown trout population. Journal of Fish Biology **65**: 106-121.

Olsson, M. and Madsen, T. (1996). Costs of mating with infertile males selects for late emergence in female sand lizards (*Lacerta agilis* L). Copeia **1996**: 462-464.

Olsson, M., Birkhead, T., and Shine, R. (1999). Can relaxed time constraints on sperm production eliminate protandry in an ectotherm? Biological Journal of the Linnean Society **66**: 159-170.

Ombredane, D., Bagliniere, J. L., and Marchand, F. (1998). The effects of Passive Integrated Transponder tags on survival and growth of juvenile brown trout (*Salmo trutta* L.) and their use for studying movement in a small river. Hydrobiologia **372**: 99-106.

Parker, G. A. (1992). The evolution of sexual size dimorphism in fish. Journal of Fish Biology **41**: 1-20.

Peterman, R. M. (2004). Possible solutions to some challenges facing fisheries scientists and managers. Ices Journal of Marine Science **61**: 1331-1343.

Pflug, D. E. and Pauley, G. B. (1983). The movement and homing of smallmouth bass, *Micropterus dolomieu*, in Lake Sammamish, Washington. California Fish and Game **69**: 207-216.

Poos, M. S., Mandrak, N. E., and Mclaughlin, R. L. (2008). A practical framework for selecting among single-species, community-,and ecosystem-based recovery plans. Canadian Journal of Fisheries and Aquatic Sciences **65**: 2656-2666.

Porto, L. M., McLaughlin, R. L., and Noakes, D. L. G. (1999). Low-head barrier dams restrict the movements of fishes in two Lake Ontario streams. North American Journal of Fisheries Management **19**: 1028-1036.

Portt, C. B., Minns, C. K., and King, S. W. (1988). Morphological and ecological characteristics of common fishes in Ontario lakes. Canadian Manuscript Report of Fisheries and Aquatic Sciences **1991**: 37 pp.

Power, G., Brown, R. S., and Imhof, J. G. (1999). Groundwater and fish - insights from northern North America. Hydrological Processes **13**: 401-422.

Pratt, T. C., O'connor, L. M., Hallett, A. G., Mclaughlin, R. L., Katopodis, C., Hayes, D. B., and Bergstedt, R. A. (2009). Balancing aquatic habitat fragmentation and control of invasive species: Enhancing selective fish passage at sea lamprey control barriers. Transactions of the American Fisheries Society **138**: 652-665.

Prenter, J., Taylor, P. W., and Elwood, R. W. (2008). Large body size for winning and large swords for winning quickly in swordtail males, *Xiphophorus helleri*. Animal Behaviour **75**: 1981-1987.

Prentice, E. F., Flagg, T. A., and McCutcheon, C. S. (1990). Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids, pp. 317-322 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, E. D. Prince, and G. A. Winans [eds.], Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Primack, R. B. (2008). A primer of conservation biology, 4th edition. Sinauer Associates Inc., Sunderland, MA.

Pulliam, H. R. and Danielson, B. J. (1991). Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist **137**: S50-S66.

Quinn, T. P., Hendry, A. P., and Buck, G. B. (2001). Balancing natural and sexual selection in sockeye salmon: interactions between body size, reproductive opportunity and vulnerability to predation by bears. Evolutionary Ecology Research **3**: 917-937.

Quinn, T. P., Gende, S. M., Ruggerone, G. T., and Rogers, D. E. (2003). Density-dependent predation by brown bears (*Ursus arctos*) on sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences **60**: 553-562.

Regier, H. A. and Hartman, W. L. (1973). Lake Erie's fish community: 150 years of cultural stresses. Science **180**: 1248-1255.

Ricciardi, A. and Rasmussen, J. B. (1999). Extinction rates of North American freshwater fauna. Conservation Biology **13**: 1220-1222.

Richter, B. D., Braun, D. P., Mendelson, M. A., and Master, L. L. (1997). Threats to imperiled freshwater fauna. Conservation Biology **11**: 1081-1093.

Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada **191**: 382 pp.

Ridgway, M. S. and Shuter, B. J. (1996). Effects of displacement on the seasonal movements and home range characteristics of smallmouth bass in Lake Opeongo. North American Journal of Fisheries Management **16**: 371-377.

Rodriguez, M. A. (2002). Restricted movement in stream fish: The paradigm is incomplete, not lost. Ecology **83**: 1-13.

Roff, D. A. (1988). The evolution of migration and some life-history parameters in marine fishes. Environmental Biology of Fishes **22**: 133-146.

Roussel, J. M., Haro, A., and Cunjak, R. A. (2000). Field test of a new method for tracking small fishes in shallow rivers using passive integrated transponder (PIT) technology. Canadian Journal of Fisheries and Aquatic Sciences **57**: 1326-1329.

Russom, C. L., Bradbury, S. P., Broderius, S. J., Hammermeister, D. E., and Drummond, R. A. (1997). Predicting modes of toxic action from chemical structure: Acute toxicity in the fathead minnow (*Pimephales promelas*). Environmental Toxicology and Chemistry **16**: 948-967.

Salas, A. K. and Snyder, E. B. (2010). Diel fish habitat selection in a tributary stream. American Midland Naturalist **163**: 33-43.

Savalli, U. M. (2001). Sexual selection, pp. 207-221 *in* C. W. Fox, D. A. Roff, and D. J. Fairbairn [eds.], Evolutionary ecology: Concepts and case studies. Oxford University Press, New York.

Schilt, C. R. (2007). Developing fish passage and protection at hydropower dams. Applied Animal Behaviour Science **104**: 295-325.

Schlosser, I. J. (1995). Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. Ecology **76**: 908-925.

Schrank, A. J. and Rahel, F. J. (2006). Factors influencing summer movement patterns of Bonneville cutthroat trout (*Oncorhynchus clarkii utah*). Canadian Journal of Fisheries and Aquatic Sciences **63**: 660-669.

Scott, W. B. and Crossman, E. J. (1998). Freshwater fishes of Canada. Fisheries Research Board of Canada, Ottawa. Bulletin 184.

Seamons, T. R., Bentzen, P., and Quinn, T. P. (2004). The mating system of steelhead, *Oncorhynchus mykiss*, inferred by molecular analysis of parents and progeny. Environmental Biology of Fishes **69**: 333-344.

Semlitsch, R. D. (1985). Analysis of climatic factors influencing migrations of the salamander *Ambystona talpoideum*. Copeia **1985**: 477-489.

Sigourney, D. B., Horton, G. E., Dubreuil, T. L., Varaday, A. M., and Letcher, B. H. (2005). Electroshocking and PIT tagging of juvenile Atlantic salmon: Are there interactive effects on growth and survival? North American Journal of Fisheries Management **25**: 1016-1021.

Singer, M. C. (1982). Sexual selection for small size in male butterflies . American Naturalist**119**: 440-443.

Skalski, J. R., Lady, J., Townsend, R., Giorgi, A. E., Stevenson, J. R., Peven, C. M., and McDonald, R. D. (2001). Estimating in-river survival of migrating salmonid smolts using radiotelemetry. Canadian Journal of Fisheries and Aquatic Sciences **58**: 1987-1997.

Smith, B. R. and Elliott, O. R. (1953). Movement of parasitic-phase in Lakes Huron and Michigan. Transactions of the American Fisheries Society **82**: 123-128.

Smith, K. L. and Jones, M. L. (2007). When are historical data sufficient for making watershed-level streamfish management and conservation decisions? Environmental Monitoring and Assessment **135**: 291-311.

Smith, R. J. and Moore, F. R. (2005). Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behavioral Ecology and Sociobiology **57**: 231-239.

Smithson, E. B. and Johnston, C. E. (1999). Movement patterns of stream fishes in a Ouachita Highlands stream: An examination of the restricted movement paradigm. Transactions of the American Fisheries Society **128**: 847-853.

Sokal, R. R. and Rohlf, F. J. (1969). Biometry: the principles and practice of statistics in biological research. San Francisco: W.H. Freeman.

Sorensen, P. W., Vrieze, L. A., and Fine, J. M. (2003). A multi-component migratory pheromone in the sea lamprey. Fish Physiology and Biochemistry **28**: 253-257.

Swanson, H. K., Kidd, K. A., Babaluk, J. A., Wastle, R. J., Yang, P. P., Halden, N. M., and Reist, J. D. (2010). Anadromy in Arctic populations of lake trout (*Salvelinus namaycush*): Otolith microchemistry, stable isotopes, and comparisons with Arctic char (*Salvelinus alpinus*). Canadian Journal of Fisheries and Aquatic Sciences **67**: 842-853.

Tallman, R. F., Abrahams, M. V., and Chudobiak, D. H. (2002). Migration and life history alternatives in a high latitude species, the broad whitefish, *Coregonus nasus pallas*. Ecology of Freshwater Fish **11**: 101-111.

Torgersen, C. E., Price, D. M., Li, H. W., and Mcintosh, B. A. (1999). Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. Ecological Applications **9**: 301-319.

Venter, O., Brodeur, N. N., Nemiroff, L., Belland, B., Dolinsek, I. J., and Grant, J. W. A. (2006). Threats to endangered species in Canada. Bioscience **56**: 903-910.

Vucetich, J. A. and Waite, T. A. (2000). Is one migrant per generation sufficient for the genetic management of fluctuating populations? Animal Conservation **3**: 261-266.

Wang, J. (2004). Application of the one-migrant-per-generation rule to conservation and management. Conservation Biology **18**: 332-343.

Wedell, N. (1992). Protandry and mate assessment in the wartbiter *Decticus verrucivorus* (Orthoptera: Tettigoniidae). Behavioral Ecology and Sociobiology **31**: 301-308.

Werner, R. G. (1979). Homing mechanism of spawning white suckers in Wolf Lake, New York. New York Fish and Game Journal **26**: 48-58.

Werner, R. G. and Lannoo, M. J. (1994). Development of the olfactory system of the white sucker *Catostomus commersoni*, in relation to imprinting and homing: A comparison to the salmonid model. Environmental Biology of Fishes **40**: 125-140.

Wiklund, C. and Solbreck, C. (1982). Adaptive versus incidental explanations for the occurrence of protandry in a butterfly, *Leptidea sinapis* L. Evolution **36**: 56-62.

Wilson, A. J., Hutchings, J. A., and Ferguson, M. M. (2004). Dispersal in a stream dwelling salmonid: Inferences from tagging and microsatellite studies. Conservation Genetics **5**: 25-37.

Wootton, R. J. (1984). Introduction: strategies and tactics in fish reproduction, pp. 1-12 *in* G.W. Potts and R.J. Wootton [eds.], Fish Reproduction: strategies and tactics. Academic Press. London.

Wootton, R. J. (1990). Ecology of teleost fishes. Chapman and Hall, London. 404 pp.

Yamamoto, T. and Edo, K. (2006). Factors influencing the breeding activity in male masu salmon, *Oncorhynchus masou*: The relationship with body size. Environmental Biology of Fishes **75**: 375-383.

Young, M. K. (1996). Summer movements and habitat use by Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in small, montane streams. Canadian Journal of Fisheries and Aquatic Sciences **53**: 1403-1408.

Zydlewski, G. B., Haro, A., Whalen, K. G., and Mccormick, S. D. (2001). Performance of stationary and portable passive transponder detection systems for monitoring of fish movements. Journal of Fish Biology **58**: 1471-1475.

Zydlewski, G. B., Horton, G., Dubreuil, T., Letcher, B., Casey, S., and Zydlewski, J. (2006). Remote monitoring of fish in small streams: A unified approach using PIT tags. Fisheries **31**: 492-502.

Zydlewski, G. B., Zydlewski, J., and Johnson, J. (2009). Patterns of migration and residency in coastal cutthroat trout *Oncorhynchus clarkii clarkii* from two tributaries of the lower Columbia river. Journal of Fish Biology **75**: 203-222.

Appendix: Antenna efficiency and movement above the barriers

Introduction

New technologies can provide an opportunity to add to the limited information regarding the behaviour of many freshwater fishes (Roussel et al. 2000). One such technology, PIT-tags, is increasingly being used to study the movement behaviour and habitat use in fishes (Aymes and Rives 2009). This relatively low-cost technology allows the collection of detailed behavioural information of large numbers of individuals at various spatial scales (Castro-Santos et al. 1996), and has been used successfully in studies on a variety of species (Ombredane et al. 1998; Greenberg and Giller 2000, Fischer et al. 2001, Zydlewski et al. 2001, Breen et al. 2009, Zydlewski et al. 2009). Each tag has a unique identification code, making it possible to assign the data gathered to a specific individual of known biology (Zydlewski et al. 2006), allowing fisheries managers to gather information on various life history characteristics, as well as follow dynamic populations in natural systems (Armstrong et al. 1996).

Proper interpretation of biological data collected by PIT-tag antennae is dependent upon detection efficiency (Aymes and Rives 2009). In particular, poor detection efficiency can result in flawed biological interpretation of the data (Aymes and Rives 2009), undermining successful conservation and recovery plans reliant upon available knowledge regarding the biology, ecology, and the life history of a species (Abell 2002; Poos et al. 2008). Although detection efficiency can be affected by many factors, such as the orientation of the PIT tag relative to the plane of the antenna, fish swimming speed, individual fish behaviour, and environmental conditions that affect flow conditions (i.e. storms) (Zydlewski et al. 2006; Aymes and Rives 2009), many studies using similar methods report detection efficiencies between 92 - 99% (Armstrong et al. 1996; Castro-Santos et al. 1996; Nunnallee et al. 1998; Zydlewski et al. 2001; Axel et al. 2005; Zydlewski et al. 2006; Connolly et al. 2008; Aymes and Rives 2009).

The goal of this chapter was to estimate antenna efficiency of the lower (downstream) antenna arrays, and to quantify the number of individuals traversing the upstream barrier. Because I am primarily using PIT-tags to analyze the movement behaviour and habitat use of fishes, I quantified my efficiency at detecting the movement of fish; *i.e.* the probability that fish leaving the six streams were detected by antennae at the mouths of those streams. Furthermore, because I am also interested in the effect of these barriers on fragmenting populations, I also quantify the number of individuals of each species that both reach the upper barrier, as well as the numbers that traversed the upstream barrier.

Methods

Antenna detection efficiency

Quantifying detection efficiency of the lower arrays entailed 2 steps: 1) estimating the number of individuals detected on at least one antenna of the lower arrays, and 2) calculating antenna efficiency as the percentage of individuals detected by at least one antenna on the lower arrays over the total number of individuals in the analysis. Antenna detection efficiency at the lower arrays was quantified three ways: 1) using only fish that were detected or captured in a stream other than the one in which it was tagged (n = 154;

category 4 only) to quantify my best estimate of antenna efficiency; 2) using the complete sample of PIT-tagged fish (*n* = 5120), including those used in the translocation experiments to quantify a lower estimate of antenna efficiency; and 3) using only individuals known to have left the streams (*n* = 2060; categories 3 and 4 from chapter 1) to quantify an upper estimate of antenna efficiency.

First, my best estimate of antenna efficiency was quantified using only fish that were detected or captured in a stream other than the one in which it was tagged. Only inter-movements within a reproductive season were considered. To be included in this sample, fish had to be detected entering a second stream, or captured in a net in a stream other than their original stream. Each individual was then scored as either being detected or not on at least one antenna of the lower array in their original stream of capture (i.e. leaving the stream). Detection efficiency was calculated as the percentage of individuals detected by at least one antenna on the lower arrays over the total number of individuals exhibiting inter-stream movement. Hence, I assessed the fish while leaving their original stream as my best unbiased estimate of detection efficiency. Second, my lower estimate of detection efficiency was quantified using all PIT-tagged fishes in this study. Detection efficiency was calculated as the percentage of individuals detected by at least one antenna on the lower arrays of their original stream over the total number of individuals PIT-tagged. This estimate will likely underestimate real detection efficiency because it includes individuals that died in the streams, purely stream resident fish that were never detected after tagging or never reached the lower arrays, fish that shed their tags, and any possible tag malfunctions. Finally, my upper estimate of antenna efficiency was quantified using only those individuals that were detected leaving their original streams (categories 3 and 4 from Chapter 1). Detection efficiency in this case was calculated as the percentage of individuals detected by at least one antenna on the lower arrays of their original stream over the total number of individuals leaving their original stream. However, detection efficiency of this sample will be positively biased because fish had to be detected leaving their stream or entering a new stream to be included in the calculation.

Movement to and above upstream barrier

Telemetry data from the upstream antennae arrays were used to determine the number of PIT-tagged individuals that reached the low-head barrier, as well as the number of individuals that traversed the barrier. Data were then summarized by species and year.

Results

Antenna detection efficiency

My best estimate of antenna efficiency was calculated as the percentage of PIT-tagged individuals exhibiting inter-stream movement detected on at least one antenna of their original stream. Overall, of all individuals exhibiting inter-stream movement within a reproductive season (n = 154), 91.6% (n = 141) were detected on at least one antenna of the lower array of their original stream.

A lower estimate of detection efficiency was calculated as the percentage of all PIT-tagged individuals detected on at least one antenna. Overall, of the 5120 PIT-tagged individuals from 26 species, including those detected or captured in subsequent years (*n* = 485), 59.8% (*n* = 3060) were detected on at least one antenna. However, this estimate also includes stream resident individuals which were detected only on the upper arrays (*n* = 747) and scored as not being detected on the lower array. When these individuals are excluded from the analysis, 70.0% of all PIT-tagged individuals (*n* = 4373) were detected on at least one antenna of the lower array.

An upper estimate of detection efficiency was calculated as the percentage of PIT-tagged individuals leaving a stream detected on at least one antenna of the lower array. Overall, of all individuals known to have left a stream (*n* = 2060), 99.1% (*n* = 2042) were detected on at least one antenna of the lower array. However, detection efficiency of these fish is likely positively biased because fish had to be detected leaving their stream or entering a new stream to be included in the calculation.

Individuals reaching and traversing in-stream barrier

The number of individuals detected at the up-stream antenna array and traversing over the barrier were low. Overall, of the 4586 PIT-tagged individuals from 26 species, 1549 (33.8%) from 15 species were detected on the up-stream antennae (Table A1). Furthermore, only 55 individuals from 6 species tagged below the barrier were detect to have moved over the barrier (Table A1).

Discussion

The PIT-tag system used in this study is an effective method to examine the movement behaviour of stream fishes. My best estimate of antenna detection efficiency in this study, calculated using individuals exhibiting inter-stream movement and detected on at least one antenna of their original stream was, 91.6%. This is comparable to the range of 92 - 99% reported in the literature using similar sized tags (Armstrong et al. 1996, Castro-Santos et al. 1996, Nunnallee et al. 1998, Axel et al. 2005, Zydlewski et al. 2006, Connolly et al. 2008, Aymes and Rives 2009). Since large amounts of biological data are generated by PIT-tag technology, detection efficiency becomes paramount in collecting reliable information (Aymes et al. 2009). Low detection efficiency results in flawed biological interpretations (Aymes et al. 2009). This is especially problematic for the success of conservation and recovery plans, which are reliant upon available knowledge regarding the biology, ecology, and the life history of a species (Abell 2002; Poos et al. 2008), or when detailed information on the population structure and life histories of a species is limited (Abell 2002).

My lower estimate of 59.8% detection efficiency was likely an underestimate because it included any natural or handling-induced mortality after tagging, as well as fish that were sedentary after tagging. Tagging-induced mortality was likely less important than natural sources, with ~1.4% of individuals dying within a few days following tagging. This value also falls within the range (0 – 5%) reported in other studies using PIT-tags (Prentice et al. 1990; Achord et al. 1996; Gries and Letcher 2002). Further, loss or shedding of PIT-tags in this study, based on individuals recaptured over the course of the three year project that had an obvious scar at the incision point, but no detectable PIT-tag, was also low (~2.7%) and comparable to studies reporting high tag retention in the literature (Ombredane et al. 1998; Roussel et al. 2000; Zydlewski et al. 2001; Bateman and Gresswell 2006). Hence, the largest sources of undetected fish were likely those dying naturally, or fish moving little or upstream after tagging. Indeed, when individuals detected only on the upper arrays were excluded from this analysis, antenna efficiency at the lower arrays increased to 70.0%. These lines of evidence suggest that detection efficiency is closer to my best estimate.

The use of a portable PIT-tag antenna in combination with the stationary system used here could potentially refine the uncertainty regarding fish that were never detected after tagging. Portable PIT-tag antennae have been used successfully to study the fine-scale movements and habitat use of individuals within a stream reach (Roussel et al. 2000; Zydlewski et al. 2001; Breen et al. 2009). Such methods are especially important in inferring the movement behaviour and life history of fishes showing restricted movement, particularly smaller-bodied fishes (Breen et al. 2009). In this study, ~30% of all PIT-tagged individuals were never detected after tagging (see Chapter 1). Although natural mortality is probably a significant factor, it is unlikely the only cause. The use of a portable PIT-tag antenna in combination with the system in this study could be used to detect individuals that remained between the two stationary antennae, and hence separating out individuals with restricted movement from natural mortality, increasing overall detection efficiency. However, the use of a portable PIT-tag antenna is labour intensive, and is limited to smaller and shallower streams (Breen et al. 2009). Furthermore, in streams with little habitat complexity, some fish might flee due to the close proximity of the antenna (Cookingham and Ruetz 2008), which could adversely affecting overall detection efficiency by overestimating the number of fish categorized as undetected.

In summary, this study illustrates the potential use of PIT-tag technology as an efficient, low-cost method to gather vital information on the life history and biology of freshwater fishes. Detection efficiency in this study was high, and comparable to those reported in the literature. The largest source of uncertainty was most likely natural steam mortality, as well as fish with restricted movement that were never detected on any antennae. Interpretation of results from this study provides valuable insight into the movement behaviour and life history of stream fishes.

Table A1: The number of PIT-tagged individuals reaching the upper antennae, summarized by species and study year, as well as the total number of individuals detected ascending the barrier for each species.

	# reaching upper barrier				# ascending barrier
Species	**2005**	**2006**	**2007**	**Total**	
Brown bullhead	1	2	7	10	
Brown trout	16	4		20	1
Brook charr	51	13	17	81	5
Creek chub	190	52	70	312	7
Common shiner	8	9	14	31	
Lake chub	1			1	
Logperch	1		1	2	
Largemouth bass		1		1	
Longnose dace	6	3	3	12	
Pumpkinseed	2	11	2	15	
Rock bass	16	14	10	40	
Rainbow trout	169	72	20	261	21
Sea lamprey	22	275	74	371	2
Smallmouth bass	2	4	5	11	
White sucker	49	196	136	381	19
Total	534	656	359	1549	55

Appendices

Appendix I: Summary of physical features, and sampling and re-sampling effort, for each stream and year of the project.

	Streams														
Variables	Covert			Grafton			Shelter Valley			Colborne			Salem		
Year	2005	2006	2007	2005	2006	2007	2005	2006	2007	2005	2006	2007	2005	2006	2007
Stream features															
Discharge (m^3s^{-1})	0.09	0.29	0.17	0.16	0.68	0.39	0.62	1.52	1.14	0.31	1.05	0.73	0.16	0.31	0.22
Width (m)	3.71	3.70	3.40	4.08	4.36	4.15	9.33	9.49	9.05	5.87	6.32	6.14	6.09	6.10	6.19
Depth (m)	0.17	0.27	0.22	0.20	0.30	0.25	0.26	0.38	0.40	0.27	0.39	0.37	0.54*	0.32	0.28
Velocity(m/s)	0.14	0.29	0.23	0.20	0.52	0.38	0.26	0.42	0.31	0.20	0.43	0.32	0.05	0.16	0.13
Water Temp. (^{0}C)	15.5	14.1	14.1	15.1	14.2	14.1	16.4	15.0		17.8	16.5	16.5	14.9	15.4	15.3
Dist. to barrier (km)	1.1			0.4			0.6			0.9			2.1		
Sediment type															
lower reach	bedrock			silt/sand			silt			silt			silt		
upper reach	gravel			gravel/cobble			sand/gravel			bedrock/gravel			sand/gravel		
Tagging effort															

Start[a]	104	102	121	97	102	121	102	93	121	98	102	121	97	102	121
Netting (days)	53	67	30	59	57	29	84[b]	76	32	81[b]	70	30	61	66	20
Fish caught	1256	1071	768	421	927	1180	631	543	627	432	1262	933	260	647	132
Fish tagged	438	149	128	168	103	105	458	407	166	197	262	159	243	340	49
Detection effort															
Upper (Start date)[a]	106	85	115	123	83	110	123	86	107	126	83	111	117	86	111
Effort (days)	72	95	63	57	97	69	56	163[d]	100[e]	53	163[d]	65	61	94	69
Lower (Start date)[a]	129	83	114	124	83	107	127	85	104	106	84	104	124	86	104
Effort (days)	49	97	64	56	97	72	62	161[d]	107[e]	139[c]	170[d]	121[e]	121[c]	169[d]	103[e]

Note: * The presence of several beaver dams in the study reach likely affected the flow regime for Salem creek in 2005. ([a]) Julian date, ([b]) two nets were used. Antennae in place until: ([c]) Sept 2005, ([d]) Sept 2006, and ([e]) Aug 2007.

Appendix II: Secondary sexual traits used to identify males (and females when noted) of the 37 species captured in this study.

Species	Name	Secondary sexual trait
alewife	*Alosa pseudoharengus*	—
banded killifish	*Fundulus diaphanous*	intensive bluish-green colouration (males), females are pale
blacknose dace[1]	*Rhinichthys atratulus*	rust-red colouration on sides of body
bluntnose minnow[1]	*Pimephales notatus*	nuptial tubercles on snout
brook charr	*Salvelinus fontinalis*	pronounced hook (kype) on lower jaw
brook lamprey	*Lampetra lamottei*	—
brook stickleback[1]	*Culaea inconstans*	jet black body and fins (sometimes tinged with copper), faint reddish colour on pelvic fins
brown bullhead	*Ameiurus nebulosus*	—
brown trout	*Salmo trutta*	pronounced hook (kype) on lower jaw
central stoneroller	*Campostoma anomalum*	nuptial tubercles over most of the body, orange fins
chinook salmon	*Oncorhynchus tshawytscha*	pronounced hook (kype) on lower jaw
coho salmon	*Oncorhynchus kisutch*	pronounced hook (kype) on lower jaw, brilliant red sides
common shiner[1]	*Luxilus cornutus*	nuptial tubercles on snout
creek chub[1]	*Semotilus atromaculatus*	nuptial tubercles on snout
emerald shiner	*Notropis atherinoides*	nuptial tubercles on pectoral fins
fantailed darter	*Etheostoma flabellare*	dorsal spines tipped with yellow or orange fleshy knobs
fathead minnow[1]	*Pimephales promelas*	nuptial tubercles on snout
golden shiner[1]	*Notemigonus crysoleucas*	nuptial tubercles on head, body, and all fins
hornyhead chub	*Nocomis biguttatus*	nuptial tubercles covering the entire head, red spot behind the eye
Johnny darter[1]	*Etheostoma nigrum*	black anterior half of the body
lake chub[1]	*Couesius plumbeus*	red mark at the base of the pectoral fin
largemouth bass	*Micropterus salmoides*	—

logperch	*Percina caprodes*	—
longnose dace[1]	*Rhinichthys cataractae*	orange-red on the corners of the mouth, tips of the pectoral, pelvic, or anal fins
mottled sculpin	*Cottus bairdii*	dark band with broad orange distal edge on first dorsal fin
northern pike	*Esox lucius*	—
northern redbelly dace[1]	*Phoxinus eos*	flanks brilliant red below the midlateral band
pumpkinseed[1]	*Lepomis gibbosus*	—
rainbow smelt[1]	*Osmerus mordax mordax*	small nuptial tubercles on head, body, and fins
rainbow trout	*Oncorhynchus mykiss*	pronounced hook (kype) on lower jaw
rock bass[1]	*Ambloplites rupestris*	margins of the pelvic and anal fins are black (males) or yellowish-white (females)
round goby[1]	*Neogobius melanostomus*	charcoal black, white or yellow edge on dorsal or tail fin
sea lamprey[1]	*Petromyzon marinus*	prominent ridge on dorsal sides of body
smallmouth bass	*Micropterus dolomieui*	—
threespine stickleback	*Gasterosteus aculeatus*	blue eyes, red sides and belly
white sucker[1]	*Catostomus commersonii*	nuptial tubercles on anal and caudal fins
yellow perch	*Perca flavescens*	lower fins suffused with orange to bright red

Note: [1]Species included in the analysis of protandry for Chapter 2.

Appendix III: The number of individuals captured in the streams (excluding recaptures and sea lamprey used in release experiment) during the study summarized by species, gender, and total number per species, with the number of individuals PIT-tagged between brackets.

Species	Female	Male	Unknown	Juvenile	Total
alewife			5		5
banded killifish[1]			17		17
blacknose dace[1]	573	354	271 (2)	54	1252 (2)
bluntnose minnow[1]	400	265	28	2	695
brook lamprey[1]	2		6		8
brook stickleback[1]	106	80	144	24	354
brook trout		4 (4)	89 (86)	23 (13)	116 (103)
brown bullhead	7 (7)		109 (109)	59 (51)	175 (167)
brown trout			5 (4)	73 (45)	78 (49)
central stoneroller	1 (1)				1 (1)
chinook salmon				230 (8)	230 (8)
coho salmon				1	1
common shiner	196 (7)	79 (64)	11	28	314 (71)
creek chub	1121 (459)	226 (220)	63	307	1717 (679)
emerald shiner[1]	28	24 (1)	198 (2)	25	275 (3)
fantailed darter[1]		1	1		2
fathead minnow[1]	446	245	115	26	832
golden shiner[1]	35 (2)	48	30 (3)	6	119 (5)
hornyhead chub		1 (1)			1 (1)
Johnny darter[1]	67	44	82	23	216

lake chub	49 (42)	52 (39)	4		105 (81)
largemouth bass	1 (1)		9 (9)	1	11 (10)
logperch	8 (5)	3 (3)	2 (2)	1	14 (10)
longnose dace[1]	686 (34)	1117 (5)	217 (3)	10	2030 (42)
mottled sculpin[1]	5	8	35 (1)	7	55 (1)
northern pike			2 (2)	1 (1)	3 (3)
northern redbelly dace[1]	700	448	225	15	1388
pumpkinseed	47 (11)	46 (17)	84 (38)	31	208 (66)
rainbow smelt	10 (7)	16 (8)	4 (4)		30 (19)
rainbow trout	24 (17)	58 (44)	24 (22)	2035 (1156)	2141 (1239)
rock bass	66 (64)	36 (34)	238 (224)	49	389 (322)
round goby	16 (6)	12 (1)	25 (2)	347	400 (9)
sea lamprey	197 (195)	289 (288)	4 (4)		490 (487)
smallmouth bass	2 (2)	2 (2)	9 (9)		13 (13)
threespine stickleback[1]			14		14
white sucker	349 (313)	345 (294)	275 (265)	528 (280)	1497 (1152)
yellow perch	1	8 (5)	167 (36)	3	179 (41)
Total	5143 (1173)	3811 (1030)	2512 (827)	3909 (1554)	15375 (4584)

Note: [1]species categorized as small-bodied, with mean fork length of all individuals < 75mm. Brook lamprey were included as small-bodied fishes because their narrow body cavity prevented the use of PIT-tags.

Appendix IV: The number of individuals captured (excluding sea lamprey used in release experiment) during the study summarized by species and gender, with the number of mature individuals between brackets, as well as the overall proportion of immature individuals (Immature) for species with at least 20 individuals.

Species	**Female**	**Male**	**Unknown**	**Juvenile**	**Immature**
alewife			5		—
banded killifish			17		—
blacknose dace	573 (476)	354 (332)	271	54	0.35
bluntnose minnow	400 (258)	265 (245)	28	2	0.28
brook lamprey	2 (2)		6		—
brook stickleback	106 (106)	80 (77)	144	24	0.48
brook charr		4	89	23	1.00
brown bullhead	7 (7)		109	59	0.96
brown trout			5	73	1.00
central stoneroller	1 (1)				—
chinook salmon				230	1.00
coho salmon				1	—
common shiner	196 (139)	79 (67)	11	28	0.34
creek chub	1121 (750)	226(216)	63	307	0.44
emerald shiner	28 (21)	24 (24)	198	25	0.84
fantailed darter		1 (1)	1		—
fathead minnow	446 (337)	245 (180)	115	26	0.38
golden shiner	35 (35)	48 (42)	30	6	0.35
hornyhead chub		1 (1)			—
Johnny darter	67 (58)	44 (44)	82	23	0.53
lake chub	49 (24)	52 (23)	4		0.55
largemouth bass	1 (1)		9	1	—

logperch	8 (8)	3 (3)	2	1	—
longnose dace	686 (641)	1117 (956)	217	10	0.21
mottled sculpin	5 (5)	8 (8)	35	7	0.76
northern pike			2	1	—
northern redbelly dace	700 (647)	448 (409)	225	15	0.24
pumpkinseed	47 (40)	46 (34)	84	31	0.64
rainbow smelt	10 (10)	16 (16)	4		0.13
rainbow trout	24 (20)	58 (49)	24	2035	0.97
rockbass	66 (65)	36 (34)	238	49	0.75
round goby	16 (11)	12 (7)	25	347	0.96
sea lamprey	197 (197)	289(289)	4		0.01
smallmouth bass	2 (2)	2 (2)	9		—
threespine stickleback			14		—
white sucker	349 (320)	345 (298)	275	528	0.59
yellow perch	1	8	167	3	0.95
Total	5143 (4182)	3811(3365)	2512	3909	0.51

Appendix IV: Numbers of individuals captured during the study and used in the analysis of sex-biased arrival timing, summarized by species, study stream, year, and gender. F = females, M = males, U = unknown sex, and J = juveniles.

		2005				**2006**				**2007**			
Species	**Stream**	**F**	**M**	**U**	**J**	**F**	**M**	**U**	**J**	**F**	**M**	**U**	**J**
bluntnose minnow	Covert									5	5		
	Colborne					263	111			95	129	16	
blacknose dace	Covert	71	90		1	47	38	21	4	37	31	2	1
	Grafton	11	8							163	82		3
	Sh. Valley	49	10	3									
	Colborne					6	17	7					
brook stickleback	Colborne									9	19		
creek chub	Covert	346	99		9	56	22		33	182	28		36
	Grafton	97	21		15	48	9	2	45	48	5	7	34
	Sh. Valley					5	6		1				
	Colborne					73	7	18	50	58	8	1	23
common shiner	Covert	19	9		6					31	15		
	Grafton	18	10	9						63	12		1
	Sh. Valley					17	5		7				

fathead minnow	Grafton					102	68	42	18	133	24		2
	Colborne					45	52			51	66		
	Salem					43	12						
round goby	Colborne									10	11	7	98
golden shiner	Colborne					6	14		3				
Johnny darter	Grafton									12	9		
lake chub	Salem	28	33	4		20	25						
longnose dace	Covert	167	237	3	4	196	384	3	1	104	172	3	2
	Grafton									14	18		
	Sh. Valley	17	15			7	18						
	Colborne					10	23						
northern redbelly dace	Covert					47	21	6		11	18	5	
	Grafton	13	30	10		182	135	38	2	248	137	11	1
	Colborne					16	13	5		31	30	2	1
pumpkinseed	Sh. Valley					10	13	5	1				
rock bass	Colborne					20	10	7	13	19	18	4	4
rainbow smelt	Sh. Valley					6	12						
sea lamprey	Grafton					13	15			26	19		

	Sh. Valley					40	85			21	14		
	Salem					61	90						
white sucker	Covert					37	40	4	9	11	19	2	3
	Grafton	30	11	8	14	15	9		41	11	10	1	
	Sh. Valley					70	67	1	5	52	72		2
	Colborne	55	32	8	11	68	84	7	69	45	46	1	
	Salem									15	18	3	44
Grand total		**921**	**605**	**45**	**60**	**1529**	**1405**	**166**	**302**	**1505**	**1035**	**65**	**255**