Fish Community Responses to the Land Use Change and Environmental Variability in Estuaries

by

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A thesis submitted in conformity with the requirements
for the degree of Doctor of Philosophy
Department of Ecology and Evolutionary Biology
University of Toronto

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2018

Abstract

Understanding how species communities respond to land use and environmental change over space and time is necessary given the rapidly changing environment that threaten species persistence. In intrinsically dynamic environments such as estuaries, the spatial and temporal environmental variability at the interface of freshwater and marine ecosystems result in species that persist with morphological or physiological adaptations to these changing environmental conditions. Yet, estuarine fish communities are facing further change as a result of the loss of functional connectivity through stream fragmentation due to culverts that impede fish passage upstream, and land use change as well as climate change among estuaries that reduce habitat quality. It is unknown how the extent of environmental change due to land use and climate change in estuaries and their associated watersheds affect estuarine fish communities in addition to natural variability.

In this thesis, I determine how fish communities in estuaries respond to land use impact and environmental variability at the stream and watershed levels. The functional connectivity of species is impacted by stream fragmentation due to culverts upstream of New Brunswick estuaries and their watersheds. I show that the potential functional connectivity of species varies according to migratory traits and the ontogeny of species. In the Miramichi watershed, I assess how forest harvesting and weather fluctuations affect the density of juvenile Atlantic salmon

(*Salmo salar*) at the watershed level. I demonstrate that accounting for the upstream forest harvesting have cumulative impacts on juvenile Atlantic salmon through each catchment downstream and over time. Within and among the estuaries, I find evidence that fish communities shift according to environmental change.

My findings relating to the effects of land use and environmental variability from streams to the watersheds would result in a better predictive capacity of how estuarine fish communities will potentially change or persist.

Acknowledgments

This work would not have been possible without the support and help of many people throughout the past four years. First and foremost, I would like to sincerely thank my supervisor Dr. Marie-Josée Fortin, who has allowed me to grow both personally and academically through her guidance, patience, and mentorship. I would also like to thank my committee members, Drs. Don Jackson and Keith Somers, who have contributed invaluable insight to my research.

I would also like to thank both current and former members of the Fortin lab for your friendship and support throughout the years: Aaron Hall, Alex Martensen, Amanda Xuereb, Ariel Greiner, Carina Firkowski, Cassidy D'Aloia, Chris Blackford, Chris Edge, Colin Daniel, Emily Darling, Jonathan Ruppert, Ilona Naujokaitis-Lewis, Kate Kirby, Korryn Bodner, Lanna Jin, Luke Frishkoff, Sandy Watts, and Stephen MacFarlane. I must specifically thank Dr. Julia Linke, whose work has been the primary foundation of my research. In addition, her networking eventually opened doors for me, when I met Roland Cormier, Dr. Simon Courtenay, Monica Boudreau, Marie-Hélène Thériault, and Carole Godin who have become important collaborators in many of my chapters. Datasets were provided by Fisheries and Oceans Canada (Chapter 2: Carole Godin; Chapter 3: Scott Douglas; Chapters 4 and 5: Monica Boudreau, Marie-Hélène Thériault) and Natural Resources Canada. Furthermore, Dr. Dan McKenney, Pia Papadopol, and Kevin Lawrence have greatly helped with the preparation of the ANUSPLIN data. I would like to thank Monica Boudreau for enthusiastically showing me the East Coast and the Community Aquatic Monitoring Program sampling, which allowed me to finally experience my scenic study system in person.

I would like to extend my thanks to Don for inviting me to his Friday morning lab discussions. They have immersed my mind in aquatic ecosystems every week. I would also like to thank current and former members of the Jackson lab–I felt as if I was always a part of the lab.

Past undergraduate students in the Fortin lab, Roxane Jaffray and Sita Ganesh, have been helpful by exploring aspects of my dataset and provided insight of other trends in this study system. I thank Karen Alofs for providing additional morphometric photos that were used in my analysis.

I would like to thank the NSERC Canadian Network for Aquatic Ecosystem Services for both funding and enriching my PhD experience. The networking opportunities have provided me with new pathways for collaborating and learning, and through this process, creating friendship across the country within the network.

Finally, I am indebted to my family and friends. I owe any of my success to my Mom and Dad. All your love, encouragement, and support has kept me going and without that, I would not be here today. And to all who have crossed paths with me during these years, you have contributed in meaningful ways. Words cannot truly express how I feel because you have positively impacted my life.

Chapter Acknowledgments

This thesis is comprised of four chapters that are currently in review or in preparation for submission to peer-reviewed journals. The design, analyses, and manuscript preparation were all carried out by the first author and PhD candidate. Co-authors of the chapters contributed to the conceptual discussions, datasets, and participated in the review and editing of the manuscripts.

1. **Chin, A.T.M.**, Cormier, R., Godin, C., Fortin, M.-J. Determining potential functional connectivity of fish species with diadromous and non-diadromous life history traits. *Landscape Ecology*. In review. (Chapter 2)

2. **Chin, A.T.M.**, Linke, J., Cormier, R., Fortin, M.-J. Juvenile Atlantic salmon (*Salmo salar*) response to land use change and weather fluctuation in the Miramichi watershed in New Brunswick. In preparation. (Chapter 3)

3. **Chin, A.T.M.**, Linke, J., Boudreau, M., Thériault, M.-H., Courtenay, S.C., Cormier, R., Fortin, M.-J. Beta diversity changes in estuarine fish communities due to environmental change. *Marine Ecology Progress Series*. In review. (Chapter 4)

4. **Chin, A.T.M.**, Linke, J., Boudreau, M., Thériault, M.-H., Courtenay, S.C., Cormier, R., Fortin, M.-J. Functional groups of fish communities shift with environmental change in estuaries. *Canadian Journal of Fisheries and Aquatic Sciences*. In review. (Chapter 5)

The following publications are related to work conducted at the University of Toronto during my PhD:

1. Sutherland, I.J., Villamagna, A., Ouellet Dallaire, C., Bennett, E.E., **Chin, A.T.M.**, Young, A., Lamothe, K.A., Tomscha, S.A., and Cormier, R. Undervalued and under pressure: a plea for greater attention toward regulating ecosystem services. *Ecological Indicators*. In press.
2. Lamothe, K.A., Bourne, B., **Chin, A.T.M.**, Daoust, K., Dieleman, C.M., Ouellet Dallaire, C., Tomscha, S.A. Are research networks worth the time for graduate students? *The Bulletin of the Ecological Society of America*. In press.

3. Nitoslawski, S., **Chin, A.T.M.**, Chan, A., Creed, I., Fyles, J., Parkins, J., Teichert, S., Weber, M. Demographics and social values as a driver of change in the Canadian boreal region. *Environmental Reviews*. In review.

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Chapter 1

1 Introduction

Understanding species persistence is necessary due to a rapidly changing climate and anthropogenic disturbances such as land use change that threaten ecosystems (Tilman et al. 1994, Parmesan and Yohe 2003, Berg et al. 2010). Habitat quality and the amount of habitat available may change due to environmental variability, habitat modification and removal (i.e., land use change), as well as the loss of connectivity (Taylor et al. 1993, 2006, Moilanen and Hanski 1998, Jackson et al. 2009, Hanski 2011). For migratory species, persistence based on survival and reproduction is imperative throughout multiple habitats that are essential to complete their life cycle (Small-Lorenz et al. 2013). In terrestrial and aquatic ecosystems, multiple habitats face greater anthropogenic impact (Halpern et al. 2008). Estuarine ecosystems, which are at the interface of freshwater and marine ecosystems, support many migratory species that are transient through this habitat (Beck et al. 2001). However, estuaries are one of the most threatened ecosystems due to anthropogenic activities in coastal areas (Kennish 2002) and upstream in associated watersheds (Vitousek et al. 1997). While the intrinsically dynamic environmental gradient of estuaries from freshwater and marine ecosystems results in species that persist with morphological or physiological adaptations to these changing environmental conditions (Cognetti and Maltagliati 2000, Elliott and Quintino 2007), extreme environmental change and the loss of habitat ultimately affect the function and structure of estuarine communities (Elliott and Quintino 2007, Madeira et al. 2012). As a result, it is unknown how the extent of environmental change due to land use and climate change in estuaries and their associated watersheds will affect species communities in combination to natural variability (Kennish 2002). Understanding such combined effects on species dispersal and their habitat would therefore inform us as well on in species abundance and composition responses at the metacommunity level.

1.1 Detecting change via metacommunities

Current changes in species community composition are influenced by both natural and anthropogenic factors. As such, the main goal of community ecology is to understand the processes that drive the patterns of species abundance, diversity, and composition in communities (McGill et al. 2006, Urban et al. 2008, Vellend 2010). While historically, community ecology mostly focused on local-based processes—the niche concept by Hutchinson and MacArthur in the 1950s and 1960s and species interactions, such as competition and predation in species-pairs relationships (Hutchinson 1957, Hutchinson and MacArthur 1959, MacArthur 1968)—nowadays, there is a growing understanding that regional and broader scale studies are needed to better understand local-scale patterns (Holyoak et al. 2005, Ricklefs 2008, Vellend 2010, Dray et al. 2012). As a result, the issue of scale and the spatial heterogeneity of habitat quality are explicitly incorporated in the study of communities as metacommunities (Leibold et al. 2004, Holyoak et al. 2005, Ricklefs 2008). The metacommunity concept becomes useful to link across multiple spatial scales by understanding that community composition in a heterogeneous landscape is linked by dispersal of potentially interacting species (Leibold et al. 2004, Holyoak et al. 2005, Ricklefs 2008). Yet, understanding the role that environmental variability plays in the composition of species communities through space and time remains a fundamental question in ecology (Sutherland et al. 2013). This is especially challenging with natural and anthropogenic changes that have effects on dispersal and habitat quality across space and time (Gilman et al. 2010, Crook et al. 2015).

In aquatic ecosystems, fish communities can be used as indicators to assess the effect of natural and anthropogenic stressors because their life histories are well-known and they are present in a wide range of environmental conditions (Karr 1981, Jackson et al. 2001, Feyrer et al. 2015). Although other taxa that have been used as indicators in estuaries (e.g., diatoms (Cooper 2009), macrophytes (Patrício et al. 2009), macroinvertebrates (Hale et al. 2004)), fish communities could be easily sampled and identified with a known response to environmental and anthropogenic changes due to stressors such as toxicity as well as being commonly found in aquatic ecosystems (Whitfield and Elliott 2002). Due to stressors, fish communities are under threat by both current and future land use and environmental changes in estuaries with their associated watersheds. As such, fish abundance and species composition changes are the result of changing abiotic conditions such as water and habitat quality, as well as physical barriers that limit dispersal through the landscape (Angermeier and Karr 1986, Perkin and Gido 2012). Permanent barriers result in differences in species community composition due to the loss of connectivity (Perkin and Gido 2012, Edge et al. 2017). In addition, abiotic conditions can indirectly affect biotic factors such as increased primary production and species movement that consequently affect trophic levels, habitat structure, predation, parasitism, and competition (Alpine and Cloern 1992, Gilliam and Fraser 2001, Holomuzki et al. 2010). Given that the change in community composition can be detected, fish community responses can be used to assess the impact of environmental change. Thus, the study of changes in fish communities applied in a metacommunity approach allow a better understanding of land use impacts by first quantifying the response and then identifying the underlying processes.

1.2 Land use change and environmental variability in estuaries

Effects of land use influence the ability of species to disperse through the landscape to reach optimal habitat. Dispersal is critical for the long-term survival of populations, which allow individuals to find suitable breeding habitat, and maintain genetic diversity (Kokko and López-Sepulcre 2006). This is true for terrestrial but for aquatic species as well. Given the number of migratory species present in estuaries, it is necessary to understand the effects on their dispersal upstream of estuaries in streams. Indeed, road crossings with culverts implemented in the stream network adversely affect the movement of fish (Warren and Pardew 1998, Perkin and Gido 2012). Thus, barriers in stream networks limit the dispersal of fish, particularly diadromous species that must migrate across estuaries through both freshwater and marine habitat to complete their life cycle (Bunn and Arthington 2002, Rolls et al. 2014). Yet functional connectivity, which is based on a species' ability to disperse through the landscape, is required to ensure species persistence within stream networks (Tischendorf and Fahrig 2000, Fagan 2002, Heino et al. 2015). Furthermore, upstream habitat may be reduced as warming temperatures under climate change do not provide suitable habitat for cool- and cold-water species to spawn, and the ability of these species to reach these cooler habitats is unfavorably affected depending on their functional connectivity (Marshall and Randhir 2008). Climate change could further affect functional connectivity due to the timing of migrations resulting from temperature changes as well the loss or gain of connectivity through hydrologic flow changes (Jaeger et al. 2014, Poesch et al. 2016).

In naturally dynamic systems such as estuaries, communities are adapted to the temporal frequency of environmental variability (Elliott and Whitfield 2011). For example, estuaries experience frequent tidal changes and seasonality that lead to dramatic changes in environmental conditions, where species are able to persist with physiological and morphological adaptations to salinity changes (Cognetti and Maltagliati 2000, Elliott and Quintino 2007). These changes in salinity levels, however, can also come from freshwater discharge with runoff that may indirectly affect community composition due to water quality and the quality and quantity of fish habitat (Gillanders and Kingsford 2002). In addition, the increased precipitation in Atlantic Canada from climate change will indirectly affect the amount of runoff that will impact estuaries downstream within watersheds as well as salinity levels in estuaries (Najjar et al. 2000, Nugent and Matthews 2012). Therefore, it is necessary to differentiate the indirect effects of these environmental changes in estuaries from the natural variability matching the correct spatio-temporal scales.

Anthropogenic land use in watersheds upstream of estuaries also has effects on fish communities in estuaries that affect habitat quality. For instance, the effect of runoff from agricultural land use leads to nutrient over-enrichment of nitrogen and phosphorus in aquatic ecosystems causing a loss of biodiversity due to eutrophication (Carpenter et al. 1998, Elser et al. 2007), which is still evident in nearshore coastal ecosystems (Cloern 2001, Woodland et al. 2015). Thus, the magnitude of effects of land use on fish communities is mainly dependent on weather events and the spatial relationship upstream, which makes testable predictions complex.

1.3 Thesis and research objectives

For my PhD thesis, I aimed to determine how estuarine fish metacommunities respond to land use impact and environmental variability in their associated streams and watersheds in New Brunswick as it affects the overall quality and amount of habitat in estuaries, which is directly linked to functioning fish metacommunities. First, fish movement through estuaries is further restricted due to barriers in streams, such that dispersal is necessary for the persistence of metacommunities (Erős 2017). Fish communities in New Brunswick estuaries and the Atlantic region of North America are diverse with non-diadromous and diadromous species (Limburg and Waldman 2009). As a result, there are differences among species given these migratory traits and dispersal ability, and in turn, variable functional connectivity among species (Wolter and Arlinghaus 2003). Second, Atlantic salmon (*Salmo salar*) is a diadromous species that is recreationally important in the Atlantic region of Canada (DFO 2018). However, certain Atlantic salmon populations are considered endangered in the inner Bay of Fundy in New Brunswick due to land use (e.g., forestry and stream fragmentation due to culverts) and climate change (DFO 2010). Yet, adult Atlantic salmon are stronger swimmers than other fish species (Calles and Greenberg 2005), hence such stronger swimmers are advantageous for dispersal. Therefore, the Atlantic salmon could be used as a model species of the impacts of land use and climate as their complex life cycle is associated with changes to terrestrial and aquatic habitat. Then, such findings could be compared to other diadromous species that are experiencing potentially greater impact due to their weaker swimming abilities to disperse. Finally, estuaries are transitional habitat between freshwater and marine ecosystems that link the dispersal of migratory species between these habitats (Beck et al. 2001). These transitional waters serve as nursery, spawning, and feeding grounds for species (Franco et al. 2008). Land use changes and extreme environmental change in estuaries ultimately affect the quality and amount of habitat through differences in the environmental gradient, thus posing a risk to transient species that rely on estuaries to persist (Kappel 2005, Waycott et al. 2009).

To address such threats to estuarine ecosystems, findings from my thesis relating to the effects of land use and environmental variability scaled from streams to the watersheds would aid in developing better predictive capacity, relating to the scale and extent of change, of how estuarine fish communities from the species to metacommunity level will potentially change or persist. By improving predictive capacity, a risk assessment framework could then be developed with the extent of impacts (Williams et al. 2008). Therefore, I hypothesize that change in fish metacommunities can be used as an indicator of land use and environmental changes in estuarine ecosystems. Given the importance of dispersal and habitat for a functioning metacommunity, I predict that impacts on the components of metacommunities (i.e., dispersal and habitat) would result in changes to fish communities in estuaries and their associated watersheds. Furthermore, my thesis is structured according to ecological units (i.e., species to metacommunities) (Jax 2006) based on the increasing complexity of interactions between the units. This arrangement would assess the cumulative effects of land use and environmental changes on fish metacommunities as the interactions between ecological units increase.

In Chapter 2, I first focus on the impact of stream fragmentation due to culverts on movement of fish species through the stream network. The objective of this chapter is to assess how stream fragmentation due to culverts affect the potential functional connectivity of various fish species differently based on migration and ontogeny. Stream networks are fragmented by land use change due to obstacles such as culverts and dams, which negatively reduce connectivity for fish passage (Hall et al. 2011). Access to habitat therefore becomes limited further upstream due to the cumulative impact of fragmentation as diadromous species move upstream to spawning grounds (Bunn and Arthington 2002, Rolls et al. 2014). Yet, the degree of functional connectivity of fish species, such as non-diadromous species, to pass through obstacles based on swimming strength to reach critical habitat is mostly unknown as this varies among ontogeny and species. As the degree of functional connectivity varies across species due to their swimming ability, it will in turn affect their persistence. I hypothesize that the potential functional connectivity of diadromous and non-diadromous species is affected according to their size as adults versus juveniles and their swimming ability. Quantifying the potential functional connectivity for different species will further the understanding of the effects of stream fragmentation on specific species due to variable swimming strength and ontogeny.

In Chapter 3, I investigate the effects of land use and weather fluctuations on the density of juvenile Atlantic salmon at the watershed level. The objective of this chapter is to determine the spatio-temporal scales at which changes in juvenile Atlantic salmon density as a response to forestry land use change and weather conditions in the Miramichi watershed can be detected. Precipitation regimes in watersheds are expected to change with increased rainfall due to climate change in Atlantic Canada and consequently increased stream discharge (Zhang et al. 2000). Land use upstream of estuaries leads to runoff, which has indirect effects on fish habitat and water quality that negatively affect the survival of juvenile Atlantic salmon. For example, sedimentation can adversely affect the survival to emergence of Atlantic salmon eggs (Lapointe et al. 2004). In particular, when compared to other life stages, Atlantic salmon juveniles are sensitive to pollution such as contaminants, heavy metals, and acidity (McCormick et al. 1998, Leduc et al. 2009). Forest harvesting potentially affects juvenile Atlantic salmon (*Salmo salar*) habitat in the Miramichi watershed. Such land use changes could have a spatial or temporal cumulative effect from the forest harvesting due to the extent of the watershed as well as the response of the population. I hypothesize that the response of density will be negatively correlated with the cumulative intensity of land use change and environmental change over space and time. I predict that the response of density will be negatively associated with the cumulative intensity of land use and environmental change. Dendritic networks are cumulative from upstream to downstream, and thus it is important to consider the spatial and temporal relationship of stressors within a watershed.

Finally, in Chapters 4 and 5, I examine how fish communities change due to estuarine environmental condition, such as salinity. Estuarine aquatic ecosystems are resilient to the naturally dynamic variability of intertidal and seasonal changes (Dauvin 2007, Elliott and Whitfield 2011). Yet, it is uncertain how the magnitude of environmental change will adversely affect the ability of estuarine fish communities to persist. Environmental changes such as increased precipitation in watersheds will decrease salinity levels in estuaries from an increase of freshwater input (Swansburg et al. 2004b). These potential long-term environmental changes will ultimately affect the survival of fish species across communities with specific salinity tolerances. Changes in species composition and reductions in abundances due to environmental change reduce functional diversity, thereby decreasing the insurance effect that is maintained by biodiversity (Folke et al. 2004, Gonzalez et al. 2009). Furthermore, functional redundancy of traits prevents the substantial loss of ecosystem function in communities such that species performing the same function can be replaced by another (Fonseca and Ganade 2001, Buisson et al. 2013). Therefore, the functional group approach allows the analysis of community composition changes and their response to environmental change by focusing on functional traits such as morphology, physiology, behavior, and life history (Mouillot et al. 2013). These community composition changes can be measured with beta diversity (Whittaker 1972, Baselga 2010). Beta diversity can indeed measure species replacement (species turnover) along environmental gradients, which can inform us of the locations associated with greater environmental change (Baselga 2010).

In Chapter 4, I assess how beta diversity changes in estuarine fish communities due to environmental change over space and time as such changes could be related to species persistence. Specifically, the objective is to investigate how species turnover over space and time in estuaries is influenced by changes in salinity, water temperature, dissolved oxygen, and eelgrass over years. I hypothesize that spatial turnover is driven by spatial heterogeneity across estuaries, and temporal turnover is driven by environmental changes over time. These differences in species turnover are mainly based on the changes due to environmental gradients over space (i.e., across watersheds) and time (i.e., responding to regional weather conditions).

In Chapter 5, I investigate how fish functional groups respond to environmental spatio-temporal changes within and across estuaries. The objective here is to determine how the functional group response that is best explained by local or regional environmental gradients is associated with these changing environmental conditions. I hypothesize that estuarine fish functional groups are sensitive indicators of environmental change. As a sensitive indicator, these changing abundance in functional groups would relate to the environmental change. Overall, environmental gradients present from freshwater to the brackish water ecosystem of estuaries elucidate community composition changes over space and time.

My thesis uses data from long-term monitoring programs that are often supported by large teams that would otherwise be impractical and impossible with only the principal investigators to collect data. The sufficient data collected addresses questions relating to changes in community composition over space and time (Magurran et al. 2010). As such, I approach the questions of my thesis using the advantages of monitoring programs from the long-term temporal changes of species communities and environmental conditions with a broad-scale spatial analysis. I use multiple datasets in a nested framework to encompass areas spanning from the mouth of estuaries to the headwaters, in addition to comparing variation among watersheds and estuaries. First, the dataset in Chapter 2 is gathered from teams of volunteers surveying multiple watersheds to detect the impact of culverts in the stream network, in which I assessed the culvert dataset from Fisheries and Oceans Canada in addition to a literature review of the fish species inventory within three watersheds (Turcotte-Lanteigne and Ferguson 2008, LeBlanc et al. 2009). In Chapter 3, to detect changes in abundance of a fish species in a watershed, I use the Fisheries and Oceans Canada monitoring of juvenile Atlantic Salmon (*Salmo salar*) in the Miramichi watershed (Moore and Chaput 2007). In Chapters 4 and 5, the estuaries in New Brunswick is monitored by the Community Monitoring Aquatic Monitoring Program, coordinated by the Southern Gulf of St. Lawrence Coalition on Sustainability and Fisheries and Oceans Canada, which establishes baseline conditions of estuarine fish communities (Weldon et al. 2005). Although missing observations remain as potential issues for long-term monitoring programs, by cover a wider spatial extent, I could substitute the missing temporal observations (Thomas 1996).

Altogether, my analytical Chapters 2 to 5 demonstrate the importance of the cumulative effects from the stream level to the watershed level to assess land use and environmental change in estuarine fish communities over space and time. Under a species-specific approach, such as

Chapter 2 and focusing on a single species in Chapter 3, there would be a better understanding of how individual species are affected by land use and environmental change. In Chapter 4, a community approach would provide a broad-scale approach within and across estuaries. In Chapter 5, I consider the importance of metacommunities as the spatial scales account for the potential dispersal of species. In Chapter 6, I synthesize my overall findings to provide summarized recommendations accounting for the broader conclusions of the chapters together to ensure species persistence.

Chapter 2

2 Determining Potential Functional Connectivity of Fish Species with Diadromous and Non-diadromous Life History Traits

2.1 Abstract

Road crossings over streams with perched culverts have become a prominent feature of the landscape that restrict upstream movement of fish. The effects of stream fragmentation due to culverts on the potential functional connectivity of various fish species may be determined by their life history traits. Depending on the location of the spawning habitat, certain species encounter more obstacles to swim upstream from the estuaries to the headwaters, such as diadromous species which require both freshwater and marine habitat. By contrast, non-diadromous species will still encounter obstacles swimming upstream at any point in the stream network. The ability of many species to pass through the culverts due to the swimming strength is unknown. Here, the total length of species was used as a morphometric approach as a surrogate of swimming ability. The amount of stream reach was analyzed for 24 species by calculating the Dendritic Connectivity Index (DCI) to assess the overall potential functional connectivity of the stream networks in three watersheds of New Brunswick (Canada) for each species to pass through culverts located by Fisheries and Oceans Canada. The findings show that non-diadromous species were negatively affected by stream fragmentation more than diadromous species. Diadromous species also experience greater variability of functional connectivity in stream networks due to differences in ontogeny and migration patterns. Conservation should reflect the amount of accessible habitat in all life stages. The findings emphasize that a species-based approach is necessary to inform policy and management in the development of fish passage standards.

2.2 Introduction

Given the increase in road networks globally (Strano et al. 2017), the ubiquity of road crossings has become a prominent feature of the landscape (Angermeier et al. 2004). Culverts are commonly installed to provide crossings over streams, but perched culverts which have an outfall are the result of either being improperly designed or poorly installed (Gibson et al. 2005), and may be the result of erosion over time in the streambed below the structure (Park et al. 2008). Specifically, perched culverts that are associated with road crossings restrict fish passage by disrupting natural hydrology and are also physical barriers due to the vertical drop (Burford et al. 2009, Mahlum et al. 2014). This habitat fragmentation affects endangered diadromous species such as Atlantic salmon (*Salmo salar*) in the inner Bay of Fundy in New Brunswick (DFO 2010), and other smaller diadromous species in the North American Atlantic coast (Limburg and Waldman 2009). Yet, options for restoring or deciding where to remove culverts within stream networks may be limited due to the sheer number of culverts within the landscape (Kemp and O'Hanley 2010, Anderson et al. 2012, Neeson et al. 2015).

Stream fragmentation impacts the persistence of fish species by impeding movement throughout the stream network (Perkin and Gido 2011, Januchowski-Hartley et al. 2013). Stream networks are fragmented by land use change due to obstacles such as culverts and dams, which negatively reduce connectivity for fish passage (Hall et al. 2011, Januchowski-Hartley et al. 2014). Access to habitat, therefore, becomes limited further upstream due to the cumulative impact of fragmentation as diadromous species move upstream to spawning grounds or such as juvenile American eels (*Anguilla rostrata*) moving upstream to mature (Bunn and Arthington 2002, Rolls et al. 2014), as well as non-diadromous species to access to their habitat (Warren and Pardew 1998). The ability of species to access their habitat given the landscape characteristics is known as functional connectivity (Taylor et al. 1993, 2006). Maintaining functional connectivity for each species is crucial to allow dispersal throughout the habitat in the stream network (Perkin and Gido 2012). However, the degree of functional connectivity of other fish species to pass through obstacles based on swimming strength to reach habitat is unknown for most species but is critical to consider (Branco et al. 2014). Functional connectivity varies among species due to their swimming ability and it will consequently affect their persistence.

Prioritizing restoration is required to evaluate effective actions as a result of the finite resources to do so and the numerous culverts in the landscape. Decisions are based on the severity of specific culverts to prevent fish passage, and by removing the barrier, how much habitat becomes accessible in the stream network (Anderson et al. 2012). Given that functional connectivity varies among species, optimal restoration would account for the removal of barriers that benefit the greatest number of species while considering the connectivity of invasive species (Neeson et al. 2015). Each barrier would therefore be assessed according to the passability of each species. However, passability information is lacking as the swimming ability, which can be used to infer the ability to overcome the hydrological modification due to culverts, is unknown for most species.

A morphological approach could be applied to estimate the current reach for each species. The body size of species has been related to the dispersal distances and swimming strength (Beamish 1978, Plaut 2000, Radinger and Wolter 2014). Larger species tend to have greater swimming ability as a result of endurance and critical swimming speed (Beamish 1978). The critical swimming speed of species, which is associated with the speed at which fatigue occurs (Webb 1971, Brett and Glass 1973), has been a factor to consider when determining the passability of culverts (Peake 2004). Furthermore, the ontogeny of species from juveniles to adults would also vary the swimming strength between life stages (Wolter and Arlinghaus 2003), and the shift in habitat for diadromous species (Anderson et al. 2013). Therefore, functional connectivity can be determined by the passability of culverts accounting for the swimming strength of species and ontogeny, as well as the upstream dispersal patterns which varies through life stages.

The objective is to use a surrogate approach based on a morphological trait of the fish species that is available to estimate and quantify the amount of reach available due to the potential functional connectivity if these culvert barriers are passable. We hypothesize that the potential functional connectivity of diadromous and non-diadromous species is affected by their size as adults versus juveniles and their swimming ability. We predict that the intensity of stream fragmentation with increasing number of perched culverts affects weaker swimming species more than stronger swimming species. Quantifying the potential functional connectivity for different species will further the understanding of the effects of stream fragmentation on specific functional traits. A morphological approach could result in a broader guideline to allow the passage of all species in a watershed. Management action could be focused on restoring or removing culverts that promote access for the greatest number of species.

2.3 Methods

2.3.1 Study area

We studied the stream networks of three focal temperate watersheds that drain into the Northumberland Strait region of New Brunswick, Canada (Fig. 2.1). The total stream length and watershed coverage of Scoudouc (137 km; 165 km^2), Shediac (277 km; 221 km^2), and Richibucto (285 km; 304 km^2) vary in size. Consistently within all three of these watersheds, a total of 24 species are known to reside in the freshwater streams and estuaries (Turcotte-Lanteigne and Ferguson 2008, LeBlanc et al. 2009) (Table 2.1).

Culverts were mapped and surveyed by Fisheries and Oceans Canada in the summers of 2008 to 20010. Culverts were surveyed upstream from the estuary up to the headwaters to record the drop height at the outfall (hereinafter ‘drop height’) during low flow, which represents the period with the lowest functional connectivity. Potential locations were determined with the road crossing data provided by Service New Brunswick and were verified if the culvert was at a road crossing. Natural falls or other types of man-made structures that may be potential barriers to fish passage due to the drop were not considered in both the surveys and the analysis. Other variables were measured such as the material, shape, diameter, and length of the culvert, but these were not incorporated in the analysis due to the lack of hydrological measurements (e.g., depth of water and slope) that would need to be incorporated to determine possible flow rate differences that would affect the passability of these culverts. Stream networks of the three watersheds were provided by Fisheries and Oceans Canada to calculate Strahler order of segments and the length of stream segments.

2.3.2 Passability

We used a morphometric trait to infer swimming strength based on the body length of each species measured as total length. We contrasted the effect of fragmentation on the potential functional connectivity of juvenile and adult life stages of each species. The maximum total length of each species for the two life stages was derived from FishBase (Froese and Pauly

2015), literature, and body length of species by measuring specimens collected at the Royal Ontario Museum.

Using the total length of species, we determined if the perched culvert was passible or impassible after a threshold. If half the total length of the species was less than the culvert drop height, it was considered impassible (0 probability). Passability would then range to being partially passable at 0.7 or 0.8 probability, the latter if the species has leaping abilities. Here, we differentiated leaping abilities as a higher probability due to the advantage of overcoming obstacles such as dams (Meixler et al. 2009). We set this reference of passability as it is similar to previous findings that were based on body lengths of individuals, when individuals with a body length twice the drop height of a perched culvert could clear the barrier (Holthe et al. 2005, Mueller et al. 2008, Prenosil et al. 2016). We further grouped species according to the NCBI taxonomy of the closest sequence homologues and the PhyloT tree tool with equal branch lengths to visualize in iTOL v3 (Letunic and Bork 2016). We use the phylogeny to compare closely related species and assume similar body size to determine if there is variation in dendritic connectivity index (DCI) scores (Cote et al. 2009) in the comparisons.

We also accounted for the anguilliform swimming locomotion of sea lamprey (*Petromyzon marinus*) and American eel (*Anguilla rostrata*). Passability was determined by the height of the species from the dorsal to ventral side, when individuals with half the height of the encountered drop height of the perched culvert was considered impassable. Lampreys and eels have relatively low burst speeds compared to other species (Russon and Kemp 2011), and natural barriers raised only a few centimeters with a vertical drop have shown to be impassable for juvenile eels (Jessop 1995).

2.3.3 Quantifying potential functional connectivity

We quantified the potential functional connectivity of the stream networks using the dendritic connectivity index (DCI) developed by Cote et al. (2009). The DCI accounts for the migratory life history of species if they are diadromous (DCI_d) or potadromous (DCI_p) for migrations (Cote et al. 2009). Diadromous species, calculated by the DCI_d, encounter obstacles from the start at the estuary to the headwaters upstream. The DCI_d is defined by the following from Cote et al. (2009):

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

where c_{ij} is the connectivity between segments *i* and *j*, *l* is the length between segments *i* and *j*, and *L* is total length of the stream sections.

Here, we assume that non-diadromous species are potadromous and are represented by $\mathrm{DCI_p}$ given that the species traverses through any point in the stream network to reach accessible habitat. The $\mathrm{DCI_p}$ is defined as follows from Cote et al. (2009):

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

where c_{ij} is the connectivity between segments *i* and *j*, *l* is the length between segments *i* and *j*, and *L* is total length of the stream sections.

Overall, our DCI scores indicate the amount of connectivity in the stream network during low flow, ranging from 0 (no connectivity) to 100 (full connectivity). DCI can be further analyzed according to the connectivity of stream segment relative to the entire stream network using $\mathrm{DCI_d}$ at a different points (Cote et al. 2009), and we indicate these stream segment scores as $\mathrm{DCI_s}$. We used the FiPEX extension (version 10.23) in ArcGIS (version 10.2) to calculate the DCI.

2.4 Results

2.4.1 Culverts in the stream network

In Scoudouc watershed with a Strahler stream order of four, there were ten culverts. In Shediac watershed with a Strahler stream order of five, there were 30 culverts. In Richibucto, there were 119 culverts in the watershed of a Strahler stream order of five. These culverts in the watersheds were potentially in the direct line from the ocean to spawning grounds in headwaters for species. Drop heights ranged from 0 to 110 cm. A total of three culverts (one in Shediac, two in Richibucto) were considered impassable in our analysis. The majority of the culverts in all three watersheds were in headwater stream segments (Fig. 2.A.1).

2.4.2 Potential functional connectivity

Potential functional connectivity assumed that dispersal occurred in the entire watershed, where all culverts could have been encountered for all species and life stages. Overall potential functional connectivity was highest in Scoudouc, which was the least impacted stream network, with Dendritic Connectivity Index (DCI) scores ranging from 73.1 to 97.2. In Shediac, the stream network with the moderate number of culverts, DCI scores ranged from 43.5 to 82.9. In Richibucto, the stream network with the highest number of culverts, DCI scores ranged from 44.4 to 84.3.

The variability of DCI scores within species between adults and juveniles varied among the three watersheds. For non-diadromous species, variability of DCI scores was greatest in Richibucto and the least in Scoudouc and Shediac (Fig. 2.2). By contrast, diadromous species maintained variability of DCI scores in all three watersheds (Fig. 2.2). The exception occurred with American eel (*Anguilla rostrata*) for diadromous species given that this species is catadromous with juveniles swimming upstream. Variability of DCI scores did not differ among taxonomic groups, unless there was a difference in diadromous versus non-diadromous species (Fig. 2.B.1).

Comparing the potential functional connectivity measured as Dendritic Connectivity Index scores of stream segments (DCI_s) for ninespine stickleback (*Pungitius pungitius*) as the weakest swimmer and Atlantic salmon (*Salmo salar*) as the strongest swimmer to demonstrate the contrast in variability of potential functional connectivity, the effect of culverts impeding fish passage for juveniles and adults was prominent with the former species among individual stream segments (Fig. 2.3). Both juveniles and adults were equally affected by stream fragmentation due to culverts in Scoudouc and Shediac (Fig. 2.3). The cumulative impacts of encountering culverts was unpronounced in the less fragmented stream network of Scoudouc for both species where impassable segments were due to individual culverts (Fig. 2.3). By contrast, Shediac and Richibucto showed a stronger negative cumulative impact across the entire stream networks for ninespine stickleback, but Atlantic salmon was mostly impacted at individual stream segments in headwater branches (Fig. 2.3).

The effect of culverts reducing the minimum potential functional connectivity for juveniles and adults was generally greatest in the headwaters with a stream order of 1 (Fig. 2.4).

Higher stream orders tend to have higher potential functional connectivity for both juveniles and adults, with the exception of segments in Scoudouc (stream order 2) and Shediac (stream order 3) represented by the median DCI_s scores (Fig. 2.4). However, the cumulative effect of culverts as potential functional connectivity for juveniles and adults of both species decreased from the higher stream orders to the headwaters was particularly noticeable in Richibucto as the watershed with greatest number of culverts (Fig. 2.4).

The potential functional connectivity of ninespine stickleback was lower than Atlantic salmon within the stream segments in all stream orders (Fig. 2.4). Impassable segments with low DCI_s were present in headwaters for adult Atlantic salmon as outliers (Fig. 2.4). By contrast, low DCI_s scores in headwaters were not outliers for juvenile and adult ninespine stickleback, with the exception in Shediac in a second-order stream segment.

2.5 Discussion

We assessed the potential functional connectivity of 24 species in three watersheds with varying number of culverts impeding fish passage through each of the stream networks and quantified using Dendritic Connectivity Index (DCI) scores. We estimated the swimming ability of the species to pass through culverts using a morphological approach based on body size accounting for the total length of species during juvenile and adult life stages. Depending where the culverts are located in the headwaters or the main channels could have different impacts on the overall connectivity of the stream network. This variation in potential functional connectivity was dependent on the ontogeny of juveniles and adults as well as the migration pattern of species (Januchowski-Hartley et al. 2014).

Non-diadromous species that are weaker swimmers tend to have similar potential functional connectivity. Smaller species are more likely to disperse less given their smaller body size (Radinger and Wolter 2014). Likewise, the variation in body size of juveniles to adults was similar among the non-diadromous species. An exception of the variation is the strongest non-diadromous swimming species in the three watersheds, white perch (*Morone americana*), due to the large size in which adults can grow to a maximum total length of 58.0 cm (Page and Burr 2011). Given the stronger swimming abilities of adult white perch than juveniles, adult individuals are less impacted by stream fragmentation as they are more likely to pass the barriers. By contrast, juveniles and adults of weaker swimming non-diadromous species are equally affected in watersheds that have numerous culverts, such as Richibucto. In less fragmented watersheds, adults could potentially pass more barriers in the network overall with greater reach accessibility and thus the possibility of overcoming barriers varies more between juveniles and adults.

We found that diadromous species experience greater variation in potential functional connectivity in the watersheds between juveniles and adults as a result of the differences in migration patterns more than taxonomic relatedness. For anadromous species, juveniles are non-diadromous swimming throughout any point in the stream network and become migratory as adults. Therefore, with the larger adult sizes, anadromous adult individuals are stronger to swim upstream and are more likely overcome culvert barriers. DCI scores are typically higher for anadromous species as a result of this trait for adults. By contrast, catadromous species such as eels, are more likely to be affected by stream fragmentation for juveniles as they are migratory to swim upstream, but adults swim downstream and are non-migratory for most of their life stage. Furthermore, juvenile eels as elvers are weaker swimmers with a short burst speed (McCleave 1980). This difference is due to the greater hindrance from culverts impeding fish passage for catadromous species during the juvenile life stage when they are weaker swimmers.

Swimming mode varies for sea lamprey (*Petromyzon marinus*) and American eel (*Anguilla rostrata*) compared to other species in the watershed potentially allowing for other opportunities to bypass culverts. Sea lamprey and American eel exhibit anguilliform locomotion with undulating motion throughout the entire body length (Tytell 2004). Other species in the watersheds are subcarangiform swimmers, which utilize only a portion of the body length for propulsion, is optimal for thrust (Sfakiotakis et al. 1999). As a result of the efficient and enhanced subcarangiform locomotion, anguilliform locomotion has lower hydromechanical efficiency (Blake 2004), and thus the latter could be more sensitive to altered hydrological regimes due to culverts. However, it is also documented that eels are capable of transitioning onto land for a short period of time (Gillis 1998), and connectivity between culverts could be maintained. Furthermore, American eel elvers and adult sea lamprey are also known to exhibit climbing abilities (Linton et al. 2007, Reinhardt and Binder 2009), which could instead bypass culverts that are present in the stream network. Therefore, there are additional ways due to the swimming locomotion of these species such that culverts do not necessarily impede passage, which were unaccounted for in our analysis.

Encountering culverts throughout the stream network is different for diadromous and non-diadromous species, which are reflected in the DCI scores. Diadromous species cumulatively encounter culverts upstream from the mouth of the estuary consecutively towards the headwaters and non-diadromous species would cumulatively encounter culverts along any point throughout the stream network. In particular, culverts located centrally in the stream network are likely to be traversed more frequently for non-diadromous species. By contrast, culverts located near the mouth of the estuaries are more likely to be encountered and must be traversed through to the headwaters for diadromous species. These differences may explain why Shediac has lower functional connectivity for non-diadromous species than Richibucto despite the latter stream network having more culverts. Our findings differ from Cote et al. (2009) as we found potential functional connectivity reduced more so for non-diadromous species when compared to diadromous species, which may be the result of their hypothetical stream network with fewer stream branching. Overall, this difference may be due to the cumulative encounter of many culverts in our stream network.

The dendritic connectivity index could be interpreted as the amount of habitat reachable for each species given that the DCI score is a proportion of available stream reach. As such, the degree of habitat loss due to perched culverts that impede fish passage may inform the decline of species' productivity (Perkin and Gido 2011, Januchowski-Hartley et al. 2013). By preventing fish from accessing critical habitat, for example, would reduce the ability of species to persist at all life stages (Erkinaro et al. 2017). Our results suggest that the response curves of declining productivity (i.e., reproduction, growth, and survival; DFO 2012) over the stream network due to an increase in a stressor, such as barriers causing stream fragmentation, could vary according to individual species and ontogeny. Understanding these productivity-stressor curves are necessary to better maintain productive fisheries (DFO 2014). Given that several of the species in this study are listed as species at risk in the region, such as the striped bass of special concern (COSEWIC 2012a), the threatened American eel (COSEWIC 2012b), and the endangered Atlantic salmon in the Inner Bay of Fundy (COSEWIC 2010), restoring connectivity could benefit the persistence of these species. Furthermore, the threshold at which productivity begins to significantly decline should be known to mitigate these adverse effects (DFO 2014) on a species by species basis.

Although we focused on the drop height as only one aspect of culverts that may limit fish passage, our findings demonstrated that a single parameter could have profound differences for the potential functional connectivity of species. Given the complexity of hydrology and temporal dynamics of connectivity, the differences among species could change if other parameters were included. For example, it is known that the circular culvert diameter impacts the discharge within culverts (Toman et al. 2014). The ability of fish to pass through varying degrees of flow rate depends on the amount of water, which varies through time. At certain times, the culvert may become passable under ideal flow conditions for certain species. Unfortunately, for the weakest swimming species, passability may still be impossible.

Temporal change and seasonality would change the window of opportunity that could potentially allow sections to be functionally connected for certain species. Intermediate flow may be desirable as low flow rates reduce connectivity whereas high flow rates may be insurmountable for passage, both of which can be altered through culverts. Low flow rates in temperate rivers may reduce the motivation of salmonids for passage (Stuart 1964) or that the swimming is impossible with no water flowing (Gibson et al. 2005). Swimming capability through the culvert may only be possible if swimming strength exceeds the flow rate, which may be difficult with higher flow rates for weaker swimmers (Richmond et al. 2007). The ideal flow rate may change accordingly with the season as well as weather events (Piehl et al. 1988). Therefore, a properly constructed culvert for fish passage (i.e., providing adequate stream depth, flow, and preventing downstream erosion at the culvert) should account for all flow rates and seasonality.

Conservation should reflect the amount of accessible habitat in all life stages. Although juveniles would not be expected to disperse through the entire stream network in a generation, understanding the amount of reach is informative in the event of habitat destruction. Population persistence relies on the dispersal to other parts of the watershed. Given different life history strategies, species may need to disperse from one headwater to another, or one tributary to another in the event of habitat loss. By understanding the impacts of stream fragmentation due to culverts on specific fish species throughout the watershed, management could prioritize the removal of barriers depending on the species being affected. A localized strategic approach could also involve a maintenance and replacement plan for the culverts or barriers that are most detrimental for most species or the weakest species in a given system. This would optimize restoration efforts over time as resources are available while avoiding the use of resources for culverts or barriers that are the least problematic.

2.6 Tables

Table 2.1. List of species of fish found in all three focal watersheds in Richibucto, Scoudouc, and Shediac (New Brunswick) (Turcotte-Lanteigne and Ferguson 2008, LeBlanc et al. 2009, Froese and Pauly 2015). The total of length of juveniles and adults are from FishBase (Froese and Pauly 2015), literature, and the specimen collection from the Royal Ontario Museum (ROM).

Common name	Species code	Scientific name	Juvenile length (cm)	Adult length (cm)	References
American eel*[1,b]	AEE	*Anguilla rostrata*	1.5	3.9	ROM
Alewife*	ALE	*Alosa pseudoharengus*	13.7	40.0	(Jessop 1985)
American shad*	ASH	*Alosa sapidissima*	11.8	76.0	(O'Leary and Kynard 1986)
Slimy sculpin	SSC	*Cottus cognatus*	3.2	12.1	(Brandt and Madon 1986)
Central mudminnow	CMU	*Umbra limi*	2.0	14.0	(Schilling et al. 2006)
Blacknose dace	BDA	*Rhinichthys atratulus*	2.0	12.4	(Gibbons and Gee 1972, Nelson et al. 2003)
Common shiner	CSH	*Notropis cornutus*	3.9	18.0	(Werner et al. 1977, Leslie et al. 1986)
Creek chub	CCH	*Semotilus atromaculatus*	7.9	30.3	(Magnan and FitzGerald 1984)
Fathead minnow	FMI	*Pimephales promelas*	3.7	10.1	(Panter et al. 2002)
Finescale dace	FDA	*Chrosomus neogaeus*	3.0	11.0	(Stasiak 1978, Chivers and Smith 1994)
Lake chub	LCH	*Couesius plumbeus*	2.5	23.0	(Fuiman and Baker 1981)

Table 2.1. continued

Common name	Species code	Scientific name	Juvenile length (cm)	Adult length (cm)	References
Northern redbelly dace	NRD	*Chrosomus eos*	3.2	8.0	(Kelsch 1994)
Pearl dace	PDA	*Semotilus margarita*	5.7	16.0	(Johnson and Johnson 1982, He and Kitchell 2011)
Banded killifish	BKI	*Fundulus diaphanus*	4.0	13.0	(Rozas and Odum 1987)
Mummichog	MUM	*Fundulus heteroclitus*	4.0	15.0	(Dunkelberger et al. 1980, Smith and Able 1994)
Fourspine stickleback*	FSS	*Apeltes quadracus*	2.0	6.4	(Blouw and Hagen 1981)
Ninespine stickleback	NSS	*Pungitius pungitius*	4.6	9.0	(Poulin and FitzGerald 1987)
Threespine stickleback*	TSS	*Gasterosteus aculeatus*	3.1	11.0	(Poulin and FitzGerald 1987, Garenc et al. 1999)
Rainbow smelt*	RSM	*Osmerus mordax*	0.7	35.6	(Siefert 1972)
Striped bass*,[a]	SBA	*Morone saxatilis*	11.1	200.0	(Serafy and Harrell 1993, Beasley and Hightower 2000)
White perch	WPE	*Morone americana*	6.5	49.5	(Kraus and Secor 2004)
Sea lamprey*,[1]	SLA	*Petromyzon marinus*	1.1	2.1	ROM
Atlantic salmon*,[c]	ASA	*Salmo salar*	12.7	150.0	(L'Abée-Lund 1988)

Table 2.1. continued

Common name	Species code	Scientific name	Juvenile length (cm)	Adult length (cm)	References
Brook trout*	BTR	*Salvelinus fontinalis*	5.0	86.0	(Tang and Boisclair 1995, Beasley and Hightower 2000)

* Diadromous species

[1] Dorsal to ventral length was measured

[a] Special concern status

[b] Threatened status

[c] Endangered status

2.7 Figures

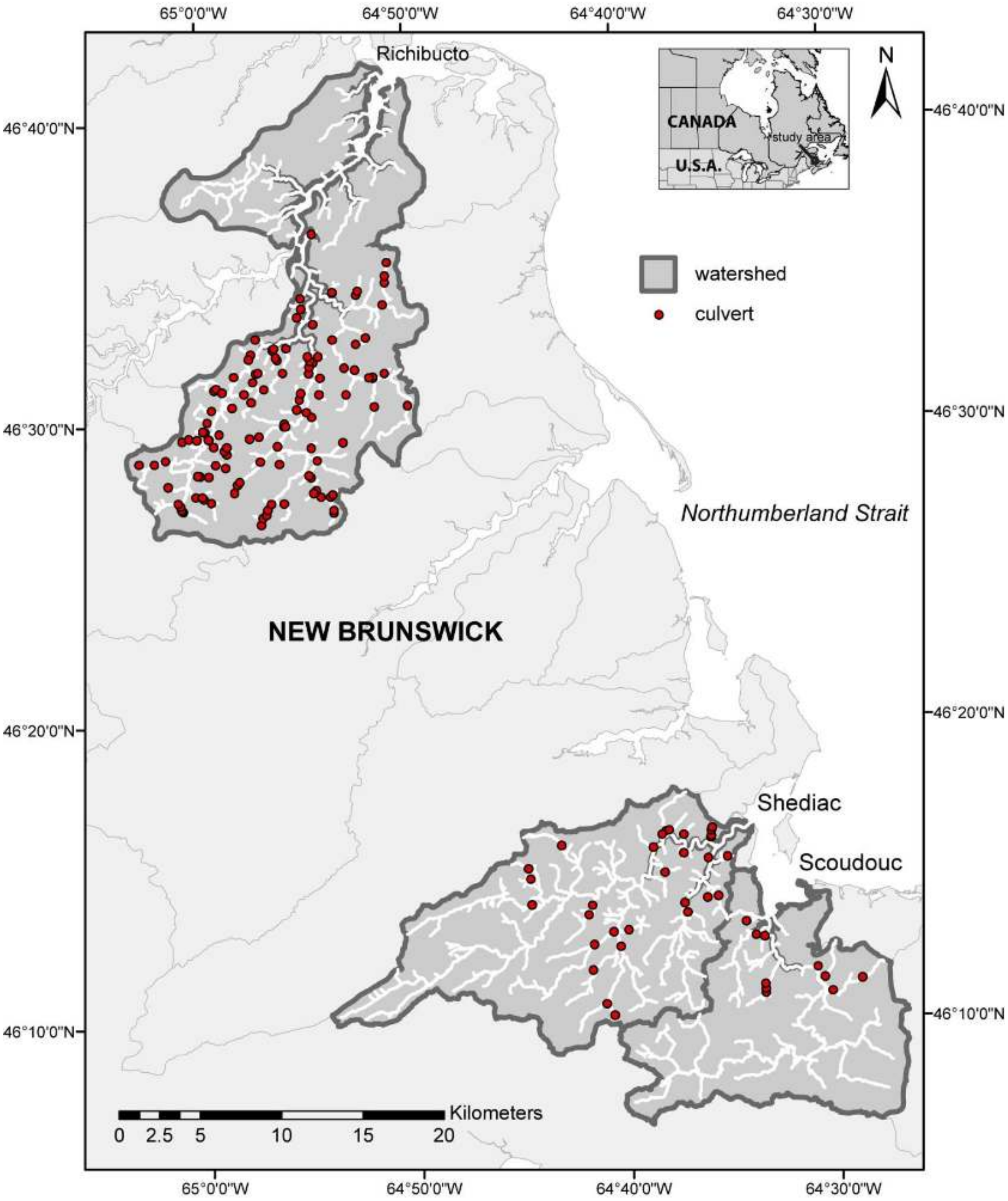

Fig. 2.1. Location of culverts surveyed in 2008 to 2010 by Fisheries and Oceans Canada (DFO) in the stream networks of Richibucto (*n* = 119 culverts), Shediac (*n* = 30 culverts) and Scoudouc (*n* = 10 culverts) watersheds in New Brunswick, Canada.

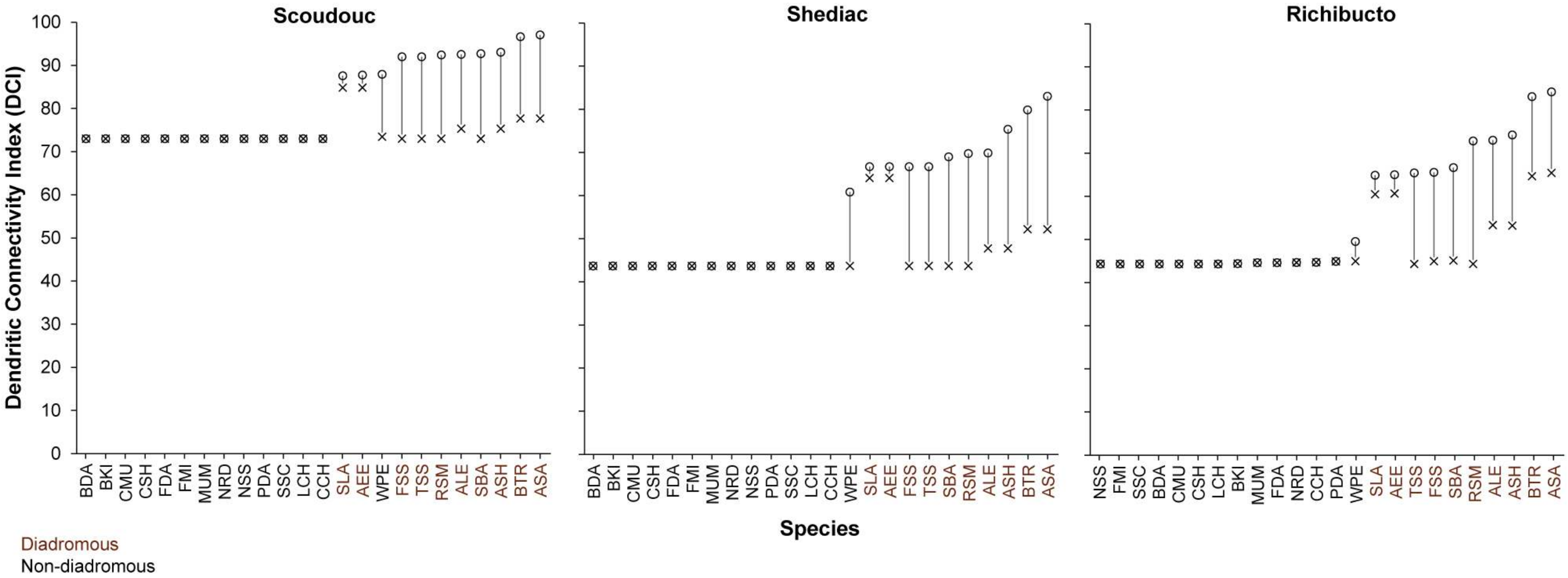

Fig. 2.2. Dendritic Connectivity Index (DCI) scores for all 24 species within the three watersheds accounting for the ontogeny of juveniles (cross) and adults (open circles).

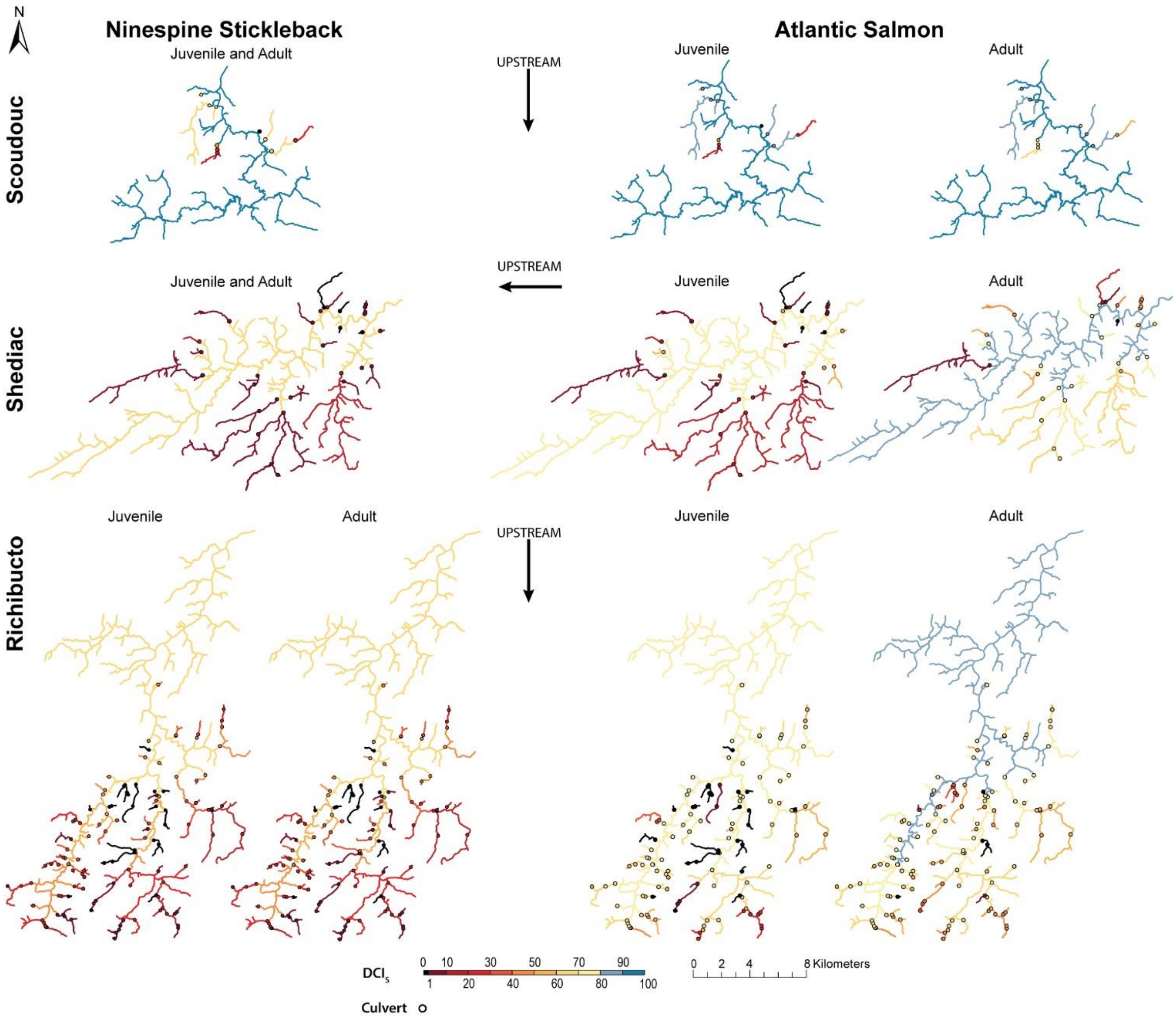

Fig. 2.3. Maximum potential functional connectivity of juvenile and adult fish at the watershed level measured with the Dendritic Connectivity Index for stream segments (DCIs) comparing the weakest swimming species (ninespine stickleback, non-diadromous).

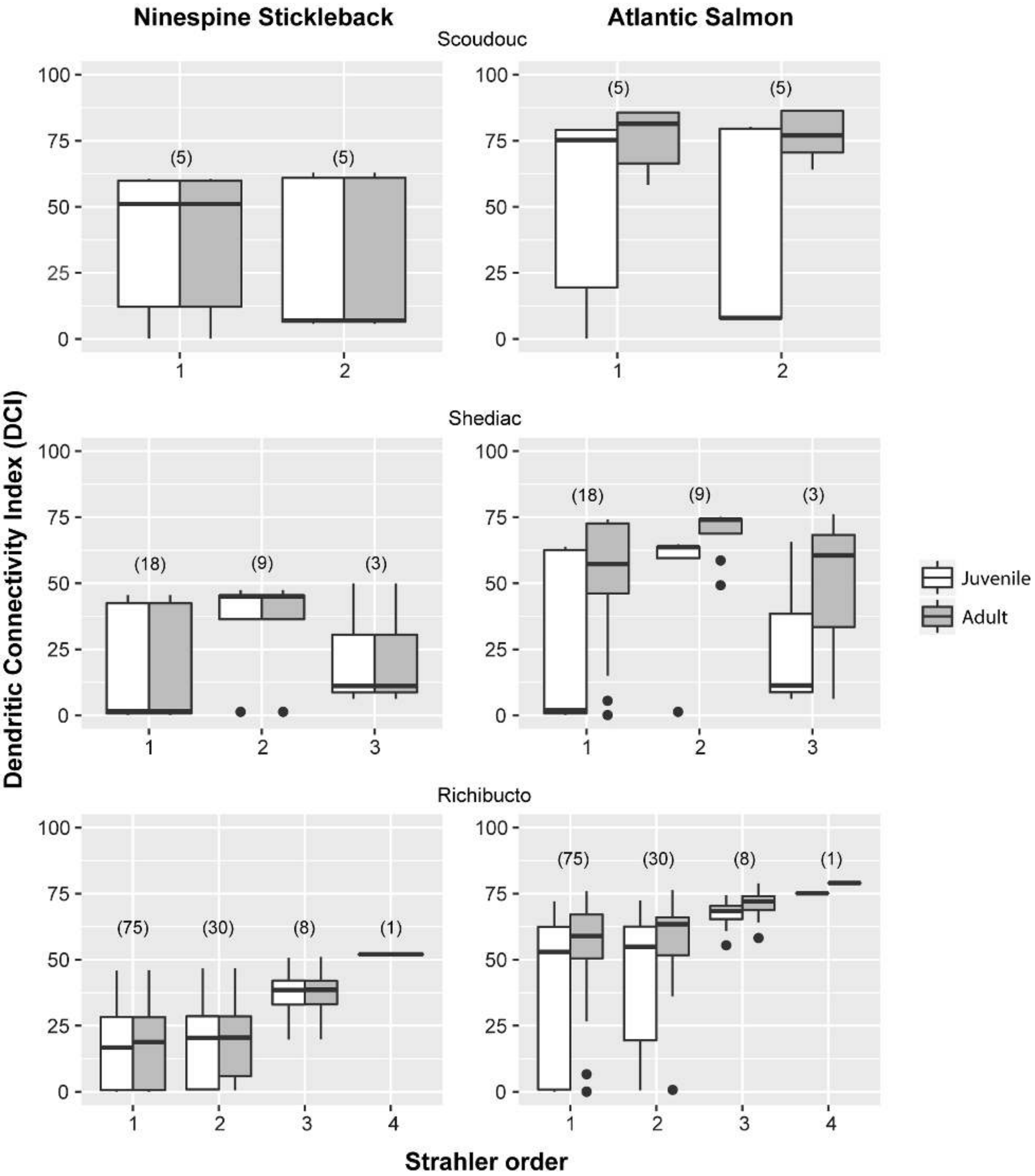

Fig. 2.4. Boxplots of the maximum Dendritic Connectivity Index stream segment (DCI_s) scores upstream of barriers for juvenile and adult ninespine stickleback and Atlantic salmon in relation to the Strahler orders of the segments in the three watersheds. The number of culverts located in the Strahler stream segments are indicated in brackets.

2.8 Appendix A

2.8.1 Culvert density in stream segments

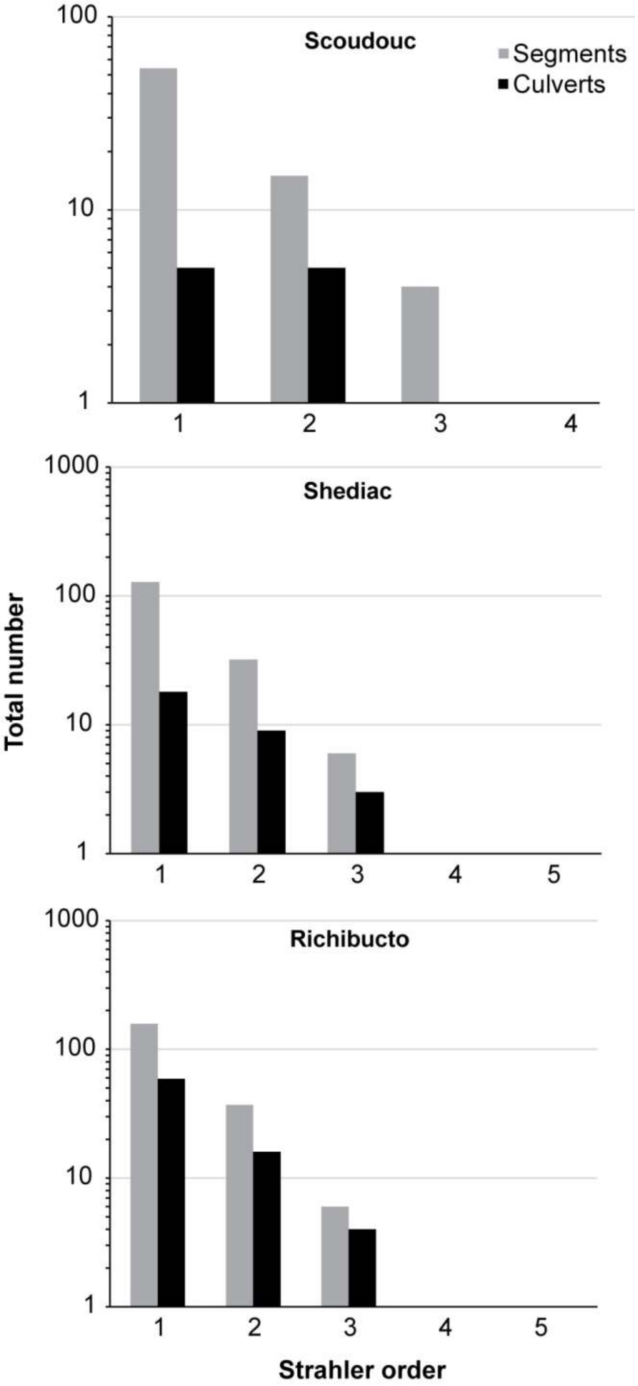

Fig. 2.A.1. Density of culverts (Richibucto: *n* = 119 culverts, Shediac: *n* = 30 culverts, Scoudouc: *n* = 10 culverts) and the total number of stream segments based on the Strahler order in the three watersheds.

2.9 Appendix B

2.9.1 Phylogeny of species

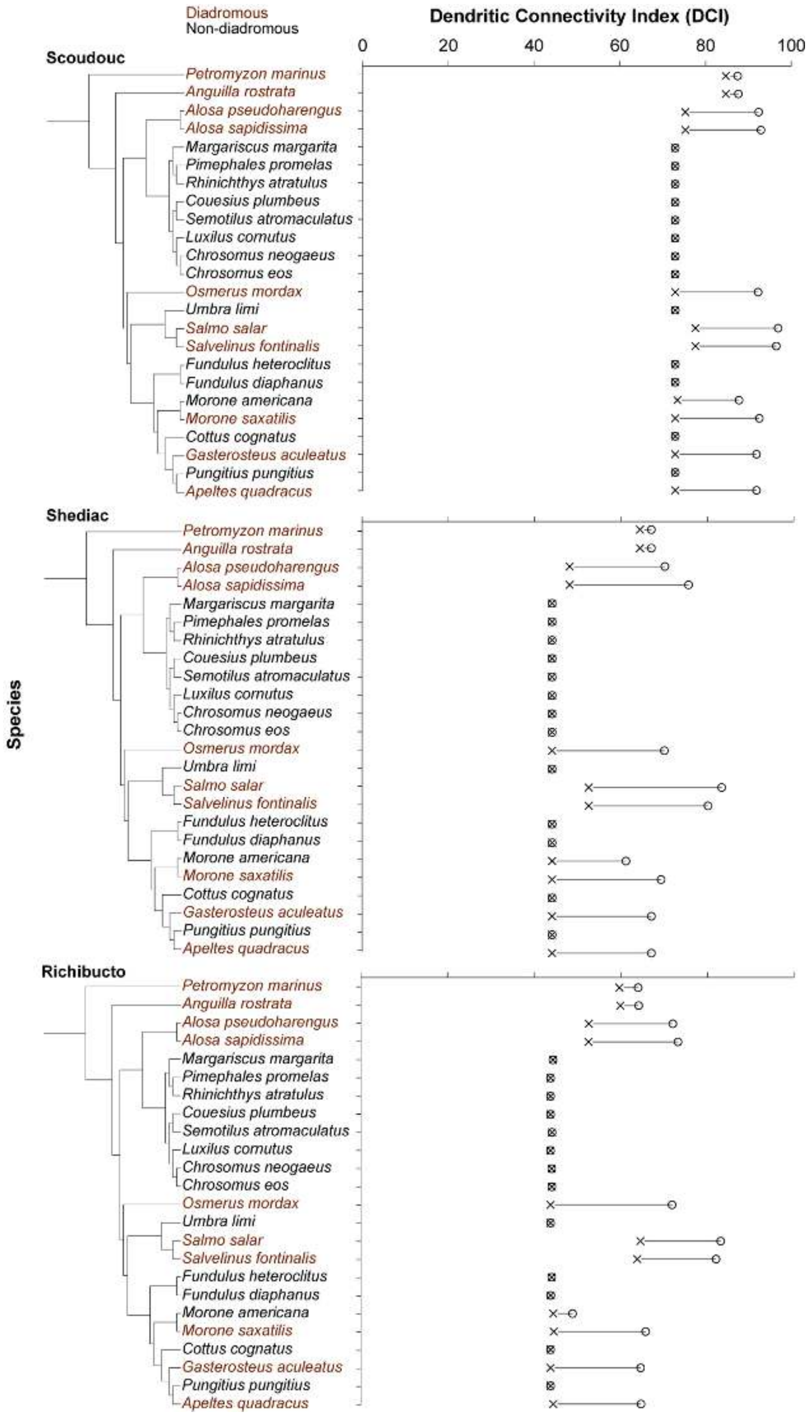

Fig. 2.B.1. Dendritic Connectivity Index (DCI) scores for the 24 species in the three watersheds in relation to their phylogenetic tree accounting for the ontogeny of juveniles (cross) and adults (open circle).

Chapter 3

3 Juvenile Atlantic Salmon (*Salmo salar*) Response to Land Use Change and Weather Fluctuation in the Miramichi Watershed in New Brunswick

3.1 Abstract

The Atlantic salmon (*Salmo salar*) is influenced by land use changes and weather changes that affect species persistence. Both the cumulative effects of land use change (e.g., forest harvesting) and weather fluctuations could adversely affect the habitat quality and amount of cool-water fish, such as juvenile Atlantic salmon. Cumulative effects over space and time of forest harvesting from upstream to downstream also alter fish habitat. We determined how juvenile Atlantic salmon density responds to forest harvesting in addition to weather conditions at the catchment level. We used sampled densities of juvenile Atlantic salmon densities of age-0 fry, age-1 parr, and age-2 parr in the Miramichi watershed of New Brunswick (Canada) in 22 catchments from 2000-2010. We assessed the effects of weather condition using maximum summer air temperature and precipitation during the months of July-August, and the annual amount of forest harvested in each catchment. We accounted for yearly time lags of weather conditions and upstream to downstream accumulation of the amount of forest harvesting due to the cumulative impact over space and time. We compared the upstream to downstream (directional) spatial effects to non-directional effects to determine key spatial scales of influence among and within catchments. We found that age-1 parr were the most sensitive to forest harvesting in all time lags. Furthermore, the effect of directional spatial patterns account for a difference of 3.9% explained variance of juvenile age-class abundance among catchments. Our results highlight the importance to account for the spatial and temporal complexity of stream networks that may affect the persistence of juvenile Atlantic salmon.

3.2 Introduction

Anadromous fish species are facing global climate change throughout their migration routes (Roessig et al. 2004). For anadromous species, both freshwater habitat for spawning and marine habitat for the maturation of adults are needed to complete their life cycle (Fleming 1996). Additional factors such as fishing pressure, diseases and parasites, the loss of connectivity to critical spawning habitat due to barriers in streams, and the reduction of habitat quality and amount due to land use changes have contributed to the decline of anadromous and non-diadromous populations alike (Parrish et al. 1998, Gibson et al. 2005, Bilotta et al. 2017, Forseth et al. 2017). Yet, climate change and anthropogenic activities impact all life stages and habitat for Atlantic salmon (*Salmo salar*) (Ottersen et al. 2001, Klemetsen et al. 2003, Harvey et al. 2017). Of particular importance is juvenile Atlantic salmon due to their development in freshwater during the fry and parr stage, which may be adversely affected by water quality in streams as well as land use changes in watersheds.

Climate change is expected to increase the water temperature of streams due to warming air temperatures in the Atlantic region of Canada (Swansburg et al. 2004a). Stream temperature is known to be a strongly correlated with air temperature (Langan et al. 2001, Caissie 2006). Moreover, the warming water temperatures have suggested to be thermal barriers for other salmonids such as brook trout (*Salvelinus fontinalis*) (Meisner 1990), which could similarly impact other cool-water fish species such as Atlantic salmon. The maximum water temperature causing thermal stress for Atlantic salmon is known to be 28 °C, with sustained periods of 10 minutes at this temperature resulting in mortality (Elliott and Elliott 2010). For juvenile Atlantic salmon parr, thermal stress occurs between 22 and 28 °C at which feeding behaviour is negatively impacted and ultimately affecting persistence (Elliott and Elliott 2010). Therefore, warming stream temperatures associated with the climate change and prolonged periods of extreme temperatures may adversely affect growth and survival of juvenile Atlantic salmon during summer months (Daigle et al. 2015).

Precipitation regimes in watersheds are expected to change with increased rainfall due to climate change across Canada (Zhang et al. 2000). Hydrologic regimes potentially affect the spatial distribution of juvenile Atlantic salmon due to streamflow (Jonsson and Jonsson 2009). Under high flow, juvenile stages such as parr could use high flow with the deeper water to evade predators as well as increase foraging opportunities due to greater inflow (Thorpe et al. 1992, Kemp et al. 2003). However, high flow events have been shown to displace juvenile fry and alevin stages of Atlantic salmon (Jonsson and Jonsson 2009). By contrast, low flows could result in stress for juvenile Atlantic salmon due to shallow waters and the likelihood of warmer water temperatures (Swansburg et al. 2004b).

Land use change, such as forest harvesting, may also impact hydrologic conditions that affect juvenile Atlantic salmon survival. For example, methods such as clear-cutting exposes the soil to greater solar radiation and thus warming soil temperatures (Hashimoto and Suzuki 2004). In turn, the warmer ground also increases the stream water temperature due to clear-cutting within catchments (Brown and Krygier 1970). Furthermore, loss of forest cover leads to a reduction in the amount of precipitation that goes into the groundwater component but increases the amount going into surface overflow, leading to increased hydrologic response and also greater temperature variation (Jones and Grant 1996, Mellina et al. 2002, Gomi et al. 2006). As the water flows down into the streams due to groundwater discharge, these areas pose a risk to Atlantic salmon (Kurylyk et al. 2015). Upstream warming also warm downstream sites (Cole and Newton 2013), thus it is important to consider the spatial dendritic network for catchments to better understand the effects of forest harvesting.

Land use upstream and precipitation leads to increased runoff events, which has effects on fish habitat and water quality that negatively affect the survival of juvenile Atlantic salmon. For example, sedimentation can adversely affect the survival to emergence of Atlantic salmon eggs (Lapointe et al. 2004). In particular, Atlantic salmon juveniles are sensitive to pollution compared to other life stages (McCormick et al. 1998, Leduc et al. 2009). However, it is unclear how runoff combined with increased precipitation with varying duration and intensity will affect the survival of juvenile Atlantic salmon in streams. The persistence of salmon populations is dependent on whether the upstream effects of runoff will adversely impact habitats downstream. These changes to the abundance of juvenile Atlantic salmon could further result in declining populations by reducing recruitment (Jonsson et al. 1998). Dendritic stream networks are also cumulative from upstream to downstream, and thus it is important to consider the spatial relationship of stressors within a watershed.

Yet, due to the cumulative effects of forest harvesting, in addition to the weather conditions at the catchment level, we hypothesize that juvenile Atlantic salmon density is affected by the cumulative impact of forest harvesting combined with weather conditions over space and time. Given all the disturbances and climate change that affect juvenile Atlantic salmon, certain populations of Atlantic salmon are recognized as endangered, such as those in the inner Bay of Fundy in Atlantic Canada (DFO 2010, Marshall 2014). Nonetheless, elsewhere in the Atlantic region, the Miramichi River of New Brunswick (Canada) is the most productive river of Atlantic salmon in North America, but it is under threat of such changes (Cunjak and Newbury 2005). To address the effects of forest harvesting and weather conditions, we used juvenile Atlantic salmon densities of age-0 fry, age-1 parr, and age-2 parr that were sampled in the Miramichi watershed of New Brunswick (Canada) from 2000 to 2010. Given the changes in abundance from one age class into the next age class each year, we also compare differences between time lags accounting for the cumulative effects of the land use due to forest harvesting. Such analyses accounting for the cumulative changes of forest harvesting and weather conditions over space and time will provide a better prediction of the impacts on forest harvesting on juvenile Atlantic salmon in a rapidly changing environment in stream networks and watersheds.

3.3 Methods

3.3.1 Study area

Our study area is located in the 13,496 km^2 Miramichi watershed in New Brunswick, Canada. The watershed is in a temperate forest biome as defined by the Hansen et al. (2010) forest cover loss biomes and considered part of the Acadian forest (Loo and Ives 2003). The Acadian forest in Miramichi is mainly comprised of coniferous (red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) Mill.) and deciduous species (yellow birch (*Betula alleghaniensis* Britt.), sugar maple (*Acer saccharum* Marsh.), trembling aspen (*Populus tremuloides* Michx.) (Loo and Ives 2003, Aubé 2008). In this region, commercial forest harvesting has been a prominent part of the economy of the region since 200 years ago, with clear-cutting being the most common method of harvesting (Loo and Ives 2003, Aubé 2008).

Hence, we used the Hansen et al. (2013) global dataset of forest cover loss (Linke et al. 2017). We summarized the dataset in our study area from summers of 2000 to 2010 to create annual forest loss data. Given that the region engages in active fire suppression along with disturbance salvage logging, we assumed that the annual forest loss was due to harvest. Harvest rates were calculated and summarized in each watershed catchment as ha/km^2/year. We then accounted for the total spatial and temporal accumulation of forest harvesting rate each year in each catchment of the Miramichi watershed upstream to downstream. Therefore, the most downstream catchments account for the total rate of forest harvesting upstream in the Miramichi watershed, in contrast to the most upstream catchments that account for total rate of forest harvesting within the catchment.

3.3.2 Atlantic salmon data

Juvenile Atlantic salmon (*Salmo salar*) density in the freshwater sections of the Miramichi watershed were annually sampled by Fisheries and Oceans Canada in 53 fixed sites selected with a complete time series during 2000-2010 (Fig. 3.1). A total of 53 sampling sites were located within 22 catchments of the Miramichi watershed. Overall, the total focal catchment area comprised of the sampling sites in the Miramichi watershed covered 5,582 km^2. The catchments varied in size from 65 km^2 to 629 km^2. Electrofishing surveys were conducted on average around August 17 and 18 as open or closed sites (Moore and Chaput 2007). At open sites without barrier nets, electrofishing was timed to approximately 500 seconds when the electrofishing unit was on, which covers an approximate area of 200 m^2 (Chaput et al. 2005). At closed sites, a removal method was used with upstream and downstream barrier nets to enclose the area to prevent immigration or emigration of individuals from the sampling area using 5 mm nylon netting (30 to 45 m in length × 1.2 m high). The area would be swept three to five times to remove all fish in the enclosed area during each sweep, with a minimum of 30-minute intervals. A population estimate was determined for the area using the Zippin (1956) method. Juvenile salmon were categorized as fry (age-0), small parr (age-1), and large parr (age-2). Here, density is reported as fish per 100 m^2 converted from catch per unit effort by calibrating with the closed sites to estimate density (Chaput et al. 2005).

3.3.3 Environmental condition

We retrieved ANUSPLIN climate data (Hopkinson et al. 2011, McKenney et al. 2011) to determine annual mean maximum daily air temperature and total monthly precipitation between July and August (summer) in 1 km × 1 km spatial grids over the study area from 2000 to 2010. These months coincide with the highest temperatures of the year in our study area. Maximum daily temperature was determined at each sampling site and averaged among the sites within each catchment for each year. Total precipitation was summed for all grids within a catchment for each year and standardized as mm/ha for each catchment.

3.3.4 Statistical analyses

We performed redundancy analyses (RDA; Legendre and Legendre, 2012) with predictors using the summarized environmental variables (mean daily maximum temperature in July and August, total precipitation in the months of July and August standardized by catchment area), the total cumulative amount of forest loss each year from 2000 to 2010, and key spatial predictors. Then, the response variables were the mean density of age classes (age-0 fry, age-1 parr, age-2 parr) in a catchment averaged each year from 2000 to 2010 to determine sensitivity to the predictors. No collinearity was present at $r > 0.7$.

To account for the key spatial scales of processes that affect salmon density over the study area, we used spatial predictors derived from eigenvector maps. We compared eigenvector maps based on Moran's eigenvector maps (MEMs) and asymmetric eigenvector maps (AEMs). MEMs account for the symmetrical effect of spatial processes that are non-directional in the watershed (e.g., amount of forest loss assuming there is no upstream bias for harvesting) (Dray et al. 2012). The MEMs first considered the spatial coordinates of each catchment based on their centroid. The Euclidean distances were calculated between each catchment as the spatial relationship and decomposed using a truncated distance matrix from the minimum spanning distance. By contrast, asymmetric eigenvector maps account for directional spatial processes (Blanchet et al. 2008a). Here, we used AEMs to assess the effect of upstream catchments on downstream catchments. We considered the spatial connection between upstream to downstream catchments for the directionality using the stream network and summarized the catchments as a connectivity matrix. Overall, eigenvector maps are synthetic spatial variables representing spatial scales, where lower eigenvalues (i.e., MEM1 or AEM1) indicate broad-scale patterns spanning across the watershed, moderate eigenvalues (i.e., MEM10 or AEM10) indicate intermediate-scale patterns spanning between multiple catchments, and higher eigenvalues indicate fine-scale patterns (i.e., MEM21 or AEM21) between catchments. The total number of eigenvector variables was 21 (total number of catchments - 1) and using a forward selection process, we retained broad, intermediate, and fine-spatial scales relating to the reduced eigenvector map variables. We performed partial redundancy analyses (pRDAs) by partitioning the variance due to the environment and space, and compared the variance explained by the two alternative models of MEM and AEM. Significance of RDAs was tested with 999 Monte Carlo permutations.

We assessed the effects of time lags of environmental condition variables (mean daily maximum temperature in July and August of sites in catchment, total precipitation in the months of July and August standardized by catchment area, cumulative annual rate of forest harvest standardized by catchment area) on the densities of each age class by comparing generalized linear mixed models (GLMMs) with Gaussian error distribution. All variables were standardized with z-scores. For fixed effects, an interaction of the amount of forest harvest and mean maximum daily temperature and total precipitation was included in the models. We considered the effect of weather with forest harvesting rate through this interaction term. We used catchments as random factors to account for the potential spatial effect within the same catchment on the response variable each year. We constructed reduced models with all possible combinations of the variables (full model) based on Akaike's information criterion (AIC; Burnham and Anderson, 2002). We lagged the environmental variables beginning at lag 0 (current environmental condition) yearly to a maximum of one year before the age class, resulting in one time lag for age-0, two time lags for age-1 parr, and three time lags for age-2 parr. To determine the 95% confidence intervals (CI) of fixed factors and if there was a significant effect on the response variable, we bootstrapped the best reduced models with 200 replications, where a non-overlapping 95% CI with 0 was considered a significant effect. We determined the variance explained by fixed factors in the best reduced model by calculating the marginal R^2 ($R^2_{\mathrm{GLMM(m)}}$), and the conditional R^2 ($R^2_{\mathrm{GLMM(c)}}$) pertaining to variance explained by both fixed and random factors (Nakagawa and Schielzeth 2013).

All analyses were performed with R (R Core Team 2014). We ran the RDA analysis with the *vegan* package (Oksanen et al. 2015), forward selection with *packfor* (Dray et al. 2013), AEM with *AEM* (Blanchet et al. 2014), MEM with *adespatial* (Dray et al. 2017), and GLMM with *lme4* (Bates et al. 2015).

3.4 Results

Over the study, the environmental variability of yearly summer (July and August from 2000 to 2010) mean maximum daily air temperature ranged from 22.8 to 25.2 °C. Yearly summer catchment precipitation varied from 228 mm to 528 mm. Rate of forest harvesting ranged from 0.5 to 15.9 ha/catchment km^2/year. Average fry (age-0) density varied from 0 to 199.9 fish/100 m^2 in catchments per year, average small parr (age-1) density varied from 0 to 57.8 fish/100 m^2 in catchments per year, and average large parr (age-2) density varied from 0 to 19.8 fish/100 m^2 in catchments per year.

3.4.1 Impact of timing due to weather and forest harvesting on juvenile Atlantic salmon density

Based on the generalized linear mixed models (GLMMs), the current cumulative rate of annual forest harvested had a significant negative effect on the density of fry (age-0; Table 3.1). The lagged maximum temperature interacting with annual forest loss had a significant effect on the density of fry (age-0; Table 3.1). The effect of current annual forest harvesting had a negative effect on the density of small parr (age-1; Table 3.1). Lagged precipitation significantly affected the density of small parr (age-1; Table 3.1). The interaction of temperature and forest harvesting lagged one year was significant for all parr age classes, and forest harvesting negatively affected small parr (age-1) in all models (Table 3.1). Generally, lagged higher maximum temperatures increased the density of all parr age classes (Table. 3.1).

Overall, fixed factors mainly explained the variance of age-1 parr ranging from 9.2 to 16.8% (Table 3.1) compared to other age classes. With the time lags, the variance explained by the fixed factors gradually decreased for age-1 parr (Table 3.1). By contrast, fixed factors explained less of the variance for age-0 fry ($R^2_{\text{GLMM(m)}} = 2.6\text{-}3.3\%$) and age-2 parr (($R^2_{\text{GLMM(m)}} = 0.08\text{-}0.5\%$); Table 3.1).

3.4.2 Cumulative impact of space upstream to downstream on juvenile Atlantic salmon density

Based on the redundancy analyses (RDA), when considering the average environmental condition of all years, there was a negative association with the cumulative amount of forest harvesting and the density of parr (age-1, age-2; Fig. 3.2). The density of fry was positively associated with greater precipitation (Fig. 3.2). Maximum daily temperature was negatively associated with the densities of all parr age classes (Fig. 3.2). These relationships between the response and predictor variables were comparable between the MEM and AEM spatial models (Fig. 3.2). The two spatial models showed associations between broad to intermediate spatial scales over the study area and mean daily maximum air temperature (MEM3, MEM14; AEM4, AEM13). Similarly, precipitation was associated between intermediate spatial scale of catchments (MEM15, AEM16), as well as forest harvesting (MEM14, AEM16). The variance of explained from the MEM model ($R^2_{\mathrm{adj}} = 0.455$) was lower than the AEM model ($R^2_{\mathrm{adj}} = 0.570$; Table 3.2) accounting for the directionality of the network of catchments. The AEM model explained greater variance for both environment and space than the MEM model (Table 3.2). In terms of variance due to space, the AEM model accounted for 3.9% more variation than the non-directional MEM model.

3.5 Discussion

We found evidence that the density of juvenile Atlantic salmon age-1 parr responds the most to environmental change. Age-1 parr were more sensitive to environmental gradients such as summer air temperature and precipitation. However, the lagged effect of forest harvesting had an effect on the densities of fry. Furthermore, the spatial and temporal cumulative effects of forest harvesting account for entire watershed as a key scale in response to changes in parr density in our temperate forest study area.

The response of age-0 fry and age-1 parr to forest harvesting and environmental condition varied indicating different potential effects on life stages. It is possible that the impact on fry densities due to forest harvesting impacts survival, but the effects are evident later for age-1 parr. Associated effects of forest harvesting include reduced spawning success due to the increase in fine sedimentation, which reduces spawning gravel and oxygenated water (Hicks et al. 1991, Greig et al. 2005). Thus, to avoid these less favourable areas with high sedimentation, salmon may be spawning elsewhere from such sites. Forest harvesting, however, may be beneficial to juvenile salmon through the intentional creation of shelter with large woody debris to increase habitat complexity (Hicks et al. 1991, Crook and Robertson 1999). For example, juvenile Coho salmon (*Oncorhynchus kisutch*) in Oregon streams are found in natural dammed pool habitats when there are full-stream-width structures as critical wintering habitat to provide preferential stream flow and a pool depth that prevents freezing (Hicks et al. 1991, Nickelson et al. 1992). Although the influence or amount of woody debris were not measured in our study, this could be an indirect effect of forest harvesting depending on the method of harvest and if debris were retained. Finally, the rate of forest harvesting attributed to age-0 fry may have resulted in the subsequent decrease in density of age-1 parr in following years.

The density of age-1 parr responded to increasing air temperature with a lagged effect. When survival of parr is associated with warming, slight increases in water temperature have shown to be beneficial for parr due to increased growth rates and longer growing season (Jonsson et al. 2001, Elliott and Elliott 2010). The optimal water temperature for the growth of Atlantic salmon parr is around 16 to 20 °C, with increased food consumption relating to growth (Jonsson et al. 2001). The tolerance, however, is at 22 to 28 °C before there is thermal stress for Atlantic salmon parr and smolts (Elliott and Elliott 2010). If the water temperature was warmer in the surrounding area outside the sampling sites, it may be possible that the sites in our study were cool thermal refugia for parr and hence the greater densities as individuals congregate in cooler areas during high air temperature events. Atlantic salmon parr are capable of seeking cooler thermal refuges during thermal stress events (Dugdale et al. 2016). This mismatch of air temperature and water temperature may be due to the topology of the area which results in cool groundwater seepage that would provide important cool-water refugia (Breau et al. 2007). Similarly, if the water temperatures were within the optimal range, then the higher density of parr may be due to habitat preference.

The cumulative effect of forest harvesting upstream to downstream as analyzed in the asymmetric eigenvector maps did not greatly enhance the models to explain the response of juvenile Atlantic salmon across catchments in our study area. It may be possible that the low elevational gradient relating to a possible association of the flow rate between sites retained much of the variation of juvenile densities between catchments. There is an elevational of around 470 m where the Miramichi River originates (Moore and Chaput 2007), which could be considered a relatively levelled elevational gradient among sites considering all the catchments. Mobile juvenile Atlantic salmon parr may preferentially seek suitable habitat, relying on the environmental condition. Thus, we found that the spatial scales without directionality provided similar results to directional spatial scales as good predictors of the response of juvenile salmon to forest harvesting and weather conditions. This result highlights the importance of local scale at the catchment level as well as the dispersal of salmon to seek suitable habitat.

Although our study did not assess habitat at a microclimate perspective, forest harvesting could potentially influence the results at a local scale at the site level. Our results summarize the changes occurring at the catchment level. At the local scale, there are many other site characteristics that could influence habitat quality for cool-water species with thermal refugia (Kurylyk et al. 2015). For instance, immediate riparian shading could provide areas of thermal refugia for cool-water species due to the cooler water temperatures, which experimental shading could lower water temperature by 2 to 4 °C (Ebersole et al. 2003). Therefore, preventing direct solar radiation on streams by maintaining forest canopy could benefit adjacent juvenile salmon habitat through cooling water temperatures. Furthermore, cold groundwater seepage are also important aspects of the environment that may provide thermal refugia (Kurylyk et al. 2014). Similar to our study, age-1 parr have shown to aggregate in higher densities as a result of cool-water sources during high temperature events in the Miramichi (Breau et al. 2007). As such, these habitat characteristics could potentially aid in the persistence of local populations of juvenile salmon.

Our study provides several points for the management of forest harvesting. The spatial and temporal cumulative impacts should be considered among the entire watershed. While there are effects of forest harvesting immediately within catchments, as our analysis at the catchment scale relate to important variables such as air maximum temperature, precipitation, and forest harvesting that affect juvenile salmon density. For example, immediate buffers in streams for forest harvesting could be beneficial to maintain cooler stream temperatures (Bourque and Pomeroy 2001). However, we found that there are the cumulative spatial and temporal effects that are usually unaccounted for in the entire watershed among catchments. Current regulations in New Brunswick that require a 30 m buffer for forest harvesting from a watercourse (New Brunswick Department of the Environment 2012) would likely be insufficient to buffer the effects of forest harvesting for cumulative spatial impact upstream of a catchment as the current buffer regulation is only relevant adjacent to the watercourse. Furthermore, the cumulative temporal impact is especially important given the recovery time for stream water temperatures to return to pre-harvest levels through the regrowth of vegetation (Johnson and Jones 2000).

Overall, upstream forest harvesting has cumulative impacts through each catchment downstream and the total amount harvested upstream in each catchment should be considered.

Our findings show the importance of considering the spatial (i.e., upstream effects) and temporal (i.e., time lags) as well as cumulative effects of forest harvesting and weather condition on juvenile Atlantic salmon densities in catchments to watersheds. The spatial and temporal changes associated with forest harvesting and weather condition influence juvenile Atlantic salmon density within catchments, but also cumulatively across upstream to downstream catchments. Finally, maintaining cool-water refugia would be essential to ensure species persistence in a warming climate with anthropogenic land use change that exacerbates these risks to cool-water species.

3.6 Tables

Table 3.1. Generalized linear mixed effect models (GLMMs) for juvenile Atlantic salmon (*Salmo salar*) density as a response due to the effects of significant annual environmental variables (annual forest harvesting = area loss, mean daily maximum air temperature = temp, summer precipitation = precip) using time lags as separate models from 2000 to 2010 in catchments with the model coefficient and confidence intervals. Catchments (*n* = 22) were treated as a random effect. Fixed factors have been standardized with *z*-scores. $R^2_{\text{GLMM(c)}}$ is the variance explained by fixed and random effects. $R^2_{\text{GLMM(m)}}$ is the variance explained by fixed effects. Significant variables are indicated in bold.

Response	***n*** **(22 catchments × no. of years)**	$R^2_{\text{GLMM(c)}}$	$R^2_{\text{GLMM(m)}}$	**Variable**	**Regression coefficient**	**Intercept**	**Lower 95% CI**	**Upper 95% CI**
Age-0								
Lag 0	242	0.408	0.026	**Area loss**	-0.16	72.9	59.8	85.4
Lag 1	220	0.438	0.033	**Temp * Area loss**	-0.031	70.6	59.7	85.9
Age-1								
Lag 0	242	0.561	0.168	**Temp**	0.63	22.6	19.1	26.1
				Area loss	-0.12	22.6	18.75	27.2
Lag 1	220	0.539	0.152	**Precip**	0.0006	22.2	17.0	27.2
				Area loss	-0.13	22.3	18.5	26.9
Lag 2	198	0.524	0.092	**Area loss**	-0.11	20.6	16.8	24.3
Age-2								
Lag 0	242	0.325	0.0005	**Temp**	0.029	5.9	4.6	7.1
Lag 1	220	0.316	0.002	**Precip**	-0.0001	6.0	4.7	7.3
Lag 2	198	0.291	0.0007	**Precip**	0.0008	6.0	4.6	7.4
Lag 3	176	0.262	0.008	**Temp**	0.13	6.1	4.7	7.8

Table 3.2. Variation explained by average density of juvenile Atlantic salmon (*Salmo salar*) age classes in response to the environmental variables (env.) from 2000 to 2010 compared with spatial predictors (Moran's eigenvector maps (MEM), asymmetrical eigenvector maps (AEM)) across 22 catchments retained as two alternative models.

Model	**R^2_{adj}**	**Variance explained**			**Variance unexplained**
		Environment	**Shared**	**Space**	
Env. + MEM	0.455*	0.246 (air temperature, precipitation, forest harvesting)	0	0.324 (MEM3, MEM6, MEM14, MEM15)	0.545
Env. + AEM	0.570*	0.352 (air temperature, precipitation, forest harvesting)	0	0.363 (AEM4, AEM10, AEM13, AEM16 AEM20)	0.430

* $p < 0.001$

3.7 Figures

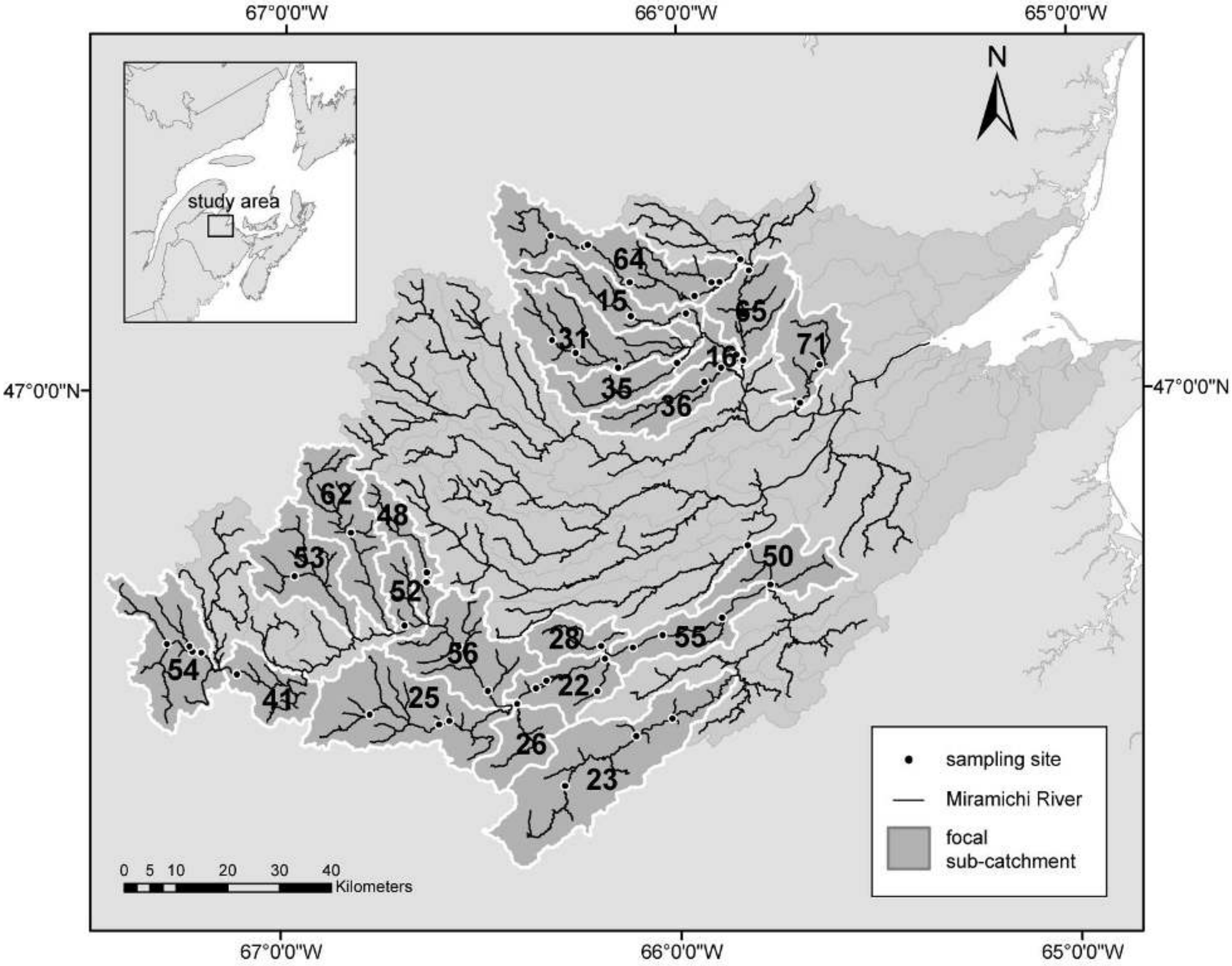

Fig. 3.1. Sampling sites ($n = 53$) for juvenile Atlantic salmon (*Salmo salar*) in the Miramichi watershed from 2000 to 2010. Focal catchments ($n = 22$) in darker grey and their identification numbers in the Miramichi watershed are indicated.

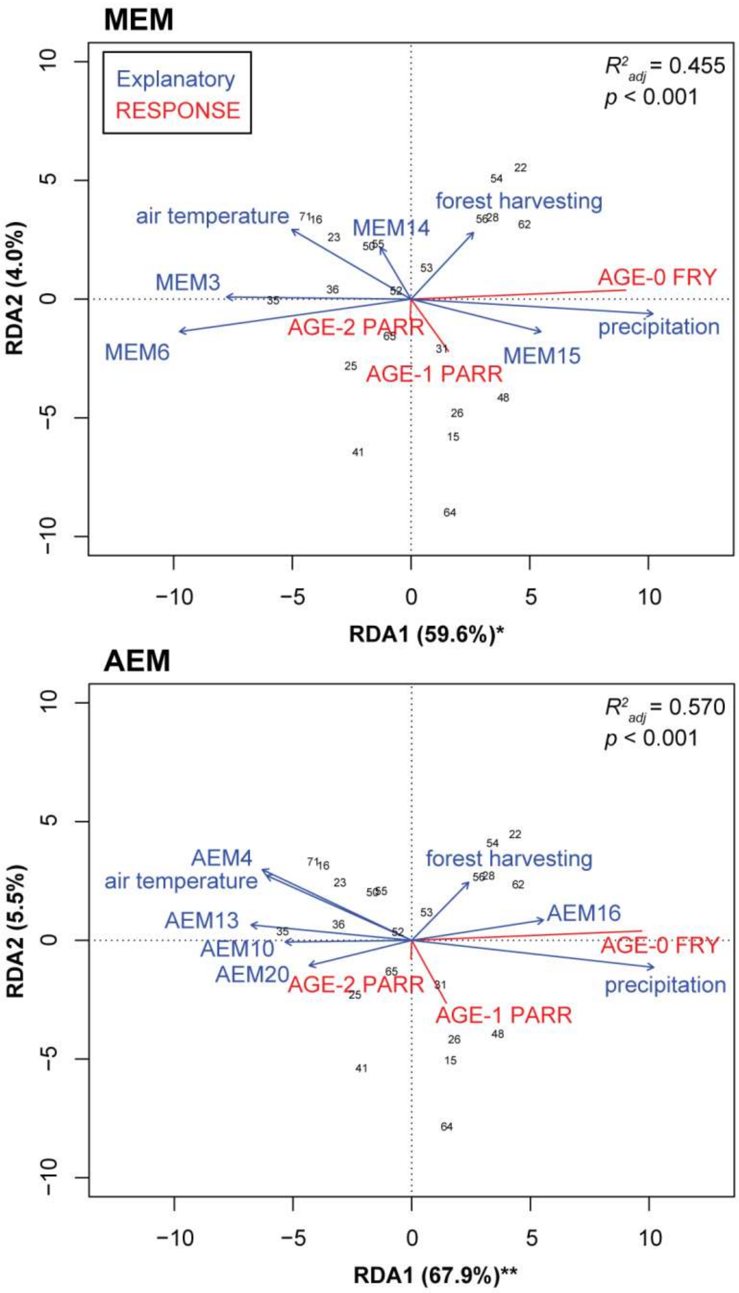

Fig. 3.2. Redundancy analyses (RDAs) of significant environmental (temperature = average daily maximum air temperature); precipitation = total precipitation/standardized with catchment area; forest harvesting = cumulative forest harvest from 2000 to 2010/standardized with catchment area) and spatial variables with juvenile Atlantic salmon (*Salmo salar*) age classes (age-0 fry, age-1 parr, age-2 parr) as response variables averaged from all years (2000-2010) in 22 catchments (catchment number is indicated). Significance of RDAs was tested with 999 Monte Carlo permutations.

3.8 Appendix A

3.8.1 Atlantic salmon sampling

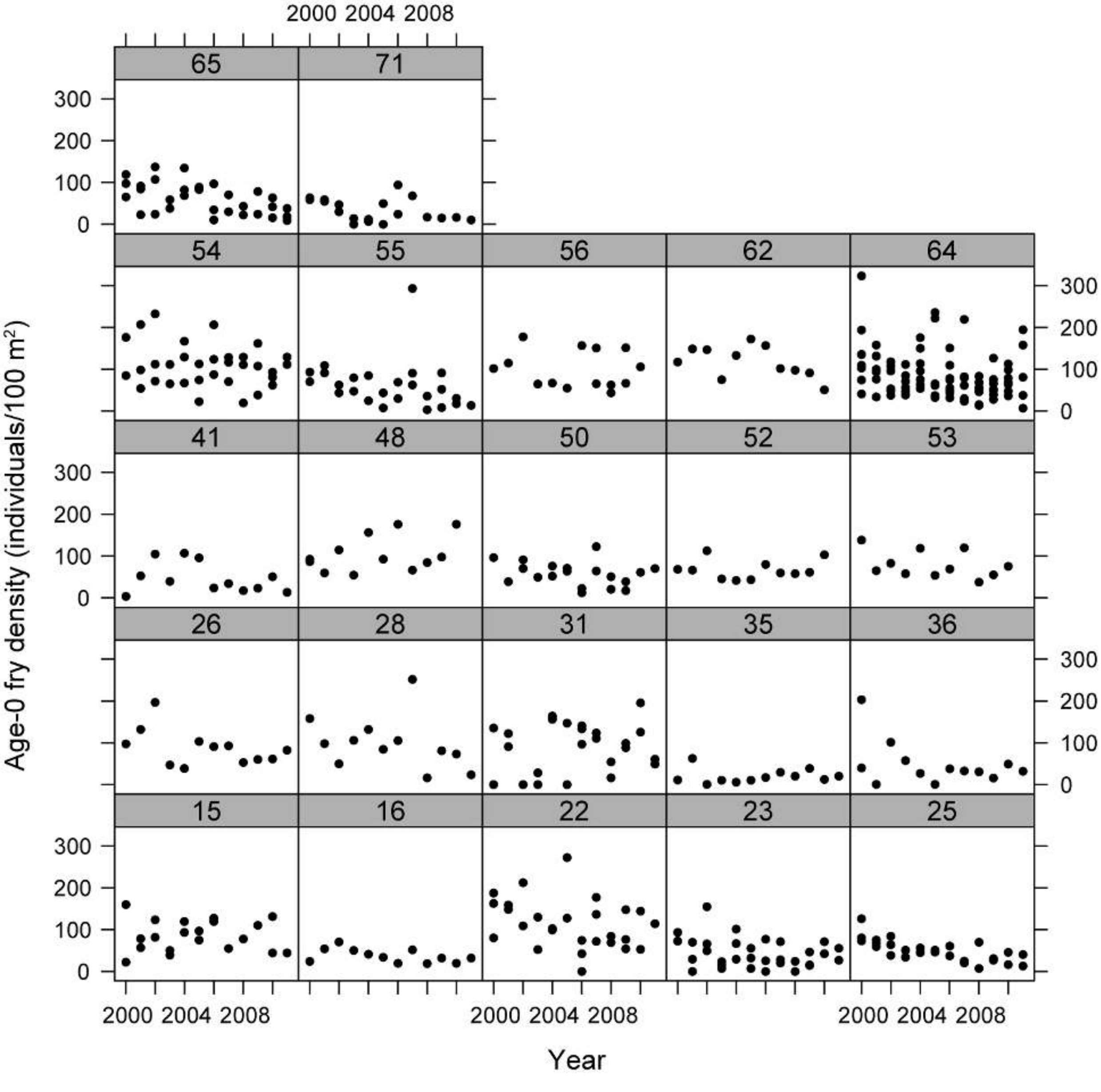

Fig. 3.A.1. Scatterplot of age-0 Atlantic salmon (*Salmo salar*) fry density in sampling sites (n = 53 sites) over time from 2000-2010 in each of the 22 catchments (catchment identification numbers are indicated in the grey box—see Fig. 3.1 for locations).

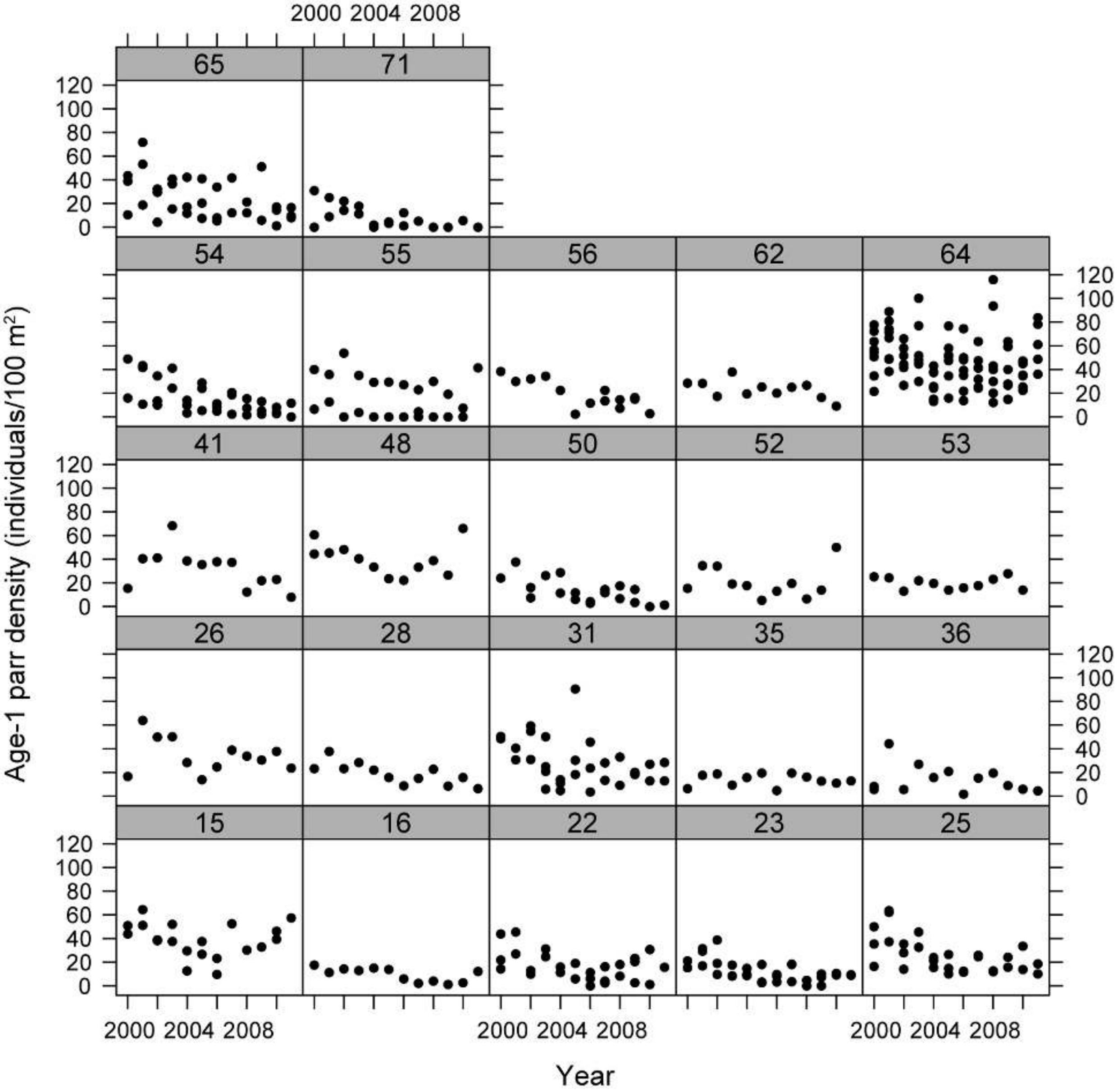

Fig. 3.A.2. Scatterplot of age-1 Atlantic salmon (*Salmo salar*) parr density in sampling sites (*n* = 53 sites) over time from 2000-2010 in each of the 22 catchments (catchment identification numbers are indicated in the grey box—see Fig. 3.1 for locations).

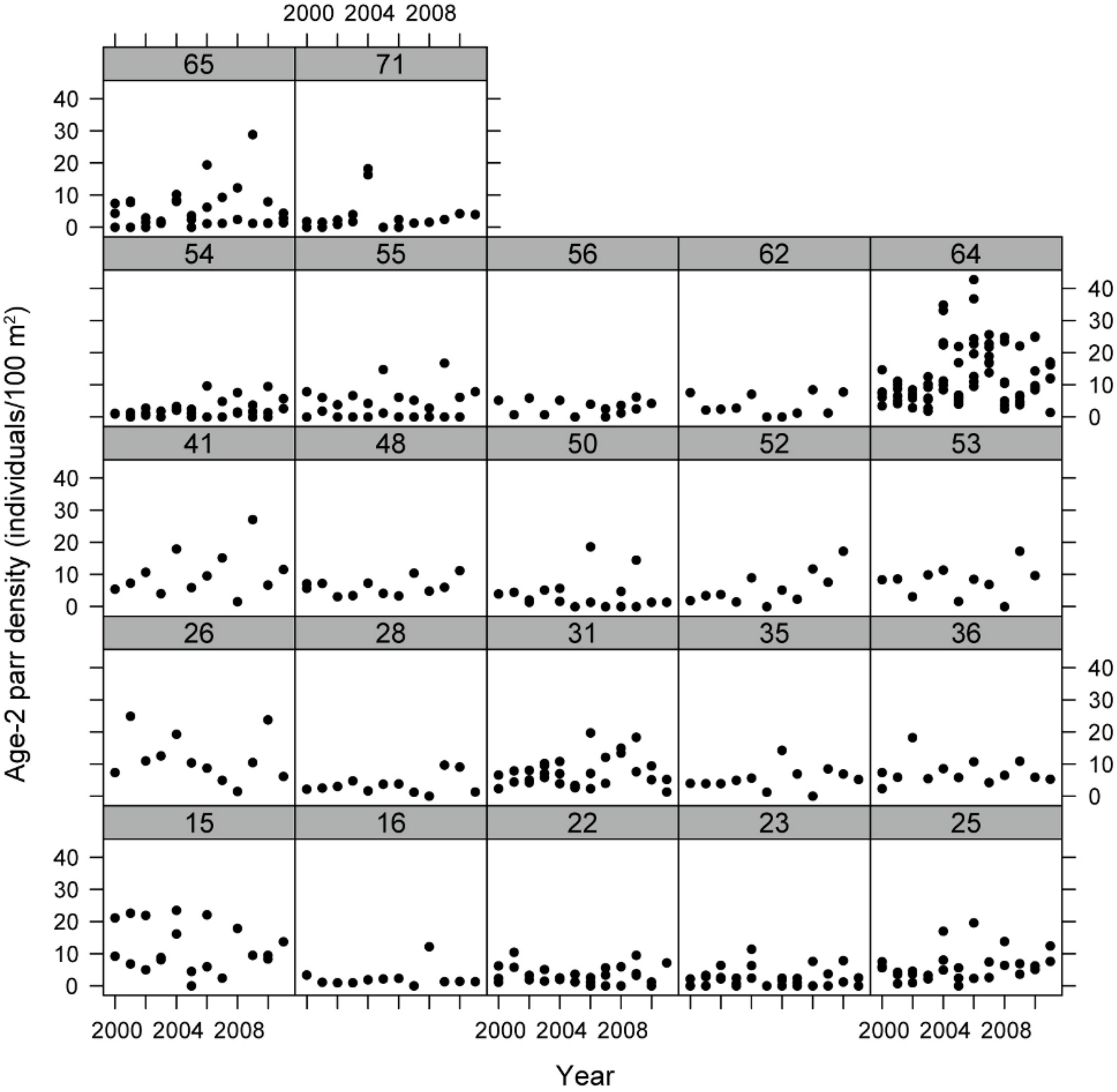

Fig. 3.A.3. Scatterplot of age-2 Atlantic salmon (*Salmo salar*) parr density in sampling sites (*n* = 53 sites) over time from 2000-2010 in each of the 22 catchments (catchment identification numbers are indicated in the grey box—see Fig. 3.1 for locations).

Chapter 4

4 Beta Diversity Changes in Estuarine Fish Communities due to Environmental Change

4.1 Abstract

Estuarine ecosystems are intrinsically resilient to the dynamic fluctuations of environmental conditions. Yet, it is unknown how the changes in environmental variability associated with climate change will affect fish communities. We assessed how species turnover over space and time in estuaries is influenced by changes in environmental conditions over years. We used fish abundances and water quality sampled at 42 stations among seven estuaries in New Brunswick (Canada) from 2005 to 2012 to estimate: (1) spatial turnover between stations based on the local contribution to beta diversity (LCBD) index; and (2) temporal turnover from year to year based on β-Sørensen. Beta diversity was mainly structured over space between stations by temperature variability within the year and over time due to environmental condition from the previous year as a result of changes among sites in the annual variability of salinity, dissolved oxygen, and water temperature at sampling stations. Species contribution to spatial beta diversity (SCBD) were attributed to four key species across all years, which were sensitive to dissolved oxygen. The current environmental condition of dissolved oxygen, temperature, salinity, and eelgrass (*Zostera marina*) affect temporal turnover year to year. When each year is analyzed separately, the estuaries with the greatest annual summer temperature fluctuations within a station contribute the most to spatial beta diversity between estuaries. Understanding how fish community structure responds to changes in environmental conditions can help inform changes to estuarine resources in the face of a rapidly changing environment.

4.2 Introduction

In naturally dynamic systems such as estuaries, species are adapted to changing environmental conditions (Elliott and Whitfield 2011). Estuaries experience tidal and seasonal changes that lead to dramatic changes in salinity and temperature, through which fish species are able to persist with physiological and morphological adaptations (Cognetti and Maltagliati 2000, Elliott and Quintino 2007). While euryhaline species are adapted to tidal and seasonal salinity fluctuations, their response to greater temporal and spatial salinity changes due to climate change could be variable.

Climate change is expected to directly increase the variability and duration of changes in salinity affecting the availability of suitable habitat for different species (Robins et al. 2016). Extreme changes in salinity from intense precipitation and storm events have been predicted for the mid-Atlantic region of North America (Najjar et al. 2000). Other coastal marine ecosystems are already showing effects of low salinity due to freshwater inflow from flood events associated with snowmelt or rain events (Huang et al. 2014a, 2014b). In addition, long-term changes related to sea-level rises are anticipated to result in saltwater encroachment in coastal areas including saltwater intrusion into freshwater aquifers further upstream (Werner and Simmons 2009, Hong and Shen 2012).

There may also be indirect effects of environmental changes to fish assemblages due to changes in water quality and the quality and quantity of fish habitat, such as eelgrass beds (*Zostera marina*). Eelgrass is particularly sensitive to salinity with niche of optimal salinity ranging between 20 to 26; however, salinity between 5 to 35 and even freshwater can be tolerated for brief periods (DFO 2009a). Additionally, increases in magnitude and frequency of high (30 °C) water temperature events increases the mortality of eelgrass in temperate estuaries, potentially past the point of recovery (Carr et al. 2012). Eelgrass beds provide structured habitat used by various invertebrate and fish species as spawning, nursery and foraging grounds (Heck et al. 1995, DFO 2009a). Thus, the size and number of eelgrass beds due to salinity and temperature conditions would indirectly affect fish communities by changing prey abundance (i.e., invertebrates) and fish habitat (Boström and Bonsdorff 1997, Namba et al. 2018).

Fish community composition changes over space and time can be quantified using beta diversity (Whittaker 1972, Baselga 2010). Beta diversity could be partitioned in two ways as nestedness or turnover (Baselga 2010). Nestedness can be used to describe species loss or gain within a subset of the species composition and compare species richness (Baselga 2010, Legendre 2014). Species turnover, also known as species replacement, along spatial and temporal gradients can be used to identify locations associated with greater environmental change (Baselga 2010). For example, these environmental gradients could be present in estuaries through salinity and temperature changes over space and time. Environmental gradients, therefore, play a major role in turnover of fish assemblages in estuaries (Henriques et al. 2017a).

Spatial gradients in salinity occur along estuaries due to freshwater input from watersheds upstream mixing with saltwater from the ocean. Salinity gradients and the effect on species assemblages have been assessed in large temperate estuaries with well-defined gradients, such as Chesapeake Bay (e.g., Jung and Houde 2003), the Severn (e.g., Potter et al. 1986), and the Giround (e.g., Pasquaud et al. 2012) as well as smaller estuaries such as those along the European Atlantic coast (e.g., Nicolas et al. 2010). In larger estuarine systems, spatial turnover of species communities is evident due to the defined salinity gradient (e.g., Wagner 1999, Martino and Able 2003, Giberto et al. 2007). Anthropogenic bathymetric changes to smaller estuaries have been shown to alter tides (e.g., Winterwerp et al. 2013). In smaller watersheds, the salinity gradient could be more sensitive to sudden changes from intense weather events and sea-level rise over a smaller area but the extent of this effect is unknown. In fact, predicted climate change in eastern Canada is expected to impact all estuaries in the region with salinity and temperature changes (Zhang et al. 2000, Swansburg et al. 2004a), and thus it is critical to determine the current structure of fish communities across smaller estuaries.

The objective in this chapter is to determine how fish communities in small, temperate estuaries are structured by environmental gradients over space and time in summer to predict changes that may be expected with climate change. We first determined how nektonic fish beta diversity varies with environmental changes over time from June to August in 2005 to 2012 across a region of estuaries in the southern Gulf of Saint Lawrence, Canada. Second, we assessed which environmental variables are associated with beta diversity changes over space and time. Such analyses will provide a current baseline of fish community structure against which the effects of climate change may be detected.

4.3 Methods

4.3.1 Study area

Our study focused on seven temperate estuaries of the eastern coast of New Brunswick along the Northumberland Strait region of the southern Gulf of Saint Lawrence (latitudes 46.1° – 47.8°; longitudes -63.8° – -65.0°; Fig. 4.1). The associated watersheds of the estuaries ranged from 150 to 510 km^2. Substrates in these estuaries are generally sand and mud and the predominant macrophyte is eelgrass (*Zostera marina*).

4.3.2 Sampling

We used fish and environmental data collected from the Community Aquatic Monitoring Program (CAMP), which is coordinated by the Southern Gulf of St. Lawrence Coalition on Sustainability and Fisheries and Oceans Canada (Weldon et al. 2005). Adult fish sampled once monthly in June-August 2005-2012 by beach seine (30 × 2 m; 6 mm mesh) were enumerated by species at six fixed sampling stations within each estuary. Fish communities at each station were summarized by the annual average catch of all months. Sampling stations were chosen within comparable estuaries but stations were different to span a range of environmental gradients and macrophyte vegetation. Given that each location is different in terms of bathymetry, the target sampling area encompassed a 15 × 15 m block bordering shore with one sample each month per station. Species were counted in a live box submerged in water and then released back into the estuary. Eelgrass coverage at each sample location were estimated using a 50 cm × 50 cm quadrat thrown randomly three times within the area seined. Eelgrass coverage is a score ranging zero to five from the quadrat sampling with zero as none and five indicating full coverage. At each station, water temperature, dissolved oxygen, and salinity were recorded using a portable meter (YSI Meter Model 85) at one-half to two-thirds of the depth down from the water surface and ca. 7 m from shore in the beach seine area. Tidal stage during a sampling event was recorded with five levels enumerated from: high tide, incoming, mid-tide, outgoing, and low tide.

4.3.3 Beta diversity

Beta diversity is a measure used to compare variations in species composition over space and time as species nestedness or turnover (Baselga 2010). Using species turnover (replacement), we partitioned total spatial beta diversity in two ways (Legendre and De Cáceres 2013). First, spatial beta diversity was calculated based on the local contribution to beta diversity (LCBD) index that assesses specific stations that contribute the most to spatial beta diversity among all 42 stations (7 estuaries and 6 stations/estuary) using the overall average abundance of species from 2005 to 2012. LCBD represents the uniqueness of community composition in sampling stations across the sampling region and it would identify stations with significantly different community composition (Legendre and De Cáceres 2013). Then LCBD was calculated over the 42 stations for each year separately. Second, species that contribute the most to spatial beta diversity each year can be assessed using the species contribution to beta diversity (SCBD; Legendre and De Cáceres 2013). The SCBD would identify specific species that mainly drive the spatial turnover. Before running the analyses for LCBD and SCBD, we applied a Hellinger transformation to the abundance data (Legendre and De Cáceres 2013). Temporal turnover was measured using the Sørensen pairwise beta diversity (β-Sørensen; Baselga 2010) index comparing year-to-year turnover considering all the 42 sampling stations for each sampling station from 2005 to 2012.

4.3.4 Relationship of beta diversity to environmental conditions

We determined periods of significant environmental change from the predictors during our study period from 2005 to 2012. Significantly different years of salinity, water temperature, and dissolved oxygen were assessed using a one-way analysis of variance (ANOVA). We further investigated the potential effect of the tidal cycle on salinity for each year associated with the timing of sampling during tides by performing a two-way ANOVA (factors are tidal stage: high tide, incoming, mid-tide, outgoing, low tide; and year). Significant year-to-year differences of the amount of eelgrass coverage were not calculated as it is based on random quadrats instead of resampled quadrats.

We assessed which environmental variables as predictors affect beta diversity (spatial turnover response variable is LCBD and temporal turnover is β-Sørensen where each sample in the data matrix is one site in one year) of our study using generalized linear mixed models (GLMMs) with Gaussian error distribution due to the normal distribution of data. Normality was verified with Q-Q plots and collinearity between environmental variables was checked with a Pearson correlation matrix. To model temporal turnover in species composition (here measured with β-Sørensen between consecutive years), we built two alternative models where the predictor variables are the current year (current env.) and the previous year (lag env.). We were interested in determining which year of the turnover difference had a greater influence on species composition changes over time. The current year of environmental condition refers to the end of each year-to-year turnover whereas the time lag refers to the beginning of each year-to-year turnover. Overall, the current year of environmental condition refers to the time period from 2006 to 2012 and the lag year of environmental condition refers to the time period from 2005 to 2011. Fixed factors were environmental and habitat variables such as salinity, dissolved oxygen, temperature, and eelgrass coverage. We further analyzed within-year environmental variability at each station by determining the interquartile ranges (IQR) for environmental condition as a fixed factor. Each estuary had variable levels of fluctuations of salinity from 2005 to 2012 (Fig. A.4.1). Estuaries of the sampling stations were treated as random factors to account for the potential spatial effect of a group of stations within the same estuary on the response variable. From a full model containing all of the fixed factors, we constructed reduced models with all possible combinations of the variables based on Akaike's information criterion (AIC; Burnham and Anderson 2002). We compared the full model with the reduced model using a chi-square test. We performed bootstrapping of the best reduced models with 200 replications to determine the 95% confidence intervals (CI) of fixed factors. If the 95% CI did not overlap with 0, then the fixed factor was considered to have a significant effect on the response variable. R^2 values were calculated to determine the variance explained by the best reduced model based on the methods described in Nakagawa and Schielzeth (2013). We then calculated $R^2_{\mathrm{GLMM(m)}}$, which is the marginal R^2 pertaining to the variance explained by fixed factors, and $R^2_{\mathrm{GLMM(c)}}$, which is the conditional R^2 pertaining to the variance explained by both fixed and random factors (Nakagawa and Schielzeth 2013).

We assessed which environmental variables as predictors affect species contribution to beta diversity as the response with each entry in the data matrix as each year using generalized linear models (GLMs) for Gaussian (normal) data. We checked for normality and removed predictors that are collinear, which reduced to four predictor variables: dissolved oxygen, dissolved oxygen IQR, salinity IQR, and temperature IQR. To model species contribution to beta diversity each year, we built two alternative models where the predictor variables are the current year (current env.) and the previous year (lag env.). The current year of environmental condition spans from 2006 to 2012. The previous year of environmental condition spans from 2005 to

2011. Due to small sample sizes, we compared models with AIC corrected for small sample sizes (AIC_C; Burnham and Anderson 2002).

All analyses were performed using the program R version 3.1.0 (R Core Team 2014). We partitioned beta diversity into turnover using the *betapart* package in R (Baselga et al. 2013). We analyzed LCBD and SCBD values using the *beta.div* package in Legendre and De Cáceres (2013). Generalized linear mixed models were constructed using the *lme4* package in Bates et al. (2015).

4.4 Results

The Community Aquatic Monitoring Program (CAMP) has detected 26 species of adult fish across the seven focal estuaries. Over all months (June, July, August) and years (the eight years 2005-2012) sampled, the number of species ranged from six to 17 species per sampling station.

4.4.1 Environmental condition

Water temperature varied from a minimum of 15.8 °C to 27.3 °C from 2005 to 2012 (Fig. 4.2). The lowest water temperature was recorded in Jourimain and the highest was in Cocagne, both in 2005. Water temperature significantly varied across 2005 to 2012 ($F_{7,328} = 11.4$, $p < 0.001$; Fig. 2) with a significant decrease from 2007 to 2008 ($p < 0.001$; Fig. 4.2). There was a significant increase in water temperature from 2009 to 2010 ($p < 0.001$; Fig. 4.2), followed by a significant decrease from 2010 to 2011 ($p < 0.001$; Fig. 4.2), and finally a significant increase from 2011 to 2012 ($p < 0.001$; Fig. 4.2). Within-year variability of water temperature at a station measured as interquartile ranges (IQR) differed year to year from 2005 to 2012 within the 42 sites. Water temperature IQR was significantly different from 2005 to 2012 ($F_{7,328} = 8.2$, $p < 0.001$). Year-to-year difference of water temperature IQR significantly varied from 2010 to 2011 ($p < 0.001$).

Annual mean salinity fluctuated from a minimum of 5.4 to 28.6 from 2005 to 2012 (Fig. 4.2). The lowest salinity was recorded in St. Louis-de-Kent in 2011 in contrast to the highest salinity in Lamèque during 2010. Significant variation occurred for salinity across 2005 to 2012 ($F_{7,328} = 4.3$, $p < 0.001$; Fig. 4.2). Recorded salinity dropped significantly from 2007 to 2008 and 2010 to 2011, and increased from 2011 to 2012 (all $p < 0.001$; Fig. 4.2). Salinity IQR significantly varied across 2005 to 2012 ($F_{7,328} = 5.5$, $p < 0.001$). The year-to-year difference of salinity IQR marginally varied from 2007 to 2008 ($p = 0.056$). We found that there was a significant effect of the tidal cycle (five levels: enumerated from high tide, incoming, mid-tide, outgoing, low tide) on salinity during the sampling years (eight levels: 2005 to 2012) using a two-way ANOVA ($F_{23,765} = 3.4$, $p < 0.001$; sampling did not always occur during a specific tidal cycle for certain years). Furthermore, although there was a significant effect based on the sampling done during a specific tidal cycle, a post-hoc analysis of this interaction was only significantly different from 2005 to 2006 (Tukey post-hoc test: $p < 0.001$). Therefore, the majority of years with the exception of 2005 to 2006 were sampled across all tidal cycles to capture the environmental change of salinity.

Dissolved oxygen varied from 2.8 mg L^{-1} to 12.7 mg L^{-1} (Fig. 4.2). Dissolved oxygen significantly varied across 2005 to 2012 ($F_{7,328} = 10.3$, $p < 0.001$; Fig. 4.2), when 2006 was significantly lower than 2007 ($p < 0.001$) and 2011 was significantly higher than 2012 ($p < 0.001$; Fig. 2). The lowest levels of dissolved oxygen were found in Lamèque during 2005 and the highest levels of dissolved oxygen were found in Bouctouche during 2008. Dissolved oxygen IQR significantly varied from 2005 to 2012 ($F_{7,328} = 2.8$, $p = 0.007$), with the year-to-year variability significantly different from 2011 to 2012 ($p = 0.003$).

The amount of eelgrass varied from an annual average score of zero when eelgrass was absent in 113 observations in certain stations within the seven estuaries over the years sampled from 2005 to 2012 (Fig. 4.2). In contrast to the absence of eelgrass, there was a maximum annual average score of 3.25 for eelgrass coverage, which was in Caraquet during 2006.

4.4.2 Spatial beta diversity

Local contribution to beta diversity (LCBD) values measured across all years ranged from 0.005 to 0.0418 and we found four sampling stations that had significant LCBD values (Fig. 4.3). These significantly different sites were found within the estuaries of Saint-Louis-de-Kent and Cape Jourimain. When the LCBD was calculated each year from 2005 to 2012 for the 42 stations, stations in Jourimain contributed to beta diversity every year (Fig. 4.A.1).

We found six species contributing greater than the overall mean beta diversity (SCBD) value (0.037; Table 4.1) considering all years from 2005 to 2012. SCBD values ranged from 0 to 0.227 (Table 4.1). Four species contributed greater than the mean beta diversity between stations obtained considering all years from 2005 to 2012 (Table 4.1). A total of nine different species contributed greater than the mean beta diversity value at any one year (Table 4.1).

4.4.3 Temporal beta diversity

Temporal turnover considering all stations measured as β-Sørensen of year-to-year changes in community composition was significantly different from 2005 to 2012 ($F_{6, 246} = 316.9$, $p < 0.001$). All year-to-year comparisons were significantly different (Bonferroni correction: $p < 0.001$) with the exception of 2008-2009 and 2009-2010 (Bonferroni correction: $p > 0.05$). Two periods, 2006-2007 and 2011-2012, showed markedly low temporal turnover, in contrast to 2005-2006 with high temporal turnover (Fig. 4.4). Overall, temporal turnover considering all stations responded similarly over time between stations and among estuaries (Fig. 4.4).

4.4.4 Relationship of beta diversity to environmental change

The reduced generalized linear mixed model with estuaries as a random effect for the local contribution to beta diversity (LCBD) values contained only temperature IQR (Table 4.2). The full model was not significantly different than the reduced model with temperature IQR ($\chi^2 = 2.98$, df = 7, $p = 0.89$). The reduced model explained 43.3% of the variation ($R^2_{\mathrm{GLMM(c)}}$) of LCBD values, temperature IQR explained 0.08% of the variation ($R^2_{\mathrm{GLMM(m)}}$), and estuaries as a random effect explained 43.22% of the variation.

For temporal turnover (β-Sørensen) considering all stations with year-to-year variation of species communities and the current year for environmental condition for fixed effects and estuaries as a random effect, the reduced model contained dissolved oxygen, temperature, salinity, dissolved oxygen IQR, and eelgrass (Table 4.2). The full model was not significantly different than the reduced model ($\chi^2 = 1.70$, df = 3, $p = 0.64$). The reduced model explained 11.7% of the variation ($R^2_{\mathrm{GLMM(c)}}$) of β-Sørensen values all due to the environmental condition.

For the time lag of one year for environmental condition and its effect on β-Sørensen values, the reduced model with estuaries as a random effect contained salinity IQR, temperature IQR, dissolved oxygen IQR, and temperature (Table 4.2). The time lag of one year for the effect of temperature on temporal turnover was not significant (Table 4.2). The reduced model was not significantly different than the full model ($\chi^2 = 1.91$, df = 4, $p = 0.75$). The reduced model explained 23.0% of the variation ($R^2_{\text{GLMM(c)}}$). The fixed factors explained 21.8% of the variation ($R^2_{\text{GLMM(m)}}$) and the random effect of estuaries explained 1.2% of the variation.

Species contribution to beta diversity each year was affected by the current environmental condition of dissolved oxygen from 2006 to 2012 (Table 4.3). The four species that responded to dissolved oxygen (Table 4.3) also corresponded to the species that consistently contributed to beta diversity greater than the mean SCBD between stations considering all years from 2005 to 2012 (Table 4.1). Mummichog (*Fundulus heteroclitus*) and Atlantic Silverside (*Menidia menidia*) contributed less to beta diversity with increasing dissolved oxygen, whereas Fourspine Stickleback (*Apeltes quadracus*) and Threespine Stickleback (*Gasterosteus aculeatus*) contributed more to beta diversity with increasing dissolved oxygen. By contrast, species contribution to beta diversity was unaffected by the environmental condition of the previous year as none of the variables were significant.

4.5 Discussion

We found that the amount of eelgrass, salinity, water temperature, and dissolved oxygen gradients over time are related to the environmental condition leading to temporal turnover as fish composition changes. Previously, it has been shown that other seagrasses in estuaries are sensitive to extreme fluctuations in salinity and water temperature (e.g., Montague and Ley 1993, Glemarec et al. 1997, Fernández-Torquemada and Sánchez-Lizaso 2005). Consequently, the increased mortality of seagrasses leads to greater decay of organic matter, thus reducing dissolved oxygen levels through the decomposition of detritus (D'Avanzo et al. 1996). Due to these changing dissolved oxygen levels and reduction in habitat in estuaries, temporal turnover occurs through species replacement for persistent species that can tolerate lower oxygen conditions (Pihl et al. 1991).

Spatial turnover of each year measured as the local contribution to beta diversity (LCBD) was highly influenced by the variability of water temperature. By contrast, temporal turnover of year-to-year variation in fish communities was mostly driven by water temperature, salinity, the amount of eelgrass, and dissolved oxygen during the current year of environmental condition. The environmental condition of a time lag of one year contributed to temporal turnover due to variability of salinity, temperature, and dissolved oxygen. Furthermore, locations along a geographical region, here based on the estuary, affected temporal turnover each year. Each individual estuary had different environmental gradients and variability over space and time that could be influenced by the shape and size of the estuary. For example, smaller and broader estuaries would potentially have shorter environmental gradients of temperature compared to larger and longer estuaries. These differences may contribute to the magnitude of change of environmental condition within each estuary. Therefore, spatial and temporal turnover of fish communities are commonly driven by temperature changes in our study area.

Dissolved oxygen during a current year of the environmental condition affects year-to-year temporal turnover. During the study period, dissolved oxygen in the estuaries fluctuated to levels below 8.0 mg L^{-1}. The interim recommended guideline for dissolved oxygen in estuarine waters is a minimum of 8.0 mg L^{-1} or lower if natural processes resulted in this decrease (Canadian Council of Ministers of the Environment 1999). Given that the estuaries within this study area fluctuated below the interim guideline, the lower dissolved oxygen levels may be due to eutrophication caused by potential anthropogenic impact in several of the estuaries of New Brunswick (Schmidt et al. 2012). In contrast to the Canadian Council of Ministers of the Environment (1999) recommended interim guideline of 8.0 mg L^{-1}, several studies have recommended lower thresholds for aquacultures in coastal waters (e.g., Brooks and Mahnken 2003, Page et al. 2005). The effects of hypoxic conditions begin to affect the metabolism of species between 2.0 and 4.0 mg L^{-1}, and mortality occurs below 0.5-2.0 mg L^{-1} (Gray et al. 2002, Vaquer-Sunyer and Duarte 2008). Prolonged variability away from the norm would favour species tolerance of lower dissolved oxygen levels and ultimately a shift in assemblage composition.

Species composition changes over time examined throughout several years measured as species contribution to spatial beta diversity (SCBD) were attributed to four key species across all years: mummichog (*Fundulus heteroclitus*), Atlantic silverside (*Menidia menidia*), fourspine stickleback (*Apeltes quadracus*), and threespine stickleback (*Gasterosteus aculeatus*). Species able to tolerate a wide range of environmental conditions, such as *F. heteroclitus*, contributed to beta diversity between stations in all years. *Fundulus heteroclitus* is known to be tolerant to environmental changes such as fluctuating temperatures, salinity, and low levels of dissolved oxygen as well as pollutants (Abraham 1985, Marshall et al. 1999, Weis 2002, Stierhoff et al. 2003). Given that *F. heteroclitus* is adapted to low dissolved oxygen, it would contribute more to beta diversity during these periods. Due to the turnover of other species unable to tolerate lower dissolved oxygen, *F. heteroclitus* becomes abundant at particular sites. For example, sites that are impacted by anthropogenic activities, such as agriculture with signs of eutrophication and showing hypoxic conditions, tend to be dominated by *F. heteroclitus* (Finley et al. 2009). The dominance of *F. heteroclitus* during these conditions may be due to their ability to gulp air at the surface of water and thereby survive low oxygen conditions (Stierhoff et al. 2003). In contrast to hypoxic conditions, the dominance of *F. heteroclitus* would be reduced during normoxic conditions. Despite these periods of prominent environmental change, *F. heteroclitus* is able to persist and remains as an important part of the community composition in estuaries.

Similarly, the lower dissolved oxygen during sampling in 2008 resulted in species such as *Menidia menidia* contributing more to beta diversity between stations during that year. During spawning, *M. menidia* have been found congregating in areas with depleted dissolved oxygen (Middaugh et al. 1981). Spawning season for *M. menidia* in higher latitudes begins early summer (Middaugh 1981, Conover and Present 1990), which coincides with the sampling period of our study. As a result of the greater abundance of *M. menidia* associated with periods of low dissolved oxygen, species contribution to spatial beta diversity is higher during these events.

Demersal species in the Gasterosteidae family responded to high dissolved oxygen. *Apeltes quadracus* and *G. aculeatus* were sensitive to dissolved oxygen when these species were found in greater abundance and contributed to beta diversity. Eggs of *A. quadracus* have greater mortality in periods of low dissolved oxygen, which reduces the recruitment to the adult population (Poulin and FitzGerald 1989). *Gasterosteus aculeatus* has also been associated with high dissolved oxygen in European estuaries (Araújo et al. 1999, Maes et al. 2007). Thus, when looking at the current environmental condition of year-to-year changes in species composition, dissolved oxygen is an important factor to structure turnover.

Results of our analysis with one-year lag indicate that greater within-year variability of environmental conditions, specifically salinity, temperature, and dissolved oxygen, have an effect on temporal species turnover. Yet, species communities are also rapidly responding to the current environmental conditions based on the temporal turnover on the year. We found that the locations that affect spatial beta diversity the most were consistent through the years, such as sampling stations within Cape Jourimain located on the coast. These exposed stations allow for greater flushing resulting in consistent fish habitat throughout the years (Nedwell 1996).

We focused on the lag of environmental conditions, as we were interested in the effects of the environmental conditions of the previous year. The lag response of fish species turnover to environmental conditions may be due to the recruitment of adult individuals. Unfavourable environmental conditions during a year may then be linked to changes in trophic interactions of fish communities or adult condition (Neill et al. 1994, Pershing et al. 2005), leading to lower fecundity for adult individuals and therefore reducing recruitment in subsequent years. It is necessary to distinguish this lag of environmental condition from the magnitude of environmental change between years. Henriques et al. (2017) assessed the environmental dissimilarity between fish communities in estuaries worldwide, where environmental differences such as sea surface temperature structure fish species turnover. These differences within environmental gradients may elucidate how fish communities respond in estuaries. Here, we found that the environmental variability within a year, which is different than the magnitude of difference between years, also cause spatial and temporal fish species turnover in estuaries.

Spatial turnover considering all years does not change rapidly over time as communities are mainly structured by the robust environmental gradients that occur within each estuary. These salinity gradients structure fish communities in large estuaries such as Chesapeake Bay (Jung and Houde 2003), as well as small estuaries (e.g., Nicolas et al. 2010, Harrison and Whitfield 2012). Turnover in fish communities has been examined in a wide range of estuaries globally (Henriques et al. 2017a), and in upstream freshwater environmental gradients (Edge et al. 2017). Similarly, we have also found that temperature gradient changes in the smaller estuaries of New Brunswick structure fish community turnover. These variations may be driven by individual estuaries, as our results indicate that each estuary had a prominent effect on spatial turnover. First, characteristics of estuaries that potentially drive environmental variation could be due to the bathymetry, such as exposed or sheltered estuaries, resulting in varying degrees of environmental variation due to the spatial scales that structure fish communities ranging from within estuaries to the entire region (Lekve et al. 2002). Similarly, the species assemblage of our Cape Jourimain site contrasts significantly with other sites in the region as it is exposed to the sea. Second, the watersheds of the estuaries could contribute to the environmental variation affecting submergent aquatic vegetation (Li et al. 2007), which may indirectly affect fish assemblages. Future research in the bathymetry and the overall region of watersheds of the estuaries could potentially drive the environmental variation influencing spatial and temporal turnover of fish communities.

In summary, environmental variability remains an important factor that influences the structure of fish community composition in the dynamic nature of estuaries. Spatial turnover operates on a localized scale corresponding to each estuary due to an environmental gradient. Effects of large-scale changes, such as climate change leading to increased within-year variability, could have potential effects on localized changes in estuaries that affect species composition over time. These findings imply that temporal turnover is rapid annually in estuaries due to environmental variability, and shifts in species communities that occur during the year are due to sensitivity to environmental change. As a result, such climatic changes would undermine any management efforts regarding the reduction of anthropogenic pressures in estuarine ecosystems.

4.6 Tables

Table 4.1. Species contribution to spatial beta diversity (SCBD) across 42 sampling stations in each year from 2005 to 2012 and the associated ranks of the highest SCBD values for each year. Bolded ranks indicate years when SCBD was greater than the mean SCBD between stations considering all years from 2005 to 2012 (0.0370). Mean abundance of species is averaged for each year from 2005 to 2012 across 42 sampling stations.

Common name	**Scientific name**	**Mean SCBD**	**Mean abundance**	**Rank of SCBD by year**							
				‘05	**‘06**	**‘07**	**‘08**	**‘09**	**‘10**	**‘11**	**‘12**
Mummichog	*Fundulus heteroclitus*	**0.227**	135.1	**3**	**2**	**1**	**1**	**2**	**1**	**1**	**1**
Atlantic Silverside	*Menidia menidia*	**0.212**	80.2	**1**	**1**	**2**	**4**	**4**	**2**	**2**	**2**
Fourspine Stickleback	*Apeltes quadracus*	**0.168**	37.9	**2**	**3**	**3**	**2**	**1**	**3**	**3**	**3**
Threespine Stickleback	*Gasterosteus aculeatus*	**0.161**	40.5	**4**	**6**	**4**	**3**	**3**	**4**	**4**	**5**
Blackspotted Stickleback	*Gasterosteus wheatlandi*	**0.061**	17.0	**5**	**4**	7	**5**	**5**	**6**	**6**	**4**
Banded Killifish	*Fundulus diaphanus*	**0.044**	6.2	9	11	8	11	11	8	**7**	8
Ninespine Stickleback	*Pungitius pungitius*	0.035	5.3	**6**	**7**	**6**	**7**	**7**	**7**	8	9
Smooth Flounder	*Pleuronectes putnami*	0.033	3.2	8	**5**	**5**	**6**	**6**	**5**	**5**	**6**
Alewife	*Alosa pseudoharengus*	0.03	1.3	16	18	17	15	9	11	20	**7**
Winter Flounder	*Pseudopleuronectes americanus*	0.007	0.7	7	9	10	10	10	9	9	10
American Sand Lance	*Ammodytes americanus*	0.006	0.09	15	12	15	**8**	8	21	12	13
Cunner	*Tautogolabrus adspersus*	0.004	0.08	11	14	13	16	19	13	13	11
Striped Bass	*Morone saxatilis*	0.004	0.1	18	18	17	9	17	14	10	18
Rainbow Smelt	*Osmerus mordax*	0.002	0.03	17	18	17	21	16	15	20	14
Northern Pipefish	*Syngnathus fuscus*	0.002	0.08	18	8	14	21	19	12	15	22
Windowpane Flounder	*Scophthalmus aquosus*	0.001	0.02	10	18	11	13	14	10	16	12
Atlantic Tomcod	*Microgadus tomcod*	0.001	0.08	12	10	9	14	13	19	11	15
Grubby	*Myoxocephalus aenaeus*	0.001	0.01	18	18	17	21	19	18	20	17
American Eel	*Anguilla rostrata*	0	0.03	13	13	17	18	12	16	14	20
Shorthorn Sculpin	*Myoxocephalus scorpius*	0	0.01	14	17	12	20	19	21	17	19
Lake Chub	*Couesius plumbeus*	0	0.003	18	15	17	21	19	21	20	24
Trout spp.		0	0.001	18	16	16	21	19	21	20	24
Rock Gunnel	*Pholis gunnellus*	0	0.007	18	18	17	12	18	17	20	23
White Sucker	*Catostomus commersonii*	0	0.0008	18	18	17	17	19	21	18	24

Table 4.1. continued

Common name	**Scientific name**	**Mean SCBD**	**Mean abundance**	**Rank of SCBD by year**							
				‘05	‘06	‘07	‘08	‘09	‘10	‘11	‘12
Brook Trout	*Salvelinus fontinalis*	0	0.007	18	18	17	19	15	20	18	21
Cyprinidae family		0	0.0004	18	18	17	21	19	21	20	16

Table 4.2. Generalized linear mixed effect models (GLMMs) for beta diversity as a response due to the effects of significant annual environmental variables from 2005 to 2012 in 42 stations with the model coefficient and confidence intervals. Spatial turnover was analyzed as local contribution to beta diversity (LCBD). Temporal turnover (β-Sørensen) of year-to-year variation was analyzed with the environmental condition of the current year (current env.) and a time lag of one year (lag env.). Estuaries (n = 7 estuaries) were treated as a random effect. $R^2_{\mathrm{GLMM(c)}}$ is the variance explained by fixed and random effects. $R^2_{\mathrm{GLMM(m)}}$ is the variance explained by fixed effects.

Response	**Variable**	**Estimate**	**Lower 95% CI**	**Upper 95% CI**
	Random effect (spatial): **Estuaries (n = 7)**			
LCBD (spatial turnover) (n = 336, $R^2_{\mathrm{GLMM(c)}} = 0.433$, $R^2_{\mathrm{GLMM(m)}} = 0.0008$)				
	Temperature IQR	0.015	0.0082	0.022
β-Sørensen (temporal turnover – current env.) (n = 294, $R^2_{\mathrm{GLMM(c)}} = 0.117$, $R^2_{\mathrm{GLMM(m)}} = 0.117$)				
	Dissolved oxygen	0.53	0.47	0.62
	Temperature	0.48	0.36	0.61
	Salinity	0.41	0.37	0.46
	Dissolved oxygen IQR	0.38	0.36	0.40
	Eelgrass	0.37	0.36	0.38
β-Sørensen (temporal turnover – lag env.) (n = 294, $R^2_{\mathrm{GLMM(c)}} = 0.230$, $R^2_{\mathrm{GLMM(m)}} = 0.218$)				
	Salinity IQR	0.42	0.39	0.45
	Temperature IQR	0.38	0.36	0.41
	Dissolved oxygen IQR	0.36	0.34	0.37
	Temperature	0.062	-0.039	0.18

Table 4.3. Generalized linear models (GLMs) for four species contribution to beta diversity (SCBD) annually as a response due to the effects of significant annual environmental variables (current environmental condition) averaged across 42 stations each year from 2006 to 2012 (n = 7). Model coefficients, standard error (SE), and p-values of the best supported model for each species are displayed.

Species contribution to beta diversity	**Parameter**	**Estimate**	**SE**	***p*-value**
Mummichog	Intercept	0.66	0.14	0.006
	Dissolved oxygen	-0.054	0.019	0.03
Atlantic silverside	Intercept	0.86	0.17	0.004
	Dissolved oxygen	-0.083	0.022	0.01
Fourspine stickleback	Intercept	-0.14	0.086	0.16
	Dissolved oxygen	0.039	0.011	0.02
Threespine stickleback	Intercept	-0.44	0.11	0.01
	Dissolved oxygen	0.072	0.014	0.004

4.7 Figures

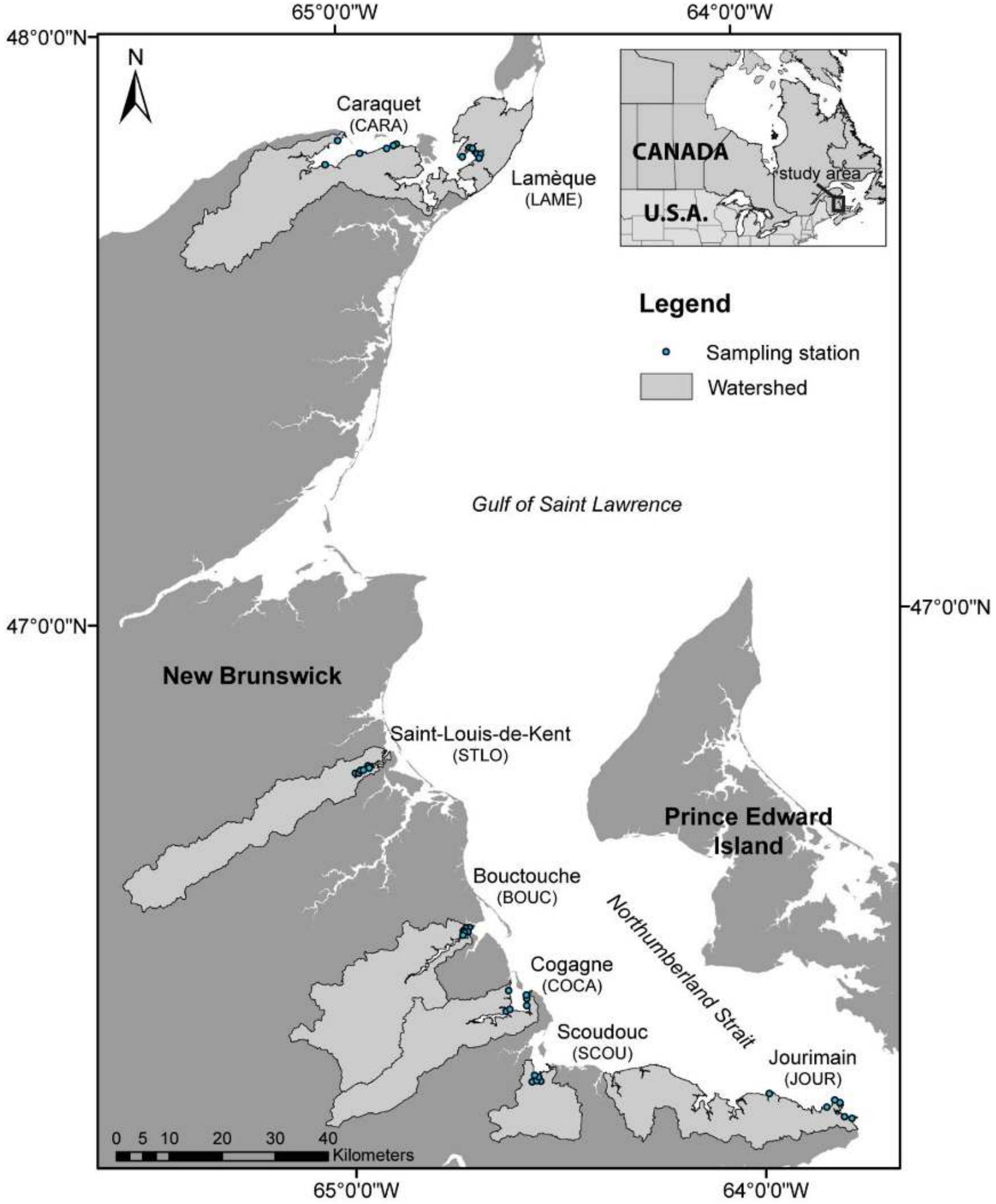

Fig. 4.1. Map of the study area with the sampling stations (*n* = 42) for the seven estuaries and associated watersheds in New Brunswick (Canada).

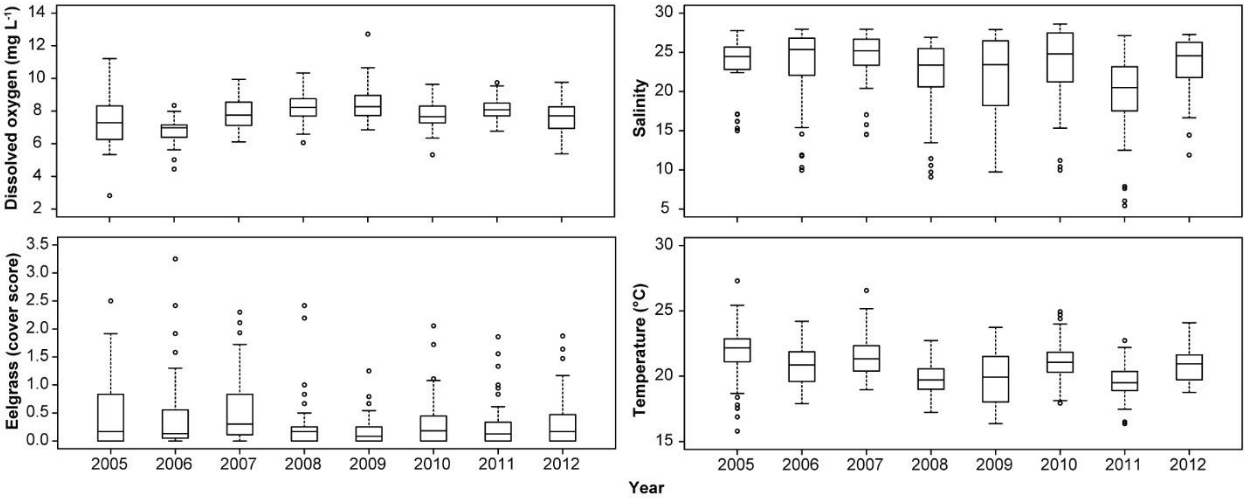

Fig. 4.2. Boxplot of dissolved oxygen, eelgrass coverage levels, salinity, and water temperature within stations in the seven focal estuaries (*n* = 42 each year) from June to August of 2005 to 2012. The box indicates the interquartile (IQR) range, the bars are the minimum and maximum, and the solid line is the median. Outliers indicated by the circles are 1.5 times the IQR. Eelgrass coverage is a score (0-5) from the quadrat sampling with 5 indicating full coverage.

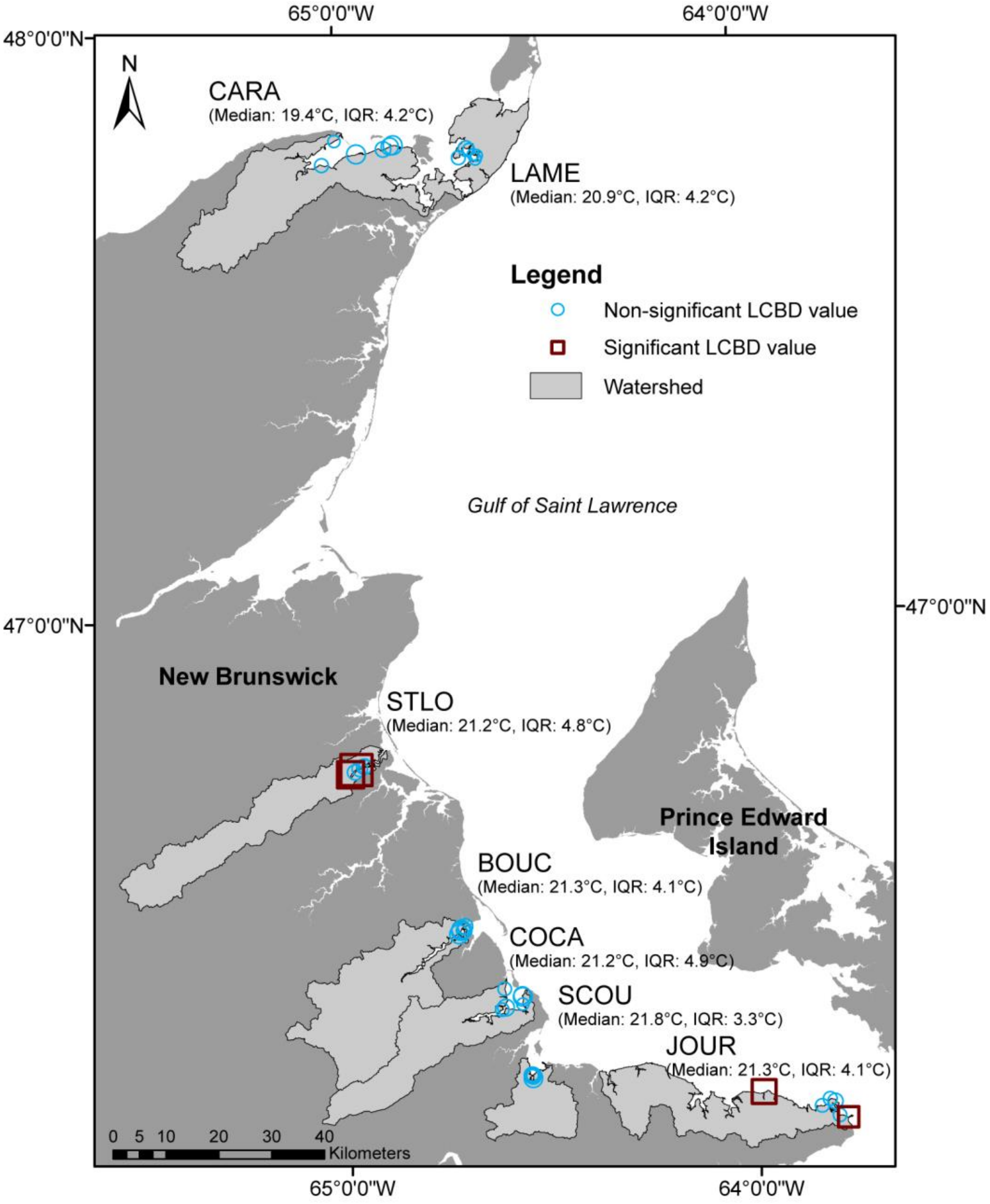

Fig. 4.3. Map of local contribution to spatial beta diversity (LCBD) represented as relative proportional symbols and significant stations across 42 sampling stations considering all years (2005 to 2012). Higher LCBD values indicate greater differences in community composition at a station compared to all sites in a region. Maximum LCBD value is 0.0418. Significant stations contributing to beta diversity were located in St. Louis-de-Kent (STLO) and Jourimain (JOUR). Median and interquartile range (IQR) of the summer water temperature within the estuaries are indicated below the name of the estuary.

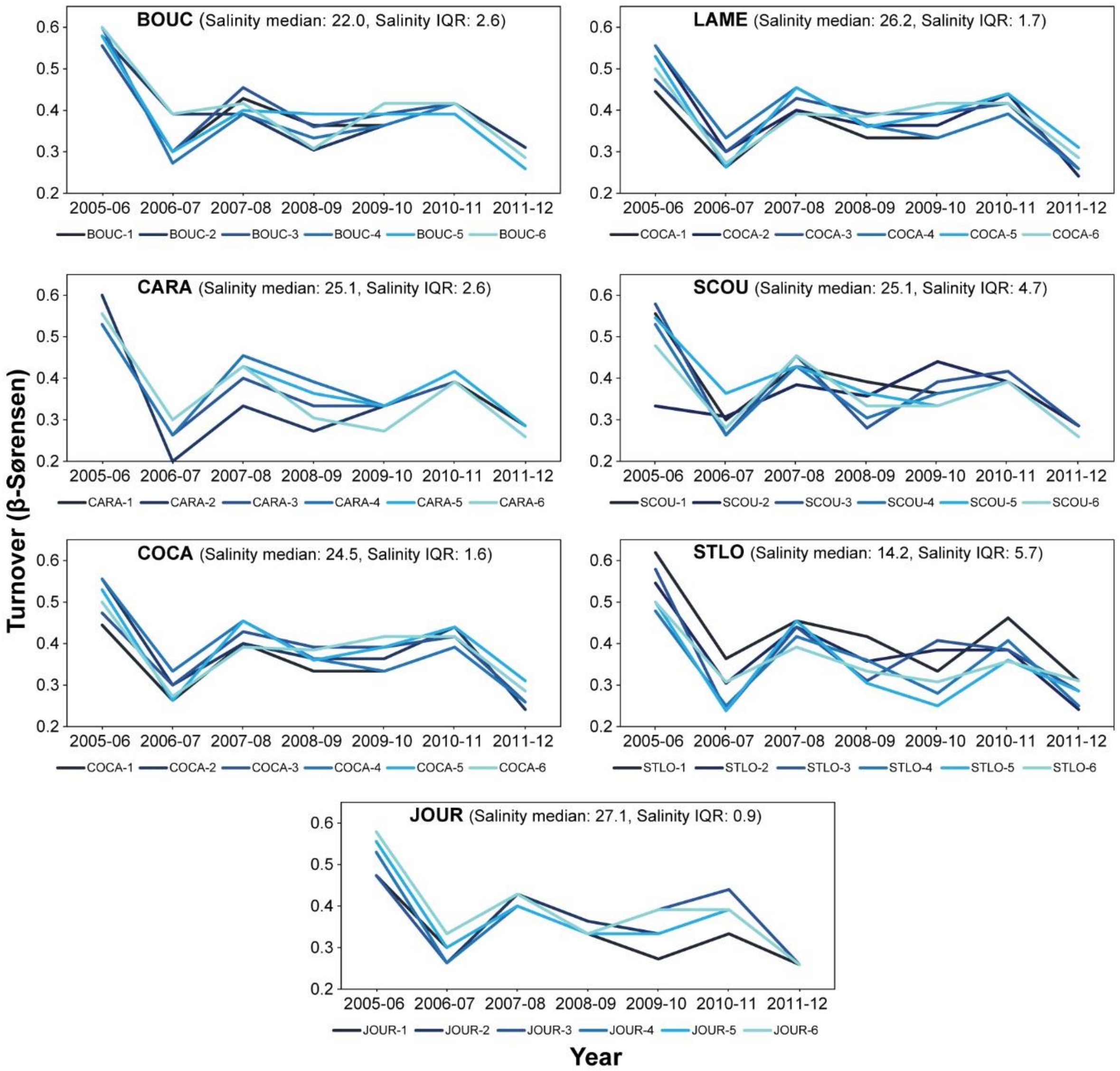

Fig. 4.4. Temporal species turnover considering all 42 stations measured as β-Sørensen of year-to-year changes in community composition from June to August of 2005 to 2012 in the six sampling stations of the seven estuaries (see Fig. 4.1 for abbreviation of estuaries). Salinity of estuaries is indicated by the median and interquartile range (IQR).

4.8 Appendix A

4.8.1 Species list

Table 4.A.1. Species detected in the Community Aquatic Monitoring Program (CAMP) in the estuaries of New Brunswick, Canada from 2005 to 2012.

Family	Common name	Scientific name
Clupeidae	Alewife	*Alosa pseudoharengus*
Anguillidae	American Eel	*Anguilla rostrata*
Ammodytidae	American Sand Lance	*Ammodytes americanus*
Atherinopsidae	Atlantic Silverside	*Menidia menidia*
Gadidae	Atlantic Tomcod	*Microgadus tomcod*
Fundulidae	Banded Killifish	*Fundulus diaphanus*
Gasterosteidae	Blackspotted Stickleback	*Gasterosteus wheatlandi*
Salmonidae	Brook Trout	*Salvelinus fontinalis*
Labridae	Cunner	*Tautogolabrus adspersus*
Cyprinidae	Cyprinidae family	
Gasterosteidae	Fourspine Stickleback	*Apeltes quadracus*
Cottidae	Grubby	*Myoxocephalus aenaeus*
Cyprinidae	Lake Chub	*Couesius plumbeus*
Fundulidae	Mummichog	*Fundulus heteroclitus*
Gasterosteidae	Ninespine Stickleback	*Pungitius pungitius*
Syngnathidae	Northern Pipefish	*Syngnathus fuscus*
Osmeridae	Rainbow Smelt	*Osmerus mordax*
Pholidae	Rock Gunnel	*Pholis gunnellus*
Cottidae	Shorthorn Sculpin	*Myoxocephalus scorpius*
Pleuronectidae	Smooth Flounder	*Pleuronectes putnami*
Moronidae	Striped Bass	*Morone saxatilis*
Gasterosteidae	Threespine Stickleback	*Gasterosteus aculeatus*
Salmonidae	Trout *sp.*	
Catostomidae	White Sucker	*Catostomus commersonii*
Scophthalmidae	Windowpane Flounder	*Scophthalmus aquosus*
Pleuronectidae	Winter Flounder	*Pseudopleuronectes americanus*

4.9 Appendix B

4.9.1 Salinity

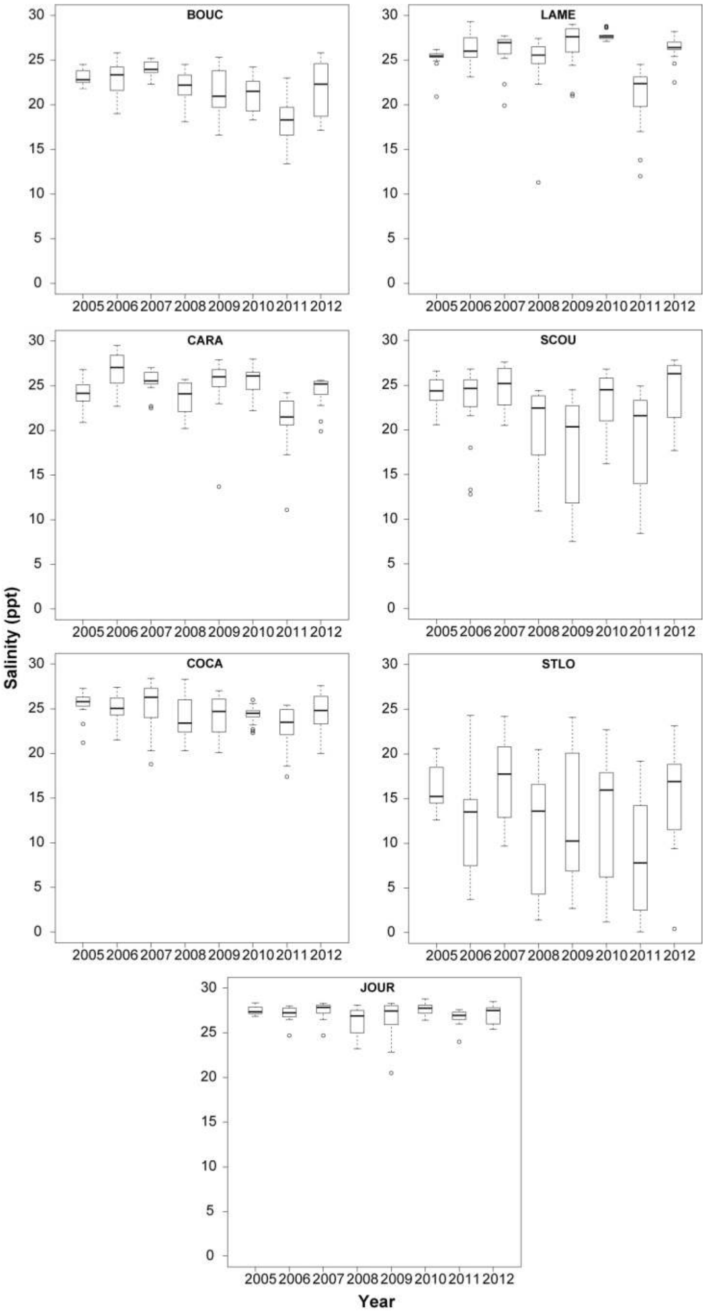

Fig. 4.B.1. Salinity at the 42 stations in the seven estuaries during each sampling event from June to August of 2005 to 2012. The box indicates the interquartile (IQR) range, the bars are the minimum and maximum, and the solid line is the median. Outliers indicated by the circles are 1.5 times the IQR.

4.10 Appendix C

4.10.1 Local contribution to spatial beta diversity each year

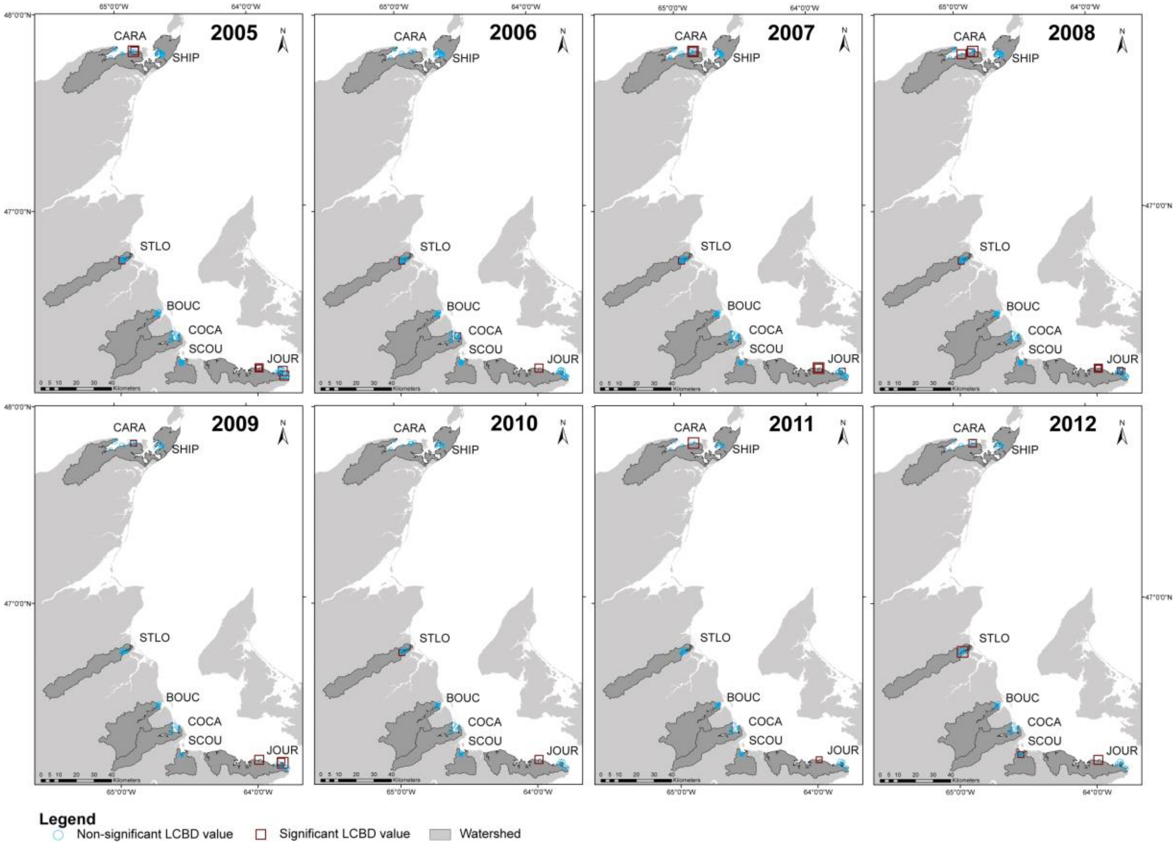

Fig. 4.C.1. Maps of local contribution to spatial beta diversity (LCBD) represented as relative proportional symbols and significant stations across 42 sampling stations considering each year (2005 to 2012). Higher LCBD values indicate greater differences in community composition at a site compared to all sites in a region in a given year. Maximum LCBD value is 0.099.

Chapter 5

5 Functional Groups of Fish Communities Shift with Environmental Change in Estuaries

5.1 Abstract

Estuaries are dynamic environments over space and time that structure fish communities adapted to this variability. Fish community responses, in terms of functional groups, could be used to determine how assemblages shift according to the effects of global climate change. However, it is uncertain how these fish communities shift locally in an estuarine environment or regionally due to comparable trends among estuaries. We compared community structure defined by taxonomy and functional groups according to average environmental variables in 17 temperate estuaries of New Brunswick (Canada) from 2004-2012. Based on redundancy analyses, the functional grouping with feeding habitat type (demersal/pelagic) explained more variation ($R^2_{\text{adj}} = 0.488$) than the taxonomic grouping ($R^2_{\text{adj}} = 0.442$) of fish assemblage according to salinity, dissolved oxygen, and macrophyte variability. Spatial scales relevant to the habitat functional groups were primarily within-estuaries. Increasing abundance of the pelagic functional group shifted with increasing salinity gradients and increasing abundance of the demersal functional group shifted with increasing temperature from 2006-2011. Our findings indicate that water salinity and temperature gradients play a significant role in structuring fish communities in small estuaries over time, and collectively occurring over a regional scale relating to the potential effects of a rapidly changing climate.

5.2 Introduction

In the face of a rapidly changing climate, environmental change is expected to affect species composition through regime shifts (Steele 1998, Chaalali et al. 2013, Holt et al. 2014). A regime shift is a sudden shift in an ecosystems and each ecosystem state is associated with an alternative stable state (Scheffer and Carpenter 2003). Such regime shifts could occur in the mid-Atlantic region of North America as predictions of increased variability of salinity as a result of intense precipitation and storm events could result in increasing freshwater flow into estuaries (Najjar et al. 2000). Intense storms may alter the geomorphology of estuaries as well as increase saltwater encroachment (Statham 2012). Furthermore, sea-level rise linked with climate change may shift estuaries towards a marine environment with saltwater encroachment producing sustained salinity (Hong and Shen 2012). Smaller estuaries may be more vulnerable to these environmental changes than large estuaries due to the greater impact on environmental gradients.

The dynamic nature of estuaries at the interface of freshwater and marine ecosystems supports and sustains biodiversity (Beck et al. 2001, Covich et al. 2004). Estuaries undergo temporal changes at various scales ranging from daily, seasonal, and annual cycles of salinity changes (Cloern and Nichols 1985, Maes et al. 2004). Species in estuaries are highly adapted to these environmental changes through morphological and physiological adaptations (Cognetti and Maltagliati 2000, Elliott and Quintino 2007, Elliott and Whitfield 2011). Fish species in estuaries have spatially dynamic distributions that vary according to their life history traits or functions. For instance, migratory fish may use estuaries as transitional waters for their migration route to their spawning areas (Paterson and Whitfield 2000, McLusky and Elliott 2004) and as important nurseries for juveniles (Paterson and Whitfield 2000).

Taxonomic response of how environmental change affects the structure of communities have been explored in traditional studies (Mouillot et al. 2013). The effects of disturbances are assumed to be unimodal at intermediate levels of disturbance (Connell 1978). An alternative approach is to use functional traits, which better describe the effects of disturbance on community structure (Mouillot et al. 2013), as there is the potential to capture changing environmental conditions that are reflected in a shift in functional groups that are more adapted to the current conditions (Potter et al. 2010, van der Linden et al. 2012). Therefore, the functional group approach, which focuses on species’ interactions with other species and the environment, allows the analysis of community composition changes and responses to environmental change by focusing on functional traits of fish such as morphology, physiology, behaviour, and life history (Mouillot et al. 2013, Gross et al. 2017). Particularly, fish functional traits have been used to examine fish community structure in other estuarine systems (Potter et al. 2015, Teichert et al. 2017, Gross et al. 2017).

Functional groups of fish have been studied to determine their sensitivity to environmental change. For example, changes to the abundance within trophic levels can help establish changes to species interactions between predators and their prey (Albouy et al. 2011). Migratory species are transient through estuaries and important environmental characteristics relating to factors such as habitat quality and connectivity critically affect their ability to spawn upstream or to mature in the ocean (e.g., Able 1998, Oliveira et al. 2012). Additionally, the feeding habitat of fish within the water column such as the pelagic or demersal zone captures the potential interactions of predator and prey within their respective habitats (e.g., Elliott et al. 2007, Franco et al. 2008). As a result, the functional group approach could capture both species responses to biotic and abiotic factors concerning the structure of fish communities (Jackson et al. 2001).

Estuarine size affects biological structuring due to the extent of environmental gradients that reflects the amount of habitat available (Nicolas et al. 2010). Catchment size also affects the amount of runoff (Vorwerk et al. 2003), thus affecting the extent of estuarine environmental gradients. The tidal influence relating to the size and bathymetry of estuaries may influence the mixing of gradients by the classification of tidal ranges with macrotidal estuaries having greater tidal influence (> 2 m) than microtidal estuaries (< 2 m; Monbet 1992, Tweedley et al. 2016). Large macrotidal estuaries are known to be structured by spatial gradients (e.g., Chesapeake Bay (Gibson and Najjar 2000), St. Lawrence (Dinauer and Mucci 2017), and the Severn (Robins et al. 2016)). However, small microtidal estuaries (e.g., Richibucto (Canadian Hydrographic Service 2017)) may have less prominent salinity gradients with increased variability due to greater mixing from both the watershed as well as the marine environment and may be structured differently for biological communities.

In this study, we hypothesize that fish functional groups in estuaries are a sensitive indicator of environmental change. We compare taxa and functional groups with their response to environmental gradients over space and time in small, temperate estuaries from 2004 to 2012 in New Brunswick, Canada. We predict that for changes in abundance of the functional groups as a sensitive indicator of environmental change would relate more to the environmental gradients than by taxonomy. Next, we determine how the functional group response that is best explained by local or regional environmental gradients responds to the changing environmental conditions from 2005 to 2011 over each year. By determining how the abundance of functional groups (feeding habitat, trophic, migratory trait) responds to current changing environmental conditions, we may develop better predictive capacity of how fish communities will change with environmental variation related due to climate change.

5.3 Methods

5.3.1 Study area

Our study area was the eastern coast of New Brunswick, Canada in the Northumberland Strait region of the southern Gulf of Saint Lawrence (latitudes 46.1° – 47.8° and longitudes -63.8° – -65.0°; Fig. 5.1). All 17 temperate estuaries had a mean tidal range of less than 2 m and therefore are classified as microtidal estuaries (Monbet 1992, Canadian Hydrographic Service 2017). The associated watersheds of these estuaries ranged from 150 to 12 530 km^2. Salinity and water temperature in the study area ranged during sampling in the months of June-August from 0.5-28.6 ppt and 16.1-26.2 °C, respectively. These estuaries consist of sand and mud substrate with eelgrass (*Zostera marina*) as the predominate macrophyte.

5.3.2 Sampling

The fish and environmental data for our study were collected by the Community Aquatic Monitoring Program (CAMP) coordinated by the Southern Gulf of St. Lawrence Coalition on Sustainability and Fisheries and Oceans Canada (Weldon et al. 2005). In each estuary, there are six fixed sampling stations (with the exception of Miramichi with four stations due to location changes over time) that survey adult fish species richness and abundance each year once a month during June to August from 2004 to 2012. Fish were sampled by beach seine (30 × 2 m; 6 mm mesh), where fish were transferred from the net into a live box and enumerated by species while submerged in water and then released back into the estuary. We selected sampling station locations within estuaries based on the natural environment and macrophyte vegetation so that stations are broadly comparable to one another. The net was hauled 15 m out from shore and then 15 m parallel to shore, encompassing an area of 225 m^2. Macrophyte vegetation at each sampling station was estimated using a quadrat (50 cm × 50 cm) with four equal sub-quadrats that was randomly thrown three times within each sampling station area. During each sampling, recordings were taken of dissolved oxygen, salinity, and water temperature (YSI Meter Model 85) at a depth of one-half to two-thirds down from the water surface and approximately 7 m from shore within the beach seine area. Water samples were collected for each sampling for nitrate, nitrite, and phosphate nutrients (for processing details, see Thériault and Courtenay (2012)). Finally, annual sediment samples were taken in August to record moisture, mean grain size, and organic matter content of the benthic substrate.

5.3.3 Fish taxa classified as functional groups

The functional groups were categorized as trophic levels (invertivore, omnivore, piscivore), feeding habitat (hereinafter "habitat") in the water column (pelagic, demersal), and migratory trait (non-diadromous, diadromous). We further explored combinations of all the functional groups to account for their different traits that are possible in species (Table 5.A.1). In total, there were seven functional groupings used in the analysis: trophic, habitat, migratory, trophic combined with habitat, trophic combined with migratory, habitat combined with migratory, and all combined. These combinations would determine which functional traits to consider to assess the abundance of such groups and their relationship with environmental change. Species traits were obtained from FishBase (Froese and Pauly 2015) based on the adult life stage.

5.3.4 Redundancy analysis

We performed multiple redundancy analyses (RDA; Legendre and Legendre 2012) with predictors using water quality, macrophyte coverage, and benthic sediments and the response using the different functional groups to assess their sensitivity to environmental gradients averaged across all months in each year from 2004 to 2012. An additional comparison to evaluate the effectiveness of functional group response was incorporated with only species and families (Fig. 5.B.1), where rare species detected in less than 5% of the sites were removed from the analyses. Fish abundances were log $(x + 1)$ transformed to reduce positive skewness. We then identified key spatial scales using Moran's Eigenvector Maps (MEMs; Dray et al. 2012) as a spatial variable in the RDA with a double-stopping criterion (Blanchet et al. 2008b) in the forward selection of significant environmental and MEM variables. MEMs are synthetic spatial variables representing spatial scales, where lower eigenvalues (i.e., MEM1) indicate broad-scale patterns spanning across the study region, moderate eigenvalues (i.e., MEM50) indicate intermediate-scale patterns spanning within estuaries, and higher eigenvalues indicate fine-scale patterns (i.e., MEM99) between stations. The total number of MEM variables was 99 (total number of sampling stations – 1) and these MEM variables were reduced through the forward selection process (Blanchet et al. 2008b) to retain broad, intermediate, and fine-spatial scales. We further performed partial redundancy analyses (pRDAs) by partitioning the variance due to the environment and space. Significance of RDAs was tested with 999 Monte Carlo permutations.

To identify the trajectories of functional group abundances across years due to the environmental condition, we analyzed the RDA trajectories between 2006 and 2011 constrained to the environmental variables over time with 16 estuaries (Bathurst Harbour was excluded as it only had one year of sampling during this period). Environmental variables and functional group abundances were summarized by averaging each estuary across the monthly sampling in stations for each year. This time period of 2006 to 2011 was selected as the environmental variables were sampled without any missing values and it includes the greatest number of sites. The RDA trajectories capture the changes of the species community composition over time (Van den Brink and Braak 1999). We chose the functional group that explained the most variance due to the environment from the partial redundancy analysis.

We performed all analyses with program R version 3.1.0 (R Core Team 2014). RDA analysis was performed using the *vegan* package (Oksanen et al. 2015) and the associated double-stopping criterion forward selection with the *packfor* (Dray et al. 2013) package. MEMs were derived from the *PCNM* package (Legendre et al. 2012).

5.4 Results

5.4.1 Average response of functional groupings with environmental conditions and spatial variables

All functional grouping models were significant ($p < 0.001$) and explained relatively more variance due to environmental change than using species ($R^2_{\text{adj}} = 0.442 – 0.488$) or family ($R^2_{\text{adj}}$

= 0.371) as a response, with the exception of the combined habitat and migratory grouping (R^2_{adj} = 0.416; Table 5.1). The variance partitioning from pRDAs indicated that environmental variables generally contribute more than spatial variables to the variation of functional groupings (Table 5.1). However, the functional grouping based on the combined trophic levels and migration had the highest amount of variance explained by space (R^2 = 0.122), whereas the habitat grouping had the highest amount of variance explained by the environment (R^2 = 0.437; Table 5.1). The habitat functional grouping, which had the most significant variation explained (R^2 = 0.488), was mainly due to salinity, widgeon grass, dissolved oxygen, eelgrass, and green algae (Fig. 2). Combining different functional groups did not yield models that explain more variation than the habitat functional grouping alone. The response of the trophic functional grouping was mainly explained by positive correlations with broad spatial scales (i.e., MEM5) of eelgrass, which indicates a gradient across the region of study stations (Fig. 5.2). Furthermore, the trophic functional group had significant spatial scales including intermediate (i.e., MEM49) and fine-spatial scales (i.e., MEM96; Fig. 5.2). For habitat functional groups, only intermediate (i.e., MEM36) and fine spatial scales (i.e., MEM96) showed significant spatial correlation with salinity and suggests the association of these groups across and within estuaries (Fig. 5.2). By contrast, the migratory functional group showed significance at broad (i.e., MEM6) and intermediate spatial scales (i.e., MEM33; Fig. 5.2).

5.4.2 Response of functional groups shifting over time

The trajectories of the habitat functional group indicated that the fish community composition in estuaries was changing along environmental gradients from 2006 to 2011, which suggests that abundances of pelagic and demersal species are responding to salinity level and temperature gradients over time based on the ends of the trajectory RDA axes (Fig. 5.3). Pelagic species were positively associated with salinity over time, as well as phosphate (Fig. 5.3). Demersal species were positively associated with macrophyte cover of eelgrass and widgeon grass as well as temperature (Fig. 5.3). Eel Ground, which is located further upstream of the Miramichi estuary, was not clustered among the other estuaries in the ordination plot but followed a similar trajectory to the other estuaries. In general, estuaries had a trajectory of returning to a community composition of fewer pelagic species due to lower salinity at certain times from 2007 to 2008 and 2010 to 2011 for specific estuaries. Overall, this trajectory model with the habitat functional group significantly explained 25.9% ($p < 0.001$) of the variance.

5.5 Discussion

The main objective of our study was to determine how fish functional groups shifted with environmental changes among temperate estuaries within a region through space and time. We found that the environmental factors structure fish communities based on their habitat in the water column mainly through water temperature and salinity levels, macrophyte coverage such as eelgrass and widgeon grass, and nutrients such as phosphate. Environmental gradients over space are restricted within each microtidal estuary. This finding also indicates that despite most estuaries being located within relatively small watersheds in our study area, there are prominent environmental gradients that define how fish communities are structured over space and time.

Due to smaller estuaries having shorter spatial environmental gradients (e.g., Strobel et al. 1994), temporal variability of the environmental gradient influenced by the watershed or the marine environment at a given station would be generally greater than a larger estuary and the structure of fish communities would be reflected by these changes over time. However, environmental variation exists within estuaries, which species are presumably tracking optimum to which they are adapted (e.g., Feyrer et al. 2015), and thus the structuring of communities is evident within these smaller estuaries. The environmental gradients exist over space and time, but are in general, similar but discrete in each estuary. For example, Strobel et al. (2000) found that small estuaries have distinct environmental conditions in the mid-Atlantic region that could be inferred for regional patterns. Consequently, species responses to environmental change in our study were represented by broad-scale patterns. Species responses behave similarly among estuaries due to these environmental changes. These relationships could be further represented by their functional group classification. Species may respond similarly to similar environmental changes in different estuaries due to specific tolerances (Feyrer et al. 2015). Fine-scale or intermediate-scale patterns would be reflected by qualities of individual estuaries that drive fish community structure.

Spatial scales due to the environmental variability remained important for structuring the fish functional groups within estuaries. Particularly, it was evident that intermediate and fine-scale patterns of environmental variation explained the abundance of habitat functional groups. Demersal and pelagic functional groups were structured within each estuary by the environmental gradients of salinity and dissolved oxygen. The influence of environmental gradient is particularly evident when contrasting the response of Eel Ground and Miramichi under the finest spatial scale structured by salinity. There is a prominent salinity gradient as Eel Ground, characterized by mainly freshwater species, is upstream of the more brackish Miramichi stations. Salinity gradients over these larger scales have been shown to structure fish communities, such as the Chesapeake Bay estuary (Wagner and Austin 1999). Similarly, specific fish species that are tolerant of lower dissolved oxygen levels have been found in gradients of low dissolved oxygen (Maes et al. 1998).

Trophic levels and migratory functional groups were also represented by broad-scale patterns of similar response to environmental changes throughout the estuaries of the study area. The similarities in functional trait response suggest a strong sensitivity to environmental gradients across a region of estuaries (Teichert et al. 2017, Fitzgerald et al. 2017). The abundances of fish within trophic levels respond to the shifts of environmental change due to conditions favouring certain trophic levels (Walther et al. 2002). For example, shifts in eelgrass coverage affect the abundance of omnivorous fish in estuaries (Adams 1976). Migratory fish are likely to be present in favourable habitat relating to temperature and salinity and thus may be sensitive to such changes due to environmental constraints (Koenigstein et al. 2016, Henriques et al. 2017b). Furthermore, salinity changes could affect the recruitment of anadromous fish species, such as striped bass (*Morone saxatilis* (Hurst and Conover 2002)).

Increasing abundances of the pelagic and demersal species were changing over time according to increasing water salinity and temperature, respectively. These shifts reflect how quickly the fish communities are capable of responding to the dynamic environment of estuaries during the year by tracking suitable habitat conditions. Therefore, the habitat functional group reflects a similar response each year to changes in salinity and water temperature over the study period. Water temperature and salinity are capable of capturing the dynamic environmental changes of estuaries, such as tidal and freshwater cycles (Thiel et al. 1995, Martino and Able 2003). The fish communities within the estuaries of the east coast of North America have also been shown to respond to salinity and water temperature over the course of 18 months (Ayvazian et al. 1992). Pelagic species such as Atlantic silverside (*Menidia menidia*) has a range of higher salinity from 24 to 32 ppt spanning from brackish to salt water (Briggs and O’Connor 1971, DFO 2009b), similar to open marine systems with higher salinity. Demersal species such as mummichog (*Fundulus heteroclitus*) are known to be temperature tolerant, which may be adaptive in to the shallow waters during low tide (Halpin 1997, Halpin and Martin 1999). Our study examined how the fish community assemblages shift according to this environmental gradient over a period of five years, in which the abundance of pelagic and demersal species changed accordingly as salinity and water temperature fluctuated over time.

Phosphate as an environmental variable that structures fish communities is likely an indirect effect through impacts on the plant community. In freshwater systems which are generally phosphate-limited, increased phosphate levels will increase primary productivity (e.g., Smith et al. 1999). In nitrate-limited environments, such as marine systems, phosphate is still capable of increasing productivity (e.g., Howarth and Marino 2006). A shift in phosphate levels may affect productivity of pelagic or benthic algae and macrophytes such as eelgrass. While eelgrass coverage may be promoted by increased phosphorous concentrations (Harlin and Thorne-Miller 1981), it may also be reduced by shading from blooms of algae which respond to the nutrient increase more quickly than eelgrass (Short et al. 1995).

Overall, within the spatial and temporal scopes of the study, our findings show that environmental variation mainly drives the fluctuations in fish communities of temperate estuaries. Salinity and temperature changes have a strong influence on the habitat functional groups of demersal and pelagic species. These influences were also observed within estuaries due to environmental gradients existing over both space and time despite these estuaries being small and microtidal. Our results may prove useful in predicting changes to the fish assemblages of small temperate estuaries in this region that will accompany climate change.

5.6 Tables

Table 5.1. Variation explained by groupings of fish communities in response to the environmental (*n* = 17) and spatial variables retained using partial redundancy analyses (pRDAs) across 100 stations in New Brunswick estuaries.

Classification	**Number of variables**			R^2_{adj}	**Variance explained**			
	Response	**Environment**	**Space**		**Environment**	**Shared**	**Space**	**Unexplained**
Taxonomic grouping								
Species	36	eelgrass, widgeon grass, green algae, temperature, salinity, organic, phosphate, nitrite	MEM5, MEM54, MEM98	0.442*	0.296	0.091	0.055	0.558
Family	18	eelgrass, widgeon grass, temperature, salinity, moisture, organic	MEM3, MEM36, MEM54, MEM81, MEM98	0.371*	0.216	0.111	0.044	0.629
Functional Grouping								
Habitat	2	eelgrass, widgeon grass, green algae, salinity, dissolved oxygen	MEM36, MEM96	0.488*	0.437	-0.050	0.101	0.512

Table 5.1 continued

Classification	Number of variables			R^2_{adj}	Variance explained			
	Response	**Environment**	**Space**		**Environment**	**Shared**	**Space**	**Unexplained**
Trophic	3	eelgrass, temperature, phosphate	MEM5, MEM49, MEM96	0.452*	0.340	0.020	0.092	0.548
Migratory	2	eelgrass, temperature, salinity, phosphate	MEM6, MEM33	0.475*	0.362	0.018	0.096	0.525
Habitat, Migratory	4	eelgrass, salinity, fucus, temperature, dissolved oxygen, phosphate	MEM5, MEM50, MEM98	0.416*	0.317	0.006	0.094	0.584
Trophic, Migratory	6	eelgrass, widgeon grass, green algae, temperature, salinity, moisture, phosphate	MEM5, MEM54, MEM96	0.454*	0.329	0.004	0.122	0.545
Habitat, Trophic, Migratory	9	eelgrass, green algae, temperature, salinity, phosphate	MEM5, MEM54, MEM96	0.447*	0.312	0.022	0.112	0.553

* $p < 0.001$

5.7 Figures

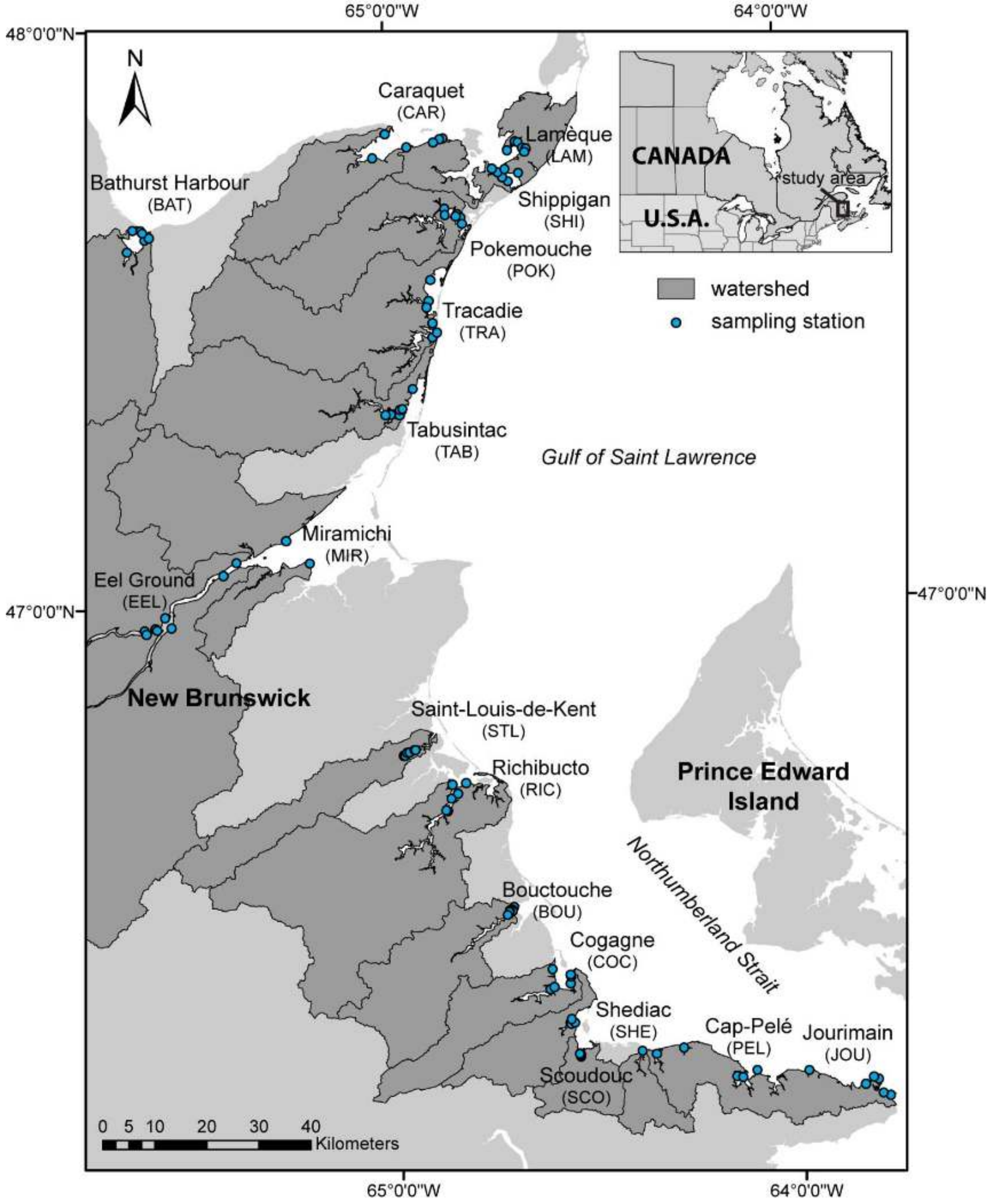

Fig. 5.1. Study area of the 17 focal estuaries and associated watersheds in New Brunswick (Canada). Each estuary consists of six sampling stations (except Miramichi with four), for a total of 100 stations from 2004 to 2012.

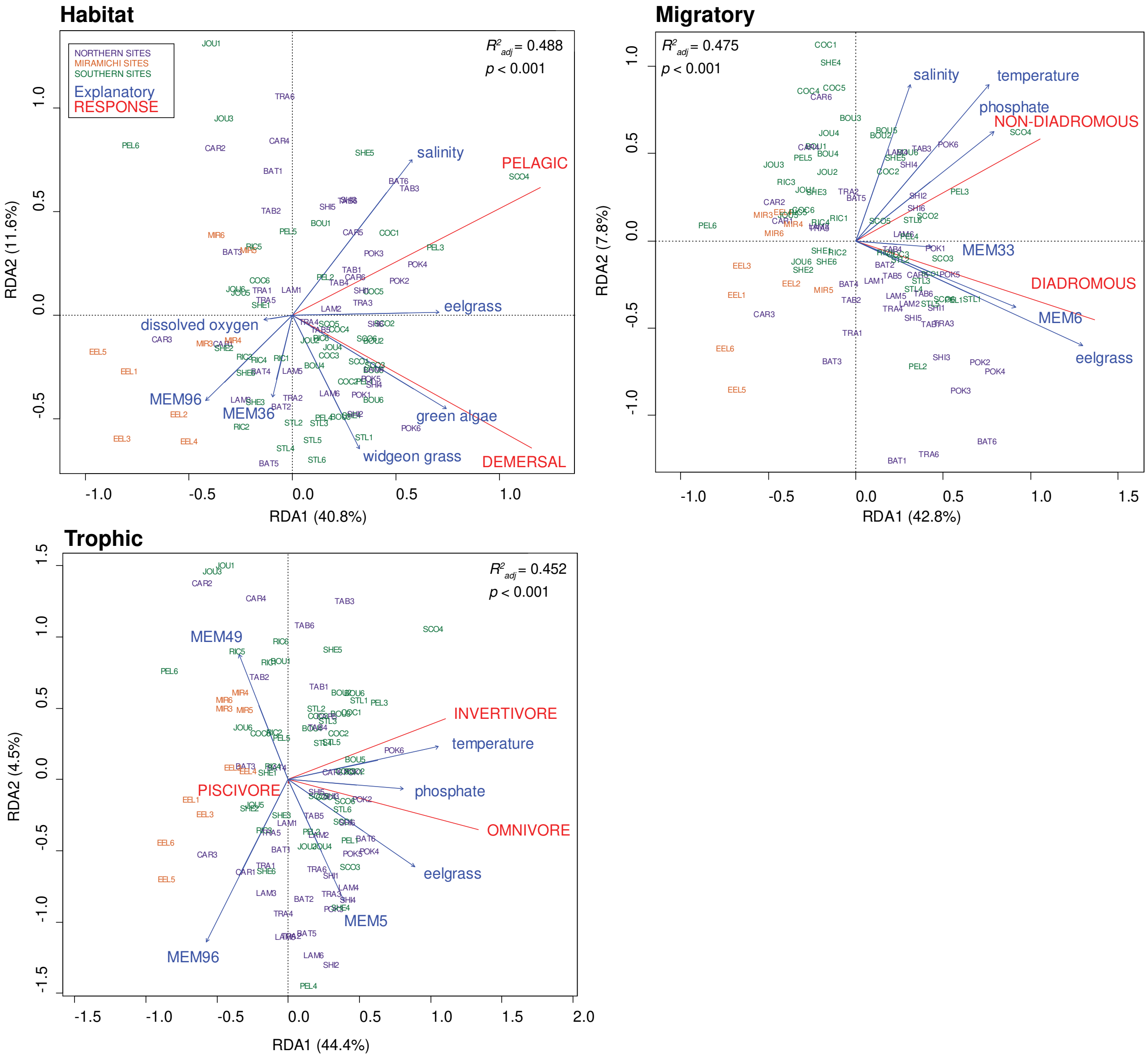

Fig. 5.2. Redundancy analyses (RDAs) of significant environmental and spatial variables with functional group abundance as response variables averaged from all years (2004-2012) in 100 stations in the Community Aquatic Monitoring Program (CAMP) in the estuaries.

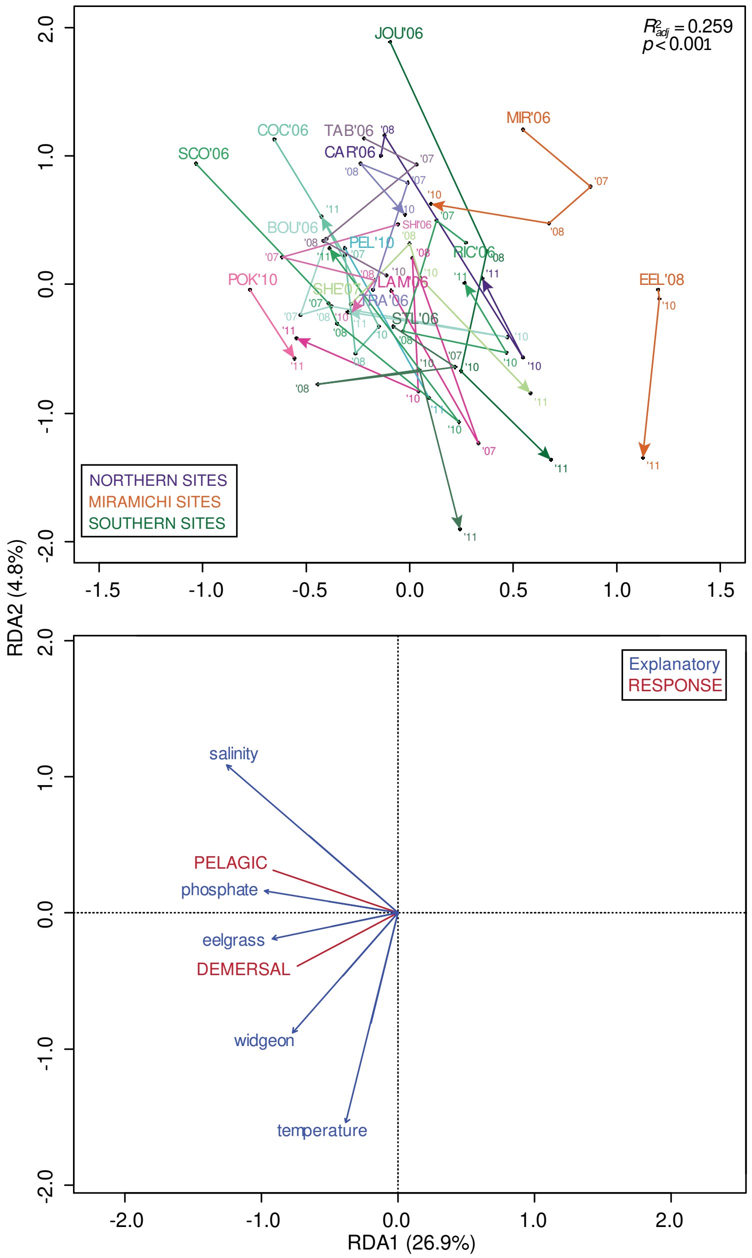

Fig. 5.3. The trajectories of 16 estuaries (see Fig. 5.1 for site codes) using a redundancy analysis (RDA) of the habitat functional groups (pelagic, demersal) as a response to environmental change annually between 2006 ('06) and 2011 ('11). The ordinations are the (A) estuary trajectories and (B) the biplot of the explanatory and response variables. Shades of purple/pink are northern estuaries, orange is the Miramichi estuary, and green/teal are southern estuaries. Significance of RDA was tested with 999 Monte Carlo permutations.

5.8 Appendix A

5.8.1 Species list

Table 5.A.1. Trophic, habitat, and migratory behaviour classification scheme of the fish taxa detected in the Community Aquatic Monitoring Program (CAMP) in the estuaries of New Brunswick, Canada from 2004 to 2012.

Family	Common name	Scientific name	Trophic level	Habitat	Migratory
Gadidae	Atlantic tomcod	*Microgadus tomcod*	Invertivore	Demersal	Diadromous
Gasterosteidae	Ninespine stickleback	*Pungitius pungitius*	Invertivore	Demersal	Diadromous
Syngnathidae	Northern pipefish	*Syngnathus fuscus*	Invertivore	Demersal	Diadromous
Anguillidae	American eel	*Anguilla rostrata*	Piscivore	Demersal	Diadromous
Salmonidae	Brook trout	*Salvelinus fontinalis*	Piscivore	Demersal	Diadromous
Moronidae	Striped bass	*Morone saxatilis*	Piscivore	Demersal	Diadromous
Clupeidae	Alewife	*Alosa pseudoharengus*	Invertivore	Pelagic	Diadromous
Clupeidae	*Alosa* spp.		Invertivore	Pelagic	Diadromous
Clupeidae	Blueback herring	*Alosa aestivalis*	Invertivore	Pelagic	Diadromous
Osmeridae	Rainbow smelt	*Osmerus mordax*	Invertivore	Pelagic	Diadromous
Gasterosteidae	Threespine stickleback	*Gasterosteus aculeatus*	Omnivore	Pelagic	Diadromous
Salmonidae	Atlantic salmon	*Salmo salar*	Piscivore	Pelagic	Diadromous
Salmonidae	Rainbow trout	*Oncorhynchus mykiss*	Piscivore	Pelagic	Diadromous
Salmonidae	Trout spp.		Piscivore	Pelagic	Diadromous
Ammodytidae	American sand lance	*Ammodytes americanus*	Invertivore	Demersal	
Fundulidae	Banded killifish	*Fundulus diaphanus*	Invertivore	Demersal	
Gasterosteidae	Blackspotted stickleback	*Gasterosteus wheatlandi*	Invertivore	Demersal	
	Flounder spp.		Invertivore	Demersal	
Gasterosteidae	Fourspine stickleback	*Apeltes quadracus*	Invertivore	Demersal	
Cottidae	Grubby	*Myoxocephalus aenaeus*	Invertivore	Demersal	
Pholidae	Rock gunnel	*Pholis gunnellus*	Invertivore	Demersal	

Table 5.A.1 continued

Family	Common name	Scientific name	Trophic level	Habitat	Migratory
Pleuronectidae	Smooth flounder	*Pleuronectes putnami*	Invertivore	Demersal	
Ictaluridae	Brown bullhead	*Ameiurus nebulosus*	Omnivore	Demersal	
Cyprinidae	Chub spp.		Omnivore	Demersal	
Labridae	Cunner	*Tautogolabrus adspersus*	Omnivore	Demersal	
Cyprinidae	Cyprinidae family		Omnivore	Demersal	
Cyprinidae	Lake chub	*Couesius plumbeus*	Omnivore	Demersal	
Fundulidae	Mummichog	*Fundulus heteroclitus*	Omnivore	Demersal	
Lotidae	Silver rockling	*Gaidropsarus argentatus*	Omnivore	Demersal	
Catostomidae	White sucker	*Catostomus commersonii*	Omnivore	Demersal	
Pleuronectidae	Winter flounder	*Pseudopleuronectes americanus*	Omnivore	Demersal	
Cottidae	Shorthorn sculpin	*Myoxocephalus scorpius*	Piscivore	Demersal	
Phycidae	White hake	*Urophycis tenuis*	Piscivore	Demersal	
Moronidae	White perch	*Morone americana*	Piscivore	Demersal	
Scophthalmidae	Windowpane flounder	*Scophthalmus aquosus*	Piscivore	Demersal	
Rajidae	Winter skate	*Leucoraja ocellata*	Piscivore	Demersal	
Atherinopsidae	Atlantic silverside	*Menidia menidia*	Invertivore	Pelagic	
Scombridae	Atlantic mackerel	*Scomber scombrus*	Piscivore	Pelagic	

Table 5.A.2. Macrophyte classification scheme for the Community Aquatic Monitoring Program (CAMP) in the estuaries of New Brunswick, Canada from 2004 to 2012.

Category	Common name	Scientific name
Eelgrass	Eelgrass	*Zostera marina*
Widgeon grass	Widgeon grass	*Ruppia maritime*
Green algae	Sea lettuce Hollow green weed Green fleece	*Ulva lactuca* *Enteromorpha intestinalis* *Codium fragile*
Brown filamentous seaweed	Brown algae	Phaeophyceae class
Brown seaweed	Tangleweed Knotted wrack	*Laminaria* spp. *Ascophyllum nodosum*
Fucus	Rockweed	*Fucus* spp.
Kelp	Kelp	*Laminaria* spp.
Green filamentous seaweed	Green algae	*Cladophora* spp.
Red filamentous seaweed	Red algae Irish moss	Rhodophyta phylum *Chondrus crispus*

5.9 Appendix B

5.9.1 Taxonomic redundancy analysis

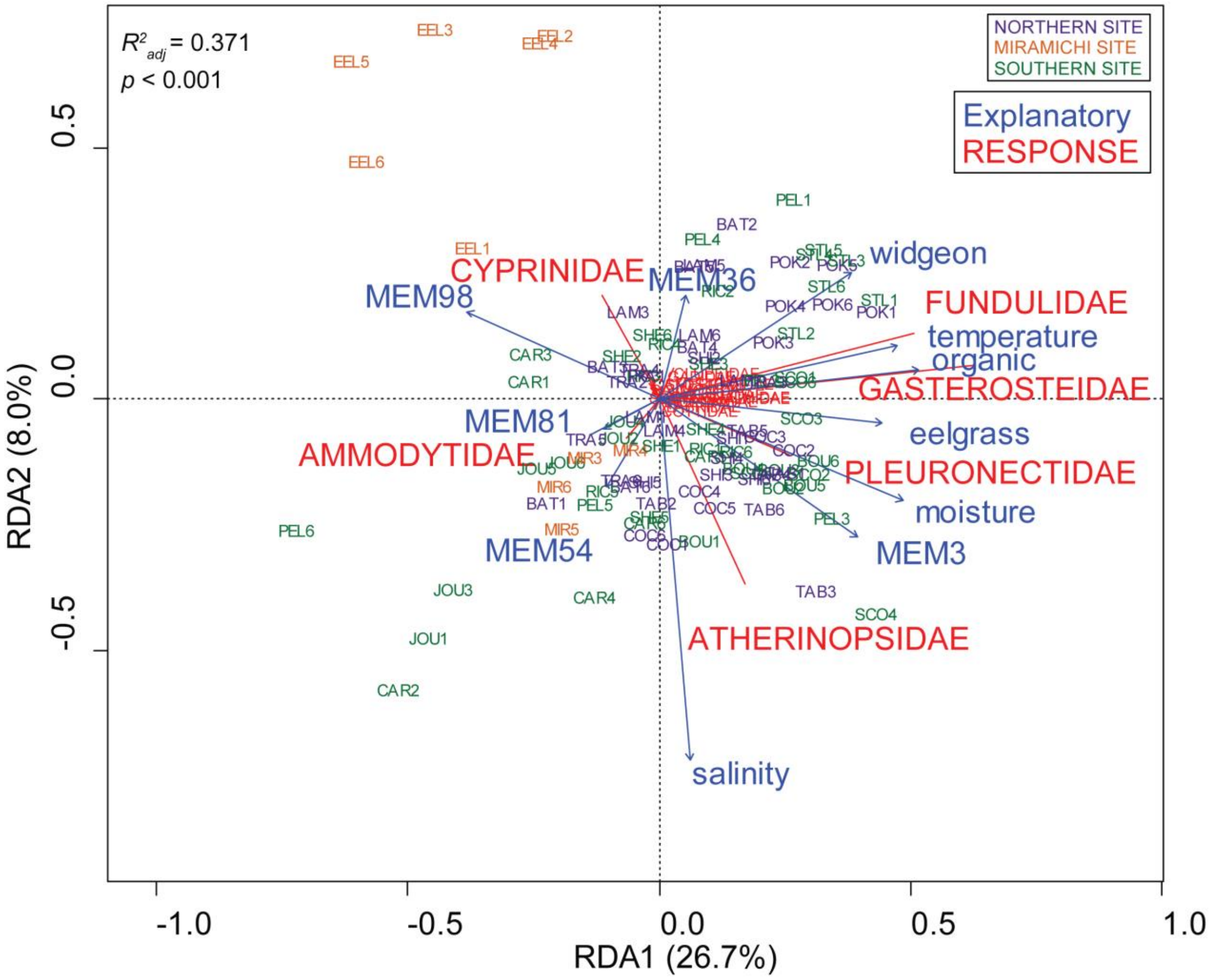

Fig. 5.B.1. Redundancy analysis (RDA) of significant environmental (eelgrass, widgeon grass, temperature, salinity, moisture, organic) and spatial (Moran's eigenvector maps (MEM)) variables with families as response variables across 100 sites in New Brunswick estuaries. Significance of the RDA was tested with 999 Monte Carlo permutations.

Chapter 6

6 Synthesis and Conclusions

6.1 Thesis summary

Environmental gradients present from freshwater to the brackish water ecosystem of estuaries aid in demonstrating that community composition changes over space and time. Anthropogenic stressors and environmental variables expected to change with a changing climate further exacerbate these baselines of environmental condition. Although my work focused on different spatial and temporal datasets ranging from stream systems to estuaries across watersheds, I addressed the broad-scale effects of the potential stressors encompassing the study region. Furthermore, time lags and temporal trends were important to indicate the effects across time within the long-term datasets.

In Chapter 2, my research focused on the potential functional connectivity of fish species affected by stream fragmentation due to culverts, which extended the application of connectivity metrics in dendritic networks due to the upstream movement of migratory species and species-specific movement accounting for ontogeny. My findings show that non-diadromous species could be negatively affected by stream fragmentation more than diadromous species. Furthermore, diadromous species also have greater variability of functional connectivity between juveniles and adult life stages as well as migration patterns. A species-based approach was necessary to consider the functional connectivity in a stream network. Findings furthered the applications of functional connectivity using a morphological trait-based analysis based on the total length of individual species. Importantly, incorporating morphometrics may inform policy changes and propose guidelines to ensure fish passage when implementing culverts in road networks to enhance productive fisheries and fish communities.

In Chapter 3, the results from this research aided in the understanding of the spatial extent that stressors have in a dynamic and rapidly changing environment within a watershed. Determining such scales was important when considering the subtle changes to species abundances caused by effects associated with forest harvesting. Catchments further downstream from headwaters experience the spatial cumulative impacts of forest harvesting, thus resulting in a lower density of juvenile Atlantic salmon (*Salmo salar*). By quantifying the magnitude of impact, metapopulation persistence due to changing environmental conditions could be predicted. In turn, these predictions could inform the prioritization of areas of conservation while considering the spatial relationship of dendritic stream networks. For example, the cumulative impact of space due to forest harvesting upstream should be considered in determining the overall impact downstream where it is the greatest. Conserving areas least susceptible to the effects of land use may become areas of refuge for species persistence, but also restoring habitat that have been greatly altered downstream.

In Chapters 4 and 5, the naturally dynamic estuarine system facilitated our understanding of the role of ecosystem shifts in estuaries from a marine or freshwater environment on changing environmental conditions. I determined how the distribution of fish communities respond to environmental change, which allows a better understanding of the effects of anthropogenic stressors that have indirect effects. First, species temporal turnover is rapid in estuaries due to environmental variability. Second, the functional groupings of fish species based on the feeding habitat respond to rapid environmental change over time. Climatic changes would undermine any management efforts to reduce anthropogenic pressures in estuarine ecosystems. Ultimately, recognizing when these ecosystem changes occur ensures the provisioning of ecosystem services that are provided by estuaries.

6.2 Contributions to estuarine research and metacommunities

My thesis furthers the understanding of threats to estuaries by broadening the scope of influential stressors in the interface of the terrestrial and aquatic environment. Although past studies investigated the effect of land use changes on freshwater or brackish-water ecosystems, they are rarely synthesized together, which is necessary to consider in ecosystems such as estuaries. By doing so, endangered species such as Atlantic salmon (*Salmo salar*) in the inner Bay of Fundy (DFO 2010) that are transient through estuaries can be used as a model example for migratory species that are impacted by culvert fragmentation in streams among other known direct stressors such as overfishing. The non-diadromous juvenile Atlantic salmon are influenced by land use and environmental conditions similarly to other fish species in the freshwater ecosystem. Furthermore, quantifying potential functional connectivity contributes to the growing field of spatial statistics and riverscape connectivity (Erős et al. 2018). Indeed, the functional connectivity of fish is vital to sustain populations, biodiversity, gene flow, and genetic diversity (Ward and Tockner 2001, Vogt et al. 2009, Storfer et al. 2010). Identifying areas where species persistence is optimized furthers the understanding of metapopulations based on quantitative changes that are adversely affected by land use which affects both dispersal and habitat quality. Ultimately, my research furthers knowledge by identifying possible locations of environmental change that relate to the conservation of aquatic ecosystem services through implementing potential guidelines in Canada based on the gained insight.

6.3 Cumulative impact and risks to estuaries

My findings show that the risks faced in estuaries exist due to the cumulative spatial and temporal extent of the stressors. In Chapter 2, the ubiquity of road crossings with culverts impacted the potential functional connectivity of many fish species while considering their ontogeny, movement and swimming strength through the stream network. These culverts were permanent structures that restrict species movement, unlike natural barriers that would appear and then degrade over time to restore functional connectivity. In Chapter 3, the upstream effects of habitat changes to juvenile Atlantic salmon (*Salmo salar*) downstream due to land use changes such as forest harvesting were mostly constant and cumulative over time. However, forest regrowth after harvesting is a slow and gradual process in temperate forests. Finally, in Chapters 4 and 5, the impact of environmental change in estuaries were region-wide in addition to the frequency of events with extreme environmental variability.

To summarize the individual risks to species persistence based on each chapter, I further synthesize the potential cumulative impact of ecological units in a nested framework of increasing complexity on species persistence by considering the chapters together (Fig. 6.1). Here, species persistence is assumed to be affected by the impacts on habitat and dispersal (Berg et al. 2010). Furthermore, given that each chapter assesses the risk to species persistence using different ecological units (i.e., from the species to community level), it could help inform biological conservation relating to specific research questions based on the ecological unit of analysis (Jax 2006). I further extend the findings of each chapter to account for possible risk to species persistence at the highest ecological unit at the metacommunity level (Fig. 6.1). By assessing the risk to species at the metacommunity level, this interpretation would include the cumulative impacts on species, dispersal, and habitat (Fig. 6.1).

In Chapter 2, the dispersal of fish species is adversely affected by stream fragmentation due to culverts when the risk to species persistence is assessed at the species level (Fig. 6.1). I further predict that the populations of species affected by stream fragmentation would result in declining populations due to the loss of functional connectivity to habitat patches and thus negatively affecting species persistence. At the metacommunity level, the loss of species with weaker swimming abilities would result in greater risk to species persistence through changing species interactions and the loss of habitat. Such habitat alteration due to land use impacts have resulted in fish community composition changes in stream due to the loss of connectivity and habitat quality (Perkin and Gido 2012, Edge et al. 2017).

In Chapter 3, forest harvesting and weather fluctuations impact juvenile Atlantic salmon density due to the greater risk to species persistence by changing habitat quality at the population level in a watershed. In addition to the findings of Chapter 2, dispersal is critical for persistence of juvenile Atlantic salmon because fry and parr are not strong dispersers (McCormick et al. 1998). Hence, the cumulative effect of both the lack of dispersal ability and loss of habitat quality result in a greater risk to species persistence at the population level for juvenile Atlantic salmon in Chapter 3 (Fig. 6.1). At the metacommunity level, even weaker swimming species (i.e., weak dispersers) would be at a greater risk to persist due to land use and environmental change through the loss of habitat.

In Chapter 4, estuarine fish communities face environmental change resulting in species turnover within and among estuaries. These changing fish communities are directly related to the changing environmental conditions as species persistence relates to the entire estuarine fish community at this ecological unit of analysis (Fig. 6.1). Given the changing environmental conditions, then in Chapter 5, a functional analysis accounts for species interactions among communities and with environmental change associated with environmental tolerances. However, environmental barriers, such as salinity and temperature beyond the tolerance of species when transitioning between estuaries, restricts species within individual estuaries (Marshall and Elliott 1998). Therefore, it is a cumulative impact by preventing species dispersal between estuaries to more suitable habitat as well as the eventual loss of habitat within estuaries due to environmental change at the metacommunity level (Fig. 6.1).

By understanding the risks to estuarine ecosystems, appropriate measures could be undertaken to either prevent or mitigate further ecosystem changes and the loss of habitat. First, prevention reduces likelihood of events that would result in harm to fish species or habitat loss (Cormier et al. 2016). Second, mitigation measures reduce the impacts to fish and fish habitat (Cormier et al. 2016). Given that climate change occurs and cannot be prevented, mitigation is required by reducing anthropogenic impacts. Anthropogenic impacts, however, can be prevented through policy and management.

In Chapter 2, my findings of reduced potential functional connectivity of fish species in stream networks indicate that the removal of specific culverts would improve overall connectivity, thus offsetting habitat loss as well as mitigating the effects of climate change to increase overall species dispersal to critical habitat. Previous work have explored how to optimize the removal of culverts by considering the budget and the amount of habitat restored by connectivity (O'Hanley and Tomberlin 2005, Neeson et al. 2015). Further consideration of the differences among species including their ontogeny and migration patterns would support this optimization process by determining the number of species that would benefit from restored connectivity. Hence, productivity of fisheries could be increased by reducing the impact of reduced connectivity (DFO 2014). The fish passage provisions of *Fisheries Act* (sections 20 and 21) and the need to recover species under the *Species at Risk Act* would benefit from a species by species approach as it would provide the basis for a more strategic approach in the development of crossing guidelines and habitat restoration initiatives.

In Chapter 3, increases in air temperature reduce the amount of suitable habitat for juvenile Atlantic salmon habitat, where habitat is further reduced by forest loss. To mitigate the effects of climate change, strategic management of forest harvesting is required across multiple catchments in a watershed. I found that the impact of spatial accumulation of the effects of land use change has implications for a dendritic network. Catchments further downstream from headwaters experience the accumulated impacts, thus posing a greater risk to juvenile Atlantic salmon populations in these catchments. However, managing within these individual downstream catchments would not be sufficient to mitigate the impacts. It would be necessary to prioritize the mitigation efforts further upstream by considering the cumulative amount of forest harvesting in upstream catchments.

Finally, in Chapters 4 and 5, estuarine fish communities are responding to changes in environmental condition. These changes in environmental condition also involve eutrophication through agricultural land use upstream of estuaries in addition to the natural variability of estuaries. Although the increasingly frequent events of extreme environmental variability cannot be prevented, eutrophication events could be reduced to mitigate further risk to ecosystem change. By determining the baseline of natural variation of fish communities in estuaries and how the response varies according to the environmental change, mitigation efforts should return the response of fish communities to the baseline.

Overall, policy objectives in Canada overlap through my chapters as they could help provide possible course of action to mitigate detrimental effects on estuarine fish communities. These efforts are directed at reversing the impact on dispersal due to culverts by enhancing upstream connectivity, and habitat change due to downstream impact of land use such as forest harvesting. The strategic mitigation measures involve managing the anthropogenic stressors as climate change will have an overarching effect in the study region. Through the gained knowledge of my thesis, we can better manage anthropogenic effects to ensure that ecosystem function is maintained in estuaries.

6.4 Future research and direction

Further research in the effects of stream fragmentation due to culverts that explicitly measures species movement would be invaluable to understand how community composition will change due the cumulative effect of culverts upstream. Using the passability rates determined in Chapter 2, habitat accessibility and availability could be verified by comparing the species composition as expected through limitations of dispersal for specific species. Furthermore, the temporal connectivity aspect is important to analyze as there are windows of opportunity throughout the year if connectivity could be maintained. To measure passability rates, radio-tagged fish would determine specific fish movement through culverts and thus provide information about timing in relation to culvert flow rates and environmental variation to determine successful fish passage (Goerig et al. 2016). Therefore, the temporal aspect of fish passage could be fine-tuned in addition with empirical data relating to species composition affected by stream fragmentation due to culverts.

Fine-scale microhabitat and spatial sampling of the environmental variability that affects juvenile Atlantic salmon abundance would complement the data from the long-term monitoring by Fisheries and Oceans Canada. Although my results were able to detect changes upstream of the sampling sites that affected salmon density, there may be changes to the environmental condition of the sites that directly affect juvenile Atlantic salmon density. The water quality samples relating to local habitat quality, such as a measurement of sedimentation size, turbidity of the water, dissolved oxygen, and water temperature (Heywood and Walling 2007) throughout the summer months would indicate the effects from forest harvesting that could otherwise affect salmon abundance.

Finally, the results from Chapters 3, 4, and 5 are derived from long-term monitoring programs which are essential to answer the complexity of trends over time. The power to detect temporal trends requires a sufficient long-term dataset that is often weighed upon the cost of such long-term monitoring programs (Caughlan 2001). Shorter time-periods may be economically cheaper for monitoring programs, but as my results indicate that time lags contained other important signals that differ from the current time period, it is recommended to have longer time periods. Therefore, the necessity of continual time lags suggests the importance of maintaining such long-term monitoring programs so that potential signals in time lags could be captured.

Overall, in addition to potential areas of research, these recommendations continue to aid in the metacommunity approach to better understand species movement and the direct and indirect impacts to their habitat. Environmental condition is dynamic over space and time, which would affect species composition changes. My thesis demonstrated the impacts to species dispersal through stream fragmentation and direct impacts to habitat through anthropogenic changes as well as the environmental changes in estuaries and their associated watersheds.

6.5 Closing remarks

In conclusion, the naturally dynamic system of estuaries provides a wide range of variability in environmental conditions to assess how species composition changes over space and time. Fish species movement through estuaries to and within upstream habitat are impacted by stream fragmentation due to culverts. Further land use changes such as forest harvesting impact the migratory Atlantic salmon (*Salmo salar*) during their juvenile life stage in watersheds. Yet, environmental condition changes impact estuaries through species community shifts of both spatial and temporal turnover. These shifts are driven by functional traits of fish species in response to the environmental change. My thesis provides a baseline of understanding of how these stressors may impact fish communities through environmental gradients and the effects of deviating away from natural norms due to anthropogenic effects and climatic change. These findings inform mitigation measures for fish communities through policy and management actions to ensure resiliency of estuarine ecosystems and their associated watersheds.

6.6 Figures

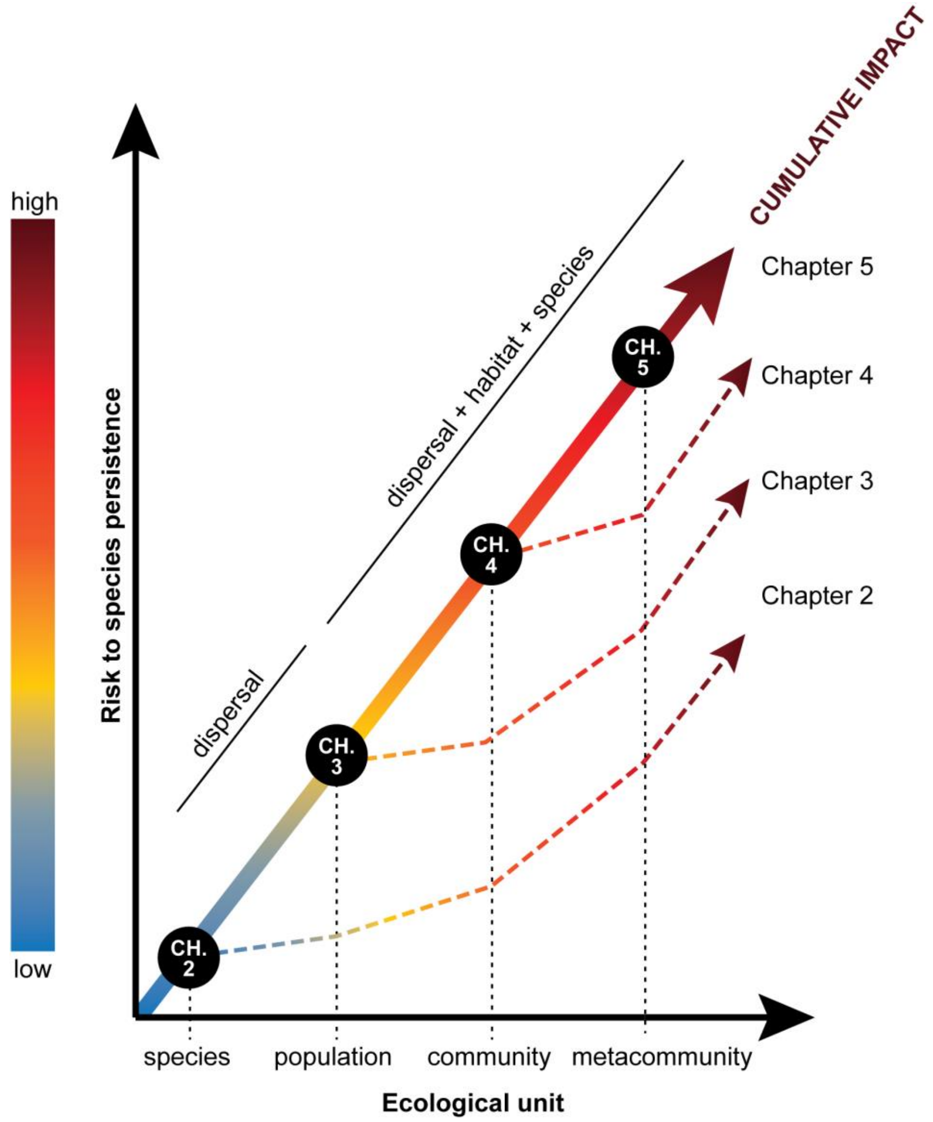

Fig. 6.1. An overview of the potential cumulative effects (thick arrow) by summarizing the results of each of the thesis chapters together at the level of the ecological unit analyzed (black circles) that lead to variable risks to species persistence. The extended interpretation relating to the risk to species persistence of individual chapters assessed at potentially higher ecological units (i.e., species to metacommunities) are indicated by the dashed lines.

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