

Fish feeding variability over space and time in natural and regulated boreal rivers

by

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### **Author's Declaration**

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners. I understand that my thesis may be made electronically available to the public.

## **Statement of Contributions**

In all cases, key ideas, primary contributions, data analysis, and interpretation were performed by the first author, and the contribution of the co-authors was through assistance with data analysis and writing advice. I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work. Additionally, I am aware of the University of Waterloo Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers in my thesis, and have obtained permission from each of the co-authors to include the above materials in my thesis.

## Abstract

Within the boreal region of Canada, river ecosystems are affected by naturally low flows in the summer months and hydropower operations, which can greatly influence the structure and function of river food webs. Few long-term studies exist that assess spatial and temporal variation in fish feeding in natural and regulated boreal rivers. Such studies would provide improved understanding of the role that temporal and spatial scale plays in the interpretation of how environmental influences such as flow affect food aquatic webs. The overall objective of this thesis was to examine factors affecting fish feeding in natural and regulated rivers, at over short and long-term and also within multiple river reaches.

In Chapter 2, fish feeding niche and stable isotope composition were compared over two reaches and ten years within the Batchawana River (a natural boreal river in northern Ontario), and in relation to flow metrics such as mean, minimum and maximum flow and temperature. Fish  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were found to be temporally invariant in upstream and downstream river reaches. Feeding niche was temporally invariant only at the lower Batchawana River reach, with a significant increase in feeding niche observed through time for the upper river reach. There was only one significant correlation between the standard deviation of  $\delta^{15}\text{N}$  and the standard deviation of mean daily flow, but no other significant correlations between fish isotope composition ( $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$ ) and select flow metrics. In Chapter 3, two rivers in south-central Newfoundland allowed for comparison of stomach contents, stable isotopes and feeding niche in normal and low flow years. During a low flow year, feeding niche decreased in the natural river and was not significantly different from that of the regulated river. The work within this thesis provides a better understanding of how fish feeding varies over space and time in natural and regulated rivers and in response to normal and low flows.

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## **General Introduction**

As open systems, rivers are intricately linked by hydrologic and geomorphic processes to the longitudinal, lateral and vertical environments (Ward 1989; Pinay 2002). Rivers are not only water, but represent the integration of local physical processes such as geography, geomorphology, climate, weather, as well as the biological communities that depend on them (Jungwirth et al. 2002). Rivers are naturally complex and support a broad diversity of aquatic species and provide a number of ecological goods and services (Cushman 1985; Sparks 1995; Karr and Chu 2000), along with having a long history of supporting the human population (Baxter 1977; Sparks 1995; Jungwirth et al. 2002). They provide an essential source of water to people in the surrounding watershed, and are used for drinking, recreation, and transportation (Sparks 1995; Jungwirth et al. 2002). Rivers are influenced by natural hydrological events, and the increasing number of human stressors such as hydropower and pollution (Ligon et al. 1995). Due to the significance of rivers for both human and ecosystem needs, it is important to make every effort to conserve them. Conserving river health and integrity depends on understanding the functional roles and linkages between riverine organisms, and the factors influencing river hydrology such as natural environmental variation and anthropogenic influences such as hydropower operations (Richter et al. 2003).

### **Life within rivers**

Life history characteristics and seasonal phenologies of riverine organisms and the structure of river communities are closely linked to environmental conditions such as temperature (Powell and Logan 2005), the timing of flood events (Sparks 1995), the inherent physical factors of the river (e.g., substrate type, current speed); (Dudley et al. 1990), and how

these vary over space and time. Natural hydrological fluctuations such as seasonal high and low flows, have a strong influence on nutrient and subsidy exchange, are responsible for shaping the river channel and for distributing sediments, influencing the availability and diversity of taxon habitats (Sparks 1995), and contributing to the structure and function of the river ecosystem (Dudley et al. 1990). Naturally variable hydrological events, such as seasonal floods and droughts, influence habitat and resource availability, biological diversity, and interactions among river organisms (Poff et al. 1997; Maddock 1999).

### *The natural flow paradigm*

Management of river systems has shifted towards a more complete understanding of the entire range of flow variability within the hydrological regime due to the importance of natural flow variability for maintaining the structure and function of river ecosystems, and the distribution and abundance of river species (Poff and Zimmerman 2010). The components of the flow regime believed to best characterize flow variability and to be responsible for maintaining the integrity of river systems are magnitude, frequency, duration, timing, and rate of change (Poff et al. 1997; Olden and Poff 2003). Magnitude refers to the quantity of water moving past a given point per unit time. Frequency of occurrence refers to the number of observations above or below a given flow magnitude over a specified time interval. Duration refers to the amount of time allocated to a particular flow event (e.g., how long a drought lasts). Timing refers to the calendar date in which a specific flow event occurs, indicating the predictability of flow events. Lastly, rate of change refers to how quickly measured flow changes from one time period to another (i.e., hourly change in magnitude); (Poff et al. 1997; Olden and Poff 2003). Accounting for natural variability within the flow regime allows for comparison of natural flow conditions to those that may be altered by human-induced changes to flow.

## **What constitutes a disturbance?**

Disturbances are rapid, prolonged, and unexpected changes in the immediate environment, exceeding the normal range of conditions to which organisms have adapted, and affecting the well-being and survival of organisms (Minshall 1988). Disturbances will affect organisms differently, depending on their size, life history characteristics, and movement capabilities (Minshall 1988; Statzner et al. 1988). While this thesis does not explicitly test for the influence of climate change on biological communities, it does touch upon the influence of temporal variations in flow on fish and invertebrates within rivers. Intra- or inter-annual variation in flow and temperature can be mediated by climatic patterns (Meyer 1999). Changes in climatic conditions are expected to alter ecosystems beyond natural ranges of environmental conditions (Kayler et al. 2015) and may interact with human mediated impacts (Gibson et al. 2005). Globally, climate change has affected the hydrological cycle through increases in temperature, changes to precipitation patterns and river discharge (Nijssen et al. 2001). At a more regional scale, climate changes can substantially alter river ecosystems through modifications to the frequency, magnitude, timing, duration and rate of change of flows, which affect the structure and function of biotic communities (Gibson et al. 2005).

To assess how biological communities respond to changing hydrological and thermal conditions, long-term studies are needed. However, few long-term, multi-species, multi-site studies have explored how food webs vary naturally and in response to altered hydrological regimes and temperature fluctuations at differing spatial and temporal scales (Daufresne and Boët 2007). Those few studies that have explored impacts over relatively long periods (>10 years) have indicated that shifts in fish and invertebrate abundance, and the timing of life cycle events were significantly correlated with temperature (Daufresne et al. 2003). For example, 1°C

increases in temperature have been correlated with declines of total invertebrate abundance by 21% (Durance and Ormerod 2007). In the St. Lawrence River, a 1.3 °C increase in water temperature was associated with a decline in discharge over the last 50 years, which modified the recruitment of both cold and warm water fish species (Hudon et al. 2010). There is a need for the completion of more long term research on fish and invertebrate community feeding niches which explicitly evaluates the direct and indirect food web effects of possible environmental stressors, such as natural and altered variation in flow.

### **General context of thesis**

The work within this thesis provides empirical testing of the relationships between components of the flow regime and fish feeding niche, in natural and regulated boreal rivers. The thesis consists of a general introduction chapter, two data chapters (Chapters 2 and 3), and a conclusion and scientific contributions chapter. At the time of thesis submission, Chapter 2 and 3 were published in *Ecohydrology*, and *River Research and Applications* (Brush et al. 2016 and Brush et al. 2014, respectively).

### **Research Objectives**

The objective of this thesis is to address the need for assessment of the perceived relationships between components of the flow regime and food web metrics in regulated and natural rivers. The environmental factors influencing fish diet, feeding niche and food chain length are examined across two reaches and ten years within a natural river in Ontario, and one reach and two years using paired dam-affected and natural rivers in Newfoundland.

## Study rivers

Cold Spring Pond, Newfoundland, is a reservoir which distributes water for hydropower production, and also is used to supply water to the West Salmon River (N48°17'244", W056°23'006"). A control structure (gate) was created between Cold Spring Pond and West Salmon River in 1981 to divert water from the West Salmon River to the hydropower facility (Scruton et al. 2008). The West Salmon River is located below the West Salmon dam at the most southern portion of Cold Spring Pond. Flow into the West Salmon is regulated seasonally and varies from 40% of the pre-project mean annual flow (MAF); (2.6 m<sup>3</sup>/s) from June 1- November 30, and 20% of the pre-project MAF (1.3 m<sup>3</sup>/s) for the remainder of the year. Within the upper reach (where the study took place), flow is kept artificially steady by the outflow from the control structure. Twillick Brook (N48°10'592", W055°57'137") is a natural, unregulated river similarly sized to the West Salmon River, with an abundance of pool and riffle habitats favourable for Atlantic salmon (*Salmo salar*), brook charr (*Salvelinus fontinalis*) and three-spined stickleback (*Gasterosteus aculeatus*) populations.

North of Sault Saint Marie, Ontario three reaches spanning over 20 km on the Batchawana River (N47.0°W84.0°) were chosen. The Batchawana River follows a natural hydrograph, with increasing flows associated with precipitation and run-off events (Marty et al. 2009; Patterson and Smokorowski 2011; Smokorowski et al. 2011). The work completed on the Batchawana River provides a better understanding of how natural levels of environmental variability can influence biological communities over space and time.

## Study taxa

Fish and invertebrates were chosen as study taxa because they are important components of the food web and are directly influenced by components of their environment (flow and temperature). Fish are easy to identify and life history information is available for most fish species (Karr 1981). Because they are relatively long-lived and mobile, fish serve as integrators of ecological processes at a range of spatial and temporal scales within rivers, providing an indication of the status of their habitats (Hynes 1970; Harris 1995). Information pertaining to fish communities as economic resources can be easily interpreted by the general public (Harris 1995). Invertebrates have been widely studied in river ecosystems, are easy to collect, and the impacts of flow modifications on community composition and diversity are known (Boon 1988; Valentin et al. 1995; Hart and Finelli 1999; Cortes et al. 2002; Jones 2010).

In Newfoundland, Atlantic salmon (*Salmo salar*) and brook charr (*Salvelinus fontinalis*), spanning available size classes, were sampled. Benthic invertebrate species collected included: Trichoptera (mainly Hydropsychidae and Philopotamidae), Plecoptera (Perlidae), Ephemeroptera (Heptageniidae), Diptera (Chironomidae and Simuliidae), Hirudinea, and freshwater mussels.

In the Batchawana River, the sampled fish community included: brook charr, rainbow trout (*Oncorhynchus mykiss*), white sucker (*Catostomus commersonii*), yellow perch (*Perca flavescens*), longnose sucker (*Catostomus catostomus*), American brook lamprey (*Lampetra appendix*), burbot (*Lota lota*), common shiner (*Luxilus cornutus*), longnose dace (*Rhinichthys cataractae*), blacknose dace (*Rhinichthys atratulus*), Northern redbelly dace (*Phoxinus eos*), creek chub (*Semotilus atromaculatus*), lake chub (*Couesius plumbeus*), slimy sculpin (*Cottus cognatus*), mottled sculpin (*Cottus bairdii*), logperch (*Percina caprodes*), trout perch (*Percopsis omiscomaycus*), brook stickleback (*Culaea inconstans*), Iowa darter (*Etheostoma exile*), and

johnny darter (*Etheostoma nigrum*). In some cases, not all fish species were captured at all sample locations. Invertebrate taxa sampled included: Ephemeroptera (Heptageniidae, Baetidae, Oligoneuriidae, Ephemerellidae), Stoneflies (Perlidae), Odonata (Gomphidae and Aeshnidae), Trichoptera (Hydropsychidae, Polycentropodidae, Philopotamidae, and Limnephilidae) and Gastropoda (*Lymnaea stagnalis* and *Promenteus exacuus*).

Following the objectives outlined above, the subsequent two chapters highlight key aspects and important findings of the thesis. Chapter 2 involves work on a natural river north of Sault Sainte Marie, Ontario, which examines long-term (10 year) data on stable isotopes of fish in relation to space, time, and selected flow and temperature metrics. Chapter 3 involves work from a natural and regulated river in Bay d'Espoir, Newfoundland where dietary and stable isotope analyses were used to investigate the influence of a low flow year on feeding ecology of resident fishes.

## **Chapter 2 Summary: Fish feeding niche characterization over space and time in a natural boreal river**

Relationships between flow, temperature and trophic metrics ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and feeding niche area) were examined using fish collected from two sites over a 10-year period from a natural, unregulated river in the boreal forest region of northern Ontario over time and space. Specifically, based on the need to characterize fish feeding at spatial and temporal scales within unaltered rivers (Poff and Zimmerman 2010) and existing literature that suggests that there are predictable relationships between flow and river community structure and function (Poff and Ward 1989), the following hypotheses were tested: (i) trophic metrics representative of feeding opportunities available to the fish community do not vary temporally; (ii) if variation in trophic metrics exists, it will be positively correlated to the variation in flow and temperature; (iii) there

will be a significant difference in fish feeding niche between low and high flow years; and (iv) consistent with the predictions of the river continuum concept (Vannote et al. 1980), the upper river reach will have smaller fish feeding niche areas and isotopic resource widths compared with the lower reach.

### **Chapter 3 Summary: The impact of low flow on riverine food webs in south-central Newfoundland**

Few studies have examined how low-flow events specifically affect the feeding ecology of fish in boreal forest rivers (Monk et al. 2008; Rolls et al. 2012). To address the knowledge gap, fish diet composition, mean and variance of fish  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , resource use and overlap were compared in a low flow and normal-flow year using data collected for fish from a pair of boreal rivers; one regulated and one unregulated. Within the regulated river, it was expected that there would be no intra-annual or inter-annual differences in resource use owing to the relative lack of flow variation, and in the natural river, it was expected that there would be high intra-annual and inter-annual differences in resource use owing to seasonal and inter-annual differences in flow. The study tested the hypotheses that: (i) there would be no inter-annual variation in resource use or overlap for fish in the regulated river, but within-river resource overlap between fish species would be higher in the low-flow year within the natural river, and (ii) resource overlap between rivers would be higher in the low-flow year.

Research explored within this thesis has provided a significant contribution to management through a better understanding of how scale and also how community diversity can affect the interpretation of fish community responses to spatial and temporal variation in temperature and flow.

## Chapter 2

### Introduction

Within natural river ecosystems, environmental factors such as temperature and flow have a clear influence on community structure and function (Poff et al. 1997; Maddock 1999; Bunn and Arthington 2002). The life history characteristics and phenologies of riverine organisms are closely linked to temperature (Powell and Logan 2005), the timing of flow events (Sparks 1995), the inherent physical factors of the river, e.g., substrate type, water velocity (Dudley et al. 1990), and how these vary over space and time. Natural hydrological fluctuations, such as seasonal high and low flows, have a strong influence on nutrient and subsidy exchange. Seasonal flows are also responsible for shaping the river channel and for distributing sediments that influence the availability and diversity of taxon habitats (Sparks 1995; Bradford and Heinonen 2008), thereby contributing to the structure of the river community (Dudley et al. 1990).

In boreal regions across the globe, changes in climate are expected to decrease precipitation and increase temperature-induced evapo-transpiration (Xenopoulos and Lodge 2006; Woo et al. 2008; Jellyman et al. 2013) and, as a result, decrease flows in lotic ecosystems (Woo et al. 2008). Such changes are predicted to directly influence the thermal and flow regimes of freshwater ecosystems (Malmqvist and Rundle 2002). While variability is a feature of all ecosystems (Holling 1973), climate change is expected to increase variability in environmental conditions such as temperature (McCarty 2001; Parmesan and Yohe 2003) and flow (Ward et al. 2015). Higher variability in flow and temperature have been associated with higher variability in invertebrate abundance and diversity (Currie et al. 2004) and lower population growth rates in salmonid fishes (Ward et al. 2015), although greater invertebrate community stability has been

documented to occur in river reaches experiencing both higher variability in flow and higher relative flood sizes (Scarsbrook 2002).

The interpretation of how environmental factors affect aquatic communities is largely dependent on spatial and temporal scale (Martinez and Lawton 1995; Jackson et al. 2001; Jackson and Füreder 2006). To date, few long-term studies of riverine fishes in aquatic communities have been completed (Woodward and Hildrew 2002), and there remains a need to collect long-term data to better understand the long-term ecological dynamics of rivers and develop flow standards (Poff and Zimmerman 2010). The studies that have been completed have typically focussed on changes in fish community structure and/or constituent population abundance (Grossman et al. 1982; Elliott and Hurley 1998; Vøllestad and Olsen 2008; Lobón-Cerviá 2012). Thus, there remains a need for more empirical studies that examine the structural factors affecting fish and their food webs at broad spatial and temporal scales (Woodward and Hildrew 2002).

Longitudinal variation in river habitat can also influence fish community composition (Troia and Gido 2013). Specifically, downstream increases in channel width and water depth, and decreases in channel gradient and bed material size can affect the distribution and abundance of fishes (Inoue and Nunokawa 2002; Tejerina-Garro et al. 2005). Thus, along the length of rivers, fish communities undergo gradual changes in composition because of abrupt or gradual physicochemical changes driving biological and habitat features (Matthews 1986). As embodied in the river continuum concept, such changes should elicit corresponding changes in river-resident biological communities as a result of changes in the patterns of nutrient loading, transport and utilization (Vannote et al. 1980).

Fish species richness generally increases along the upstream-downstream gradient within rivers because of increased habitat diversity and habitat size, e.g., wetted width (Tejerina-Garro et al. 2005). Downstream increases in habitat size, as well as tributary inputs can contribute to spatial differences in prey abundance and diversity (Vannote et al. 1980), which can broaden ecological feeding niches for fish. Where relative abundance measures of fish in the community have not been quantified, examining the ecological feeding niche is a useful way to examine community stability over space and time (Rosenfeld 2002). While the feeding niche is only one part of the total ecological niche of a species, it does provide a means of examining the response of fish communities to environmental variability over time and space. Quantifying long-term and spatial variability in fish  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and feeding niche within a natural river ecosystem will thus help evaluate whether, and how, a natural fish community responds to environmental variability.

For this study, I used fish obtained from two sites over a ten year period from a natural, unregulated river in the boreal forest region of northern Ontario to investigate relationships between flow, temperature and trophic metrics ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and feeding niche area) over time and space. Specifically, based on the need to characterize fish feeding at spatial and temporal scales within unaltered rivers (Poff and Zimmerman 2010) and existing literature which suggests that there are predictable relationships between flow and river community structure and function (Poff and Ward 1989), the following hypotheses were tested: i) trophic metrics representative of feeding opportunities available to the fish community do not vary temporally; ii) if variation in trophic metrics exists it will be positively correlated to the variation in flow and temperature, iii) there will be a significant difference in fish feeding niche between low and high flow years, and, iv) consistent with the predictions of the river continuum concept (Vannote et al. 1980), the

upper river reach will have smaller fish feeding niche areas and isotopic resource widths compared to the lower reach.

## **Methods**

### *Study reaches*

Located on the north-eastern portion of Lake Superior, Ontario, Canada, the Batchawana River is typical of the boreal region, with slightly coloured waters originating from a relatively unperturbed watershed. Samples for analysis were collected from two reaches, designated as the upper Batchawana (N 47° 10' W 84° 20') and the lower Batchawana (N 47° 01' W 84° 31'), approximately 30 river kilometers apart (Figure 2.1). The flow regime (mean annual flow: 22 m<sup>3</sup>s<sup>-1</sup>) follows a typical hydrograph for the region, with high flows at the spring freshet and in the fall (Marty et al. 2009). Substrate within the river is comprised of cobble, and small areas of gravel, and sand. Substrate grain size is larger in the upper than in the lower reaches of the river, with the upper reaches of the river having irregular patches of large boulder and bedrock. Relative channel width measurements increase from 31 m in the upper Batchawana to 36 - 44 m in the lower Batchawana. Terrestrial vegetation is typical of boreal shield species and is similar within both reaches, with dense canopy cover of speckled alder (*Alnus incana*), yellow birch (*Betula alleghaniensis*) and white spruce (*Picea glauca*).

### *Study species and sample collection*

Fish species collected and their main prey items are represented in Table 2.1. Species sampled represented a similar variety of feeding habitats (benthic, water column and generalist) as classified by the standard handbook of *Freshwater Fishes of Canada* (Scott and Crossman

1973). Collectively the sampled fish species consume various stages of aquatic invertebrates, including the larvae of midges, mayflies, dragonflies, and caddisflies (Scott and Crossman 1973). All sampled fish ranged in size from 14 to 137 mm, and approximately equal numbers of male and female fishes were sampled. As fish home range size increases allometrically with body size (Minns 1995), use of smaller bodied fish ensured samples were representative of local conditions.

Permission for fish sampling was obtained from the Great Lakes Laboratory for Fisheries and Aquatic Science/Water Science and Technology Directorate Animal Care Committee, Burlington, Ontario, Canada. Collections were made using standardized protocols employing backpack (Smith-Root Model LR-24) electrofishing methods (Bohlin et al. 1989; Meador et al. 2003; Reynolds et al. 2003) in each July of 2003-2012. Fish were sampled in locations of the river reach with depths less than 60 cm. Within a river reach of approximately 500 m<sup>2</sup>, electrofishing took place until an adequate sample had been randomly obtained (approximately 3-5 of each individual fish taxa). Consistency of the sampling crew ensured minimal year to year variation in protocol use.

#### *Stable isotope analysis*

Stable isotope values were measured for all fish and invertebrate species following methods described in Marty et al. (2009). Stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope analyses can be used to evaluate consumer dietary ecology, both at the individual and community level (Post 2002; Bearhop et al. 2004), as they integrate prey resource use over time (Bearhop et al. 2004). For fish, dorsal muscle tissue was removed from above the lateral line and posterior to the dorsal fin. Skin and bone were removed and the sample was dried in a standard

laboratory convection oven (Yamato Scientific, Model DX 600, California, USA) at 50°C for 48 hours and then ground to a powder using a mortar and pestle.

Approximately 300 µg of ground tissue was combusted for stable isotope analyses using a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108, Carlo Erba, Milan, Italy). All analyses were completed at the Environmental Isotope Laboratory, University of Waterloo (Waterloo, Ontario, Canada), with results expressed in standard  $\delta$  notation. Working internal laboratory standards were calibrated against the International Atomic Energy Agency standards CH6 for carbon and N1 and N2 for nitrogen and run as controls throughout the analysis to ensure the continued accuracy of all measurements. Analytical precision was assessed by mean differences of one in ten duplicate samples, where the mean  $\pm$  standard deviation was  $0.13 \pm 0.2$  ‰ for  $\delta^{13}\text{C}$  and  $0.17 \pm 0.2$  ‰ for  $\delta^{15}\text{N}$ .

### *Data Analysis*

Calculated flow metrics considered in the study included: minimum, maximum, mean summer flow, standard deviation of summer flow, flow variability expressed as a rate of change (Marty et al. 2009; Armanini et al. 2014), and frequency of extreme flow events. Daily summer flow metrics were calculated using available daily flow data obtained for station 02BF001 from the Water Survey of Canada website (<http://www.wsc.ec.gc.ca>). Minimum, maximum, mean and standard deviation of daily summer flow data were calculated between June 1<sup>st</sup> and August 31<sup>st</sup> within each year. Hourly flow variability ( $\text{m}^3\text{s}^{-1}\text{h}^{-1}$ ) was calculated as rate of change using the absolute difference in flow between hours (Marty et al. 2009). The mean of all the absolute differences gives the flow variability measurement for the period of interest. To calculate the

relative frequency of extreme flow events, each hourly discharge measurement ( $\text{m}^3\text{s}^{-1}$ ) was given a z-score. Extreme flow events were identified by individual hours with z-scores indicating that they deviated from mean daily summer discharge by more than  $\pm 2$  SDs. The relative frequency of extreme flow was then determined by dividing the number of observations that exceeded  $\pm 2$  SDs by the total number of observations within the period of interest. Daily water temperature data were obtained from the Ontario Ministry of Natural Resources (R. Metcalfe, personal communication). Daily water temperature data were available for all years, except 2012 where complete data were not available for the period of interest owing to equipment failure.

All stable isotope data were tested for normality using the Shapiro-Wilks W test (Zar 2010). Equality of variances between years in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data was tested using Levine's homogeneity of variance test to ensure similarity of variance in data (Zar 2010) used to subsequently calculate analytical measures. Statistical analyses were performed using Systat version 11 (Statsoft Inc. 2004) with significance set at  $\alpha = 0.05$ . The SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011) method was used in the SIAR package (version 4.1.3) to evaluate isotopic niche widths (measured as a standard ellipse area, SEA, in  $\delta^{13}\text{C}$ -  $\delta^{15}\text{N}$  space) for the fish. As a result of functional overlap between predators and prey in food webs, species in community food webs are commonly aggregated for analytical purposes (Solow and Beet 1998; Abrantes et al. 2014) as a means of reducing methodological biases that may arise in the data (Williams and Martinez 2000). Lumping fish species to calculate community metrics had little impact in overall ANOVAs because species variation represented a small portion of overall variance in our dataset (1.3 and 10.7 % for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively). The Bayesian methods used in SIAR take account of uncertainty in sampled data and incorporate sampling error, thus allowing for statistical comparisons (Jackson et al. 2011). The methods are also

ideally suited to making comparisons between different communities (Jackson et al. 2011). The estimated SEA measure is unbiased with respect to sample size (Jackson et al. 2011), but encompass only 40 % of the available data points, approximately one standard deviation in the data (Batschelet 1981). Accordingly, the SEA measures were expanded here to include two standard deviations which encompass 95 % of the data and better represent data variability (Chew 1966; Jackson et al. 2011). All SEA ellipse estimates were further adjusted for small sample sizes ( $\leq 30$ ) to obtain SEAc, which corrects for possible under-estimation of the ellipse area as a result of small sample sizes (Jackson et al. 2011; Brush et al. 2014).

Because of the implications of non-stationarity in the data implied by possible autocorrelation, data series were examined for stationarity using standard statistical techniques as described in Abraham and Ledolter (1983) prior to further statistical analyses. Specifically, the autocorrelation and partial autocorrelation functions were estimated and the significance of peaks at lags 1 through 5 was assessed using the Ljung-Box Q statistic and necessary corrective action as prescribed by Abraham and Ledolter (1983) was applied. As a final precaution, linear regression residuals were also examined for evidence of residual autocorrelation using standard statistical procedures as outlined in Abraham and Ledolter (1983).

The temporal invariability hypothesis (i) was tested by regressing the trophic metrics (SEAc, mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) against time using least-squares linear regression on both the upstream and downstream data sets (Zar 2010). Linear regression was similarly used to test hypothesis (ii) concerning the significance of relationships between variation in trophic metrics and variations in flow (SD mean daily flow, flow variability, and frequency of extreme flows) and temperature (SD mean daily temperature) metrics using the upstream and downstream data sets individually.

Flow years were categorized as either a high or low flow year, on the basis of maximum, minimum and mean daily summer flow, using K-means analysis (Zar 2010). Low flow years had mean daily summer discharges that were below  $4.5 \text{ m}^3 \text{ s}^{-1}$ , except for 2010 where limited flow data were available. Supplementary data obtained from the Water Survey of Canada gauge on the nearby Magpie River (02BD007) were used to characterize 2010 as a low flow year. A two-way ANOVA was used to test hypotheses (iii) and (iv) using trophic metrics (e.g., mean and variance of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , and SEAc) as the dependent factors and flow year type (high versus low) and river reach (upper versus lower) as the independent factors.

## Results

Mean  $\pm$  standard deviation (SD) summer discharge varied between  $3.7 \pm 1.9 \text{ m}^3 \text{ s}^{-1}$  and  $14.7 \pm 6.3 \text{ m}^3 \text{ s}^{-1}$  (Table 2.2), with maximum summer discharge being on average slightly more variable (coefficient of variation, CofV = 75.5%) than minimum summer discharge (CofV = 72.8 %). Hourly flow rate of change ranged between  $0.02 \text{ m}^3 \text{ s}^{-1} \text{ h}^{-1}$  and  $0.20 \text{ m}^3 \text{ s}^{-1} \text{ h}^{-1}$ . The frequency of extreme flows across all years ranged between 2.50 % (year 2009) to 8.50 % (year 2010). Mean  $\pm$  SD daily summer temperature varied between  $19.62 \pm 2.49 \text{ }^\circ\text{C}$  and  $22.83 \pm 2.32 \text{ }^\circ\text{C}$ , and was consistently less variable between years (CofV = 5.20 %) than mean daily summer discharge (CofV = 85.82 %). Mean  $\pm$  SD  $\delta^{13}\text{C}$  of the fish sampled from both sites ranged from  $-27.93 \pm 1.25 \text{ }^\circ\text{‰}$  to  $-24.93 \pm 1.36 \text{ }^\circ\text{‰}$ , and the mean  $\pm$  SD  $\delta^{15}\text{N}$  ranged from  $6.63 \pm 0.48 \text{ }^\circ\text{‰}$  to  $8.30 \pm 0.74 \text{ }^\circ\text{‰}$  (Table 2.3).

There was no pervasive evidence of non-stationarity in the annual data series with 12 of the 15 tested series, including those for flow, temperature and isotope measures, considered stationary (Ljung-Box Q statistic  $P < 0.5$ ). The remaining 3 series were stationary at the 0.4 level

of significance and showed no evidence of significant period to period correlations when assessed using partial autocorrelation techniques (all lag  $P < 0.05$ ). Given the lack of convincing evidence for autocorrelative structure in the data series and the implications of data loss associated with correction procedures (Abraham and Ledolter 1983), no autocorrelative corrective procedures were used.

The standard ellipse areas (SEAc) ranged between 4.12 and 17.60 (Table 2.3). There was a significant increase in SEAc through time for the upper Batchawana (regression slope = 0.62,  $R^2 = 0.62$ ,  $p < 0.01$ ; Figure 2.2). Consistent with the temporal invariance hypothesis (i), there was no significant trend ( $p = 0.28$ ) in SEAc through time for the lower Batchawana (Figure 2.2). Furthermore, there was no significant trend in mean  $\delta^{13}\text{C}$  in either the upper ( $p = 0.20$ ) or the lower ( $p = 0.07$ ) river reaches (Figure 2.3). There was also no significant temporal trend in mean  $\delta^{15}\text{N}$  in the upper ( $p = 0.15$ ) or the lower ( $p = 0.28$ ) river reaches. All tested linear regression residuals showed no evidence of autocorrelative structure.

Congruent with hypothesis (ii), where temporal variation in trophic metrics existed, there was a corresponding significant positive relationship (Figure 2.4) between variation (SD) in  $\delta^{15}\text{N}$  and variation (SD) in mean daily flow ( $R^2 = 0.49$ ,  $p = 0.03$ ) in the upper Batchawana, but not the lower Batchawana ( $R^2 = 0.14$ ,  $p = 0.28$ ). There were no other significant correlations between variation in flow and temperature and variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (all  $p > 0.05$ ). All tested linear regression residuals showed no evidence of autocorrelative structure.

The flow effect hypothesis (iii) was not substantiated by the data, with two-way ANOVA analysis indicating that fish SEAc did not differ significantly ( $p > 0.05$ ) by flow year type (Table 2.4; Figure 2.5; Figure 2.6). Data, substantiated the continuum hypothesis (iv), with two-way ANOVA indicating a significant difference in SEAc between the reaches ( $p < 0.01$ ), with mean

SEAc in the lower reach exceeding that in the upper reach (13.05 vs 7.86 ‰)(Figure 2.5).

Significant differences were observed in the variance of  $\delta^{13}\text{C}$  between river reaches ( $p < 0.01$ )

but not in the variance of  $\delta^{15}\text{N}$  ( $p > 0.05$ ).

## **Discussion**

The influence of temperature and flow on fish community trophic metrics was investigated over time and space, using a long-term dataset from a riverine ecosystem with a natural flow regime. As hypothesized, trophic metrics as represented by  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were found to be temporally invariant at both the upstream and downstream river reaches. Isotopic niche, as characterized by SEAc, was temporally invariant only at the lower Batchawana River sampling reach, with a significant increase in SEAc observed through time for the upper river reach. Where variation in the trophic metrics was observed, it was positively correlated with variation in the physical environment, as hypothesized. While SEAc did not differ between flow year types as expected, consistent with the river continuum concept (Vannote et al. 1980), fish from the lower Batchawana River had significantly higher SEAc values than fish from the upper Batchawana River.

Despite variable temperature and flow, studied trophic metrics calculated using fish community data did not vary temporally with the exception of SEAc in the upper river reach. SEAc was temporally invariant in the lower Batchawana River, yet increased through time in the upper Batchawana. Fish can be generalist feeders and so will adapt to any changes in the abundance or diversity of their prey resources brought about by inter-annual variation in flow, temperature or other environmental parameters. Dietary generalism has been shown to enhance food web stability (Polis 1991) and has been suggested to confer stability on food webs (Layer et

al. 2010), with the result that feeding niches are not likely to vary much through time as has been noted here. As a result, fish assemblages are thought to be more persistent in river reaches with little flow variability compared with those subject to high flow variability (Grossman et al. 1982) and as demonstrated by Jellyman et al. (2013), fish biomass and community structure similarly display less temporal variability within stable river reaches than at disturbed sites. In addition, fish community biomass has been shown to be temporally stable relative to individual species (Smokorowski and Kelso 2002), with such stability having implications for within-community feeding. Temporal variability in the fish community metrics may be linked to the successional processes that occur following natural seasonal disturbances that require the re-establishment of a suitable resources base (e.g., invertebrates) as pre-requisite to re-occupancy of the habitat by fish (Taylor and Warren 2001) and in that way are linked to food web stability.

Fish can be redundant in their ecological roles such that if one fish species is negatively affected by low flow (for example), through competitive release another similar fish species will be able to exploit “newly” available resources (Bolnick et al. 2010). Indeed within the assemblage of fishes considered here, there were multiple representatives of each trophic feeding guild, although benthic insectivores dominated as a group. The ability of species to varyingly exploit resources as physical conditions change is consistent with the niche compression/expansion hypothesis (MacArthur and Wilson 1967) that predicts an expansion of the habitat used by a species due to decreased competitive pressure without a major change in the feeding niche (Tracy and Christian 1986).

In addition, consuming a varying diversity or abundance of prey resources may not necessarily result in major temporal changes in tissue  $\delta^{13}\text{C}$ /  $\delta^{15}\text{N}$  of fish, because of possible similarity in isotopic composition among prey items. Mobility, short life cycles, high

reproductive rates, and the ability to encyst or to burrow into the substrate allows invertebrates to avoid or adjust to regular variations in the stream environment (Minshall et al. 1983), with the result that the available prey resource base may not vary substantially over time at any given site. Coupling between littoral and main channel habitats may further allow fish to buffer the effect of environmental variation and maintain constancy in prey selection given studies that suggest sufficient energy and taxonomic diversity at all trophic levels is present in the main channel to support functional food webs (Dettmers et al. 2001). The lack of temporal changes in fish isotope measures, therefore, may reflect the generalist feeding behaviour of fishes able to spatially average assimilated prey items.

The upper reach of the Batchawana experienced a temporal increase in fish feeding niche, with an associated increase in the variability of fish  $\delta^{15}\text{N}$  driven by mean daily flow and there was a corresponding significant temporal increase in SD  $\delta^{15}\text{N}$  (Table 2.3). As a result of the significant relationship between SD  $\delta^{15}\text{N}$  and SD mean daily flow, a temporal increase in  $\delta^{15}\text{N}$  variability results in higher SEAc via expansion of the  $\delta^{15}\text{N}$  axis. As flow variability increases, mechanical effects such as shear stress and drag forces can affect the composition and abundance of invertebrate communities, which in turn can influence predator feeding behaviour (Hart and Finelli 1999). Feeding broadly on multiple prey items (with distinct  $\delta^{15}\text{N}$  signatures) as flow variability increases (Bunn and Arthington 2002; Balcombe et al. 2005), will contribute to  $\delta^{15}\text{N}$  variability and feeding niche over time as observed here. In contrast, temporal constancy of feeding niche, fish  $\delta^{15}\text{N}$  and mean daily flow variability in the lower reach relative to the more variable upper reach emphasizes the ability of a tributary to moderate and stabilize flows (Horwitz 1978). When flows are less variable, invertebrate and fish communities tend to become more specialized (Poff and Allan 1995). Here, the consistency of feeding niche within the lower

reach may be related to influence of the Turkey Lakes watershed discharge entering above the lower reach sampling site (Beall et al. 2001).

While there was no difference in mean  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  between the reaches,  $\delta^{13}\text{C}$  was more variable in the lower reach. Higher variability in mean  $\delta^{13}\text{C}$  and larger fish feeding niche observed downstream is consistent with the river continuum concept given that the mix of energy sources (allochthonous versus autochthonous) and the downstream transport of organic material from upstream leads to probable increases in available feeding niches for downstream fish species (e.g., Vannote et al. 1980), which would result in overall broader community niches (Flaherty and Ben-David 2010). Larger ellipses in the lower Batchawana reach compared to the upper may also be explained by spatial differences in fish and invertebrate abundance and community diversity. As Goldstein and Meador (2004) have noted, fish community function is structured by longitudinal differences in habitat along the river, with the differences being evident in variations in trophic ecology. As a consequence, higher abundance and diversity of food resources should lead to feeding niche expansion as observed here. Furthermore, feeding on heterogeneous food sources should also increase variability in fish stable isotope composition and the SEAc, provided that fish are not selectively feeding on one or a few food sources.

## **Conclusion**

The study is one of few that have used long-term datasets to examine relationships between flow, temperature and trophic metrics over space and time within a natural river ecosystem. There was an increase in fish community feeding niche over time within the upper reach of the Batchawana River, however, despite natural temperature and flow variability, fish community feeding niche was temporally invariant in the lower Batchawana River. In addition, a

significant relationship was observed between variation (SD) in  $\delta^{15}\text{N}$  and variation (SD) in mean daily flow in the upper reach. Fish SEAc was larger in the lower reach compared to the upper Batchawana. Because of spatial differences in fish responses observed in this study, other studies focussing on the influence of abiotic factors (temperature and flow) on fish community structure, therefore, need to account for how different spatial and temporal scales might affect the interpretation of data. When logistically feasible, long-term studies can provide important observations on the range of natural variation within river ecosystems, and such studies can serve as important baselines against which one can compare potential future environmental changes.

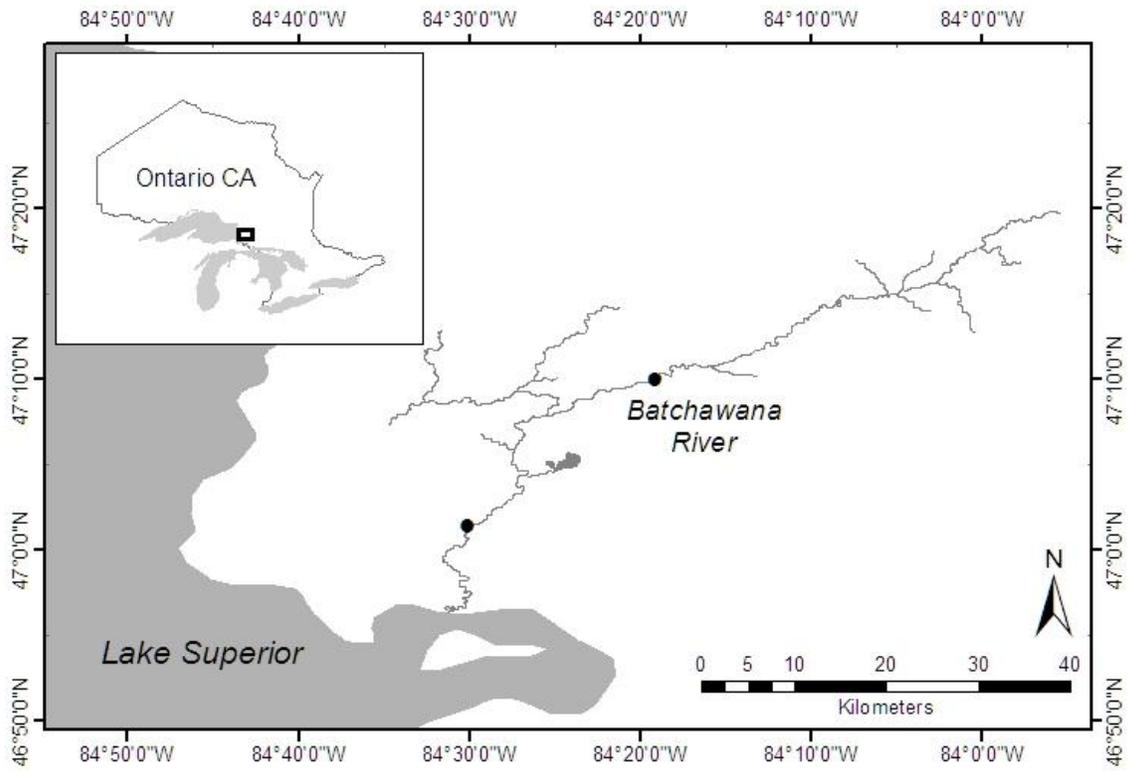


Figure 2.1. Location of sample reaches on the Batchawana River.

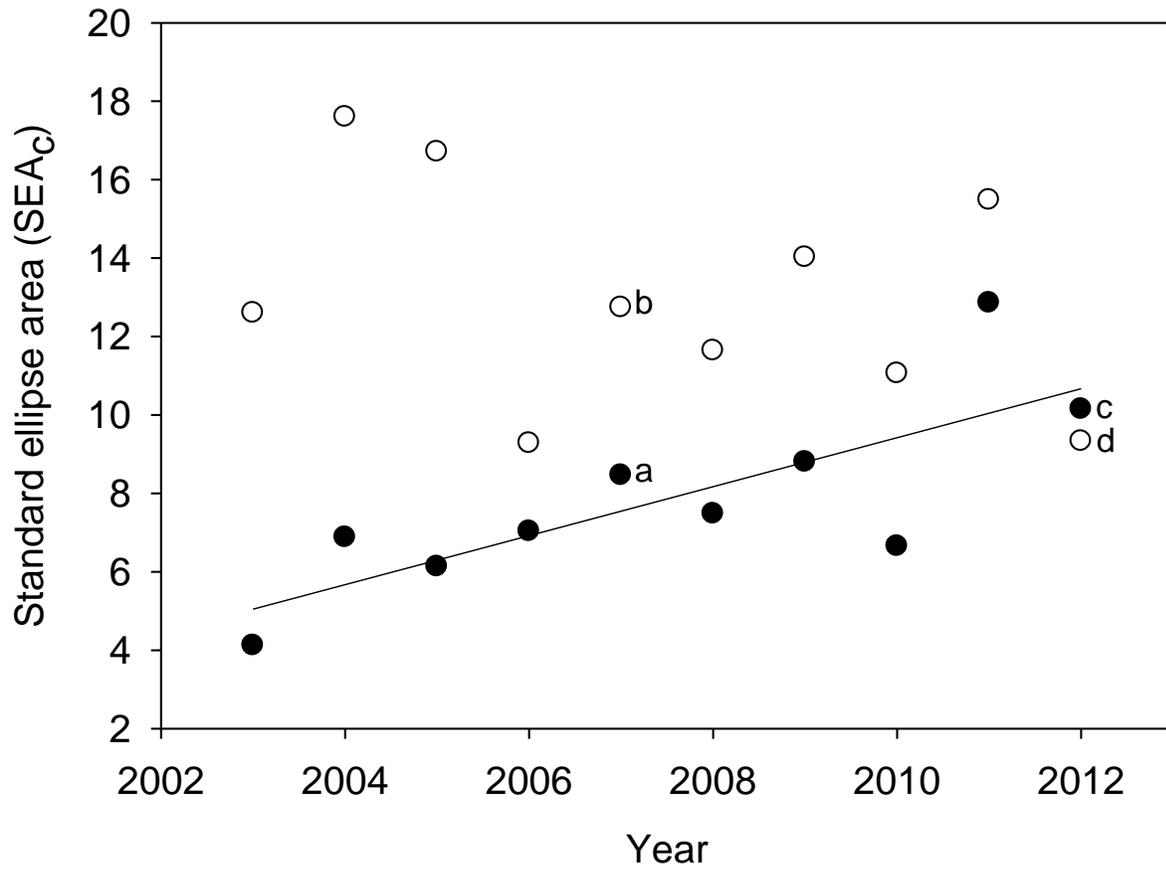


Figure 2.2. Standard ellipse areas calculated for all fish species in a given year for the upper and lower Batchawana River. The upper and lower Batchawana River are plotted as solid and open symbols, respectively.

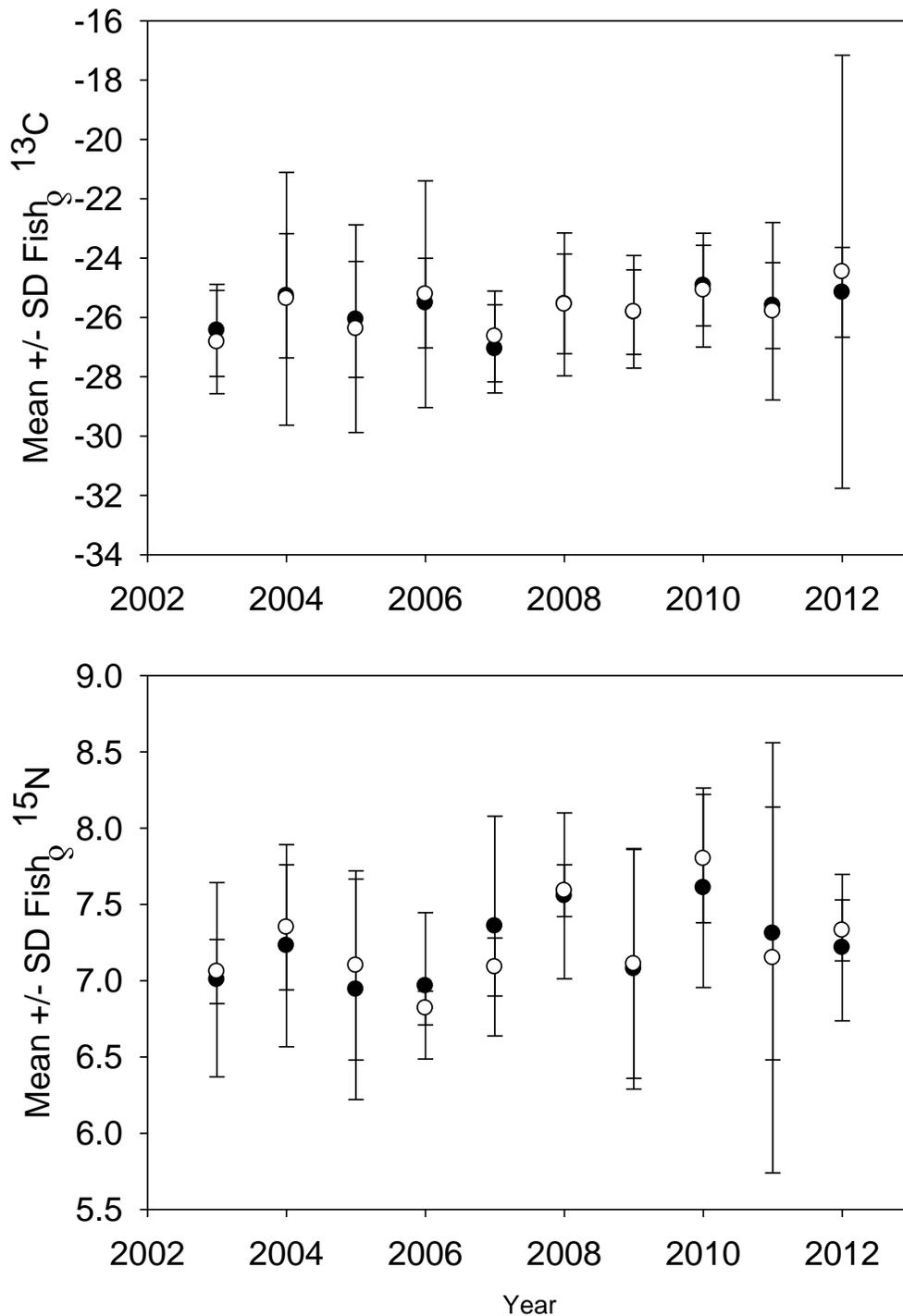


Figure 2.3. Mean  $\pm$  SD  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values computed for the sampled fish community over time. Values for the upper and lower Batchawana River are plotted as solid and open symbols, respectively.

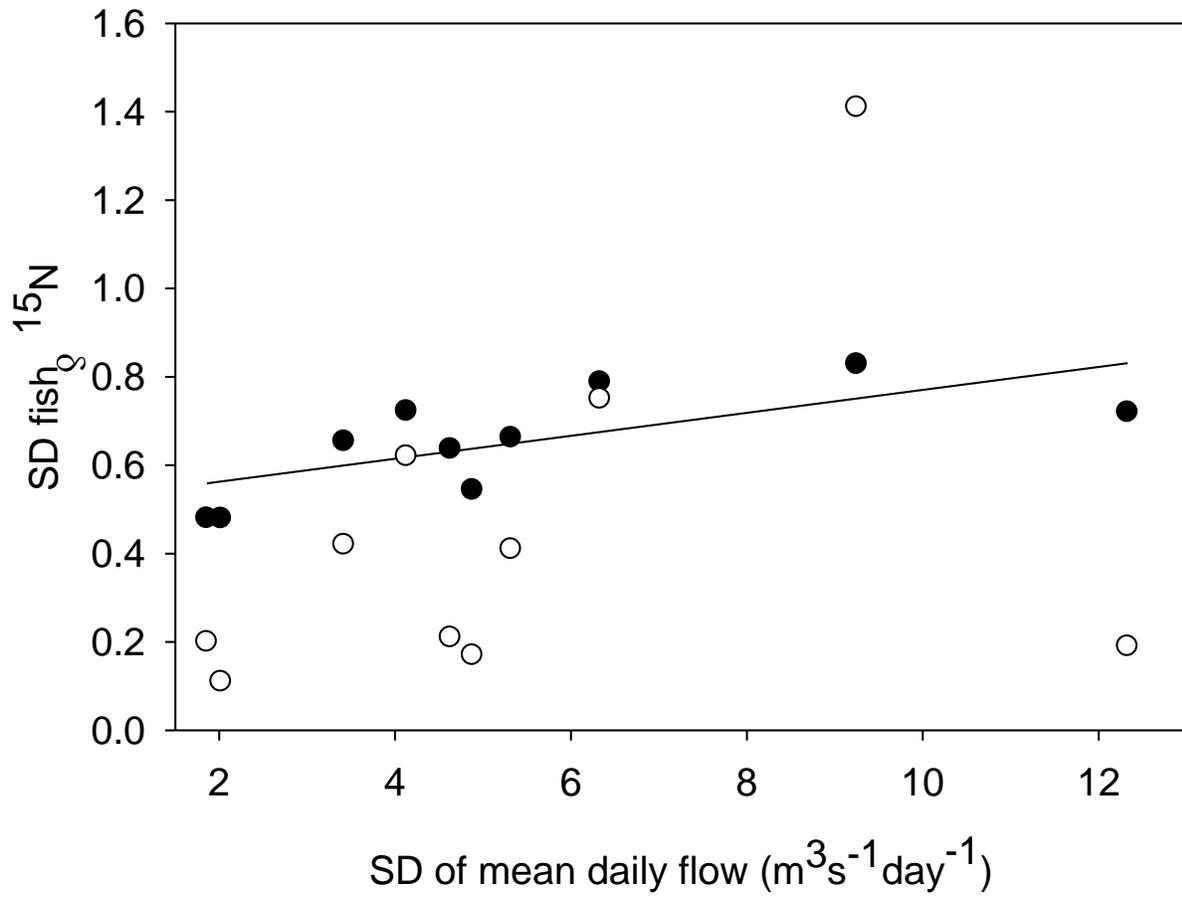


Figure 2.4. Relationship between SD  $\delta^{15}\text{N}$  of fish and SD of mean daily flow ( $\text{m}^3/\text{s}/\text{day}$ ). The upper Batchawana is represented as solid symbols and the lower Batchawana is represented by open symbols.

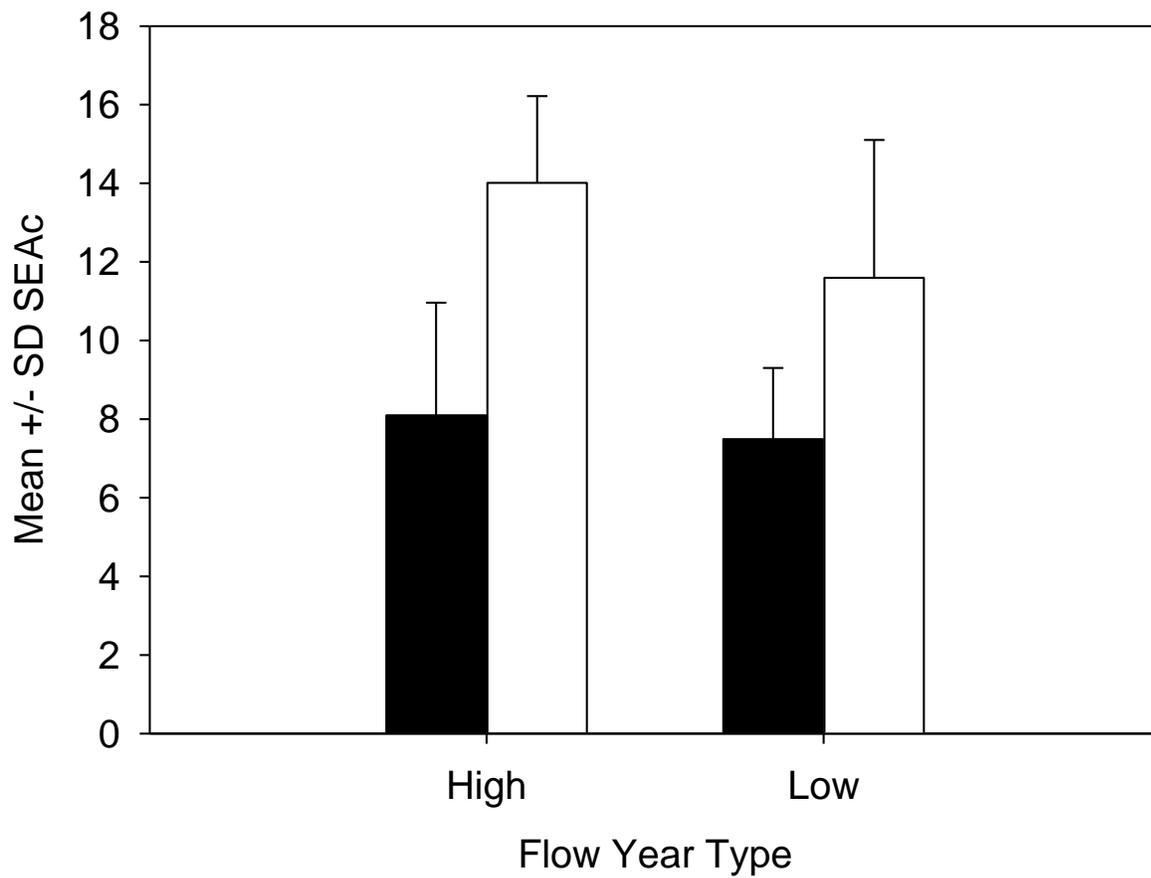


Figure 2.5. Comparison of standard ellipse area between upper and lower Batchawana River. The upper Batchawana is represented by solid bars and the lower Batchawana is represented by open bars.

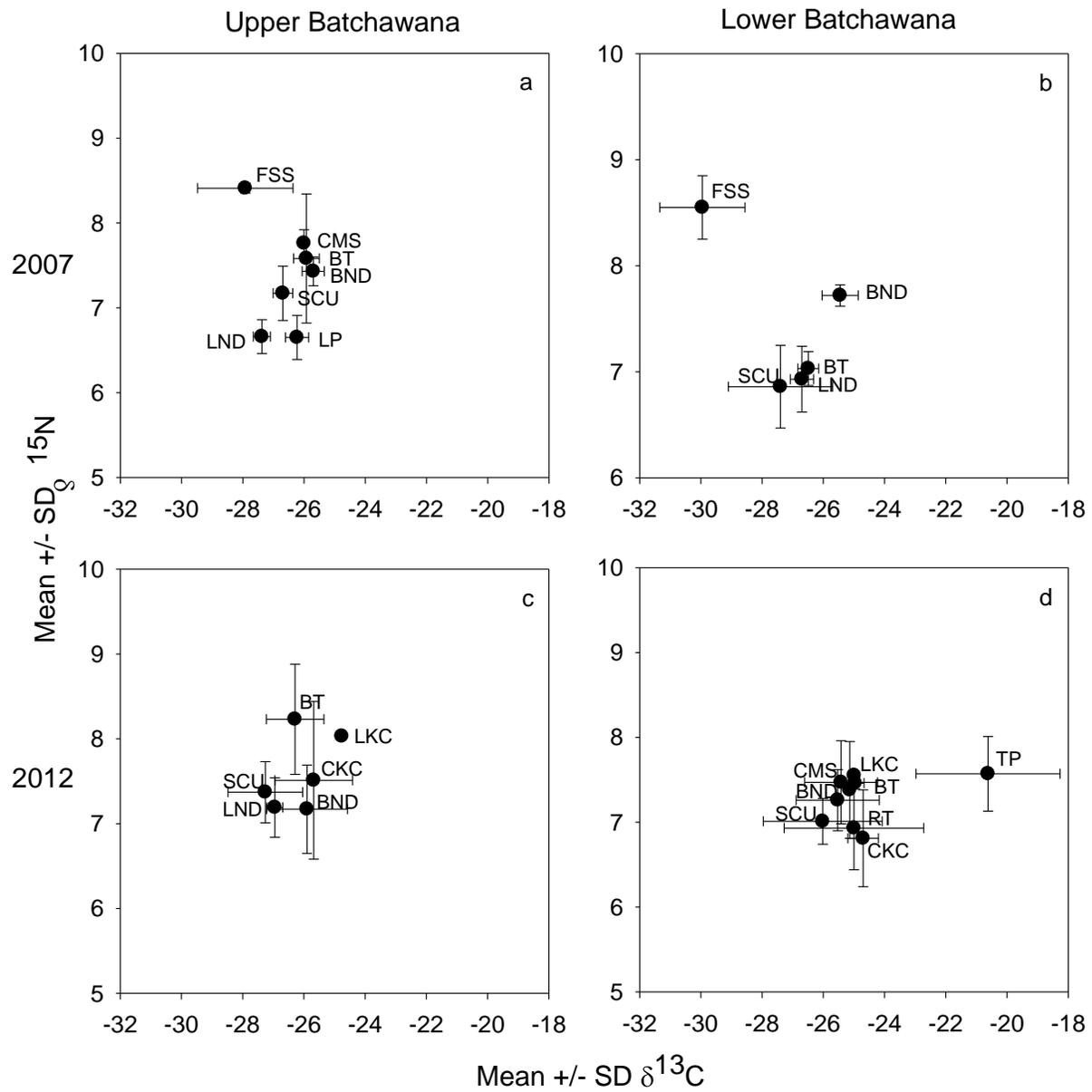


Figure 2.6. Mean  $\pm$  SD fish  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for 2007 (a high flow year) and 2012 (a low flow year) in the Batchawana River.

Table 2.1. Fish species collected and their main prey items, as described in Scott and Crossman (1973).

Fish Species	Main prey items
Longnose dace ( <i>Rhinichthys cataractae</i> )	Chironomidae, simuliidae and ephemeroptera larvae
Blacknose dace ( <i>Rhinichthys atratulus</i> )	Chironomidae larvae, diatoms and desmids also seasonally
Slimy sculpin ( <i>Cottus cognatus</i> )	Aquatic insect larvae and nymphs
Common white sucker ( <i>Catostomus commersonni</i> )	Chironomidae and trichoptera larvae and pupae, mollusca
Longnose sucker ( <i>Catostomus catostomus</i> )	Amphipoda, trichoptera, chironomidae, ephemeroptera, ostracoda, gastropoda, coleoptera
Juvenile Brook charr ( <i>Salvelinus fontinalis</i> )	Ephemeroptera, trichoptera, midge and simuliidae larvae, oligochaeta, annelida, cladocerans, amphipoda, terrestrial insects
Juvenile Rainbow trout ( <i>Oncorhynchus mykiss</i> )	Plankton, crustaceans, aquatic insects, gastropoda, annelida, and possibly fish eggs
Trout perch ( <i>Percopsis omiscomaycus</i> )	Chironomidae and ephemeroptera larvae
Creek chub ( <i>Semolitus atromaculatus</i> )	Coleoptera, ephemeroptera, trichoptera, and chironomidae larvae and adults. Cladocerans, algae, and aquatic plants are also consumed
Logperch ( <i>Percina caprodes</i> )	Cladocera, copepoda, ephemeroptera and midge larvae
Emerald shiner ( <i>Notropis atherinoides</i> )	Microcrustaceans (zooplankton), midge larvae, and algae
Northern redbelly dace ( <i>Phoxinus eos</i> )	Algae (diatoms and filamentous), zooplankton and aquatic insects
Brook stickleback ( <i>Culaea inconstans</i> )	Larvae of aquatic insects, eggs and larvae of other fish, gastropoda, oligochaeta, and algae

Table 2.2. Maximum, minimum, mean  $\pm$  standard deviation of daily summer flow (m<sup>3</sup>/s) and water temperature (°C) measured for the lower Batchawana River (Station 02BF001). Flow year type is defined with respect to maximum, minimum, and mean daily summer flow.

Year	Flow				Temperature		
	Max	Min	Mean $\pm$ SD	Flow Year Type	Max	Min	Mean $\pm$ SD
<b>2003</b>	21.4	2.9	8.7 $\pm$ 4.6	High	25.3	15.9	21.0 $\pm$ 1.8
<b>2004</b>	22.9	2.6	8.4 $\pm$ 5.3	High	26.2	13.8	19.9 $\pm$ 2.7
<b>2005</b>	18.6	1.1	4.3 $\pm$ 4.1	Low	28.8	18.3	22.8 $\pm$ 2.3
<b>2006</b>	22.2	1.7	3.8 $\pm$ 2.0	Low	27.8	17.3	22.1 $\pm$ 2.1
<b>2007</b>	75.8	1.6	8.7 $\pm$ 12.3	High	27.7	17.2	21.6 $\pm$ 2.2
<b>2008</b>	23.8	3.3	9.3 $\pm$ 4.9	High	24.6	17.1	20.8 $\pm$ 1.4
<b>2009</b>	31.6	4.6	14.7 $\pm$ 6.3	High	25.0	13.0	19.6 $\pm$ 2.5
<b>2010</b>	21.6	2.4	5.4 $\pm$ 3.4	Low	25.8	16.2	21.9 $\pm$ 2.5
<b>2011</b>	39.3	2.7	9.9 $\pm$ 9.3	High	22.6	16.1	20.1 $\pm$ 1.5
<b>2012</b>	9.24	1.6	3.7 $\pm$ 1.9	Low	--	--	--

Table 2.3. Number of fish collected (N), and calculated mean  $\pm$  SD  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and standard ellipse area (SEAc) for each year and flow year type for the upper and lower Batchawana River. A significant temporal trend was observed in SD  $\delta^{15}\text{N}$  for the upper Batchawana sample site ( $R^2 = 0.48$ ,  $p < 0.03$ ).

Year	Flow Year Type	N	Upper Batchawana			N	Lower Batchawana		
			Mean $\pm$ SD $\delta^{13}\text{C}$	Mean $\pm$ SD $\delta^{15}\text{N}$	SEAc		Mean $\pm$ SD $\delta^{13}\text{C}$	Mean $\pm$ SD $\delta^{15}\text{N}$	SEAc
2003	High	13	-27.47 $\pm$ 0.67	6.63 $\pm$ 0.48	4.12	63	-26.44 $\pm$ 1.55	7.01 $\pm$ 0.64	12.60
2004	High	23	-27.93 $\pm$ 1.25	6.99 $\pm$ 0.42	6.88	63	-25.27 $\pm$ 2.09	7.23 $\pm$ 0.66	17.60
2005	Low	43	-27.38 $\pm$ 1.23	7.29 $\pm$ 0.40	6.13	132	-26.07 $\pm$ 1.95	6.94 $\pm$ 0.72	16.71
2006	Low	26	-26.12 $\pm$ 1.31	6.97 $\pm$ 0.44	7.03	25	-25.51 $\pm$ 1.51	6.97 $\pm$ 0.48	9.28
2007	High	21	-26.55 $\pm$ 0.98	7.38 $\pm$ 0.66	8.46	17	-27.06 $\pm$ 1.49	7.36 $\pm$ 0.72	12.74
2008	High	18	-25.97 $\pm$ 1.22	7.85 $\pm$ 0.46	7.48	32	-25.54 $\pm$ 1.68	7.56 $\pm$ 0.54	11.64
2009	High	17	-26.62 $\pm$ 0.89	7.86 $\pm$ 0.75	8.80	55	-25.82 $\pm$ 1.42	7.08 $\pm$ 0.79	14.02
2010	Low	36	-27.14 $\pm$ 1.05	7.55 $\pm$ 0.52	6.65	61	-24.93 $\pm$ 1.36	7.61 $\pm$ 0.65	11.06
2011	High	20	-26.90 $\pm$ 1.31	8.30 $\pm$ 0.74	12.86	38	-25.60 $\pm$ 1.45	7.31 $\pm$ 0.83	15.48
2012	Low	27	-26.32 $\pm$ 1.21	7.46 $\pm$ 0.65	10.15	46	-25.15 $\pm$ 1.51	7.22 $\pm$ 0.48	9.33

Table 2.4. Effect of river reach, flow year type, and the interaction effect on the mean and variance fish  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and SEAc.

Independent variable	Factor	F <sub>(1,18)</sub>	p
Mean $\delta^{13}\text{C}$	River Reach	0.02	0.89
	Flow Year Type	4.52	0.05
	Interaction	0.09	0.77
Variance $\delta^{13}\text{C}$	River Reach	19.00	< 0.01
	Flow Year Type	0.30	0.59
	Interaction	0.71	0.41
Mean $\delta^{15}\text{N}$	River Reach	0.03	0.86
	Flow Year Type	0.20	0.89
	Interaction	0.19	0.67
Variance $\delta^{15}\text{N}$	River Reach	2.92	0.11
	Flow Year Type	3.09	0.10
	Interaction	0.12	0.74
Fish SEAc	River Reach	17.20	<0.01
	Flow Year Type	1.57	0.23
	Interaction	0.56	0.47

## Chapter 3

### Introduction

Climatic changes have had significant impacts on global and local hydrology, which affect the structure and function of river fish communities through effects on habitat quantity and quality, and biotic interactions (Carpenter et al. 1992; Poff et al. 1996; Bunn and Arthington, 2002; Wrona et al. 2006). Although rivers within the boreal forest region of North America commonly experience low flow in the summer months due to decreased precipitation and increased temperature relative to spring and fall (Woo et al. 2008; Ström et al. 2011), extreme low flow events are expected to become more common with climate change (Ström et al. 2011; Walters and Post, 2011). Biotic communities within boreal rivers have adapted to deal with hydrologically seasonal phenologies (Monk et al. 2008). Nevertheless, low flow events can have significant effects on the availability of riverine food resources (Matthews and Zimmerman 1990).

Disruption of the flow regime as a result of river regulation and water diversion can also lead to loss of suitable habitat and associated food sources, and in turn represents a major threat to aquatic biodiversity and production (Stanford et al. 1996). Some of the negative impacts that dams and modifications to the natural flow regime have on the physical habitat within a river include alterations to: bank and channel morphology, sediment composition, suspended matter and water temperature (Maddock 1999; Scruton et al. 2003). Within the group of studies that have focused on variable flow conditions, there are a limited number of studies that focus on the consequences of flow variation for the riverine food webs within which fish and their prey operate. Those studies of low flow effects that do exist have reported negative effects on biota such as: migration interruption, or timing modification (Caudill et al. 2007), entrainment

mortality (Benstead et al. 1999), increased potential for stranding (Scruton et al. 2005), changes to predator-prey interactions (Power et al. 1996; Bunn and Arthington 2002), changes in food chain length (Marty et al. 2009), declines in algal biomass (Blinn et al. 1995), changes in invertebrate community composition (Jones 2013), and declines in invertebrate abundance (James et al. 2008). Although knowledge gained from these studies has provided a better understanding of how modified flow conditions may affect many aspects of riverine fish ecology under forecasted changing hydrological and climate conditions, few studies have examined how low flow events specifically affect the feeding ecology of fish in boreal forest rivers (Monk et al. 2008; Rolls et al. 2012).

To address the knowledge gap, fish diet composition, mean and variance of fish  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , resource use and overlap are compared in a low flow and normal flow year using data collected for key fish species from a pair of boreal rivers, one regulated and one unregulated. Within the regulated river, it is expected there would be no intra- or inter-annual differences in resource use owing to the relative lack of flow variation, and in the natural river, high intra- and inter-annual differences in resource use owing to seasonal and inter-annual differences in flow. The following hypotheses were tested: that: i) within- river resource overlap between fish species would be higher in the low flow year, ii) as would resource overlap between rivers.

## **Methods**

Fish and representative invertebrate taxa were collected from geographically proximate (Figure 3.1), and geomorphically similar sites on the West Salmon River (N48 17' 244" W056 23' 006") and Twillick Brook (N48 10' 592" W055 57' 137") in May and August of 2011 and 2012. The West Salmon River is regulated by a control structure at the southern end of the Cold

Spring Pond reservoir that feeds the river. Flow in the West Salmon River is maintained at  $2.6 \text{ m}^3\text{s}^{-1}$  from June 1- November 30, and  $1.3 \text{ m}^3\text{s}^{-1}$  for the remainder of the year (Figure 3.2). Aside from a few short-term flow manipulation experiments (1999-2003), the flow regime has been maintained since construction in 1981 (Scruton et al. 2003; Robertson et al. 2004; Scruton et al. 2005; Scruton et al. 2008). The West Salmon River has a boulder and cobble substrate, and a variety of riffle, run and flat water habitats (Robertson et al. 2004). At  $2.5 \text{ m}^3\text{s}^{-1}$ , the West Salmon River has a wetted width that ranges from 20 - 45 m (Scruton et al. 2008). Minimal terrestrial vegetation hangs over the river banks, which are steeply sloped.

Twillick Brook is a similarly sized river (25-30 m wide and 11 km long) to the West Salmon River (approximately 30 m wide and 12.7 km long), with abundant pool and riffle habitats, but differs from the West Salmon River in the amount of riparian vegetation along the river banks. In 2011, Twillick Brook followed a natural hydrograph, with flows varying between  $2.84$  and  $7.71 \text{ m}^3\text{s}^{-1}$  in spring, and  $1.31$  and  $5.30 \text{ m}^3\text{s}^{-1}$  in summer (Water Survey of Canada). In 2012 the Twillick Brook catchment experienced above and below average summer temperatures and precipitation with the result that river discharge varied between  $1$  and  $2 \text{ m}^3\text{s}^{-1}$  from May to August, lower than levels typically experienced in the West Salmon River during the same period (Figure 3.2).

#### *Study species and sample collection*

In spring and summer of each year, approximately 30 Atlantic salmon (*Salmo salar*), and brook charr (*Salvelinus fontinalis*) were collected using standard backpack electrofishing methods (Meador et al. 2003; Reynolds et al. 2003). All fish were euthanized and measured for fork-length ( $\pm 1$  mm). Individual stomachs were removed and kept frozen for stomach content analysis.

Diet composition was quantified for all individual fish, using the method described in Cortès (1997). For each fish, stomach contents were identified to the lowest practical taxonomic level (Family or Order) and counted under a dissection microscope. The volume of each prey taxa was estimated as a proportion of total stomach volume, and each prey taxa was determined as present (1) or absent (0). For each prey item of a given type, the %number, %volume, and %frequency of occurrence were determined. An index of relative importance (IRI) for an individual prey type  $x$  was then determined as:

$$IRI_x = (\%N + \%V) * \%O \quad (1).$$

The percent index of relative importance (%IRI) for an individual prey item was calculated as:

$$\%IRI_x = (IRI_x / \sum IRI) * 100 \quad (2).$$

#### *Stable isotope analysis*

A small (0.5-2.0 g) piece of dorsal muscle tissue was excised from an area dorsal to the lateral line and posterior to the dorsal fin on each fish and frozen for stable isotope analysis (e.g., Guiguer et al. 2002). Values of  $\delta^{13}C$  and  $\delta^{15}N$  were measured for all fish following methods described in Peterson and Fry (1987) and Post (2002). Briefly, dorsal muscle tissue from all fish were dried in an oven at 50 °C for 48 hours and then ground to a powder using a mortar and pestle. Approximately 275-300  $\mu$ g of ground tissue was used for stable isotope analyses completed on a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108, Carlo Erba, Milan, Italy). All analyses were completed at the Environmental Isotope Laboratory, University of Waterloo (Waterloo, Ontario, Canada), with results expressed in standard  $\delta$  notation. Working internal laboratory standards were calibrated against the International Atomic Energy Agency standards CH6 for carbon and N1 and N2 for nitrogen and run as controls

throughout the analysis to ensure the continued accuracy of all measurements. Analytical precision was assessed by mean differences of one in ten duplicate samples, where the mean  $\pm$  standard deviation was  $0.13 \pm 0.2$  ‰ for  $\delta^{13}\text{C}$  and  $0.17 \pm 0.2$  ‰ for  $\delta^{15}\text{N}$ .

## Data Analysis

Using stomach content data (proportional IRI values), the degree of resource overlap between individual fish species and rivers was calculated with Schoener's index as:

$$D = 100 * (1 - 0.5 * (\sum |p_{xi} - p_{yi}|)) \quad (3),$$

where  $p_{xi}$  is the proportion of prey item  $i$  for predator  $x$ , and  $p_{yi}$  is the proportion of prey item  $i$  for predator  $y$ . The index will vary between 0 and 1, with values  $> 0.6$  indicating significant biological overlap or resource use (Wallace 1981; Scrimgeour and Winterbourn 1987). Schoener's index of overlap was also used with relative frequency histograms of  $\delta^{13}\text{C}$  to examine resource use similarity within and between rivers. Values of  $\delta^{13}\text{C}$  were binned into 0.5 ‰ intervals to account for analytical variability.

Where stable isotope data were used in the statistical analysis, values of fish  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were treated as dependent variables and factors such as year, season, river, and species were treated as independent variables. Preliminary analyses of linear relationships between consumer  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  and fork-length were generally non-significant ( $p > 0.05$ ). Where significant relationships were found, they were generally inconsistent with respect to sign (positive or negative slopes), explained only a small portion of the variation ( $R^2 \leq 0.43$ ), or yielded residuals inconsistent with the assumptions required of linear regression (e.g., heteroscedastic, non-normal). Given the weakness, inconsistency and statistical inadequacy of the estimated length

relationship, length was not considered further as a significant explanatory variable in subsequent statistical analyses.

Separate factorial ANOVAs were used to evaluate the influence of year, season, river and species on either fish  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$ . Equality of  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  variances between years, seasons and rivers was evaluated using Levene's test (Zar 2010). All statistical analyses were performed using Systat version 11 (Systat Software Inc. 2004), with significance set at  $\alpha = 0.05$ .

The SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011) method was used in the SIAR package (version 4.1.3) to evaluate isotopic niche widths (measured as standard ellipse areas in  $\delta^{13}\text{C}$ -  $\delta^{15}\text{N}$  space) for intra- and inter-annual comparisons of river fish populations. The standard ellipse encompasses 40 % of the data points, which represents approximately 1 SD of the data (Batschelet 1981). Ellipse areas were expanded here to include two standard deviations, which encompass 95 % of the data and better represent variability in the data (Chew 1966; Jackson et al. 2011). All  $\text{SEA}_B$  ellipse estimates were adjusted for small sample sizes ( $\leq 30$ ) to obtain  $\text{SEA}_C$ , which corrects for possible under-estimation of the ellipse area as a result of small sample sizes. The overlap area between ellipses was calculated following Jackson et al. (2011), with an overlap value of 0.6 or higher considered biologically significant (Guzzo et al. 2013).

## **Results**

A total of 528 fish were collected across all sampling dates. Fork-length of captured Atlantic salmon ranged in size from 38 -197 mm, and 45-164 mm in the West Salmon River and Twillick Brook, respectively. Brook charr ranged in size from 46 -142 mm and 36-263 mm in West Salmon River and Twillick Brook, respectively.

### *Diet analysis*

All fish fed on invertebrate prey items, with differences evident from sampling dates among species, rivers, and year (Tables 3.1A, 3.1B). Baetidae mayflies dominated in spring samples, while Simuliidae larvae appeared to be more important in summer. Overall, brook charr diet composition was more variable than that of Atlantic salmon.

In spring 2012, significant dietary similarity was observed between Atlantic salmon and brook charr in both rivers with Schoener's index values for the West Salmon River and Twillick Brook, respectively, equalling 0.94 and 0.79. Within individual rivers, other seasonal inter-specific comparisons were significantly different (all index values < 0.6). In contrast, intra-annual comparisons of  $\delta^{13}\text{C}$  histograms within individual rivers completed using Schoener's index, revealed no significant differences in resource use between seasons (all  $x > 0.6$ ). Comparisons between rivers, however, revealed similar resource use between rivers in all seasons except spring 2011 ( $x < 0.6$ ); (Table 3.2).

Fish from the West Salmon River had more negative  $\delta^{13}\text{C}$  values compared to fish in Twillick Brook (Table 3.3). In spring 2011 and 2012, mean  $\delta^{13}\text{C}$  differed significantly between rivers. In both summers, however, mean  $\delta^{13}\text{C}$  was similar in both rivers. In the spring of 2011 and 2012,  $\delta^{13}\text{C}$  variances were similar in both rivers (2011:  $F_{(1,130)} = 2.18$ ,  $p = 0.14$  in 2011, 2012:  $F_{(1,126)} = 0.001$ ,  $p = 0.97$ ). In the summer of 2011, mean  $\delta^{13}\text{C}$  was similar in both rivers, however variances differed ( $F_{(1,134)} = 12.43$ ,  $p < 0.001$ ). Whereas in summer of 2012,  $\delta^{13}\text{C}$  means and variances ( $F_{(1,134)} = 0.003$ ,  $p = 0.95$ ) were both similar (Table 3.3).

In general, fish from the West Salmon River had higher mean  $\delta^{15}\text{N}$  values compared to fish in Twillick Brook, except in the summer of 2012 (Table 3.3). Mean  $\delta^{15}\text{N}$  was not significantly different between rivers in spring 2011, or in summer 2012. In contrast,  $\delta^{15}\text{N}$  was

significantly different in summer 2011 and in spring 2012. Fish from Twillick Brook had higher  $\delta^{15}\text{N}$  variances than fish from the West Salmon River in spring 2011 ( $F_{(1,130)} = 0.50$ ,  $p < 0.01$ ) and summer 2012 ( $F_{(1,135)} = 0.46$ ,  $p < 0.01$ ), but variances were not significantly different in summer 2011 ( $F_{(1,134)} = 0.95$ ,  $p = 0.84$ ), and spring 2012 ( $F_{(1,126)} = 0.65$ ,  $p = 0.09$ ). In the West Salmon River, variances were not different between years for spring ( $F_{(1,124)} = 1.26$ ,  $p = 0.36$ ), or summer ( $F_{(1,132)} = 1.30$ ,  $p = 0.29$ ). In both years, there was a pattern of increasing  $\delta^{15}\text{N}$  variance from spring to summer, and a comparison of spring versus summer variances revealed significant differences (2011:  $F_{(1,130)} = 0.52$ ,  $p = 0.008$ ; 2012:  $F_{(1,126)} = 0.53$ ,  $p < 0.05$ ).

In Twillick Brook, spring  $\delta^{15}\text{N}$  variances were significantly different between years ( $F_{(1,132)} = 1.64$ ,  $p = 0.047$ ), whereas summer variances were similar between years ( $F_{(1,137)} = 0.64$ ,  $p = 0.06$ ). In the normal flow year (2011), spring and summer variances were not significantly different ( $F_{(1,134)} = 0.98$ ,  $p = 0.94$ ), while in the low flow year (2012), there was a significant increase in  $\delta^{15}\text{N}$  variance from spring to summer ( $F_{(1,135)} = 0.38$ ,  $p < 0.001$ ).

#### *Resource overlap*

Within the West Salmon River, the SEAc for brook charr was always higher than that for Atlantic salmon. Standard ellipse area and ellipse overlap between species was consistently lower in the spring and higher in the summer (Figure 3.3 and Table 3.4). Similarly, within Twillick Brook, the SEAc and ellipse overlap increased from spring to summer for both species and in both years. Despite a decrease in the SEAc for Atlantic salmon and an increase in the SEAc for brook charr in summer 2012 within Twillick Brook, the degree of overlap between species remained similar between years (Figure 3.4 and Table 3.4).

In both rivers, the SEAc values increased from spring to summer. In the West Salmon River, values increased from 4.07 to 5.15 in 2011, and from 3.09 to 6.61 in 2012. In Twillick

Brook, values increased from 5.74 to 9.04 from spring to summer 2011, and from 4.76 and 7.94 in 2012. Ellipse areas were always larger in Twillick Brook compared to the West Salmon River (Table 3.4). In the West Salmon River, there was a decrease in ellipse area between spring 2011 and 2012 (4.07 to 3.09), and an increase in ellipse area between summer 2011 and 2012 (5.15 to 6.61). In Twillick Brook, there was also a decrease in ellipse area between spring 2011 and 2012 (3.11 to 1.72), however, there was an increase in ellipse area between summer 2011 and 2012 (4.01 to 5.71). Area of overlap between the West Salmon River and Twillick Brook ellipses was 3.11 in spring 2011, and 4.01 in summer 2011. Overlap was lowest in spring 2012 (1.72), but highest in summer 2012 (5.71), when river flows were most similar (Figure 3.5).

## **Discussion**

As hypothesized, no intra- or inter-annual differences in trophic niche area were demonstrated within the regulated river, however, within the natural river intra- and inter-annual differences in trophic niche were found. Niche areas were larger for brook charr compared to Atlantic salmon, larger in both rivers in the spring compared to summer, and smaller in the low flow year compared to the normal flow year. As hypothesized, resource overlap between fish species was higher in the low flow year, lower in the spring and higher in the summer as a result of differences in flow, and higher between rivers in the low flow year.

Low flows arise largely due to elevated temperatures and decreased rainfall (Poff et al. 1996), and the frequency of low flow events is predicted to increase because of climate change (Vorosmarty et al. 2000; Walters and Post 2011). The reduced niche areas experienced by the community of the natural river in the low flow year, the reduction in niche areas from spring to summer in both rivers, and the increase in overlap between fish species in summer likely arise

from similar mechanisms whereby low flow decreases habitat, reduces the availability of food resources and increases intra-and inter-specific interactions for food and space (Dewson et al. 2007; Walters and Post 2011; Rolls et al. 2012). Decreasing flows generally result in a reduction in habitat space (Stanley et al. 1997; Brasher 2003) and can significantly alter benthic communities (Boulton and Lake 1992; Acuna et al. 2005; Stubbington et al. 2009). While some studies have found little or no effect (Caruso 2002; Suren et al. 2003; Dewson et al. 2007; Walters and Post 2011), others have indicated that low flow can reduce aquatic insect taxonomic richness and community composition (Englund and Malmqvist 1996; Rader and Belish 1999; Boulton 2003). Reduction of habitat area and volume can also lead to short-term increases in richness and abundance of river invertebrates (Stubbington et al. 2011) and an increase in benthic invertebrates in the drift (Minshall and Winger 1968). Low flows can decrease the densities and the distance traveled by drifting invertebrates (Rolls et al. 2012), thereby affecting prey availability for stream resident fishes. In general, however, low flows decrease invertebrate recruitment (Cowx et al. 1984), species richness and density of flow-dependent taxa (Larned et al. 2007; Haxton and Findlay 2008; Datry 2012), and the total biomass of food resources (Walters and Post 2011). As habitat decreases during low flow, the concentration of aquatic biota decreases, which results in increased potential for inter-specific interactions such as competition and predation (Rolls et al. 2012) reflected in the increasing feeding niche overlap observed in this study.

Higher inter-specific overlap in the summer may indicate increased competition for food resources between Atlantic salmon and brook charr, given that habitat area is reduced and both species utilize similar invertebrate resources (Magnan et al. 1994; Amundsen et al. 2001; Mookerji et al. 2004). One consideration, however, is that the species use slightly different

habitats. Atlantic salmon are found in faster flowing waters, and so drifting invertebrates comprise a greater percentage of their diets (Klemetsen et al. 2003). Brook charr are found in slower flowing waters, with a strong preference for cover (Cunjak and Green 1983), meaning that terrestrial subsidies may be more important to their diets when available. Resource and habitat overlap between species should increase at low flows when habitat space and the available resource base are reduced (Morse 1974). Nevertheless, the degree of overlap between Atlantic salmon and brook charr was found to be similar between years in both rivers. In summer 2012, niche area declined for Atlantic salmon while niche area for brook charr increased relative to summer 2011. The result may depend on diet differences, as in summer 2012 Atlantic salmon were dominated by Simuliidae (~72%) while in summer 2011 Chironomidae and Hydropsychidae larvae were important in the diet. Simuliidae larvae are generally inferior competitors to net-spinning Hydropsychidae (Hemphill and Cooper 1983; Hemphill 1988; Hershey and Hiltner 1988), which explains the higher abundance of Trichoptera in our diet composition samples in normal flow years. However, with reduced flow and increased temperatures, black fly larvae become more abundant (Zhang et al. 1998).

Low flows have known effects on river invertebrate communities. Under low flows (such as that experienced in summer 2012), net energy intake in drift feeding fish, such as salmonids, decreases as a consequence of reduced densities of drifting prey. Reduced availability of food resources, and increased potential for competition and predation under low flow may, therefore, hold significant negative consequences for individual and population growth as a result of the combined effect of increased metabolic demand and reduced ration (Elliott 1994; Elliott et al. 1997; Rolls et al. 2012). Low flows can also contribute to elevated instream temperatures, which pose a significant risk to salmonids. Increases in salmonid mortality have been associated with

low flows (Cunjak et al. 2013) and elevated temperatures (Hedger et al. 2012), especially during the summer (Connor et al. 2003; Gunn and Snucins 2010). It is uncertain as to how the interaction between increased temperatures, reduced habitat and resource availability will affect growth and fitness of salmonids in with changing climates, but it is clear that both temperature and resource changes will be intertwined.

## **Conclusion**

There were no intra- or inter-annual differences in trophic niche area within the regulated river, however, within the natural river intra- and inter-annual differences in trophic niche were found. Niche areas were higher for brook charr compared to Atlantic salmon, higher in the spring compared to summer in both rivers, and smaller in the low flow year compared to the normal flow year. Resource overlap between fish species was higher in the low flow year, lower in the spring and higher in the summer, and resource overlap between rivers was higher in the low flow year. High resource overlap between rivers during decreased summer flow indicates a strong effect of flow on river organisms, where both fish and their invertebrate prey resources are concerned. Multiple approaches, such as stomach content and stable isotope analysis, provide detailed short- and long-term observations of fish feeding and resource overlap that yield insights into how the food webs of natural and regulated rivers function vary under changing flow conditions.

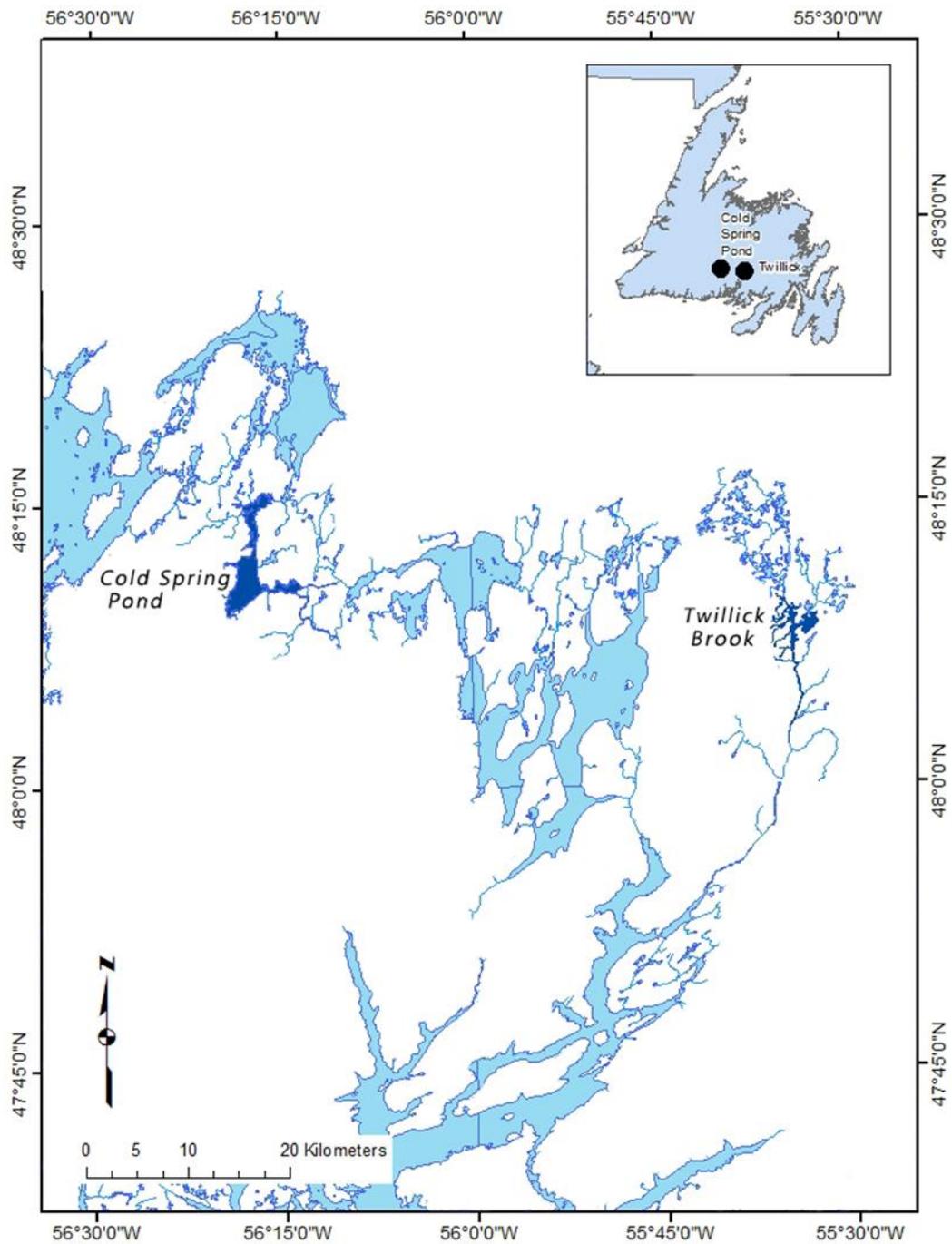


Figure 3.1. Location of sample collections on the West Salmon River and Twillick Brook.

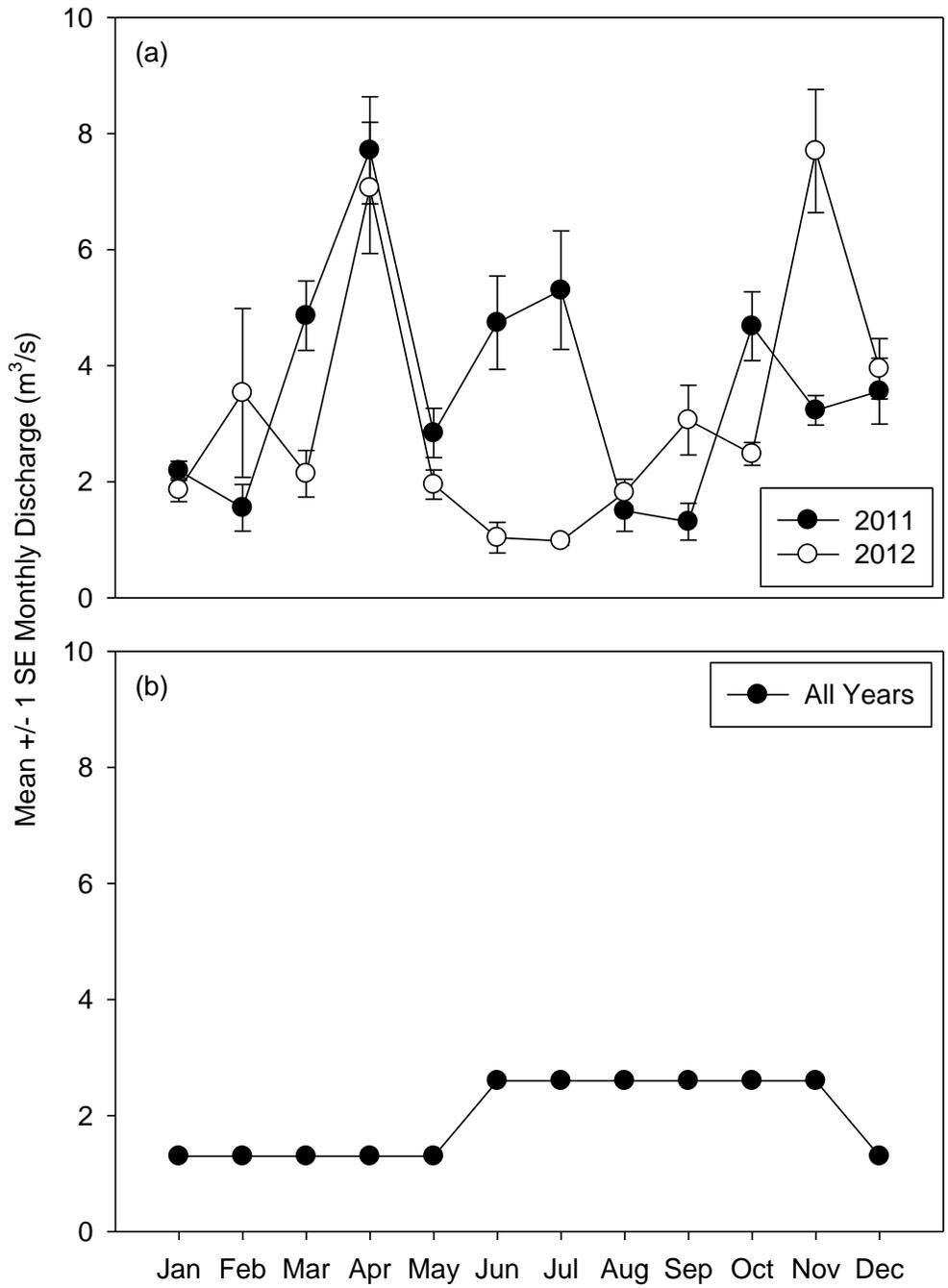


Figure 3.2. Hydrograph of monthly mean discharge ( $\text{m}^3/\text{s}$ ) in Twillick Brook (a) and the West Salmon River (b).

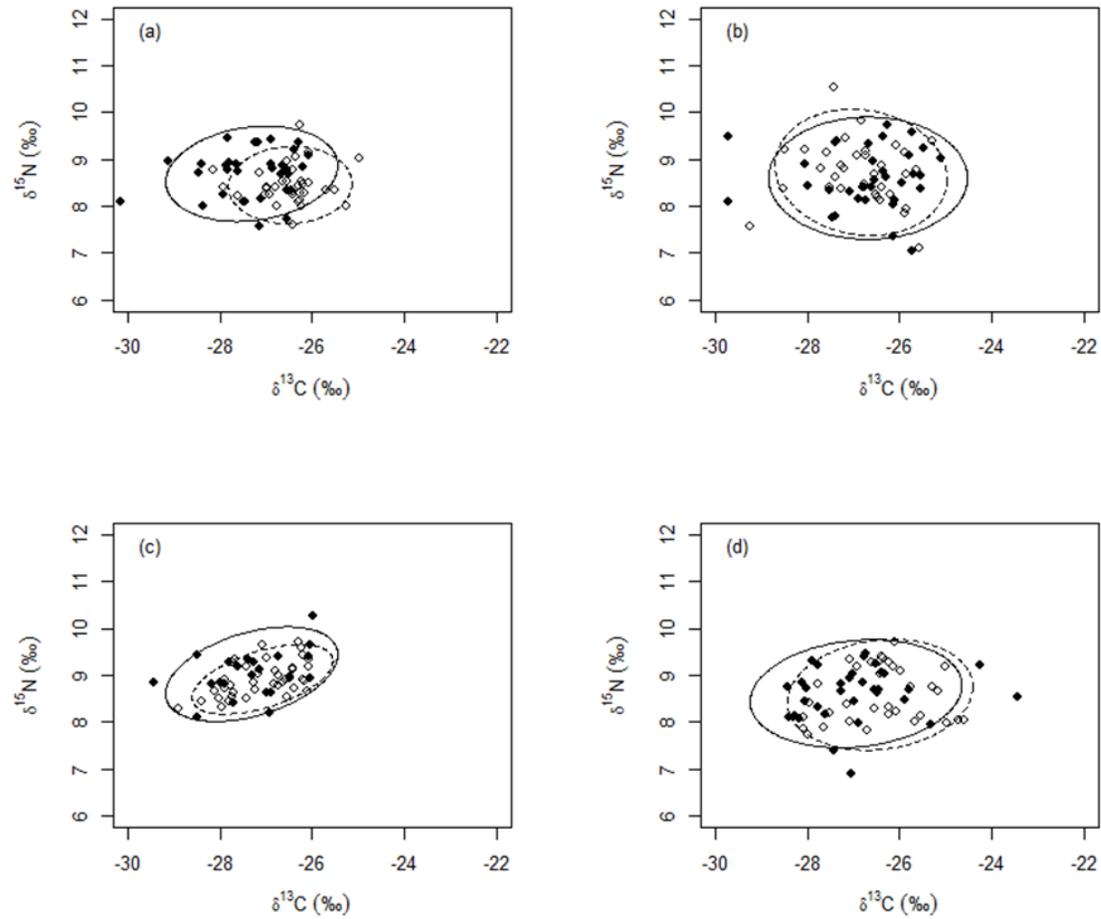


Figure 3.3. West Salmon intra-annual ellipse comparisons between Atlantic salmon and brook charr. Atlantic salmon are represented by white symbols and dashed lines while brook charr are represented by black symbols and solid lines.

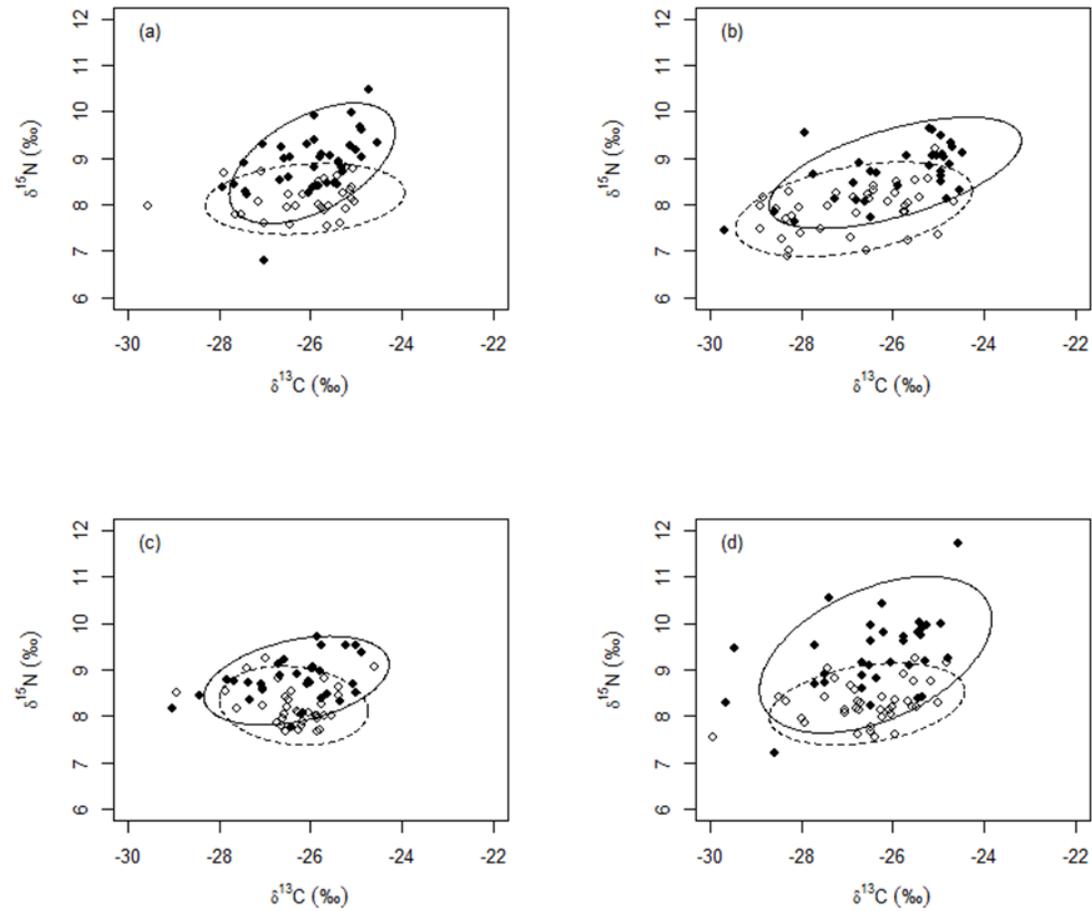


Figure 3.4. Twillick Brook intra-annual ellipse comparisons between Atlantic salmon and brook charr. Atlantic salmon are represented by white symbols and dashed lines while brook charr are represented by black symbols and solid lines.

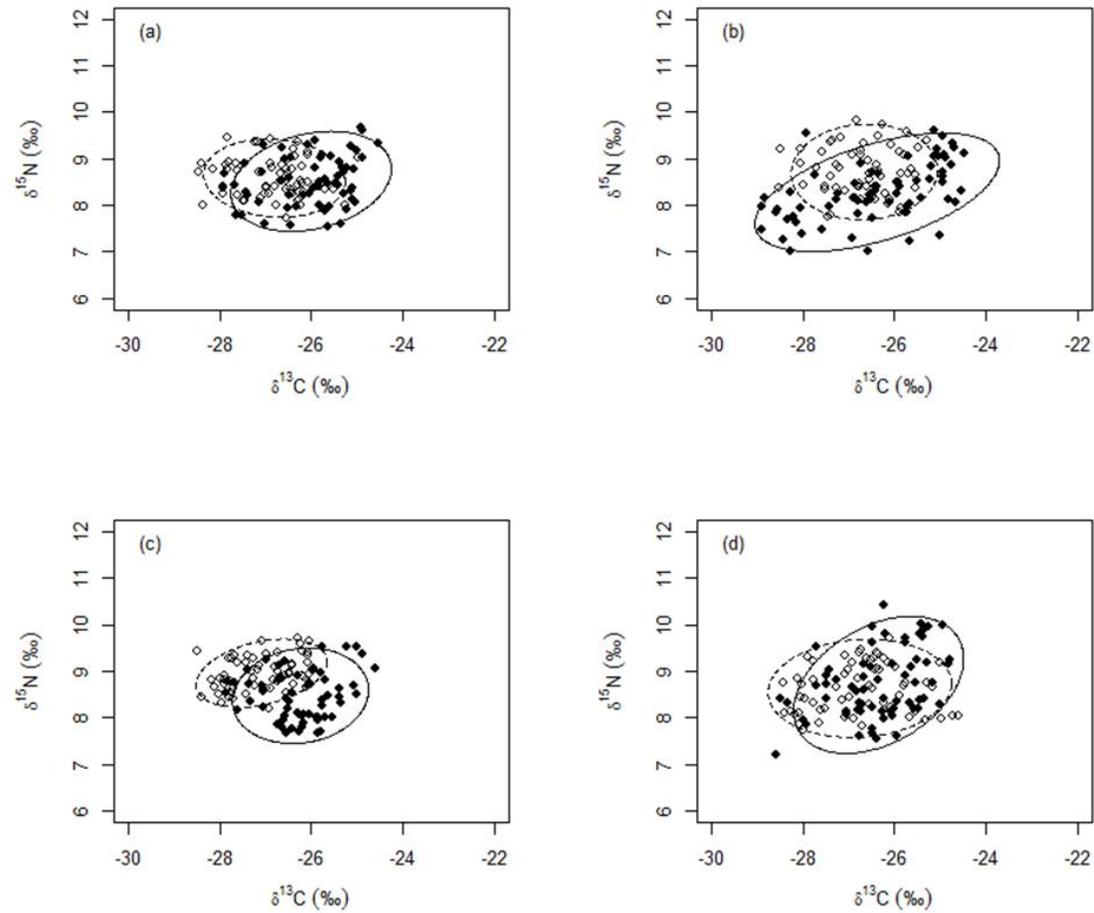


Figure 3.5. Comparison of standard ellipse area between the West Salmon River and Twillick Brook. The West Salmon River is represented by white symbols and dashed lines while Twillick Brook is represented by black symbols and solid lines.

Table 3.1A. Index of relative importance (%) of various prey items for Atlantic salmon (AS) and brook charr (BC) in spring and summer of 2011 and 2012 within the West Salmon River. Prey items comprising  $x < 3$  %IRI were pooled into an “other” category.

Prey Item	Spring 2011		Summer 2011		Spring 2012		Summer 2012	
	AS	BC	AS	BC	AS	BC	AS	BC
Hydropsychidae	51.28%				7.00%			
Philopotamidae								16.80%
Trichoptera		46.14%	9.57%	4.59%			34.47%	
Baetidae	38.19%	42.15%	5.60%	33.58%	91.03%	91.20%		
Perlidae	3.59%	5.11%						
Chironomidae			34.36%	19.80%				
Simuliidae			17.94%	23.06%			60.41%	18.58%
Hydrachnida				3.66%				
Cladocera			23.33%					
Other	6.94%	6.60%	9.20%	15.31%	1.96%	8.80%	5.12%	64.62%

Table 3.1B. Index of relative importance (%) of various prey items for Atlantic Salmon (AS) and brook charr (BC) in spring and summer of 2011 and 2012 within Twillick Brook. Prey items comprising  $x < 3$  %IRI were pooled into an “other” category.

Prey Item	Spring 2011		Summer 2011		Spring 2012		Summer 2012	
	AS	BC	AS	BC	AS	BC	AS	BC
Hydropsychidae	2.59%		57.70%					
Trichoptera		36.40%	5.82%	11.91%			4.02%	
Baetidae	64.58%	17.09%	3.34%		96.58%	75.37%		23.96%
Hymenoptera							4.89%	
Chironomidae			25.95%					
Simuliidae			3.24%				71.90%	
Oligochaeta	29.92%	7.10%				7.74%	4.36%	3.72%
Gastropoda		12.42%		70.07%				
Other	2.91%	25.25%	3.95%	18.02%	3.42%	16.89%	19.19%	72.32%

Table 3.2. Within and between river intra-and inter-annual resource overlap values, calculated using relative frequency histograms of consumer  $\delta^{13}\text{C}$ . Atlantic salmon and brook charr  $\delta^{13}\text{C}$  values were pooled for analysis. Values  $\leq 0.6$  indicate no significant overlap.

Comparison	West Salmon River	Twillick Brook
<u>Seasonal Between Years</u>		
Spring 2011 vs Summer 2011	0.78	0.63
Spring 2011 vs Spring 2012	0.81	0.77
Spring 2012 vs Summer 2012	0.80	0.71
Summer 2011 vs Summer 2012	0.77	0.94
<u>Annual Between Rivers</u>		
Spring 2011	0.46	
Summer 2011	0.63	
Spring 2012	0.62	
Summer 2012	0.77	

Table 3.3. Mean  $\pm$  1 SD stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) values of fish from the West Salmon River (WSR) and Twillick Brook (TB) in all seasons and years. Within a season, similarities and differences in mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between rivers are denoted by the use of superscripts (A, B, C, etc.).

		$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Spring 2011	WSR	$-26.89 \pm 0.90^{\text{A}}$	$8.57 \pm 0.47^{\text{A}}$
	TB	$-26.12 \pm 1.14^{\text{B}}$	$8.54 \pm 0.66^{\text{A}}$
Summer 2011	WSR	$-26.76 \pm 0.99^{\text{C}}$	$8.66 \pm 0.65^{\text{B}}$
	TB	$-26.44 \pm 1.38^{\text{C}}$	$8.27 \pm 0.67^{\text{C}}$
Spring 2012	WSR	$-27.17 \pm 0.81^{\text{D}}$	$8.96 \pm 0.42^{\text{D}}$
	TB	$-26.35 \pm 0.89^{\text{E}}$	$8.49 \pm 0.52^{\text{E}}$
Summer 2012	WSR	$-26.69 \pm 1.09^{\text{F}}$	$8.60 \pm 0.57^{\text{F}}$
	TB	$-26.48 \pm 1.15^{\text{F}}$	$8.77 \pm 0.84^{\text{F}}$

Table 3.4. Species-specific standard ellipse areas (SEAc) by fish species and area of overlap within the West Salmon River and Twillick Brook. AS = Atlantic salmon, BC = brook charr.

West Salmon River	Fish Species	SEAc	Area of ellipse overlap
Spring 2011	AS	3.46	2.70
	BC	5.87	
Summer 2011	AS	7.85	7.40
	BC	8.83	
Spring 2012	AS	3.02	3.02
	BC	5.38	
Summer 2012	AS	7.39	6.56
	BC	8.22	
<u>Twillick Brook</u>			
Spring 2011	AS	5.14	2.91
	BC	6.33	
Summer 2011	AS	7.56	4.46
	BC	8.43	
Spring 2012	AS	4.30	2.96
	BC	5.66	
Summer 2012	AS	5.62	4.05
	BC	11.98	

## **Chapter 4: General Conclusion and Recommendations for Future Research**

### **Synopsis**

Rivers are diverse and complex systems (Jungwirth et al. 2002). They have historically been used more by humans than other ecosystems (Arthington and Welcomme 1995), and provide many benefits to human societies (Sparks 1995; Jungwirth et al. 2002). Despite their ecological and economic importance, river ecosystems have experienced significant chemical, geological and biological alterations as a result of human influences, especially due to hydroelectric power generation (Efford 1974; Richter et al. 1996; Murchie et al. 2008; Poff and Zimmerman 2010).

Short-term studies have investigated the influence of hydroelectric power operations on the ecology of regulated and natural river ecosystems (Marty et al. 2009; Jones 2010; Patterson and Smokorowski 2011; Smokorowski et al. 2011; Jones 2013; Jackson et al. 2007; Delong and Thoms 2016), however few long-term studies exist. The scientific literature has suggested that there are predictable relationships between components of the flow regime and biological communities (Poff et al. 1997; Olden and Poff 2003), however this has not been empirically tested in paired natural-regulated boreal rivers.

The overall objective of this research was to address the need for assessment of how flow and temperature variations influence fish diet, feeding niche and food chain length on paired altered-and natural rivers in Newfoundland and a natural river in Ontario. This thesis comprises two studies, which tested the effect of low natural flow and regulated flow (Newfoundland), and naturally variable flow (Ontario) on the feeding ecology of fish and invertebrates measured using carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotopes, stomach contents of fish, and food chain length and fish feeding niche.

In Chapter 2, an increase in fish community feeding niche was found over time within the upper Batchawana River, however, despite natural temperature and flow variability, fish community feeding niche was temporally invariant in the lower Batchawana River. Fish feeding niche was influenced by flow variability within the upper reach but was likely moderated by tributary inputs downstream. Examining spatial variability in fish feeding and food web structure is important to account for how various environmental factors such as flow and temperature, as well as channel morphology can affect fish feeding ecology. Characterizing fish feeding at multiple reaches within rivers can help to avoid erroneous conclusions that could be made by quantifying food web metrics at single reaches within rivers. In addition, a significant negative relationship was observed between variation (SD) in  $\delta^{15}\text{N}$  and variation (SD) in mean daily flow. When logistically feasible, long-term studies can provide important information on the range of natural spatial and temporal variation within river ecosystems and how food webs respond to these variations. Such studies can serve as important baselines against which one can compare potential future environmental changes.

In Chapter 3, I found no intra- or inter-annual differences in niche area within the regulated river, however, within the natural river intra- and inter-annual differences in trophic niche were found. Brook charr had larger niche areas compared to Atlantic salmon, higher in the spring compared to summer in both rivers, and smaller in the low flow year compared to the normal flow year. Resource overlap between fish species was higher in the low flow year, lower in the spring and higher in the summer, and resource overlap between rivers was higher in the low flow year. During decreased summer flow, high resource overlap between rivers indicates a strong effect of flow on influencing the food available to river organisms, which can ultimately influence feeding ecology, fish health and overall food web structure. Multiple approaches, such

as stomach content and stable isotope analysis, provide detailed short- and long-term observations of fish feeding and resource overlap. Fish communities with more diverse communities appear to be more resistant to variable flow and temperature than those with simpler fish communities.

## **Synthesis**

Flow has been widely cited as a major determinant of food web structure and function in rivers (Poff et al. 1997; Finlay 2001; Bunn and Arthington 2002). Regular discharge pulses are critical in the dynamics of river systems (Junk et al. 1989; Puckridge et al. 1998). Rivers have been altered substantially beyond natural levels of variation due to hydropower operations, which affect hydrological and thermal regimes, as well as the feeding ecology of resident organisms (Bunn and Arthington 2002; Olden and Naiman 2010).

The natural flow paradigm asserts that maintaining ecosystem integrity is largely dependent on conserving the natural features of the flow regime (Poff et al. 1997). Management and research interests have been directed towards restoration of affected ecosystems to a natural “reference” condition in an attempt to improve integrity (Bayley 1991; Landres et al. 1999; Jungwirth et al. 2002; Poff and Zimmerman 2010).

To better understand how food web integrity may be altered by flow changes, it is important to test hypotheses related to effects of flow variation on fish feeding ecology over spatial and temporal scales. Natural environmental influences and anthropogenically-induced changes to the flow regime and consequently fish and their food resources, can affect the health and integrity of aquatic food webs.

## **Recommendations for future research**

Every river is unique and flow regimes are spatially and temporally complex (Rolls et al. 2012), therefore it may be difficult to generalize findings from one regulated or natural river to the next. The studies of river food webs in northern Ontario and Newfoundland included in this thesis have sparked many ideas and have highlighted areas that I feel provide the basis for future research. My next step is to complete a long-term assessment of feeding ecology within a regulated river and identify food web differences between the natural and regulated rivers in northern Ontario. Preliminary findings from the regulated river demonstrated significant decrease in food chain length post-ramping rate change, following the period originally studied by Marty et al. (2009). Expanding upon the work completed by Marty et al. (2009) is important because of the continued decrease in food chain length over time, which is an indication of significant food web changes that have been mediated by the change in ramping rate regime. I would also like to explore the before-after impact-control for several years post ramping rate regime change, whether differences exist between natural and regulated rivers after considering the influence of regional climate impacts.

Other studies that I feel would enhance the aforementioned studies as well as provide benefit to knowledge within the area of aquatic ecology are:

1. ***Fatty acids and proximate body condition***

Traditional body condition metrics such as Fulton's K and L-W relationships have been widely applied in fisheries research, however, rely on assumptions which may not be applicable to all species or all environments (Cone 1989). As an example, there is a loss of information when comparing L-W relationships between populations due to single statistic results, and

Fulton's K assumes that the slope of the L-W relationship is 3.0 (indicating isometric growth) which may not be the case (Cone 1989).

Lipids and their constituent fatty acids offer an additional tool to study food web dynamics and body condition. Polyunsaturated fatty acids (PUFAs) are obtained from the diet (DHA: docosahexaenoic acid and EPA: eicosapentaenoic acid), and are indicators of condition in freshwater fish because they affect growth, osmoregularity, membrane fluidity and immune responses (Arts et al. 2009; Tocher 2010). Because PUFAs such as EPA, DHA and ARA (arachidonic acid) are obtained from the diet, the availability of PUFA can be reduced under adverse environmental conditions, thus affecting organism health and condition (Arts et al. 2009).

Lipids can also provide an indication of habitat quality, as well as proximate body condition (Homyack 2010), which makes them ideal for studying the effect of hydropower operations, because of modifications to flow and temperature as well as indirectly affecting food availability (Hasler et al. 2009). Hydropeaking operations in particular, can create an energetic cost for fishes such as salmonids (Puffer et al. 2014), which can reduce feeding opportunities. Lipid or fatty acid analysis can be useful for studying the environmental stress response in fish (Wagner and Congelton 2004; Hasler et al. 2009)

Fish experiencing widely fluctuating flow conditions may have fewer fat reserves due to potentially modified ability to obtain food resources (Hasler et al. 2009). Thus, highly variable flows can affect energy usage in fish and the influence of hydropower operations on lipid storage and energy requirements in fish can be determined (Wagner and Congelton 2004). It is possible that fish exposed to higher frequency of flow changes would be unable to consume higher quality prey items, although this is yet to be determined. Comparing fatty acid composition of

fish and their prey in natural and regulated river environments would provide an understanding of lipid dynamics in response to changing environmental conditions such as temperature and flow.

## 2. *Study design*

Replication is a limitation of my study design, whereby in each individual study (Newfoundland or Ontario), only two rivers were studied –one natural and one regulated. If more time permitted and with an unlimited research budget, I would have liked to include data from multiple natural rivers, and compare it to multiple regulated rivers with similar operational regime within the same region. Increasing the number of rivers studied across Canada would allow for the determination of how downstream rivers exposed to different flow regimes will respond. Although the biological community within each river may respond differently to environmental or anthropogenic stressors, there may be some generalizations that can be made about the influence of flow variations.

Being part of HydroNet was a unique experience and I think it would have been very useful to coordinate efforts among other students in order to sample a wide range of natural and altered rivers so that multiple response variables were analyzed within the same period (stable isotope composition, growth, hydrology, geology, etc). By conducting sampling programs simultaneously, there would be more environmental variables available as explanatory factors for the biological responses (i.e., we could gain a better picture of how the biology and habitat, or hydrological or thermal regime are linked).

The work completed within this thesis, the continued research plans, and the recommendations for future work has and will contribute to a better understanding of how varying fish communities (simple and more diverse) respond to variable flow and temperature

regimes and over short and long temporal periods. Why fish feeding ecology? Fish feeding, the attainment and consumption of food, is paramount to fish survival within variable lotic ecosystems. Flow variations can directly affect the quantity and quality of prey. Anticipating how fish communities and their prey resources respond to natural and artificially low flow, and flow and temperature variations in general, will allow managers to diagnose acute and chronic food web changes that may arise due to predicted alterations to temperature and flow regimes brought about by climate changes in boreal regions of Canada.

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