Effects of Hydroelectric Dam Operation on Downstream Fish Populations

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

Chapter 2: Slimy sculpin (*Cottus cognatus*) annual growth in contrasting regulated and unregulated riverine environments.

While the research was my own, this chapter was published in a journal with co-authors K. E. Smokorowski and M. Power. KES and MP contributed financial support, some data, and editorial comments. The chapter was published as:

Slimy sculpin (*Cottus cognatus*) annual growth in contrasting regulated and unregulated riverine environments. B. Kelly, K. E. Smokorowski, and M. Power. Hydrobiologia 768: 239-253.

Chapter 6: Thermal habitat segregation among morphotypes of whitefish (*Coregonus lavaretus*: Salmonidae) and invasive vendace (*C. albula*): a mechanism for co-existence?

While the research was my own, this chapter was published in a journal with co-authors P.-A. Amundsen and M. Power. PAA and MP contributed financial support, some data, and editorial comments. The chapter was published as:

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Abstract

Naturally flowing rivers form a longitudinal gradient of physical conditions to which fish communities are adapted. Hydroelectric dams disrupt the river continuum, resulting in alterations to downstream hydrologic and thermal characteristics. Changes in physical conditions downstream from hydroelectric dams can have a variety of effects on local fish populations. However, the tendency for biological responses to be species- and system-specific complicates the development of broadly applicable management strategies. Therefore, it is necessary to conduct long-term, large-scale studies on the impacts of river regulation under different hydroelectric dam operating regimes, and to investigate the impacts on multiple species within a given system.

In this thesis I report data from two long-term, large-scale field studies (in northern Ontario and northern Norway), and investigate the impacts of river regulation on downstream fish. Specifically, the effects of river regulation on an important recreational fish, *Salvelinus fontinalis,* the forage fish community (*Cottus cognatus, Rhinichthys cataractae,* and *Percopsis omiscomaycus*), the coldwater fish guild, and native-invasive species interactions (*Coregonus lavaretus* and *Coregonus albula,* respectively) are studied. Indicators of fish health used to assess the effects include growth, condition, survival, thermal habitat and field metabolism. Potential driving forces such as changes to river discharge and water temperature are investigated to identify the causal mechanisms behind the effects on fish health.

Fish growth was higher in a northern Ontario river with a 15 MW hydropeaking dam, relative to a nearby naturally flowing river, regardless of the dam operating regime. Condition and survival varied between and among species, and between the regulated and naturally flowing river. *S. alpinus* exhibited a higher field metabolic rate in the regulated river, which was positively correlated with time spent hydropeaking. The higher growth in the regulated river was likely a result of system-specific food increases resulting from impoundment, hydropeaking, or a combination of both, while the varying responses in condition and survival were likely driven by species and life-stage specific differences in behaviour, access to food and increased energetic costs associated with daily hydropeaking. Thermal habitat differed among the two coldwater species evaluated and is likely related to species-specific temperature preferences and behaviour. Hydrologic and thermal indices explained little of the variation in fish growth, likely as a result of both the indirect and interacting effects associated with altering river discharge and temperature.

In a regulated system in northern Norway, the availability of different thermal habitats influenced the success of the invasive *C. albula*. Stable isotope evidence suggested that thermal habitat partitioning was occurring in a site where *C. albula* and *C. lavaretus* coexist, while dietary resource partitioning was occurring in a site where *C. albula* were outcompeting *C. lavaretus*, relegating them to the littoral zone.

This thesis highlights the variation in biological responses to river regulation amongst species and within systems, providing evidence for the species-specific effects of hydroelectric dam operation. The potential for both direct and indirect impacts, and the complexity of biological responses within the forage fish community, the coldwater fish guild, and between native and invasive species, necessitates the use of multiple species and multiple indicators of fish health to thoroughly characterize the effects of river regulation on fish species. Given the different habitat and temperature preferences and behavioural patterns exhibited within the fish community, it is important to manage river environments not just for specific thresholds, but to ensure the availability of a variety of different flow and thermal habitats. Maintaining the availability of a variety of habitats within the riverine environment should be considered as an important component of river management strategies.

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Chapter 1 Introduction

General context

Hydropower is an important contributor to electricity grids around the world, including in Canada and Norway, where it contributes 60% and 96% of the total electricity generated, respectively (Statistics Canada 2015; Statistics Norway 2015). The damming of rivers and operation of hydropower facilities results in significant alterations to physical parameters in downstream river reaches (Baxter 1977), which in turn impacts downstream ecosystems (Ligon et al. 1995). While numerous studies have investigated the impacts of hydroelectric dam operation on river ecosystems, general trends in the response of fish populations to river regulation remain difficult to identify (Poff & Zimmerman 2010) as these responses may be species-specific (e.g. Korman & Campana 2009; Finch et al. 2015). Therefore, simple overarching environmental flow restrictions may not be broadly effective (Arthington et al. 2006), and there is a need for long-term, large-scale studies aimed at identifying mechanistic relationships between physical alterations and biological responses (Mims & Olden 2013; Olden et al. 2014).

In this thesis I examine the impact of hydroelectric dam operation on downstream fish using data collected during large-scale long-term studies in northern Ontario and northern Norway. Hydrologic and thermal indices are calculated and investigated alongside indicators of fish health including: growth, condition, survival, thermal habitat and field metabolism, to identify causal mechanisms between hydroelectric dam-driven physical alterations and biological responses. The indicators of fish health are calculated for several morphologically diverse species with a range of behavioural characteristics and habitat preferences in order to gain a more complete understanding of the effects of river regulation on the fish community. The implications of this research are discussed within the context of river management.

Physical parameters altered by hydroelectric dam operation

A gradient of physical conditions exists along the length of a river, and aquatic communities are adapted to this gradient (Vannote et al. 1980). However, the barrier introduced by hydroelectric dams disrupts the gradient (Ward & Stanford 1983), with accompanying impacts on organisms living downstream. Specifically, the operation of hydroelectric dams can alter the five key components of the natural flow and thermal regimes: timing, magnitude, frequency, duration and rate of change (Poff et al. 1997; Olden & Naiman 2010). Hydroelectric peaking operations, in particular, induce large daily fluctuations in discharge to meet daily patterns in electricity demand (Morrison & Smokorowski 2000), and these fluctuations have no parallel in natural freshwater systems (Poff et al. 1997). Alterations to the natural flow and thermal regimes can have important implications for the biology and ecology of fish in terms of growth (Korman & Campana 2009; Bond et al. 2015; Finch et al. 2015), life history traits (Alexandre et al. 2014; Bond et al. 2015), survival of specialist species (Quinn & Kwak 2003), and the success of invasive species (Marchetti & Moyle 2001; Brown & Ford 2002).

Flow regime

Hydroelectric dam altered flows can affect downstream fish both directly and indirectly. Increased flows during hydropeaking events can directly result in increased energy expenditure resulting from increased activity (Murchie & Smokorowski 2004). Dam operations and the resulting altered flows can also indirectly alter the food available for fish (Bond et al. 2015) by increasing the abundance of invertebrates (Jones 2013) and invertebrate drift (Lauters et al. 1996; Lagarrigue et al. 2002; Patterson & Smokorowski 2011). Changes in discharge from river regulation have been shown to increase the abundance of run and riffle habitat relative to pools (Bunn & Arthington 2002), or may eliminate riffles, increasing the amount of slow velocity habitat and lacustrine environments (Bøhn & Amundsen 2001; Gjelland et al. 2007), depending on how dam operations influence river morphometry. The changes to food availability, habitat and fish behaviour all have the potential to influence fish life history characteristics and population health (Bøhn & Amundsen 2001; Alexandre et al. 2014; Bond et al. 2015).

Thermal regime

Hydroelectric dam operation can affect the thermal regime of a river in a variety of ways. Fundamentally, the construction of a dam creates a barrier to fish movement, and, barring the construction of fish passages (see review by Schilt 2007), will reduce the ability of individual fish to access thermal refuges in different parts of the river system (Hillyard & Keeley 2012). Dams also alter downstream temperatures through water releases. A surface water draw from a reservoir results in warm water being released downstream, increasing water temperatures (Lessard & Hayes 2003), while drawing water from a deeper depth can result in a cool water draw, reducing temperatures downstream (Petts 1986). Changes to downstream water temperatures can have a number of negative impacts on fish, including the local extirpation of fish species (Quinn & Kwak 2003), changes to the timing of spawning (Zhong & Power 1996), impacts to larval development (Clarkson & Childs 2000) and decreased growth rates (Saltveit 1990). However, managing dams to release water of a desired temperature may also benefit specific fish species downstream (MacDonald et al. 2012) and could potentially be used to mitigate climate change-driven river water temperature increases (Isaak et al. 2012; Null et al. 2013; Robson et al. 2013; Rheinheimer et al. 2014; Rheinheimer & Viers 2014). Given the importance of temperature on fish metabolism and physiology (Brett & Groves 1979; Kelsch & Neill 1990), growth (Neuheimer & Taggart 2007), and life-history traits (Coutant 1987), determining how altered thermal regimes impact individual fish species is an important aspect of characterizing the effects of river regulation.

Indicators of Fish Health

Growth

Growth is an important determinant of fish health, as it acts as an integrative measure, incorporating both energy inputs and outputs (Brett & Groves 1979), as well as biotic (e.g. competition) and abiotic (e.g. temperature) factors (Brett 1979). Fish growth rates and the resulting length-at-age can have important implications for inter-and intra-species interactions (Fausch & White 1981), overwinter survival (Hunt 1969) and life history traits such as age-at-maturity (Roff 1984). Alterations to downstream river environments from hydroelectric dam operations can result in either decreases (Korman & Campana 2009) or increases (Bond et al. 2015; Finch et al. 2015) to fish growth. However, impacts from river regulation on fish growth are species-specific, and, therefore, necessitate the characterization of effects on a variety of fish species with different morphologies and behaviours, as well as within different systems to more fully understand the impacts of river regulation.

In this thesis, annual growth rates were determined for four fish species from four different families, and analyzed with respect to river discharge and temperature. First, fish age was determined by identifying and counting annuli in fish otoliths. Fish growth and length-at-age were then determined by applying otolith back-calculations according to the Scale Proportional Hypothesis method (Francis 1990).

Condition

Condition is used as an indication of fish well-being and is an important tool when comparing fish populations from different environments (Bolger & Connolly 1989). It is especially useful when impacts on a population are more subtle than mortality or extirpation. River regulation in general, as well as the restrictions under which dams operate, can impact fish condition (Weisburg & Burton 1993). In this thesis, I compare fish condition between a regulated and naturally flowing river, as well as between two different hydroelectric dam operating regimes in the regulated river. Condition was assessed using several methods, depending on sample suitability. Weight-length relationships were calculated, whereby fish with a heavier weight for a given length were considered to be healthier (Anderson & Neuman 1996). Fulton's condition factor (Nash et al. 2006) and relative condition factor (Le Cren 1951) were also calculated to compare fish between and within populations, respectively. Caloric content of the muscle tissue of fish was measured, with higher caloric content indicative of higher energy storage and, therefore, better condition (Paine 1971).

Thermal habitat

Given the importance of water temperature for ectotherms such as fish, and the downstream alteration of water temperature by dams (Casado et al. 2013), quantifying the temperature at which fish live can provide valuable information on the effects of river regulation. Stable oxygen isotopes in fish otoliths can be used to provide estimates of fish thermal habitat. Oxygen isotope values in river water correspond well with values in precipitation (Kendall & Coplen 2001), which in turn are strongly correlated with temperature (Clark & Fritz 1997). Oxygen isotopes are deposited in the calcium carbonate of otoliths in equilibrium with the surrounding water, irrespective of metabolic or kinetic effects (Høie et al. 2003). Therefore, $\delta^{18}O$ values can be used to estimate the water temperature at which fish have lived (Devereux et al. 1967), if the isotopic fractionation between water and fish otoliths is known (e.g. Storm-Suke et al. 2007a). $\delta^{18}O$ values have been used to compare thermoregulation and thermal habitat use in different environments, and the associated implications for fish growth and climate change adaptation (Murdoch & Power 2013; Sinnatamby et al. 2013). However, to date this technique has not been applied towards the study of sympatric native and invasive species, or the effect of river regulation on thermal habitat use. In this thesis, thermal habitat was quantified using oxygen isotopes over the course of individual growing seasons for four of the six study species to characterize thermal habitat partitioning between native and invasive species, and the influence of river regulation on two coldwater guild fish species.

Field metabolic rate

Alterations to river flow and temperature can alter fish metabolism through increased energetic expenditures for place holding or higher activity levels (Murchie & Smokorowski 2004), or higher standard metabolism driven by higher water temperatures (Brett & Groves 1979). The δ^{13}C of otoliths can provide information on field metabolic rate, which is an estimate of the total energetic costs of standard metabolic rate, thermoregulation, locomotion, feeding, reproduction and growth (e.g. Nagy et al. 1987; Sinnatamby et al. 2015). The δ^{13}C value of otoliths is derived from ambient dissolved inorganic carbon (DIC) and respired metabolic carbon (Weidman & Millner 2000). Higher metabolic rates result in a higher concentration of metabolically derived carbon in the fish bloodstream, which diffuses into the endolymphatic fluid surrounding the otoliths, becoming incorporated in the otoliths during calcium carbonate deposition (Solomon et al. 2006). Thus, calculating the proportion of metabolic carbon contributing to the δ^{13}C otolith value provides information on the average energy expenditure of a fish, or field metabolic rate. The contribution of standard metabolic rate to field metabolic rate can be accounted for if the temperature at which fish live is known, allowing for inferences about fish activity levels. Given the potential for increased fish activity associated with the act of hydropeaking (Murchie & Smokorowski 2004), field metabolic rates are a valuable tool for investigating increased energy expenditure associated with this type of river regulation.

Study Sites

Large-scale experimental studies which investigate different flow regimes on downstream ecosystems can provide valuable information to river managers on how to restrict hydroelectric dam operations (Olden et al. 2014). To that end, in this thesis I report data obtained as part of two separate large-scale long-term studies (Amundsen et al. 1999; Smokorowski et al. 2011), one of which was also experimental in nature (Smokorowski et al. 2011).

Batchawana and Magpie Rivers, Ontario Canada

Two boreal shield rivers in northern Ontario were sampled from 2002 through 2012: the Magpie River near Wawa ON (48°4’N; 84°44’W), which has a 15 MW peaking hydroelectric facility, and the Batchawana River near Sault Ste. Marie ON (47°0’N; 84°30’W), which has a natural flow regime and acted as an environmental control. These two rivers were chosen for comparison, as they have similar drainage areas, mean annual discharges, channel morphology and nutrient concentrations (Marty et al. 2009; Smokorowski et al. 2011).

The peaking hydroelectric facility in the Magpie River is located at Steephill Falls dam and has been operational since 1989. Over the course of the study, the hydroelectric facility operated under two different hydropeaking regimes: from 2002 to 2004, the rate of increase or decrease in flow was restricted, while from 2005 through 2012 it was not. During both periods a minimum flow requirement of 7.5 $m^3 \cdot s^{-1}$ was in place (Smokorowski et al. 2011). The collection of fish data under both hydropeaking regimes in the Magpie River and over the course of the experiment in the Batchawana River enabled the comparison of impacts between hydropeaking regimes as well as a comparison between a regulated and a naturally flowing river, using a BACI (before-after, control-impact) design.

Pasvik Watercourse, northern Norway

The Pasvik watercourse forms the border between northern Norway and Russia and contains seven hydroelectric dams ranging in size from 69 GWh to 272 GWh. The damming of the system has shifted the waterway from a predominantly riverine system, to a series of lakes and reservoirs connected by slow flowing rivers (Bøhn & Amundsen 2001; Gjelland et al. 2007). Whitefish (*Coregonus lavaretus*) was the predominant fish species in the system prior to the invasion of vendace (*Coregonus albula*) in the late 1980s (Bøhn & Amundsen, 2001), following their translocation and introduction into the Pasvik headwaters three decades earlier (Amundsen et al. 1999, Bøhn et al. 2004, Præbel et al. 2013). Vendace populations have developed differently in different parts of the system, becoming abundant and outcompeting whitefish for dietary resources at some locations, while remaining low in numbers and sharing dietary resources with whitefish at other locations (Bøhn & Amundsen 2001; Bøhn et al. 2008).Two lacustrine sites, Lake Skrukkebukta and Lake Tjærebukta which have similar areas (6.6 and 5.1 km^2, respectively) and chemical compositions, but differ in depth, were sampled to investigate the causal mechanism behind the different inter-species interactions between these two sites.

Study Species

Impacts of hydroelectric dam driven changes to discharge and temperature are likely species-specific (e.g. Finch et al. 2015; Bond et al. 2015). Therefore, this study investigates the impact of hydroelectric dam river regulation on six study species which exhibit a range of morphological and behavioural characteristics as well as diet, temperature, and velocity preferences (Table 1.1). These six species each play an important role within their respective ecosystems, and, as a result of their differences, provide valuable and unique information on the impacts of river regulation. Slimy sculpin (*Cottus cognatus*) is a known sentinel species (Edwards & Cunjak 2007) and can thus indicate the impact of altered discharge and temperature regimes at local spatial scales. Brook trout (*Salvelinus fontinalis*) is an important recreational fish species (Fisheries and Oceans Canada 2010) and the research conducted here can be used to contribute to the management of the recreational brook trout fisheries in the Batchawana and Magpie Rivers. Slimy sculpin and brook trout, as members of the coldwater fish guild (Magnuson et al. 1979) can provide information on the potential for hydroelectric dam management of downstream water temperatures as a climate change mitigation strategy. Longnose dace (*Rhinichthyus cataractae*) and trout perch (*Percopsis omiscomaycus*), in addition to slimy sculpin, are the three most abundant forage fish species in the Batchawana and Magpie Rivers. A comparison of the impacts of river regulation amongst these three species provides important information on the diversity of responses which fish within the same community can exhibit towards altered discharge and temperature regimes. Both whitefish (*Coregonus lavaretus*) and vendace (*Coregonus albula*) are important commercial species (Amundsen et al. 1999; Salonen & Mutenia 2004). However, vendace is an invasive species in the Pasvik watercourse, thus an analysis of these two species can provide information on how hydroelectric dam driven river regulation affects native-invasive species interactions. These six study species together provide valuable information on the effects of hydroelectric dams on recreational and commercial fish species, coldwater fish, invasive species, and the forage fish community.

Research Objectives

Chapter 2: Slimy sculpin (Cottus cognatus) annual growth in contrasting regulated and unregulated riverine environments

To assess the impact of hydroelectric dam-altered river discharge on fish, hydrologic indices representing the five components of the flow regime were calculated for both the Batchawana and Magpie Rivers and correlated with slimy sculpin growth using a linear model. The general hypotheses for this chapter were that slimy sculpin growth would be higher in the regulated river relative to the naturally flowing river, a gradient of growth effects with distance from the dam would be seen in the regulated river, and that the frequency and magnitude of hydropeaking events would be positively related to sculpin growth. These hypotheses were derived based on the potential for hydropeaking to increase food availability for fish (Jones 2013; Bond et al. 2015), and the benthic behaviour of sculpin (Facey & Grossman 1992), which may shield them from the negative effects of increased flow. The objective of the chapter was to assess the mechanistic relationship between fish growth and river hydrology. By identifying a correlation between specific hydrologic indices and fish growth, the chapter provides information which may be applied to the formulation of environmental flow management plans within regulated rivers.

Chapter 3: Effect of hydroelectric dam river regulation on the growth, condition and survival of resident forage fish

Given the discrepancy amongst existing studies on the effects of river regulation by hydroelectric dams (Poff & Zimmerman 2010), and the likelihood of species-specific effects (e.g. Korman & Campana 2009; Finch et al. 2015), this chapter investigates the response of three forage fish species to two different hydropeaking regimes in the Magpie River, and relative to the naturally flowing Batchawana River. The general hypotheses for this chapter were that fish growth, condition and survival would differ between the Batchawana and Magpie Rivers and between hydropeaking regimes in the Magpie River, and that between-river differences would be species-specific. The hypotheses were based on the different morphological, behavioural and habitat preferences of the three study species (Table 1.1). The objective of this chapter was to characterize the diversity of responses to river regulation within the forage fish community. The data collected for this purpose will help to inform management decisions aimed at mitigating impacts on the fish community.

Chapter 4: Downstream effects of hydroelectric dam operation on fish thermal habitat use: Implications for dam management in an era of climate change

Although hydroelectric dam operation alters the downstream thermal regime (Casado et al. 2013), fish are capable of thermoregulating by relocating within a river reach to microhabitats with more suitable temperatures (Petty et al. 2012). The objective of this chapter was to determine the impact of altered thermal regimes on fish thermal habitat use. A detailed analysis of the thermal regime in both the Batchawana and Magpie rivers was conducted with respect to the five components of the thermal regime and species-specific preference, avoidance and upper incipient lethal level temperatures. Thermal habitat use by slimy sculpin and brook trout were chosen for comparison, as both these species are part of the coldwater fish guild (Magnuson et al. 1979), but exhibit different morphologies and behaviour. The hypotheses for the chapter were that fish thermal habitat would differ between rivers and between species, and that fish living at temperatures closer to their preferred temperature would exhibit higher condition. The hypotheses were based on the difference in temperature and habitat preferences between species (Table 1.1) and the potential for the cool water draw at the Steephill Falls Dam to significantly reduce downstream temperatures in the Magpie River. The results are discussed within the context of the potential use of cool water releases from hydroelectric dams to mitigate climate change driven river water temperature increases.

Chapter 5: Impact of river regulation on the growth, condition and field metabolism of brook trout (Salvelinus fontinalis)

Brook trout is an important recreational species in Canada (Fisheries and Oceans Canada 2010) and both the Batchawana and Magpie Rivers support a recreational fishery for this species. The objective of this chapter was to determine the impact of both hydropeaking regimes in the Magpie River on the length-at-age, condition and relative metabolic rate of brook trout relative to the naturally flowing Batchawana River. The hypotheses for the chapter were that brook trout length-at-age and condition would be higher in the regulated river relative to the naturally flowing river, and that field metabolic rates would be higher in the regulated river and positively correlated to time spent hydropeaking. The hypotheses were based on the potential for an increased food supply related to impoundment and/or hydroelectric dam operation (Patterson & Smokorowski, 2011; Jones 2013), and the increased activity and movement during hydropeaking events (Murchie & Smokorowski 2004) exhibited by brook trout. The information reported in the chapter can be used to inform the management of the recreational brook trout fishery in the Magpie and Batchawana Rivers.

Chapter 6: Thermal habitat segregation among whitefish morphotypes and invasive vendace: a mechanism for co-existence?

This chapter investigates how river regulation from hydroelectric dam operation can alter the inter-species interactions between a native (whitefish) and invasive (vendace) fish species. Hydroelectric dam operation alters river morphology and influences the availability of different habitats within the riverine system. A natural flow regime favours native species, while altered flows resulting from hydroelectric dam operation can facilitate the establishment of non-native species (Marchetti & Moyle 2001). In this thesis, the thermal habitat, dietary resource use patterns and field metabolic rates of the native whitefish and invasive vendace were investigated. The general hypothesis for the chapter was that these two species would exhibit thermal habitat partitioning where different thermal habitats were available and dietary partitioning would occur where different thermal habitats were not available. The chapter provides information on the mechanisms which contribute to the success of an invasive fish species.

Table 1.1 Morphology, substrate, velocity, temperature and feeding preferences of brook trout, longnose dace, slimy sculpin, trout perch, vendace and three morphotypes of whitefish.

Species	Morphology	Substrate Preference	Velocity Preference	Temperature Preference	Feeding Preferences
brook trout	Elongate trout-like body, terminal mouth[a]	Boulder, cobble, rubble[b]	Pool[c] $30, 50\ \text{cm}\cdot\text{s}^{-1}$ for juvenile and adult, respectively[d]	16.0-17.3[e]	Aquatic insect larvae, terrestrial insects, fish[a]
longnose dace	Round body, inferior mouth[a]	Boulder, cobble, rubble, gravel[b]	Riffle, rapid[b] $65\ \text{cm}\cdot\text{s}^{-1}$[d]	5.4-22.7°C[f] (entire range)	Chironomids, algae, midge and diptera larvae[g]
slimy sculpin	Laterally compressed body, mouth has protruding upper lip[a]	Boulder, cobble, rubble, bedrock, gravel, sand[b]	Riffle[b] $30\ \text{cm}\cdot\text{s}^{-1}$[d]	10-12 °C[h]	Aquatic insects, crustaceans, small fishes, aquatic vegetation [g]
trout perch	Thick body, ventral mouth[a]	Gravel, sand, boulder, cobble, rubble[b]	Pool[b]	10 – 16°C[i]	Chironomids, amphipods, mollusks, small crustaceans [g]
vendace	Long thin closely spaced gill rakers[j]	Pelagic habitat[j]	Lacustrine	9°C[k]	Zooplankton[j]
whitefish, pelagic morph	Comparatively small size, long thin closely spaced gill rakers[l]	Pelagic habitat[j]	Lacustrine	NF	Zooplankton[m]
whitefish, littoral morph	Comparatively large size, intermediate size and spacing of gill rakers[l]	Littoral habitat[j]	Lacustrine	NF	Benthic invertebrates[m]
whitefish, profundal morph	Large head, subterminal mouth, large widely spaced gill rakers[l]	Profundal habitat[j]	Lacustrine	NF	Benthic invertebrates[m]

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[a] Scott & Crossman 1973

[b] Portt et al. 1999 (preference refers to high usage)

[c] Cunjak & Green 1983

[d] Peake 2008 $\text{cm}\cdot\text{s}^{-1}$ refers to the critical velocity criteria for fishway design above which species would be unable to swim for sustained periods

[e] Cherry et al. 1977 based on an acclimation temperature of 18°C

[f] Edwards et al. 1983

[g] Richardson et al. 2001

[h] Otto & Rice 1977

[i] Coutant 1977

[j] Bøhn & Amundsen 2001

[k] Ohlberger et al. 2008

[l] Siwertsson et al. 2010

[m] Kahilainen & Østbye 2006

NF not found

Chapter 2 Slimy sculpin (*Cottus cognatus*) annual growth in contrasting regulated and unregulated riverine environments

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Introduction

Hydroelectric dams are an important source of energy in Canada, providing over 60% of the country's electricity (Statistics Canada 2013). Dams contribute significantly to the proportion of both total and renewable electricity produced, but can have major impacts on downstream physical conditions and biological communities (Sabater 2008). Hydroelectric dams alter river discharge patterns by reducing the variability of flows, changing the timing of flow events and dampening seasonal trends (Poff et al. 2007). Hydroelectric peaking operations, in particular, induce large daily fluctuations in discharge to meet daily patterns in electricity demand (Morrison & Smokorowski, 2000). While peaking gives electricity producers flexibility in responding to market forces, large daily fluctuations are a phenomenon that have no parallel in natural freshwater systems (Poff et al. 1997). Aquatic communities are adapted to the gradient of physical conditions along the length of a river (Vannote et al. 1980), and can adjust to the many discontinuities imposed by river regulation (Ward & Stanford 1983). Thus, hydroelectric operations in general (Baxter 1977), and peaking operations in particular, can have lasting impacts on downstream organisms (Cushman 1985; Moog 1993).

A variety of impacts from altered flow regimes have been identified for fish, including: mortality as a result of stranding (Hvidsten 1985; Young et al. 2011), changes in abundance (Freeman et al. 2001), an increase in invasive species (Marchetti & Moyle 2001; Brown & Ford 2002), changes in growth (Korman & Campana 2009; Bond et al. 2015), and changes in fish movement patterns (Dare et al. 2002; Murchie & Smokorowski 2004). The magnitude and direction of impacts on fish populations vary by study, and the identification of general trends in the response of biotic communities to flow alteration has proved elusive (Poff & Zimmerman 2010). The inapplicability of simple overarching and straightforward flow rules (Arthington et al. 2006) make it difficult to design and implement effective environmental flow regulations. Thus, an increase in long-term experimental studies, which focus on hydrological alterations and their impacts on biological communities, are needed to identify mechanistic relationships and facilitate ecologically-based river management (Monk et al. 2007; Mims & Olden 2013).

Fish growth is a useful individual based-metric for characterizing the effects of river regulation on downstream fish communities. The release of reservoir water from hydroelectric dams can indirectly influence fish growth as a result of altered water temperatures (Olden & Naiman 2010), increasing invertebrate drift (Lauters et al. 1996; Lagarrigue et al. 2002) and increased abundance of benthic invertebrate communities (Jones 2013). However, few studies assess the impact of river regulation on fish growth. Korman & Campana (2009) determined that reduced hourly flow fluctuations on weekends corresponded with increased daily growth in young-of-the-year rainbow trout (*Oncorhynchus mykiss*, Walbaum) in a hydropeaking river (Korman & Campana 2009), while Finch et al. (2015) found that growth of juvenile humpback chub (*Gila cypha*, Miller) had higher growth rates under hydropeaking flows relative to steady flows. Bond et al. (2015) found higher slimy sculpin (*Cottus cognatus*, Richardson) growth rates in two regulated rivers relative to eight naturally flowing nearby rivers. Given that responses to altered flow are likely species-specific, and most studies to date have been carried out over short time periods, we suggest that long-term temporal studies assessing fish growth under multiple hydropeaking regimes would provide further valuable insight into the impacts of hydropeaking on fish.

To better understand the potential impacts of flow regimes altered by hydroelectric operations on fish, we determined annual growth rates for slimy sculpin collected along a longitudinal river gradient from a pair of boreal rivers in Ontario (ON), Canada, one with a 15 MW peaking dam, the other with a natural flow regime. We assessed the impact of river regulation on fish growth under two different hydroelectric operating regimes and investigated the suitability of hydrologic indices for explaining differences in fish growth.

Slimy sculpin (hereafter referred to as “sculpin”) is a small bodied benthic fish, common throughout Canada and has been proposed as a sentinel species (Edwards & Cunjak 2007) because of its small home range (Gray et al. 2004) and site fidelity (Cunjak et al. 2005). As a result, sculpin have been shown to reflect local conditions along a river continuum (Edwards & Cunjak 2007) and can be used to indicate environmental degradation (Galloway et al. 2003). In addition, the behavioural traits of sculpin make them an interesting species with which to assess the impacts of altered flow regimes. For example, the closely related Mottled Sculpin (*C. bairdii,* Girard) have been shown to maintain position with no change in oxygen consumption at velocity ranges of up to 8 body lengths/second (Facey & Grossman 1992) by staying close to the substrate, a strategy facilitated by their large pectoral fins (Facey & Grossman 1990). Thus, sculpin may not be as susceptible as salmonids to the increased energetic demands associated with fluctuating flow regimes (Scruton et al. 2008; Cocherell et al. 2011), and may be able to take advantage of increased food availability in the regulated system.

We formulated several hypotheses for the potential responses of sculpin growth to the altered flow regime created by a hydropeaking dam with a minimum environmental flow, based on the changes to food availability in hydropeaked systems (Lauters et al. 1996; Lagarrigue et al. 2002; Jones 2013), the potential for sculpin to avoid increased energetic demands (Facey & Grossman 1992) and a previous study on sculpin growth (Bond et al. 2015). First, we hypothesized that sculpin annual growth would be higher in the regulated river than the natural river, and higher under the unrestricted ramping regime relative to the restricted ramping regime. Second, a gradient of growth effects with distance from the dam would be seen in the regulated river, with higher annual growth at sites closest to the dam, but no gradient with distance from the upstream valley segment would be seen in the naturally flowing reference river. Finally, we investigated a set of hydrologic indices proposed in the literature to identify the aspect(s) of the natural and hydropeaked flow regimes that may lead to differences in sculpin growth. Given that water releases from dams can increase lentic and lotic invertebrate abundance downstream (Jones 2013), we hypothesized that more frequent or higher discharge peaking events would indirectly increase the sculpin food supply and, therefore, hydrologic indices which capture the magnitudes and frequencies of peaking events would be positively related to sculpin growth.

Methods

Study Sites

Samples were obtained from a pair of boreal shield rivers in northern Ontario selected to assess the impact of varying hydroelectric hydropeaking regimes on downstream systems relative to a proximate river with similar physical conditions and a natural flow regime (e.g. Smokorowski et al. 2011). The Batchawana River near Sault Ste. Marie ON (47°0’N; 84°30’W) has a natural flow regime and was chosen as the comparative control to the regulated Magpie River near Wawa ON (48°4’N; 84°44’W), which has a 15 MW hydropeaking facility (Fig. 2.1).

The river reach sampled in the Batchawana River was selected on the basis of proximity and similar drainage area, geology, river geomorphology, fish species composition, historical mean annual discharge, and the availability of long-term flow gauge data (Marty et al. 2009; Smokorowski et al. 2011). We chose a section to sample within the control river that was not immediately downstream from a lake to simulate the placement of a dam within a river reach and to avoid the confounding factor of increased water temperatures often observed downstream from lake outlets (Wotton 1995).

The Steephill Falls Dam and Generating Station (SHF) are located together on the Magpie River. The SHF facility is located at a natural falls, has been operational since 1989, draws water from a depth of 10 m and has a maximum passable flow of 44 $m^3 \cdot s^{-1}$. From 1989 through 2004, regulations for the “restricted hydropeaking regime” required a minimum flow of 7.5 $m^3 \cdot s^{-1}$, and ramping restrictions of $\leq 1\ m^3 \cdot s^{-1} \cdot hr^{-1}$ from October 10th through November 15th, 2 $m^3 \cdot s^{-1} \cdot hr^{-1}$ from November 16th through the spring freshet, and no greater than a 25% increase or decrease from the previous hour’s flow from the spring freshet to October 9th (Smokorowski et al. 2011). The ramping rate restrictions were removed in the fall of 2004 (“unrestricted hydropeaking regime”), although the minimum flow requirement of 7.5 $m^3 \cdot s^{-1}$, measured at SHF was maintained. The unrestricted hydropeaking regime enabled the hydro operator to increase from the minimum required flows to the maximum passable flow through the turbines and back down again on a daily or sub-daily basis, while under the restricted hydropeaking regime, daily discharge changes of this magnitude were not possible (Smokorowski et al. 2011).

Sampling

Sculpin were collected by backpack electrofishing during July and August of 2002 through 2012 (resulting in growth estimates for the years 2002 through 2010) at randomly selected transects below SHF in the Magpie River. Randomly selected transects of 100 m in analogous river valley segments were sampled in the Batchawana River to ensure that similar habitats between rivers were sampled (Smokorowski et al. 2011). An additional site upstream of the SHF reservoir in the Magpie River was sampled as an in-river control. Sites were fished to a depth of 60 cm, which was a safe depth for backpack electrofishing in these rivers and which represents a significant proportion of the total area in both rivers. The longitudinal distance along which the river was sampled was 12 km on the Batchawana River, and 19 km on the Magpie River. Backpack electrofishing was standardized to a rate of 4 $s \cdot m^2$. The majority of fish were preserved in formalin (24-30 hrs) followed by ethanol, while a subset of fish were frozen to avoid preservation biases (Storm-Suke et al. 2007b; Kelly et al. 2006) for future stable isotope analysis. Species identification was confirmed in the lab following keys in Scott & Crossman (1973) and McAllister (1964); sex was determined by examination of the gonads, and length (mm) and weight (g) measurements were obtained. Sculpin density and biomass were calculated for each 100 m transect sampled as number of sculpin per m^2, and the total weight (g) of sculpin per m^2, respectively.

Sagittal otoliths from sculpin were removed and stored dry in plastic snap cap vials. A preliminary study showed no difference in otolith diameter (µm), radius (µm) or weight (mg) between dried, frozen, or ethanol preserved otoliths (Student's t test, $p>0.05$, data not shown). Aging was conducted with a dissecting microscope (Nikon SMZ 1000, Nikon Instruments Inc.) using whole otoliths placed in deionized water under reflected light. All otoliths were read twice by the same reader and where discrepancies existed, otoliths were polished or thin sectioned. If a discrepancy between ages persisted, the sample was removed from the analysis. Corroboration of ages included consultation with other sculpin age readers and examination of the length frequency diagram by age-class. Otolith increments consisting of an annual cycle were measured at 90 degrees from the rostral radius along a line from the nucleus towards the dorsal edge using NIS Elements software (Nikon Instruments Inc.). Only full annuli were measured, such that the partial growth during year of capture was not included in the analysis. Only the first and second full year's growth could be included in the statistical analysis due to low sample numbers of 3+, 4+ and 5+ aged fish. Growth (ΔL) was measured as the individual absolute increase in length for one annual cycle where length at age was determined by back-calculation using the scale proportional hypothesis as outlined in (Francis 1990):

$$L_i = -(a/b) + (L_c + a/b)(S_i/S_c),$$

where L_i is the length of the fish at age i, L_c is the length of the fish at capture, S_i is the radius of the otolith at age i, S_c is the radius of the otolith at capture, and a and b are the intercept and slope, respectively, of the regression of otolith radius on fish length. The regression of otolith radius on fish length was conducted separately by site within each river, given the potential for differences in growth rates and otolith formation rates amongst sites.

River discharge data were measured with data loggers (Keller 173-L pressure transducer (2002-October 2004), and Solinst Leveloggers (October 2004 through 2010)) every half hour in

2002 and every fifteen minutes thereafter from 2003 through 2010 (Metcalfe, unpublished data). Data loggers were located upstream from the SHF reservoir and at three locations downstream from SHF in the Magpie River, as well as at two locations in the Batchawana River. In addition we accessed flow data from two Water Survey of Canada gauges, 02BD007 (Magpie River) and 02BF001 (Batchawana River).

Data Analysis

Statistical analyses were completed in R (R Core Team 2014). Normal quantile-quantile plots were used to assess the normality of the data while Bartlett's test was used to assess homogeneity of variance (Bartlett 1937). Individual fish were treated as replicates within each river for between river comparisons, and within each site for among-site comparisons. Differences in first and second year annual growth and length at ages 1 and 2 between male and female sculpin were tested within each river using a Welch's t test. No significant differences were found ($p>0.05$) and male and female sculpin were pooled in subsequent analyses. A Welch's t-test (Welch, 1947) was used to test for differences in ΔL between hydropeaking regimes in the regulated river and between the regulated and natural rivers for first and second year growth. A difference in ΔL between the time periods encompassed by the two hydropeaking regimes was also tested with Welch's t test in the natural river to control for potential weather and climate related impacts. Linear regression was used to assess differences in ΔL with distance from the dam in the regulated river and distance downstream in the natural river. Distance downstream in the naturally flowing river was measured from the beginning of the river valley segment within which the randomly selected sampling transects were located. Pearson's partial correlation coefficient was used to assess whether sculpin density and biomass were significantly correlated with sculpin growth when distance downstream was controlled for.

A linear model was used to investigate more directly the impact of discharge on ΔL. Numerous hydrologic indices have been applied in the literature to characterize river flow patterns and have been used to explain differences in macroinvertebrate assemblages (Monk et al. 2007; Konrad et al. 2008; Kennen et al. 2010), fish diversity and abundance (Yang et al. 2008) and fish recruitment (Nicola et al. 2009). Here, hydrologic indices were chosen to represent each of the fundamental components of the flow regime: magnitude, timing, duration, frequency and rate of change (Richter et al. 1996; Poff et al. 1997). Nine hydrologic indices were chosen in total, corresponding to each of the nine flow regime components outlined by Olden &

Poff (2003). Each of the chosen indices is known to have a large absolute loading in a statistically significant principal components analysis for streams in the US (Olden & Poff 2003). Slight modifications from the calculations in Olden & Poff (2003) were sometimes necessary to suit study and data availability (Table 2.1.) For example, flow indices were calculated for the growing season (June 1st to September 30th) of each year in the study, rather than for the entire period of record. As well, the absolute rate of change of discharge was calculated in this study instead of a separate calculation for the rate of increase and the rate of decrease. Discharge data used to calculate the nine hydrologic indices were taken from the data logger 2.5 km below SHF in the Magpie River and from the Water Survey of Canada station 02BF001 in the Batchawana River. Multi-collinearities were identified and removed by running the model using a correlation matrix based on the Pearson product-moment correlation coefficient (R Core Team 2014). The Akaike information criterion (AIC) (Hirogutu 1974) was used to refine the linear model, balancing goodness of fit and prediction power (R package MASS; Venables & Ripley 2002). The relative importance of each of the variables included in the final model was approximated following Lindeman et al. (1980) using a ranking based on standardized regression coefficients (R package relaimpo; Grömping 2006).

Results

Sculpin (n=1163) collected from 2002 through 2012 ranged in length from 12 to 126 mm and resulted in first and second year ΔL estimates for the years 2002 through 2010. However, degradation of some otoliths from fish preserved in formalin followed by ethanol resulted in no ΔL estimates for second year growth for 2006 and only one estimate for 2008 in the Magpie River. Average sculpin ΔL ± standard deviation in the Magpie River (regulated) for first and second growth years was 47.9±8.0 and 18.6±7.3 $\text{mm}\cdot\text{yr}^{-1}$, respectively, during the restricted ramping period, and 47.5±8.1 and 19.1±7.0 $\text{mm}\cdot\text{yr}^{-1}$ during the unrestricted ramping period. In the Batchawana River (natural) sculpin ΔL for first and second growth years was 41.5±4.2, and 13.6±5.1 $\text{mm}\cdot\text{yr}^{-1}$, respectively, during the period of restricted ramping in the regulated river, and 42.1±4.9 and 15.7±5.2 $\text{mm}\cdot\text{yr}^{-1}$ during the period of unrestricted ramping in the regulated river (Fig. 2.2).

There was no difference in ΔL between hydropeaking regimes for first year growth (Welch's $t_{165.2}$=0.16, p>0.05) or second year growth (Welch's $t_{21.8}$=1.68, p>0.05) in the regulated river (Fig. 2.2). There was also no difference in ΔL between the time periods encompassed by the hydropeaking regimes for first year growth (Welch's $t_{223.7}$=1.19, $p>0.05$) or second year growth (Welch's $t_{37.2}$=1.84, $p>0.05$) in the naturally flowing river (Fig. 2.2). As such, the remainder of comparisons were computed using growth data from all years combined. There was a significant difference between ΔL in the regulated and natural river for first year growth (Welch's $t_{507.8}$=10.3, $p<0.05$) and second year growth (Welch's $t_{113.4}$=3.04, $p<0.05$), with growth in the regulated river being higher (Fig. 2.2). Variance in annual growth was significantly different between rivers for first year ΔL (Bartlett's test, K-squared$_1$=49.82, $p<0.05$) and second year ΔL (Bartlett's test, K-squared$_1$=26.11, $p<0.05$) and was higher in the regulated river (Fig. 2.2).

Both first and second year ΔL in the regulated river were significantly related to distance from the dam ($p<0.05$, r^2=0.12 and 0.19 for first and second year growth, respectively) (Fig. 2.3), with ΔL decreasing with distance downstream. A between-site ANOVA followed by Tukey's *post hoc* test showed that both first and second year sculpin growth in the regulated river decreased to rates not significantly different from the upstream control site at a distance of 4 km downstream from the dam ($F_{8,396}$=10.68, $p<0.05$). First year ΔL in the natural river was also significantly related to distance ($p<0.05$, r^2=0.03), but in contrast to the regulated river increased with distance downstream. There was no significant relationship between growth and distance for second year ΔL in the natural river. There was also no significant correlation between growth and density or biomass in either river when distance downstream was controlled for (Pearson's partial correlation coefficient, $p>0.05$).

Growth season values for the nine flow regime components included in the multiple regression are listed in Table 2.2. Consistent dam operations, and thus consistent values for the flow regime components, were expected within each flow regime. However, there were two anomalous years in the unrestricted ramping period on the regulated river: 2008 was an uncharacteristically wet year, leading to higher discharge, while 2010 was an uncharacteristically dry year, leading to lower discharge. In both those years, ramping was reduced relative to other years throughout the study period.

When explanatory power of the model relating sculpin growth to the tested hydrological indices was significant, it was low and the pattern of hydrologic indices contributing to the explanatory power was not consistent among sites. The variation in sculpin ΔL explained by the flow regime components was significant for first year ΔL in the regulated river (r^2=0.12), but not for second year ΔL. Upstream from the reservoir in the regulated river, the model was significant for both growth years ($r^2=0.25$ and 0.33, respectively) (Table 2.3). The model was also significant for both first and second year ΔL in the natural river, but explained only a small proportion of the variance in ΔL ($r^2=0.11$ and 0.11, respectively). The hydrologic indice responsible for the highest proportion of variation explained by the model differed between upstream from the reservoir (F_L1) and downstream from the dam (D_H15) in the regulated river and between the regulated and natural river (M_H1) (Table 2.2). Rate of change was positively related to ΔL in the regulated river, but negatively related to ΔL in the natural river. When the anomalous years 2008 and 2010 were removed from the data set used to estimate the model, there was no longer a significant relationship between hydrologic indices and first year ΔL in the regulated river. An ANOVA and Tukey's HSD showed that first year ΔL in 2008 was significantly higher than in years 2002 and 2010, and first year ΔL in 2009 was significantly higher than in 2010 ($F_{7,\,220}=4.07$, $p<0.05$) (Fig. 2.4). There were no significant differences in second year ΔL between years in the regulated river ($F_{5,\,44}=1.71$, $p>0.05$), however, no second year growth samples were available for 2008.

Discussion

Sculpin annual growth rates did not differ between the periods encompassed by the two different ramping rate regimes in either the regulated Magpie River or the naturally flowing Batchawana River. Growth rates differed between the rivers, with higher average annual growth rates observed in the regulated river. A decrease in growth rates for both growth years was detected with increasing distance from the dam in the regulated river, while an increase in growth rates for first year growth was observed in the naturally flowing river. Sculpin density and biomass did not account for any variation in growth beyond that which was explained by distance downstream. Tested hydrologic indices accounted for only a small proportion of the explained variation in sculpin growth in either river, and significant hydrological indices were not consistent among sites. Thus, while data obtained for sculpin indicate there are impacts associated with changing river flow regimes (natural versus regulated), sculpin in general do not indicate strong growth-flow correlations under either natural or altered flow conditions.

Flow patterns resulting from a hydropeaking regime could be expected to increase energetic costs, and thus lower growth as a result of increased movement during peak flow events (Murchie & Smokorowski 2004; Scruton et al. 2008; Cocherell et al. 2011), exposure to higher velocities (Korman & Campana 2009) and/or changes in foraging behaviour (Cocherell et al. 2011). In contrast, our higher sculpin growth in the hydropeaking river relative to the naturally flowing river could be explained by potential benefits provided by the dam and its operations, such as increased nutrient delivery (Hildebrand 1980), increased benthic invertebrate abundance (Jones 2013), changes to the thermal regime (Olden & Naiman 2010) which shift water temperatures closer to the optimum for sculpin, and maintenance of a minimum flow requirement (Weisberg & Burton 1993). In addition, sculpin display life-history traits and behaviour that may enable them to cope with increased peaking without reducing the resources allocated to growth. Below we explore the validity of these possibilities within the context of our study systems.

In the regulated river sampled in this study, the metalimnetic dam draw (Smokorowski et al. 2011) results in cooler water temperatures throughout the summer (by an average of 2.2°C) and slightly warmer temperatures throughout the winter (by an average of 1°C). While the preferred water temperature for sculpin is 10°C (Otto & Rice 1977), temperatures in both rivers routinely exceed this point in the summer and can also exceed the upper incipient (21°C; Otto & Rice 1977) and ultimate incipient lethal (26°C; Otto & Rice 1977) levels for sculpin. However, the regulated river remains cooler in the growing season relative to the natural river (1.7°C cooler on average during restricted ramping and 2.4°C cooler on average during unrestricted ramping 2.5 km below the dam). High temperatures in the natural river would cause an increase in standard metabolic rate and a reduction or cessation of feeding (e.g. Elliott 1994), resulting in less assimilated energy being allocated towards growth. The cooling effect of the metalimnetic draw in the regulated river would maintain a thermal environment conducive to sculpin feeding throughout more of the growing season, while sculpin would maintain a lower standard metabolic rate. As such, the more favourable water column temperatures in the regulated river may have reduced fish energetic costs and increased feeding opportunities, contributing to higher growth.

Food availability and foraging success, which are key determinants of fish growth, are impacted by river impoundment in general, as well as by the different hydropeaking regimes in our regulated river. Although we did not measure invertebrate abundance directly in this study, several publications have reported on this topic in detail for our two study rivers for the years encompassed by our study (Patterson & Smokorowski 2011; Jones 2013; Tuor et al. 2014; Bond et al. 2015). In our hydropeaking river, there was a higher abundance of invertebrates in the benthos (Jones 2013) relative to nearby naturally flowing rivers. In addition, stomach contents of small bodied fish (including sculpin) had a higher abundance of invertebrates in the regulated river relative to the naturally flowing river (Tuor et al. 2014). A higher abundance of invertebrates in the benthos, an important food source for sculpin (Petrosky & Waters 1975), coupled with a higher abundance of invertebrates in stomach contents suggests a higher foraging success in the regulated river, resulting in the higher observed growth. Indeed, Bond et al. (2015) found a positive correlation between sculpin growth rates and invertebrate density for a set of rivers including both the Magpie and Batchawana Rivers.

However, Tuor et al. (2014) also found a higher abundance of invertebrates in the stomach contents of small bodied fish during the unlimited ramping regime in the regulated river relative to the restricted ramping regime, and a change in the species composition of stomach contents to a higher proportion of primary consumers relative to predatory macroinvertebrates. The lack of difference in growth between the two hydropeaking regimes, despite the increase in stomach contents, suggests that increased energy intake during unlimited ramping was offset by increased energy outputs, or nutritional quality was decreased by the shift in taxonomic composition in stomach contents, or a combination of both. The possibility of increased energetic costs suggests a response threshold exists for sculpin where positive forage-related gains from increased variable flows are ultimately outweighed by the associated energetic costs of standard metabolic rate. Thus, the absence of a significant difference in sculpin growth between the two hydropeaking regimes does not mean that the two hydropeaking regimes were equivalent in their impacts on sculpin.

Invertebrate abundance in the regulated river was highest at the site closest to the dam, but decreased to levels found in natural rivers 5-8 km below the dam (Jones 2013). This coincides well with our finding that sculpin growth was highest near the dam, with growth decreasing to levels not significantly different from upstream at 4 km below the dam. In the naturally flowing Batchawana River, benthic invertebrate abundance increases with distance downstream (Jones 2013), as do our first year annual growth rate measurements for sculpin. These results may be expected based on current stream ecological theory. Cooler water temperatures, increased particulate drift and increased abundance of filter feeding invertebrates below dams (Ward & Stanford 1983; the serial discontinuity concept) would produce conditions beneficial for sculpin growth. As river water temperatures are attenuated and benthic invertebrate abundances decrease to levels similar to naturally flowing rivers with distance downstream, sculpin growth would be expected to, likewise, decrease with distance downstream. Conversely, in the middle reaches of a naturally flowing river without a significant input of particulate organic matter, the filter feeding invertebrate community may have a lower abundance relative to river reaches below a dam. As the river shifts from heterotrophy to autotrophy with distance downstream and the benthic community of collectors and grazers increases in abundance (Vannote et al. 1980, the river continuum concept), food availability for sculpin may increase, driving an increase in sculpin growth with distance downstream.

While invertebrate abundance can increase immediately below dams (Spence & Hynes 1971; Jones 2013), with consequences for productivity at higher trophic levels, the same phenomenon can occur in riverine habitats below naturally occurring lakes (Richardson & Mackay 1991; Jones 2010). The river reach sampled in the Batchawana River as a control for our regulated Magpie River was not immediately downstream from a lake. Yet, given that our study dam has a cool water draw, the ideal environmental control may not be obtainable. The outlet water from natural lakes is composed of lake surface water, which is often warmer than downstream river temperatures, increasing water temperatures immediately downstream (Wotton 1995). As discussed above, the alteration of downstream water temperatures is an important factor for coldwater species such as sculpin. Higher water temperatures from the outlet of a natural lake would increase sculpin metabolic costs relative to a lake-less river reach, potentially offsetting benefits from an increased food supply. Therefore, we chose to compare our study river with a lake-less river reach to determine the impacts of a hydroelectric dam built within a river reach as opposed to at the outlet of a lake.

During both experimental periods, the requirement of a minimum discharge (7.5 $m^3 \cdot s^{-1}$) in the regulated river remained in place, which has demonstrated benefits to fish (Weisberg & Burton 1993; Travnichek et al. 1995). The requirement often resulted in a mid-summer discharge in the regulated river above that which was experienced in the naturally flowing river (see discharge parameter M_L1, Table 2.2). In general, discharge parameters positively correlated with the frequency and duration of high discharge events were important components of the explained variation in annual growth in both rivers, suggesting that higher discharge provides benefits realized in higher sculpin growth rates. For example, Weisberg & Burton (1993) noted an increase in invertebrate abundance and increased foraging success, once a minimum flow requirement was instituted below the Conowingo Dam in Maryland, US. Therefore, continuation of the minimum discharge requirement, as well as higher mean flows (Table 2.2), may in part explain the higher annual sculpin growth rates in the regulated river relative to the natural river.

Variance in growth rates was higher in the regulated river relative to the natural river. Variability in discharge (Rand et al. 2006) and resource availability (Nislow et al. 2004) can lead to variability in energy allocation, resulting in differential growth. Invertebrate abundance and community composition differs along both lateral and longitudinal gradients in both the rivers in this study with depth and velocity being important factors contributing to the gradients in the regulated river (Jones 2013). The longitudinal gradient in invertebrate abundance in the regulated river likely contributes to the longitudinal gradient in growth in the regulated river, as discussed previously above, driving the higher variation in growth rates seen in the Magpie River.

Higher annual growth rates of sculpin in the regulated river and decreasing growth rates with distance from the dam coincide with trends between rivers reported for sculpin by Bond & Jones (2015), but not the specific growth-flow relationships reported by Korman & Campana (2009) for rainbow trout. While Korman & Campana (2009) reported an increase in daily growth with reduced ramping, sculpin growth was not higher under the restricted regime in the regulated river. The closely related Mottled Sculpin are most often found underneath the cover of rocks or clinging to substrate (Facey & Grossman 1992), with the tactical use of substrate necessitated by their poor swimming ability (Facey & Grossman 1990). Field observations in this study suggest that slimy slimy sculpin behave similarly to Mottled Sculpin, with the apparent advantage of reducing energetic expenditure even under high, hydropeaking induced discharge rates and rates of change. Thus, sculpin likely avoid the negative consequences of increased discharge by taking refuge in the substrate, while juvenile rainbow trout which maintain position during peaking events do not (Korman & Campana 2009). However, it cannot be presumed that the higher growth rates in the regulated river relative to the naturally flowing river are a beneficial response to river regulation or will necessarily lead to higher relative abundance in the regulated river, as higher sculpin growth rates in the Magpie River led to younger age at maturity and higher instantaneous mortality rates (Bond et al. 2015). To understand the impacts of hydropeaking on fish growth more fully, investigations specific to particular fish body morphologies, age-class and behavioural strategies are needed (e.g. Scruton et al. 2003; Murchie & Smokorowski 2004).

Weak correlations between hydrologic indices and annual sculpin growth rates, despite significant differences in growth rates between rivers, highlight the importance of the indirect effects of altering flow regimes on fish species. Indeed, when two anomalous years during which peaking operations were suspended are removed from our analysis, there was no significant relationship between first or second year sculpin growth and hydrologic indices in the regulated river. However, changes in flow regimes do not have ubiquitous effects for all species, as not all fish species respond equally to flow, and indirect impacts associated with flow alteration may compensate for negative impacts. Therefore, it is imperative that both biotic (Bunn & Arthington 2002) and abiotic (Cushman 1985) factors be included in study designs to properly understand the impacts of altered hydrologic regimes, and how such alterations interact with species-specific life history traits. This paper provides valuable insight into the effects of two different hydroelectric peaking regimes on the growth of a little studied but widely distributed forage fish species with benthic behaviour. Our detailed hydrologic analysis highlights the importance of direct and indirect effects of flow alteration and lends support to current ecological theories, shedding light on how the ecological impacts of hydroelectric dams are manifested by a benthic fish species.

Table 2.1 Hydrologic indices chosen for the multiple regression analysis of flow on slimy sculpin growth. All metrics were calculated for the growing season (June 1st to September 30th) for each year of the study. Metric names and definitions from Olden & Poff (2003).

Category	Component	Olden & Poff Metric	Definition	Study Calculation
Magnitude	Average	M_A1	Mean daily flow	Mean daily flow
	Low flow	M_L1	Mean minimum monthly flow	mean for all months of minimum daily flow
	High flow	M_H1	Mean maximum monthly flow	mean for all months of maximum daily flow
Frequency	Low flow	F_L1	Low flow pulse count	number of events where daily flow dips below the 25th percentile for all years
	High flow	F_H1	High flood pulse count	number of events where daily flow rises above the 75th percentile for all years
Duration	Low flow	D_L16	Low flow pulse duration	mean number of days for events in F_L1
	High flow	D_H15	High flow pulse duration	mean number of days for events in F_H1
Timing		T_L1	Day of year with annual minimum	day of year with lowest daily flow
Rate of change		R_A1/R_A3	Rise/Fall rate	mean of absolute value of hourly change

Table 2.2 Hydrologic indices and the proportion of variation explained by each in a multiple regression for slimy sculpin first and second year growth in the naturally flowing river, the regulated river and upstream of the reservoir in the regulated river. Hydrologic indices are defined in Table 1.

											Proportion of variation explained	
	Metric	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**1st year**	**2nd year**
Natural Flow	$\mathbf{M_{A}1}$	8.82	9.26	7.82	3.71	3.98	8.01	7.96	12.65	12.33	-	**0.28**
	$\mathbf{M_{L}1}$	4.5	3.30	3.84	1.86	2.06	3.12	7.81	6.63	2.70	*	-
	$\mathbf{M_{H}1}$	17.14	26.40	15.64	7.91	10.09	23.20	14.98	24.13	61.31	**0.36**	**0.41**
	$\mathbf{F_{L}1}$	6	3	3	1	3	1	3	1	4	-	-
	$\mathbf{F_{H}1}$	2	5	2	91	28	37	8	10	10	0.05	**0.1**
	$\mathbf{D_{L}16}$	4.67	7.67	9.00	1.00	1.00	2.00	2.00	7.00	2.00	-	*
	$\mathbf{D_{H}15}$	18.5	5.80	10.50	7.00	4.00	8.50	13.50	8.71	7.50	**0.15**	**0.13**
	$\mathbf{T_{L}1}$	224	255	221	238	259	249	250	269	213	0.27	0.07
	$\mathbf{R_{A}1/R_{A}3}$	0.12	0.08	0.05	0.03	0.04	0.133	0.175	0.13	0.08	0.18	-
Growth	**1st year ± SD**	43.1±4.7	37.7±4.8	39.2±7.7	39.5±3.2	40.5±3.8	36.7±1.2	38.4±4.7	40.2±5.8	42.8±4.2		
	2nd year ± SD	22.7	16.0±4.9	11.8±4.6	14.1±3.5	12.9±3.1	13.6±4.8	17.2±2.8	15.9±2.7	17.0±4.0		
Regulated Down-stream	$\mathbf{M_{A}1}$	14.97	12.48	17.30	13.42	12.41	18.30	23.48	12.68	2.93	**0.21**	not sig.
	$\mathbf{M_{L}1}$	6.98	8.19	8.79	7.34	5.63	9.37	10.42	5.62	1.78	**0.16**	*
	$\mathbf{M_{H}1}$	29.44	20.65	27.18	20.08	22.48	28.38	42.33	20.82	5.69	*	*
	$\mathbf{F_{L}1}$	7	3	11	9	14	0	5	14	2	**0.07**	not sig.
	$\mathbf{F_{H}1}$	8	4	12	5	5	10	8	8	0	**0.10**	not sig.
	$\mathbf{D_{L}16}$	1.43	4.67	1.91	1.89	2.79	0.00	2.60	2.79	60.00	0.11	not sig.
	$\mathbf{D_{H}15}$	3.13	3.50	4.83	3.80	3.20	4.80	9.00	2.50	0.00	**0.23**	not sig.
	$\mathbf{T_{L}1}$	166	266	234	153	186	182	228	176	239	-	not sig.
	$\mathbf{R_{A}1/R_{A}3}$	0.56	0.33	1.24	1.8	2	2.4	1.8	1.7	0.08	**0.12**	not sig.
Growth	**1st year ± SD**	44.1±8.0	46.0±8.7	44.5±5.0	44.4±7.7	45.2± 10.5	47.3±9.5	52.4±6.8	49.4±9.9	44.5±6.9		
	2nd year ± SD	15.7±4.4	19.8±6.6	11.6±1.6	12.9±1.5	ND	17.97±5.8	20.7	23.4±8.9	19.2±5.6		

Table 2.2 continued

											Proportion of variation explained	
	Metric	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**1st year**	**2nd year**
Regulated - upstream	**M_A1**	ND	4.94	5.72	4.42	5.59	6.08	16.84	7.68	2.08	-	**0.3**
	M_L1	ND	4.05	4.65	3.06	4.03	4.18	10.17	5.54	1.36	*	*
	M_H1	ND	9.94	7.49	6.06	8.23	9.38	33.58	11.61	1.77	*	*
	F_L1	ND	2	0	1	1	0	1	0	1	**0.64**	-
	F_H1	ND	2	1	1	2	0	1	2	0	-	*
	D_L16	ND	3	0	76	24	0	10	0	124	-	*
	D_H15	ND	4	5	21	13	0	82	24	0	*	**0.36**
	T_L1	ND	256	220	270	265	249	272	232	220	**0.24**	0.34
	R_A1/R_A3	ND	0.014	0.011	0.022	0.026	0	0.081	0.035	0.0082	0.12	*
Growth	**1st year ± SD**	ND	51.1±4.2	44.7±5.6	43.1	ND	48.3±5.9	46.5±7.4	44.5±4.5	54.5±3.6		
	2nd year ± SD	ND	ND	10.2±4.6	15.6±1.8	ND	ND	23.1	18.3±3.7	18.8±2.5		

*removed because of a singularity with another independent variable as identified by a correlation matrix

- removed by AIC

bold numbers in the last two columns denote a positive relationship

ND denotes no data

Table 2.3 Multiple linear regression relating first and second year annual slimy sculpin growth to hydrologic indices. The linear regression results are for the models outlined in Table 2.

	Growth year	F statistic	degrees of freedom	p-value	Multiple r^2
Natural Flow	1	5.47	5, 230	<0.05	0.11
	2	2.81	5, 116	<0.05	0.11
Regulated downstream	1	4.79	7, 252	<0.05	0.12
	2	0.76	7, 54	>0.05	NA
Regulated upstream	1	5.62	3, 50	<0.05	0.25
	2	3.75	3, 22	<0.05	0.33

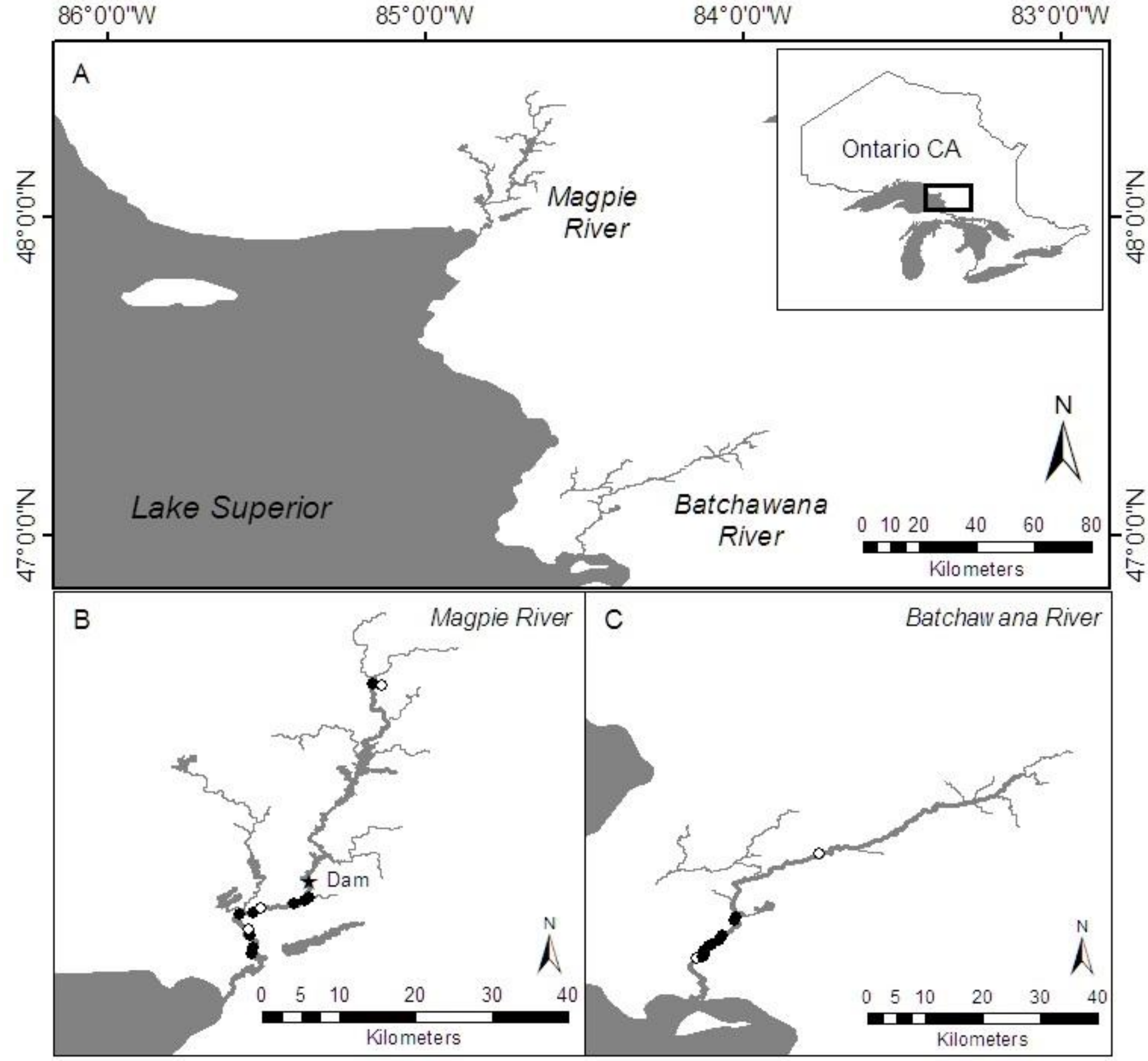

Figure 2.1 Magpie (regulated) and Batchawana (natural) Rivers in Ontario, Canada (A). Sampling sites are denoted by solid circles (●) and data logger locations are denoted by hollow circles (○) in the Magpie (B) and Batchawana (C) Rivers.

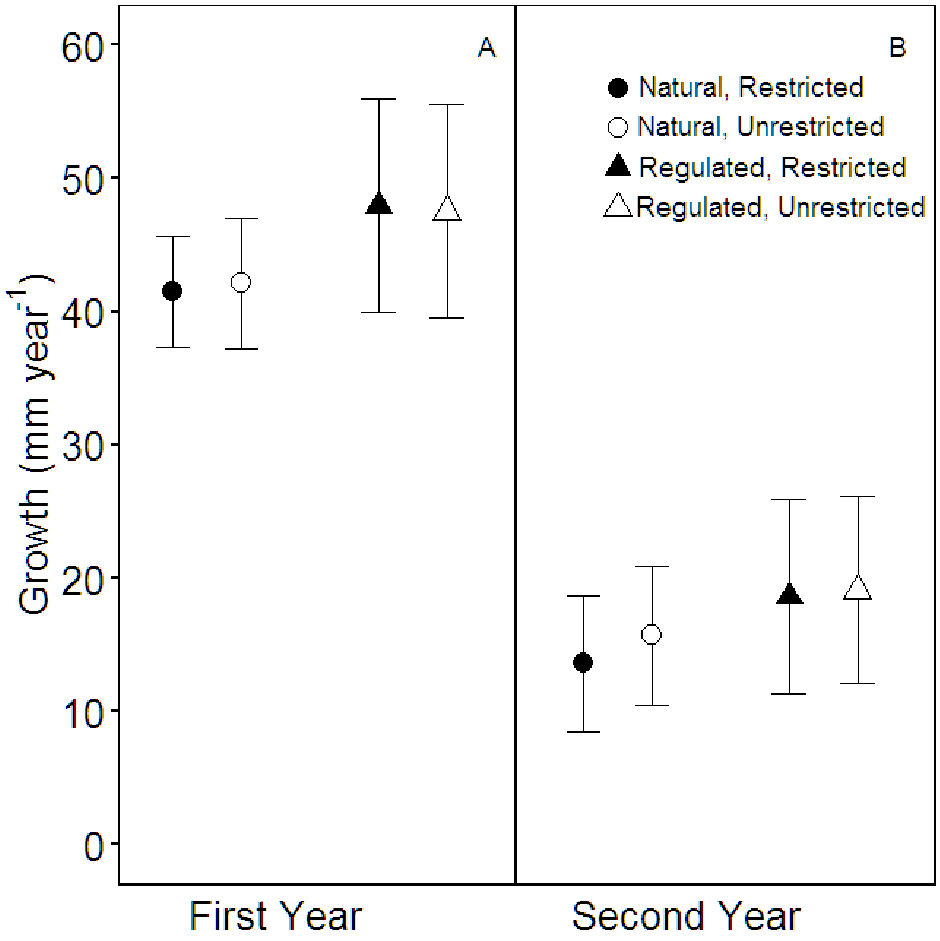

Figure 2.2 Annual first (A) and second (B) year growth (mm·year $^{-1}$) with error bars indicating ± standard deviation for the naturally flowing Batchawana River (circles) and the regulated Magpie River (triangles). Closed symbols indicate growth for the period of restricted hydropeaking regime, while open symbols indicate growth for the unrestricted hydropeaking regime in the regulated river. The same time periods were analyzed in the naturally flowing river and are similarly represented with open and closed symbols.

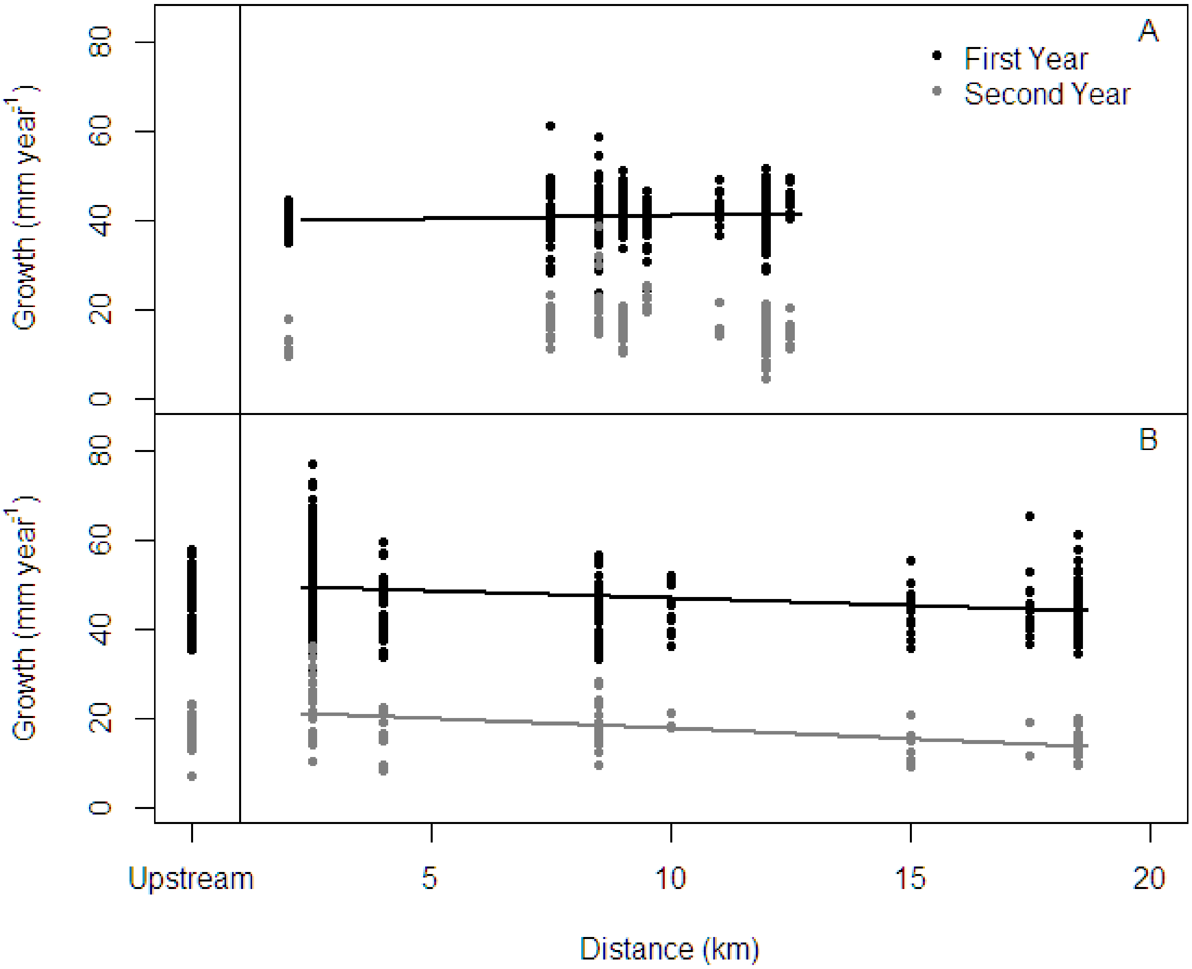

Figure 2.3 First and second year growth for Sculpin in the naturally flowing Batchawana River (A) and the regulated Magpie River (B) along a longitudinal gradient. Distance is measured from the dam in the regulated river and from the beginning of the river valley segment in the naturally flowing river. Regression lines are included where the relationship between growth and distance is significant.

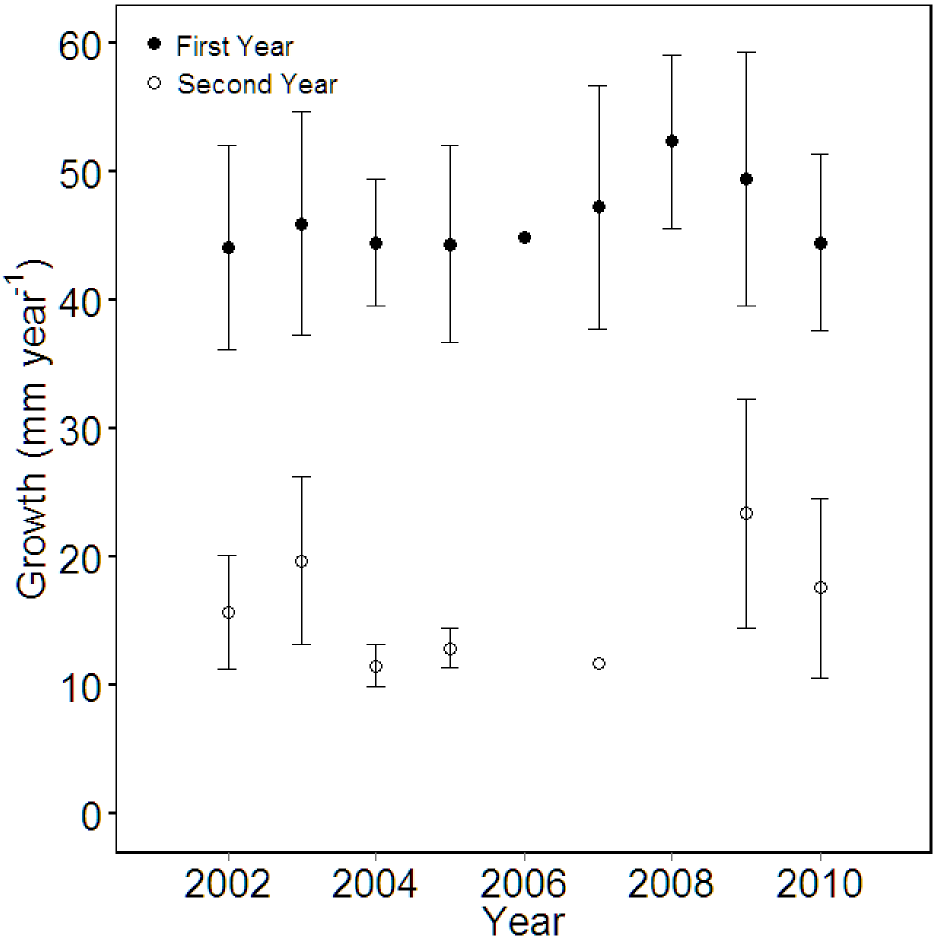

Figure 2.4 Sculpin first and second year growth ± standard deviation by year in the regulated Magpie River. First year ΔL in 2008 was significantly higher than in years 2002 and 2010, and first year ΔL in 2009 was significantly higher than in 2010 ($F_{7, 220}=4.07$, $p<0.05$)

Chapter 3 Effect of hydroelectric dam river regulation on growth, condition and survival of resident forage fish

Introduction

River regulation resulting from the construction and operation of hydroelectric dams can have significant impacts on downstream ecosystems (Sabater 2008). Physical parameters such as river discharge (Cushman 1985), and water temperature (Lessard & Hayes 2003) are affected by hydroelectric dam operation, and biological communities adapt to those physical alterations (Vannote et al. 1980). Biological responses can be manifested at the population and community level, resulting in changes to fish abundance (Bain et al. 1988; Moog 1993; Freeman et al. 2001) and diversity (de Mérona et al. 2005; Smokorowski et al. 2011; Freedman et al. 2014), with less tolerant species becoming extirpated from downstream river reaches (Quinn & Kwak 2003). However, responses to physical alterations may also be manifested at the individual level through changes in growth rates (e.g. Korman & Campana 2009; Kelly et al. 2015a) and life history traits (e.g. Alexandre et al. 2014; Bond et al. 2015), with significant consequences for both species population dynamics and aquatic ecosystems.

Recent studies have focused on the impacts of river regulation on individual level metrics, noting species-specific effects. For example, river regulation and peaking operations have been found to decrease the growth rate of young-of-the-year rainbow trout (*Onchorynchus mykiss*) (Korman & Campana 2009) and Iberian barbel (*Luciobarbus bocagei*) (Alexandre et al. 2014), and increase the growth rates of slimy sculpin (*Cottus cognatus*) (Bond et al. 2015; Kelly et al. 2015a) and humpback chub (*Gila cypha*) (Finch et al. 2015). River regulation can also result in earlier maturation and higher instantaneous mortality rates in slimy sculpin (Bond et al. 2015), but has also been found to decrease gonadal activity and increase longevity in Iberian barbel (Alexandre et al. 2014). The causal mechanisms attributed to observed changes in growth rates and life history traits vary among studies, but include: discharge rates and patterns (Korman & Campana 2009; Kelly et al. 2015a), river water temperature (Kelly et al. 2015a) and nutrient delivery and food supply (Bond et al. 2015). Despite differences in biological responses and the driving forces behind them, studies to date have largely focused on single species within a given river. Investigating the effects of river regulation on the growth, condition and survival of multiple species simultaneously will provide a more comprehensive understanding of the impact of river regulation on the fish community, and would provide valuable information on how best to modify hydroelectric dam operations to minimize possible negative effects on downstream ecosystems.

To address this knowledge gap, the growth rates ($\text{mm}\cdot\text{yr}^{-1}$), condition and survival of three fish species were investigated over a ten year period in a river regulated by a 15 MW hydropeaking dam, and a nearby similarly sized naturally flowing river. During the study, the dam operated under two different hydropeaking regimes: one where the hourly rate of change in discharge was restricted, and one where it was not. The three fish species chosen: slimy sculpin, longnose dace (*Rhinichthys cataractae*), and trout perch (*Percopsis omiscomaycus*), are the three most abundant forage fish species in both rivers and represent three different families of fishes (Cottidae, Cyprinidae, Percopsidae), thus they constitute an important component of the fish community and the riverine ecosystem. The species differ in their body morphology, temperature, habitat and feeding preferences (Table 3.1), and thus may reflect the impact of river regulation on taxa that occupy different ecological niches.

Our objective was to test for between-river and between-hydropeaking regime differences in growth, condition and survival within species and, where differences exist, investigate the consistency of the differences amongst species. In addition, given that hydroelectric dams significantly alter downstream discharge patterns (Smokorowski et al. 2011) and river water temperature (Olden & Naiman 2010; Casado et al. 2013), whether discharge and temperature impact species differently within the study systems was tested. In general, it was hypothesized that growth, condition and survival would differ between rivers for each species. Specifically, it was hypothesized that (i) growth and condition of slimy sculpin and longnose dace would be higher in the regulated river and under the unrestricted ramping regime, given their preference for rapidly flowing water (Bradbury et al. 1999; Portt et al. 1999) and the potential for increased food supply resulting from hydropeaking (Bond et al. 2015), while the growth and condition of trout perch would be lower in the regulated river and under the unrestricted ramping regime given their preference for pools (Portt et al. 1999). Also hypothesized was that (ii) survival would be lower for longnose dace and slimy sculpin in the regulated river, given that high growth and condition may be related to altered life history characteristics and shorter life spans in these two rivers (Bond et al. 2015). Trout perch survival would also be lower in the regulated river, resulting from a less favourable flow regime based on this species' preferences. As well, it was hypothesized that (iii) longnose dace and slimy sculpin growth would be positively related to mean discharge given the possibility of increased food availability related to hydropeaking (Bond et al. 2015), the preference of the former for areas of swift flowing waters (Bradbury et al. 1999) and the demonstrated ability of the latter to avoid the energetic costs of faster flowing waters (e.g., Kelly et al. 2015a). However, it was hypothesized that trout perch growth would be negatively related to discharge given their preference for pools (Portt et al. 1999), where access to an increased food supply from hydropeaking induced invertebrate drift may be limited. Lastly, it was hypothesized that (iv) slimy sculpin and longnose dace growth would be negatively related to river water temperature given their preference for cooler water (Otto & Rice 1977; Bradbury et al. 1999), while trout perch growth would not be related to river water temperature.

Methods

Sampling sites

Sampling took place during the summer months from 2002 through 2012 in the Batchawana River near Sault Ste. Marie, ON (47°0’N; 84°30’W) and the Magpie River near Wawa, ON (48°4’N; 84°44’W) (Fig. 3.1). The two rivers were chosen for comparison because of their proximity, their similarity in terms of drainage area, mean annual discharge, chemical composition, and fish community composition (Smokorowski et al. 2011). The Magpie River has a 15 MW hydroelectric peaking dam, while the Batchawana River has a natural flow regime. During the period encompassed by this study, the hydroelectric dam at the Steephill Falls Generating Facility operated under two different hydropeaking regimes. From 2002 through 2004, regulations for the “restricted hydropeaking regime” required ramping restrictions of ≤ 1 $m^3 \cdot s^{-1} \cdot hr^{-1}$ from October 10th through November 15th, 2 $m^3 \cdot s^{-1} \cdot hr^{-1}$ from November 16th through the spring freshet, and no greater than a 25% increase or decrease from the previous hour’s flow from the spring freshet to October 9th (Smokorowski et al. 2011). The ramping rate restrictions were removed in October 2004 (“unrestricted hydropeaking regime”). During both operating regimes a minimum flow regulation of 7.5 $m^3 \cdot s^{-1}$ was in place.

Sampling

Randomly selected 100 m transects in analogous river valley segments were fished in both rivers (Smokorowski et al. 2011). Eight sites were sampled downstream from the hydroelectric dam in the regulated river and within an analogous reach in the naturally flowing river. As a result of unforeseen circumstances (e.g. road washouts during major weather events), not all eight sites were sampled each year in each river. Fish were captured by backpack electrofishing to a depth of 60 cm, with depths ≤60 cm representing the majority of the area encompassed by these shallow, partially wadeable rivers (Smokorowski et al. 2011). A standard shocking rate of 4 $s\cdot m^{-2}$ was used. In addition to the routine random sampling, additional fish were caught for a separate stable isotope study (Marty et al. 2009). The samples were used to increase the sample size of aged fish used in this study, but were not included in annual survival calculations. Fish for the stable isotope study were frozen, while all others were preserved in formalin followed by ethanol. Fish were weighed and measured in the lab, dissected and sexed, and their otoliths were removed for aging. No significant differences were found between male and female specimens of slimy sculpin and trout perch in terms of growth or length at age in either river (Welch's t test, $p>0.05$) and therefore, male and female specimens were pooled in subsequent analyses. Given the difficulty of determining sex for the longnose dace caught, a test for sex related differences in growth and length at age for this species was not conducted. In order to maintain consistency, male and female specimens of longnose dace were pooled for subsequent analyses.

Physical parameters

Mean daily river discharge was obtained from two Water Survey of Canada gauges, 02BD007 (Magpie River) and 02BF001 (Batchawana River). River water temperature data were obtained from study placed Solinst Leveloggers located at the Water Survey of Canada gauges in both the Magpie and Batchawana Rivers (Fig. 3.1) that recorded every half hour in 2002 and every 15 min thereafter from 2003 through 2010 (Smokorowski et al. 2011). Discharge and temperature parameters were calculated for each year by averaging mean daily discharge and mean daily water temperature from June 1st to September 30th.

Aging

Aging was completed by immersing whole otoliths in a 50% by volume glycerol-deionized water solution and viewing the otoliths under a dissecting microscope (Nikon SMZ 1000, Nikon Instruments Inc.). Only sagittal otoliths were used for slimy sculpin and trout perch, while sagittal and lapilli otoliths were used for longnose dace, depending on availability. All otoliths were read at least twice by the same reader and where discrepancies between aging existed (<5%), otoliths were not used.

Measurements for growth back calculations were made along the clearest radius (which was consistent within species) using NIS Elements software (Nikon Instruments Inc., Melville NY). Length at age *i* was back-calculated for each species using the scale proportional hypothesis (Francis 1990):

$$L_i = -(a/b) + (L_c + a/b)(S_i/S_c),$$

where L_i is length at age *i*, L_c is length at capture, S_i is otolith radius at length *i*, S_c is otolith radius at capture, and a and b are the intercept and slope of the otolith radius-on-length relationship, respectively. In order to standardize otolith back-calculations, otolith measurements obtained from longnose dace lapilli otoliths were converted to sagittal measurements using the linear relationship between the lapilli and sagittal radii ($p<0.05$, $r^2=0.75$). Average annual growth rate (ΔL) was calculated as the difference in fish length for one annual cycle from the beginning of spring to the end of winter.

Estimates of annual survival were conducted using the R package fishmethods (Nelson 2015). Annual survival ± 95% confidence intervals were estimated using the Chapman-Robson method (Chapman & Robson 1960).

Statistical analysis

All statistical analyses were conducted in R (R Core Team 2014). Heterogeneity of variance was determined using Bartlett's test (Bartlett 1937), while normality was confirmed with the Shapiro-Wilks test (Royston 1982). Given the recently documented and pronounced effect of ramping impacts on fish and invertebrate community characteristics immediately below the dam on the Magpie River (Bond et al. 2015; Kelly et al. 2015a), data for the sample transect closest to the dam (2.5 km downstream) were removed from all subsequent analyses to avoid biasing river comparisons. Estimates of ΔL were compared between rivers and hydropeaking periods for each species using a two-way ANOVA with a significant interaction between river and hydropeaking period signifying an impact on fish growth from the hydropeaking regime (e.g. Marty et al. 2009). Fish condition (weight-length relationship) was assessed for each species using an ANCOVA with river and hydropeaking regime as categorical variables. To balance the sample sizes used in the statistical comparisons, a maximum of 200 specimens per species, river and hydropeaking period were randomly sampled from the dataset to complete the ANCOVA analysis. To avoid the confounding factor of including fish with a lifespan that encompassed both hydropeaking periods, condition estimates were conducted using fish caught in 2002-2004 for the unrestricted period, and fish caught in 2009 to 2012 for the restricted period. Partial correlation analysis was used to assess the significance of the correlation between ΔL and mean summer daily discharge and water temperature when the effect of the other variable was controlled. An ANCOVA was used to determine if the correlations between ΔL and mean summer daily discharge and water temperature differed between species, by including species as the categorical variable.

Results

Longnose dace and slimy sculpin were caught in all transects sampled within each river, most frequently in habitats characterized as runs or riffles with fast flowing water. Trout perch were caught less frequently, mainly in pools and slow moving water. Within the subset of aged fish, longnose dace attained ages of 5 and 3 in the Magpie and Batchawana Rivers, respectively (n=697), slimy sculpin attained ages of 4 and 5, respectively (n=1076), while trout perch attained the age of 3 in both rivers (n=633).

Otolith derived back-calculations yielded a high enough sample size of first and second year ΔL estimates for statistical analysis for each species. Longnose dace ΔL was significantly higher in the Magpie River relative to the Batchawana River for both first and second year ΔL (Table 3.2). Hydropeaking regime was not a significant factor in determining longnose dace ΔL and there was no significant interaction between river and hydropeaking regime. Slimy sculpin ΔL was significantly higher in the Magpie River relative to the Batchawana River for first year ΔL, while hydropeaking regime and the interaction between river and hydropeaking regime were not significant (Table 3.2). For slimy sculpin second year ΔL, there was no significant difference between rivers, and no significant interaction between river and hydropeaking period. First year trout perch ΔL was significantly higher in the Magpie River and significantly higher during the unrestricted hydropeaking regime in both rivers, while the interaction between river and hydropeaking regime was not significant (Table 3.2). There was no significant difference in ΔL between rivers or hydropeaking regimes for second year trout perch ΔL.

Analysis of the weight-length relationship for longnose dace and slimy sculpin resulted in significantly different slopes and intercepts between rivers (Table 3.3). There was a significant interaction between river and hydropeaking regime for both species, such that during the unrestricted hydropeaking regime smaller fish were lighter, but gained weight faster relative to during the restricted ramping period in the regulated river and both periods in the naturally flowing river. The trout perch weight-length relationship slope and intercept also differed between rivers such that smaller fish in the regulated river were lighter, but gained weight faster relative to the naturally flowing river (Table 3.3). Hydropeaking regime did not have a significant impact on the trout perch weight-length relationship, and there was no interaction between river and hydropeaking regime.

Annual survival was calculated for the unrestricted hydropeaking period only, as some sample sizes during the restricted hydropeaking period were insufficient for the calculation. Annual survival was higher in the Batchawana River relative to the Magpie River for both slimy sculpin and longnose dace, with no overlap in the 95% confidence intervals within species (Fig. 3.2). Annual survival was similar between rivers for trout perch.

River mean summer discharge and temperature, where significant ($p<0.05$), explained little of the variation in first and second year ΔL in the three species in this study (Table 3.4; Fig. 3.3, 3.4). Mean summer discharge was significantly correlated with first year ΔL in the Magpie River, while mean water temperature was significantly correlated with first year ΔL in the Batchawana River for all three species. In general, second year ΔL was less often correlated with either mean summer discharge or river water temperature. All correlations, where significant, were positive except for the correlation between longnose dace first year ΔL and mean summer discharge. The slope and intercepts of the linear relations for first year ΔL varied by species for mean summer discharge, while only the slopes varied by species for mean summer temperature (Table 3.5). For second year ΔL, the slope and intercept varied by species for mean summer discharge but not mean summer temperature.

Discussion

The three forage fish species investigated in this study exhibited differences in ΔL, condition and survival between rivers; however the differences were not always consistent among species. ΔL was higher in the regulated Magpie River relative to the naturally flowing Batchawana River for both first and second year ΔL for longnose dace, but only first year ΔL for trout perch and slimy sculpin. River and hydropeaking regime were significant factors for the weight-length relationship of longnose dace and slimy sculpin, while only river was a significant factor for the trout perch weight-length relationship. Survival was higher in the naturally flowing Batchawana River relative to the Magpie River for both longnose dace and slimy sculpin, but similar between rivers for trout perch. River discharge and temperature, where significant, explained little of the variation in ΔL. Discharge was more often significantly correlated with ΔL in the Magpie River, while temperature was more often significantly correlated with ΔL in the Batchawana River for all three species. Significant differences among species in the slopes of the discharge- and temperature- ΔL relationships indicate that the effects on fish of hydroelectric dam altered hydrologic and thermal regimes can differ amongst species.

Fish species evolve life-history traits in response to environmental variability (Winemiller 2005) and can exhibit phenotypic plasticity in traits based on physical conditions (e.g. Blanck & Lamouroux 2007). For example, higher environmental variability within a natural riverine environment can lead to a fish community dominated by species with a shorter life span, a smaller body size and earlier sexual maturation (Schlosser 1990). However, the practice of hydropeaking results in discharge patterns which have no corollary in natural systems (Poff et al. 1997). Variability in discharge in hydropeaked systems can increase at the sub-daily scale but decrease inter- and intra- annually. Meanwhile, variability in both daily and annual temperature can decrease as a result of hydropeaking (Casado et al. 2013). And as demonstrated here, such differences in the variability of physical conditions can result in changes to fish life-history traits (e.g. survival) and individual-based metrics (e.g. growth and condition).

A decrease in flow variability driven by river regulation resulted in a decrease in growth rates and condition, and an increase in longevity in Iberian barbel (Alexandre et al. 2014), while hydropeaking resulted in decreased survival, longevity and size in Andalucian barbel (*Barbus sclateri*) (Del Mar Torralva et al. 1997). As well, hydropeaking can result in either a decrease (Korman & Campana 2009), or an increase in fish growth (Bond et al. 2015; Finch et al. 2015; Kelly et al. 2015a). In our study, although growth was higher for all three species in the regulated river, differences in fish condition and survival between rivers did not show similar trends among species. Thus, while previous studies have demonstrated that the response of fish to river regulation can differ between river systems, our study demonstrates that fish species within the same system can exhibit different biological responses to the same river regulation regime.

The differences in ΔL and condition between rivers may be related to food availability. Invertebrate abundance was found to be higher in the regulated river relative to the naturally flowing river (Jones 2013), and Bond et al. (2015) found a significant relationship between slimy sculpin growth and invertebrate density in the Magpie River. Thus, higher food availability may have led to the higher growth rates exhibited by all three species in the regulated river. And while slimy sculpin and trout perch showed higher *ΔL* in the unrestricted ramping period for second, and first year *ΔL*, respectively, the same trend was seen in the naturally flowing river for both species over the same time period. Thus, while hydropeaking in general did have an impact on growth, there was no detectable difference in impact between hydropeaking regimes.

In contrast, river regulation and hydropeaking regime did have a significant impact on the weight-length relationship of longnose dace and slimy sculpin, while river regulation alone had a significant impact on the weight-length relationship of trout perch. Specifically, river regulation altered the allometric nature of the weight-length relationship, increasing the value of the exponent, b, relative to the naturally flowing river for all three species, while unrestricted hydropeaking increased b relative to restricted hydropeaking for longnose dace and slimy sculpin. The differences in the weight-length relationships between rivers and hydropeaking regimes may be related to a difference in both the abundance and accessibility of food resources between rivers. Condition indices can be correlated with different prey items for fish of different lengths, as a result of ontogenetic diet shifts (Liao et al. 1995). And, although invertebrate abundance was higher in the regulated river (Jones 2013), and hydropeaking can increase invertebrate drift (Lauters et al. 1996; Lagarrigue et al. 2002; Patterson & Smokorowski 2011), food resources may not be equally available to all fish size classes. Jones (2013) found that the nearshore varial zone in the Magpie River generally had lower invertebrate abundance relative to areas in the permanently wetted zone, while in the Batchawana River, invertebrate densities tended to be highest in the nearshore zone. Small (YOY) longnose dace and slimy sculpin are most frequently caught along the river margins (B. Kelly, unpublished data), where invertebrate density is highest in the Batchawana River, while longnose dace migrate to the variable zone in the Magpie River during hydropeaking events, where invertebrate abundance is lower (Bond & Jones 2015). Thus, the difference in the weight-length relationships between rivers and between hydropeaking regimes is likely reflective of the changing accessibility of food resources during the hydropeaking cycle on a daily basis, and on a more long-term basis as fish grow.

The comparable annual survival of trout perch between rivers but higher growth in the regulated river, suggests that hydropeaking did not have a negative impact on this species, despite their habitat preference of slower moving water (Portt et al. 1999) and the tendency for river regulation to increase the amount of run and riffle habitat relative to pools (Bunn & Arthington 2002). Thus, despite the sub-daily changes in discharge in the regulated river, sufficient areas of slow moving water or pools may remain during hydropeaking periods that provide trout perch with a refuge in order to avoid the potential negative impacts of being routinely exposed to high discharge events.

Although trout perch exhibited similar annual survival between rivers, longnose dace and slimy sculpin showed lower survival in the regulated river relative to the naturally flowing river. The lower survival in the regulated river may be driven by higher mortality of fish which are less able to deal with large flow fluctuations (Del Mar Torralva et al. 1997), given that both these species inhabit riffles (Portt et al. 1999) where they would be more exposed to hydropeaking events relative to trout perch. For example, newly emerged longnose dace are most often found in slower velocity water along stream margins (Gee & Northcote 1963), which are areas that would shift or disappear daily under a hydropeaking regime. It is also possible that these two species are exhibiting a shift in life-history characteristics in the Magpie River, whereby more rapid growth and higher condition are coupled with younger age-at-maturity and decreased longevity, relative to the Batchawana River. The mechanism was suggested by Bond et al. (2015) for slimy sculpin in the Magpie River, and is consistent with the lower survival of longnose dace and slimy sculpin in the Magpie River.

Where the relationship between ΔL and river discharge and temperature was significant, it explained little of the variation in ΔL. In general, given the heterogeneous nature of riverine environments (Fausch et al. 2002), mean summer discharge and river water temperature estimates likely fail to characterize the full range of habitats available to fish. As well, increased metabolic costs driven by altered discharge (e.g. Murchie & Smokorowski 2004; Korman & Campana 2009) and temperature may be offset by increases in food availability associated with river regulation (Patterson & Smokorowski 2011; Jones 2013) and hydropeaking (Lauters et al. 1996; Lagarrigue et al. 2002), resulting in a weak correlation between fish growth and river discharge and temperature. Increased food availability may also be driving the positive correlation between temperature and fish growth in the naturally flowing Batchawana River. Warmer water temperatures in a given year can increase invertebrate production (e.g. Plante & Downing 1989) as long as species-specific upper thermal thresholds are not exceeded (Sweeney and Vannote 1978), increasing food availability for fish. Species-specific preferences and behaviours likely play a role as well. For example, the negative relationship between discharge and Magpie River longnose dace first year ΔL may be related to the sensitivity of small longnose dace to high velocity environments (Gee & Northcote 1963).

River regulation can decrease the diversity of downstream fish communities (Freedman et al. 2014), and this was found for the regulated Magpie River relative to the naturally flowing Batchawana River (Smokorowski et al. 2011). While the effect of river regulation on multiple fish species was documented, this study does not take into account species which may have been extirpated after the dam first became operational (e.g. Quinn & Kwak 2003). As well, the three forage fish species chosen all have a wide distribution, ranging from eastern Canada to British Columbia and north to the Yukon and Northwest Territories (Scott & Crossman 1973). The ability of these species to persist across such a wide range of geographical and climatic environments is indicative of an ecological plasticity that allows them to thrive under a variety of temperature and flow conditions. Therefore, while information on multiple species was provided, these results may underestimate the impacts of hydropeaking in this case given that specialist or sensitive species were not included.

While previous papers have shown the impacts of river regulation on the growth and condition of individual species, this study provides information on the species-specific differences in responses within a given fish community. Our results highlight the need to consider the impact of river regulation on multiple fish species within a given system when attempting to determine effective management strategies to maintain ecosystem integrity. Given the species-specific response to hydropeaking, management strategies aimed at maintaining flow and habitat heterogeneity within the riverine environment may best ensure that species with a variety of habitat preferences and life-history strategies can persist in this environment.

Table 3.1. Morphology, substrate, velocity and temperature preferences of longnose dace, slimy sculpin and trout perch.

Species	Morphology	Substrate Preference	Velocity Preference	Temperature Preference	Feeding Preferences
longnose dace	Round body, inferior mouth[a]	Boulder, cobble, rubble, gravel[b]	Riffle, rapid[b] 65 cm^{-s}	5.4-22.7°C[c] (entire range)	Chironomids, algae, midge and diptera larvae[f]
slimy sculpin	Laterally compressed body, mouth has protruding upper lip[a]	Boulder, cobble, rubble, bedrock, gravel, sand[b]	Riffle[b] 30 cm^{-s}	10-12 °C [d]	Aquatic insects, crustaceans, small fishes, aquatic vegetation [f]
trout perch	Thick body, ventral mouth[a]	Gravel, sand, boulder, cobble, rubble[b]	Pool[b] NA*	10 – 16°C [e]	Chironomids, amphipods, mollusks, small crustaceans [f]

[a] Scott and Crossman (1973)
[b] Portt et al. 1999 (preference refers to high and medium usage), cm^{-s} give critical velocity critieria for fishway design above which species would be unable to swim for sustained periods as given in Peake (2008)
[c] Edwards et al. 1983
[d] Otto and Rice 1977
[e] Coutant 1977
[f] Richardson et al. 2001
*No estimate available

Table 3.2. Results of two way ANOVA for first year and second year growth within species using river and hydropeaking regime as independent factors.

Parameter	Species	River	Hydropeaking Regime	Annual Growth (mm·yr^{-1})	ANOVA	F	Degrees of freedom	p-value
First year annual growth	longnose dace	Regulated	Restricted	38.1±5.6	River	18.0	1	<0.01
			Unrestricted	38.4±5.4	hydropeaking period	0.3	1	0.58
		Natural	Restricted	35.8±4.0	Interaction	0.0	1	0.98
			Unrestricted	36.1±4.8				
	slimy sculpin	Regulated	Restricted	44.9±5.3	River	39.6	1	<0.01
			Unrestricted	45.1±5.9	hydropeaking period	0.8	1	0.37
		Natural	Restricted	41.8±4.2	Interaction	0.2	1	0.68
			Unrestricted	42.4±4.5				
	trout perch	Regulated	Restricted	45.1±5.8	River	32.3	1	<0.01
			Unrestricted	47.3±6.1	hydropeaking period	11.1	1	<0.01
		Natural	Restricted	40.6±5.2	Interaction	0.0	1	0.99
			Unrestricted	42.3±4.4				
Second year annual growth	longnose dace	Regulated	Restricted	21.5±3.1	River	38.0	1	<0.01
			Unrestricted	20.9±4.8	hydropeaking period	0.3	1	0.61
		Natural	Restricted	16.9±3.0	Interaction	0.0	1	0.90
			Unrestricted	16.6±3.7				
	slimy sculpin	Regulated	Restricted	15.1±4.3	River	2.0	1	0.16
			Unrestricted	16.5±4.7	hydropeaking period	4.0	1	0.05
		Natural	Restricted	13.6±5.1	Interaction	0.1	1	0.74
			Unrestricted	15.5±5.1				
	trout perch	Regulated	Restricted	17.2±4.4	River	2.3	1	0.13
			Unrestricted	15.6±5.2	hydropeaking period	1.9	1	0.17
		Natural	Restricted	15.8±3.0	Interaction	0.6	1	0.45
			Unrestricted	15.0±3.2				

Table 3.3. ANCOVA results for the comparison of weight-length relationships for longnose dace, slimy sculpin and trout perch, using river and hydropeaking regime as categorical variables.

Species	Comparison	F	t statistic	Degrees of freedom	p-value
longnose dace		6295.00		7, 557	<0.01
	River intercept		2.49		0.01
	Hydropeaking regime intercept		1.32		0.19
	River slope		3.09		<0.01
	Hydropeaking regime slope		0.92		0.36
	River x regime intercept		2.87		<0.01
	River x regime slope		2.86		<0.01
slimy sculpin		12190.0		7, 634	<0.01
	River intercept		8.33		<0.01
	Hydropeaking regime intercept		0.78		0.44
	River slope		9.35		<0.01
	Hydropeaking regime slope		0.13		0.89
	River x regime intercept		5.13		<0.01
	River x regime slope		5.00		<0.01
trout perch		2890.0		7, 433	<0.01
	River intercept		3.43		<0.01
	Hydropeaking regime intercept		0.80		0.42
	River slope		3.20		<0.01
	Hydropeaking regime slope		0.38		0.71
	River x regime intercept		1.24		0.22
	River x regime slope		1.16		0.25

Table 3.4. Pearson partial correlation coefficients for the correlation between first and second year growth and mean summer discharge ($m^3 \cdot s^{-1}$) and temperature (°C) for longnose dace, slimy sculpin and trout perch. Mean summer temperature was controlled for in the correlation coefficient calculation between growth and discharge, while mean summer discharge was controlled for in the correlation coefficient calculation between growth and temperature. Bold lettering indicates a significant correlation.

Parameter	Species	Growth year	River	Pearson partial coefficient	p-value	Test statistic
Discharge	longnose dace	First	Natural	0.004	0.95	0.06
			Regulated	**-0.17**	**0.05**	**-1.99**
		Second	Natural	0.15	0.06	1.87
			Regulated	-0.069	0.68	-0.4
	slimy sculpin	First	Natural	0.05	0.41	0.83
			Regulated	**0.38**	**<0.01**	**6.16**
		Second	Natural	0.13	0.16	1.39
			Regulated	0.12	0.38	0.87
	trout perch	First	Natural	-0.07	0.22	-1.22
			Regulated	**0.32**	**0.03**	**2.19**
		Second	**Natural**	**0.26**	**0.03**	**2.25**
			Regulated	0.28	0.28	1.07
Temperature	longnose dace	First	**Natural**	**0.28**	**<0.01**	**4.65**
			Regulated	-0.006	0.95	-0.064
		Second	Natural	-0.01	0.90	-0.12
			Regulated	0.13	0.45	0.76
	slimy sculpin	First	**Natural**	**0.19**	**<0.01**	**3.18**
			Regulated	0.08	0.25	1.15
		Second	**Natural**	**0.22**	**0.01**	**2.51**
			Regulated	0.07	0.59	0.53
	trout perch	First	**Natural**	**0.15**	**<0.01**	**2.62**
			Regulated	**0.44**	**<0.01**	**3.17**
		Second	**Natural**	**0.25**	**0.03**	**2.13**
			Regulated	-0.14	0.60	-0.52

Table 3.5. ANCOVA results for comparison of the relationship between annual growth and discharge and temperature among species.

		F statistic	p-value
first year annual growth	discharge intercept	39.01	<0.01
	discharge slope	189.82	<0.01
	temperature intercept	2.74	0.09
	temperature slope	7.71	<0.01
second year annual growth	discharge intercept	74.97	<0.01
	discharge slope	7.64	<0.01
	temperature intercept	1.32	0.25
	temperature slope	0.04	0.96

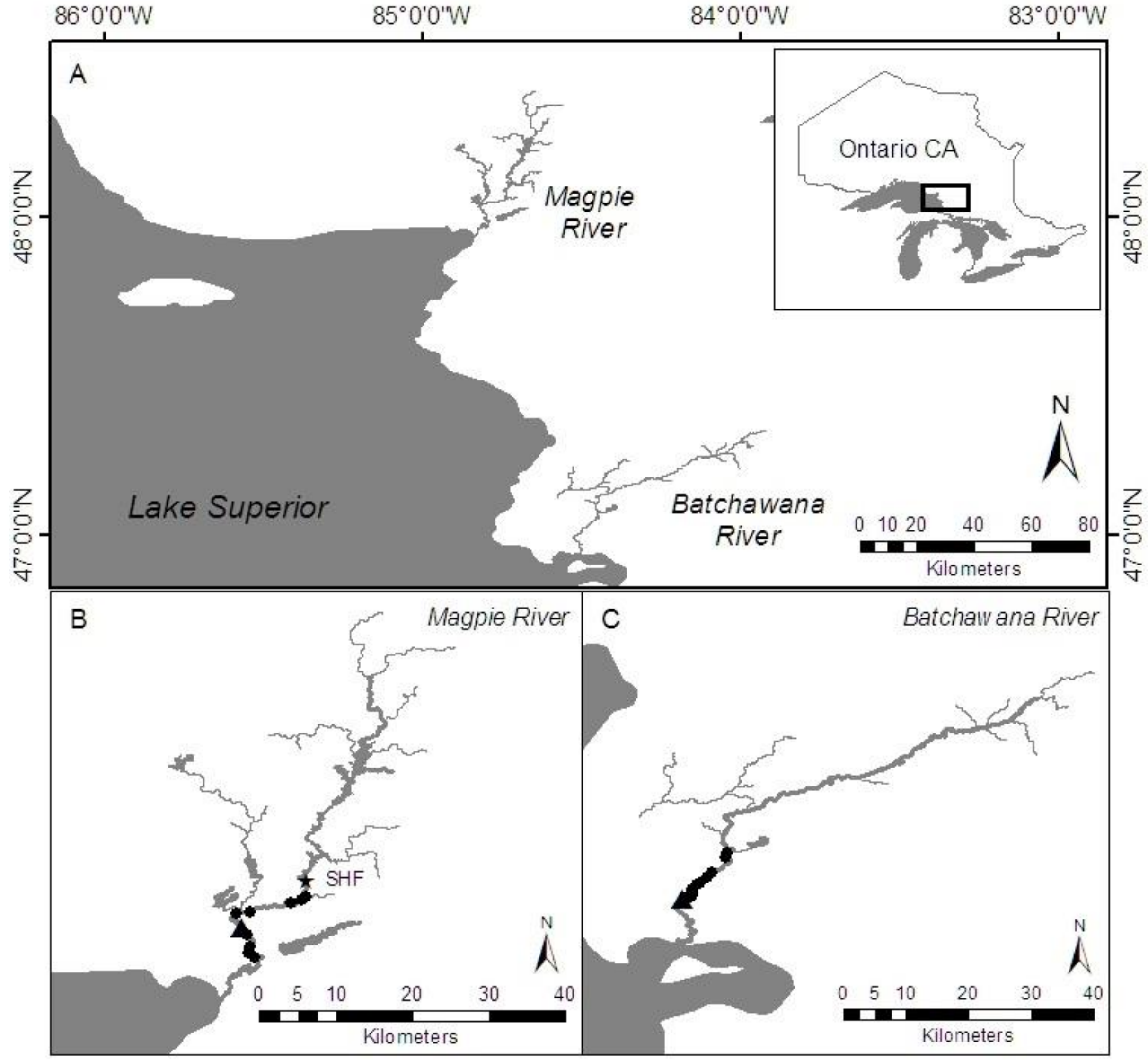

Figure 3.1. Magpie (regulated) and Batchawana (natural) Rivers in Ontario, Canada (A). Sampling sites are denoted by solid circles (●) and locations where discharge and temperature data were collected are denoted by triangles (▲) in the Magpie (B) and Batchawana (C) Rivers. The Steephill Falls (SHF) dam and generating facility in the Magpie River is indicated with a star.

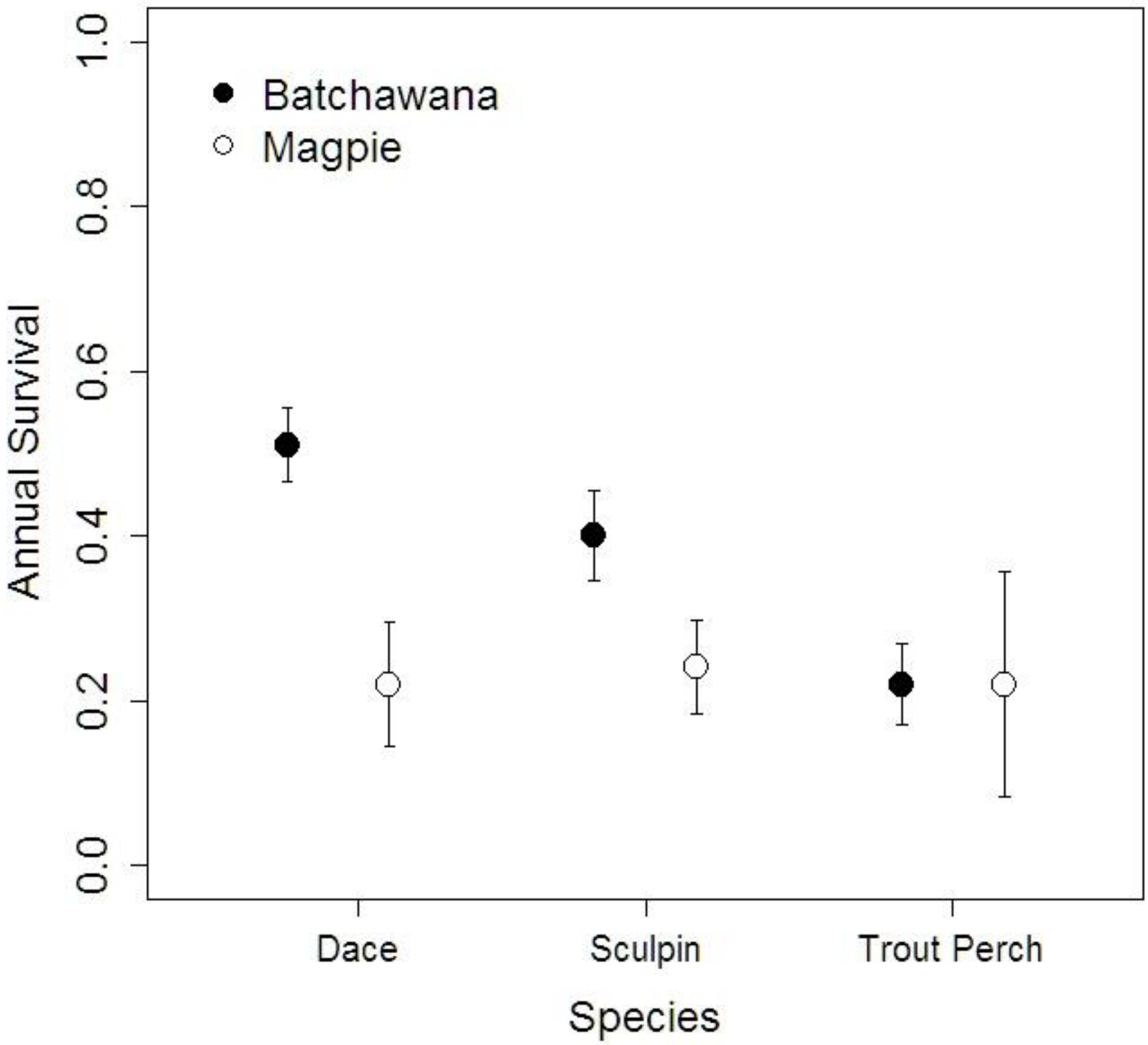

Figure 3.2. Annual survival ± 95% confidence intervals of longnose dace, slimy sculpin and trout perch in the naturally flowing Batchawana River (●) and the regulated Magpie River (○). Annual survival was calculated using fish caught in the unrestricted ramping period only.

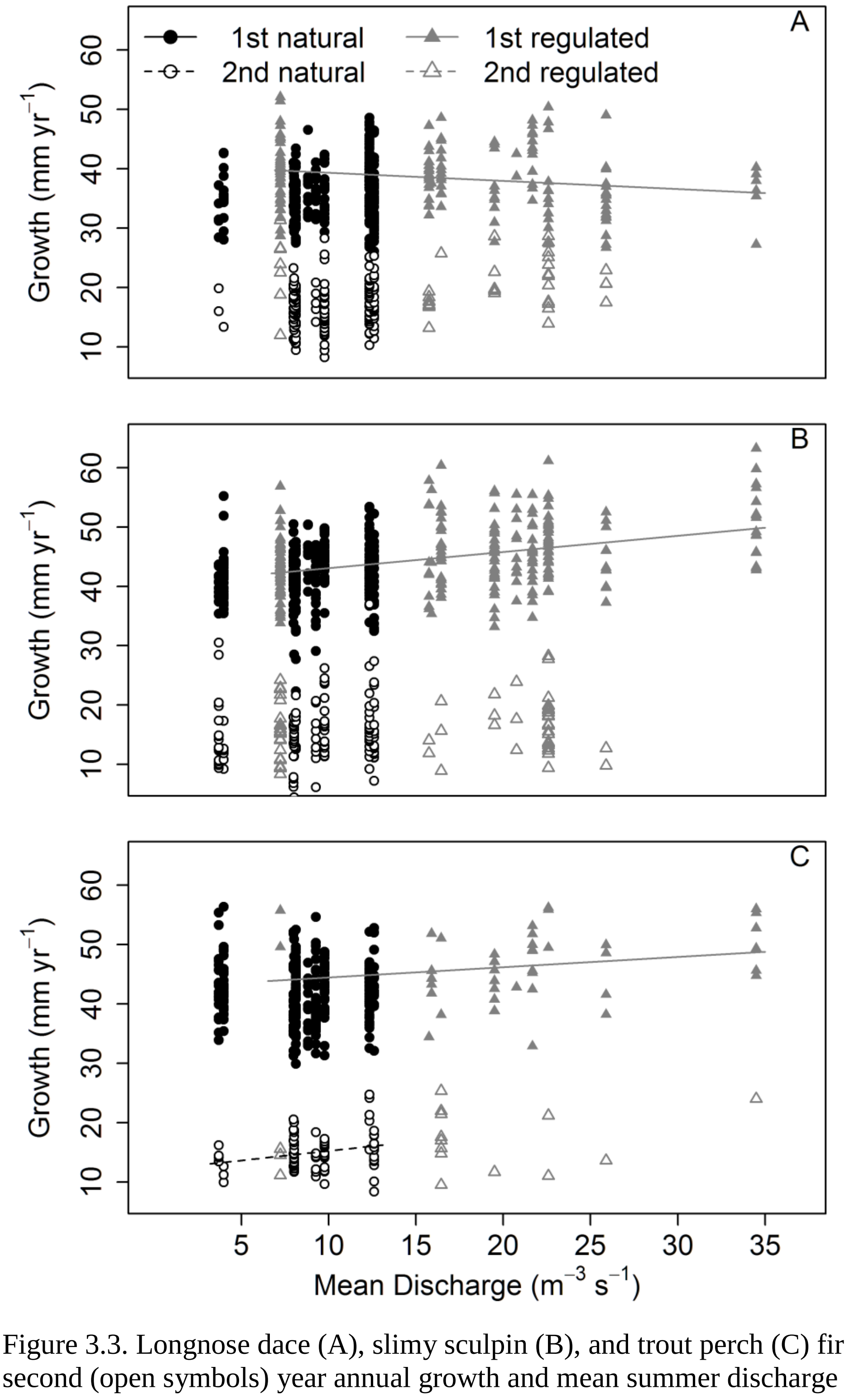

Figure 3.3. Longnose dace (A), slimy sculpin (B), and trout perch (C) first (solid symbols) and second (open symbols) year annual growth and mean summer discharge ($m^3 \cdot s^{-1}$) in the naturally flowing Batchawana (○) and regulated Magpie (Δ) Rivers. Lines indicate significant correlations where mean summer temperature was controlled for ($p<0.05$).

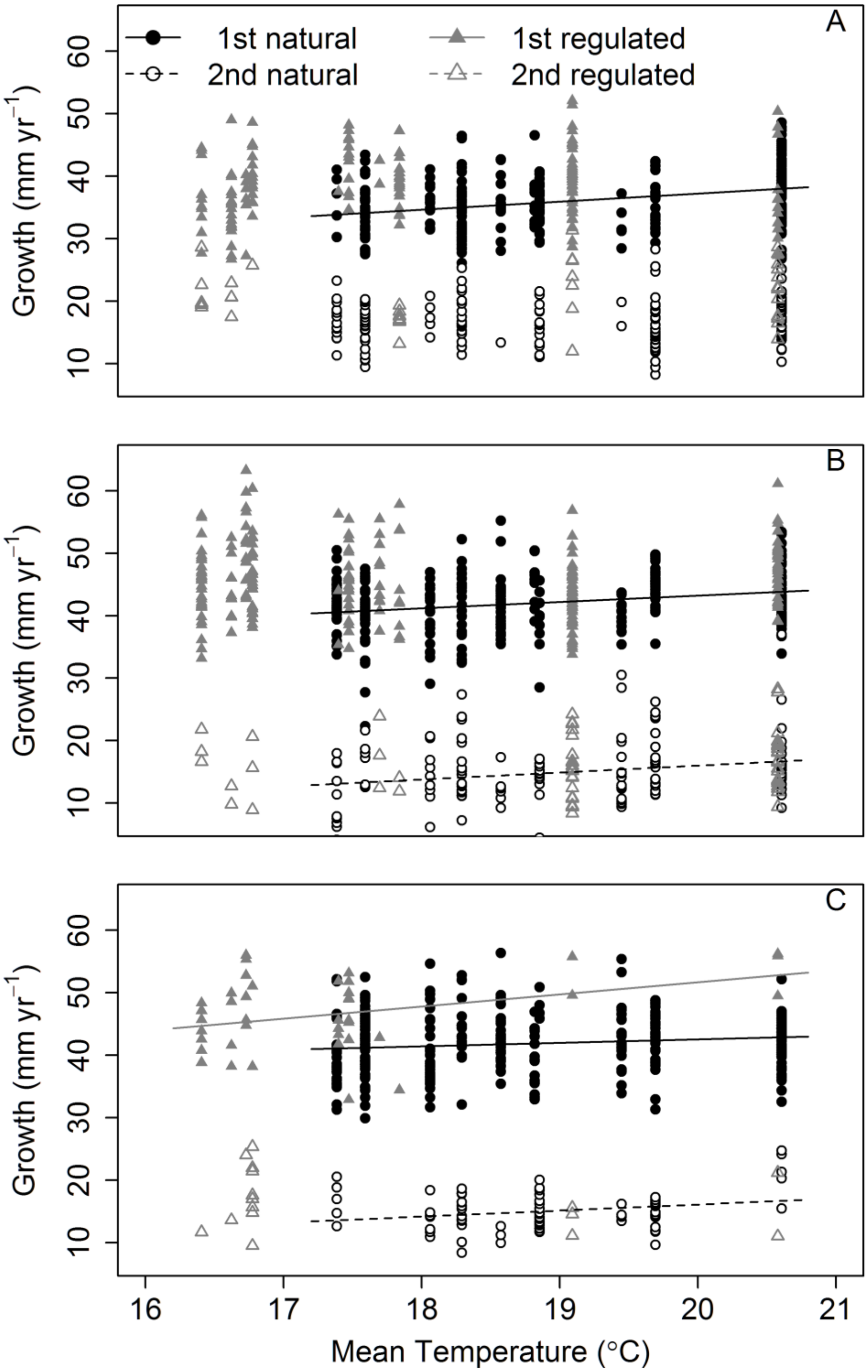

Figure 3.4. Longnose dace (A), slimy sculpin (B), and trout perch (C) first (solid symbols) and second (open symbols) year annual growth and mean summer temperature (°C) in the naturally flowing Batchawana (○) and regulated Magpie (Δ) Rivers. Lines indicate significant correlations where mean summer discharge was controlled for ($p<0.05$).

Chapter 4 Downstream effects of hydroelectric dam operation on thermal habitat use by brook trout (*Salvelinus fontinalis*) and slimy sculpin (*Cottus cognatus*)

Introduction

Hydroelectric dam operations alter river discharge and temperature downstream from dams (Baxter 1977; Ward & Stanford 1983), and these physical alterations can affect aquatic communities living in downstream river reaches (Sabater 2008; Poff & Zimmerman 2010). Temperature is a particularly important parameter for ectotherms such as fish, given its influence on metabolism and physiology (Brett & Groves 1979; Kelsch & Neill 1990), growth (Neuheimer & Taggart 2007), and life-history traits (Coutant 1987). In addition to increases or decreases in downstream water temperatures (Baxter 1977), dam operation can shift the timing and magnitude of thermal events relative to a natural flow regime (Petts 1986). Given the influence of temperature on fish physiology and the extent to which downstream water temperatures are impacted by hydroelectric dam operation, a detailed analysis of altered thermal regimes is a prerequisite for understanding the impacts of river regulation on fish communities (Caissie 2006; Olden & Naiman 2010).

A number of negative effects on fish resulting from cold water releases from dams have been documented, such as the local extirpation of warm water fishes (Quinn & Kwak 2003), delays in spawning (Zhong & Power 1996), impacts to larval development (Clarkson & Childs 2000) and decreased growth rates (Saltveit 1990). However, temperature preferences and avoidance thresholds are species and life-history stage specific (Cherry et al. 1977), and positive impacts of coldwater releases from dams documented for stenothermic species will support fisheries management objectives for those species (Clarke et al. 2008). Given the conservation value of many coldwater fish species (e.g. Connelly & Brown 1991) several recent studies have proposed the management of hydroelectric dams for cold water releases as a potential mitigation strategy for climate change (Isaak et al. 2012; Null et al. 2013; Robson et al. 2013; Rheinheimer et al. 2014; Rheinheimer & Viers 2014), given the increases in stream temperature already measured (Kaushal et al. 2010; Isaak et al. 2012) and the projected future increases in stream temperatures (van Vliet et al. 2013).

Assessing the feasibility of managed river temperatures for providing benefits to downstream fish communities is difficult given the complex nature of temperature dynamics in these systems. Rivers are heterogeneous environments, where water temperature is driven by both external forcing and internal structure (Poole & Berman 2001). Longitudinal (Casado et al. 2013) and lateral (Clark et al. 1999) temperature gradients exist as well as depth gradients within pools (Neilsen et al. 1994). Groundwater inputs can also have significant localized influence on temperature (Ebersole et al. 2003; Dugdale et al. 2015) as does riparian cover (Theurer et al. 1985).

The availability of different thermal habitats within rivers enables fish to thermoregulate by migrating to areas with more suitable temperatures when needed (Berman & Quinn 1991; Petty et al. 2012). When preferred thermal habitat is unavailable, or unattainable as a result of habitat fragmentation, fish can spend short periods of time at temperatures above their upper incipient lethal levels (Dickerson & Vinyard 1999; Wehrly et al. 2007) provided periodic temperature decreases occur to enable fish recovery (Schrank et al. 2003). Therefore, commonly used parameters such as daily mean and maximum river channel temperature may not be representative of the realized thermal habitat of a given fish, or predictive of fish densities, given that they do not accurately represent the variability in available thermal habitat (Hillyard & Keeley 2012; Butryn et al. 2013; Snyder et al. 2015). Determination of the water temperatures used by fish below dams and a detailed characterization of the riverine thermal regime are, therefore, both necessary for understanding how fish respond to the thermal alterations caused by hydroelectric dam operation.

In this study, water temperature data and realized fish thermal habitat (temperature use) were examined in a regulated and a naturally flowing river. The regulated river has a 15 MW peaking hydroelectric dam with a metalimnetic (cool water) draw. Frequently used temperature metrics such as mean, minimum and maximum daily temperature (Butryn et al. 2013), as well as metrics representing species-specific thresholds for preferred, avoidance and upper incipient lethal temperatures were calculated. Temperature use analysis of two coldwater species (brook trout (*Salvelinus* *fontinalis*) and slimy sculpin (*Cottus cognatus*)) found in the same river reaches (Scott & Crossman 1973), but exhibiting different behavioral and life-history strategies was conducted. Oxygen stable isotope analysis of fish otoliths was used to determine the mean temperature experienced over the course of the growing season. The objective was to determine the effect of river regulation on fish thermal habitat use within the context of current river management questions, namely the feasibility of using hydroelectric dams to mitigate water temperature increases associated with climate change. It was hypothesized that: (i) the thermal regime downstream from the cool water draw in the regulated river would result in lower water temperatures and a more suitable thermal regime for both species, as determined by species-specific thresholds. Accordingly, (ii) the thermal regime in the regulated river would result in lower temperatures experienced by both species relative to the naturally flowing river, but (iii) brook trout and slimy sculpin would inhabit significantly different temperatures based on species-specific temperature preferences and behavior. As well, it was hypothesized that (iv) Brook Trout would inhabit consistent temperatures through the growing season, given their propensity to thermoregulate (Petty et al. 2012), while Slimy Sculpin temperature experienced would reflect seasonal changes in river water temperature. It was hypothesized that these behavioural tendencies would result in a lack of detectable ontogenetic shift in temperature use in either species between mean first and second growing season. Given that temperature alterations can become attenuated with distance from the dam (e.g. Webb & Walling 1993), and slimy sculpin are a proven sentinel species for local conditions (e.g. Galloway et al. 2003; Gray et al. 2004), it was hypothesized that (v) slimy sculpin living further from the dam would inhabit warmer water temperatures. Finally, it was hypothesized that (vi) fish condition would be correlated with temperature use such that fish with a realized thermal habitat closer to the species-specific thermal preference would have higher condition.

Methods

Study Sites

The regulated Magpie River near Wawa ON (48°4’N; 84°44’W), with a 15 MW dam, and the naturally flowing Batchawana River near Sault Ste. Marie ON (47°0’N; 84°30’W) were sampled for this study (Fig. 4.1). The Batchawana River was chosen as a field control given the similar discharge volumes, water chemistry and fish communities in the two rivers (Smokorowski et al. 2011). Over the time span encompassed by this study, the Steephill Falls waterpower facility (SHF) on the Magpie River had operating restrictions consisting of a minimum flow requirement of 7.5 $m^3 \cdot s^{-1}$, and a maximum passable flow through the turbines of 44 $m^3 \cdot s^{-1}$. The SHF has a metalimnetic water draw and operates as a hydropeaking facility, increasing and decreasing river discharge within those restrictions to align hydroelectricity production with daily patterns of electricity demand in Ontario.

Sampling

Sampling for slimy sculpin and young-of-the-year (YOY) brook trout was conducted in July of 2011 and 2012 in the Batchawana River, and August of 2011 and 2012 in the Magpie River. Sampling transects of 100 m length were chosen randomly from analogous valley segments in each river (Smokorowski et al. 2011). Distance downstream in the regulated river was measured from the SHF, while distance downstream in the naturally flowing river was measured from the beginning of the river valley segment within which the sampling transects were located. Fish were caught by backpack electrofishing to a depth of 60 cm at a standard rate of 4 $s \cdot m^{-2}$. Sampling for adult brook trout was conducted in both rivers in October of each year by angling. Fish specimens were identified to species using keys in Scott & Crossman (1973) and McAllister (1964), then weighed (g) and measured (mm) prior to freezing for storage until dissections were conducted. Water samples were collected from the thalweg of the river at a depth of 30 cm for oxygen stable isotope analysis (Storm-Suke et al. 2007a) at each sampling site on the day of sampling during July and August, as well as on one sampling date during winter.

Temperature Data

Water temperature was measured year round approximately 30 cm from the substrate in the thalweg of the river. Solinst Leveloggers (Solinst, Canada) were used to log temperature at 15 minute intervals. Four data loggers were placed in the Magpie River, with one upstream of the SHF reservoir, and the remaining three placed at 2.5, 7.5 and 13.5 km downstream from the dam (Fig. 4.1). The data logger in the Batchawana River was located at the Water Survey of Canada Station (02BF001).

Mean Temperature Experienced

Oxygen stable isotope measurements obtained from otoliths were used to quantify thermal habitat use (e.g. Murdoch & Power 2013; Kahilainen et al. 2014; Sinnatamby et al. 2013), as this method enables the determination of temperature use in YOY and small-bodied fishes that have not attained sufficient size for tagging or telemetry methods. In addition to analyzing otoliths from YOY fish, which provided temperature estimates from otolith formation to date of capture, otoliths from fish aged ≥ 2+ were subsampled to estimate temperature experienced during full growing seasons from 2008 to 2011. By using fish ≥ 2+, samples from multiple growing seasons per specimen were obtained, enabling us to check for ontogenetic shifts in temperature use. The comparison between YOY and first full summer estimates was used to deduce whether thermal habitat use was consistent over the growing season. For simplicity, temperature estimates from YOY otoliths will be referred to as “partial” season estimates, while estimates produced for entire growing seasons from fish ≥ 2+ are referred to as “full” season estimates.

Sagittal otoliths were removed from slimy sculpin and brook trout using forceps, rinsed with deionized water, dried at room temperature, and then stored in plastic snap cap vials. YOY otoliths were weighed and then either analyzed whole for $\delta^{18}O$, or, if too large, were homogenized using a mortar and pestle then subsampled. Otoliths from ≥ 2+ aged fish were placed in epoxy, sulcus side down, on a glass microscope slide and polished to expose inner annuli. Aging was conducted under reflected light using a dissecting scope and each otolith was aged at least twice by the same reader. In addition, brook trout ages were corroborated by a second, independent reader and the age and seasonality of deposition zones in slimy sculpin otoliths were confirmed by analyzing alternating opaque and translucent zones using oxygen stable isotopes (e.g. Høie et al. 2004a). Ultimately, only first and second growing season (as defined above) could be analyzed for fish ≥ 2+ as a result of small sample sizes for 3+ slimy sculpin, and insufficient otolith material for the third growing season in brook trout otoliths.

First and second summer otolith material deposited during the growing season were delineated in Image J (Schneider et al. 2012), then milled with a MicroMill Sampling System (New Wave Research, Fremont, California, US). A minimum of 50 μg of otolith material was analyzed per growing season. Otolith oxygen isotope ($\delta^{18}O_{oto}$)

samples and water oxygen isotope ($\delta^{18}O_{H2O}$) samples were analyzed on an IsoPrime multiflow isotope ratio mass spectrometer (GV Instruments/Micromass, Manchester, UK) with a precision of ±0.2‰, at the University of Waterloo Environmental Isotope Laboratory (UWEIL). A precision of ±0.2‰ equates to a temperature range of ±0.8°C. The epoxy used to embed the otoliths produces no $\delta^{18}O$ signature (B. Kelly *unpbl. data*) and therefore would not contaminate the otolith isotope values. $\delta^{18}O_{H2O}$ values were measured relative to Vienna standard mean ocean water (VSMOW) and converted to Vienna Pee Dee Belemnite (VPDB) following Coplen et al. (1983). Temperature experienced was estimated using a linear salmonid-specific fractionation equation (Storm-Suke et al. 2007a) that included samples originally collected in the Magpie River. Mean $\delta^{18}O_{H2O}$ values for 2011 and 2012 in each river were used in the fractionation equation for otolith samples corresponding to those years. For otolith samples from earlier years, the relationship between air temperature and the $\delta^{18}O$ value of precipitation developed for Eastern Canada by Fritz et al. (1987) was used to estimate $\delta^{18}O_{H2O}$ values such that

$$\delta^{18}O_{i} = \delta^{18}O_{0} + 0.43 * \Delta T,$$

Where $\delta^{18}O_{i}$ represents the $\delta^{18}O$ value for year *i*, $\delta^{18}O_{0}$ represents the river specific mean of $\delta^{18}O$ values for 2011 and 2012, and ΔT represents the difference in mean annual air temperature between year *i* and the mean of 2011-2012.

Statistical Analysis

Daily and hourly summer water temperature data were analyzed for the years for which growth season temperature estimates were obtained from fish otoliths (2008 through 2012). Data logger malfunction in low water levels in 2010 prevented the computation of diagnostics calculated with hourly data beyond July 27th for this year. Thus, for inter-year comparison purposes, daily mean, minimum and maximum temperatures for all years were calculated from May 1st through July 27th. Among-site differences downstream in the regulated river in minimum, mean and maximum water temperatures were tested with an ANOVA followed by Tukey's HSD *post hoc* test. Significant differences in thermal metrics were tested with a two-way ANOVA with year and river as categorical variables.

Hourly water temperature data were used to characterize the thermal regime (e.g. Olden & Naiman 2010), of both rivers using species-specific temperature thresholds in relation to the five components of the natural flow regime (frequency, magnitude, timing, duration and rate of change; Poff et al. 1997). For slimy sculpin, the lab derived preference (10-13°C), avoidance (21°C), and upper incipient lethal level (UIL=23.5°C) from Otto & Rice (1977) based on an acclimation temperature of 15°C were used in the calculations. For brook trout, a large number of temperature parameter estimates are available in the literature and are summarized by Coutant (1977) and Wismer & Christie (1987). Estimates were chosen based on the similarity of the lab or field conditions in the cited studies to those in our study, resulting in a preference range of 16.0-17.3°C (Cherry et al. 1977, based on an acclimation temperature of 18°C), an avoidance temperature of 20°C (Smith & Saunders 1958), and an upper incipient lethal level of 25.3°C (Fry et al. 1946). The thermal regime components were calculated as frequency of event occurrence (temperatures that fell within the preferred range or above the avoidance or UIL threshold), average duration (hours) at or above the avoidance or UIL threshold, magnitude (°C) above the avoidance or UIL threshold, and rate of change (°C hr^{-1}) in the hour prior to exceeding a threshold.

Daily water temperature data were used to calculate mean growing season water temperature. Missing data from 2010 were replaced with daily water temperature estimates produced using a linear least squares model (r^2=0.93, Batchawana River; r^2=0.88, Magpie River) based on mean daily water discharge ($m^3 \cdot s^{-1}$) (Water Survey of Canada station 02BF001 in the Batchawana River and station 02BD007 in the Magpie River) and a seven day moving average of mean daily air temperature (Government of Canada station 6057591 in Sault Ste. Marie and station 6059407 in Wawa). Mean growing season water temperature was calculated as the average of all mean daily water temperatures where the mean daily water temperature was ≥ 3°C. A threshold temperature of 3°C for both species was selected, as this corresponds to the lower limit for brook trout growth (Power 1980). No lower growth limit for slimy sculpin could be found in the literature. Partial growing season mean water temperatures were similarly calculated using data up to date of capture. An ANCOVA was used to test for a correlation between mean growing season water temperature and mean temperature experienced for both species controlling for river.

Brook trout and slimy sculpin in each river were tested for isometric growth (e.g. Wootton 1991) and condition factor was subsequently computed using Fulton's condition factor where isometric growth prevailed (e.g. Nash et al. 2006; brook trout) or using relative condition (slimy sculpin) following Le Cren (1951) where allometric growth prevailed. Where allometric growth prevailed, only within river comparisons of condition were completed.

River temperature data and otolith derived temperature use estimates were tested for normality using the Shapiro Wilk test (Royston 1982), and for homogeneity of variance using Bartlett's test (Bartlett 1937). A repeated measures analysis was used to test for differences between first and second growing season temperature use within individuals ≥ 2+. An ANOVA (Chambers 1992) was used to test for differences in temperature experienced between rivers with year as a categorical variable. Welch's t test was used to test for differences in temperature use between species, and between partial and full growing season estimates. A linear model was used to test for a correlation between temperature experienced and distance downstream for full and partial season slimy sculpin temperature use estimates, and an ANOVA followed by Tukey's HSD *post hoc* test were used to test for differences in temperature use among sites within rivers. Finally, to determine if fish living closer to their preferred temperature exhibited higher condition, linear models were used to test for a correlation between fish condition and the absolute difference between experienced temperature and preferred temperature. This analysis was conducted for both full and partial season estimates.

Results

Thermal Regime

Average mean, minimum, and maximum daily water temperatures (Fig. 4.2) downstream in the regulated river were significantly cooler relative to the naturally flowing river (ANOVA, $F_{1,4}$=102.1, $p<0.05$, mean; $F_{1,4}$=90.6, $p<0.05$, minimum; $F_{1,4}$=123.2, $p<0.05$, maximum), with year (ANOVA, $F_{1,4}$=26.5, $p<0.05$, mean; $F_{1,4}$=26.2, $p<0.05$, minimum; $F_{1,4}$=28.1, $p<0.05$, maximum), and the interaction between river and year being significant (ANOVA, $F_{1,4}$=11.5, $p<0.05$, mean; $F_{1,4}$=11.3, $p<0.05$, minimum;

$F_{1,4}$=11.2, $p<0.05$, maximum). Downstream water temperatures in the regulated river were also significantly cooler relative to upstream temperatures within the same river for all three parameters (Welch's paired t_{439}=25.34, $p<0.05$, mean; Welch's paired t_{439}=24.34, $p<0.05$, minimum; Welch's paired t_{439}=26.09, $p<0.05$, maximum) (Fig. 4.3). There was no significant difference in mean daily water temperature amongst downstream sites ($F_{2,1317}$=0.5, $p>0.05$). However there were significant differences between minimum ($F_{2,1317}$=4.9, $p<0.05$) and maximum ($F_{2,1317}$=6.7, $p<0.05$) daily temperatures. Tukey's HSD *post hoc* test revealed that minimum daily temperatures 13.5 km downstream were significantly lower relative to 2.5 km downstream, while maximum daily temperatures were significantly higher 13.5 km downstream relative to 2.5 and 7.5 km downstream.

Thermal regime parameters calculated according to species-specific thresholds provided results consistent with those for mean temperatures. For example, avoidance temperatures were most often, and for the longest duration, exceeded in the naturally flowing river for both species, with the difference in average magnitude above avoidance temperature being significant between the naturally flowing river and downstream in the regulated river ($F_{2,12}$=7.8, $p<0.05$, Tukey HSD, slimy sculpin; $F_{2,12}$=2.7, $p<0.05$, Tukey HSD, brook trout). The downstream segment of the regulated river never exceeded the UIL for either species. When the naturally flowing river did exceed the UIL, it did not do so for more than 24 hours, with the average magnitude above was usually below 1°C. The upstream site in the regulated river exhibited intermediate values between the downstream and the naturally flowing river with regards to the frequency, average duration and magnitude of events where the avoidance and upper incipient lethal temperatures were exceeded. The frequency and average duration of events where temperatures were within the preferred range of slimy sculpin varied between years, and between and within rivers, yielding no pattern where one site consistently provided greater lengths of time in the preferred range. For brook trout, water temperatures were most frequently within their preferred temperature range in the downstream segment of the regulated river ($F_{2,12}$=4.2, $p<0.05$). A comprehensive summary of thermal regime parameters are available for slimy sculpin in Table 4.1 and for brook trout in Table 4.2.

Thermal habitat

Otolith derived mean temperature use by slimy sculpin ± standard deviation was 18.9±1.7, 12.3±3.0, and 12.1±2.5 °C for partial, first full and second full season estimates, respectively, in the regulated river, and 20.6±1.8, 16.4±2.2, and 14.3±2.2 in the unregulated river (Fig. 4.4A). Mean temperature use by brook trout ± standard deviation was 19.6±1.6, 17.1±5.3, and 15.9±3.1 °C for partial, first full and second full season estimates, respectively, in the regulated river, and 20.5±2.2, 17.07±2.9, and 19.3±5.2°C in the unregulated river (Fig. 4.4B). Slimy sculpin used significantly lower temperatures over the course of the full growing season in the regulated river relative to the naturally flowing river (ANOVA, $F_{1,37}=19.9$, $p<0.05$). Year was a significant factor (ANOVA, $F_{2,37}=7.9$, $p<0.05$) with temperature estimates in 2010 being significantly warmer relative to 2009 and 2011. There was no significant difference in full season temperature use by brook trout between rivers (ANOVA, $F_{1,20}=1.04$, $p>0.05$), or amongst years (ANOVA, $F_{3,20}=1.80$, $p>0.05$).

Partial season temperature estimates were not significantly different between species in the regulated (Welch's $t_{32.1}=1.4$, $p>0.05$) or naturally flowing river (Welch's t $test_{54.9}=0.3$, $p>0.05$). Full season temperature estimates were significantly different between species in the regulated river, with slimy sculpin experiencing lower temperatures relative to brook trout (Welch's t test, $t_{19.7}=3.4$, $p<0.05$). However, full season temperature estimates were not significantly different between species in the naturally flowing river (Welch's $t_{14.6}=1.9$, $p>0.05$).

A repeated measures ANOVA showed no significant difference between the first and second full season temperature use estimates for slimy sculpin ($F_{1,8}=0.9$, $p>0.05$, Batchawana; $F_{1,9}=0.3$, $p>0.05$, Magpie) or brook trout ($F_{1,4}=0.4$, $p>0.05$, Batchawana; $F_{1,6}=0.5$, $p>0.05$, Magpie) in either river. Slimy sculpin partial and first full season temperature estimates were significantly different in both rivers with partial estimates being warmer (Welch's $t_{11.3}=8.1$, $p<0.05$, natural flow; Welch's $t_{13.1}=8.7$, $p<0.07$, regulated). This was also true for brook trout in the naturally flowing river, whereas there was no significant difference in the regulated river (Welch's $t_{6.3}=2.74$, $p<0.05$, natural flow; Welch's $t_{6.5}=1.2$, $p>0.05$ regulated).

Slimy sculpin temperature use in the regulated river showed no significant correlation with distance downstream for either partial or full season estimates ($p > 0.05$). Despite no longitudinal trend in temperature use, there were significant differences in mean temperature use amongst sites for both partial ($F_{6,41} = 5.35$, $p < 0.05$) and full season estimates (ANOVA, $F_{2,20} = 4.6$, $p < 0.05$) in the regulated river (Fig. 4.5A). In the naturally flowing river, partial and full temperature use estimates were not significantly correlated to distance downstream ($p > 0.05$), and there were no significant differences amongst sites ($F_{5,37} = 1.79$, $p > 0.05$, YOY; $F_{2,14} = 0.40$, $p > 0.05$, full season) (Fig. 4.5B).

There was no significant correlation ($p > 0.05$) between the proximity of temperature use to preferred water temperature and condition of slimy sculpin (Fig. 4.6A) or brook trout (Fig. 4.6B), i.e. fish living at temperatures closer to their preferred temperature did not exhibit higher condition.

Discussion

Thermal regime

Thermal regime parameters such as mean, minimum and maximum daily water temperatures, as well as parameters calculated based on biologically relevant species-specific thresholds indicate that the metalimnetic (cool water) draw at the SHF provides a more suitable thermal environment for both species downstream from the dam in the regulated river relative to upstream and the naturally flowing river. The frequency and duration of temperatures above the avoidance and UIL thresholds for both species was higher upstream in the regulated river and in the naturally flowing river relative to downstream in the regulated river. Thus, barring the availability of thermal refuges, fish in the naturally flowing river would have experienced unsuitably high temperatures for longer periods of time relative to fish downstream from the reservoir in the regulated river. However, it is important to note that temperature logger numbers (see methods) were limited, and thus measured river temperature data may not fully represent the range or quality of thermal habitat available to fish within either river.

Thermal Habitat

Thermal regime parameters indicative of more suitable temperatures downstream in the regulated river relative to the naturally flowing river corresponded with significantly cooler thermal habitat use in the regulated river by slimy sculpin, but not brook trout. Full season temperature use estimates for both species in the regulated river, and brook trout in the naturally flowing river, accord well with their literature documented preferred temperatures (Cherry et al. 1977). And while partial and full season estimates were not significantly different in the Magpie River for brook trout, they were significantly different in both rivers for slimy sculpin. The differing results obtained between species are likely driven by species-specific behavioral strategies and temperature preferences.

Slimy sculpin are a small bodied benthic fish with poor swimming abilities (e.g. see Facey & Grossman 1990 who studied the closely related *C. bairdii*) and a small home range size (Gray et al. 2004). There was no significant correlation between distance downstream and temperature experienced by slimy sculpin. However, despite higher variability in daily temperatures 13.5 km downstream compared with 2.5 km downstream, there was no significant difference in mean daily temperature. Thus, based on temperatures measured by the data loggers, the lack of longitudinal trend in temperature use may be expected. Nonetheless, the between-river, site-specific, and temporal (partial vs full season) differences in temperature use by slimy sculpin in this study suggest that they experience locally available temperatures, and are not actively selecting preferred temperatures as would be the case if slimy sculpin were behaviourally thermoregulating. This is not to suggest that slimy sculpin are insensitive to temperature, as their densities can be higher in cooler river reaches, relative to warmer sections (Edwards & Cunjak 2007). But within a given river reach with a temperature range within the tolerance limits of slimy sculpin, their low mobility appears to inhibit active thermoregulation.

In contrast to slimy sculpin, brook trout are a more mobile species and are known to behaviourally thermoregulate, actively moving to areas within their preferred water temperature range (Baird & Kreuger 2003; Petty et al. 2012). The proximity between estimates of temperature use and literature-based temperature preferences and the lack of significant difference in temperature use estimates between rivers, suggests that brook trout in both rivers thermoregulate by seeking habitat with specific temperatures. However, brook trout are also known to select habitat based on cover (Petty et al. 2012), flow (Murchie & Smokorowski 2004), and inter-and intra-species interactions (Fausch &

White 1981; Tremblay & Magnan 1991). Given the high variability in full season temperature use estimates (Fig. 4.4), it is likely that any or all of these additional factors interact with temperature to determine brook trout habitat choice (e.g. Walsh et al. 1988; Magoulick & Wilzbach 1998).

The consistent use of higher water temperatures by brook trout relative to slimy sculpin reflects the difference in preferred temperatures between species (Cherry et al. 1977; Otto & Rice 1977). In addition to the difference in the degree to which each species behaviourally thermoregulates, these species have different microhabitat preferences. Slimy sculpin are often found in rocky areas of runs and riffles, using substrate for cover (Scott & Crossman 1973), while brook trout are often found underneath overhanging cover or within pools (Griffith 1972; Cunjak & Green 1983). Thus, despite the fact that these two stenothermic species are often found sympatrically in river reaches, their different thermal and microhabitat preferences underscore the importance of habitat complexity within riverine environments.

The majority (90%) of partial season temperature use estimates, and many full season estimates were above laboratory determined preferences, in both species. Yet fish inhabiting temperatures closer to their preferred range did not exhibit significantly higher condition. At temperatures above those preferred, higher metabolic rates would lead to higher energy expenditure for maintenance functions, and less energy available to contribute to energy storage (growth/condition), assuming constant ration levels (e.g. Brett & Groves 1979). However, hydroelectric dams simultaneously alter multiple downstream parameters impacting factors such as food availability (e,g. invertebrate abundance, Jones 2013) and fish energy expenditure (e.g. Murchie & Smokorowski 2004). In addition, optimum temperatures can increase to a certain extent based on energy intake and food type (Elliott & Hurley 2000). Thus, while the difference between preferred and realized temperature was not correlated with condition, thermal habitat is still an important factor when considered as part of the interplay amongst changes to food availability and energetic demands caused by river regulation.

Otolith derived estimates for temperature experienced by YOY fish fell consistently around laboratory derived avoidance temperature estimates. It is possible that otolith-derived growing season temperature use estimates overestimate temperature experienced in these rivers. Deposition of otolith material is dependent on resting metabolic rate, and can result in higher deposition rates at higher temperatures (Wright 1991; Wright et al. 2001). The use of an average across the entire growing season does not account for higher deposition rates at higher temperatures and therefore a higher proportion of otolith material from periods of time spent at higher temperatures. As well, fish can spend short periods of time above their avoidance temperatures (Schrank et al. 2003), which could bias our mean estimates upwards. For example, brook trout have been observed to feed in the early evening (Walsh et al. 1988), corresponding with peak daily water temperatures (Casado et al. 2013). This behavior would increase the mean temperature at which fish lived, but may not have a detrimental effect if fish spent other parts of the day in cooler thermal refugia (Schrank et al. 2003). With regards to YOY slimy sculpin, they are caught along the stream edges (e.g. see Smokorowski et al. 2011 for methods), where summer water temperatures can be higher relative to the main channel (Clark et al. 1999; Webb et al. 2008). Thus, our otolith derived temperature estimates are not unrealistic based on the behavior and habitat of fish in these systems.

Implications for dam management

The selective release of cool water from dams is being used successfully to provide more favorable spawning temperatures for sockeye salmon (*Onchorynchus nerka*) below a dam (MacDonald et al. 2012) and has been suggested as a strategy to mitigate climate induced stream warming (Isaak et al. 2012; Null et al. 2013; Robson et al. 2013; Rheinheimer et al. 2014; Rheinheimer & Viers 2014). However, prior to widespread adaptation of management strategies aimed at decreasing downstream temperatures through dam operation, several caveats need to be considered. Primarily, the fragmentation of thermal refuges by barriers such as hydroelectric dams already impacts the accessibility of cooler temperatures to fish (Hillyard & Keeley 2012). Assuming continued river regulation, many issues remain. This study demonstrates the discrepancy between realized thermal habitat between two species within the coldwater fish guild (e.g. Scott & Crossman 1973; Magnuson et al. 1979), suggesting that operating hydroelectric dams to thermally benefit multiple species rather than one species alone will be complicated. Despite significant reductions in water temperature as a result of river regulation, the continued role of external forcing on river water temperature (e.g. air temperature; Poole & Berman 2001) is evident short distances downstream from the dam (greater daily range of temperatures 13.5 km downstream in this study; see also Webb & Walling 1993; Casado et al. 2013). As well, the use of dam water releases to mitigate climate-driven temperature increases presumes the ability to maintain consistent dam operations under a changing climate, including changes to precipitation, evapotranspiration and runoff (Chu et al. 2005; Oni et al. 2012). For example, unexpectedly low water levels in 2010 forced the Steephill Falls operators to stop generating electricity and use a surface spill to try and maintain downstream water levels. A surface spill would not decrease downstream temperatures in the same way as a coolwater draw, thus dam operators may not be able to continuously mitigate downstream water temperatures during extreme low flow years. Despite the localized impact of cool water releases on downstream temperatures, modelling studies suggest that these decreases could be overwhelmed by climate warming (Isaak et al. 2012; Null et al. 2013). Thus, when attempting to mitigate climate change impacts, a holistic and adaptive approach to dam management which maintains heterogeneity within the riverine environment may provide better results for the fish community as a whole, rather than one focused on temperature alone. While actively managing a dam for desired downstream temperatures has proven effective for a single species as determined by spawning success (MacDonald et al. 2012), additional approaches such as managing land use and restoring riparian vegetation (Kurylyk et al. 2014) also provide thermal benefits and have the potential for synergistic effects when applied together (Robson et al. 2013).

In this study, the hydroelectric dam coolwater draw resulted in significantly cooler temperatures downstream, creating a more suitable thermal regime for coldwater fish species relative to a nearby naturally flowing river. However, our two study species use habitat differently, resulting in significantly different realized thermal habitat. Thus, species-specific differences in temperature, habitat preference, and behavior suggest that using hydroelectric dams to alter river water temperatures and mitigate climate change impacts on the fish community will be complicated. A more holistic approach to river management which focuses on maintaining the complexity of the riverine environment may better serve conservation goals when multiple fish species are of concern.

Table 4.1 Slimy sculpin thresholds for preferred (10-13°C), avoidance (>21°C) and upper incipient lethal (UIL) (>23.5°C) temperatures (see methods) described according to the five components of the thermal regime: timing (number of days to first occurrence), frequency (total number of events), average duration, magnitude (above avoidance and UIL threshold), and rate of change (during the hour prior to exceeding the threshold). Measurements were collected from May through September in the naturally flowing Batchawana River, upstream of the reservoir in the regulated Magpie River, and 2.5 km downstream from the Steep Hill Falls water power facility in the regulated river. Parameters are calculated from May 1st to July 27th.

		Preferred (10-13°C)			Avoidance (>21°C)					Upper Incipient Lethal Temperature (>23.5°C)				
Year	Site	First Day	Freq-uency	Average Duration (hrs)	First Day	Freq-uency	Average Duration (hrs)	Magnitude Above (°C)	Rate of Change ($m^3 \cdot s^{-1} \cdot hr^{-1}$)	First Day	Freq-uency	Average Duration (hrs)	Magnitude Above (°C)	Rate of Change ($m^3 \cdot s^{-1} \cdot hr^{-1}$)
2008	natural	153	3	52	177	11	49.2	1.2	0.24	218	2	13.5	0.5	0.3
	upstream	145	6	56.7	145	6	28.2	0.37	0.16	NA	0	NA	NA	NA
	downstream	133	16	29.3	225	0	NA	NA	NA	NA	0	NA	NA	NA
2009	natural	128	17	21.7	168	10	21	1.3	0.18	174	3	10.7	0.7	0.3
	upstream	141	7	37.1	141	8	20.5	0.58	0.23	NA	0	NA	NA	NA
	downstream	147	8	45.5	NA	0	NA	NA	NA	NA	0	NA	NA	NA
2010	natural	127	4	46.5	143	14	90.8	2.4	0.19	145	33	15.3	0.9	0.3
	upstream	121	11	29.6	121	31	39.6	1.75	0.4	146	33	8.3	0.8	0.4
	downstream	136	7	23.3	191	16	33	0.73	0.24	NA	0	NA	NA	NA
2011	natural	128	8	32.5	183	7	123	1.4	0.36	199	12	8.75	0.3	0.2
	upstream	139	6	43.7	139	5	171.8	1.8	0.22	198	15	16.8	0.7	0.2
	downstream	151	12	22.8	200	10	14.3	0.64	0.26	NA	0	NA	NA	NA
2012	natural	123	6	31.5	145	12	116.7	2.9	0.26	175	15	61.1	1.3	0.3
	upstream	129	4	44.8	129	14	68.9	1.4	0.24	186	16	5.6	0.4	0.2
	downstream	140	7	37.1	206	2	5.5	0.07	0.2	NA	0	NA	NA	NA

Table 4.2 Brook trout thresholds for preferred (16-17.3°C), avoidance (>20°C) and upper incipient lethal (UIL) (>25.3°C) temperatures (see methods) described according to the five components of the thermal regime: timing (number of days to first occurrence), frequency (total number of events), average duration, magnitude (above avoidance and UIL threshold), and rate of change (during the hour prior to exceeding the threshold). Measurements were collected from May through September in the naturally flowing Batchawana River, upstream of the reservoir in the regulated Magpie River, and 2.5 km downstream from the Steep Hill Falls water power facility in the regulated river. Parameters are calculated from May 1st to July 27th.

		Preferred (16-17.3°C)			Avoidance (>20°C)					Upper Incipient Lethal Temperature (25.3°C)				
Year	Site	First Day	Freq-uency	Average Duration (hrs)	First Day	Freq-uency	Average Duration (hrs)	Magnitude Above (°C)	Rate of Change ($m^3 \cdot s^{-1} \cdot hr^{-1}$)	First Day	Freq-uency	Average Duration (hrs)	Magnitude Above (°C)	Rate of Change ($m^3 \cdot s^{-1} \cdot hr^{-1}$)
2008	natural	161	10	18.0	176	13	59.5	1.7	0.3	NA	0	0	0	0
	upstream	161	9	27.6	201	3	156.0	0.8	0.1	NA	0	0	0	0
	downstream	158	31	13.9	204	10	11.8	0.3	0.1	NA	0	0	0	0
2009	natural	162	8	10.8	167	14	34.0	1.2	0.2	NA	0	0	0	0
	upstream	165	3	17.0	172	14	29.5	0.9	0.2	NA	0	0	0	0
	downstream	173	27	22.1	NA	0	0	0	0	NA	0	0	0	0
2010	natural	138	3	15.7	141	13	115.0	2.8	0.3	145	8	4.9	0.5	0.3
	upstream	138	8	5.6	144	21	70.0	2.4	0.3	147	5	3.4	0.3	0.3
	downstream	147	12	18.2	175	7	112.0	1.3	0.2	NA	0	0	0	0
2011	natural	140	21	10.1	159	15	67.0	2.1	0.2	NA	0	0	0	0
	upstream	157	7	18.1	168	5	185.0	2.6	0.3	220	1	2.0	0.03	0.1
	downstream	167	23	9.2	194	17	21.9	0.9	0.2	NA	0	0	0	0
2012	natural	133	10	12.0	141	8	198.0	3.6	0.3	184	28	9.3	0.6	0.3
	upstream	141	22	12.3	162	9	130.0	2.0	0.2	NA	0	0	0	0
	downstream	156	15	6.5	189	14	15.1	0.4	0.2	NA	0	0	0	0

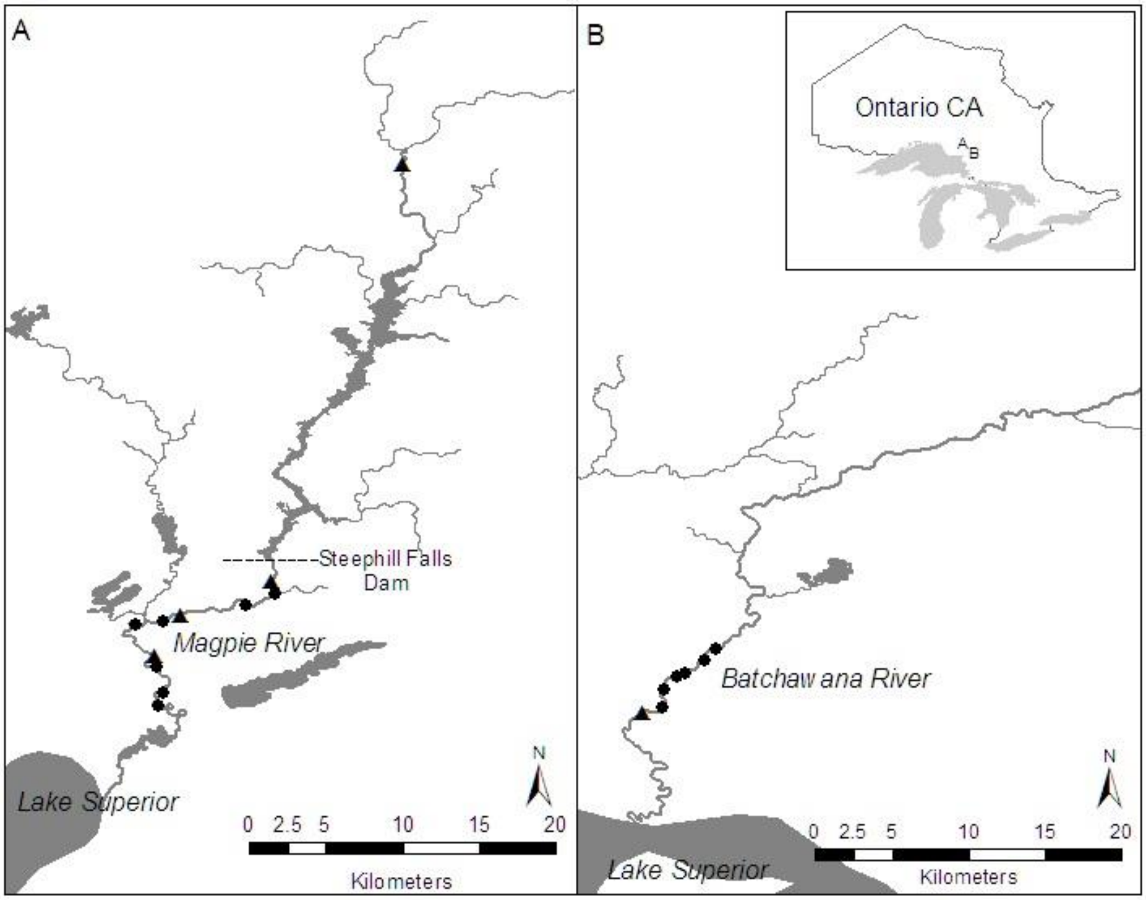

Figure 4.1. Location of the regulated Magpie River (A) and naturally flowing Batchawana River (B) in Ontario, Canada (inset). Fish sampling sites are denoted by circles (●) and water temperature logger locations are denoted by triangles (▲).

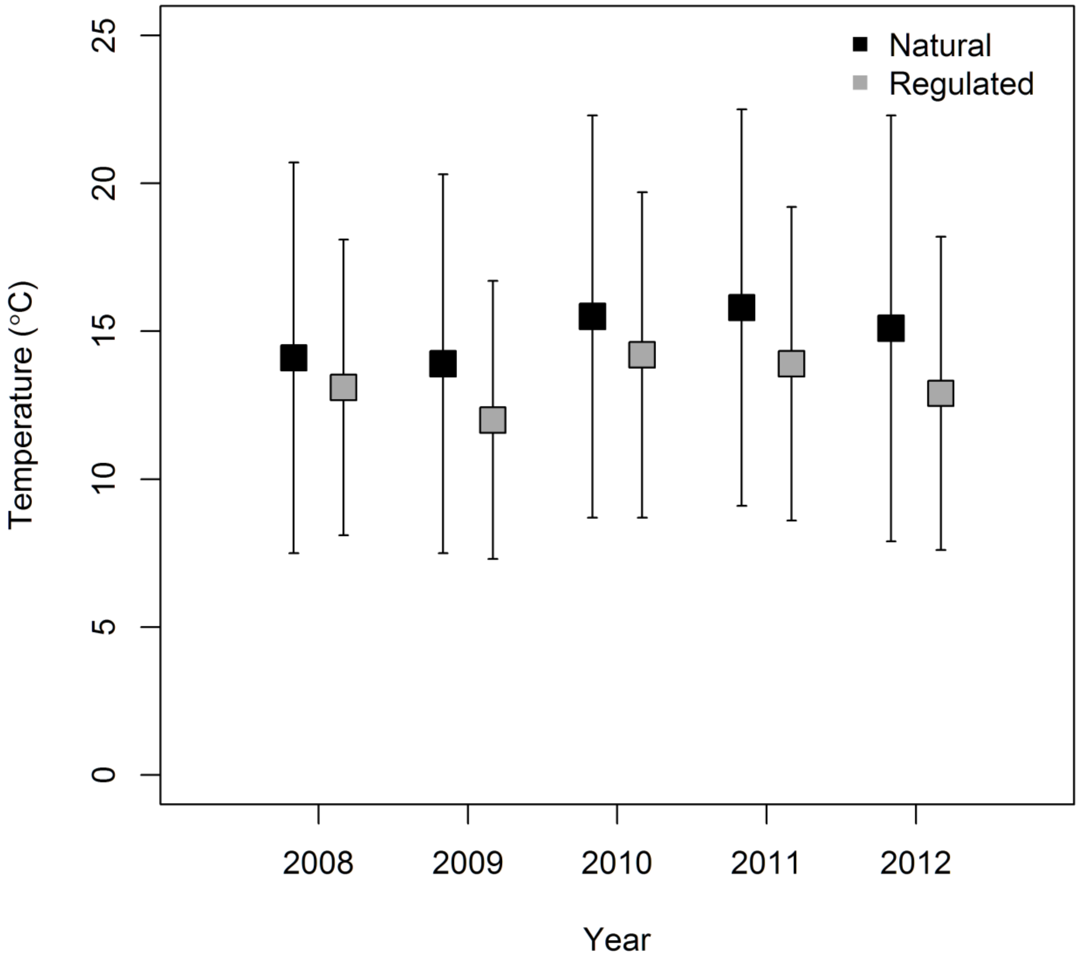

Figure 4.2. Mean daily growing season water temperature (°C ± standard deviation) 13.5 km downstream from the reservoir in the regulated Magpie River (■) and in the naturally flowing Batchawana River (■). Growing season is defined as the period of time when the mean daily river water temperature is ≥ 3°C.

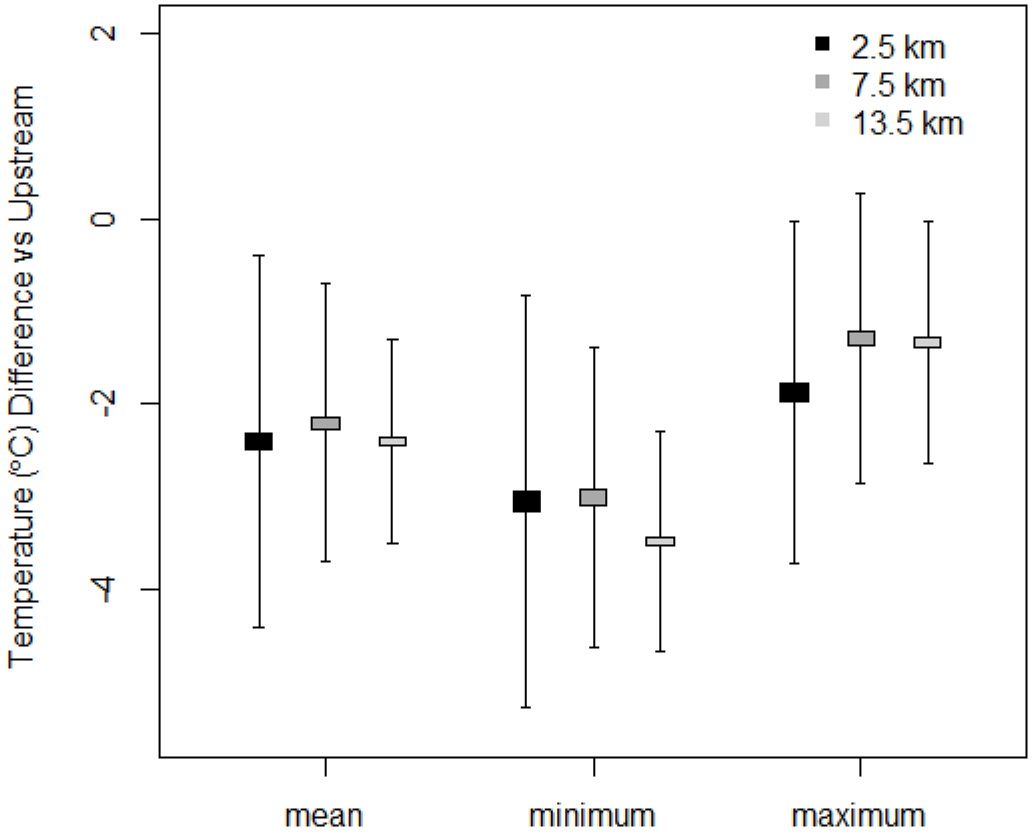

Figure 4.3. Differences in the mean, minimum and maximum daily temperatures 2.5 (■), 7.5 (■), and 13.5 (■) km downstream from the dam, relative to the site upstream from the reservoir in the regulated Magpie River. Bars define the mean ± standard error. Whiskers define the mean ± one standard deviation.

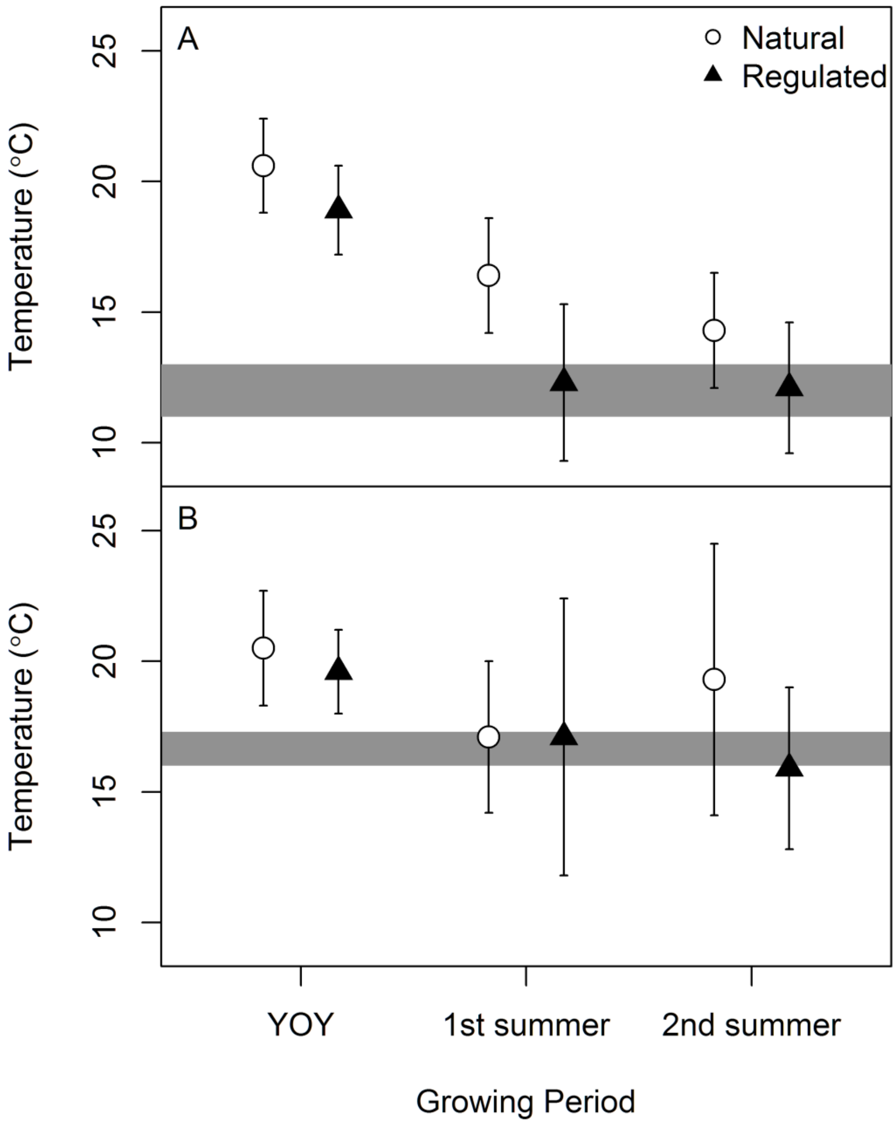

Figure 4.4. Estimates of young-of-the-year (YOY) and first and second growing season mean ± standard deviation water temperature experienced by slimy sculpin (A) and brook trout (B) in the regulated Magpie (▲) and naturally flowing Batchawana (○) Rivers. Grey bars indicate species-specific temperature preference.

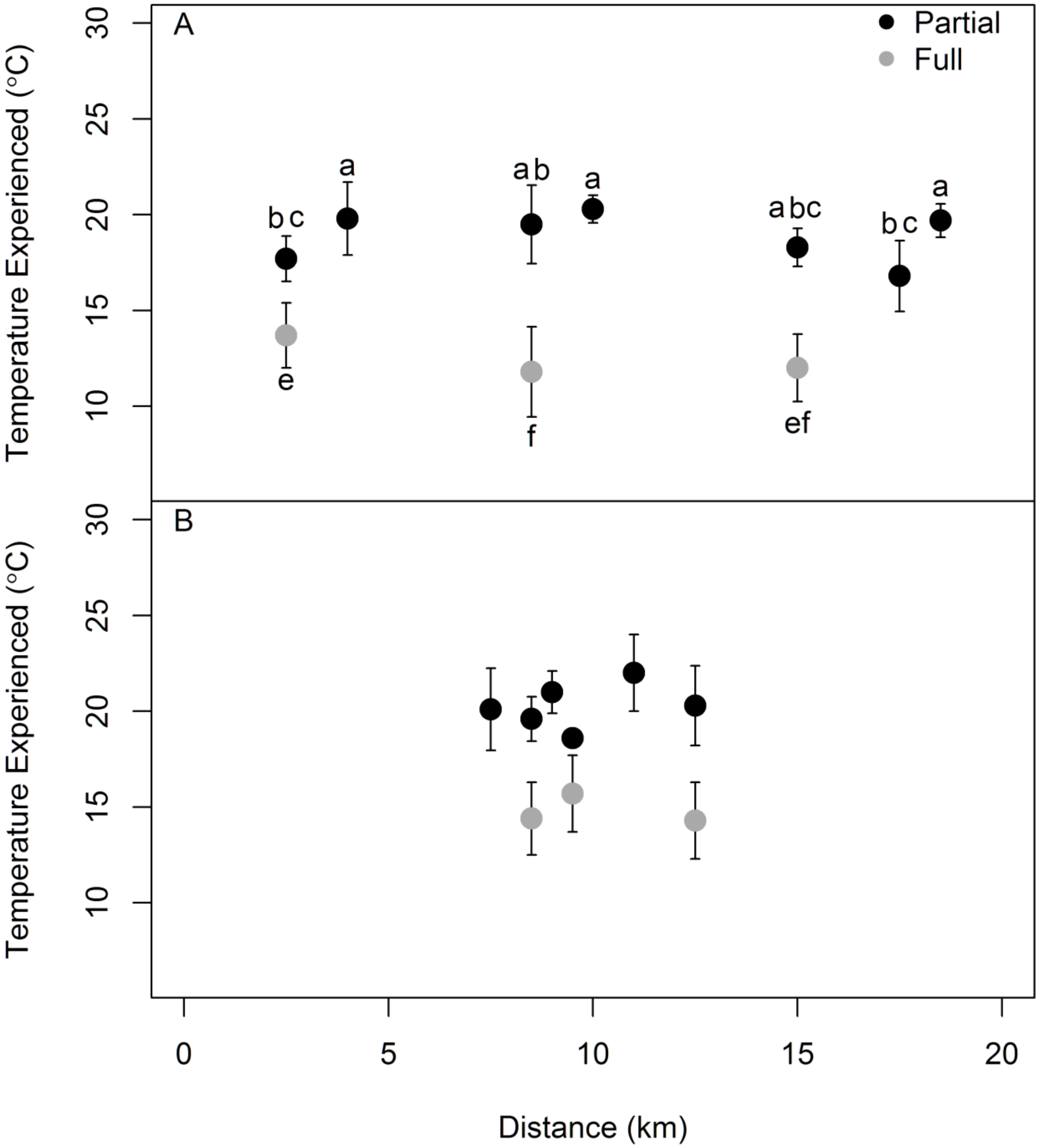

Figure 4.5. Estimates of mean water temperature experienced (°C) during partial (●) and full growing seasons (●) for slimy sculpin in the regulated Magpie (A) and the natural Batchawana (B) Rivers by distance downstream. Letters indicate sites which are not significantly different from each other. No significant differences were found amongst sites in the natural river.

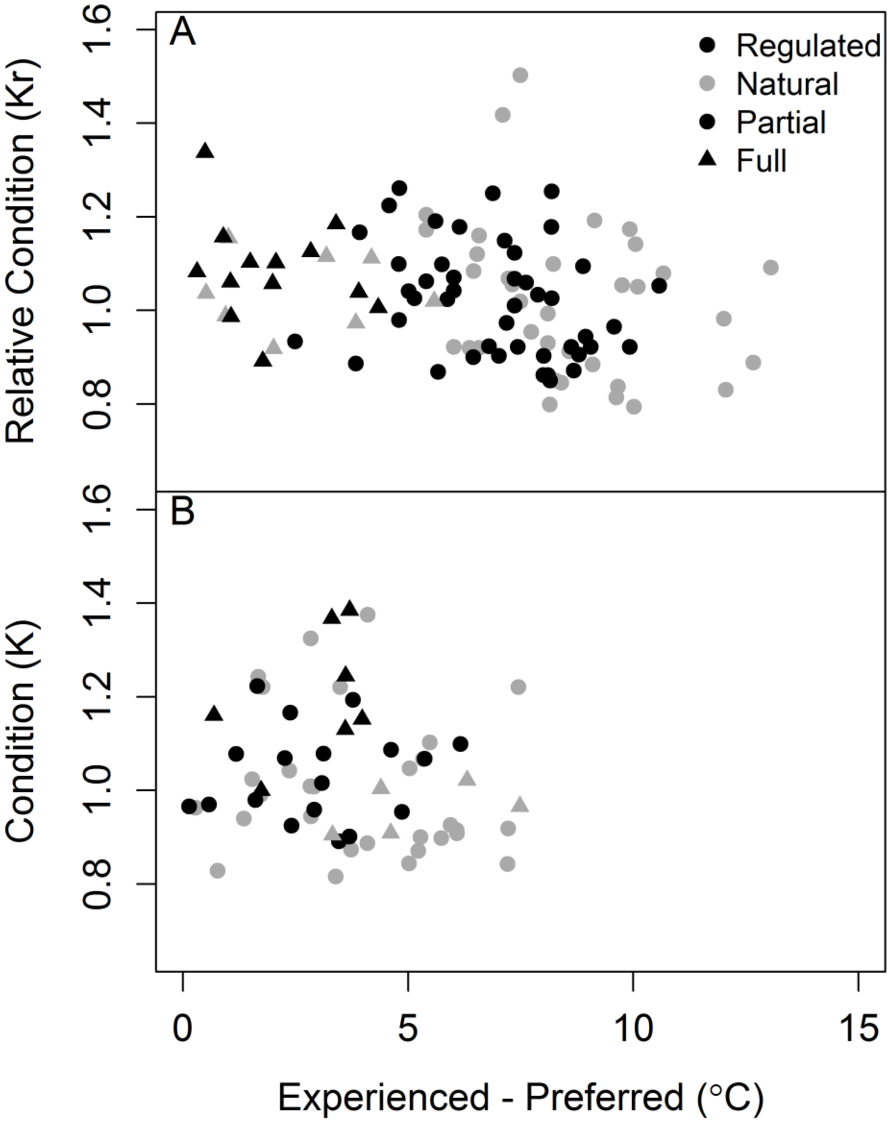

Figure 4.6. Fish condition relative to the difference between mean water temperature experienced and preferred temperature for partial (circles) and full (triangles) season slimy sculpin (A) and brook trout (B) in the regulated Magpie (●) and natural Batchawana (●) Rivers. Condition is calculated as relative condition for slimy sculpin and Fulton's condition factor for brook trout.

Chapter 5 Impact of river regulation on the growth, condition and field metabolism of brook trout (*Salvelinus fontinalis*)

Introduction

The Laurentian Great Lakes and their tributaries are important for a variety of economic and recreational interests, including: recreation (Allan et al. 2015), sport, commercial and aboriginal fishing (Cooke & Murchie 2013; Tufts et al. 2015), electricity production (Kelly et al. 2015b; Tidwell & Pebbles 2015) and irrigation (Mubako et al. 2013). Balancing the competing needs of multiple users, while protecting the biological communities within these systems, is essential to ensuring their ecological integrity. For example, hydroelectric dams in Ontario are an important contributor to the electricity grid, supplying approximately 60% of the total electricity produced in 2014 (Statistics Canada 2015), while recreational fishing in Ontario has an important socioeconomic impact, involving close to 1 million resident anglers and generating direct expenditures of close to 1 billion dollars annually (Fisheries and Oceans Canada 2010). However, hydroelectric dam operation can have significant impacts on downstream fish populations (e.g. Haxton et al. 2015), which could in turn reduce the viability of recreational fisheries. Thus, it is necessary to evaluate the impact of hydroelectricity production on downstream fish populations to balance competing economic interests, and ensure the sustainability of recreational fisheries and the integrity of river ecosystems.

Brook trout (*Salvelinus fontinalis*) is an important recreational fishery species in Canada (Fisheries and Oceans Canada 2010). They are often found in river environments with cool, clean water (Power 1980), in pools, or underneath overhanging cover (Griffith 1972; Cunjak & Green 1983). Previous studies have shown that hydroelectric dam operation, and specifically hydropeaking, whereby dam operators rapidly change discharge to match daily electricity demands (Morrison & Smokorowski 2000), can affect fish. For example, discharge increases may cause an increase in fish movement and thus metabolic demands (Taylor & Cooke 2012; Taylor et al. 2014), while stranding and mortality can occur during discharge decreases (Hvidsten 1985; Saltveit et al. 2001). Adult brook trout have been found to increase their activity during the discharge increase phase of hydropeaking events (Scruton et al. 2003; Murchie & Smokorowski 2004), while young-of-the-year (YOY) brook trout have been found to move laterally to inhabit newly wetted areas (Bond & Jones 2015). Given the amount of time spent in a state of rapid discharge increase in hydropeaked systems (Smokorowski et al. 2011), the resultant increased activity and movement of brook trout has the potential to increase their metabolic costs and energy output (Scruton et al. 2003; Murchie & Smokorowski 2004), reducing the amount of energy available to allocate towards growth, storage and reproduction.

Although hydropeaking may increase the energetic costs of fish living downstream from dams, it is possible that river regulation can also provide a benefit for some fish populations. A higher food supply for fish may be available downstream from dams in the form of increased invertebrate abundance (Jones 2013) and invertebrate drift (Cushman 1985; Lauters et al. 1996; Lagarrigue et al. 2002; Patterson & Smokorowski 2011). Studies have documented increased growth rates in slimy sculpin (*Cottus cognatus*) (Bond et al. 2015; Kelly et al. 2015a) and humpback chub (*Gila cypha*) (Finch et al. 2015) downstream from dams, with increased food supply being a likely causal factor (Bond et al. 2015). However, lower growth rates in rainbow trout (*Oncorhynchus mykiss*) have also been found as a result of hydropeaking (Korman & Campana 2009). Given the species-specific impacts, it is important to evaluate the effects of dam operation on individual species, especially for those of recreational and conservation importance.

In this study the length-at-age and condition of brook trout was examined in a river with a 15 MW hydropeaking facility and contrasted to the same measurements obtained from contemporarily sampled brook trout in a nearby naturally flowing river. The field metabolism of the two populations was also examined, inferred from the contribution of metabolically derived carbon in otolith $\delta^{13}C$. The data was used to test several hypotheses, including that: (i) brook trout length-at-age and condition would be higher in the regulated river relative to the naturally flowing river as a result of increased food supply (Patterson & Smokorowski 2011; Jones 2013), and (ii) field metabolic rate would be higher in the regulated river as a result of increased activity and movement stimulated by hydropeaking events (Murchie & Smokorowski 2004; Bond & Jones 2015). The causal mechanisms driving variation in field metabolic rate were further investigated by quantifying the correlation between field metabolic rate and thermal habitat and river discharge. It was hypothesized that estimates of field metabolic rate would be positively correlated with: (iii) the temperature of the river water inhabited by fish, given the temperature dependence of fish metabolic rates (Brett & Groves 1979) and the ability of hydroelectric dams to significantly alter downstream river water temperatures (Olden and Naiman 2010), and (iv) the amount of time spent hydropeaking in the regulated river, as brook trout relative activity is positively correlated with discharge increases (Murchie & Smokorowski 2004).

Methods

Study Sites

Two tributaries of Lake Superior in northern Ontario were sampled for this study: one with a 15 MW hydropeaking facility (the Magpie River near Wawa ON, 48°4’N; 84°44’W) and one with a natural flow regime (the Batchawana River near Sault Ste. Marie ON, 47°0’N; 84°30’W) (Fig. 5.1). The Batchawana River was chosen as a natural control for the Magpie River, given that the two rivers have similar historical mean annual discharge, geology, chemical compositions, and biological communities (Marty et al. 2009; Smokorowski et al. 2011). Both resident (riverine) and coaster (migratory between lentic and lotic environments) populations of brook trout have been documented in tributaries of Lake Superior (Leonard et al. 2013). Therefore, river segments where fish return migrations from Lake Superior were prevented by a large water fall at the downstream end were sampled to avoid the confounding factor of growth and condition differences likely to exist between resident and coaster populations (Robillard et al. 2011).

The Steephill Falls generating station (SHF) in the Magpie River has a coolwater draw at 10 m depth and a maximum passable turbine discharge of 44 $m^3 \cdot s^{-1}$, although spill flow could be higher. Throughout the study period a minimum flow requirement of 7.5 $m^3 \cdot s^{-1}$ was in place. However, the study period encompasses two different hydropeaking regimes. A “restricted” hydropeaking regime was in place up to October 2004 during which time ramping restrictions of ≤ 1 $m^3 \cdot s^{-1} \cdot hr^{-1}$ from October 10th through November 15th, 2 $m^3 \cdot s^{-1} \cdot hr^{-1}$ from November 16th through the spring freshet, and no greater than a 25% increase or decrease from the previous hour’s flow from the spring freshet to October 9th were in place (Smokorowski et al. 2011). An “unrestricted” hydropeaking regime was in place from 2005 on, during which time there was no restriction on the rate of increase and decrease of discharge. This enabled the dam operators to alter discharge from the minimum allowable flow to the maximum passable flow through the turbines on a sub-daily basis (Smokorowski et al. 2011).

Randomly selected transects of 100 m were sampled in both rivers in analogous river reaches by backpack electrofishing in July and August from 2002 to 2012, effectively targeting YOY brook trout (e.g. Bond & Jones 2015). Brook trout older than 0+ were targeted in the autumn of each year by angling. Specimens which were used for stable isotope analysis were frozen until dissection to avoid preservation biases (Kelly et al. 2006; Storm-Suke et al. 2007b), while all other specimens were preserved in formalin for 24 – 30 hrs, followed by ethanol. Upon dissection, fork-length (mm) and weight (g) were recorded. Dorsal muscle tissue was dissected from frozen samples for stable isotope and caloric content analysis. Otoliths were removed using forceps, rinsed with deionized water, air dried and stored in snap cap vials until aging and stable isotope analysis.

Length-at-age

Sagittal otoliths were aged under reflected light using a dissecting microscope (Nikon SMZ 1000, Nikon Instruments Inc.). All otoliths were read twice by the same reader, and where annuli were difficult to determine, otoliths were epoxied to microscope slides and polished to clarify. Ages were corroborated by a second, independent reader. Otolith increments consisting of an annual cycle were measured at 90 degrees from the rostral radius along a line from the nucleus towards the dorsal edge using NIS Elements software (Nikon Instruments Inc.). Length-at-age was determined by back-calculation using the scale proportional hypothesis as outlined in (Francis 1990):

$$L_i = -(a/b) + (L_c + a/b)(S_i/S_c),$$

where L_i is the length of the fish at age i, L_c is the length of the fish at capture, S_i is the radius of the otolith at age i, S_c is the radius of the otolith at capture, and a and b are the intercept and slope, respectively, of the regression of otolith radius on fish length. The regression of otolith radius on fish length was conducted separately for each river, given the potential for differences in growth rates and otolith formation rates between populations.

Condition

Brook trout condition was assessed using two methods: (i) examination of weight-length relationships (Anderson & Neuman 1996), and (ii) quantification of the caloric content (calories$\cdot$g^{-1}) of muscle tissue (Paine 1971). Weight-length regressions incorporated the entire size range of brook trout caught, but only pre-preservation measurements were used, given that preservation type can affect both length and weight (Anderson & Neuman 1996). Caloric content analysis was restricted to adult, male specimens caught in the fall given the influence of fish size, sex and season on this parameter (Meakins 1976), and the higher number of samples from male specimens available. Dorsal muscle tissue used for caloric content analysis was dried at 50°C for 48 hrs, ground to obtain a homogenized sample, formed into a pellet and analyzed using a Parr Semi-micro Calorimeter 6725 (Parr Instrument Company, Moline, IL). Between-river condition comparisons using both methods were limited to the unrestricted ramping period for which a larger number of specimens were available.

Metabolism

The δ^{13}C of otoliths ($\delta^{13}C_{oto}$) is driven mainly by the dissolved inorganic carbon (DIC) δ^{13}C (~ 80%) of inhabited waters, with the remainder contributed by metabolically derived carbon (Weidman & Millner 2000; Høie et al. 2003; Solomon et al. 2006; Elsdon et al. 2010). An increase in metabolic rate results in an increased concentration of metabolically derived carbon in the bloodstream and endolymphatic fluid, leading to an increased concentration in the otolith (Solomon et al. 2006). Thus, the carbon isotope measurement of the otolith ($\delta^{13}C_{oto}$) can be used to make inferences about fish metabolism from the calculation of *M*, i.e. the contribution of metabolically derived carbon to the $\delta^{13}C_{oto}$ value (e.g. Lin et al. 2012; Kahilainen et al. 2014; Kelly et al. 2015c; Sinnatamby et al. 2015). Field metabolism (*M*), as estimated using $\delta^{13}C_{oto}$,will represent an average energy expenditure of fish and incorporate the energetic costs of standard metabolic rate, thermoregulation, locomotion, feeding, reproduction and growth (e.g., Nagy 1987; Sinnatamby et al. 2015).To estimate the contribution of metabolically derived carbon to $\delta^{13}C_{oto}$, the δ^{13}C values of the otolith, fish muscle tissue (as a proxy for respired carbon) and river water DIC are required (e.g. McConnaughy et al. 1997).

YOY brook trout otoliths were weighed and then either analyzed whole for $\delta^{13}C$, or, if too large, were homogenized using a mortar and pestle, then subsampled. Summer growth season otolith material from brook trout >0+ was delineated in Image J (Schneider et al. 2012), then milled with a MicroMill Sampling System (New Wave Research, Fremont, California, US) following methods described in Kelly et al. (2015c). Mass spectrometer operating capabilities necessitated a minimum of 50 µg of otolith material per sample for $\delta^{13}C$ analysis. This enabled us to analyze $\delta^{13}C$ from only the first and second summer growth zones for brook trout aged >0+.

Water samples for the stable isotope analysis of DIC were collected multiple times through the summer of each growing season. Samples were collected in glass bottles in the thalweg of the river at a depth of 30 cm (Storm-Suke et al. 2007a), and refrigerated in the dark until analysed at the University of Waterloo Environmental Isotope Laboratory (UWEIL) following standardized protocols described in Guiguer et al. (2003). To account for spatial and temporal variability, an average water DIC isotope value was calculated per year and used to estimate *M* as described below.

All isotope samples were analysed at the UWEIL and are reported in standard δ notation:

$$\delta = [(R_{sample} - R_{standard}) / R_{standard}] \times 1000 \text{ (‰)}.$$

$\delta^{13}C_{oto}$ was analysed on an IsoPrime multiflow isotope ratio mass spectrometer (GV Instruments/Micromass, Manchester, UK). Muscle tissue $\delta^{13}C$ ($\delta^{13}C_{mus}$) was analysed with a 4010 Elemental Analyser (Costech Instruments, Italy) coupled to a Delta Plus XL (Thermo-Finnigan, Germany) having a precision of 0.2‰ (UWEIL). Water samples were analysed on an IsoPrime multiflow isotope ratio mass spectrometer (GV Instruments/Micromass, Manchester, UK). All samples were analysed relative to Vienna Pee Dee Belemnite (VPDB) with an analytical precision of 0.2‰ (UWEIL).

The proportion of metabolic carbon (*M*) contributing to $\delta^{13}C_{oto}$ was calculated following McConnaughy et al. (1997) as:

$$M(\delta^{13}C_{resp}) + (1-M)(\delta^{13}C_{DIC}) = \delta^{13}C_{oto} - \Delta$$

where *M* is the fraction of respired carbon contributing to $\delta^{13}C_{oto}$, $\delta^{13}C_{resp}$ is the isotopic value of the respired carbon and Δ is the fractionation between tissue HCO_3^- and the otolith. $\delta^{13}C_{resp}$ was assumed to be equivalent to $\delta^{13}C_{mus}$ (Post 2002) and a value of 2.7

for Δ was used (Romanek et al. 1992) following common practice (Høie et al. 2004b; Sinnatamby et al. 2014; Kelly et al. 2015c). The $\delta^{13}C_{mus}$ value was used when calculating *M* for both first and second growing seasons in brook trout aged >0+. For 0+ brook trout, a river-specific mean value calculated from samples collected for a stable isotope study spanning the same time frame as this study was used (J. Brush unpublished data). $\delta^{13}C_{oto}$ values used to calculate *M*, resulted in an average value of *M* for the time period of otolith formation to catch date for YOY specimens, and the summer growing season for subsampled otoliths from brook trout >0+. Availability of unpreserved otolith samples enabled the calculation of *M* for the unrestricted hydropeaking period only.

Realized thermal habitat was defined as the mean temperature experienced by the fish over the course of the summer growing season and was estimated using otolith oxygen stable isotope analysis. Briefly, ground or milled otolith samples (see above) were analyzed for $\delta^{18}O$ according to Guiguer et al. (2003). Otolith $\delta^{18}O$ ($\delta^{18}O_{oto}$) and water $\delta^{18}O$ ($\delta^{18}O_{H2O}$) were analysed on an IsoPrime multiflow isotope ratio mass spectrometer (GV Instruments/Micromass). $\delta^{18}O_{oto}$ was measured relative to VPDB, while $\delta^{18}O_{H2O}$ was measured relative to Vienna standard mean oceanic water (VSMOW) and converted to VPDB following Coplen et al. (1983). $\delta^{18}O$ values were applied within a genus-specific fractionation equation (Storm-Suke et al. 2007a) to estimate individual temperature use (e.g. Kelly et al. 2015c; Sinnatamby et al. 2013).

Statistical Analysis

All statistical analyses were completed in R (R Core Team 2014). Data were assessed for normality using the Shapiro Wilks test (Shapiro & Wilk 1965) and homogeneity of variance was assessed using Bartlett's test (Bartlett 1937). Significant differences between rivers and hydropeaking regimes in length-at-age were tested for using a two-way ANOVA. Weight-length relationships were assessed using an ANCOVA (Chambers 1992) with river as the categorical variable. Differences in brook trout caloric content were tested with Welch's t test (Welch 1947).

Differences in *M* between rivers were tested with an ANOVA, with summer (first or second) as the independent factor. Only fish >0+ were included given that YOY samples had different capture dates and could not be compared directly. An ANCOVA was used to test for a correlation between *M* and river water temperature use by fish (realized thermal habitat), with river and life stage (YOY, first or second summer) as categorical variables. An ANCOVA was used to test for a correlation between *M* and the amount of time spent up-ramping (the discharge increase phase of a hydropeaking event), with river and life stage as categorical variables. Up-ramping was defined as an increase in discharge of $>0.25\ m^3 \cdot s^{-1} \cdot hr^{-1}$ from the previous hourly flow (Smokorowski et al. 2011). It was used as an index of hydropeaking rather than calculating total time spent hydropeaking, given the connection between increased brook trout activity and up-ramping (Murchie & Smokorowski 2004), and the consistency in daily hydropeaking patterns during the unrestricted hydropeaking regime period of the study. Time spent up-ramping was calculated for the period from June 1st to September 30th using hourly discharge data from the Water Survey of Canada (02BD007 Magpie River, and 02BF001 Batchawana River). As the Batchawana River has a natural flow, events where discharge increased by $>0.25\ m^3 \cdot s^{-1} \cdot hr^{-1}$ were driven by precipitation rather than by increasing releases of water from a dam during a peaking event. For YOY fish, the amount of time during which the river was in an up-ramping state was calculated up to the date of capture rather than to September 30th.

Results

Length-at-age

Captured brook trout in both rivers varied in age from 0+ to 5+. In the Magpie River, brook trout lengths varied from 38 to 364 mm (n=136), while in the Batchawana River, lengths varied from 25 to 365 mm (n=329). Comparisons of length-at-age between rivers and hydropeaking regimes could only be assessed for fish in age-classes I, II and III, as a result of low sample sizes for fish in age classes IV and V. Mean length-at-age was higher in the Magpie River relative to the Batchawana River for age-classes I, II and III ($p \leq 0.01$), while hydropeaking regime, and the interaction between hydropeaking regime and river were not significant (Table 5.1; Fig. 5.2).

Condition

There was a significant difference between rivers in the slopes and intercepts of the ln-transformed weight-length relationship ($F_{3,86}=7733$, $p<0.05$, $r^2=0.99$), with brook trout in the Magpie River (b=3.15) increasing in weight for a given length at a higher rate relative to brook trout in the Batchawana River (b=3.00) (Fig. 5.3). Average caloric content ± standard deviation was 4606.4 ± 122.7 calories·g^{-1} in the Batchawana River, and 4638.8 ± 110.9 calories·g^{-1} in the Magpie River. There was no significant difference between rivers in muscle tissue caloric content (Welch's $t_{3.4}$=0.41, $p>0.05$).

Metabolism

M varied from 16.5 to 38.0 % in the Batchawana River, and from 27.3 to 40.5 % in the Magpie River. *M* differed significantly between rivers ($F_{1,14}$=57.7, $p<0.05$) and between first and second summers ($F_{1,14}$=20.9, $p<0.05$), with mean *M* being significantly higher in the Magpie River (33.3±3.5 %) relative to the Batchawana (27.6±6.7 %) and significantly lower in the second summer in both rivers. There was no significant interaction between river and summer (first or second) ($F_{1,14}$=2.5, $p>0.05$). There was no significant correlation between *M* and mean temperature use ($p>0.05$), and river and life-stage were not significant categorical variables in the *M*-temperature relationship ($p>0.05$) (Fig. 5.4). *M* was significantly correlated with time spent up-ramping ($p<0.05$), while life-stage and the interactions between *M* and river, and river and life stage were also significant ($p<0.05$, r^2=0.76) (Fig. 5.5).

Thermal Habitat

Mean temperature use by brook trout ± standard deviation was 19.6±1.6, 17.1±5.3, and 15.9±3.1 °C for YOY, first and second growth season estimates, respectively, in the regulated river, and 20.5±2.2, 17.07±2.9, and 19.3±5.2°C in the unregulated river. A between river comparison of temperature use by fish >0+ showed no significant difference (ANOVA, $F_{1,17}$=0.9, $p>0.05$). Different catch dates prevented a comparison between rivers for 0+ fish.

Discussion

Longer length-at-age and higher condition based on weight-length relationships were found in the regulated Magpie River relative to the naturally flowing Batchawana River. *M* was also higher in the Magpie River relative to the Batchawana River and was positively, significantly correlated with time spent up-ramping. While there was a difference in length-at-age between rivers, there was no significant difference between hydropeaking regimes in the Magpie River, or the time period encompassed by the hydropeaking regimes in the Batchawana River. Thus, while river regulation in general has an impact on brook trout, the differences in the rate of change of discharge between the hydropeaking regimes tested in this study did not result in an additional measureable impact on brook trout length-at-age.

The longer mean length-at-age, and heavier weight of large brook trout in the regulated Magpie River relative to the naturally flowing Batchawana River are likely related to food availability. Brook trout eat a wide variety of food including a large proportion of aquatic insects and insect larvae (Scott & Crossman 1973). There is a higher invertebrate abundance (Jones 2013) and drift (Patterson & Smokorowski 2011) downstream from the Steephill Falls dam, including a higher proportion of lentic invertebrates, relative to nearby naturally flowing rivers (Jones 2013). A significant proportion of invertebrates downstream from the dam probably originated in the reservoir, or is supported by reservoir-derived seston (Jones 2013), and, therefore, is a consequence of the dam construction and reservoir creation. However, hydropeaking as a form of river regulation may also impact food availability. Hydropeaking can increase invertebrate drift (Lauters et al. 1996; Lagarrigue et al. 2002), and fish feeding downstream from a dam (Lagarrigue et al. 2002). Brook trout are drift feeders (e.g. Fausch & White 1981) and higher food availability, whether driven by impoundment in general, or hydropeaking in particular, may result in increased foraging success in the Magpie River. For example, in addition to the higher invertebrate abundance in the Magpie River (Jones 2013), Tuor et al. (2014) found a higher abundance of invertebrates within the stomach contents of small bodied fish, including YOY brook trout, in the Magpie River relative to the Batchawana River. Therefore, a larger food supply coupled with higher foraging success resulted in a higher proportion of energy intake allocated towards growth, leading to higher length-at-age in the Magpie River.

Despite significant differences in length-at-age and weight-length relationships between rivers, there was no significant difference in caloric content. This may be a function of the time of year when the fish used for caloric content were caught. The mature adult male fish used in the comparison were caught in the fall, prior to spawning, but may have begun partitioning energy sources away from storage and towards reproduction in both rivers (Scott & Crossman 1973). Additionally, while a higher ration can drive fish growth, the lipid content of fish muscle tissue is dependent on the lipid content of the food consumed by fish, not the amount of food consumed (Shearer et al.

1997). Lipids are the primary source of energy for fish during aerobic activity (Shearer et al. 1997; Kieffer et al. 1998). A higher energy intake would not necessarily result in higher lipid storage and higher caloric content if energy stores were consumed as a result of the increased activity exhibited by brook trout in the Magpie River (see below).

Our estimates of *M* were within the range reported in other field based studies (Kahilainen et al. 2014; Kelly et al. 2015c; Sinnatamby et al. 2015) and were significantly higher in the Magpie River relative to the Batchawana River. *M* values were not significantly related to temperatures used by the fish (realized thermal habitat), however, there was also no significant difference in the temperature of brook trout thermal habitat between these two rivers. Thus, the between-river differences in *M* were not driven by temperature, but by increased activity (e.g. Sherwood & Rose 2003) occurring during hydropeaking events (Murchie & Smokorowski 2004) as evidenced by the positive correlation between time spent up-ramping and *M*. As aerobic metabolic activity increases during hydropeaking events (Murchie & Smokorowski 2004), a higher respiration rate would result in a higher concentration of metabolically derived carbon in the blood stream which would diffuse into the endolymphatic fluid and become incorporated in the otolith during calcification (Solomon et al. 2006).

Despite the higher activity and the higher energy expenditure indicated by the higher contribution of metabolically derived carbon to $\delta^{13}C_{oto}$, brook trout in the regulated river were still able to allocate more resources towards growth relative to the Batchawana River. Higher growth may have been driven by the larger food supply in the Magpie River (see above), which provided a greater potential energy source for brook trout. The increased activity during hydropeaking events may be driven in part by increased foraging during periods of increased flow (Murchie & Smokorowski 2004), and the greater availability of prey in faster flowing habitats (e.g. Dedual & Collier 1995). Studies with brown trout (*Salmo trutta*) have similarly shown higher food consumption rates during hydropeaking flow pulses as an opportunistic response to increased prey availability (Rocaspana et al. 2016), effectively coupling the two opposing impacts of increased food supply in the form of drift, and increased energy expenditure driven by hydropeaking. However, regulation-derived increases in activity (metabolic demands) may not always be offset by increases in food supply, making generalizations about dam impacts difficult. As Korman and Campana (2009) note, hydropeaking was associated with lower growth in YOY rainbow trout in the Colorado River. Given the likelihood of differences among systems, species-specific responses to river regulation in general, and hydropeaking in particular, and the potential interaction of multiple factors, it is important to characterize impacts on food supply, thermal habitat and fish activity at the species level.

While food supply and activity are two factors likely driving the differences in length-at-age and relative metabolic rates between rivers, additional factors such as fishing pressure and invasive species may also play a role. Differing sport and conservation fishing limits between the two rivers (Government of Ontario 2015) combined with the potential for higher fishing pressure in the Batchawana, given its easier river access via a parallel road, could cause a shift in the size structure of brook trout in the Batchawana River (e.g. see review by Lewin et al. 2006). As well, several specimens of the invasive species rainbow trout were caught in the Batchawana River, but not the Magpie River during this study. The emergence of rainbow trout fry in the spring can reduce the growth rates of YOY brook trout as a result of competition for food (Rose 1986; Marschall & Crowder 1996). However, a detailed study on relative fishing pressure differences and the rainbow trout population impacts in the Batchawana River are needed to determine the extent to which these factors may independently contribute to the overall growth differences observed in this study.

Conclusion

Brook trout length-at-age, condition and metabolic rates differed significantly between the Magpie and Batchawana Rivers. However, no difference in length-at-age between the restricted and unrestricted form of hydropeaking was detected. Brook trout in the regulated Magpie River exhibited longer length-at-age and heavier weight at longer lengths, but no difference in muscle tissue caloric content. Time spent up-ramping was correlated with relatively higher field metabolic rates in brook trout, but the higher food supply associated with river regulation may have offset the energetic costs associated with this increased activity. The potential for interacting effects between increased food supply and increased activity on brook trout growth, condition and caloric content suggest that both food availability and brook trout activity should be examined in detail when designing regulations for dam operations.

Table 5.1 ANOVA results for comparison of brook trout length-at-age between rivers.

Length-at-age	Variable	Degrees of freedom	F statistic	p-value
1	River	1	13.19	<0.01
	Hydropeaking regime	1	0.06	0.81
	River x regime	1	0.23	0.63
2	River	1	12.48	<0.01
	Hydropeaking regime	1	0.08	0.78
	River x regime	1	0.00	0.99
3	River	1	7.62	0.01
	Hydropeaking regime	1	0.76	0.39
	River x regime	1	<0.01	0.96

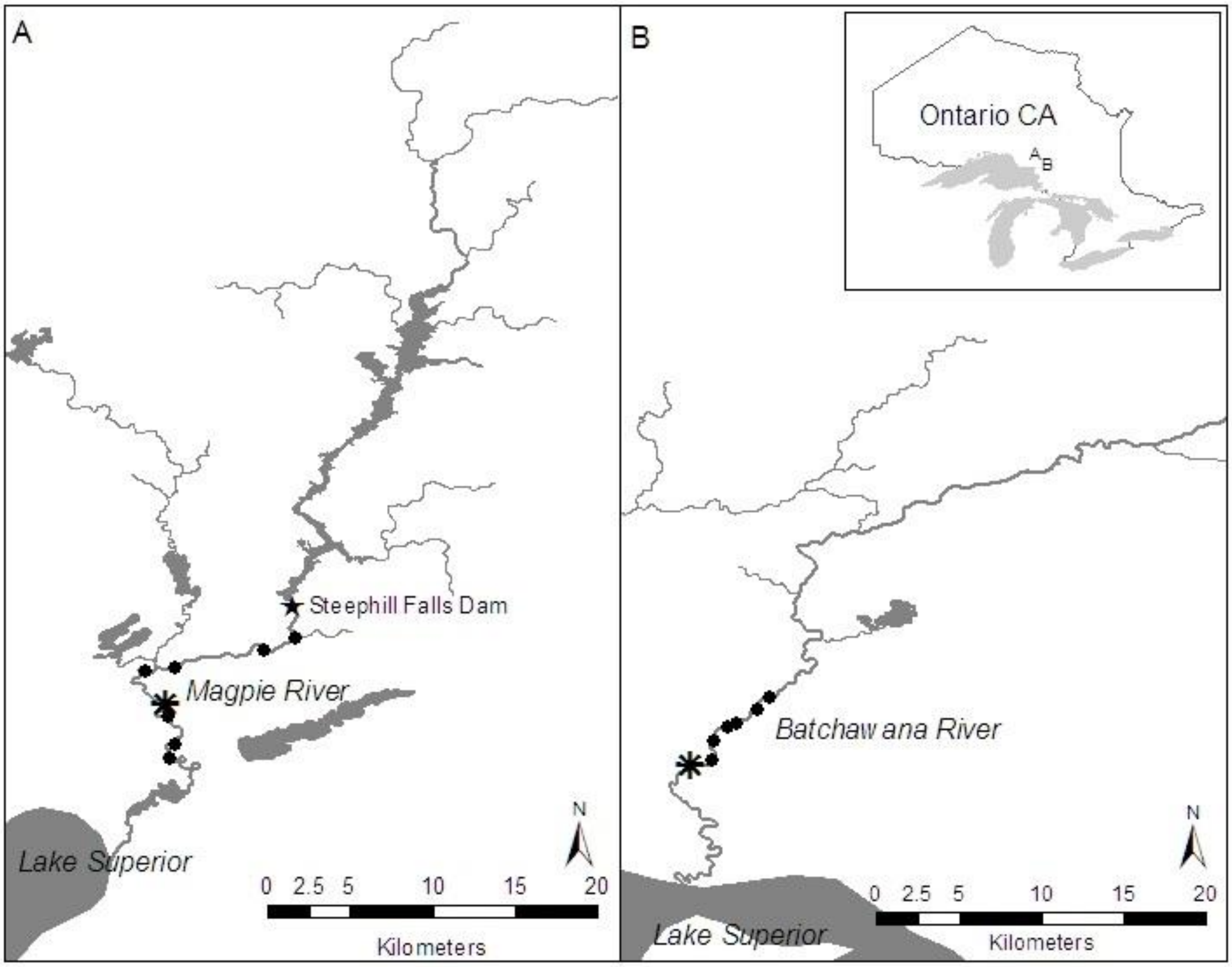

Figure 5.1. Location of the regulated Magpie River (A) and naturally flowing Batchawana River (B) in Ontario, Canada (inset). Fish sampling sites are denoted by circles (●) and river discharge logger locations are denoted by an asterisk (*).

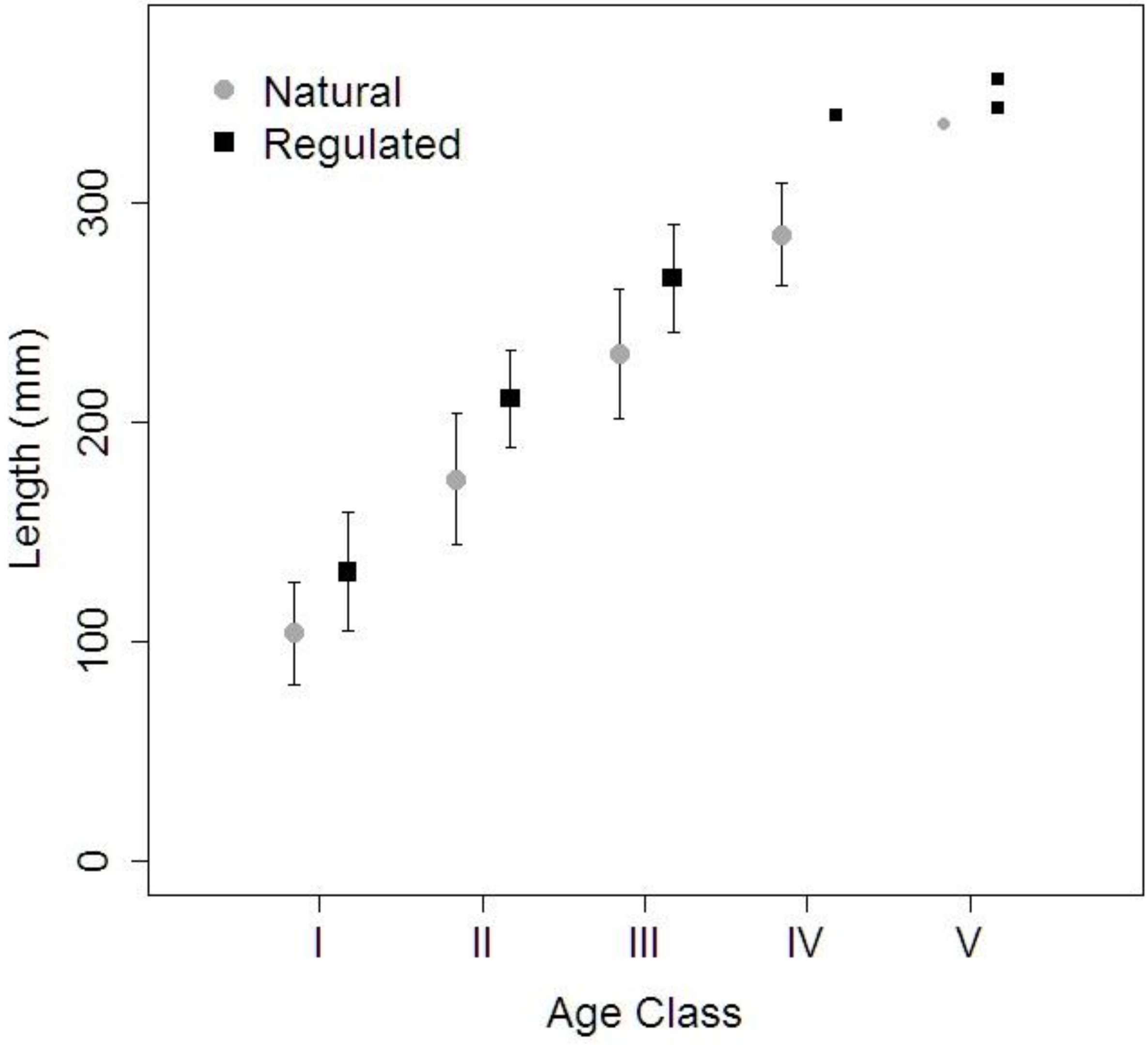

Figure 5.2. Length-at-age (mm) for brook trout in the naturally flowing Batchawana River (●) and the regulated Magpie River (■).

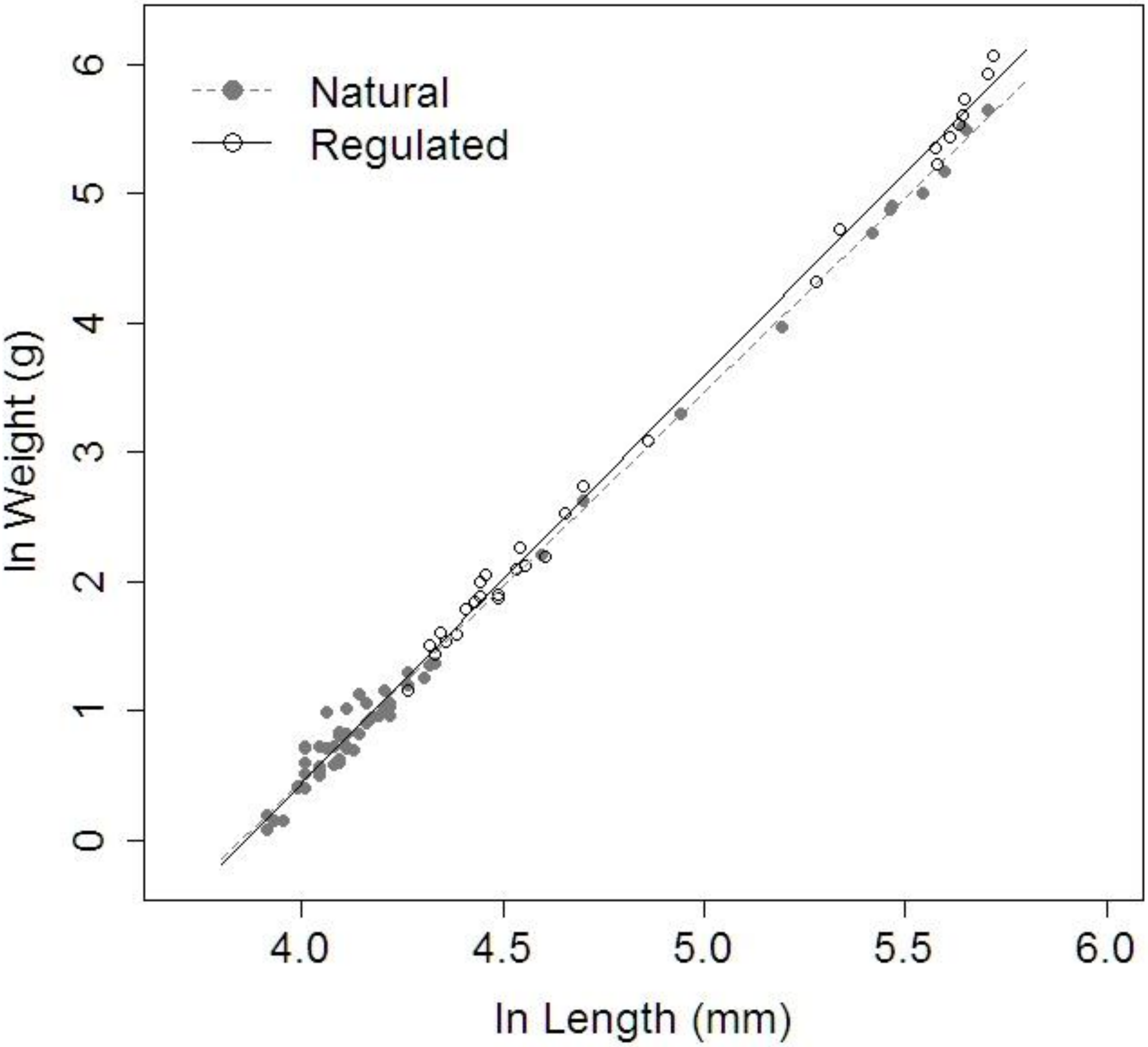

Figure 5.3. Weight-length relationships for brook trout in the naturally flowing Batchawana River (●) and the regulated Magpie River (○).

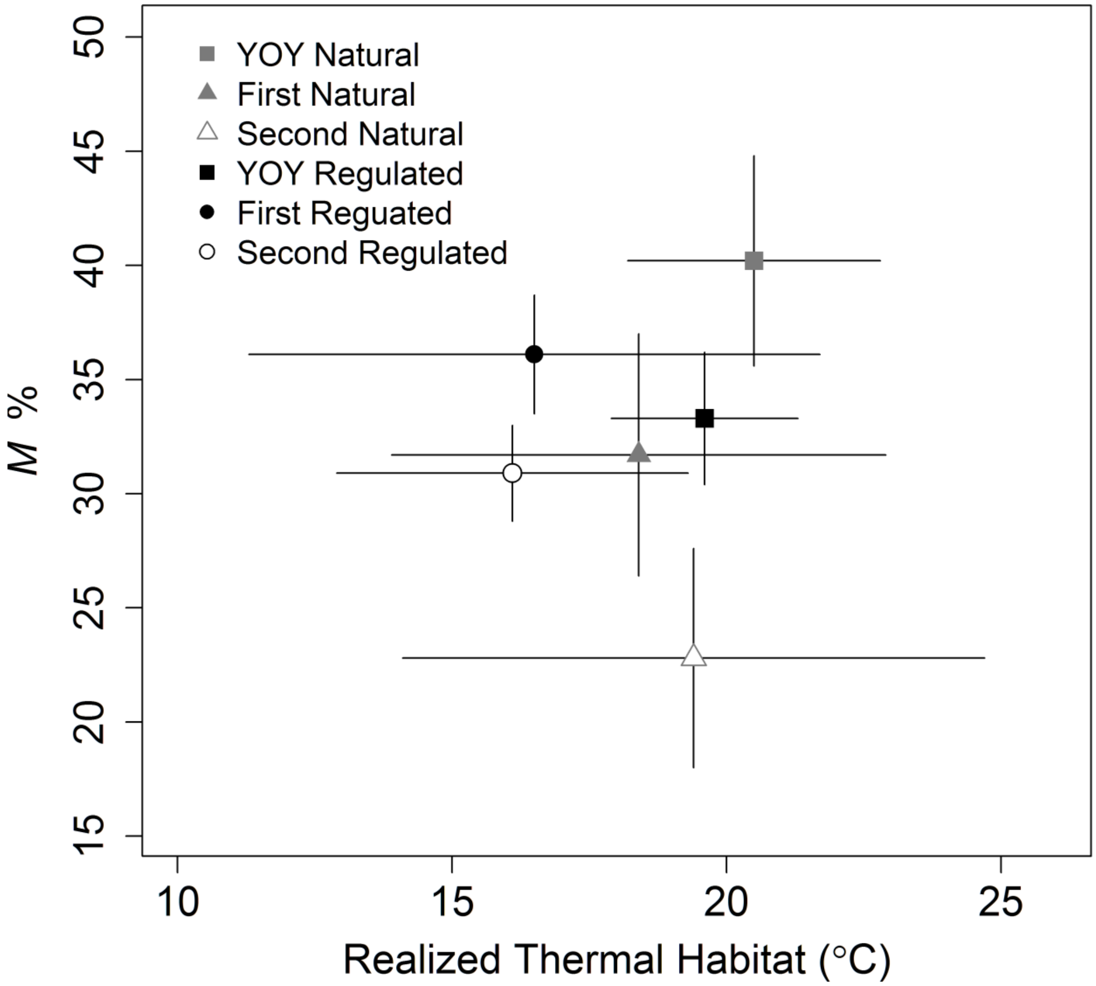

Figure 5.4. The proportion of metabolic carbon (*M*) contributing to $\delta^{13}C_{oto}$ ± standard deviation to realized thermal habitat (°C) ± standard deviation in the naturally flowing Batchawana River (grey symbols) and the regulated Magpie River (black symbols).

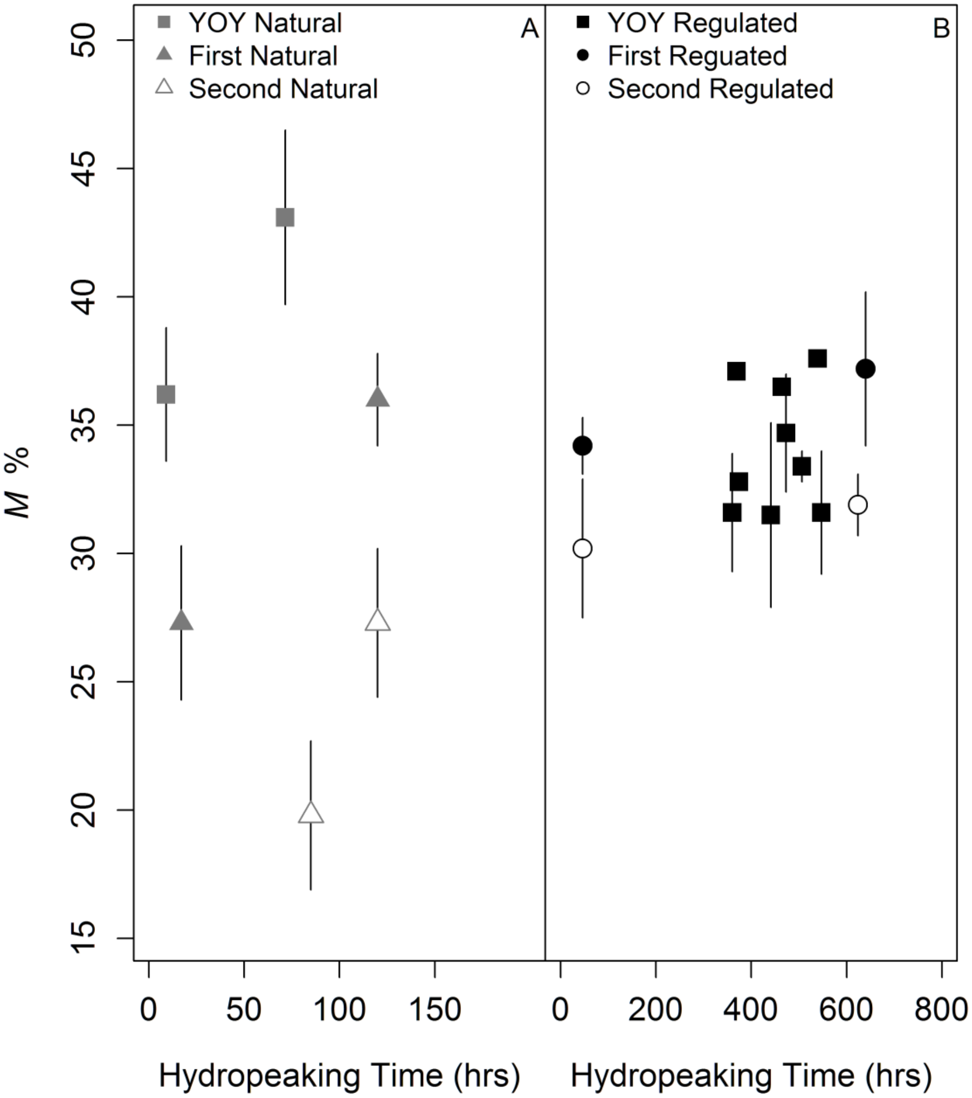

Figure 5.5. The proportion of metabolic carbon (*M*) contributing to $\delta^{13}C_{oto}$ ± standard deviation relative to time spent hydropeaking (hrs), in the naturally flowing Batchawana River (grey symbols) (A) and the regulated Magpie River (black symbols) (B). Note the different ranges in the x axes.

Chapter 6 Thermal habitat segregation among native whitefish morphotypes and invasive vendace: a mechanism for co-existence?

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Introduction

Aquatic invasive species (AIS) can have a variety of effects on the ecosystems they invade, such as alterations of nutrient cycling (Arnott & Vanni 1996), changes in food web structure (Vander Zanden et al. 1999) and replacement of native species (Hill & Lodge 1999). Stable isotope analysis has been used extensively to study the impacts of AIS (see review by Coucherousset et al. 2012), but has been limited almost entirely to the use of nitrogen and carbon from muscle tissue, focusing on dietary resource use (e.g. Zambrano et al. 2010; Jackson et al. 2012; Layman & Allgeier 2012). However, the niche space of two species may overlap simultaneously along more than one axis (Hutchinson 1957; Pianka 1981). Expanding investigations to additional niche axes such as temperature use can provide valuable information on the interactions between invasive and native species, and may be accomplished by the application of stable isotope analysis to other elements and tissues.

Stable oxygen isotopes in fish otoliths are potential tools for identifying differences in thermal habitat between invasive and native species. Otoliths are composed mainly of calcium carbonate deposited around an organic matrix of protein (Campana & Neilson 1985). They are considered metabolically inert and can provide an environmental chronology throughout the life of the fish (Campana 1999). Oxygen isotopes are deposited in otoliths in equilibrium with the surrounding water, irrespective of metabolic or kinetic effects (Høie et al. 2003). Therefore, δ^{18}O values can be used to estimate the water temperature at which fish have lived (Devereux et al. 1967). Furthermore, as the δ^{13}C value of otoliths is derived from ambient dissolved inorganic carbon (DIC) and respired metabolic carbon (Weidman & Millner 2000), otoliths can provide information on habitat (Pruell et al. 2010), diet (Elsdon et al. 2010; Nelson et al. 2011) and metabolic rate (Lin et al. 2012; Sinnatamby et al. 2015).

Temperature has a profound effect on fish metabolism and, therefore, on fitness and eventual reproductive success (Fry 1947). When possible, fish will choose a narrow range of temperatures to inhabit (Coutant 1977), may compete for preferred temperatures (Magnuson et al. 1979), and partition diet and thermal habitat resources among species (Crowder et al. 1981; Olson et al. 1988; Urban & Brandt 1993; Atrill & Power 2004). Differences in both standard and field metabolic rates at a given temperature are indicative of physiological adaptations which can play a role in enabling the coexistence of closely related species (Ohlberger et al. 2008). Thus, here we use stable oxygen and carbon isotopes to investigate inter-and intra-specific temperature use and concomitant differences in diet and metabolism by a native whitefish species (*Coregonus lavaretus*) and invasive vendace (*Coregonus albula*) in two lacustrine sites within the Pasvik watercourse in northern Norway. To our knowledge, this is the first time oxygen and carbon stable isotopes from otoliths have been used as a tool to examine potential differences in temperature use between sympatric invasive and native fishes.

Three different morphotypes of whitefish are present in the Pasvik system and are specialized for feeding in either the pelagic, littoral or profundal habitat (Siwertsson et al. 2010). Whitefish was the predominant fish species prior to the invasion of vendace in the late 1980s (Bøhn & Amundsen 2001), following their translocation and introduction into the Pasvik headwaters three decades earlier (Amundsen et al. 1999; Bøhn et al. 2004; Præbel et al. 2013). Vendace is a zooplankton specialist and achieved different levels of success in different locations within the system. Vendace outcompeted whitefish for zooplankton and relegated the pelagic whitefish morphotype to feeding in littoral and profundal habitats in an upstream site, Lake Tjærebukta (hereafter referred to as the "ID" site for "invasive dominant") (Bøhn et al. 2008). In contrast, vendace and pelagic whitefish largely shared pelagic prey resources in a downstream site, Lake Skrukkebukta (hereafter referred to as the "CE" site for "co-existence") (Bøhn & Amundsen 2001). Lake Skrukkebukta and Lake Tjærebukta have similar areas (6.6 and 5.1 km^2, respectively) and chemical compositions, but differ in depth, with Lake Skrukkebukta being deeper than Lake Tjærebukta. The lack of a distinct dietary resource partitioning in the downstream site coupled with catch data suggests that microhabitat segregation may enable vendace and whitefish to coexist at the Skrukkebukta site (Gjelland et al. 2007). Thermal stratification of the two lacustrine environments ensures a range of available temperatures and provides an opportunity to further investigate habitat segregation using stable oxygen and carbon isotopes.

We explored several hypotheses regarding thermal habitat and otolith $\delta^{13}C$ differences among whitefish morphotypes and vendace. First, we hypothesized that thermal habitat will not differ strongly among morphotypes or between species in the ID site, where vendace are dominant, and the available space below the thermocline is limited. We further hypothesized that in the CE site, with its greater range of available thermal habitats, whitefish and vendace would exhibit thermal niche separation. Thus, the profundal whitefish morphotype would inhabit the coldest thermal habitat, the pelagic morphotype would inhabit water with intermediate temperatures, and the littoral morphotype and vendace would inhabit the warmest thermal habitat. We also hypothesized that $\delta^{13}C$ values would differ between sites, with differences driven by dietary resources as reflected in the $\delta^{13}C$ values of fish muscle tissue. Finally, we hypothesized that metabolic rates, as inferred from otolith $\delta^{13}C$ values, would differ among morphotypes, between species and between sites and would be positively related to temperature use, given that standard metabolic rate is temperature dependent (Brett & Groves 1979).

Methods

Sampling

The Pasvik watercourse (Fig. 6.1) forms the border between northern Norway and Russia and contains seven hydroelectric dams. The damming of the system has shifted the waterway from a predominantly riverine system, to a series of lakes and reservoirs connected by slow flowing rivers (Bøhn & Amundsen 2001; Gjelland et al. 2007). Within the Pasvik watercourse, the ID site and the CE site were sampled via gill netting from 12 to 16 September 2013. Temperature profiles were collected at each site using a YSI 556 multiprobe temperature probe (YSI Ltd., Hampshire, UK). Water samples for the analysis of $\delta^{18}O$ ($\delta^{18}O_{H2O}$) and $\delta^{13}C$ of DIC ($\delta^{13}C_{DIC}$) were collected from three locations within the littoral zone (30 cm below surface), two locations within the pelagic zone (at 5 m depth) and two locations within the profundal zone (at 20 m depth) in each site.

Fish were collected using gill nets (mesh size 6-45 mm knot to knot) set overnight in pelagic, littoral and profundal habitats, as defined in Bøhn et al. (2008), where the pelagic zone consisted of surface waters to a depth of 6 m in the deepest part of the lake, the littoral zone was considered to be shoreline areas to a depth of 5 m, and the profundal zone was defined as the bottom 2 m in the deepest part of the lake. Permission for the gill net fishing in the two lakes was obtained from the County Governor of Finnmark, which is the official fishing right owner on Government land in Finnmark county. Fish were dissected on site and whitefish morphotypes were identified by gill raker number as DR (densely rakered, pelagic specialized morphotype), LSR (large sparsely rakered, littoral specialized morphotype) and SSR (small sparsely rakered, profundal specialized morphotype) following Siwertsson et al. (2010). Given the known preservation biases on otolith oxygen isotope measurements (Storm-Suke et al. 2007b), for a subset of fish spanning the length range of fish caught, one sagittal otolith was dried and stored in a plastic snap-cap vial for stable isotope analysis. The other sagittal otolith was removed and preserved in ethanol and used for aging. Dorsal fish muscle tissue was removed and frozen on site, then transported and dried in the lab at 60°C for 24 hours for stable isotope analysis.

For the CE and ID sites, respectively, n=43 and n=19 otoliths were analysed (Table 6.1). Although efforts were made to analyse three to four otoliths from each age range for each species and morphotype, this was often not possible owing to the population structure and capture selection of vendace and whitefish at each site. For example, no SSR specimens were caught in the ID lake, while SSR specimens caught in the CE lake were often older than 4+. Vendace caught in both lakes were mainly of ages 1+ and 2+, which is typical for these sites (Amundsen et al. 2012).

Otolith preparation

Whole otoliths were aged by two separate readers under a dissecting microscope. Age discrepancies occurred in less than 10% of the samples, and where they did occur, the sample was not used. Summer growth zones (opaque under reflected light) were used for analysis since this zone would largely overlap with the period of summer thermal stratification in the lakes. Once aged and photographed, otoliths were mounted sulcus side down on glass microscope slides and polished to expose inner annuli. Summer growth zones were delineated using Image J (Schneider et al. 2012), then transferred to a MicroMill Sampling System (New Wave Research, California, USA) where samples were milled with a computer controlled drill. The entire summer portion of the dorsal side of the otolith was milled and collected for each summer growth zone and the sample was used to infer average temperature used by the fish over the course of the growing season. Samples up to and including the fourth growth season were collected where the age of the fish permitted. Full summer zone widths beyond the fourth summer in fish 5+ and older yielded sample sizes too small (<50 µg) for individual analysis and were not used. Milled otolith material was roasted under a continuous flow of helium at 350°C for 1 hour (Guiguer et al. 2003) to remove organic material. Samples were then acidified with 100% ortho-phosphoric acid to produce CO_2 and equilibrated in a water bath at 90°C for 3 hours prior to isotope analysis (Guiguer et al. 2003).

Stable isotope analysis

All isotope samples were analysed at the University of Waterloo Environmental Isotope Laboratory (UWEIL) and are reported in standard δ notation:

$$\delta = [(R_{sample} - R_{standard}) / R_{standard}] \times 1000\ (‰).$$

Muscle tissue $\delta^{13}C$ ($\delta^{13}C_{mus}$) was analysed relative to Vienna Pee Dee Belemnite (VPDB) with a 4010 Elemental Analyser (Costech Instruments, Italy) coupled to a Delta Plus XL (Thermo-Finnigan, Germany) having a precision of 0.2‰ (UWEIL). Water samples were analysed on an IsoPrime multiflow isotope ratio mass spectrometer (GV Instruments/Micromass, Manchester, UK). All $\delta^{18}O_{H2O}$ values were measured relative to Vienna standard mean oceanic water (VSMOW) and all $\delta^{13}C_{DIC}$ measured relative to VPDB. Both $\delta^{18}O_{H2O}$ and $\delta^{13}C_{DIC}$ were analysed with a precision of 0.2‰ (UWEIL). $\delta^{18}O_{H2O}$ (VSMOW) was converted to VPDB following Coplen et al. (1983). Otolith $\delta^{13}C$ ($\delta^{13}C_{oto}$) and $\delta^{18}O$ ($\delta^{18}O_{oto}$) were analysed on an IsoPrime multiflow isotope ratio mass spectrometer (GV Instruments/Micromass, Manchester, UK) with an analytical precision of 0.2‰ (UWEIL), which is equivalent to 0.8°C following conversion to temperature estimates.

Temperature estimates

$\delta^{18}O_{oto}$ and $\delta^{18}O_{H2O}$ values were used to estimate average water temperature used by the fish over the course of the growing season. No species-specific fractionation equation exists for whitefish or vendace. Given that differences in physiology among fish species may affect the relationship between temperature and oxygen fractionation in otoliths on a species-specific basis (Høie et al. 2004b; Rowell et al. 2005; Storm-Suke et al. 2007a), following Kahilainen et al. (2014) we selected the non-linear fractionation equation developed for Arctic charr (*Salvelinus alpinus)*, by Godiksen et al. (2010). $\delta^{18}O_{H2O}$ values necessary for determining individual fractionation values were assigned to fish based on their known preferred feeding habitat (pelagic, littoral or profundal), and on their capture location.

Statistical analyses

All analyses were performed in R (R Core Team 2014). A Shapiro-Wilk test (Royston 1982) and a normal quantile-quantile plot were used to assess the normality of the data while Bartlett's test was used to assess homogeneity of variance (Bartlett 1937). A repeated measures ANOVA (Chambers et al. 1992) was used to determine if sampling zone (first, second, third or fourth summer) was a significant factor for $\delta^{18}O_{oto}$, $\delta^{13}C_{oto}$ or temperature estimates among and within individuals, and no significant differences were found ($p>0.05$). Therefore, where temperature or $\delta^{13}C_{oto}$ measurements were made for multiple years for an individual fish, these estimates were averaged and the average was used in tests for differences between sites, among morphotypes and between species. Welch's t-test (Hollander & Wolfe 1973) was used to assess differences in average temperature used and $\delta^{13}C_{oto}$ between sites. An ANOVA followed by Tukey's *post hoc* HSD test (Yandell 1997) was used to test for differences within sites among morphotypes and between species. When using an ANOVA, the whitefish morphotypes were always included separately, analogous to testing differences among four separate species.

Differences in temperature estimates derived by *a priori* assignment of $\delta^{18}O_{H2O}$ values by known preferred feeding habitat and on the basis of capture depth were tested using a paired t test where fish were grouped by morphotype and species.

To test for significant relationships between $\delta^{13}C_{mus}$ and $\delta^{13}C_{oto}$, an ANCOVA with site and species/morphotype as categorical variables was used, where a positive correlation would indicate respiration of dietary carbon and, thus, that dietary differences influence $\delta^{13}C_{oto}$ values. Only the outer edge of the otolith comprising the last summer of growth was used when comparing $\delta^{13}C_{mus}$ and $\delta^{13}C_{oto}$ so that the timing of isotope incorporation into muscle tissue and otolith carbonate matched. This resulted in smaller sample numbers relative to the $\delta^{18}O_{oto}$ analysis (Table 6.1), given that the outer otolith edge did not always provide enough material to be run. The proportion of metabolic carbon (*M*) contributing to $\delta^{13}C_{oto}$ was calculated following McConnaughy et al. (1997) as:

$$M(\delta^{13}C_{resp}) + (1-M)(\delta^{13}C_{DIC}) = \delta^{13}C_{oto} - \Delta$$

where *M* is the fraction of respired carbon contributing to $\delta^{13}C_{oto}$, $\delta^{13}C_{resp}$ is the isotopic value of the respired carbon and Δ is the fractionation between tissue HCO_3^- and the otolith. We assumed $\delta^{13}C_{resp}$ to be equivalent to $\delta^{13}C_{mus}$ (Post 2002) and used a value of 2.7 for Δ (Romanek et al. 1992) following Høie et al. (2004b).

Results

Temperature profiles

Temperature profiles showed a temperature of 13°C in the epilimnion for both lakes, decreasing towards the profundal zone to 8°C in the ID lake and to 6.3°C in the CE lake. The thermocline, defined as the depth at which the greatest temperature change occurs, was located between 17 and 18 m depth in both lakes, where water temperatures decreased from approximately 12°C to 9°C (Fig. 6.1B and 6.1C). Based on our definition of the pelagic, littoral and profundal zones (see Methods), the pelagic and littoral habitats in both sites were entirely within the mixed layer where the temperature at the time of sampling was 13°C. The profundal habitat sampled in the ID lake was also mainly within the mixed layer, due to the limited area below the thermocline at this site. However, the profundal zone sampled in the CE lake was below the thermocline with water temperatures below 9°C.

Temperature estimates

Significant differences in temperature estimates calculated based on the assignment of $\delta^{18}O_{H2O}$ values by preferred feeding habitat or capture location were found for DR whitefish ($t_{63}=-4.04$, $p<0.05$), SSR whitefish ($t_{31}=2.08$, $p<0.05$) and vendace ($t_{35}=3.13$, $p<0.05$) in the CE site and LSR whitefish in the ID site ($t_{15}=3.98$, $p<0.05$). The mean difference between temperature estimates exceeded the analytical precision of the mass spectrometer (0.8°C) only for LSR whitefish (2.8°C), and this difference did not change the outcome of the within- and between-site statistical comparisons. As such, estimates based on known preferred feeding habitat were used for the analysis, given the known discrepancies between catch location and average temperature use (Power et al. 2012).

A repeated measures ANOVA found no relationship between age and thermal habitat. When within-individual variation was excluded, a significant correlation was still not found between age and $\delta^{18}O_{oto}$ or temperature ($p>0.05$). Therefore, average temperature use is reported, and comparisons in temperature estimates within and between sites were computed using the mean temperature use for each individual.

A significant difference in temperature use by vendace was observed between sites ($t_{19}=-3.06$, $p<0.05$), with lower temperatures used in the CE lake (Fig. 6.2). In contrast, no significant difference in temperature use was found between sites for DR ($t_{6.9}=0.88$, $p>0.05$) or LSR ($t_{7}=-1.80$, $p<0.05$). Within the CE site, significant differences in temperature use were found between vendace and DR, and between SSR and DR ($F_{3,40}=4.01$, $p<0.05$, Tukey’s HSD), with DR using warmer temperatures in each case (10.6°C on average relative to 8.0°C for vendace and 7.5°C for SSR). Mean temperature use by LSR in the CE site (9.4°C) was also warmer relative to SSR and vendace, but not significantly so. No significant differences existed in temperature use between species or among morphotypes in the ID site ($F_{2,15}=0.57$, $p>0.05$), although mean temperature use by DR (9.5°C) was slightly below vendace (11.2°C) and SSR (11.2°C).

Stable carbon isotopes

To avoid the confounding factor of slightly different baselines for both $\delta^{13}C_{H2O}$ and the $\delta^{13}C$ values of primary consumers between lakes, we did not conduct between-lake comparisons for $\delta^{13}C_{oto}$. The pattern of significant differences within sites for $\delta^{13}C_{oto}$ values was different from that of $\delta^{18}O_{oto}$, such that LSR was significantly enriched relative to DR and vendace, and DR was significantly enriched relative to vendace ($F_{3,40}=11.3$, $p<0.05$; Fig. 6.3). No significant differences were found among morphotypes or species in the ID site ($F_{2,15}=1.5$, $p>0.05$), although a similar pattern emerged, with LSR having the most enriched values and vendace having the most depleted values.

Mean ± standard deviation $\delta^{13}C_{mus}$ values were –26.4±0.7, -23.8±1.4, -27.0±0.8, and -27.2±0.4 for DR, LSR, SSR and vendace, respectively, in the CE site. In the ID site, $\delta^{13}C_{mus}$ values were -25.6±1.0, -25.8±2.3, and -26.8±0.3 for DR, LSR and vendace, respectively. Within the CE site, LSR $\delta^{13}C_{mus}$ values were significantly enriched relative to all other morphotypes/species ($F_{3,27}=20.49$, $p<0.05$), while no significant differences occurred within the ID site ($F_{2,12}=2.148$, $p>0.05$). There was a significant positive relationship between $\delta^{13}C_{oto}$ and $\delta^{13}C_{mus}$, with the interaction between $\delta^{13}C_{mus}$ and location being significant ($F_{13,31}=4.9$, $p<0.05$, $r^2=0.53$) (Fig. 6.4).

The mean vendace *M* value was significantly higher in the CE site relative to the ID site ($t_{11.4}=4.5$, $p<0.05$; Fig. 6.5), but did not differ significantly between sites for DR ($t_{14.1}=1.5$, $p>0.05$) or LSR ($t_{2.4}=-1.4$, $p>0.05$). Within the CE site, vendace had a significantly higher *M* compared to LSR and SSR (ANOVA, $F_{3,26}=5.6$, $p<0.05$). No significant differences among morphotypes or between species were observed at the ID site (ANOVA, $F_{2,12}=3.1$, $p>0.05$), although vendace had the lowest *M* value within that site.

Discussion

Temperature estimates

Differences in thermal habitat use and concomitant differences in dietary resource use and metabolic rates between sympatric native and invasive species were found in the Pasvik system. Temperature estimates calculated from $\delta^{18}O_{oto}$ values are realistic based on temperatures measured in the field in 2013, published data (<12°C to 18°C ; Amundsen et al. 1999) and historical values for the epilimnion in the system (12°C; Puro-Tahvanainen et al. 2011). Temperature estimates also coincided with expected values for LSR and SSR based on the habitats within which they were caught and the measured temperatures of those habitats. For example, the SSR morphotype individuals analysed here were caught in the profundal zone in the CE site and used temperatures only available below the thermocline, while the LSR morphotype individuals were caught in the pelagic and littoral zones and used temperatures indicative of those habitats.

Temperature use by vendace in the ID site was similar to those predominating in the pelagic zone (11.2°C), whereas vendace caught in the CE site used lower than expected temperatures (8.0°C), given that most were caught in the pelagic zone. Indeed, historical catch data from Gjelland et al. (2007) and Liso et al. (2013), indicated that vendace inhabited the upper pelagic zone (0-6m) while pelagic whitefish inhabited the lower pelagic zone (6-12m, Gjelland et al. 2007; 4-20m Liso et al. 2013) during the overnight period. However, diel vertical migrations (DVM) by vendace, as outlined by Gjelland et al. (2009) in the CE site, may explain the discrepancy between catch data and otolith-based thermal habitat estimates. DVM behaviour by vendace, whereby they inhabit cooler, deeper water during the day, would explain the significant difference in temperature use estimates between DR and vendace. The differentiation in temperature use between DR and vendace in the CE site supports the suggestion that habitat segregation enables the coexistence of the pelagic whitefish morphotype and vendace at this site (Gjelland et al. 2007).

Our temperature estimates are similar to those of Kahilainen et al. (2014) and corroborate their findings that the SSR morphotype uses colder temperatures than the LSR and DR morphotypes. Thus, despite small sample sizes, particularly in the ID lake, our results correspond well with previous otolith-derived temperature estimates as well as measured lake temperatures, as detailed above. However, given our limited sample sizes, our results may not be generalized to encompass other lakes, specifically those with different geomorphologies and thermal habitat availability. Indeed, while Kahilainen et al. (2014) found a pronounced ontogenetic shift towards cooler temperatures with increased age in the SSR and DR morphotypes, and a shift to reduced variability in temperature with age in the LSR morphotype, we found no relationship between age and thermal habitat. In the ID site, the lack of ontogenetic shift may be explained by limited habitat as this site is not as deep (maximum depth of 26 m compared with 38 m for the CE site) and has low dissolved oxygen below the thermocline (mean of 2.7 mg L^{-1} below the thermocline; Kahilainen, *pers. comm.*), resulting in a limited range of suitable thermal habitat. In the CE site, inter- and intra-species interactions may influence thermal habitat use (e.g. Magnuson et al. 1979) and diet (e.g. Bøhn et al. 2008), restricting the resources which whitefish morphotypes and vendace are able to exploit, thus precluding ontogenetic shifts in thermal habitat. Therefore, lake-specific studies are likely necessary to characterize the life history stage specific thermal habitat of whitefish and vendace.

Stable carbon isotopes

$\delta^{13}C_{oto}$ values and their variation provide an opportunity to evaluate dietary and metabolic differences among morphotypes and between species at both sites. $\delta^{13}C_{oto}$ is thought to be driven mainly by DIC $\delta^{13}C$ values (~80%), with the remainder contributed by metabolically derived carbon (Weidman & Millner 2000; Høie et al. 2003; Solomon et al. 2006; Elsdon et al. 2010). As expected, we found a significant positive relationship between $\delta^{13}C_{oto}$ and $\delta^{13}C_{mus}$, suggesting that respired dietary carbon has a significant influence on otolith $\delta^{13}C$ values in whitefish and vendace. Enriched $\delta^{13}C_{oto}$ and $\delta^{13}C_{mus}$ values, indicative of a higher littoral contribution to diet, were found for LSR in the CE site (Fig. 6.3), a finding supported by stomach contents data (Bøhn & Amundsen 2001) and reported habitat use (Bøhn & Amundsen 2004).

The dietary resource use and thermal habitat data suggest that resource partitioning between species is occurring at the CE site. Complementary use of diet and habitat resources has been found in other salmonids (e.g. *Salvelinus namaycush*, *S. alpinus*, *Salmo trutta* and *Onchorynchus tshawytscha*) (Olson et al. 1988; Power et al. 2007), as well as between native and invasive fishes (Crowder et al. 1981), with seasonal changes in thermal stratification affecting the nature of resource partitioning between food and habitat (Urban & Brandt 1993; Power et al. 2007). In the CE site, low dietary overlap within each species/morphotype comparison (Liso et al. 2011; Bøhn & Amundsen 2001; $\delta^{13}C_{mus}$ data this study), and/or low thermal habitat overlap, indicates resource use segregation along at least one niche axis (e.g. Hutchinson 1957). An exception may be the lack of significant difference in both thermal habitat and diet inferred from stable isotopes between vendace and SSR. However, similar ^{13}C baseline values in the profundal and pelagic zones may have prevented us from differentiating diets based in those two habitats (B. Kelly, unpubl. data). In the ID site, the complementarity of resource use breaks down, as no thermal habitat segregation was detected, and dietary overlap was high (no significant difference among species/morphotypes in $\delta^{13}C_{oto}$ or $\delta^{13}C_{mus}$; see also Liso et al. 2013). The lack of resource partitioning in the ID site coincides with low catch numbers for DR and LSR, which together comprised 9% of the total catch (Liso et al. 2013 reporting catch data from 2008). In contrast, DR and LSR whitefish made up 42% of the total catch in the CE site

(Liso et al. 2013), suggesting that complementarity of resource use enables the coexistence of vendace and whitefish at that site.

In addition to providing insight into dietary resource use, $\delta^{13}C_{oto}$ can be used to make inferences about metabolic rate from the calculation of *M*, i.e., the contribution of metabolically derived carbon to $\delta^{13}C_{oto}$ (e.g. Lin et al. 2012; Kahilainen et al. 2014; Sinnatamby et al. 2015). Higher values of *M* indicate higher metabolic rates, as an increase in metabolic rate results in an increased concentration of metabolically derived carbon in the bloodstream and endolymphatic fluid (Solomon et al. 2006). Values of *M* at both our sites are high relative to laboratory studies (17-32%) (Høie et al. 2003; Solomon et al. 2006; Tohse & Mugiya 2006; Elsdon et al. 2010), but overlapped with field-based ranges reported by Sinnatamby et al. (2015) (15.7 to 45.1%) and Kahilainen et al. (2014) (26 to 35%). The pattern of *M* values among whitefish morphotypes also coincides with that found by Kahilainen et al. (2014), with DR having the highest values of *M*, LSR having intermediate values and SSR having lowest values.

Vendace *M* values were significantly higher in the CE site relative to the ID site, and within the CE site they were significantly higher than LSR and SSR values. The higher *M* values for vendace occupying lower temperatures suggests that these *M* values are driven by activity (e.g. Sherwood & Rose 2003) rather than temperature-dependent standard metabolic rate. DVM behaviour contributes to activity and field metabolic rate (Brett & Groves 1979) and is consistent with the higher *M* values, as bioenergetics modelling has indicated that vendace expend more energy performing DVM relative to remaining in either the hypolimnion or the metalimnion throughout the day (Busch et al. 2011).

Implications for invasive-native species interactions

Segregation of thermal habitat between vendace and DR provides an explanation for the coexistence of both species in the CE pelagic habitat, unlike the ID site where vendace are dominant. As vendace are considered superior competitors over whitefish (Bøhn & Amundsen 2001), the shift by vendace to cooler waters in the CE lake was presumably driven by factors other than competitive interactions with DR whitefish. Gjelland et al. (2009) argued that DVM by coregonids in the CE site resulted from foraging at light levels which lower predation risk from piscivores such as pike (*Esox* *lucius*), perch (*Perca fluviatilis*), burbot (*Lota lota*) (Amundsen et al. 2003) and brown trout (*Salmo trutta* L.) (Jensen et al. 2004). However, studies have shown that vendace DVM can also be driven by temperature preferences (Mehner et al. 2010) and bioenergetics in addition to predator avoidance (Mehner et al. 2007). The temperatures used by vendace in the CE lake correspond with those found for vendace performing DVM in other sites (6-9°C; Mehner et al. 2010). While higher values of *M* in the CE lake suggest that DVM does not optimize energy use (e.g. Busch et al. 2011), we cannot entirely rule out bioenergetics, since DVM can lead to growth rates higher than if vendace remained in the hypolimnion (Busch et al. 2011). Therefore, we argue that, while predator avoidance may be the dominant force driving DVM in the CE lake, temperature preferences and bioenergetic factors also play a role, creating a complex system of trade-offs between competing costs and benefits (Mehner 2012), with factors shifting in importance through the growing season (Gjelland et al. 2009).

A likely consequence of the thermal habitat segregation observed here is the alteration of competitive dynamics between vendace and whitefish for dietary resources. Specifically, thermal habitat segregation facilitates the maintenance of a zooplankton-based diet for DR in the CE lake rather than a littoral-based diet (Bøhn & Amundsen 2001). The lack of significant difference in thermal habitat in the ID lake, where DR numbers have been reduced (Liso et al. 2013) and DR have been relegated to feeding in the littoral zone (Bøhn & Amundsen 2004), suggests that available thermal habitat is an important factor influencing the interactions between the native and invasive species in the Pasvik watercourse.

In conclusion, our study documents thermal habitat segregation and an accompanying dietary resource partitioning between a native and an invasive sympatric fish species. Where a larger volume of suitable habitat below the thermocline was available, thermal habitat segregation enabled both species to coexist and feed in the pelagic zone. Where a limited availability of thermal habitats precluded extensive thermal habitat segregation there was less evidence for partitioning of food resources and catches of the native fish species were drastically reduced. Thus, lake morphology and the ability of fish species to exploit different thermal habitats can fundamentally alter competitive interactions between native and invasive fishes. Our results demonstrate the importance of considering temperature when investigating invasive fishes and the utility of stable oxygen and carbon isotope analysis in achieving this.

Table 6.1 Sample data for whitefish morphotypes DR (pelagic zone specialized), LSR (littoral zone specialized), SSR (profundal zone specialized) and vendace at the Skrukkebukta (CE) and Tjærebukta (ID) sampling sites. The pelagic zone consisted of surface waters to a depth of 6m in the deepest part of the lake, the littoral zone was considered to be shoreline areas to a depth of 5m, and the profundal zone was defined as the bottom 2m in the deepest part of the lake. Water stable isotope values are the mean of two samples for the pelagic and profundal zones, and three values for the littoral zone. Sample numbers refer to the number analysed for δ^{18}O, while the sample number in brackets refers to the number analysed for a correlation between $\delta^{13}C_{oto}$ and $\delta^{13}C_{mus}$ and the calculation of *M*.

	Species / Morphotype		Habitat			Age				Length	Wet weight
Site		n	Pelagic	Littoral	Profundal	1+	2+	3+	4+	(mm)	(g)
CE	DR	16 (13)	13	3	0	3	8	1	4	117 - 207	15.1 - 90.3
	LSR	10 (8)	0	10	0	1	2	3	4	90 - 215	6.2 – 106.0
	SSR	7 (3)	0	0	7	0	2	1	4	110 - 151	10.8 - 32.9
	Vendace	10 (6)	9	0	2	5	3	2	1	119 - 157	15 - 36.8
	$\delta^{18}O_{H2O}$ (‰)		-11.87	-11.85	-12.30						
	$\delta^{13}C_{H2O}$ (‰)		-9.67	-8.76	-11.70						
ID	DR	4 (4)	2	2	0	2	2	0	0	116 - 162	13.7 - 40.5
	LSR	4 (3)	2	2	0	0	2	2	0	156 - 189	39 - 66.3
	SSR	0									
	Vendace	11 (8)	7	0	4	4	4	3	0	99 - 147	7.6 - 26.6
	$\delta^{18}O_{H2O}$ (‰)		-11.36	-11.31	-12.55						
	$\delta^{13}C_{H2O}$ (‰)		-10.22	-9.57	-16.11						

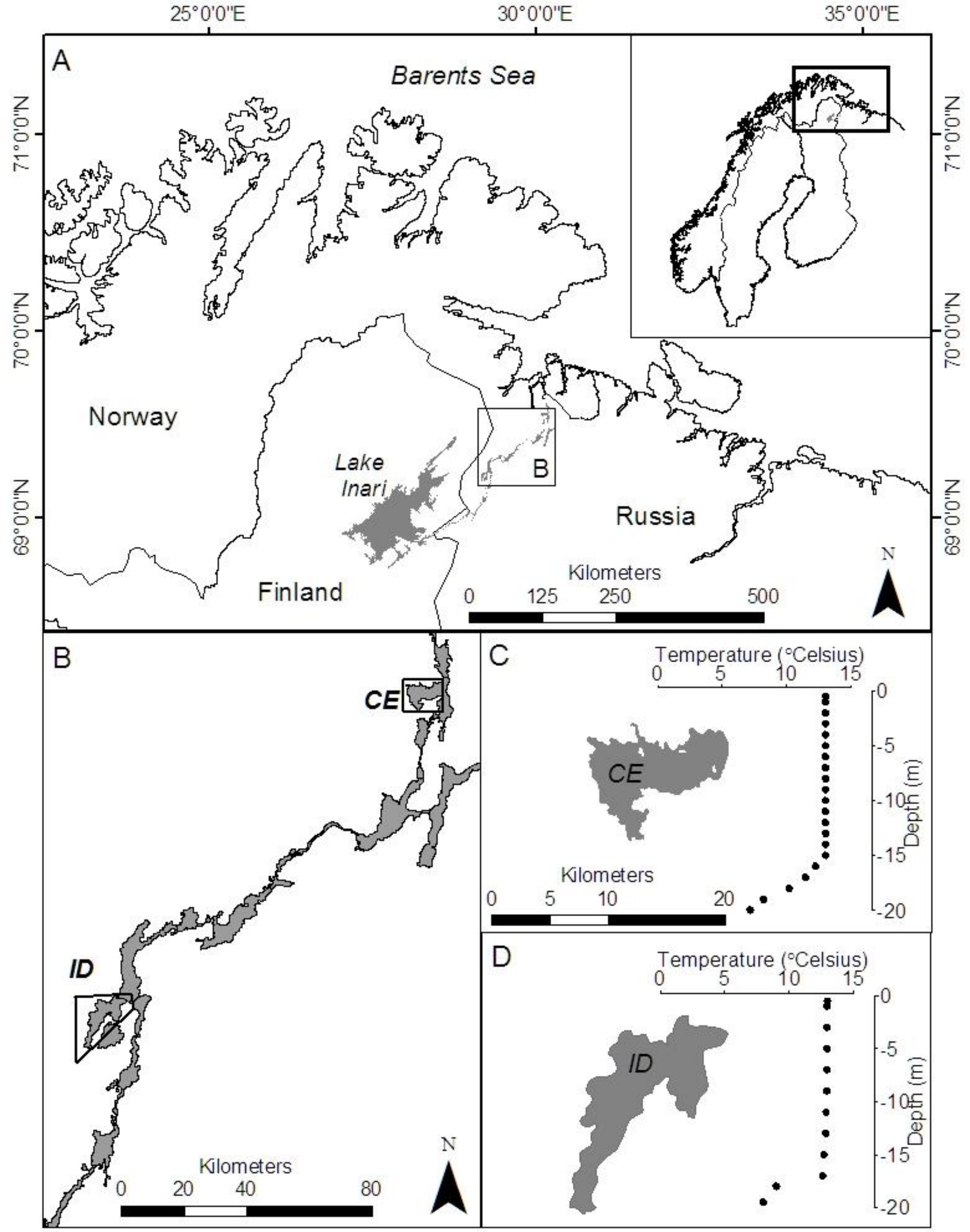

Figure 6.1 Location of the Pasvik watercourse within the northern Fenno-Scandinavian peninsula (A) and the Pasvik watercourse (B). Lake Skrukkebukta (CE) map and thermocline are illustrated in panel C, and Lake Tjærebukta (ID) map and thermocline in panel D.

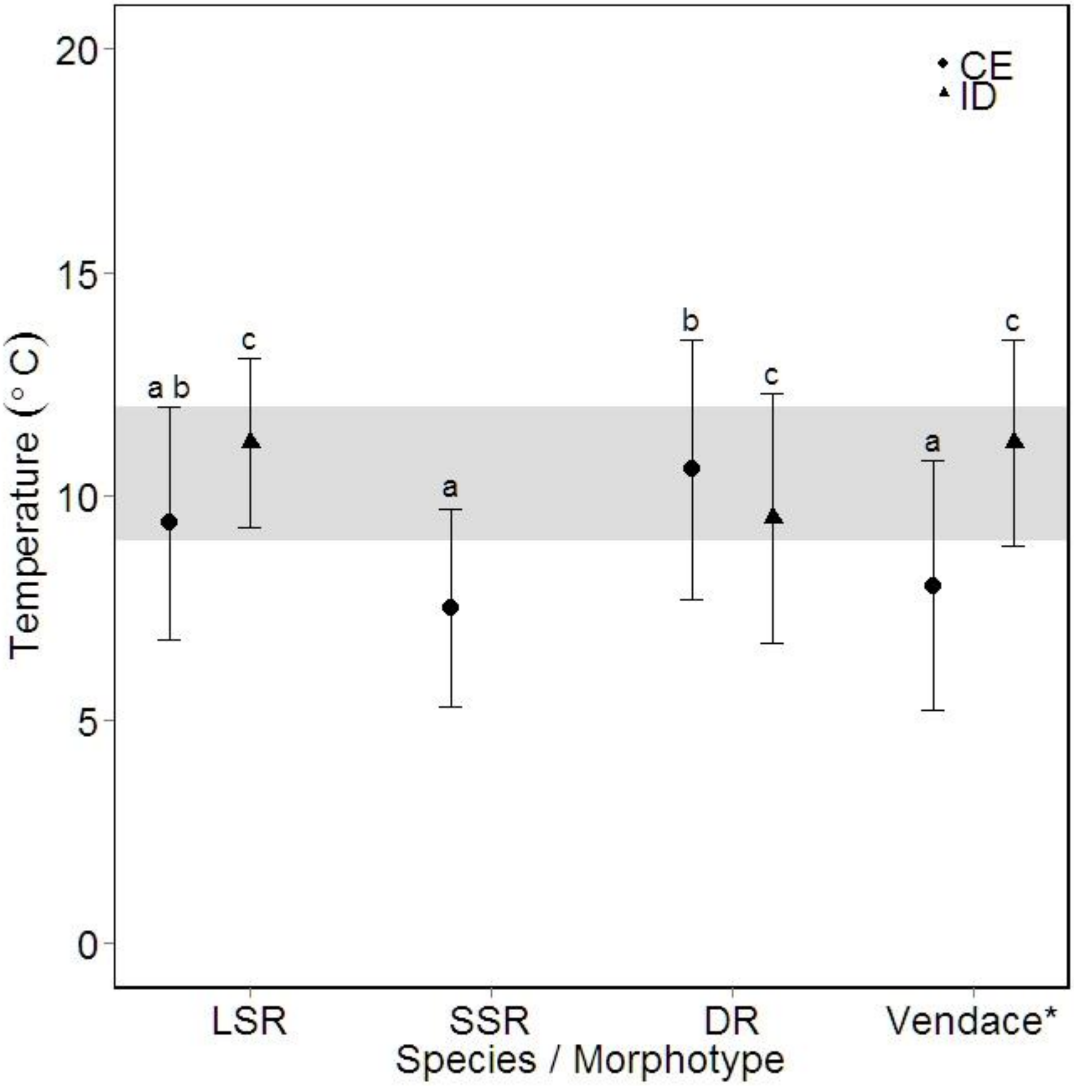

Figure 6.2. Mean (± standard deviation) temperature estimates for whitefish morphotypes DR (pelagic zone specialized), LSR (littoral zone specialized), SSR (profundal zone specialized) and vendace in the CE (co-existence, Lake Skrukkebukta; ●) and the ID (invasive-dominated, Lake Tjærebukta; ▲) site. The grey area illustrates the temperature range encompassed by the thermocline as defined by the depth over which the greatest temperature change occurs. No SSR whitefish morphotypes were caught in the ID site. The * symbol beside the Species/Morphotype label indicates a significant difference between sites. Matching letters within the graph indicate no significant difference between morphotypes/species within site.

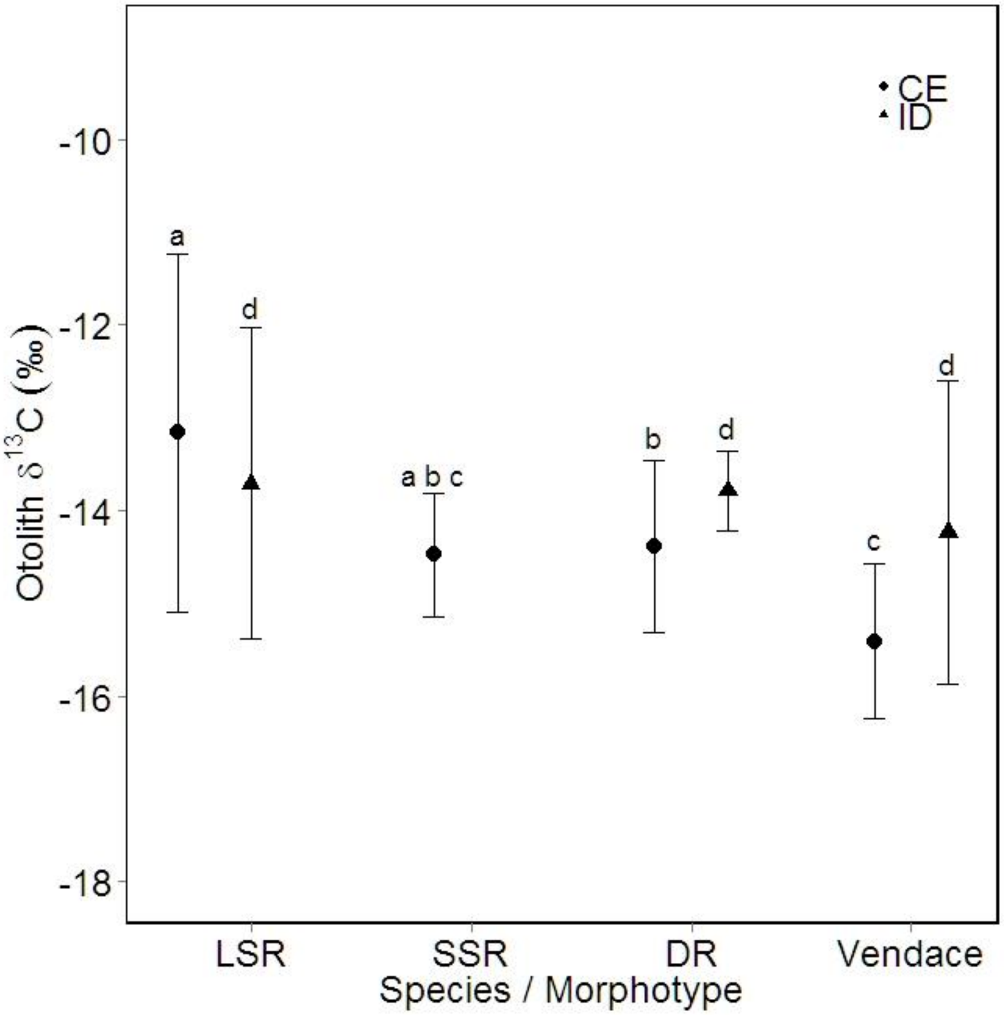

Figure 6.3. Mean (± standard deviation) otolith full growth season δ^{13}C values for whitefish morphotypes DR (pelagic zone specialized), LSR (littoral zone specialized), SSR (profundal zone specialized) and vendace in the CE lake (co-existence, Lake Skrukkebukta; ●) and the ID lake (invasive-dominated, Lake Tjærebukta; ▲).No SSR whitefish morphotypes were caught in the ID site. Matching letters within the graph indicate no significant difference between morphotypes/species within site.

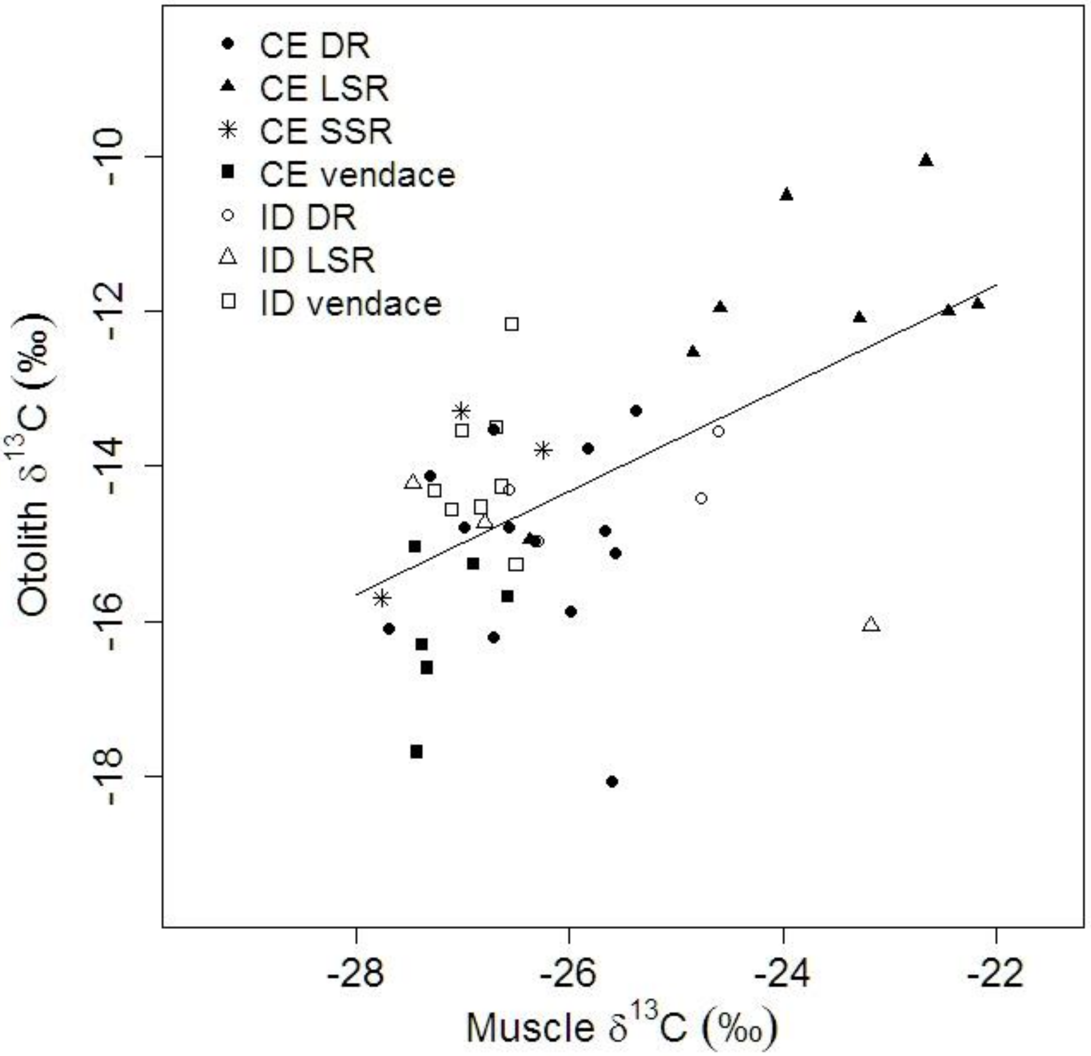

Figure 6.4. Muscle δ^{13}C values and otolith δ^{13}C values taken from the last growing season to date of capture for whitefish morphotypes DR (pelagic zone specialized), LSR (littoral zone specialized), SSR (profundal zone specialized) and vendace in the CE lake (solid symbols) and in the ID lake (open symbols). CE represents Lake Skrukkebukta, where vendace and whitefish co-existed, while ID represents Lake Tjærebukta where vendace was dominant.

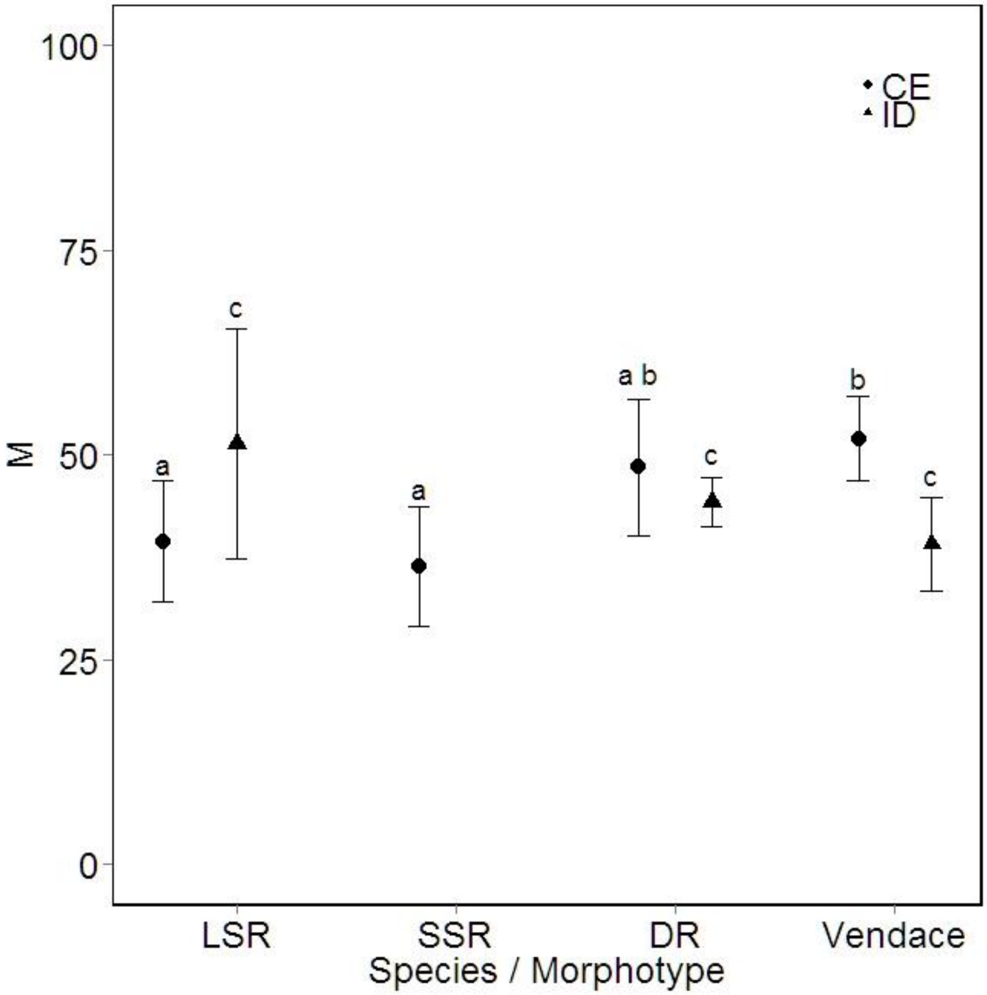

Figure 6.5. Mean (± standard deviation) percent contribution of metabolic carbon (*M*) to the otolith $\delta^{13}C$ value for whitefish morphotypes DR (pelagic zone specialized), LSR (littoral zone specialized), SSR (profundal zone specialized) and vendace in the CE lake (co-existence, Lake Skrukkebukta; ●) and in the ID lake (invasive-dominated, Lake Tjærebukta; ▲).No SSR whitefish morphotypes were caught in the ID site. Matching letters within the graph indicate no significant difference between morphotypes/species within site.

Chapter 7 General Conclusions

Synopsis

Determining the effects of hydroelectric dam-altered river discharge and temperature on downstream fish populations is essential for the management of river ecosystems (Baxter 1977; Ward & Stanford 1983; Olden & Naiman 2010). Effects on fish can be species-specific and depend on life-history characteristics and behaviour (e.g. Korman & Campana 2009; Alexandre et al. 2014; Bond et al. 2015). Accordingly, in this thesis I investigated the influence of hydroelectric dam operation on six fish species and the causal mechanisms driving them. The results of this investigation are reported in five data chapters, and briefly summarized below.

Slimy sculpin (*Cottus cognatus*) are an important sentinel species (Gray et al. 2004; Edwards & Cunjak 2007) which can be used to evaluate local effects of environmental and anthropogenic disturbances. Thus, this species was used to determine the impacts of hydroelectric dam-altered discharge along a longitudinal gradient downstream from a 15 MW hydropeaking dam, with comparisons made to a nearby naturally flowing river (Chapter 2). Slimy sculpin annual growth rates did not differ between hydropeaking regimes but did differ between rivers, with higher average annual growth rates observed in the regulated hydropeaking river. Decreases in growth rates were detected with increasing distance from the dam in the regulated river, while an increase in growth rate with distance downstream was observed for first year growth in the naturally flowing river. Tested hydrologic indices accounted for only a small proportion of the variation in slimy sculpin growth, and significant hydrological indices were not consistent between rivers. Thus, while data obtained for slimy sculpin indicate there are effects associated with changing river flow regimes (natural versus regulated), slimy sculpin in general do not indicate strong growth-flow correlations under either natural or altered flow conditions.

In addition to using slimy sculpin to investigate the effects of hydroelectric dam operation on fish populations, two additional members of the forage fish community were used to identify among-species, within-system differences in response to altered physical conditions: longnose dace (*Rhinichthys cataractae*) and trout perch (*Percopsis omiscomaycus*) (Chapter 3). The three species exhibited differences in growth, condition and survival between the regulated river and the naturally flowing river. However, the differences were not always consistent among species. Similar to slimy sculpin, longnose dace and trout perch exhibited higher growth in the regulated river, while there was no difference in growth for either species between the two hydropeaking regimes. However, hydropeaking regime altered the allometric nature of the weight-length relationship for longnose dace and slimy sculpin condition, with unrestricted hydropeaking resulting in a higher exponent (b) relative to the unrestricted hydropeaking regime. For trout perch, b was higher in the regulated river, while the weight-length relationship did not differ between hydropeaking regimes for this species. Survival in the regulated river was lower for longnose dace and slimy sculpin compared to the naturally flowing river, but similar between rivers for trout perch. Mean summer discharge was significantly correlated with growth for all three species in the regulated river, while mean summer river temperature was significantly correlated with growth in the naturally flowing river. Even when significant correlations were found, temperature and discharge explained little of the variation in growth for the three species.

The influence of hydroelectric dam altered river water temperature was further tested using two species from the coldwater fish guild, slimy sculpin and brook trout (*Salvelinus fontinalis*) (Chapter 4). The thermal regime downstream from the dam in the regulated river was determined to be more suitable for both species based on species-specific thermal thresholds. However, temperature use was significantly different between rivers for slimy sculpin only. As well, slimy sculpin inhabited significantly cooler water relative to brook trout. Both spatial and temporal analysis of temperature use suggested that brook trout thermoregulate by inhabiting temperatures close to their known thermal preference, while slimy sculpin inhabit temperatures indicative of their local environment. Temperature use was not correlated with condition for either species.

The growth, condition and relative metabolism of brook trout were compared between the regulated Magpie River and the naturally flowing Batchawana River in Chapter 5. There were significant differences in brook trout length-at-age, condition and relative metabolism between rivers. Length-at-age did not differ between hydropeaking regimes. Both the weight-length exponent and growth were higher in the regulated river, and brook trout were heavier at longer lengths. Caloric content did not differ between rivers, while field metabolism was higher in the regulated river and was positively correlated with time spent in the discharge increase phase of hydropeaking events. Differences in brook trout growth were likely the result of differing food availability between rivers, with a higher food supply offsetting the increased metabolic costs associated with hydropeaking.

In Chapter 6, the relative success of the invasive species vendace (*Coregonus albula*) at two sites in the regulated Pasvik watercourse, Norway, was investigated. Mean temperature use by vendace over the course of the growing season was significantly different between the two sites, with vendace inhabiting lower temperature water in the site where they co-existed with whitefish. Temperature use by whitefish morphotypes (*Coregonus lavaretus*) did not differ between sites, but differed among morphotypes in the site where whitefish and vendace coexisted. Otolith and muscle tissue stable isotope analyses suggested that thermal habitat partitioning was occurring in the site where vendace and whitefish successfully coexist, while dietary resource partitioning was occurring where vendace dominate the pelagic zone. Field metabolism differed between sites for both species, likely resulting from differences in fish activity between sites driven by diel vertical migrations in the deeper site. The availability of different thermal habitats facilitates the co-existence of invasive vendace and native whitefish by reducing competition for food through thermal habitat partitioning.

Synthesis

Based on the analysis in the five data chapters within this thesis, several overarching conclusions can be drawn regarding the effects of river regulation on downstream fish populations:

1. *The impacts of river regulation vary by fish species*

Fish responses to the physical alterations downstream from hydroelectric dams differed when evaluated according to annual survival, condition, field metabolism and thermal habitat. This occurred within the forage fish community (Chapter 3), the coldwater fish guild (Chapter 4) and between native and invasive species (Chapter 6). Differential responses were driven by species-specific preferences and behaviour (Table 1.1, Chapters 3, 4, 6).

2. *The impacts of river regulation vary within fish species*

Using multiple indicators of fish health revealed the conflicting nature of effects from river regulation within a species. Potential positive and negative effects were found, such that higher growth, but lower survival (Chapter 3), or higher growth and higher field metabolism (Chapter 6) were exhibited by the same species in the regulated river. Therefore, multiple indicators of fish health are necessary to characterize the impacts of river regulation on a given species.

3. *Hydrologic and thermal indices do not capture the complexity of responses exhibited by fish species*

Alterations to the physical environment downstream from the dam resulted in both direct and indirect effects on fish species. Hydrologic and thermal indices failed to explain a large proportion of the variation in fish growth, given the indirect effects of hydrologic and thermal alterations and the integrative nature of indicators of fish health. While species-specific discharge and thermal thresholds remain important for developing management strategies, the availability and quantity of different habitat types was also important for fish population health (Chapter 4) and inter-species interactions (Chapter 6), and should be incorporated into evaluations of river regulation on fish communities.

4. *Multiple species and multiple indicators are needed to characterize the impacts of river regulation on downstream fish populations*

Given the variation in effects among and within species, multiple fish species must be investigated using multiple indicators of fish health to characterize the impacts of river regulation within a given system. Physical alterations to discharge and temperature should be characterized according to species-specific thresholds and relative availability of different habitats. As alterations driven by hydroelectric dam operation can have both direct and indirect effects, indicators of fish health need to be considered within the context of additional parameters such as fish food availability. The complexity of riverine systems necessitates continued efforts towards the completion of long-term, large-scale studies which include the sampling of multiple species and the evaluation of multiple parameters to fully characterize the impacts of river regulation.

Future Directions

This thesis characterized the effects of river regulation using multiple indicators of fish health and six fish species. As with all scientific studies, the results discussed in the thesis generated additional research questions. Several possibilities for future research are discussed in detail below.

- This thesis highlighted the importance of changes to food availability driven by river regulation and/or hydropeaking (Lauters et al. 1996; Lagarrigue et al. 2002; Patterson & Smokorowski 2011; Jones 2013) for fish growth, and for mitigating the costs of increased energetic outputs. However, based on the invertebrate community composition (Jones

2013), increases in invertebrate abundance are likely driven in part by inputs from the reservoir (Jones 2013). Long-term decreases in fish growth in regulated system lakes have been documented and are likely linked to reductions in reservoir nutrient dynamics and productivity (Milbrink et al. 2011). Therefore, characterizing the link between the reservoir ecosystem and downstream fish growth in the Magpie River in further detail would provide valuable information for managing both upstream and downstream ecosystems, i.e. is downstream productivity dependent on reservoir productivity? And, would changes to reservoir productivity affect fish growth downstream in the Magpie River? It may be worthwhile to monitor both reservoir and river ecosystem dynamics long-term, to inform river management strategies, should a long-term decrease in fish growth be detected (e.g. Milbrink et al 2011).

- This thesis addressed multiple indicators of fish health including growth, condition, survival and relative metabolic rate. However, hydroelectric dams can also affect aspects of fish maturity and reproduction. For example, studies have found younger age-at-maturity for slimy sculpin (Bond et al. 2015), as well as decreased gonadal activity in Iberian barbel (Alexandre et al. 2014). Given that there is the potential for hydroelectric dam-induced physical alterations to affect the reproductive characteristics of fish, it would be informative to collect data on the reproductive success of fish living downstream from the 15 MW dam in the Magpie River, compared to the naturally flowing Batchawana River. Several metrics such as age-at-maturity, fecundity, spawning frequency and timing, egg size and larval growth rates could be investigated. Comparisons would be especially interesting within the forage fish community as longnose dace and trout perch are known to spawn multiple times per season, while slimy sculpin do not. Determining the response of reproductive parameters to altered river discharge and temperature, combined with the analyses completed in this thesis would provide information on the impacts of river regulation for the entire fish life cycle.

- The calculation of detailed hydrologic and thermal indices in this thesis quantified the extent to which hydroelectric dam operation alters discharge and temperatures downstream. The 15 minute intervals over which the data loggers recorded temperature and discharge provide a comprehensive picture of the temporal heterogeneity of river discharge and temperature. However, given the limitations on the number of data loggers within the rivers, the data analysis in this thesis fails to characterize the full spatial heterogeneity of river velocity at different discharges as well as river temperature. River heterogeneity has been characterized within rivers relative to woody debris and substrate (Lepori et al. 2005; Palmer et al. 2010) and across rivers within regions (Poff et al. 2007). However, a comprehensive study of the heterogeneity in velocity and temperature, at both low and high flows in the regulated river, coupled with an assessment of fish habitat use, could provide a more complete picture of how habitat availability and use changes at different points in the hydropeaking cycle. Given the safety constraints of sampling at high flows, the habitat availability aspect could be addressed with detailed modelling studies (e.g. Torgersen et al. 1999; Bouchard & Boisclair 2007), while telemetry methods may be used to characterize fish habitat use (e.g. Murchie & Smokorowski 2004; Cocherell et al. 2010).

- To date, studies on the impact of hydroelectric dams on downstream fish communities have focused on abundance and community composition (Bain et al. 1988; Freeman et al. 2001) or conducted a detailed analysis on a single species (e.g. Korman & Campana 2009; Bond et al. 2015; Finch et al. 2015). This thesis highlighted the potential for within-system, species-specific biological responses at the individual level. Yet, this analysis was confined to the most abundant species within two boreal forest rivers in northern Ontario. There remains a need to characterize different responses within the fish community to river regulation in river systems of varying sizes, from different geographic regions, and under different dam operating regimes. This would provide valuable information on the impacts of river regulation on different fish communities and would be useful for developing river management strategies.

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