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Ecological effects of flow and temperature regimes on fish communities in temperate rivers

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Résumé

Les organismes aquatiques sont adaptés à une grande variabilité hydrique et thermique des rivières. Malgré ceci, la régulation des eaux suscite des changements aux débits qui peuvent provoquer des impacts négatifs sur la biodiversité et les processus écologiques en rivière. Celle-ci peut aussi causer des modifications au niveau des régimes thermiques et des caractéristiques de l'habitat du poisson. Des données environnementales et biologiques décrivant l'habitat du poisson existent, mais elles sont incomplètes pour plusieurs rivières au Canada et de faible qualité, limitant les relations quantitatives débit-température-poissons à un petit nombre de rivières ou à une région étudiée.

La recherche menée dans le cadre de mon doctorat concerne les impacts de la génération d'hydroélectricité sur les rivières; soit les changements aux régimes hydriques et thermiques reliés à la régulation des eaux sur la variation des communautés ichtyologiques qui habitent les rivières régulées et naturelles au Canada. Suite à une comparaison d'échantillonnage de pêche, une méthode constante pour obtenir des bons estimés de poisson (richesse, densité et biomasse des espèces) a été établie pour évaluer la structure de la communauté de poissons pour l'ensemble des rivières ciblées par l'étude. Afin de mieux comprendre ces changements environnementaux, les principales composantes décrivant ces régimes ont été identifiées et l'altération des régimes hydriques pour certaines rivières régulées a été quantifiée. Ces résultats ont servi à établir la relation significative entre le degré de changement biotique et le degré de changement hydrique pour illustrer les différences entre les régimes de régulation. Pour faire un complément aux indices biotiques déjà calculés pour l'ensemble des communautés de poissons (diversité, densité et biomasse des espèces par rivière), les différences au niveau des guildes de poissons ont été quantifiées pour expliquer les divers effets écologiques dus aux changements de régimes hydriques et thermiques provenant de la gestion des barrages. Ces derniers résultats servent à prédire pour quels traits écologiques ou groupes d'espèces de poissons les composantes hydriques et thermiques sont importantes. De plus, ces derniers résultats ont servi à mettre en valeur les variables décrivant les régimes thermiques qui ne sont pas toujours inclues dans les études hydro-écologiques. L'ensemble des résultats de cette thèse ont des retombées importantes sur la gestion des rivières en évaluant, de façon cohérente, l'impact de la régulation des rivières sur les communautés de poissons et en développant des outils de prévision pour la restauration des écosystèmes riverains.

Mots-clés: variation biotique, régimes hydrologiques, régimes thermiques, poissons, rivières canadiennes.

Abstract

Widespread anthropogenic impacts to river ecosystems are currently changing the naturaly variability of flow and temperature regimes, with potentially important repercussions on the stability and function of aquatic communities. Although fish community responses to flow alterations from river regulation have been quantified in the past (e.g. late maturation of salmonid populations due to attenuated flows or stranding of fishes from down-ramping flows), the scarcity of high quality, long-term data, especially in Canadian rivers, has limited our understanding of the effect this has had on other environmental drivers and fish community structure across this heterogenous landscape. Using extensive field surveying across unregulated and regulated rivers in Alberta, Ontario, Québec, and New Brunswick coupled with data from national, provincial, and private flow and water temperature gauge networks, I showed the effects of flow and thermal regimes on fish diversity, density, biomass, and different types of ecological guilds. I also examined the extent to which different regulation practices have modulated the response of riverine fish to the combined effect of changes to flow and thermal regimes.

To first establish a methodology for quantifying fish community structure across rivers, I generated reliable site-specific species richness, density, and biomass metrics that combined measures from two commonly used surveying methods. To then quantify the response of these fish community metrics to river regulation, I defined daily and hourly flow indices based on river flow conditions, developed hydrologic regime variables that described dominant patterns of flow variation, and calculated flow alterations based on the difference in multivariate space of these hydrologic regime variables for regulated rivers from reference flow conditions. By applying this same approach to fish community metrics, I identified a significant positive relationship between biotic and flow alterations and showed a separation between the two most distinct flow regulation types, run-of-river (ROR) and hydro-peaking. To tease apart the relative importance of each environmental driver for establishing fish communities across river regimes, I provided quantitive thermal indices based on river water temperatures and developed thermal variables akin to those described for flow regimes. To evaluate whether quantitative fish guild estimates, rather than total river biomass or density estimates, would respond more strongly to river thermal regimes, I compared the response of different types of fish guilds to flow and thermal regimes across rivers, including those subjected to river regulation. All fish guild models performed better relative to studying total river estimates, confirming the use of trait-environmental relationships for studying fish community responses across rivers. I also found that integrating thermal regimes in hydro-ecological studies is critical in predicting fish guild responses across rivers.

Collectively, these findings have important repercussions for river management, as they provide comprehensive assessments of the environmental variables driving fish community responses, inform the potential range of ecological consequences of anthropogenic alterations on natural flow regimes, and contribute to establishing more transferable predictions for restoring impacted rivers. More broadly, the thesis results are important given future global climate warming, its synergistic effects with other anthropogenic stressors, and ongoing scarcity for water and energy sources.

Keywords: biotic variation, hydrologic regimes, thermal regimes, fish, Canadian rivers.

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List of acronyms and abbreviations

AB: Alberta

BC: British Columbia

CDEA: Comité de Déontologie de l'Expérimentation sur les Animaux

CPUE: Catch Per Unit Effort

Cum R^2_{adj}: Cumulative adjusted R^2

D: Daily (daily flows)

E: Electrofishing

ELOHA: Ecological Limits of Hydrologic Alteration

FQRNT: Le Fonds de Recherche du Québec – Nature et Technologies

GRIL: Groupe de Recherche Interuniversitaire en Limnologie et en Environnement Aquatique

H: Hourly (hourly flows)

IHA: Indicators of Hydrologic Alteration

NB: New Brunswick

NFP: Natural Flow Paradigm

NSERC: Natural Sciences and Engineering Research Council of Canada

ON: Ontario

PC: Principal Component

PCA: Principal Component Analysis

pRDA: partial Redundancy Analysis

P/A: presence or absence

QC: Québec

RDA: Redundancy Analysis

R^2_{adj}: adjusted R^2

R^2_{CV}: cross-validation R^2

ROR: run-of-river

SD: Standard Deviation

V: Visual (snorkelling survey)

For my family

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Preface

NSERC HydroNet is a national research network whose overall mission is to provide government and industry with the knowledge and tools necessary for minimizing the effects of hydroelectric installations and river regulation on aquatic ecosystems, thereby promoting sustainable development of hydropower in Canada. NSERC HydroNet identified several research challenges, among them, the absence of comprehensive, good-quality data that would enable inter-riverine comparisons of fish community structure and their environmental drivers (Boisclair et al. 2015). The range of regulation practices further complicated relationships that attempted to quantify and predict the overall impact of hydroelectric installations on river ecosystems.

To address these limitations, the present thesis examines the ecological effects of flow and thermal regimes for a subset of unregulated and regulated Canadian rivers surveyed for NSERC HydroNet. Four years of extensive field surveying was conducted across selected rivers to obtain *in-situ* estimates of fish community structure and local physical attributes. Additional river-scale physical drivers, notably river flow and thermal regimes, were quantified from national, regional databases, data disclosed by industry partners (NB Power, Brookfield, Trans-Alta, BC Hydro), and HydroNet collaborators (M. Lapointe and A. St-Hilaire labs at McGill and INRS, respectively). The rivers surveyed also represented different points within the river regulation continuum, from unregulated to heavily regulated, allowing us to better understand the effects of river alteration on fish community structure. With the help of this research partnership, the completed thesis provides some of the answers and tools necessary for more effective river flow management, as per NSERC HydroNet's mission.

Thesis format and style

The manuscript-based thesis consists of three manuscripts, of which I am the lead author. A general introduction provides the overall context that motivated this research, as well as an overview of the literature that supports the research questions. With advice from my supervisors, I contributed to the conception, planning, data collection, data analyses, and preparation of all thesis manuscripts. A general conclusion synthesizes key thesis findings and closes on future research questions and implications for river management and restoration. Each thesis chapter has either been published or submitted for review in peer-reviewed journals. The three manuscripts are as follows:

C. J. Macnaughton, S. Harvey- Lavoie, C. Senay, G. Lanthier, G. Bourque, P. Legendre, D. Boisclair (2015) A comparison of electrofishing and visual surveying methods for estimating fish community structure in temperate rivers. *River Research and Applications* **31**:1040-1051. doi: 10.1002/rra.2787.

C. J. Macnaughton, F. McLaughlin, G. Bourque, C. Senay, G. Lanthier, S. Harvey- Lavoie, P. Legendre, M. Lapointe, D. Boisclair (2015) The effect of regional hydrologic alteration on fish community structure in regulated rivers. *River Research and Applications*, special edition Ecohydraulics. doi: 10.1002/rra.2991.

C. J. Macnaughton, C. Senay, I. Dolinsek, G. Bourque, A. Maheu, G. Lanthier, S. Harvey-Lavoie, J. Asselin, P. Legendre and D. Boisclair (*in review*) Using guilds to assess fish community response to hydrological and thermal regimes across temperate rivers. (Re-submitted May, 2016 to Freshwater Biology).

Statement of contribution

As the lead author of all three manuscripts, I conceived and designed the work, participated in the collection of field data, conducted the analyses, interpreted the results, drafted, and revised the manuscripts. C. Senay, G. Lanthier, G. Bourque, and S. Harvey-Lavoie contributed to collecting fish and environmental field data used in all three thesis chapters, as well as sourcing databases for hydrologic data. Additional contributions to the development of hydrologic and thermal indices used in the 2nd and 3rd chapters were made by F. McLaughlin and A. Maheu, respectively. C. Senay, G. Lanthier, G. Bourque, S. Harvey-Lavoie, I. Dolinsek, J. Asselin, and I contributed to the fish guilds developed in the 3rd chapter. Revisions to the work for content and integrity of results and final approval of the version published were provided by all authors, including supervisors, P. Legendre and D. Boisclair.


Photo: Bull River, British Columbia 2012

General Introduction

Anthropogenic threats to ecosystem services

Overwhelming human demand for fresh water threatens the ecosystem services (e.g. food production based on artisanal and commercial fisheries, aquaculture, floodplain agriculture etc.) on which millions of humans depend directly for water, food, secure housing, quality of life, health, and prosperity (Postel and Richter 2003, Arthington 2012). Heavily populated areas worldwide pose an even greater threat to these ecosystem services and biodiversity, as many dams and diversions are in close proximity to these areas. Indeed, a synthesis of threats to world rivers has found that greater than 83% of the land surface surrounding aquatic systems has been significantly influenced by human activities (Vörösmarty et al. 2010). Hydroelectric infrastructure, for example, has altered many river systems and resulted in changes to the physical, chemical, and biological processes, which include the disruption of most ecological processes and loss of biodiversity occurring in these regulated environments (Poff 1997, Nilsson et al. 2005). Extensive ecological alteration resulting from river regulation for hydroelectric purposes has thus led to concern for the viability of maintaining and restoring healthy river ecosystems (Dudgeon et al. 2005, Vörösmarty et al. 2010); not only because of the substantial ecological costs mentioned, but also because impacts on the productivity of fisheries and water resources may lead to socio-economic losses (Postel and Richter 2003).

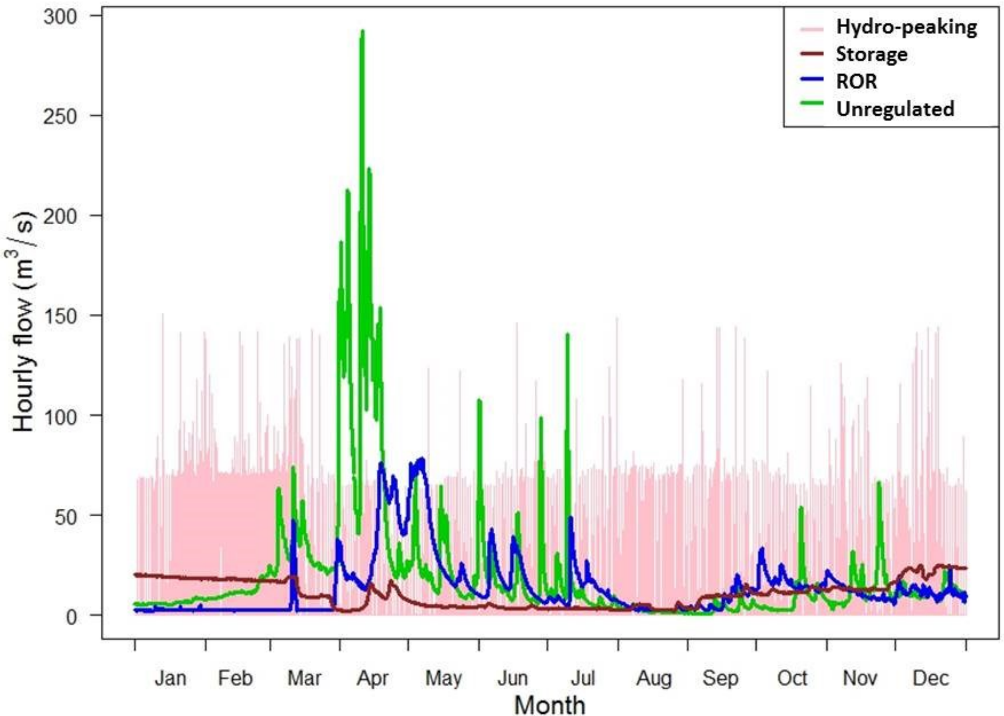
Aquatic organisms are generally adapted to a wide range of natural variability of flows and temperatures (Allan 1995), however, defining natural variability is often complicated by the widespread historical anthropogenic impacts on many rivers. Although much effort and resources have been allocated to quantifying fish community responses to flow alterations from river regulation (Webb et al. 2013), the scarcity of high quality, long-term data, especially in Canadian rivers, has limited our understanding of the effects these modifications and different regulation practices have had on other environmental drivers and fish communities across this heterogenous landscape. To successfully curtail future ecological changes occurring across river systems, a better understanding of the complex interactions among flow and water temperature regimes and how these shape the ecological integrity of river systems is therefore needed (Olden and Naiman 2010).

Ecological responses to flow regimes and flow alteration

As delineated in the Natural Flow Paradigm (NFP; Poff et al. 1997), the ecological integrity (biodiversity, production, and sustainability) of riverine ecosystems is a function of their natural dynamic character. As such, the variability in flow regime has become fundamental to the biological study and practical management of lotic systems (Richter et al. 1996). The flow regime varies geographically in response to climate (precipitation and temperature), catchment properties, and runoff (geomorphology and position in river network) (Poff 1996, Poff 2009, Poff and Zimmerman 2010). For example, the organization of fish assemblages is constrained, not only by local processes (e.g. hydraulic conditions or riparian canopy cover), but also by landscape-scale habitat variables, which include broad hydrologic patterns (e.g. spring floods) and available species pools (Poff and Allan 1995, Poff 1996, Guisan and Thuiller 2005, Mims and Olden 2013, Senay et al. 2016). Though local environmental variables (e.g. water velocity, water depth, and sediment size) have been found to drive the largest part of intra-riverine fish species distribution variation among the suite of lateral-, longitudinal-, or physiographic-scale variables (Bouchard and Boisclair 2008), regional differences and river regulation may affect the relative contribution of these local variables (Senay et al. 2015). As a result, models developed for a system are not necessarily transferable to another.

The flow regime also varies temporally. In many existing hydro-ecological studies, basic statistics using weekly or yearly averages are sufficient to characterize relationships between flow regimes and ecological functioning. However, such analyses based on coarse temporal scales may miss the more rapidly occurring biological responses to flow changes (Olden and Poff 2003). For example, indices capturing hourly variations in river flow are needed to capture the extent that hydrologic alteration resulting from regulation practices alter flows on an hourly basis. The range and variation of flows over time and space can, therefore, be used as a template for understanding current ecological processes, resulting evolutionary adaptations (Lytle and Poff 2004), and the requirements to maintain the natural biodiversity of aquatic and riparian ecosystems (Bunn and Arthington 2002).

This concept of maintaining flow variation to sustain the ecosystem and associated biodiversity has led to a paradigm shift in ecosystem management away from a single species with static habitat requirements (e.g. minimum flows), to whole ecosystems, in which the assemblage of species could be sustained by a dynamic flow regime (Poff 2009). According to Poff et al. (1997), there are five critical components of flow regime that regulate ecological processes in river ecosystems: the magnitude, frequency, duration, timing, and rate of change (flashiness) of hydrologic conditions. These components encompass the range of natural flow variability and include specific hydrologic events, such as floods or droughts, which are integral to the health of river ecosystems (Poff et al. 1997). In northern latitudes, the natural flow regime is modulated by climatic processes, revealing seasonal periodicity (i.e. spring floods and droughts) and occasional flow peaks as a result of large storms. By contrast, regulated systems will generally hold back water for later use (e.g. power generation), allow surplus water to spill over weirs, and cause downstream flow regimes to be altered. Regulated flows from dams may also vary according to the dam operation practices, resulting in differences in the magnitude and periodicity of downstream flows (Figure 1). As such, dams and operation practices or regulation types, from run-of-river (ROR) to storage with or without peaking (hydro-peaking or storage, respectively), are known to cause multiple changes to fish populations (Anderson et al. 2006, Renöfält et al. 2010), via diverse alterations to water quality and hydrologic regimes (Freeman et al. 2001, Dudgeon et al. 2005). ROR type systems appear to have the least impact on stream ecology because patterns of water release are designed with minimal water storage, often resulting in flows mimicking natural regimes (Bratrich et al. 2004, Habit et al. 2007). Conversely, hydro-peaking and storage regulation types may have large storage volumes in upstream reservoirs and release water gradually over the course of the day or all-at-once, at peak times to match daily hydropower consumption needs (Cushman 1985). The resulting flows from these regulation types have been shown to shift temporally, resulting in significant seasonal high flow attenuation and enhancement of low flows, especially over winter months (McManamay et al. 2012a, McLaughlin et al. 2014). Other studies have also confirmed the occurrence of reduced flow variability and increased flow constancy when comparing with pre-dam flow records (Mims and Olden 2013).



Bourque, 2014

Figure 1. Hydrographs representing the differences in annual flows between unregulated and regulated rivers: ROR, storage, and hydro-peaking regulation types. Hydrographs depict flow data from four rivers studied and source hourly flow data to illustrate daily, seasonal, and annual hydrologic trends.

Numerous case studies provide the foundation for the scientific understanding that many types of flow alterations (e.g. alterations of flow magnitude, frequency, and timing) induce a variety of ecological responses (Bunn and Arthington 2002, Postel and Richter 2003, Mims and Olden 2013). Hydro-peaking events, typified by the rapid and large release of water from dams, have been shown to directly impact fish populations through strandings along the changing channel margins (Bradford 1997, Halleraker et al. 2003), downstream displacements (Scruton et al. 2008), reduced spawning and rearing success due to dewatering of redds (nests), and obstructed migration (Anderson et al. 2006, Young et al. 2011). Flow alterations may also exert indirect effects through the loss or reduction of suitable habitats (Vehanen 2000). At the population and community levels, flow alterations have been shown to disrupt environmental cues that influence the maturation and spawning of riverine fishes, resulting in lower recruitment and decreases in adult abundance and species richness (Humphries and Lake 2000, Humphries et al. 2008). Trait-based approaches have also been used to advance our understanding of stream fish community distribution through the community-level relationships between species traits and river habitat variables, including those resulting from flow regulation (Vannote and Sweeney 1980, Lamouroux and Souchon 2002, Frimpong and Angermeier 2010a). For example, benthic or pelagic fish guilds were found to follow gradients in mean daily flows and their variability, notably, mean baseflows, number of zero-flow days, high-flow pulses, among other low-flow hydrology metrics observed across catchments where flows were regulated (Arthington et al. 2014). While high-flow pulses below dams may cause some fish mortality (Young et al. 2011), they may also cleanse gravel beds, rejuvenate spawning and foraging habitats, and may reconnect channel-floodplain habitats, ultimately benefiting the system long-term (Poff 2009). Understanding how temporal fluctuations in environmental conditions and alterations to flow variability may contribute to the rejuvenation and maintenance of habitat quality and overall ecosystem health is the cornerstone to implementing more effective flow programs (Annear et al. 2004).

Quantifying flow regimes and flow alteration

With the recognition that ubiquitous flow alterations threaten biodiversity and ecosystem functions of rivers on a global scale, the development of quantitative indices characterizing the various types of flow alteration has been essential to management and conservation efforts. Though empirical studies have revealed quantitative relationships between various kinds of flow alteration and ecological responses, a review found that 70% of studies focused on either alteration of flow magnitude or the effects of high flow stabilisation (Poff and Zimmerman 2010). There remain several additional limitations to addressing the effects of flow alteration on fish communities in regulated rivers. For one, hydrologic alterations are generally quantified as the difference between current and reference conditions, as inferred from historical flow data (Richter et al. 1996, Magilligan and Nislow 2005). The absence of such historical data for certain systems or suitable reference sites inherently limits the accuracy of estimates relevant for quantifying the degree of flow alteration (Lloyd et al. 2003, McManamay et al. 2012a). Moreover, different authors have highlighted the importance of choosing relevant flow indices to best represent dominant patterns of hydrologic variability (Olden and Poff 2003) or to address the fundamental dimensions of the flow regime driving patterns of fish occurrence (Mims and Olden 2012). *A priori* selection of flow indices to represent ecologically meaningful facets of the flow regime may, however, limit the chances of exploring other possible unknown flow-ecological relationships. As such, adopting a multivariate approach to quantifying flow alterations may foster the development of more comprehensive environmental flow standards for regulated rivers sharing similar hydrographic characteristics.

The Ecological Limits of Hydrologic Alteration (ELOHA) framework proposes the development of regional flow standards derived from observed relationships between altered hydrologic parameters and ecological responses across river systems. This framework assumes that rivers sharing similar hydrology (within a same hydrographic region or flow class) may be compared for evaluating the relative effects of regulation on natural flow dynamics (Arthington et al. 2006, Poff et al. 2010). ELOHA, thus, measures observed deviations of regulated flows from reference conditions and develops flow alteration-ecological relationships for different river types, eliminating the reliance on historical data (McManamay et al. 2012a, McManamay et al. 2012b). Building on the ELOHA concept, these deviations from reference may then be synthesized into river-level hydrologic alterations, resulting in more comprehensive composites of river flow alterations.

Ecological responses to water temperatures and thermal alteration

The significance of water temperature in riverine ecosystems has been widely acknowledged (Coutant 1999, Caissie 2006, McCullough et al. 2009). Water temperature controls almost all rate reactions (chemical and biological) and is thus a strong influence on biological systems at all levels; influencing responses at the molecular, organismal, population, and community levels. At the molecular level, genetic adaptations augment a fish's capacity for anaerobic metabolism, anti-oxidative defense, and protect molecular functions by heat shock proteins, further bolstering thermal tolerance (survival) for local populations (Portner 2002). At the organismal level, responses to water temperatures depend on thermal tolerance and sub-lethal effects (e.g. growth, reproduction, and intergenerational effects) (McCullough et al. 2009). Organisms are often constrained by particular temperature ranges and thus limited in their distribution to a certain range of latitudes and altitudes. However, these organisms may tolerate thermal environments where temperatures briefly exceed levels that could be damaging, if experienced over longer time periods and fluctuate, rather than remain constant (Caissie 2006). The annual temperature range in temperate rivers is typically between 0 and 25°C, which approaches the minimal and maximal thermal tolerances of fishes adapted to these environments, respectively (Matthews and Zimmerman 1990). The extent of diel temperature variation is usually greatest in streams of small to intermediate size (between 1 and 9 °C; Vannote and Sweeney 1980) due to day vs. night changes in air temperature and absorption of solar radiation during the day (Allan 1995). Indeed, fish have evolved to fit into "thermal niches" to optimize physiological, ecological, and reproductive performance in their native habitats (Coutant 1987). Under natural conditions, fish may also be adapted to temperature variability and/or temperature maxima by a combination of selective microhabitat use (i.e. thermal refugia created from groundwater upwelling and/or cold water flumes from small order streams) and diel behavioural partitioning, allowing fish to compensate for physiological heat stress associated with high temperatures (Coutant 1999). For example, both brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*) behaviourally thermoregulate by preferentially occupying cooler areas such as tributaries when ambient temperatures exceed their upper tolerances (Cunjak et al. 2011).

High temperatures produce stress effects that are the result of not only the magnitude of the temperature, but the duration of the exposure (Coutant 1987, Caissie 2006). Studies have revealed the influence of fluctuating temperatures relative to constant ones in controlling the balance between the growth of organisms vs. mortality (Hokanson et al. 1977). Moreover, the influence of cumulative exposure to adverse high temperatures in a fluctuating regime may produce mortality from successive thermal cycles (McCullough et al. 2009). Responses may also differ among life stages of species, prior experience to ranges in water temperatures, and any previous or concurrent exposures to multiple stressors like low dissolved oxygen. These factors ultimately result in complex ecological responses to thermal regimes (Caissie 2006). Although water temperature seems to be associated with the movement of some salmonids, there are a wide range of movement behaviours through time that are not simply explained by water temperature alone. It is suggested that a combination of water temperature change, weight or condition factor (K: length-weight relationship; Cunjak et al. 1990), river flow, turbidity, fish density, availability of cover, photoperiod, presence of thermal refuges, fishing pressure, among many others may collectively stimulate or reduce movement (McCullough et al. 2009).

The impoundment of rivers in temperate zones typically alters thermal regimes even in large rivers and the depth of water release from the dam (i.e. epilimnetic (warm) vs. hypolimnetic (cold) water release from thermally stratified reservoirs) has a great influence on downstream temperatures (Ward 1985, Allan 1995, Olden and Naiman 2010). Thermal stratification along the longitudinal axis of natural rivers is generally uncommon. However, if the flow through a reservoir is relatively slow, it may lead to thermal stratification typical of lakes, whereby reservoir surface temperatures are generally much warmer while deeper waters remain relatively cool. Water downstream of reservoirs therefore tends to be warmer overall (increase in mean annual water temperatures), with a decrease in the range of annual temperature variation (Ward 1985, Allan 1995). In the summer, water temperatures may be cooler and annual cycles delayed (Caissie 2006). In northern climates, the most significant thermal alteration is thought to occur over the winter, where warm water released during the winter is problematic because winter freezing may occasionally not occur. As a result, salmonid egg hatching may be advanced by as much as 50 days, ultimately impacting salmonid population survival (Caissie 2006). The range of anthropogenic impacts on thermal regimes and resulting fish communities is dependent on the type of flow regulation (amount and timing of heat load delivered) and on the sensitivity of rivers to human modifications (Poole and Berman 2001).

The type of river regulation (ROR, storage, and hydro-peaking), the slope of the river, and the depth of water release (outflows) may also affect downstream thermal regimes (Caissie 2006, Webb et al. 2008). For example, fluctuating water releases by dams from outflows located beneath the thermocline in reservoirs may result in highly variable and depressed summer water temperatures. In some cases, large dams have been known to intentionally manage thermal regimes by selectively releasing cold water from deep reservoirs to promote optimal sport fishing opportunities (e.g. salmonids) (Olden and Naiman 2010). Nevertheless, substantial thermal alteration in regulated rivers is known to locally decrease the range of fish assemblages like cold water fishes and influence the growth of fishes downstream of reservoirs (Vannote and Sweeney 1980, Coutant 1987, Allan 1995), impacting overall fisheries and aquatic resources (Caissie 2006). Conversely, smaller dams with little storage volumes (e.g. ROR type systems) may cause increases in downstream water temperatures by releasing warmer surface waters over weirs. The degree to which altered thermal regimes varies is therefore an important consideration when discussing the gamut of ecological responses to thermal alterations. However, conversations centered on environmental flows have yet to include mitigating thermal degradation in rivers (Olden and Naiman 2010), let alone consider specific thermal alterations stemming from different regulation practices.

Quantifying thermal regimes and thermal alteration

More recently, an increase in water temperatures is thought to be one of the main predicted changes stemming from climate change. In fact, it is expected to increase over the next 50 years, especially in higher latitudes (McCullough et al. 2009). A number of studies have also suggested that the climate in North America may lead to an increase in the frequency that water temperatures exceed suitable temperature ranges for cold water fishes (Mather et al. 2008). There have been several attempts at differentiating water temperature variations due to climate change from those due to the background of land-use impacts, including hydroelectric projects (Schindler 2001, McCullough et al. 2009). This recent research effort has demonstrated the urgent need for reliable water temperature measurements and highlighted current research challenges facing freshwater ecologists. The limited number of temperature gauging stations, especially in Canada, has been a substantial impediment to acquiring suitable thermal data (Guillemette et al. 2011). Though studies have used predictive models to estimate water temperatures at ungauged sites in Canadian rivers (Guillemette et al. 2011), a greater network of temperature gauges may better serve to elucidate the role of thermal alteration due to climate change vs. river regulation on freshwater fisheries. Furthermore, a comprehensive quantification of the thermal characteristics of rivers is needed (Caissie 2006). In fact, few studies have looked at the impacts of river regulation beyond their influence on the annual or seasonal magnitude of river thermal regimes (Arismendi et al. 2013). Using the NFP's characterization of flow regimes (Poff et al. 1997), unregulated and regulated rivers may be described according to similar components representing the magnitude, frequency, duration, timing and rate of change in water temperatures. This approach should enable more comprehensive assessments of thermal modifications arising from river regulation, as different metrics describing thermal regimes may have distinct ecological implications. Predictive models describing relationships between thermal modifications and fish responses for a given region may also constitute an important management tool.

Ecological responses to flow-temperature interactions

Variation in water temperatures in major rivers is caused by complex interactions between climate and hydrologic changes, major climate patterns, and increasing anthropogenic impacts stemming from impoundment and dam construction, among other human-related activities (Webb et al. 2008). Although dialogue on how best to define and manage environmental flows is promising, these discussions are primarily focused on water quantity without explicitly considering components of water quality such as water temperature, a fundamental ecological variable (Olden and Naiman 2010). It is widely recognised that dams impact thermal regimes and the relationship between discharge, temperature and many other water quality variables (e.g. dissolved oxygen, water pH) exists (Nilsson and Renöfält 2008). However, very few empirical studies attempt to consider hydrologic and thermal variability simultaneously, and explicitly link them to the functioning of aquatic ecosystems (Harris et al. 2000). Indeed, there is evidence that the effects of flow regulation include reduced summer water temperatures due to hypolimnetic discharge from dams and reduced frequency and duration of low flows. These may, in turn, limit opportunities for fish spawning, lower densities of potential prey sources, and possibly flush larvae and juveniles downstream, thereby affecting recruitment (Rolls et al. 2013). In this example, however, thermal regimes were considered as a function of altered flow regimes and not as independent drivers of fish community change. As such, changes in thermal regimes are inherently linked with river regulation and are confounded with changes arising from other potential sources of anthropogenic disturbances like climate change. The ecological response of thermal alteration in regulated rivers is not straightforward and conflicting results have been reported in the literature. A more comprehensive quantification of thermal regimes, akin to that done for flow regimes (i.e. flow components and indices) may provide the information needed to understand how flow and thermal regimes interact to affect fish communities, which and to what extent components of the thermal regime are changed when rivers are regulated, and how multiple anthropogenic stressors influence fish communities.

Thesis objectives

The present thesis broadly examines the relationships between fish community metrics (species diversity, density, and biomass) and environmental drivers (flow and thermal regimes) in unregulated and regulated rivers across the Canadian landscape. The metrics estimated varied according to the organismal scale examined (species composition, phylogenetic association or fish guilds based on ecological traits) and the spatial scales of both biotic and abiotic conditions analysed (sites or rivers). Results from the thesis may be used to explain and predict the effects of flow and temperature regime variability or the degree of river alteration on downstream fish communities for rivers of a same size and that share similar biotic and abiotic conditions. For each chapter, river selection was based on available data at the moment of analysis (chapter 1) or the research question at hand (chapters 2 and 3). As such, the number of rivers between thesis chapters varies, and results and interpretations obtained may only be employed within the scope or geographical context set out by each chapter.

To first establish a methodology for quantifying fish community structure across rivers, I generated site-specific species richness, density, and biomass metrics that combined measures from two commonly used surveying methods, electrofishing and visual surveys (snorkelling). Multiple paired electrofishing and visual surveys were conducted in 18 temperate Canadian rivers in order to obtain community-wide fish estimates from both methods. Site- and river-scale abiotic conditions (flow velocity, cloud cover, and water temperature) were also considered when comparing differences between surveying methods on sequential sampling dates. Results from this first chapter thus accounted for surveying biases and provided the framework for obtaining the best (greatest) species richness, density, and biomass estimates per site (fish response matrices) that underpinned all other thesis objectives.

For the second chapter, the Ecological Limits of Hydrologic Alteration framework (ELOHA; Poff et al. 2010) served to quantify hydrologic alteration scores for ecologically-relevant flow indices across 10 regulated and 14 unregulated Canadian rivers. In the absence of historical flow data, this framework proposes that unregulated rivers within a same flow class serve as the reference condition, from which observed relationships between altered hydrologic parameters and ecological responses across river systems are compared. Site-specific fish density and biomass estimates obtained in the first chapter and extended to include additional rivers were used to derive river-specific biotic alteration scores relative to unregulated river conditions. This approach not only examined the relationship between river-specific hydrologic alteration scores and the associated biotic responses across a range of regulated flow regimes, but also provided a separation between the two most distinct flow regulation types, ROR and hydro-peaking.

The objectives for the third chapter built on the previous chapter, by evaluating whether fish guilds based on different ecological traits, rather than total river biomass or density estimates, would respond more strongly to river flow and thermal regimes. Site-specific fish data measured for previous chapters were used to derive quantitative fish guilds representing morphologic, trophic, reproductive, habitat, and behavioural traits across 25 unregulated and regulated rivers. To tease apart the relative importance of each environmental driver for establishing fish communities across river regimes, I provided quantitive thermal indices based on river water temperatures and developed thermal variables akin to those described for flow regimes. By identifying the flow and thermal variables that best explained and predicted the types of fish guilds across rivers, I gained a better understanding of the dominant patterns of flow and thermal variation driving fish communities across our rivers, including those resulting from river regulation. The use of guilds in environmental assessments further ensures that predictions of fish-environmental interactions are transferable between rivers.

Alterations to river and habitat environments are highly variable geographically and among flow regulation types. The direction and severity of ecological effects are therefore dependent on these contexts, which explain why fish-environmental interaction models are only developed for a specific river or region. Collectively, these findings have important repercussions for river management. They provide comprehensive assessments of the environmental variables driving fish community responses across temperate rivers of small to intermediate size, improve the knowledge used to understand of the effects of hydroelectric dams and river regulation on fishes in these same rivers, and contribute to establishing more transferable predictions for restoring impacted rivers. More broadly, the thesis results are important given future global climate warming, its synergistic effects with other anthropogenic stressors (Schindler 2001), and ongoing scarcity for water and energy sources.

Chapter 1: A comparison of electrofishing and visual surveying methods for estimating fish community structure in temperate rivers

Photo: Snorkelling survey, Granite compensation channel, Newfoundland 2010

A comparison of electrofishing and visual surveying methods for estimating fish community structure in temperate rivers

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Abstract

Studies designed to describe fish community structure in shallow riverine environments typically rely on electrofishing and/or visual (snorkelling) surveying, but few have addressed the performances of these two methods at estimating relative fish density and biomass across wide ranges of geography, taxonomy and life history stages. Multiple paired electrofishing and visual surveys were conducted in 18 temperate Canadian rivers in order to obtain community-wide density and biomass estimates from both methods. Partial canonical multivariate analyses were computed for the paired fish community matrices comparing the results of both surveying methods at the taxonomic levels of family, genus and species, as well as size classes within families and species, to assess the particular effectiveness of each sampling method. Although electrofishing estimates of family and species richness were greater, snorkelling surveys tended to generate higher density and biomass estimates for different size classes of many salmonid and cyprinid species. Moreover, mean river biomass estimates derived from visual surveying matched those obtained from our best mean river biomass estimates arising from the two methods combined. This study provides empirical evidence that electrofishing and visual survey methods generate different types of information when assessing fish community structure at the family level or by size classes. Our results provide ample background information for determining the most reliable sampling method for quantifying a particular fish community assemblage, which is fundamental to fisheries management and research.

Keywords: sampling methods, snorkelling, fish density, biomass, species richness.

Introduction

Determining how best to quantify fish populations, be it with measures of species richness, abundance or production, is the first requirement and often the most difficult step to developing scientifically sound monitoring and management programs or population dynamic models (Meador et al. 2003, Peterson et al. 2004, Korman et al. 2009). Various methods are used to sample fish in rivers, but all ultimately provide biased representations of the true species assemblage and size composition. In particular, by altering the sampling mode (e.g. passive vs. active capture) or targeting species that differ in their ecology and life history (e.g. size class and behaviour) or preferred habitats (e.g. sandy vs. boulder substrate, moderate vs. slow water velocities and low vs. high water turbidity), relative sampling efficiencies will change and generate conflicting estimates of fish abundance (Miranda and Schramm 2008). It is therefore difficult to decide what sampling method or combination thereof should be used to conduct censuses of riverine fish populations. With anthropogenic changes occurring in freshwater systems (Vörösmarty et al. 2010), it is essential to the maintenance and/or improvement of fish populations that efforts are targeted at refining our knowledge of the advantages and limitations of different sampling methods over a wide range of river types (Korman et al. 2009).

Many ecological studies have used electrofishing and snorkelling surveys for estimating population density, species richness, growth or production of freshwater fishes in small and shallow riverine areas (i.e. < 2 m depth; Griffith 1981, Hankin and Reeves 1988, Mullner et al. 1998, Joyce and Hubert 2003). Electrofishing is particularly useful for the precise identification and measurement of individuals within a population, including cryptic species that may not be easily detected visually (Willis 2001). However, this sampling method may have low estimated efficiency for sampling density or biomass (capture efficiency), particularly for small (Reynolds

1996) and shoaling fish like some cyprinids and catostomids (Kimmel and Argent 2006), potentially leading to underestimates of overall community densities. By contrast, visual surveys of freshwater fish populations appear to be fairly reliable when compared with electrofishing provided that certain conditions (i.e. few macrophytes or emerging plants, homogeneous substrate and high water visibility) are present at the time of sampling (Helfman 1983). However, snorkelling surveys also have several shortcomings, including problems with accurate species identification, counting and estimating the size of fishes (Brock 1982). These inherent sampling biases have been quantified for some species, notably salmonids (Gardiner 1984, Joyce and Hubert 2003), but to our knowledge, no studies have yet attempted to assess sampling differences for entire fish communities across a wide range of temperate rivers.

Cunjak et al. (1988) compared abundances of juvenile Atlantic salmon (*Salmo salar*) as estimated by electrofishing and snorkelling in three rivers in eastern Canada and revealed that snorkelling counts consistently underestimated density, especially for younger and/or smaller fish which frequented shallow stream margins where underwater enumeration was difficult. Visual surveying has also been found to underestimate several other salmonids (1+ coho salmon (*Oncorhynchus kisutch*), steelhead trout (*Oncorhynchus mykiss*), bull (*Salvelinus malma*), cutthroat (*Oncorhynchus clarkii*), rainbow (*Oncorhynchus mykiss*), brown (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) relative to electrofishing, although estimates from both methods are generally well correlated ($r > 0.90$; Hankin and Reeves 1988, Wildman and Neumann 2003, Thurow et al. 2006). Despite the differences in abundance estimates, length-frequency distributions obtained by either method are fairly similar (Wildman and Neumann 2003). In addition to demonstrating sampling differences among various salmonid species across selected rivers, these studies, like many others, generally compare fish abundance and/or diversity counts, rather than deriving biomass estimates between surveying methods.

The apparent consensus in the literature is that sampling biases are influenced by a number of factors, from the composition of the fish community (species, individual size, and behaviour), to environmental descriptors (water temperature, visibility, and weather) that characterize the sampling site and time (Gardiner 1984, Reynolds 1996, Meador et al. 2003, Korman et al. 2009). Most authors suggested the need for more comprehensive evaluations of the relative performance of these sampling methods for a wider range of species, river, and habitat type. In an attempt to address these knowledge gaps, the objectives of this study are: 1) to evaluate the performances of electrofishing and snorkelling methods for estimating relative fish community richness, density, and biomass in selected systems; and 2) establish background information guiding the choice of the most suitable sampling method for the inventory of fish populations essential for fisheries management and research. This study is intended to provide information that will facilitate standardized comparisons among studies employing similar methodologies.

Materials and methods

Study sites

Eighteen small to intermediate rivers (wetted river width ranging from 17 to 116 m) comprising four in Alberta, five in Ontario, six in Québec and three in New Brunswick were selected based on sampling feasibility and river accessibility (Figure 1). Specifically, sampling was based on the ability to survey wadeable stretches of river across the entire wetted width and road access (> 2 access points to the river). Between 25 and 50 relatively homogeneous sampling sites, measuring on average 299 ± 7.49 m² (5.08 m ± 0.44 m × 59.19 m ± 3.59 m, mean ± SD;

width × length) were surveyed per river, for a total of 663 sites. Sampling sites broadly represented a uniform habitat type, which was visually assessed and categorized into run, riffle or pool according to Jowett (1993). Sampling sites were spread along 10-15 km river segments, with a 60-m minimum buffer between sites to ensure that fish would not be displaced as a result of our sampling efforts, thus ensuring that sites were independent from one another. The position of the first sampling site on a river segment was randomly selected prior to field surveying, either on the left or right shores or the middle stretch, and subsequent sites were positioned following a systematic design (i.e. left shore, middle, right shore, left shore). The middle stretch was determined by taking the mid-point of the wetted river width.

Sampling protocol

Field work was carried out during summer months (late June to late August) in 2011 and 2012. Paired single-pass electrofishing and snorkelling surveys were conducted at each site, for a total of 1326 surveys (two surveys per site). Paired single-pass electrofishing and snorkelling surveys were carried out at each site, in random order and at roughly the same time between 09:00 and 17:00 on consecutive days, with a minimum 24-hr recovery interval to allow fish to re-establish themselves after a surveying event. The single-pass electrofishing approach has been shown to effectively sample fish abundance (Edwards et al. 2003) and allowed for a greater survey area covered in each of the 18 rivers. To increase the accuracy of species identification and length estimation under water for electrofishing and snorkelling methods, surveyors were trained in the field full-time for a month prior to data collection. To further decrease the incidence of surveyor bias, only those surveyors that successfully identified and estimated fishes in underwater training sessions were allowed to conduct snorkelling surveys. Surveyor differences among snorkelling or electrofishing teams were, however, not evaluated in this study.

Electrofishing surveys were administered in accordance to Ontario Ministry of Natural Resources (OMNR; Jones 2011) policy standards using a Smith-Root LR-24 backpack electrofishing unit (Smith-Root®, Vancouver, WA). An electrofishing operator, flanked by two assistants who collected stunned fish into Smith-Root® trapezoid dipnets (4” wide back, 14” wide x 17” long and 8” deep and of ¼” mesh size), proceeded at a rate of 3 s/m² in an upstream zigzag fashion, covering an effective sampling zone of approximately 300 m². Electrofishing parameters such as voltage, frequency for sampling whole fish communities and shocking seconds were adjusted in function of water conductivity to produce a constant average power of 200 W, of 60 Hz, and over a mean time of 913.26 ± 74.61 shocking seconds. Setting constant parameters ensured that sampling effort was standardized across electrofishing sampling events as well as between electrofishing teams (four teams in total). Captured fish were identified to species and their lengths (total body length, ±0.1 cm) and masses (wet blotted weight, ± 0.1g) were measured after completion of electrofishing at a given site. Fish were then allowed to recover from handling stress and released back to their place of capture. Visual surveys were conducted using two divers swimming upstream in a slow (6 s/m²), zigzag-like fashion (Cunjak et al. 1988), along 60 m marked transects (2.5 m width each), covering approximately 300 m², over an average of 1920 ± 314.4 s. Fish species identification and total length were recorded *in-situ* in 5-cm class increments.

Physical variables

At the end of individual visual and electrofishing surveys, the physical variables of each site were estimated: (i) flow velocity (m/s), taken at 40% of the total water depth and (ii) depth (cm) were measured with a Marsh-McBirney Flo-Mate 2000 flow meter and wading rod (Hach Company, Loveland, CO, USA); (iii) water temperature (°C) was measured with YSI Model 30 handheld conductivity meter (YSI inc., Yellow Springs, OH, USA); (iv) and proportion cloud cover was assessed visually as the percentage of clouds occupying the sky at the time of the survey. These physical descriptors may have differed between paired electrofishing and visual surveys because the surveys were conducted on different days. Water temperature and cloud cover were measured once by site and survey, whereas mean flow velocities and depths were determined 10 times by site and survey (randomly dispersed throughout each site). All of these variables were retained for analysis for the purpose of removing their confounding effect on the observed differences between surveying methods. Other site variables were measured for each site, but were not included in this study because 1) habitat specific variables (e.g. vegetation and substrate cover) did not differ within our 24 hour sampling period and 2) our study aims at comparing fish community estimates between sampling methods across 18 rivers, rather than assessing which environmental variables best predict overall fish communities. Furthermore, weather conditions such as heavy rainfall were considered when choosing survey times. For example, more time between surveying events was given for rivers that suddenly increased in flows and were more turbid due to rainfall, allowing affected rivers to regain pre-rainfall conditions. As such, water turbidity and flow conditions reflected average summer conditions for a given river and deemed similar between surveying events. Conductivity measurements adjusted for water temperature were also taken for each site using an YSI handheld conductivity meter (YSI inc., Yellow Springs, OH, USA).

Fish matrices

Species richness was tabulated by counting the number of different species represented in a site. Density estimates were determined as the total number of each species observed for each site of 300 m² multiplied by 100 (i.e. the number of a given species/100 m²), while species biomass estimates were calculated by adding individually measured fish masses for species at any given site multiplied by 100 (i.e. the total mass in grams for a given species/100 m²). Mass-length relationships derived from electrofishing data were calculated for each species per river and used to estimate mass from length for all fish recorded during visual surveys (Le Cren 1951). The sampling design (i.e. single-pass electrofishing without block nets or visual surveys in open sites) was not suitable for ascertaining absolute species density and biomass estimates for each site sampled; therefore, all values presented herein represent relative site estimates. Additionally, taxon occurrence (*N*) refers to the number of sites where a given family, species or species-by-size-class was observed with either sampling method, removing the cases of non-occurrences. Total densities and biomasses for a given species were categorized by 5-cm size classes (i.e. 1: 0-5 cm, 2: 5-10 cm, 3: 10-15 cm, 4: 15-20 cm, and 5: 20-25 cm), thus creating species-by-size-class density and biomass matrices, for both surveying methods. Densities and biomasses for each species were therefore merged into 5-cm size class increments to provide the information required for assessing sampling differences, from small to larger fish, inter-, and intra-specifically.

Statistical analyses

Wilcoxon matched-pairs signed-rank tests were computed on tabulated species richness to test whether these scores differed significantly between sampling methods across sites. The richness scores were calculated using all 55 species observed in the 663 sites.

Fish density and biomass data from paired surveys were compiled for each of 15 fish families, the 27 most prevalent species (species present in all rivers), and 101 species-by-size-class combinations across all sites, resulting in 12 fish community matrices (i.e. three taxonomic levels for densities and three for biomasses; six matrices per surveying method). The fish data were Hellinger transformed, which consists of expressing the density or biomass data as relative values per site and taking the square root of these values (Legendre and Gallagher 2001). This data transformation meant that subsequent analyses were not affected by double zeros and a more meaningful analysis is obtained because "no ecological conclusion can be drawn from the simultaneous absence of a species at two sites" or in our case, at one site using two surveying methods (Legendre and Legendre 2012 section 7.2.2). Forward selection of physical variables (standardized survey means for flow velocity, water depth, water temperature, and cloud cover) was conducted using redundancy analysis (RDA) to select the best explanatory variables for the model describing each fish community matrix (packfor package in R, Blanchet et al. 2008, Dray et al. 2011).

Partial canonical multivariate analyses of variance, conducted for related samples using partial redundancy analyses (pRDA: Legendre and Legendre 2012 section 11.1.10), were performed on each fish community matrices (e.g. family biomass estimates for electrofishing vs. visual surveying) to assess the effect of sampling method, while controlling for the effects of selected physical variables and paired surveys per site (i.e. the fact that each site had been sampled twice). For each significant multivariate pRDA, univariate family-, species-, and species-by-size-class specific pRDA were conducted and corrected for multiple testing using the Hochberg correction (Hochberg 1988). Univariate pRDA enabled the identification of which densities or biomasses significantly differed between sampling methods, for the various taxa.

Cumulative fit R^2 were also calculated using the *goodness* function from the multivariate pRDA for each taxon: families, species, and species-by-size-classes (vegan package, Oksanen et al. 2011, Legendre and Legendre 2012 section 9.3). Taxa with cumulative fit R^2 values above community average were considered as being well explained by the multivariate model, and therefore as being differently sampled by the two sampling methods. Taxa with cumulative fit values above community average are displayed as the proportion of the cumulative fit value of a particular taxon over the sum total of all cumulative fit values for all taxa. Odds ratios, which are descriptive statistics used to denote the strength of the difference between surveying estimates, were also calculated for significantly different density and biomass estimates from each surveying method. All tests of significance for pRDA analyses were conducted using permutation tests involving 9999 permutations of the residuals under the reduced model using the function *anova.cca* of the vegan package (Oksanen et al. 2011).

Our "best species biomass matrix" was derived by selecting the largest estimate obtained when comparing electrofishing and snorkelling surveys at each site; these estimates were then averaged by river (number of rivers = 18). Similarly, total fish biomasses averaged by river were calculated for electrofishing and visual surveys, respectively, and a linear relationship between each of our sampling methods and our best possible outcome was drawn. Model II regressions were computed to compare our "best mean river biomass estimates" to those obtained from electrofishing and visual surveys (Legendre and Legendre 2012, section 10.3.2). We used function lmodel2 to compute model II simple linear regressions using the major axis method (MA), as well as parametric 95% confidence intervals for the slope and intercept parameters, which were used to determine whether model slopes and intercepts differed significantly from a 1:1 slope and a 0 intercept, respectively (lmodel2 package Legendre 2011) in (R version 2.13.2, R Development Core Team 2014).

Results

On average, rivers were 45 m wide, of low water velocity (0.36 m/s), shallow depth (39.70 cm), warm water temperature (18.5 °C), moderate cloud cover (42%) and elevated temperature-adjusted conductivity (148.14 µS/m; Table 1). None of the physical variables met the assumptions of normality before or after transformation, therefore careful consideration of each of these variables and their impact on predicting the distribution of fishes for each of the models was conducted prior to carrying out the analyses described in the next paragraph.

Surveying differences for estimating community structure

Across all 663 sites, species richness differed significantly between sampling methods (Wilcoxon signed rank test: $p < 0.001$), with average species richness for electrofishing sampling greater (mean = 3.67, range = 0-12 species per site) than for visual surveying (mean = 3.37, range = 0-12 species per site). Of the 55 species recorded, 48 were observed using snorkelling while all but *Hybognathus regius* were counted during electrofishing. Species nearly or completely absent from visual surveys included: *Anguilla rostrata*, *Ameiurus nebulosus*, *Umbra limi*, *Esox masquinongy*, *Ichthyomyzon fossor*, *Petromyzon marinus*, *Moxostoma macrolepidotum*, *Lota lota,* and *Lethenteron appendix*.

All physical variables (water velocity, depth, water temperature and cloud cover; Table 1) were deemed significant (in all tests, $p \leq 0.005$) and retained by forward selection for all 12 fish community matrices. There was a significant difference in family densities and biomasses between electrofishing and visual surveys (multivariate pRDA tests, $p < 0.005$). Density and biomass estimates for Percopsidae, Cottidae, Umbridae, Lottidae, Anguillidae, and Petromyzontidae were significantly greater for electrofishing suveys, while the reverse was true for Salmonidae (univariate pRDA tests with Hochberg correction, $p \leq 0.05$, Figure 2). Gasterosteid snorkelling density and biomass were between 3.0 and 6.5 times greater than electrofishing estimates (univariate pRDA tests with Hochberg correction, $p = 0.06$ and $p = 0.058$ respectively). Cumulative fit values for density or biomass estimates echoed these results, with Cottidae (29.25%), Umbridae (7.09%), Lottidae (13.01%), Anguillidae (8.80%), and Petromyzontidae (20.25%), each contributing more than community average to the global model (cumulative fit values for biomass estimates displayed and illustrated by shaded bars in Figure 2). Density and biomass differences occuring for these families therefore explained the greatest cumulative proportion of variation between the two sampling methods.

For 16 of the 27 more prevalent species listed in Table 2, significant differences for species densities and/or biomasses were found between electrofishing and visual surveys (multivariate pRDA tests, $p < 0.005$ and univariate pRDA with Hochberg correction, $p < 0.05$, Figure 3). The salmonids *S. salar*, *Prosopium williamsoni* and *Oncorhynchus spp.,* and several cyprinid shoaling species, namely *Luxilus cornutus, Semotilus corporalis, Rhinichthys atratulus,* and *Exoglossum maxillingua*, were found to have over 1.5 times greater visual density estimates for salmonids or a 2 to 10-fold increase in snorkelling density estimates for cyprinids. Electrofishing density estimates were at least 1.5 times greater than visual estimates for cryptic species like *L. lota*, *Etheostoma spp.*, *Cottus spp.,* and *Percopsis omiscomaycus,* in addition to *S. trutta, Ambloplites rupestris* and *Rhinichthys cataractae*. Of these species, *P. williamsoni* (9.29%), *R. cataractae* (15.05%), *Cottus spp.* (18.59%) and *L. cornutus* (8.46%) had the greatest cumulative fit values derived from both density and biomass species matrices (cumulative fit values for density estimates displayed and illustrated by shaded bars in Figure 3). Likewise, biomass estimates were significantly different between sampling methods for all the same species in addition to *S. fontinalis* (univariate pRDA tests with Hochberg correction, $p < 0.05$), save for *S. trutta* ($p = 0.075$).

Thus far, all size classes were merged to give total family and species averages for electrofishing and visual surveys. Consistent with previous family- and species-level results, there was a significant difference in species by size-class densities and biomasses between electrofishing and visual surveys for sculpins, several salmonid and cyprinid species by 5 cm size increments (multivariate pRDA tests, $p < 0.005$). For example, juvenile *S. salar* (1: 0-5 cm, 2: 5-10 cm) had approximately 1.5 to 4 times greater visual relative density and biomass estimates, respectively, than electrofishing surveys (univariate pRDA tests, $p < 0.008$), while the reverse was true for relative density estimates for juvenile *S. trutta* of 5-10 cm (univariate pRDA tests, $p = 0.03$, Figure 4). Likewise, smaller *R. cataractae* (2: 5-10 cm) had between 2 and 3 times higher density and biomass estimates for electrofishing surveys (univariate pRDA tests, $p = 0.008$), while juvenile *R. atratulus* (1: 0-5 cm and 2: 5-10 cm), *L. cornutus* (1: 0-5 cm, 2: 5-10 cm and 3: 10-15 cm), *Nocomis biguttatus* (1: 0-5 cm) and *S. corporalis* (1: 0-5 cm and 3: 10-15 cm) all had greater density and biomass estimates for visual sampling (univariate pRDA tests, $p < 0.008$, Figure 5). Snorkelling yielded overall greater density and biomass estimates for larger salmonid species and for adults, save for the trout species *Salvelinus malma* and *S. trutta*, which revealed greater densities and biomasses across size classes for electrofishing surveys and larger *S. salar* and *S. fontinalis* individuals, which showed similar sampling outcomes. Not only were snorkelling biomass and density estimates at least 1.5 times greater for larger cyprinids (*S. corporalis*, *L. cornutus*, *E. maxillingua* and *S. atromaculatus* of 3: 10-15 cm and

4: 15-20 cm size classes), certain size classes (*S. corporalis* of 10-15 and 15- 20 cm and *L. cornutus* of 10-15 cm) were totally unrepresented in electrofishing surveys. Cumulative fit values greater than the community average for both biomasses and densities were seen for *Cottus spp.* measuring between 5-10 cm (30.41%), *L. cornutus* of 0-5 cm (16.79%), and 10-15 cm (9.26%), *R. cataractae* of 5-10 cm (25.25%), and *R. atratulus* of 0-5 cm (19.72%) (cumulative fit values for density estimates displayed and illustrated by shaded bars in Figure 5).

Inter-river sampling differences

The “best mean river biomass estimates” obtained from combining the snorkelling and electrofishing survey data were regressed against mean biomass estimates calculated from visual or electrofishing surveys. Type II regressions quantifying the relationship between our “best mean river biomass estimates” and those derived from visual ($r = 0.98$, slope = 1.09, intercept = 0.27, two-tailed $p < 0.001$; Figure 6A) or electrofishing surveys ($r = 0.68$, slope = 4.69, intercept = -1.11, two-tailed $p = 0.002$; Figure 6B) were significant. The slope derived from the regression between our “best mean river biomass estimates” in relation to those from visual sampling was not significantly different from a slope of 1, but the intercept significantly differed from the origin of 0, indicating that mean estimates obtained through snorkelling closely approximated “best mean river biomass estimates”. The slope and intercept obtained when regressing “best mean river biomass estimates” against mean river biomass estimates for electrofishing were significantly different from the 1:1 relationship. Biomass estimates derived from electrofishing were more variable than those from the snorkelling surveys, as indicated by the lower correlation coefficient.

Discussion

Our results quantify the respective performances of electrofishing and snorkelling methods for estimating fish species richness, as well as population densities and biomasses for each family, species, and selected species and size classes sampled across several Canadian rivers. When attempting to quantify species richness of sampling sites, electrofishing yields superior results relative to visual surveys. In particular, all species but *Hybognathus regius* were detected in electrofishing surveys, while species characterized by behavioural or cryptic colouration were nearly or totally absent from visual surveys. In fact, significantly different estimates of densities and biomasses between sampling methods were found for known cryptic families, including the Cottidae, Lottidae, Anguillidae, and Petromyzontidae. These results support earlier studies that found visual surveying to significantly underestimate cryptic fish densities (Willis 2001). Species like *A. rostrata*, *L. lota,* and all lamprey species, especially larval or ammocete life history stages, typically shelter under boulders, inhabit crevices or burrow into the soft muddy or sandy stream bottoms (Scott and Crossman 1973, Bernatchez and Giroux 2000). *A. nebulosus*, *U. limi,* and Cottidae species are relatively small species, coloured to blend in well with surrounding substrate and vegetation, ostensibly negatively biasing visual surveys. Likewise, *R. cataractae* had significantly higher density and biomass estimates in electrofishing surveys, likely resulting from this species' tendency to shelter under gravel and cobble substrate, thereby limiting their detection when snorkelling.

While sampling via electrofishing may be favoured for assessing overall fish community richness and/or detecting the presence of elusive or incidental species, visual surveying is significantly more efficient at estimating densities and biomasses of salmonid and gasterosteid, and to a lesser extent, centrarchid and esocid families. Salmonid species such as *S. salar*, *P.*

williamsoni, *O. mykiss,* and *Oncorhynchus* hybrids (rainbow and cutthroat trout hybrids) were best assessed in snorkelling surveys, despite earlier findings suggesting that fish with fine scales, as is the case with salmonids, tend to be more easily detected by electrofishing than fish with coarse scales (e.g. cyprinids; Meador et al. 2003). These authors suggested that coarser scales offer more protection from galvanotaxis than finer scales, which implies that electrofishing surveys are inefficient at collecting cyprinid species and better suited for salmonids within a site. However, in our study, salmonid species such as *S. salar*, *P. williamsoni*, *O. mykiss,* and *Oncorhynchus* hybrids were best sampled with snorkelling surveys. Our results are thus more aligned with the findings of Heimbuch et al. (1997), who showed that salmonids, centrachids, and some cyprinids may be able to detect and avoid the electrical field outside of the effective shocking radius (approximately 1 m radius). Such was also the case in the present dataset for *P. williamsoni*, *M. dolomieui, A. rupestris* ranging 0-10 cm, *E. lucius, S. corporalis*, *E. maxillingua*, *L. cornutus* and, *R. atratulus*. All these species save for *P. williamsoni*, which occasionally school in deeper runs, are solitary and conspicuously occupy the water column, also facilitating their enumeration in underwater visual surveying. Furthermore, schooling fishes like juvenile gasterosteids and shoals of small to intermediate-sized catostomids and cyprinids, like *R. atratulus* (0-5 and 5-10 cm size classes), *L. cornutus* (0-5, 5-10 and 10-15 cm), and *S. corporalis* (0-5 and 5-10 cm) are often found in vegetated habitats along the shallow banks of rivers, which would normally suggest that detection while snorkelling would be impaired and lower density estimates generated. However, when combined with the fact that smaller fish have a higher chance of escaping electrofishing dipnets and appropriate time was accorded to visually assess high densities of fishes, it is not surprising that visual density estimates for these smaller size classes are close to double those obtained via electrofishing.

When evaluating differences between electrofishing and visual surveys for certain species over a range of size classes, sampling method outcomes are more variable. In this study, density and biomass estimates of juvenile *S. salar* life stages ranging approximately from 0 to 10 cm in total length are significantly greater for visual surveys than for electrofishing estimates, but when *S. salar* measuring between 10 and 20 cm are sampled, both sampling methods yield similar density and biomass estimates. These findings contradict those of Cunjak et al. (1988), who found that snorkelling provided significantly lower juvenile salmonid densities. Though not supported for *S. salar* fry and parr life stages in this study, higher estimates were generated via electrofishing relative to snorkelling surveys of *S. trutta*, *S. fontinalis*, *S. malma*, in keeping with earlier studies (Wildman and Neumann 2003, Thurow et al. 2006). Our results suggest that *P. williamsoni*, *O. mykiss,* and *Oncorhynchus* hybrids are best sampled via snorkelling survey and this observation holds especially true for the largest individuals sampled in this dataset (size range from 10 to 25 cm). These observations oppose previous assertions that electrofishing often yields samples that overrepresented large fish and underrepresented small fish (Mullner et al. 1998). Rather, it is our opinion that discrepancies in estimates for larger individuals between snorkelling and electrofishing surveys arise from: 1) avoidance of the electrical field from outside the shock radius and 2) specific habitat preferences for deeper pools or fast flowing runs, which limit the range of application of backpack electrofishing.

The relationships between the mean relative biomass variations for our “best mean river biomass estimates” with those obtained from visual or electrofishing surveys, show that snorkelling estimates most closely resemble our “best mean river biomass estimates”, while those derived from electrofishing surveys are more variable. Because large shoals of juvenile fish and bigger individuals account for the greatest portion of relative biomass estimates for any given site or river, we suggest that snorkelling surveys may best capture biomass estimates for a river and should be the preferred choice, should one want to estimate fish production within a particular river. Electrofishing may also be more variable because it is more dependent on site physical conditions that vary between rivers (i.e. water depth and conductivity), which may limit electrofishing sampling efficiency, especially for detecting large individuals. Further research on the relationship between electrofishing surveying estimates and local and river-scale physical conditions may explain some of the variability observed in our study. Likewise, geographic variation in method performance may constitute an important consideration for future studies, especially when water conductivity moderates electrofishing outputs and is shown to vary substantially between rivers.

These results provide the data and analysis needed for informing future research and management practices. For example, our study reveals that for larger salmonids, *P. williamsoni*, *O. mykiss,* and *Oncorhynchus* hybrids, snorkelling surveys yield higher estimates, while certain families and/or species surveyed exhibiting cryptic colouration or behaviour (e.g., Cottidae species, *A. rostrata*, *L. lota*, *A. nebulosus,* and *U. limi*) are best sampled via electrofishing methods. As such, the largest estimates obtained across taxa may guide the choice of surveying method. With the information generated from each surveying method, recommendations may be inferred, but prescribing a comprehensive guiding framework is more complex as it is contingent on the particular objectives and limitations (e.g. logistical constraints, habitat conditions) set out by the study.

Certain training and/or operational costs may limit the scope of a study. In particular, substantial training to meet certification requirements and greater resources (i.e. personalized gear and time and money spent transporting gear) allocated for personnel conducting electrofishing surveys will often result in a fewer number of sites or rivers covered during the survey. Conversely, visual surveying is generally considered low-cost and does not harm fish, but requires that snorkelers be properly trained for correct species identification and accurate size estimation for a given river. Although challenging, our experience is that proper training is possible, thus providing us with a reliable, non-invasive census of the fish community sampled per river.

This study is unique in that it compared electrofishing and snorkelling surveying methods for the estimation fish species richness, density, and biomass across a wide range of temperate rivers in Canada. By controlling for the effects of experimental and abiotic factors, electrofishing and snorkelling fish estimates were directly compared and displayed in such a way that one may select the most suitable sampling method for estimating specific families, species and size classes in selected systems. Of particular interest is the reliability of snorkelling surveying methods for generating reliable fish biomass estimates, proxies that may inform river fish production, which is fundamental to fisheries management and research.

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work reported herein was conducted in accordance with the guidelines of the University of Montreal CDEA permit number for 2011 (CDEA 11-072) and 2012 (CDEA 12-063) and was approved by Alberta Tourism, Parks and Recreation (scientific fishing permit # 11-108, #11-0215FR and #12-2669FR), Ministère des Resources Naturelles et de la Faune (scientific fishing permits # 2011-06-07-005-S-P and 2012-06-01-003-00-S-P), Fisheries and Oceans Canada (scientific licence # SG-NBT-12-091), the Ontario Ministry of Natural Resources (scientific fishing permit # 106837) and permission from Ontario Parks.

Table 1. Environmental river attributes and mean physical variables listed by river and sampling method (E: Electrofishing, V: Visual). Rivers are grouped by province and numbers in brackets refer to the number of sites sampled in each river. Adjusted conductivity is corrected for water temperature.

River (no sites)	Latitude	Longitude	Mean wetted width (m)	Mean adjusted conductivity (µS)	Mean flow velocities (m/s)		Mean water depth (cm)		Mean water temperature (°C)		Mean cloud cover (% coverage)	
					E	V	E	V	E	V	E	V
Castle (42)	49.527	-114.0397	46.39	237.71	0.56	0.52	40.51	38.58	14.62	17.39	32.00	27.75
Waterton (47)	49.39543	-113.62527	41.29	188.02	0.37	0.37	40.71	40.31	13.47	15.79	29.22	19.84
Elbow (46)	51.001544	-114.4984	35.3	377.5	0.59	0.57	36.91	37.21	9.08	11.22	33.98	24.51
Kananaskis (47)	50.895217	-115.151383	25.47	333.08	0.38	0.37	33.32	31.91	8.72	10.53	27.5	25.33
Magpie (30)	47.98803	-84.79094	45.5	118.75	0.31	0.33	41.17	39.81	18.84	18.47	57.73	51.3
Batchawana (43)	47.03394	-84.48171	50.34	145.25	0.37	0.37	45.77	45.43	21.02	21.28	53.93	49.64
Goulais (30)	46.74951	-84.07173	35.8	65.4	0.12	0.12	41.68	40.48	21.71	22.5	54.84	50.63
Aubinadong (40)	46.91232	-83.43875	40.8	208.57	0.34	0.33	46.48	47.83	22.5	21.69	48.1	53.5
Mississagi (36)	46.87428	-83.33037	89.89	170.52	0.22	0.22	40.99	43.55	21.07	20.96	44.24	43.68
Sainte-Anne (30)	46.66526	-72.11772	116.12	55.41	0.23	0.26	40.13	39.94	22.47	23.35	60.83	51,00
Saint-Jean (49)	48.230617	-70.220283	31.08	152.24	0.54	0.57	44.88	48.24	18.48	18.51	56.53	43.57
Petit Saguenay (25)	48.197667	-70.058167	33.54	129.74	0.43	0.43	49.86	50.81	19.99	19.95	33.13	65.21
Etchemin (40)	46.67858	-71.07941	81.51	139.86	0.29	0.26	37.68	35.77	23.67	23.26	35.75	18.75
Bécancour (50)	46.24103	-71.49765	37.24	156,00	0.27	0.26	48.06	45.54	22.6	21.78	44.2	38.1
Au Saumon (50)	45.62213	-71.39175	54.95	91.25	0.25	0.24	33.11	34.34	21.4	21.39	53.8	54.1
Dee (30)	47.12905	-67.00243	14.33	25.93	0.5	0.45	33.08	31.8	18.89	19.89	51.67	44.83
Serpentine (30)	47.20297	-66.82289	20.43	26.6	0.37	0.37	28.36	28.03	17.02	18.1	38.00	24.52
Gulquac (30)	46.95862	-67.15582	16.8	44.66	0.43	0.36	32.4	33.22	16.41	17.8	35.17	50.67

Table 2. Prevalent species listed by province and river of provenance. QC: Québec, ON: Ontario, NB: New Brunswick and AB: Alberta.

Species	**Provenance (province and rivers)**	
Atlantic salmon *Salmo salar* L., 1756	QC, NB	St Jean, Petit Saguenay, Dee, Serpentine, Gulquac
Blacknose dace *Rhinichthys atratulus* (Hermann, 1804)	QC, ON, NB	Au Saumon, Bécancour, Etchemin, Petit Saguenay, St Jean, Batchawana, Goulais, Magpie, Aubinadong, Serpentine, Dee, Gulquac,
Bluntnose minnow *Pimephales notatus* (Rafinesque, 1820)	QC, ON	Au Saumon, Bécancour, Goulais, Mississagi, Aubinadong
Brook stickleback *Culaea inconstans*(Kirtland, 1840)	QC, ON, NB	Etchemnin, Batchawana, Goulais, Magpie, Gulquac
Brook trout *Salvelinus fontinalis* (Mitchill, 1814)	QC, ON, NB, AB	Au Saumon, Bécancour, Etchemin, Petit Saguenay, St Jean, Batchawana, Goulais, Magpie, Mississagi, Aubinadong, Serpentine, Dee, Gulquac, Elbow, Kananaskis
Brown trout *Salmo trutta* L., 1758	AB	Castle, Waterton, Kananaksis, Elbow
Bull trout *Salvelinus malma* (Walbaum, 1792)	AB	Castle, Waterton, Kananaksis, Elbow
Burbot *Lota lota* (Linnaeus, 1758)	QC, ON, AB	Au Saumon, Goulais, Magpie, Mississagi, Aubinadong, Waterton, Castle
Common shiner *Luxilus cornutus*(Mitchill, 1817)	QC, ON, NB	Au Saumon, Bécancour, Etchemin, St- Anne, Goulais, Mississagi, Aubinadong, Batchawana, Dee, Gulquac
Creek chub *Semolitus atromaculatus*(Mitchill, 1818)	QC, ON, NB	Au Saumon, Bécancour, Etchemin, Petit Saguenay, St- Jean, St- Anne, Aubinadong, Batchawana, Mississagi, Goulais, Dee, Serpentine, Gulquac
Cutlips minnow *Exoglossum maxillingua*(Lesueur, 1817)	QC	Bécancour, Etchemin, St- Anne
Darter spp. (Tessellated, Johnny darters) *Etheostoma spp.(*Rafinesque, 1820)	QC, ON	Au Saumon, St- Anne, Goulais
Fallfish *Semotilus corporalis*(Mitchill, 1817)	QC, NB	Au Saumon, Bécancour, Petit Sagunenay, St- Jean, St- Anne, Etchemin, Dee, Gulquac
Fantail darter *Etheostoma flabellare* Rafinesque, 1819	QC	St- Anne, Bécancour
Lake chub *Couesius plumbeus*(Agassiz, 1850)	QC, ON, NB, AB	Au Saumon, Batchawana, Magpie, Mississagi, Aubinadong, Serpentine, Dee, Gulquac, Waterton
Logperch *Percina caprodes* (Rafinesque, 1818)	QC, ON	Au Saumon, Bécancour, Etchemin, St- Anne, Batchawana, Goulais, Magpie
Longnose dace *Rhinichthys cataractae* (Valenciennes, 1842)	QC, ON, AB	Au Saumon, Bécancour, Etchemin, Petit Saguenay, St- Jean, St- Anne, Aubinadong, Batchawana, Mississagi, Goulais, Magpie, Elbow, Waterton, Castle, Kananaskis
Mountain whitefish *Prosopium williamsoni* (Girard, 1856)	AB	Castle, Waterton, Kananaksis, Elbow
Northern pike *Esox lucius* L., 1758	QC, ON	Au Saumon, Bécancour, Mississagi, Magpie, Aubinadong
Rainbow trout *Onchorynchus mykiss* (Walbaum, 1792)	ON, AB	Batchawana, Castle, Waterton, Kananaksis, Elbow
Rainbow-Cutthroat hybrid (raincut) *Onchorynchus spp.* (Richardson, 1836)	AB	Castle, Waterton
Rock bass *Ambloplites rupestris* (Rafinesque, 1817)	QC, ON	Au Saumon, Bécancour, St- Anne, Goulais, Mississagi, Aubinadong
Sculpin spp. (Slimy and Mottled sculpins) *Cottus spp.* (Girard,1850)	QC, ON, NB	Bécancour, Aubinadong, Batchawana, Goulais, Mississagi, Magpie, Dee, Gulquac, Serpentine
Smallmouth bass *Micropterus dolomieu* Lacepède, 1802	QC, ON	Au Saumon, St- Anne, Bécancour, Goulais, Mississagi, Aubinadong
Sucker spp. (Longnose, White and Mountain suckers) *Catostomus spp.* Lesueur, 1817	QC, ON, NB, AB	Au Saumon, Bécancour, Etchemin, Petit Saguenay, St- Jean, St- Anne, Batchawana, Aubinadong, Mississagi, Goulais, Magpie, Dee, Gulquac, Serpentine, Castle, Waterton
Threespine stickleback *Gasterosteus aculeatus* L., 1758	QC, NB	St- Jean, Dee, Gulquac, Serpentine
Trout-perch *Percopsis omiscomaycus* (Walbaum, 1792)	QC, ON, AB	St- Anne, Aubinadong, Batchawana, Goulais, Magpie, Mississagi, Castle, Waterton

Figure 1. Map of Canada displaying the 18 rivers studied, grouped by province (A). Alberta (inset B): Castle, Waterton, Elbow and Kananaskis Rivers; Ontario (inset C): Magpie, Goulais, Batchawana, Aubinadong and Mississagi Rivers; Québec (inset D): Sainte-Anne, Etchemin, Bécancour, Au Saumon, Saint-Jean and Petit Saguenay Rivers; New Brunswick (inset D): Dee, Gulquac and Serpentine Rivers.

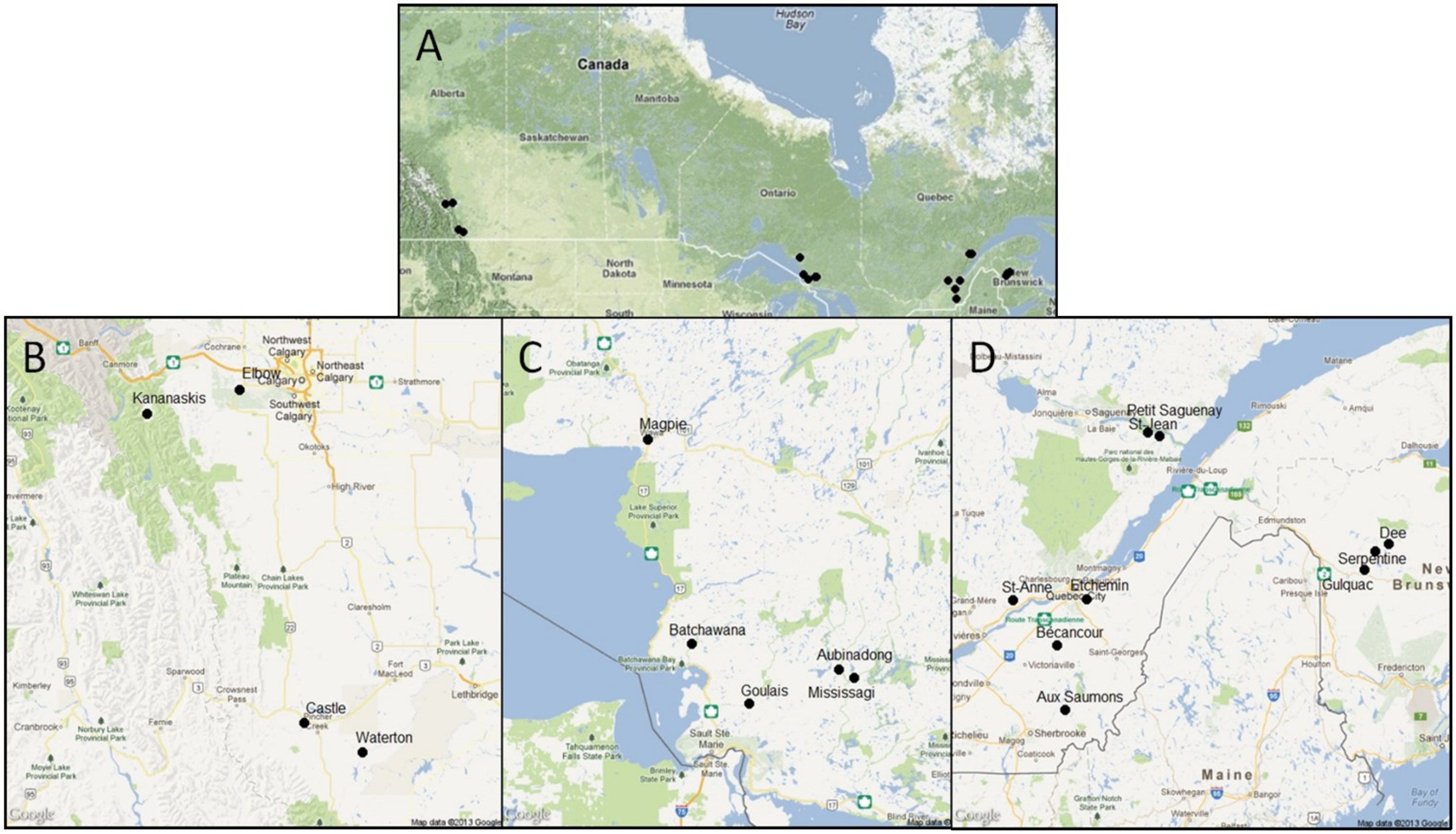

A
Canada
Hudson Bay
Alberta
Manitoba
Saskatchewan
Ontario
Quebec
Montana
North Dakota
Minnesota
New Brunswick
Maine
B
Elbow
Kananaskis
Castle
Waterton
C
Magpie
Batchawana
Aubinadong
Goulais
Mississagi
D
Petit Saguenay
St-Jean
Dee
Serpentine
Gulquac
St-Anne
Etchemin
Becancour
Aux Saumons
Maine
New Brunsw

Figure 2. Median relative family density (A) and biomass (B) estimates per 100 m² (abscissa), for electrofishing and visual sampling methods. Shaded bars indicate the families that are well explained by the global model and differ notably between the two sampling methods (cumulative fit for families). *N*: taxon occurrence *: pRDA tests with Hochberg correction, $p \leq 0.05$ between sampling methods.

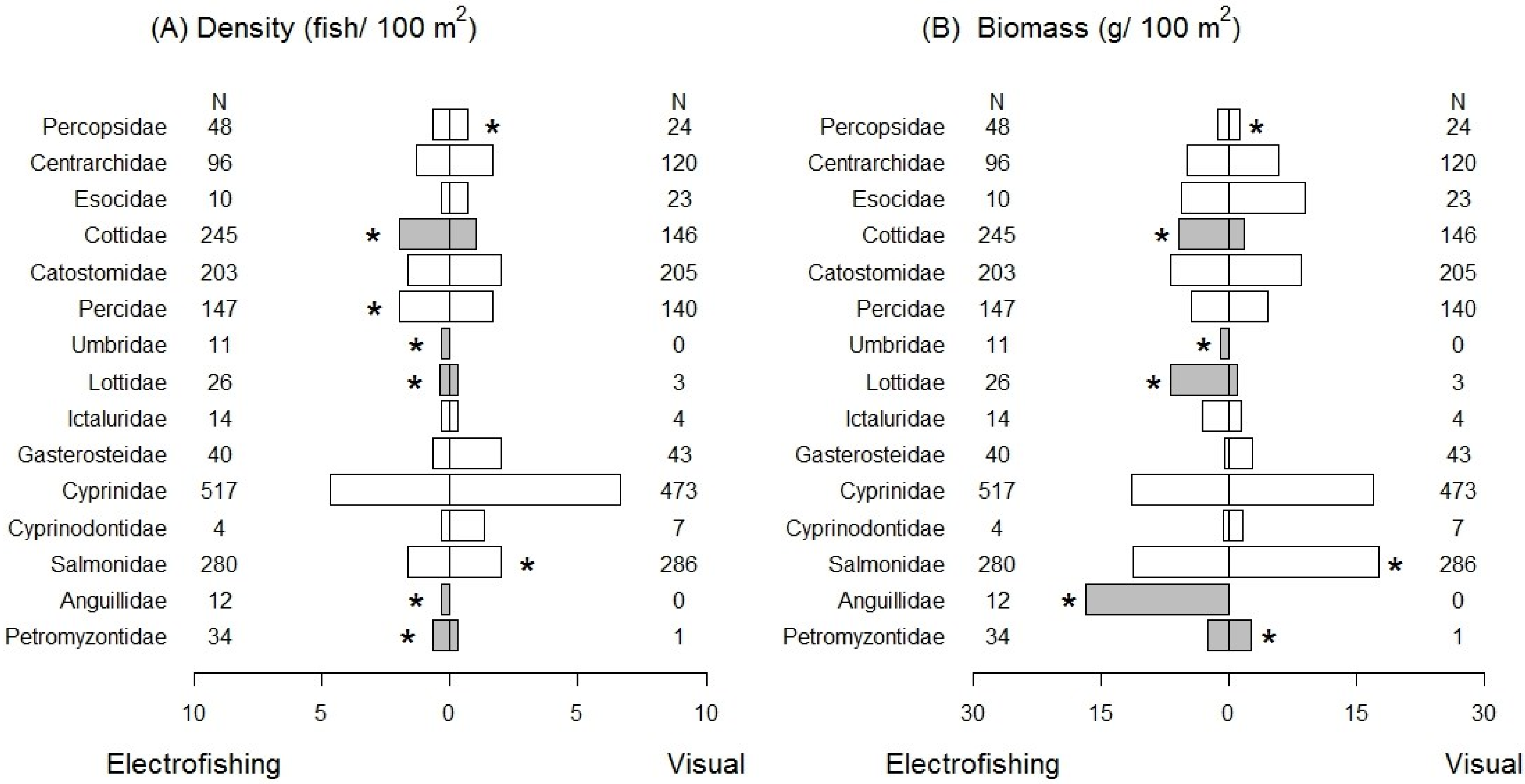

(A) Density (fish/ 100 m2)
(B) Biomass (g/ 100 m2)
N
N
Percopsidae 48 * 24
Centrarchidae 96 120
Esocidae 10 23
Cottidae * 245 146
Catostomidae 203 205
Percidae * 147 140
Umbridae * 11 0
Lottidae * 26 3
Ictaluridae 14 4
Gasterosteidae 40 43
Cyprinidae 517 473
Cyprinodontidae 4 7
Salmonidae 280 * 286
Anguillidae * 12 0
Petromyzontidae * 34 1
10
5
0
5
10
30
15
0
15
30
Electrofishing
Visual

Figure 3. Median relative species density (A) and biomass (B) estimates per 100 m², for electrofishing and visual sampling methods. See caption of Figure 2.

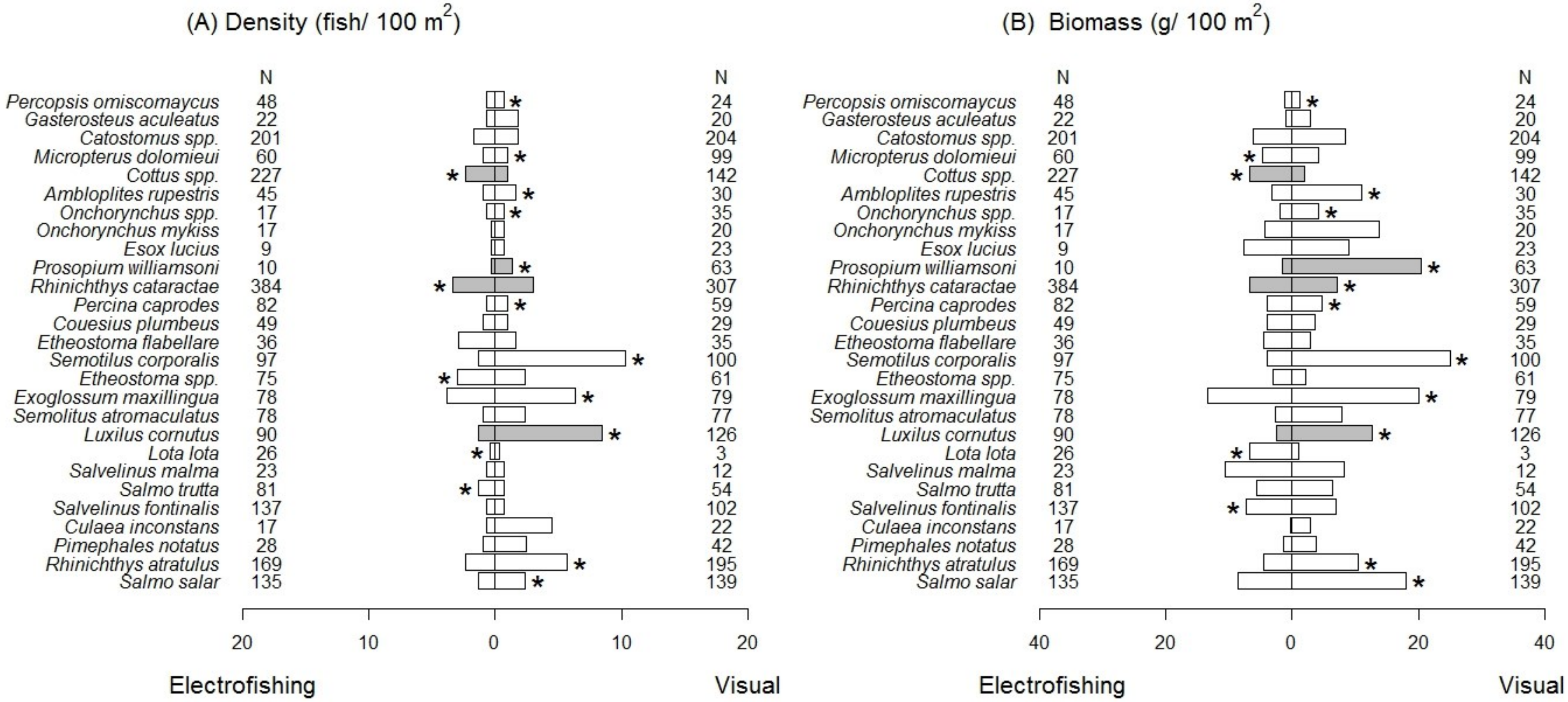

(A) Density (fish/ 100 m^2)
(B) Biomass (g/ 100 m^2)
N
N
Percopsis omiscomaycus 48 24
Gasterosteus aculeatus 22 20
Catostomus spp. 201 204
Micropterus dolomieui 60 99
Cottus spp. 227 142
Ambloplites rupestris 45 30
Onchorynchus spp. 17 35
Onchorynchus mykiss 17 20
Esox lucius 9 23
Prosopium williamsoni 10 63
Rhinichthys cataractae 384 307
Percina caprodes 82 59
Couesius plumbeus 49 29
Etheostoma flabellare 36 35
Semotilus corporalis 97 100
Etheostoma spp. 75 61
Exoglossum maxillingua 78 79
Semolitus atromaculatus 78 77
Luxilus cornutus 90 126
Lota lota 26 3
Salvelinus malma 23 12
Salmo trutta 81 54
Salvelinus fontinalis 137 102
Culaea inconstans 17 22
Pimephales notatus 28 42
Rhinichthys atratulus 169 195
Salmo salar 135 139
20 10 0 10 20
40 20 0 20 40
Electrofishing
Visual
Electrofishing
Visual

Figure 4. Median salmonid (size class) relative density (A) and biomass (B) estimates per 100 m², for electrofishing and visual sampling methods. See caption of Figure 2. (1: 0-5 cm, 2: 5-10 cm, 3: 10-15 cm, 4: 15-20 cm and 5: 20-25 cm).

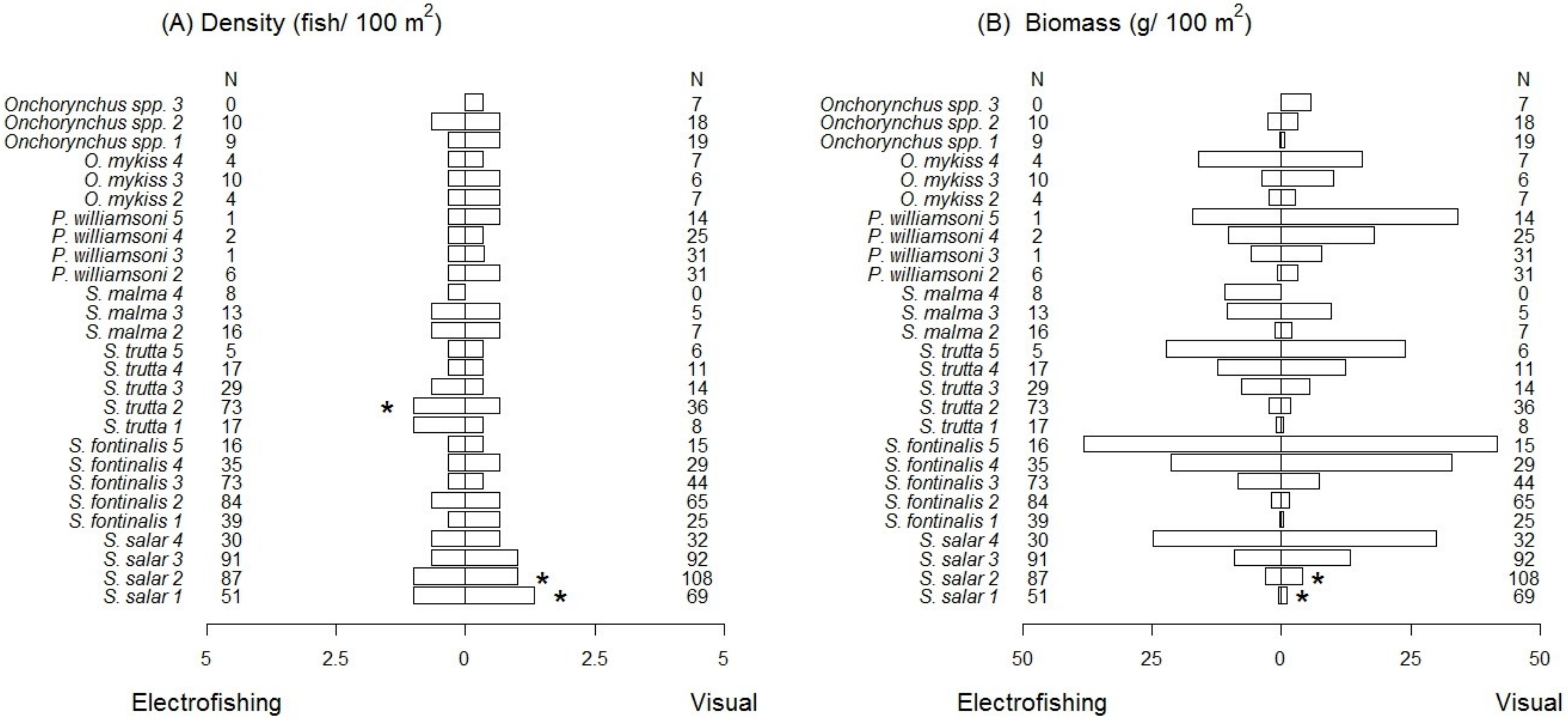

(A) Density (fish/ 100 m2)
(B) Biomass (g/ 100 m2)
N
N
Onchorynchus spp. 3 0 7
Onchorynchus spp. 2 10 18
Onchorynchus spp. 1 9 19
O. mykiss 4 4 7
O. mykiss 3 10 6
O. mykiss 2 4 7
P. williamsoni 5 1 14
P. williamsoni 4 2 25
P. williamsoni 3 1 31
P. williamsoni 2 6 31
S. malma 4 8 0
S. malma 3 13 5
S. malma 2 16 7
S. trutta 5 5 6
S. trutta 4 17 11
S. trutta 3 29 14
S. trutta 2 73 36
S. trutta 1 17 8
S. fontinalis 5 16 15
S. fontinalis 4 35 29
S. fontinalis 3 73 44
S. fontinalis 2 84 65
S. fontinalis 1 39 25
S. salar 4 30 32
S. salar 3 91 92
S. salar 2 87 108
S. salar 1 51 69
*
*
*
5
2.5
0
2.5
5
50
25
0
25
50
Electrofishing
Visual
Electrofishing
Visual

Figure 5. Median cyprinid (size class) relative density (A) and biomass (B) estimates per 100 m², for electrofishing and visual sampling methods. See caption of Figure 2. (1: 0-5 cm, 2: 5-10 cm, 3: 10-15 cm, 4: 15-20 cm and 5: 20-25 cm).

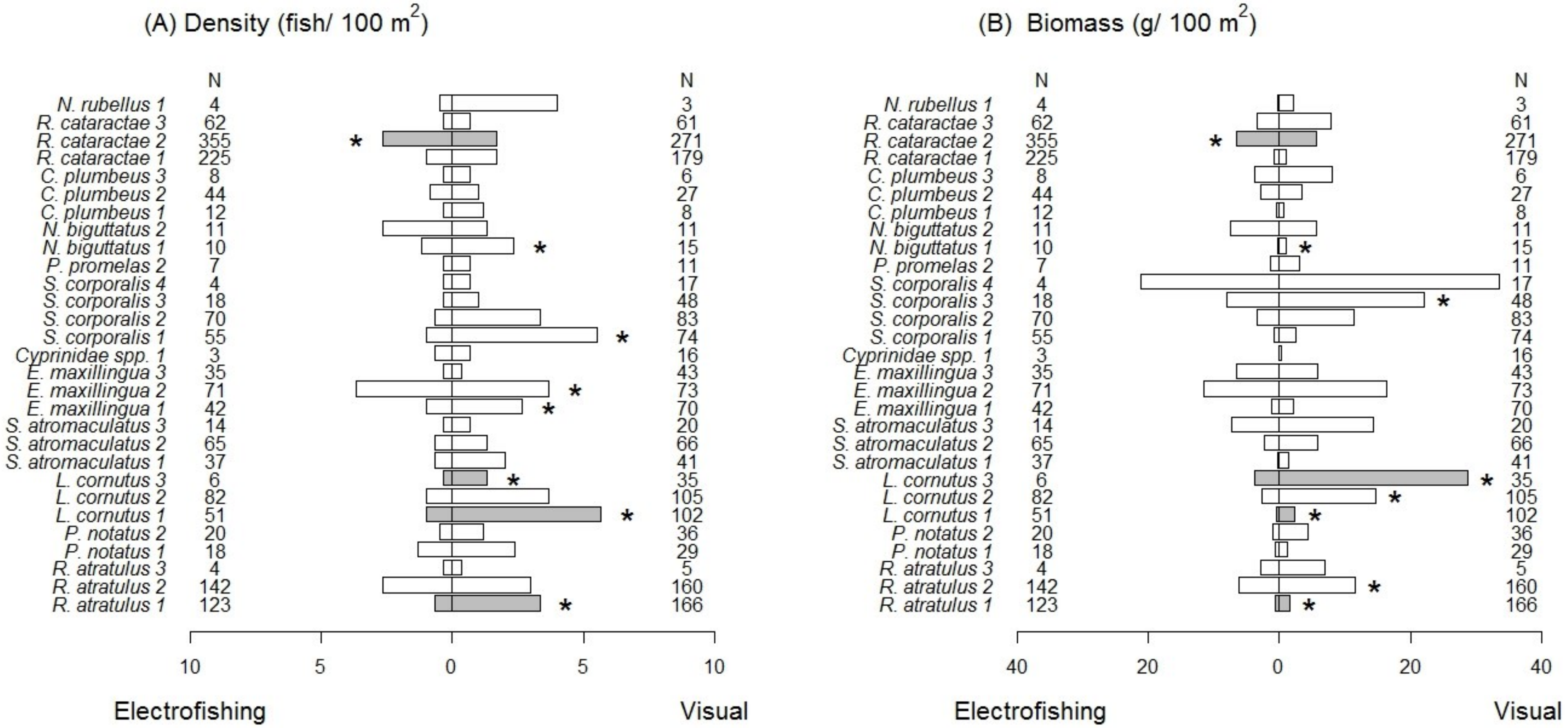
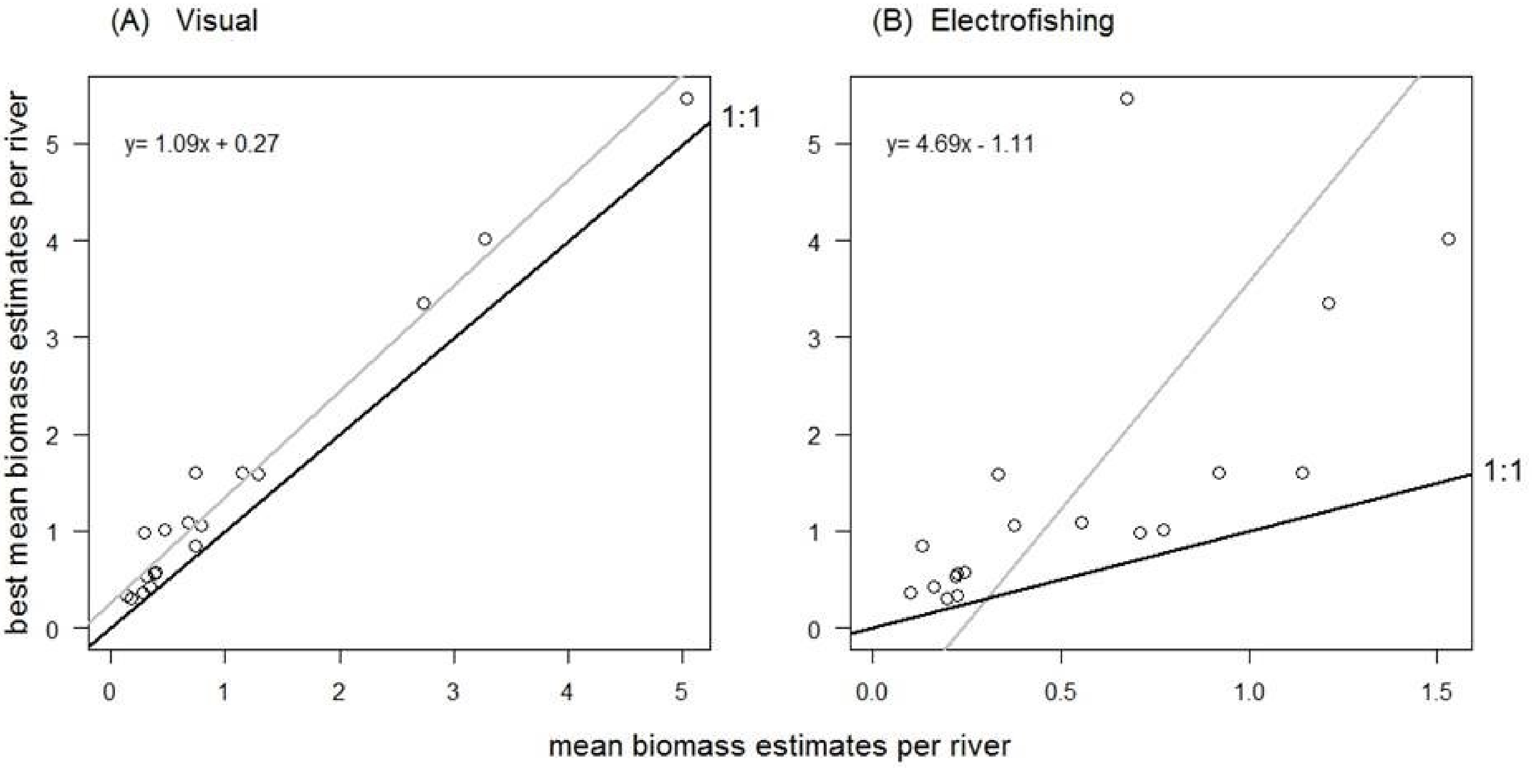
(A) Density (fish/ 100 m²)
(B) Biomass (g/ 100 m²)
N
N
N. rubellus 1
R. cataractae 3
R. cataractae 2
R. cataractae 1
C. plumbeus 3
C. plumbeus 2
C. plumbeus 1
N. biguttatus 2
N. biguttatus 1
P. promelas 2
S. corporalis 4
S. corporalis 3
S. corporalis 2
S. corporalis 1
Cyprinidae spp. 1
E. maxillingua 3
E. maxillingua 2
E. maxillingua 1
S. atromaculatus 3
S. atromaculatus 2
S. atromaculatus 1
L. cornutus 3
L. cornutus 2
L. cornutus 1
P. notatus 2
P. notatus 1
R. atratulus 3
R. atratulus 2
R. atratulus 1
4 62 355 225 8 44 12 11 10 7 4 18 70 55 3 35 71 42 14 65 37 6 82 51 20 18 4 142 123
3 61 271 179 6 27 8 11 15 11 17 48 83 74 16 43 73 70 20 66 41 35 105 102 36 29 5 160 166
*
10 5 0 5 10
40 20 0 20 40
Electrofishing
Visual

Figure 6. Major axis model II regressions displaying mean relative biomass per river for the "best mean biomass estimates" in relation to mean relative biomass estimates derived from visual sampling (A) and electrofishing (B) methods. Grey lines indicate the major axis regression line for the model and black lines represent the 1:1 relationships


(A) Visual
(B) Electrofishing
y= 1.09x + 0.27
y= 4.69x - 1.11
1:1
1:1
best mean biomass estimates per river
mean biomass estimates per river
0
1
2
3
4
5
0.0
0.5
1.0
1.5

Connecting Statement 1

Representing the most reliable fish estimates for all species surveyed within a site is the first important step, before evaluating any river fish community-environment relationship. In this first chapter, I controlled for the effects of experimental and abiotic factors that often play a significant role in surveying efficacy among sites and/or rivers and showed that a combination of data derived from electrofishing and visual surveying methods provided more complete representations of site-specific fish richness, density, and biomass estimates. Specifically, results from this first chapter culminated in response matrices that represented the greatest species estimates generated from both sampling methods. As fish surveying in rivers continued, response matrices were expanded to reflect new site richness, density, and biomass estimates obtained by taking the greatest estimates between surveying methods for each new site. As such, the results from the first chapter provided the methodology that underpinned all other thesis contributions and collaborative NSERC HydroNet published work.

Chapter 2: The effects of regional hydrologic alteration on fish community structure in regulated rivers

Photo: Electrofishing survey, Waterton River, Alberta 2012

The effects of hydrologic alteration on fish community structure in regulated rivers

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Abstract

Alterations to river hydrologic regimes resulting from damming and flow regulation are known to have negative consequences for freshwater communities downstream from dams. However, little has been done to develop a comprehensive approach to assess the effects of hydrologic alterations on fish communities across a wide range of river flow regimes, between different regulation types (ROR, storage, and hydro-peaking), and for rivers without pre-regulation data. We used daily and hourly flow data from gauges located in 10 regulated and 14 unregulated Canadian rivers and quantified multivariate scores of hydrologic alteration for regulated rivers by combining deviations of ecologically-relevant flow indices from reference conditions. Extensive fish community surveys were conducted to estimate the abundance, biomass, diversity indices, and habitat guild representation for all species sampled. The fish data contributed to the derivation of similar multivariate biotic alteration scores relative to reference or unregulated rivers. Our results indicate that significant biotic alterations are directly related to increasing flow alteration scores, with a separation between the two most distinct flow regulation types, run-of-river (ROR) and hydro-peaking. These results thus provide a comprehensive assessment of the flow-response alteration relationship between regulation practices, which may better inform future environmental flow management guidelines.

Keywords: biotic alteration scores, flow alteration scores, hydrologic indices, natural flow regime, ELOHA framework.

Introduction

Anthropogenic changes in the frequency and severity of flows beyond predictable natural ranges, referred to as flow alteration, disrupt the physical conditions determining riverine population and community structures (Resh et al. 1988, Nilsson et al. 2005, Anderson et al. 2006). Flow regulation results in temporal homogenisation through decreases in flow magnitude maxima, increases in annual baseflows, greater flashiness, and a reduction of the number of flow reversals relative to unregulated conditions (Magilligan and Nislow 2005, McLaughlin et al. 2014). As such, alterations to the magnitudes, seasonal patterning, and temporal variability of flows by damming and other interventions are known to have a variety of ecological and evolutionary consequences for riverine fishes, at the individual (Bain et al. 1988, Bradford et al. 2011), population (Bunn and Arthington 2002), and community levels.

Dams and associated regulation practices, from run-of-river (ROR) to storage with or without peaking (hydro-peaking or storage), have been shown to elicit multiple changes to fish populations (Anderson et al. 2006, Renöfält et al. 2010) via alterations to water quality and hydrologic regimes (Freeman et al. 2001, Dudgeon et al. 2005). ROR type systems appear to have the least impacts on stream ecology because patterns of water release result in flows mimicking natural regimes (Bratrich et al. 2004, Habit et al. 2007). Conversely, hydro-peaking events, typified by the rapid and large release of water from a dam timed to match daily hydropower consumption needs (Cushman 1985), have been shown to directly impact fish populations through strandings along the changing channel margins (Bradford 1997, Halleraker et al. 2003), downstream displacements (Scruton et al. 2008), reduced spawning and rearing success due to dewatering of redds (nests), and obstructed migration (Young et al. 2011). Flow alterations may also exert indirect effects through the loss or reduction of suitable habitats

(Vehanen 2000). At the population level, alterations to the flow regime in regulated rivers have been shown to disrupt environmental cues that influence the maturation and spawning of riverine fishes, resulting in lower recruitment and decreases in adult abundance, and species richness (Humphries and Lake 2000, Humphries et al. 2008). At the community level, benthic or pelagic guilds of fishes were follow gradients in mean daily flows and their variability, baseflow, number of zero-flow days and high-flow pulses, among many others describing the low-flow hydrology across 20 catchments where flows were regulated (Arthington et al. 2014).

Despite substantial advancements made by previous studies, there remain several limitations to addressing the effects of flow alteration on fish communities in regulated rivers. For one, hydrologic alterations are generally quantified as the difference between current and reference conditions, as inferred from historical flow data (Richter et al. 1996, Magilligan and Nislow 2005). The absence of such historical data or suitable reference rivers representing unregulated conditions, among other factors affecting pre- and post-flow comparisons, inherently limits the accuracy of estimates of the degree of flow alteration in certain systems (Lloyd et al. 2003, McManamay et al. 2012a). Various hydrologic indices have been used to characterize river flows, but these classifications often incorporate redundant indices (Olden and Poff 2003), and it is difficult to directly link one aspect of river flows to a particular response in fish communities. *A priori* selection of flow indices used to describe hydrologic alterations may also limit the scope of ecological interpretations by focusing primarily on well-established flow-ecological relationships at the expense of less understood facets of the flow regime that may structure fish communities. In addition, index-specific flow alterations and the various biological responses have been inconsistently quantified between studies, often generating interpretations limited to the context of a specific study (Poff and Zimmerman 2010). Given the fact that the severities and directions of ecological responses vary between systems, these limitations emphasize the lack of comprehensive approaches to quantifying flow alterations and their impacts on biota.

The Ecological Limits of Hydrologic Alteration (ELOHA) framework proposes the development of flow standards based on observed trends between altered hydrologic parameters and ecological responses across river systems within a same flow class (Arthington et al. 2006, Poff et al. 2010). Given that rivers sharing similar hydrology should provide bases for evaluating the relative effects of regulation on natural flow dynamics, unregulated rivers may serve as reference conditions and observed flow deviations from these conditions may then be used to develop alteration-ecological relationships for different rivers, eliminating the reliance on historical data (Poff et al. 2010, McManamay et al. 2012a, McManamay et al. 2012b). Building on the ELOHA concept, individual deviations of ecologically-relevant flow indices (Poff et al. 1997) from reference may be combined to obtain river-specific, multivariate hydrologic alteration scores, resulting in more comprehensive composites of river flow alterations.

Our goal is to quantify the relationship between biotic and flow alteration across regulated flow regimes by expanding on the ELOHA framework of shared hydrology for establishing reference conditions. We predict that the degree of biotic alteration will be positively related to that of hydrologic alteration, with the greatest alterations occurring for regulation practices that most alter natural regimes (i.e. storage and/or hydro-peaking). The range of regulation practices under consideration represents different endpoints along the flow regulation continuum, therefore, changes of fish community metrics resulting from flow alteration may also differ among regulation practices. A better understanding of the flow-response alteration relationships between regulation practices may, thus, inform future environmental flow management guidelines.

Materials and methods

Rivers and sampling protocol

Fish community surveys were conducted during the summer months (late June to August) from 2011 to 2013, in 10 regulated and 14 unregulated Canadian rivers (Appendix A). Rivers surveyed included five rivers in Ontario, 16 in Québec and three in New Brunswick (Figure 1). River selection proceeded by first identifying older hydropower facilities across Canada (>40 years since construction) and narrowing this selection by flow regulation practices (ROR, storage, and hydro-peaking), as determined by the Canadian Dam Association and provincial governmental agencies. Rivers where hydrologic gauges were located within 15 km of potential study sites were then retained. Lastly, rivers were selected based on sampling feasibility and river accessibility. Specifically, sampling was based on the ability to survey wadeable stretches of river across the entire wetted width and road access (>2 access points to the river).

In each river, 25-50 300 m² sites were surveyed, for a total number of sites combining all rivers of N = 829. For regulated rivers, study sites were positioned below dams and hydrologic gauges. For unregulated rivers, sites were placed in river reaches that shared similar geomorphological traits with regulated rivers (e.g. river width and depth, alluvial, non-branching rivers) and located upstream from major tributaries (M. Lapointe, personal communication 2010). For each river studied, sites surveyed were distributed along ~5-12 km river stretches, enabling us to extrapolate local impacts of flow regulation in rivers downstream from dams.

Paired single-pass electrofishing and snorkelling surveys were carried out in random order, at roughly the same time between 08:30 and 18:00 on consecutive days, with a minimum 24-hr recovery interval to allow fish to re-establish themselves after a sampling event. Electrofishing surveys were conducted by teams of three using an LR-24 backpack electrofishing unit (Smith-Root®, Vancouver, WA). Captured fish were identified to species, weighed (wet blotted weight, ± 0.1 g), measured (total length, ±0.1 cm), and released. Visual surveys were conducted by two observers snorkelling upstream and surveying the sites at a rate of ~6 s/m². Species were identified, recorded, and total lengths were estimated in 5-cm increments. Mass-length relationships derived from the electrofishing data were calculated for each species per river and used to estimate the masses of fish recorded during the visual surveys (Le Cren 1951). Selection of sampling sites and specific details pertaining to surveying methodology are described in Macnaughton *et al.* 2015.

Regulation types

ROR, storage without and with hydro-peaking were treated as three points along a continuous range of flow regulation regimes. We defined these types based on the resultant hydrologic alteration, dam type, and specific operational characteristics (Appendix A). In ROR-type systems, a small upstream reservoir volume relative to mean flows may occur, but does not store more water than required for power production for a single day, resulting in downstream flows similar to a natural regime. Conversely, storage type systems were defined as having larger storage volumes that allow for temporal shifts of the natural seasonal runoff volumes, resulting in significant seasonal high flow attenuation and enhancement of low flows, especially over the winter months. Hydro-peaking type systems were defined as exhibiting frequent periods of significant hourly or diel hydrologic fluctuations over a year, caused by rapid opening and closing of reservoir release structures (Cushman 1985, Flodmark et al. 2004). Precise, quantitative thresholds distinguishing these regulation types are not internationally accepted, so we assigned "types" to our rivers based on preliminary analyses of the regulated hydrographs (after McLaughlin et al. 2014).

Hydrologic Indices

Daily and hourly flow data were obtained from the Centre de l'Expertise Hydrique du Québec (CEHQ) and the Water Survey of Canada (HYDAT) national flow gauge networks, and industry partners. We analyzed a 12-year time series (1997-2009) to control for the effects of temporal and climate variability on subsequent analyses and to detect differences in indices summarized across flow records (Kennard et al. 2010). Hydrologic indices for describing ecologically important characteristics of flow regimes are commonly used in riverine research. These include indices that depict the seasonal patterning of flows; timing of extreme flows; the frequency, predictability, and duration of floods, droughts, and intermittent flows; daily, seasonal, and annual flow variability; and rates of change (Poff et al. 1997). Flow indices representing ecologically relevant components of the hydrographs for our rivers included among others, the Indicators of Hydrologic Alteration (IHA; Richter 1997). All flow indices described by Olden and Poff (2003), in addition to those created to capture hourly variations in the flow record, were calculated for each of the rivers surveyed for a total of 211 flow indices. Prior to analysis, flow indices were evaluated for indetermination (e.g. index calculating the number of days above 7x median flows when a river never reached this threshold), computational, and mathematical errors (e.g. coefficient of variation for circular data). In general, all flow indices were assessed for aberrant values (outliers) across all rivers and those that exhibited any type of problem, computationally or other, were deemed lower quality and not included in further analyses. A preliminary removal of low-quality flow indices (i.e. indices that did not exhibit any inter-river variability or had skewed data due to winter ice conditions) reduced the number of indices to 105, with 101 derived from daily flows (D) and the remaining 4 from hourly flows (H). The 105 daily flow indices were grouped by component, representing 1-daily flow magnitude, 2-frequency, 3-duration, 4-timing, and 5-rate of change of hydrologic regimes. The inclusion of hourly flow indices is thought to capture the extent of hydrologic alteration resulting from hydro-peaking practices, which often alter flows on an hourly basis to meet energy demands. As such, the sixth flow components included the four hourly flow indices. All flow metrics expressed as discharge units (volume per time) were normalized by dividing these indices by the median flow (daily or hourly as appropriate) for the available flow records (McManamay et al. 2012c).

Hydrologic class analysis was initially carried out on data from 96 unregulated rivers from across Canada, representing five flow classes that comprised three western and two eastern flow class regions (McLaughlin et al. 2014). The 14 unregulated rivers in our study represented a subset of the rivers within the two eastern regions, distributed between East1 (N = 27) and East2 (N = 18). When grouping all of the unregulated rivers from the two eastern regions described in McLaughlin *et al.* 2014, the pooled flow distributions (principal component scores) were not bimodal. As such, the 14 unregulated rivers, which are a subset of these 45 rivers, were considered as belonging to a single reference flow class. As more unregulated rivers contributed to the reference flow class, the variability observed across unregulated river flow regimes increased and we bettered our chances of capturing the extent that natural flow regimes vary for that reference flow class. Altered flows for regulated rivers were, thus, more conservatively and reliably detected, as they were defined against a broader, rather than narrower, reference flow class. As we did not have an even representation of regulated rivers by regulation type, all regulated rivers were compared within the same multivariate space.

Biotic Attributes

For the electrofishing and visual surveys, density estimates were calculated for the species sampled at each site. All individuals recorded were also assigned to a size category (small: <5 cm; medium: 5 to 20 cm; large: 20 to 90 cm) for each river. Site-, species-, and size category-specific biomass estimates were generated by summing either the masses recorded during the electrofishing surveys or the mass estimates inferred from the observed length-weight relationships applied to the visual survey data. The data collected via the sampling method that yielded larger density or biomass estimates for each species and size category at each site were used to calculate the total species densities and biomasses in each of the rivers studied. These total river fish density and biomass attributes therefore represented the greatest estimates for each species and likely minimized any biases from the two sampling methods (Macnaughton et al. 2015a). Species and family richness were estimated by counting the numbers of species and families detected in each river. Shannon's (H) and Simpson's (D) diversity indices were derived from the estimated species biomass and densities using the *vegan* package (Oksanen et al. 2011) for R (R Development Core Team2014). In addition, Hill's $N1$ and $N2$ indices describing the effective number of species (Hill 1973) were calculated for each river as:

$N1 = \exp(H)$ and

$N2 = 1/D$

Proportions of family-level representation in each river were calculated as the ratio of family to total biomass. Rare or under-represented families (yielding <0.1% of total biomass and density) were omitted from this analysis, leaving 12 family proportion attributes. Lastly, a habitat guild attribute was calculated by taking the ratio of species categorized as demersal or benthopelagic to the total number of species observed in each river. In total, we calculated 25 biotic attributes that were grouped to represent: 1-fish quantity, 2-diversity, 3-composition, and 4-proportional representation of two habitat guilds (Appendix B). Prior to analyses, attributes representing fish quantity, composition, and habitat guilds were log-transformed to normalize their distributions.

Statistical Analysis

Characterizing flow alteration for our regulated systems first involved identifying the range observed for hydrologic indices across each of the six flow components (daily flow magnitude, frequency, duration, timing, rate and hourly flows), done by river. This was performed by conducting six separate principal component analyses (PCA) on the correlation matrices for each of the components characterizing the flow regime across all 24 rivers. For each flow component, river PC scores along significant PC axes (PC1 or both PC1 and PC2) evaluated using the broken-stick rule (Legendre and Legendre 2012) were retained for a total of 10 PC axes. Performing separate PCAs for each of the flow components ensured that indices describing major sources of variation within each hydrologic subset contributed to the retained PCs and that subjectivity associated with the process of selecting the indices was reduced. Flow indices that contributed the most to the significant PC axes (i.e. top loaders) were also identified to explain dominant patterns of variation for each of the flow components measured in our rivers (Appendix C). Likewise, the correlation matrices of each of the four groups of fish community attributes were subjected to PCA to identify the greatest portion of variation within each of the groups of fish attributes across all rivers. All significant PCs for each of the groups of fish attributes were retained for a total of 5 axes, and fish community attributes contributing significantly to each of these axes were identified.

Reference conditions describing natural hydrologic variability and fish community structure were established by calculating the means and covariance matrices separately for the six flow components (10 PC axes) and four fish groups (5 PC axes) for the 14 unregulated rivers. Mahalanobis (1936) generalized distances were calculated for each of the rivers (Legendre and Legendre 2012). This distance computes the deviation between two points in multivariate space whose axes are not orthogonal, thereby taking into account the correlations among indices (Legendre and Legendre 2012). Hotelling's T^2 statistic was used to determine whether this distance for each of the regulated rivers differed significantly from reference conditions. A regulated river was considered flow-altered if the distance of the hydrologic alteration inferred from flow PCs from reference conditions (alteration scores), was significantly greater than what can be expected from that of unregulated rivers. Likewise, a river was considered biotic-altered if biotic alteration inferred from biotic PCs was significantly greater than expected. A schematic of how the alteration scores were calculated is provided in Figure 2. A Model II linear regression was computed by permutation ($N = 999$), using the major axis (MA) method and 95% CI for the slope and intercept parameters, to compare the biotic and hydrologic alteration scores of all regulated rivers. Model II regressions are generally used when the two variables in the regression equation are not controlled by the researcher and errors on the X and Y axes are relatively important, as is the case for the flow and biotic alteration scores calculated (Legendre 2013). Assuming that the relationship is linear, it may be possible to suggest a flow alteration threshold above which significant biotic alteration may occur. All statistical analyses were performed in R Language (R Development Core Team 2014).

Results

PCA conducted for each of the flow components across all 24 rivers yielded a minimum of 10 significant PC axes (≤ 2 axes per flow component retained). In each of these 6 PCAs, the axes explained from 61.63% to 91.23% of the variance. Flow indices that contributed the most (top loaders) for each of the flow components on PC1 and PC2, respectively, were: MA3 and nML6 (flow magnitude), FH1 (flow frequency), DL12 and DH6 (flow duration), TA2 and TH2 (flow timing), RA7 and nRA1 (flow rate), and RL2 and MA60 (hourly flows). The cumulative portion of variation attributed to statistically significant PC axes for each of the four fish groups ranged from 49-99%. Biotic attributes that represented the top loaders for significant PC axes were: total biomass of medium and small-sized fishes, total fish biomasses and densities (fish quantity); Shannon diversity indices (fish diversity); the proportion of esocid and lottid families on PC1, and the proportion of salmonid, cyprinid, ictalurid and anguillid families on PC2 (fish composition); and proportional difference of both habitat guilds. These PC axes (10 and 5 axes describing flow components and fish groups, respectively) were then combined into river-specific alteration scores.

Several regulated rivers were significantly different from hydrologic and/or biotic reference conditions. Significant hydrologic alteration scores were found for hydro-peaking rivers (Magpie and Mississagi), storage systems (Dee, Serpentine, and Saint-Francois), and ROR systems (Coaticook and Saint-Jean; Table 1). However, the biotic alteration scores of only hydro-peaking rivers and a single storage river diverged significantly from reference conditions. The lowest hydrologic and biotic alteration scores were found for ROR and storage regulation types, which were within natural variability as measured from hydrologic and biotic means and variance for unregulated rivers (± SD: 3.03 ± 0.34 and 2.11 ± 0.45, respectively).

Across the significantly flow-altered rivers, general patterns of attenuation of the natural flow regime were observed (data not shown). In particular, daily flow magnitudes representing the variability in daily flows (MA3) and high flow discharge (MH15), the top loadings on PC1, were greatly decreased from flow reference conditions for all regulated rivers, with hydro-peaking and storage rivers exhibiting up to a four-fold decrease in high flows. Slightly higher indices characterizing baseflows (ML17) and mean minimum monthly flows for the month of June (nML6) were also seen in several regulated rivers, most notably hydro-peaking systems. Across our regulated rivers, the predictability (TA2) and constancy (TA1) of flows were both increased relative to means for unregulated rivers. For the hydro-peaking rivers, the number of day-to-day changes in daily flows (RA8) more than doubled, but for storage-type rivers, Dee and Serpentine, this index decreased five-fold. Particular to hydro-peaking rivers were indices describing hourly flow fluctuations, namely the coefficient of hourly variation (MA60), which was 24 and 3.5 times greater for the Mississagi and Magpie Rivers, respectively. For all other regulated rivers, this index was lower than the mean for unregulated rivers. In addition, the Mississagi River had a significantly smaller hourly low flow flashy index (RL2) than the regional average, which indicated that minimum hourly flows for this river were much less than in the unregulated rivers. Lastly, storage systems demonstrated decreases in negative change (nRA7) or in the rise rates in flows (nRA1), both indicated some degree of flow stabilization.

The direction of deviations for biotic attributes from the unregulated reference conditions varied between rivers and regulation practices (Table 2). About half (58%) of all biotic attributes decreased from the means for unregulated rivers, with the Mississagi (hydro-peaking) and Saint-Francois (storage) rivers exhibiting the greatest frequencies of negative deviations (13 out of 16 attributes). These rivers, along with the Magpie (hydro-peaking), demonstrated similar trends with respect to fish size attributes. Proportions of salmonids, cyprinids and ictalurids, which were generally small-bodied, were all decreased relative to reference conditions. For the hydro-peaking rivers, the proportions of esocids and lottids, both generally large-bodied, were greater than the reference conditions.

Model II regression produced a significant positive linear relationship between biotic and flow alteration scores (r = 0.94, two-tailed p-value = 0.007), with the two hydro-peaking rivers exhibiting the greatest alterations overall (Figure 3). Despite significant differences in flow alteration scores for many of the regulated rivers, ROR and storage systems tended to cluster in close proximity to the biotic mean for unregulated rivers. Flow indices and biotic attributes for each of the unregulated rivers were quantified, as were multivariate scores for each of the unregulated rivers from reference conditions. Though not truly “altered”, unregulated rivers were depicted within the same multivariate space to show the variability in scores among rivers, rather than simply illustrate their collective position at origin.

Although the overall relationship was driven by one of the hydro-peaking rivers, the linear relationship between biotic and hydrologic alteration scores remained marginally significant when the outlier was excluded (r = 0.65, two-tailed p-value = 0.06). It is also important to note that the removal of hydro-peaking rivers from the analysis may not yield a significant relationship. However, should we consider hydro-peaking practices as part of the flow regulation continuum; the relationship suggests a potential flow alteration threshold that may bring about significant biotic alterations.

Discussion

Our results indicate that for a given reference flow class, regulated rivers generally exhibit flow indices that suggest flows are altered well beyond their natural parameters. Both hydrologic and biotic alteration scores for hydro-peaking systems differed significantly from unregulated rivers, while most run-of-river and certain storage regulation practices were not associated with significant alterations. These findings show that flow alterations will drive significant biotic alterations for certain regulation types. However, the lack of data points in the moderate to high ranges of flow alteration scores in our study precludes us from suggesting a generalized threshold at this time.

In hydro-peaking rivers, biotic attributes including total fish biomasses and densities, biomass of medium and small-sized fishes, and the proportions of salmonid, cyprinid, and ictalurid families all decreased relative to means for unregulated rivers. However, the proportions of large-bodied esocids and lottids in these same rivers increased significantly, implying that the effects of hydrologic alteration are strongly mediated by taxonomic differences. Mims and Olden (2012) demonstrated that the prevalence of opportunistic (i.e. small-bodied species with early maturation) or periodic (i.e. long-lived and large-bodied species) life history strategies were influenced by key hydrologic metrics, albeit in opposite directions. Frequencies of opportunistic strategists were negatively related to flow predictability and seasonality, while the frequencies of periodic strategists were positively related to high flow seasonality and/or predictable, high duration flow events (Mims and Olden 2012). In the hydro-peaking rivers studied, an increase in the observed predictability and constancy of flow metrics pointed to an increase in flow stability, which may result in increased proportions of larger-bodied taxa. Because opportunists likely have a selective advantage in environments subjected to frequent and intense disturbances (i.e. hydro-peaking) relative to periodic strategists (Winemiller and Rose 1992), it is not surprising that we detected changes in the relative proportions of small- to large-bodied fish biomasses. The inclusion of hourly flow data for deriving hydrologic alteration scores also added to capturing variability related to hydro-peaking regulation. For instance, we detected an increase in both inter- and intra-diel flow variability, as well as hourly low flashy floods over 24-hour periods in hydro-peaking rivers.

The flow in the Saint-Francois River, like most of the storage systems in our data set, was significantly altered, but the inconsistency with which significant biotic alterations was observed across storage systems point to factors other than flow regulation influencing fish communities. In fact, the Saint-Francois River is dammed at several different points, which may alter the fish community attributes as much as the regulation type. Despite demonstrating substantial biotic alterations from reference, the attributes quantified may not capture the full extent of community responses to low and moderate levels of hydrologic alteration. To fully understand the ecological effects of flow alteration, larger datasets that span broader ranges of biotic responses and hydrologic alterations are needed.

The effects of altered flow regimes on fish species are likely confounded by other factors comprising both the physical environment and the ecological traits of individual species (e.g. migratory patterns/behaviours) (Poff and Zimmerman 2010). In the Dee and Serpentine rivers (storage), the observed increases in the proportion of salmonids relative to the reference condition may be attributed to several factors, both anthropogenic and environmental. On the one hand, the occurrence of large fishes (between 20-30 cm standard length) detected downstream of the dams may be the result of periodic “flushing” of water from the reservoirs to increase the downstream potential for generating hydropower. In this scenario, the larger salmonids such as landlocked Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) sampled were assumed to have been entrained downstream. This idea is supported by increases in indices representing the magnitudes of high flow volumes in the Dee and Serpentine rivers. On the other hand, the prevalence of suitable salmonid habitats (i.e. habitats characterized by cold, clear and moderately fast waters; Bjornn and Reiser 1991) and stocking programs in these rivers (see Appendix A) may also explain the proportions of salmonids observed in these rivers.

Using flow classifications derived from unregulated rivers provides an ecologically relevant foundation upon which a framework for environmental flow management standards may be developed (McManamay et al. 2012b). Expansions on the ELOHA concept have enabled more comprehensive composites of river flow alterations that highlight the flow indices deviating significantly from unregulated conditions, while relating hydrologic patterns to regional flow classes. Different authors have highlighted the importance of choosing relevant flow indices to best represent dominant patterns of hydrologic variability (Olden and Poff 2003) or to address the fundamental dimensions of the flow regime driving patterns of fish occurrence (Mims and Olden 2012). By avoiding restrictive *a priori* selection of indices describing hydrology and fish communities, subjectivity and potential misrepresentation of flow-ecological relationships are largely avoided. We do recognize that our analysis may produce some degree of uncertainty for deriving biotic and flow alteration scores, but we believe that the gains of having composite scores summarizing multiple components of alteration outweigh this uncertainty. Our results do not demonstrate direct relationships between single flow indices and individual ecological responses for particular rivers. However, we are able to determine significant changes from reference conditions for both flow indices and fish community attributes and inform the biotic responses to certain types of flow alteration and regulation type. Moreover, we have described a framework, upon which alterations may be estimated and used to predict the direction of environmental variable/stressor-community response alteration relationships. As such, the applications of this framework may also extend into other fields concerned with anthropogenic impacts on ecosystem structure and function.

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Table 1. Flow and fish alteration scores and associated p-values for the 10 regulated rivers. Significant differences between flow and fish alteration scores and the reference conditions are given in bold. Flow and fish means and SD for unregulated rivers are 3.03 ± SD 0.34 and 2.11 ± SD 0.45, respectively.

River	Regulation type	Flow alteration score	p.value	Fish alteration score	p.value
Magpie	Hydro-peaking	55.66	**< 0.001**	7.00	**0.008**
Mississagi	Hydro-peaking	129.34	**< 0.001**	15.95	**< 0.001**
Coaticook	ROR	20.062	**0.007**	1.35	0.94
Du Sud	ROR	1.94	0.99	2.24	0.67
Etchemin	ROR	3.97	0.72	2.22	0.68
Saint-Jean	ROR	12.19	**0.044**	2.81	0.46
Dee	Storage	21.44	**0.006**	1.24	0.96
Kiamika	Storage	6.94	0.25	2.30	0.65
Serpentine	Storage	19.90	**0.007**	2.58	0.54
Saint-Francois	Storage	12.93	**0.036**	5.42	**0.040**

Table 2. Direction of the deviations from biotic reference conditions for attributes representing the largest portion of variation on significant principal components axes (PC1 and PC2) in the regulated rivers.

Attributes representing PC axes	Peaking		ROR				Storage			
	Magpie	Mississagi	Coaticook	Du Sud	Etchemin	Saint-Jean	Dee	Kiamika	Serpentine	Saint-Francois
Tot. biomass of M-sized fishes	-	-	+	+	+	-	+	+	+	-
Tot. fish biomass	-	-	+	+	+	-	+	+	+	+
Tot. fish density	-	-	+	+	+	-	-	+	-	-
Tot. biomass of S-sized fishes	-	-	+	+	+	-	-	+	-	-
Shannon diversity index (B)	-	+	+	+	-	-	-	+	-	-
Hill diversity index N1 (B)	-	+	-	+	-	-	-	+	-	-
Shannon diversity index (D)	-	+	-	+	+	-	-	+	-	+
Species richness	-	+	-	+	-	-	-	+	-	-
Proportion of Esocidae	+	+	-	-	-	-	-	-	-	-
Proportion of Lottidae	+	+	-	-	-	-	-	-	-	-
Proportion of Salmonidae	-	-	-	-	-	+	+	-	+	-
Proportion of Cyprinidae	-	-	+	+	+	-	-	-	-	-
Proportion of Ictaluriadae	-	-	-	+	+	-	+	+	-	-
Proportion of Anguillidae	-	-	-	-	-	+	-	-	-	-
Proportion of demersal species	-	-	-	-	-	+	-	+	-	+
Proportion of benthopelagic species	+	+	+	+	+	-	+	-	+	-

Figure 1. Map of Southeastern Canada featuring the 24 study systems comprising 10 regulated (★) and 14 unregulated (◊) rivers.

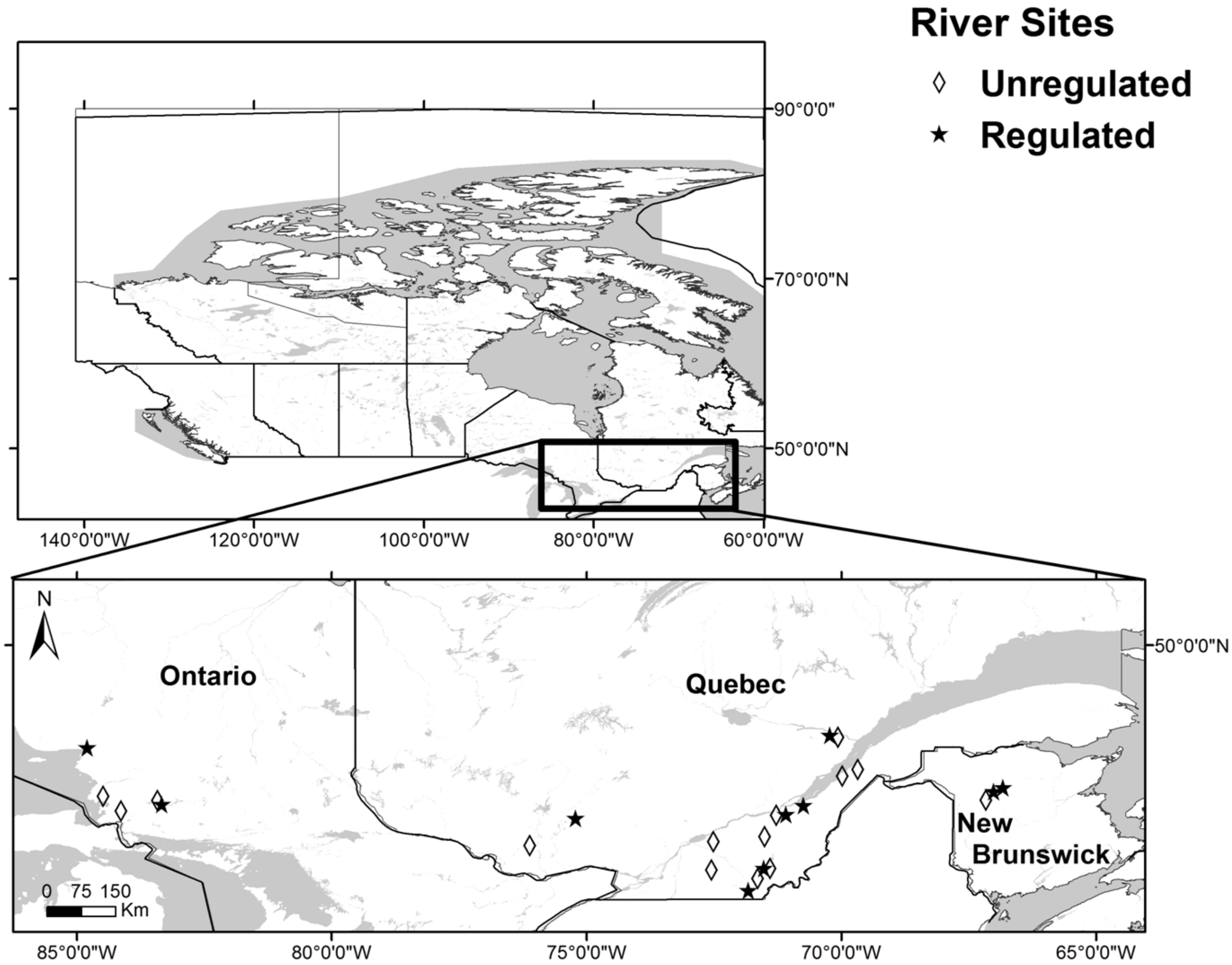
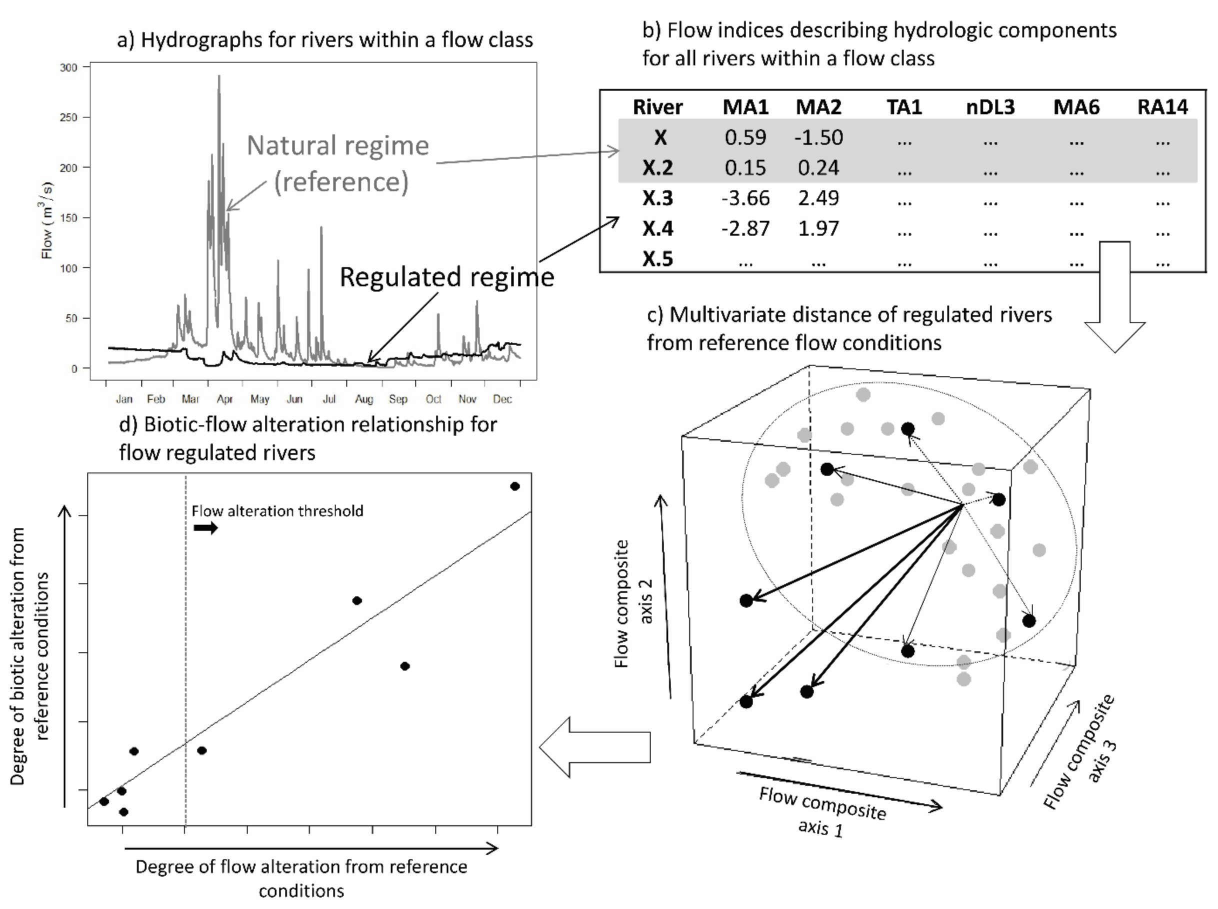
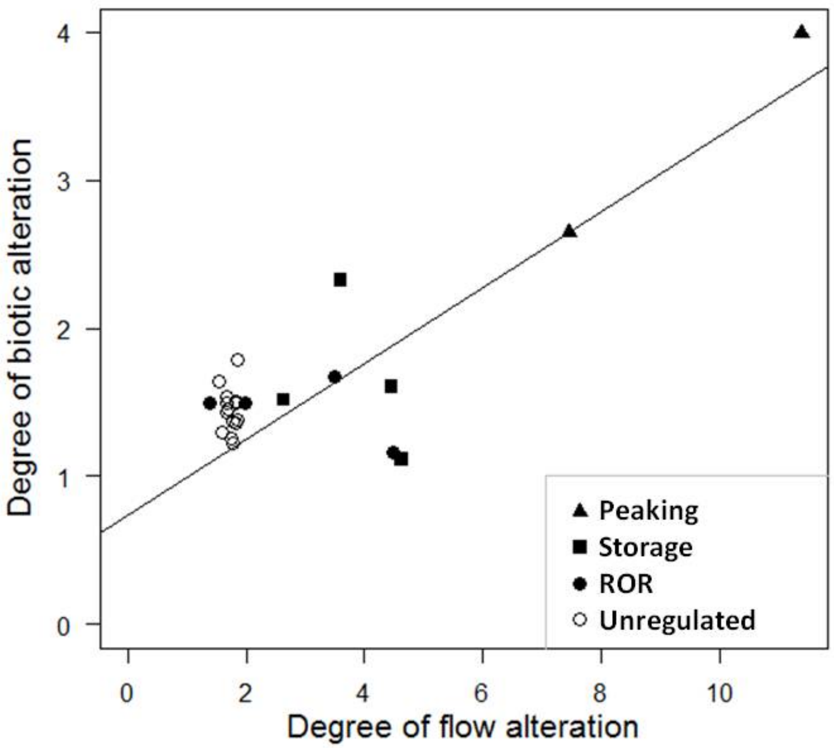

River Sites
◊ Unregulated
★ Regulated
90°0'0"
70°0'0"N
50°0'0"N
140°0'0"W
120°0'0"W
100°0'0"W
80°0'0"W
60°0'0"W
N
Ontario
Quebec
New Brunswick
0 75 150
Km
50°0'0"N
85°0'0"W
80°0'0"W
75°0'0"W
70°0'0"W
65°0'0"W

Figure 2. (a) Hydrographs depicting unregulated (reference) and regulated regimes for rivers belonging to a given flow class. (b) Table of the flow indices that describe each of the flow components by rivers, for a given flow class. PCA were conducted for each of the flow components, yielding PC axes representing dominant patterns of flow variability by flow component, for all rivers within a flow class. (c) Multivariate plot of the dominant patterns of flow variability for all rivers. Multivariate flow distances were calculated for each of the regulated rivers from the reference flow conditions, represented by the origin of all arrows within the reference ellipse. (d) Biotic-flow alteration score relationship for regulated rivers using the multivariate flow distances previously calculated. Biotic alteration scores for these same regulated rivers were derived in the same manner as was done for flow alteration scores. The dashed line refers to the flow alteration threshold, where points to the right of the line are rivers that are significantly altered from the reference flow conditions.



River	MA1	MA2	TA1	nDL3	MA6	RA14
X	0.59	-1.50	...	...	...	...
X.2	0.15	0.24	...	...	...	...
X.3	-3.66	2.49	...	...	...	...
X.4	-2.87	1.97	...	...	...	...
X.5	...	...	...	...	...	...

Figure 3. Major axis regression relationships between the degree of biotic and flow alteration (biotic and flow alteration scores, square root-transformed) across all 10 regulated rivers, derived from all 105 daily and hourly flow indices. Rivers depicting Peaking (▲), Storage (■), ROR (●) types of regulation regimes as well as unregulated rivers (○) are illustrated.


4
3
2
1
0
Degree of biotic alteration
0
2
4
6
8
10
Degree of flow alteration
▲ Peaking
■ Storage
● ROR
○ Unregulated

Connecting Statement 2

The flow alteration research discussed in the second chapter quantified a number of ecologically-relevant flow indices and biotic attributes for unregulated and regulated rivers and calculated significant deviations for each index and attribute from reference conditions. By further developpiong this framework into comprehensive alterations for regulated rivers, I identified a significant positive relationship between biotic and flow alterations, providing a separation between the two most distinct flow regulation types, ROR and hydro-peaking. The downside of developping multivariate alterations, however, is reduced interpretability of results. Specifically, our results do not directly demonstrate relationships between any one flow index and individual ecological responses for particular rivers.

The third chapter addresses this limitation by comparing fish guild-environment relationships across unregulated and regulated rivers. To tease apart the relative importance of each environmental driver for establishing fish communities across river regimes, I provided quantitive thermal indices based on river water temperatures and developed thermal variables akin to those described for flow regimes. To evaluate whether quantitative fish guild estimates, rather than total river biomass or density estimates, would respond more strongly to river thermal regimes, I compared the response of different types of fish guilds to flow and thermal regimes across rivers, including those subjected to river regulation. These results provide interpretations at the guild level that facilitates comparisons across rivers.

Chapter 3: Using guilds to assess fish community response to hydrologic and thermal regimes across 25 Canadian temperate rivers

Photo: Saint-Jean River, Québec 2011

Using guilds to assess fish community response to hydrologic and thermal regimes across 25 Canadian temperate rivers

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Summary

1. Although well-known interactions among river hydrologic and thermal regimes have been described, both have yet to be analysed together for assessing guild responses across temperate rivers. A comparison of the different types of fish guilds responses to environmental variables might highlight the ecological traits most susceptible to current and future environmental change stemming from flow regulation.
2. Extensive field surveys were conducted across 25 unregulated and regulated rivers to estimate river species densities and biomasses. Fish estimates were subsequently grouped into type of guilds representing morphologic, trophic, reproductive, habitat, and behavioural traits or groups of related species (i.e. phylogenetic associations). River hydrologic data was paired with thermal data derived from *in-situ* water temperature loggers to generate indices characterizing hydrologic and thermal regimes in each of the rivers surveyed. Redundancy analyses (RDA) served to compare types of guild responses to dominant patterns of varying hydrologic and thermal regimes.
3. Fish guild data were significantly explained (R^2_{Adj} = 25-44%) and predicted (R^2_{CV} = 35-76%) by explanatory variables representing river hydrologic and thermal regimes across rivers, whereas total fish density and biomass were not. All fish guild models performed better relative to studying phylogenetic associations, confirming that guild models based on trait-environmental relationships were better performing than those based on phylogeny. Results also showed that the models describing habitat and trophic guilds had the greatest explanatory powers (R^2_{Adj} = 0.44 and R^2_{Adj} = 0.41, respectively),

suggesting that the traits representing these guilds were more closely associated with variables depicting river flow and thermal variability than other guild traits.

4. Flow and thermal variables representing the magnitude of summer water temperatures and intra-annual flow variability were consistently selected as independent drivers of fish guild models (> 86% of models), pointing to the importance of integrating thermal regimes in hydro-ecological studies.
5. The biomass of guilds representing species' habitat preferences for specific water velocities and temperatures, tolerance for anthropogenic disturbances, and water clarity were driven by the magnitude of summer water temperatures and flow variability. By ranking the different habitat guilds along low to high summer water temperature magnitudes, for example, the guilds most related to changes in temperature magnitudes were identified, indicating that the conservation of groups of species most vulnerable to increases in water temperatures and variability may be prioritized. Differences between unregulated vs. regulated rivers also revealed how more constant summer water temperatures and lower flow variability for downstream regulated river habitats led to generally warmer and less variable conditions, favouring certain habitat guilds over others.
6. These findings identified the different guild trait-environment relationships across rivers and highlighted the importance of more comprehensive hydrologic and thermal regime conservation, on which management efforts focused on maintaining the ecological integrity of rivers should rely.

Key-words: ecological traits, flow indices, trait-environment relationships, thermal indices, regulated rivers.

Introduction

Guilds were originally defined as groups of species that exploit the same environmental resources in a similar way (e.g. foliage gleaning guild; Root 1967). Species traits have since been used to establish general rules in community ecology, linking groups of species through shared ecological traits along environmental or landscape gradients (Poff 1997, Mathieson et al. 2000, Lamouroux et al. 2002, Frimpong and Angermeier 2010b). Though grouping fishes by feeding modes (trophic groups) may be one of the oldest attempted non-taxonomic classification of fishes, guilds have since been expanded to group species that share morphological (Winemiller 1991, Reyjol et al. 2008) and reproductive traits (Balon 1975, Winemiller 2005), or specific river flow or hydraulic preferences (Cattanéo 2005, Lamouroux and Cattanéo 2006, Arthington et al. 2014). As such, guilds have long served as the "basic building blocks" of communities, focusing on groups of co-occurring species with particular trait-environment relationships, which reveal a structure not attributable simply to species composition and phylogeny (Hawkins and MacMahon 1989, Simberloff and Dayan 1991). Although phylogenetic relationship may be an indication of shared abilities or constraints, the notion that it can predict ecological function is under debate (Walter and Ikonen 1989). Trait-based approaches, however, are independent of phylogenetic associations and may infer causal relationships rather than relying on classifications related to selected traits.

Recently, guilds have been used to describe the community response to environmental perturbation, as they are thought to respond to environmental change in a more predictable manner than individual species (Austen et al. 1994). Fish traits such as trophic position and feeding behaviour (Karr 1981, Schlosser 1982), reproductive attributes (Balon 1975, Aarts and Nienhuis 2003, Winemiller 2005), and habitat preferences (Leonard and Orth 1988, Aadland

1993, Malavasi et al. 2004, Welcomme et al. 2006) have often been chosen to group species into guilds because of the known community-level relationships between these traits and river habitat variables, including those resulting from flow regulation (Vannote and Sweeney 1980, Lamouroux and Souchon 2002, Humphries et al. 2008). Morphological guilds have also been developed since fish morphology is quite variable and known to reflect aspects of the foraging behaviour and habitat use (Winemiller 1991, Ibañez et al. 2007, Reyjol et al. 2008). To date, however, comparing the relationships between the different types of guilds and variables reflecting environmental change are lacking. Such an analysis may highlight the guilds most susceptible to environmental change via a better understanding of these trait-environment relationships and increase our capacity to predict the effects of environmental change related to river regulation on these communities (Welcomme et al. 2006, Webb et al. 2010, Michel and Knouft 2014).

Numerous environmental attributes are known to affect the structure of river fish assemblages. In particular, specific guilds may be affected by variables relating to and including the biogeography, water temperature (Jackson and Harvey 1989, Malavasi et al. 2004), nutrient levels such as the abundance of organic substrates (Schlosser 1982), geomorphology, and river flow (Poff and Allan 1995, Ibarra et al. 2003, Lamouroux and Cattanéo 2006). Of these, catchment area and hydrologic regimes have often been cited as the most important environmental variables driving guild composition (i.e. the types of traits describing the guilds and proportion of species represented within) in lotic systems, implicating anthropogenic influences such as land-use and flow regulation in changing the structure of fish assemblages (Bunn and Arthington 2002, Ibarra et al. 2003, Welcomme et al. 2006, Rolls and Arthington 2014, Taylor et al. 2014). For example, benthic or pelagic guilds of fishes were associated with gradients in mean daily flows and their variability, baseflow, number of zero-flow days and high-flow pulses, among many others describing the low-flow hydrology across 20 catchments where flows were regulated (Arthington et al. 2014).

Although evidence pointing to changes in guild composition resulting from flow regulation has been acknowledged, the dynamics of river thermal regimes and the extent that thermal alteration due to river regulation affects fish communities remain poorly described (Murchie et al. 2008, Olden and Naiman 2010, Arismendi et al. 2013). Reyjol *et al*. (2001) did show that water temperature and flow regulation both influenced the progressive replacement of Salmoniforms by Cypriniforms from unregulated to regulated sites. However, a more comprehensive quantification of thermal regimes, beyond the scope of sampling fish during specific time periods or preferences/tolerances for certain water temperatures, and across a range of rivers remains a major challenge to understanding changes in fish community organization stemming from river regulation.

The significance of water temperature in riverine ecosystems has been widely acknowledged (Coutant 1999, Caissie 2006, McCullough et al. 2009). However, the limited number of temperature gauging stations, especially in Canada, has been a substantial impediment to acquiring suitable thermal data across temperate rivers (Guillemette et al. 2011, Maheu et al. in press). Integrating thermal regimes is therefore a vital step forward into setting more comprehensive environmental flow programs, as hydrologic regimes alone may not provide all the conditions required to understand the complex and interactive influences of hydrologic and thermal regimes (Puckridge et al. 1998, Olden and Naiman 2010).

This paper examines the relationships between guilds representing different ecological traits, phylogenetic associations, and environmental variables, notably those describing temperate river regimes. Specifically, the present objectives are to: 1) characterize hydrologic and thermal regimes across 25 rivers; 2) compare the relationships between guild models based on morphologic, trophic, reproductive, habitat, and behavioural traits with flow and thermal river variables; 3) contrast these relationships with those found using either phylogenetic associations or total fish community estimates (i.e. river densities or biomasses); and 4) identify the flow and thermal variables that best explain and predict fish guild densities and biomasses for each of the fish guild models across unregulated and regulated rivers. By achieving these objectives, we may identify the specific flow and thermal variables for understanding how freshwater fish communities respond to environmental changes stemming from river regulation.

Materials and Methods

River fish densities and biomasses were estimated along with flow and thermal regimes across 25 Canadian temperate, unregulated and regulated rivers. Five fish guild models each based on morphologic, trophic, reproductive, habitat preferences, behavioural traits and one model representing phylogenetic associations were collated from literature to compare the relationships among guild models and between guilds of a given model with explanatory variables describing river hydrologic and thermal regimes.

River segments, sites, and surveying methodology

A total of 25 river segments were selected based on surveying feasibility (i.e. wadeable stretches of river across the entire wetted width) and road access, across three rivers in Alberta, five in Ontario, 14 in Québec and three in New Brunswick (Figure 1). River segments ranged from 5-27 km in length (Mississagi and Kananaskis rivers, respectively; mean = 12.3 km, standard deviation = 6.1 km). Of these, 14 rivers were unregulated while the remaining 11 were regulated for hydro-electric purposes (Table 1). Regulated rivers differed according to three flow management practices: run-of-river (ROR), storage with and without hydro-peaking. ROR type rivers generally have a small reservoir, where water flows freely though turbines and has little to no effect on downstream hydrologic regimes (Bratrich et al. 2004). Conversely, storage with and without hydro-peaking practices have large storage reservoirs that allow managers to release water upon demand (i.e. for irrigation or for hydropower demands), temporally shifting the natural hydrologic regime and attenuating seasonal high flows. Hydro-peaking type rivers additionally provoke frequent and rapid flow peaks that are timed to match daily consumption needs, causing significant flow alteration (Zimmerman et al. 2010) and subsequent ecological impacts (Bond et al. 2015, Macnaughton et al. 2015b, Senay et al. 2016). Despite the variability in hydrologic regimes stemming from regulation, all unregulated and regulated rivers segments were analysed together to assess the overall effect of river hydrologic and thermal regimes on fish guild models. To ensure that the fish communities surveyed downstream from dams had been interacting over a long period of time, rivers with older dams (40+ years) were selected.

For the 25 river segments studied, a total of 870 sites were surveyed, each measuring approximately 300 m² (~5 by 60 m, width and length of a site), with a distance of 60 to 100 m separating successive surveying sites. The fish data and sampling for these sites are largely the same as described in previous thesis chapters. The position of the first sampling site was randomly selected prior to field surveying and subsequent sites were positioned following a systematic design (i.e. left shore, middle, right shore, left shore). Fish community surveys were conducted during the summer months (late June to early September) from 2011 to 2013.

Paired single-pass electrofishing and snorkelling surveys were carried out at each site, in random order and at roughly the same time between 08:30 and 18:00 on consecutive days, with a minimum 24-hr recovery interval to allow fish to re-establish themselves after a surveying event. Electrofishing surveys were conducted by teams of three, moving upstream in a zigzag fashion. LR-24 backpack electrofishing units (Smith-Root, Vancouver, WA) were used in accordance with Ontario Ministry of Natural Resources (OMNR) policy standards (Jones 2011). After each survey, fish captured were identified, measured (total length, ± 0.1 cm), and weighed (wet blotted weight, ± 0.1 g). Visual surveys were conducted using two trained divers, swimming slowly upstream (approximate speed of 6 s/m^2). Species were identified and lengths estimated by 5 cm-increment size classes throughout each visual survey. Specific information pertaining to electrofishing and snorkelling surveying methods and parameters have been detailed (Macnaughton et al. 2015a, Senay et al. 2016).

For both electrofishing and visual surveys, fish density estimates were calculated for every species (fish ≥ 3 mm in total length) collected at each site. Site- and species-specific biomass estimates were generated by summing either the masses recorded during the electrofishing surveys or the mass estimates inferred from the observed length-weight relationships applied to the visual survey data (Le Cren 1951). The data for each species collected via the sampling method that yielded larger density or biomass estimates at each site were retained. Fish densities and biomasses per site therefore represented the greatest estimates for each species and likely minimized any species-specific biases of the two sampling methods (Macnaughton et al. 2015a).

Fish variables

Considering the large numbers of species present across the rivers (57 species) and the variation of their traits, the guild analyses described below were conducted on an extensive list of traits selected to represent the range of fish species occurring in the rivers (Table S1,

Appendix D). Quantitative ecological traits (e.g. trophic position ranging from 1 to ~4) were standardized (i.e. centred and reduced) prior to cluster analysis. K-means partitioning was then conducted on species' ecological traits ascribed to each of the type of guilds and a range of simple structure indices (SSI criterion; Oksanen et al. 2011) along with expert knowledge were used to guide the number of ecologically relevant guilds. For example, 10 ecological traits representing fish habitat preferences (e.g. preference for cold, cool, and warm water temperatures or tolerance to/for anthropogenic disturbances and turbidity levels) were coded for every species surveyed. K-means partitioning analysis conducted on these traits by species (SSI criterion suggested six groups) along with expert knowledge on the groups of species obtained, resulted in seven habitat guilds (Table S5, Appendix H). Phylogenetic distances between the fish species surveyed (Hubert et al. 2008) was also established and served as our null hypothesis.

Site- and species-specific density and biomass estimates described above were then used to derive mean river densities and biomasses for each of the guilds (e.g. density and biomass for each of the seven habitat guilds). Total fish density and biomass estimates per river segment were also calculated. Guild density and biomass estimates per river segment, along with total estimates (i.e. fish densities and biomasses per river segment) were subsequently transformed using the fourth root to achieve more normalized distributions.

Hydrologic indices

Daily and hourly flow data were obtained from the Centre d'Expertise Hydrique du Québec (CEHQ) and HYDAT from the Water Survey of Canada (2013) national flow gauge networks, and hydro-electric companies: Trans-Alta, Brookfield Renewable Power and NB Power. We analysed a 13-year time series (1997-2009) that reflected the effects of temporal and climate variability on the hydrologic regime and the multi-year index differences characterizing the 25 rivers (Kennard et al. 2010). Flow indices representing ecologically relevant components of the hydrologic regime (magnitude, frequency, duration, timing and rate of change of daily and hourly flows) included, among others, the Indicators of Hydrologic Alteration (IHA; Richter 1997, Olden and Poff 2003). All flow indices described by McLaughlin *et al.* (2014), in addition to those created to capture hourly variations in the flow record (Zimmerman et al. 2010, Macnaughton et al. 2015b), were calculated for each of the rivers surveyed for a total of 211 flow indices. Flow indices expressed as discharge units (volume per time) were normalized by dividing these indices by the median flow (daily or hourly as appropriate) for the available flow records (McManamay et al. 2012c). A preliminary removal of flow indices that did not exhibit any inter-river variability or had skewed data due to winter ice conditions reduced the number of indices to 77. Together, these indices described the magnitude (42), frequency (6), duration (15), timing (4) and rate of change (10) of river flows.

Thermal indices

Summer water temperatures were measured using temperature data loggers (Hobo Pendant Temp, precision of ± 0.5°C, ONSET® Computer Corporation) anchored along the 25 river segments. For 22 of the 25 river segments, temperature data loggers were placed between the most upstream and downstream sites. For the three remaining river segments, loggers were located 22 to 69 km away from sites (Table 1). Loggers were deployed in riffle, run or shallow pool river habitats to limit any potential water temperature anomalies that may arise from placing loggers in deep pools, shallow shore habitats and/or tributaries. Loggers were set to record ambient water temperatures every 15 minutes, from early June to late-September in 2013, save for the Elbow, Bécancour and Waterton rivers, for which loggers were placed in rivers over similar time periods in 2006, 2012 and 2014, respectively. Due to atypical flooding events in

Alberta in 2013 (Phillips 2013), many loggers were lost, limiting the use of temperature data in those rivers. Between 3 and 15 temperature loggers were retrieved and used to calculate summer thermal profiles for each of the rivers studied. Water temperature data extracted from loggers were checked for erroneous measurements (i.e. air exposure), which were removed from thermal profiles. Loggers with <5 days of data removed were kept, and data from these loggers were averaged per day and hour, for each of the loggers, to derive a total of 294 thermal indices describing all components of thermal regime (magnitude, variance, frequency, duration, timing and rate of change of daily and hourly temperatures (Olden and Naiman 2010). Median values per thermal index were calculated for each river from all retained loggers to further decrease the incidence of local thermal anomalies.

Of the 294 thermal indices calculated, 21 indices were selected to reliably represent the river average thermal regime from a single summer, the biological relevance, and the type of thermal alteration expected for regulated rivers. For example, thermal indices were based on the warmest week rather than on the warmest day because the former is more consistent between years than the warmest day. These 21 indices described the magnitude (7), variance (6), frequency (1), duration (2), timing (1) and rate of change (4) of water temperatures for the month of July or for a standardized 9-week summer period, which was centred on the warmest week for unregulated rivers to allow inter-river comparisons (Table 2).

Statistical analyses

To reduce the number of explanatory variables chosen to represent hydrologic and thermal regimes across the rivers surveyed, we ran several principal component analyses (PCA), ensuring that the number of observations (i.e. 25 rivers) was greater than the number of explanatory variables selected. Specifically, the 77 hydrologic indices characterizing the hydrologic regime for the 25 rivers were summarized by conducting five separate PCAs on the correlation matrices for each of the hydrologic regime components (magnitude, frequency, duration, timing, and rate of change). River scores for PC axes describing a greater fraction of the variation than the broken-stick null model were retained (Legendre and Legendre 2012). Performing separate PCAs for each of the hydrologic regime components ensured that indices describing major sources of variation within each component contributed to the retained PC axes, and that subjectivity associated with the process of selecting individual indices was reduced. Flow indices that contributed the most to the retained PC axes (i.e. top loaders) were identified to explain dominant patterns of flow variation measured in our rivers as described by each of the flow components.

Likewise, the 21 thermal indices characterizing each river's thermal regime were subjected to PCAs to identify the main axes of variation within each thermal regime component across all rivers. Due to small number of thermal indices describing the frequency (1), duration (2) and timing (1) of water temperatures, these thermal regime components were grouped with other correlated components and three PCAs on thermal indices were conducted instead of a possible six: 1- magnitude, frequency, and duration ($n = 10$); 2- variance ($n = 6$); and 3- timing and rate of change ($n = 5$). PC axes retained were selected as done for hydrologic indices. Top thermal loaders were identified for each retained thermal PC axis. Correlations between hydrologic and thermal PC axes were computed to assess whether the explanatory variables summarizing hydrologic and thermal regimes were highly correlated with one another at $r > 0.8$ (correlation threshold; P. Legendre, personal communication March, 2016).

Redundancy analyses (RDA) with 9999 permutations (Legendre and Legendre, 2012) were used to assess the relationships between river biomass and density estimates for each of the types of guilds based on morphologic, trophic, reproductive, habitat, behavioural traits, and phylogenetic associations (6 response matrices), and hydrologic and thermal PC axes (12 explanatory variables). Additional relationships using the total river density and biomass estimates as response variables (2 vectors) were also conducted to compare with multivariate fish guild models. A permutational forward selection of explanatory variables was subsequently conducted for significant relationships to identify the best variables for the model describing each response matrix and vector (Blanchet et al. 2008, Dray et al. 2011). The proportion of variation explained by selected explanatory variables for each of the response matrices was determined using a cumulative adjusted R^2 ($CumR^2_{Adj}$). Individual canonical axes were also tested for significance to determine whether axes represented variations that were more explained than random (Legendre and Legendre 2012). For the leading fish guild model (greatest R^2_{Adj}), the response matrix and explanatory variables were plotted in reduced space (correlation biplot), where the focus is on the relationships among habitat guilds, explanatory variables (flow and thermal PCs), and each other. A distance biplot was also illustrated to show the relationships between explanatory variables and the position of our rivers, as well between unregulated and regulated rivers in reduced space. To facilitate interpretation, RDA 1 and RDA 2 axes were rotated to project the first selected environmental variable on RDA 1. This was done by calculating the angle between RDA 1 and this selected variable and rotating all other points in the figure along this angle.

Each model's ability to predict new responses from selected explanatory variables was quantified using the cross-validation R^2 (R^2_{CV}) via a leave-one-out cross-validation approach

(Guénard et al. 2013). R^2_{CV} is bound between $-\infty$ and 1, where $R^2_{CV} = 1$ when predictions perfectly match the observations and $R^2_{CV} \leq 0$ when predictions are inaccurate or no better than what would be expected from chance alone. All statistical analyses were performed in R (R Core Team 2014).

Results

Description of fish guilds

The eight morphologic guilds differed from one another with respect to traits describing general body shape (discoid, cylindrical or eel-like), the mouth position (subterminal vs. terminal), and fin types, sizes, and placements (soft or spiny dorsal rays, large pectoral fins and abdominal pelvic fins, respectively; Table S2, Appendix E). The six trophic guilds revealed the shared species diet preferences and associated trophic level, with a particular distinction between guilds that eat small prey and generally shift their diet ontogenetically, have moderate trophic levels, and prey on larger fishes, amphibians and mammals (Table S3, Appendix F). The eight reproductive guilds generally grouped traits that depicted reproductive behaviours (nest building and/or guarding), spawning time (fall or summer), fecundity level and age of maturity, and spawning habitat preferences (marine, riffles or shallow waters; Table S4, Appendix G). The seven habitat guilds differed from one another with respect to preferences for warm, cool or cold water temperatures, slow-moving or riffle water velocities and tolerance levels to water turbidity and/or anthropogenic perturbations (Table S5, Appendix H). The six behavioural guilds depicted fishes that shared similar feeding (grazing, pursuit or sorting), migratory (anadromous), and other (territorial or schooling) behaviours (Table S6, Appendix I). Lastly, the phylogenetic groups were based on the phylogenetic distances between freshwater species in Canada (Hubert et al. 2008) and cut at seven groups to facilitate the comparison of relationships between different types of traits describing guilds (Table S7, Appendix J).

Characterization of hydrologic and thermal regimes

The PCAs conducted separately for each of the flow and thermal components resulted in a total of 12 PC axes (9 and 3 PC axes describing flow and thermal components, respectively) that represented between 61-85% of the variation in the groups of indices (Table 3). The magnitude of summer water temperatures (PC1 Magnitude of temperatures) combined thermal indices that described the cumulative degree days at mid-summer (DD_midsum), the summer average in daily mean water temperatures (MSmn), and the July average in daily mean water temperatures (MOmn7). The intra-annual flow variability (PC1 Magnitude of flows) depicted the difference in extreme flows within a year: the variability in daily flows (MA3), the ratio between maximum annual flow and median flow (MH14), and the ratio between the mean of the upper quartile and median flow (MH27). Only 2 pairs of PC axes had correlation coefficients at the $r \geq 0.8$ level, suggesting that explanatory variables were not redundant. Exceptions were found for correlations between variables describing the intra-annual flow variability (PC1 Magnitude of flows) with the proportion of rise days (PC2 Rate of change of flows; $r = 0.80$), and the flashiness of summer water temperatures (PC1 Rate of change of temperatures) with the fall rate of flows (PC1 Rate of change of flows; $r = 0.84$).

Comparison of fish guild models

The PC axes describing the flow and thermal components significantly explained fish density and biomass estimates for all guild models (a total of 12 models representing densities and biomasses of guilds and phylogenetic associations). Since the results for fish guild models using biomass estimates were comparable to and slightly better than those using density estimates, our results focused on the former fish guild models. The greatest R^2_{Adj} values were found for habitat and trophic types of guilds ($R^2_{Adj} = 0.44$ and 0.41; p-values = 0.001 and 0.002, respectively), however all guild models yielded comparable values (range of $R^2_{Adj} = 0.26\text{-}0.44$; Figure 2). Our results further showed that all guild models outperformed the null hypothesis (phylogenetic groups $R^2_{Adj} = 0.26$); this suggests the presence of functional relationships not attributable simply to phylogeny. In addition, selected environmental variables did not significantly explain total river density and biomass fish estimates (p-values = 0.22 and 0.69, respectively). Furthermore, fitting non-linear relationships (canonical correlation analysis (CCA) or multivariate regression trees (MRT)) were not as powerful or predictive, suggesting that RDAs were an appropriate tool to investigate the various guild relationships with selected environmental variables.

The explanatory variables most often selected by fish guild models (>86% of models) were the magnitude of summer water temperatures (solid black bars, Figure 2) followed by the intra-annual flow variability or the difference in the extreme flows within a year (thinly-spaced dashed lines, Figure 2). Highly correlated flow and thermal variables describing the proportion of rise days (PC2 Rate of change of flows), fall rates of flows (PC1 Rate of change of flows) and flashiness of summer water temperatures (PC1 Rate of change of temperatures) were not selected in any of the fish guild models. When habitat and trophic guild models were computed without the thermal components, the flow components significantly explained biomass estimates. However, these model strengths based on R^2_{Adj} were 13 and 20% lower without thermal components, respectively. The same was true when flow PCs were removed from the analyses (9 and 10% lower, respectively).

Variables selected by forward selection significantly predicted the different types of guild models (R^2_{CV} values; black points, Figure 2). The best predictive model (largest R^2_{CV}) was found for phylogenetic associations ($R^2_{CV} = 0.73$), but these results were likely driven by the uneven distribution of rare species within a guild (e.g. a single group composed of *Fundulus diaphanus* or a few species belonging to the petromyzontids and gasterosteids groups, respectively). When phylogenetic predictive models were conducted for groups with > 50% presences across rivers, the model's predictive power decreased to $R^2_{CV} = 0.09$. Lastly, explanatory and predictive power results were fairly comparable, suggesting that the models were not overfitted and good at explaining and predicting the effects that selected flow and thermal variables had on different fish guilds.

Habitat guild-environmental relationships

The habitat guild model served as an example to illustrate the relationships between the biomasses of habitat guilds and flow and thermal PC axes (Figure 3; correlation biplot). The magnitude of summer water temperatures, the intra-annual flow variability, and the long-term flow variability explained approximately 39% of the variation of habitat guilds constrained on the first two redundancy axes (RDA 1 = 33% and RDA 2 = 13%). Specifically, the biomass of species that preferred habitats with warm to cool water temperatures and macrophyte cover (habitat guild 1) was related with higher magnitude of summer temperatures, whereas the biomass of species that preferred cold water temperatures (habitat guild 3) was related with lower water temperature magnitudes. Greater flow variability was also shown to drive guilds of fishes preferring riffle type habitats (habitat guilds 3 and 4), while lower flow variability was related with guilds of fishes preferring warm and turbid habitats with cover and are more tolerant to perturbation (habitat guilds 1 and 5). This suggests that fishes that prefer warm, turbid waters and more tolerant to perturbations are likely to thrive in rivers where flows are more constant and generally warmer during summer months (i.e. regulated rivers). With the exception of two rivers (Kananaskis and Elbow Rivers; triangle and circle icons to the far left of the inset figure), all rivers exhibited moderate to high magnitude of summer temperatures and flow variability. Despite these findings, no discernible general pattern was observed between regulated and unregulated rivers within the same constrained space (Figure 3; inset).

Discussion

Characterization of river regimes

By quantifying river hydrologic and thermal regimes separately, we showed which independent drivers significantly explained and predicted the density and biomass across fish guild types. Specifically, our results are among the first to point to the importance of indices describing the magnitude of summer water temperatures and those depicting the intra-annual variability in flows for driving guild composition. Given that habitat guild model strength was decreased when either selected flow or thermal variables were omitted from the analyses and that selected flow and thermal variables were not highly correlated with one another, we demonstrated the importance of integrating thermal regimes in hydro-ecological studies. These findings align with previous assertions that the interplay of variables describing river hydrologic and thermal regimes is crucial in shaping fish community structure (Reyjol et al. 2001, Murchie et al. 2008, Olden and Naiman 2010).

Furthermore, using flow index analyses (McManamay et al. 2012c, Macnaughton et al. 2015b) as a conceptual template allowed us to depict river thermal regimes as a suite of thermal indices that capture the range of conditions characterizing summer water temperatures and reduce the number of redundant indices among them. The magnitude of summer water temperatures was consistently selected first across guild models, giving importance to thermal indices, notably, those that describe the cumulative degree days at mid-summer, the average daily mean in water temperatures, and the July average in daily mean water temperatures. We further identified dominant patterns of water temperature variability (i.e. daily range and flashiness of summer water temperatures) that may have had an effect on fish community organization. Due to the similarity in ecological traits describing types of groupings, such as traits depicting spawning habitat preferences (habitat guilds) and type of spawning substrate, water velocities and depths (reproductive guilds), we expect that similar relationships with explanatory variables may have occurred between type of fish guilds. This might explain why differences in model outputs (R^2_{Adj}) were subtle among guild types. These results collectively suggest that thermal regimes are crucial when developing fish guild models because thermal regime-trait relationships exist between them.

Fish guild models

All fish guild models were significantly explained and predicted by explanatory variables representing river hydrologic and thermal regimes across rivers, whereas total fish density and biomass were not. They also performed better relative to studying phylogenetic associations, suggesting that models based on trait-environmental relationships were better than those based on phylogeny, further supporting the original "basic building blocks" guild concept (Simberloff and Dayan 1991). This is to be expected seeing as the distribution of species differed in the rivers surveyed across Canada, while the ecological roles and functional attributes shared by species may not have across this same geographical extent. Furthermore, there is evidence from across the plant and animal kingdoms that ecological traits or functional groupings are better at explaining variation compared to phylogenetic associations, as they are more responsive to proximate environmental factors (Walter and Ikonen 1989, Weiher et al. 1998, Mathieson et al. 2000, Frimpong and Angermeier 2010b). Our results were thus in line with much of the guild literature.

We had expected that guilds grouping species according to preferences for habitat conditions may be linked to flow and/or thermal variables, as was the case for Lamouroux and Cattanéo (2006), Arthington *et al.* (2014), and Rolls and Arthington (2014). Although habitat guilds had the greatest R^2_{Adj}, all explanatory fish guild models yielded significant results, pointing to the existence of functional relationships between the flow and thermal variables identified and the range of species traits encompassed between the different types of guilds. Predictive model results further supported these findings, indicating that fish guild models were accurately predicted by the selected flow and thermal variables across rivers. Though phylogenetic and reproductive fish guild models yielded the largest R^2_{CV}, we have reason to believe that the models' predictive power may have been substantially influenced by species prevalence (i.e. the proportion of rivers where a species was surveyed), resulting in poorly performing models that, otherwise, would be viewed as powerful (Olden et al. 2002).

Applications of habitat guild-environmental relationships

Habitat guild relationships with selected explanatory variables were observed. For example, the habitat guild that preferred cold water, riffle-type habitats and was intolerant to environmental perturbations was related with high annual flow variability and low magnitudes of summer temperatures. As such, species representing this guild, which included sculpins (*Cottus cognatus, Cottus ricei*) and salmonids (*Oncorhynchus clarkii, Oncorhynchus mykiss, Salmo salar, Salmo trutta, Salvelinus confluentus, Salvelinus fontinalis*), may be more vulnerable to anthropogenic perturbations via significant decreases in variables describing annual flow variability or increases in the cumulative degree days at mid-summer or the summer average in daily mean water temperatures. As river regulation in our systems tends to decrease river flow variability (McLaughlin et al. 2014) and contribute to general patterns of thermal alteration, such as reducing water temperature variability and increasing the magnitude in the late summer temperatures (Maheu et al. in press), conservation efforts may begin with these more vulnerable habitat guilds, because trait-based intolerances to perturbations may be linked with habitat preferences characteristic of unregulated systems. In other words, planned modifications to unregulated systems may seriously impact guilds preferring cold and faster moving habitats via the stabilization of natural flows and increased summer water temperatures that often occurs with river regulation. By ranking the different habitat guilds along summer water temperature magnitudes, for example, we were able to determine the guilds most susceptible to changes in temperature magnitudes, indicating that the conservation of groups of species most vulnerable to increases in water temperatures and variability should be prioritized. Further research, however, is needed to quantify the causal relationships between specific guilds and the environmental drivers concerned in order to better understand the degree to which these guilds may potentially be impacted.

The importance of summer water temperature regimes for understanding the organization of different types of guilds has been elucidated here, but year-round thermal regimes is likely important for fish assemblages that rely on different thermal cues for initiating various physiological and behavioural activities (e.g. spawning and recruitment of fishes, timing and availability of resources, cold water thermal tolerances; Elliott 1982, Rolls et al. 2013). Our results also revealed some degree of regional discrimination as glacier-fed rivers located in

Alberta (Kananaskis and Elbow rivers) were strongly associated with low summer temperature variability; this result seems to be an artefact resulting from the absence of great temperature variability during the summer months for these rivers, especially when compared to rivers located in southern Quebec. The study's large spatial scale and short time-period (summer months) might also explain why general patterns of water quality and quantity were not observed between regulated and unregulated rivers. A preliminary investigation of thermal profiles across our regulated rivers suggested that the variability in water temperatures was either reduced or increased, depending on the flow management practices adopted: storage or hydro-peaking regulation practices, respectively (Maheu et al. in press). In fact, we found that certain regulated rivers were associated with high flow variability while others were not, suggesting that differences in river regulation practices may have played a role in driving fish guild composition. However, a preliminary analysis assessing the proportions of explained variation from selected environmental variables vs. regulation practices (ROR, storage and hydro-peaking) showed that while flow and temperature variables significantly explained fish habitat guilds, regulation practices did not. Although the habitat guilds that preferred warm water temperatures were associated with regulated rivers, future research considerations should include geographical location of the river and/or headwaters, timing of surveys, and equal representation among regulation practices.

Implications for river management

Another important contribution of this study centred on the identification of ecologically relevant thermal indices and the value of both hydrologic and thermal regimes in driving the river fish guild responses. The European Water Framework Directive (WFD) outputs have been known to greatly improve the assessment of different stressors including river regulation on the ecological integrity of systems (Hering et al. 2010). The use of trait-based approaches in this study also contributes to developing transferable methods for establishing stressor-trait relationships across large geographical areas. From an applied standpoint, our findings identified the different guild trait-environment relationships for a large number of rivers and highlighted the importance of comprehensive hydrologic and thermal regime conservation on which management efforts focused on maintaining the ecological integrity of rivers should rely. Furthermore, the observed trait-environment relationships may aid in mitigating the effects of modifying hydrologic regimes with selective water release from dam outflows, benefitting specific guilds via either hypolimnetic (cold) or epilimnetic (warm) water release from reservoirs (Olden and Naiman 2010). Now that we have shown the importance of thermal regimes, quantified separately from hydrologic regimes, we may begin to attempt adaptive flow and thermal management strategies to better conserve ecosystem resources.

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Table 1. Description of the 25 Canadian rivers surveyed: province, regulation type (run-of-river (ROR), storage, hydro-peaking), watershed area, length of river surveyed, position vis-à-vis dams if applicable, flow gauges, and thermal loggers.

River	Province	Regulation type	Watershed area (km²)	Length of river segments surveyed (km)	Distance of river segment to dam (km)	Distance of river segment to flow gauge (km)	Distance of river segment to thermal logger (km)
Elbow	Alberta	unregulated	791	22.3	NA	0.0	33.0
Kananaskis	Alberta	hydro-peaking	362	27.4	3.0	1.0	0.7
Waterton	Alberta	storage	1631	23.7	0.7	2.4	22.0
Dee	New Brunswick	storage	141	13.7	0.2	0.2	0.01
Gulquac	New Brunswick	unregulated	110	8.8	NA	62.0	8.9
Serpentine	New Brunswick	storage	47	18.2	0.2	0.2	0.0
Aubinadong	Ontario	unregulated	1440	9.8	NA	1.0	0.05
Batchawana	Ontario	unregulated	1190	7.8	NA	0.0	0.0
Goulais	Ontario	unregulated	1637	7.2	NA	15.0	0.0
Magpie	Ontario	hydro-peaking	1930	10.0	8.0	8.0	4.09
Mississagi	Ontario	hydro-peaking	4040	4.9	8.0	8.0	5.46
Au Saumon	Québec	unregulated	738	8.2	NA	0.0	0.0
Bécancour	Québec	unregulated	917	12.7	NA	0.0	69.0
Coaticook	Québec	ROR	362	7.8	1.0	11.0	0.0
Du Loup	Québec	unregulated	515	7.0	NA	3.0	4.46
Du Sud	Québec	ROR	821	15.4	1.0	0.2	0.0
Eaton	Québec	unregulated	646	10.2	NA	1.5	0.0

Etchemin	Québec	ROR	1160	6.8	3.0	1.7	0.0
Kiamika	Québec	storage	702	14.8	0.3	3.3	0.04
Nicolet	Québec	unregulated	1550	18.8	NA	0.0	0.0
Noire	Québec	unregulated	401	12.9	NA	24.0	0.0
Ouelle	Québec	unregulated	796	7.4	NA	3.5	2.83
Petit Saguenay	Québec	unregulated	712	6.0	NA	10.0	0.0
Picanoc	Québec	unregulated	1290	9.2	NA	3.1	0.6
St Francois	Québec	storage	2940	7.9	6.0	9.0	3.54

Table 2. Identification of the 21 thermal indices calculated to characterize the thermal regime across the 25 rivers.

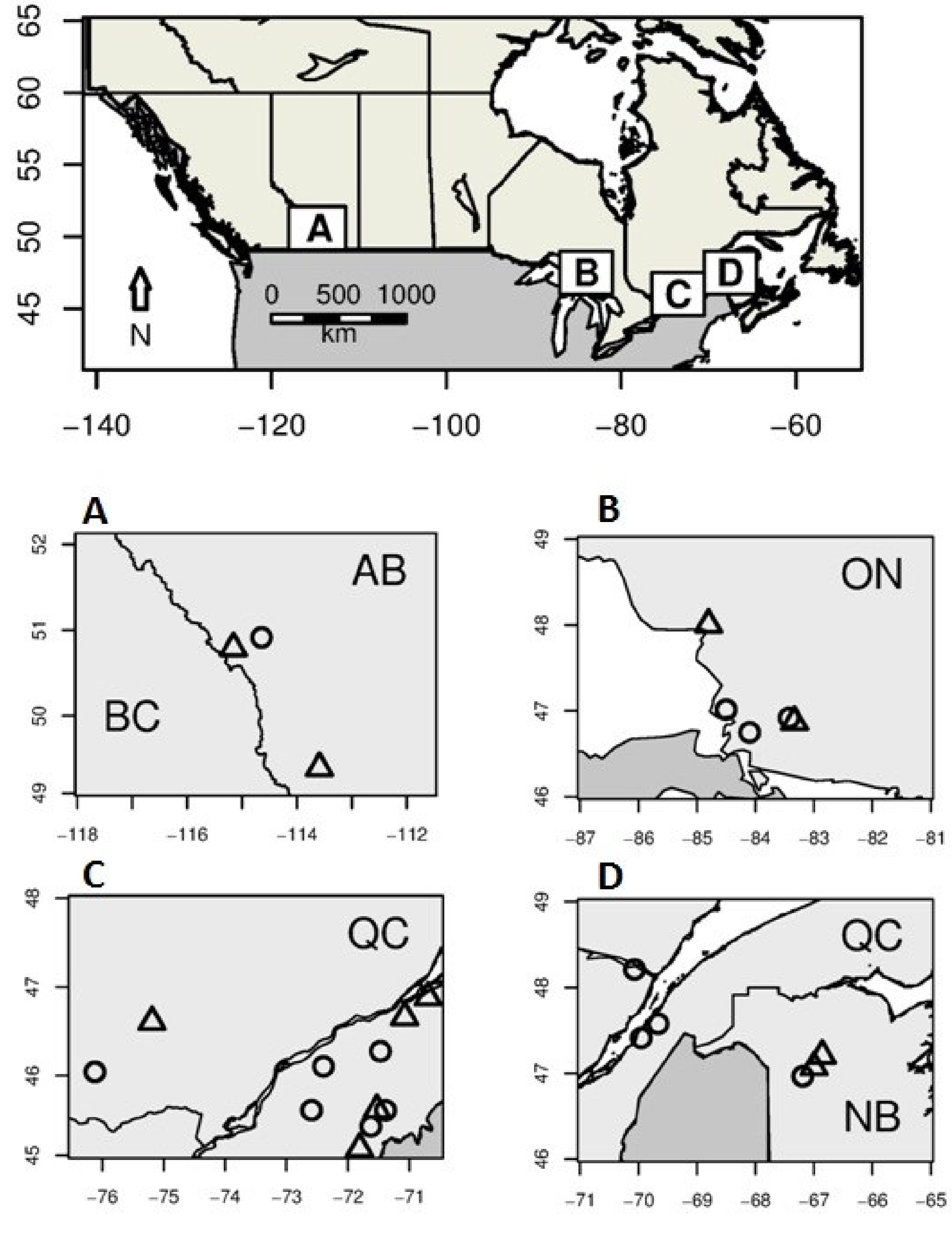
Component	Name of index	Data	Description	Units	Period of time
Magnitude	MOmn7	Daily	Monthly average in daily mean water temperature	°C	July
	MOmin7	Daily	Monthly average in daily minimum water temperature	°C	July
	MOmax7	Daily	Monthly average in daily maximum water temperature	°C	July
	MSmn	Daily	Average daily mean water temperature	°C	Summer
	MWmax	Daily	Maximum weekly average in daily mean water temperature (during TWmax)	°C	Summer
	DD_midsum	Daily	Cumulative degree-days at mid-summer (week TWmax-4 to TWmax inclusively)	°C-days	Summer
	DD	Daily	Cumulative degree-days	°C-days	Summer
Variance	RNGmn7	Hourly	Monthly average daily range (daily max-daily min)	°C	July
	RNGmax7	Hourly	Monthly maximum daily range (daily max-daily min)	°C	July
	RNGSmn	Hourly	Mean daily range during summer period	°C	Summer
	RNGSmin	Hourly	Minimum daily range during summer period	°C	Summer
	RNGSmax	Hourly	Maximum daily range during summer period	°C	Summer
	AMPLW	Daily	Median of weekly amplitude (max. daily mean water temperature - min. daily mean water temperature)	°C	Summer
Timing	TWmax	Daily	Timing of maximum weekly average in daily mean water temperature (MWmax)	Week number	Summer

Rate of change	RARev	Hourly	Average number of reversals per day during summer period for upstream-most logger	number of reversals	Summer
	RAPos	Daily	90th percentile of positive changes in daily mean water temperature	°C	Summer
	RANeg	Daily	90th percentile of absolute negative changes in daily mean water temperature	°C	Summer
	RARatio	Daily	Absolute value of ratio between RAPos and RANeg	none	Summer
Frequency	FDmax25	Daily	Number of days where daily maximum water temperature was above 25 °C	days	Summer
Duration	FDconsmax25	Daily	Maximum number of consecutive days where daily maximum water temperature was above 25°C	days	Summer
	FDconsmax_min20	Daily	Maximum number of consecutive days where daily minimum water temperature was above 20°C	days	Summer

Table 3. Results of PCAs computed independently on groups of flow and thermal indices; the number of indices per group is shown in brackets. Central columns: the top loaders for the first (1, 2 or 3) axes in each analysis are listed. Right: proportion of variation of the stated group of indices accounted for by 1, 2 or 3 PCA axes.

Flow and thermal components (# indices)	**Principal component axes**			**Cumulative variation explained (%)**
	PC1 Description (Top loaders)	**PC2 Description (Top loaders)**	**PC3 Description (Top loaders)**	
Magnitude of flows (42)	Intra-annual flow variability (MA3, MH14, MH27)	Intra vs. inter- year variability in monthly flows (MA31, MA33, MA40)	Long-term flow variability (MH17, MA7, MA8, MH9)	72
Frequency of flows (6)	Flood frequency (FH8, FH1, FH5)	-	-	68
Duration of flows (15)	Magnitude of spring flood (DH13, DH12)	Low exceedence flows (DL14)	-	78
Timing of flows (4)	Predictability of daily flows (TA2, TH2)	-	-	61
Rate of change of flows (10)	Fall rate of flows (RA7, nRA3)	Proportion of rise days (RA5)	-	83
Magnitude of temperatures (10)	Magnitude of summer water temperatures (DD_midsum, MSmn, MOmn7)	-	-	85
Variance of temperatures (6)	Daily range in temperatures over summer (RNGmax7, RNGSmn, RNGmn7, RNGSmax)	-	-	81
Rate of change of temperatures (5)	Flashiness of summer water temperatures (RANeg, RARev)	-	-	65

Figure 1. Map of the study area showing the 25 rivers surveyed in Canada (principal map). Enlarged views depict rivers located in A) Alberta (AB), B) Ontario (ON), C) Québec (QC), and D) New Brunswick (NB). Open circles and triangles refer to unregulated and regulated rivers, respectively.


65
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−114
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−72
−71
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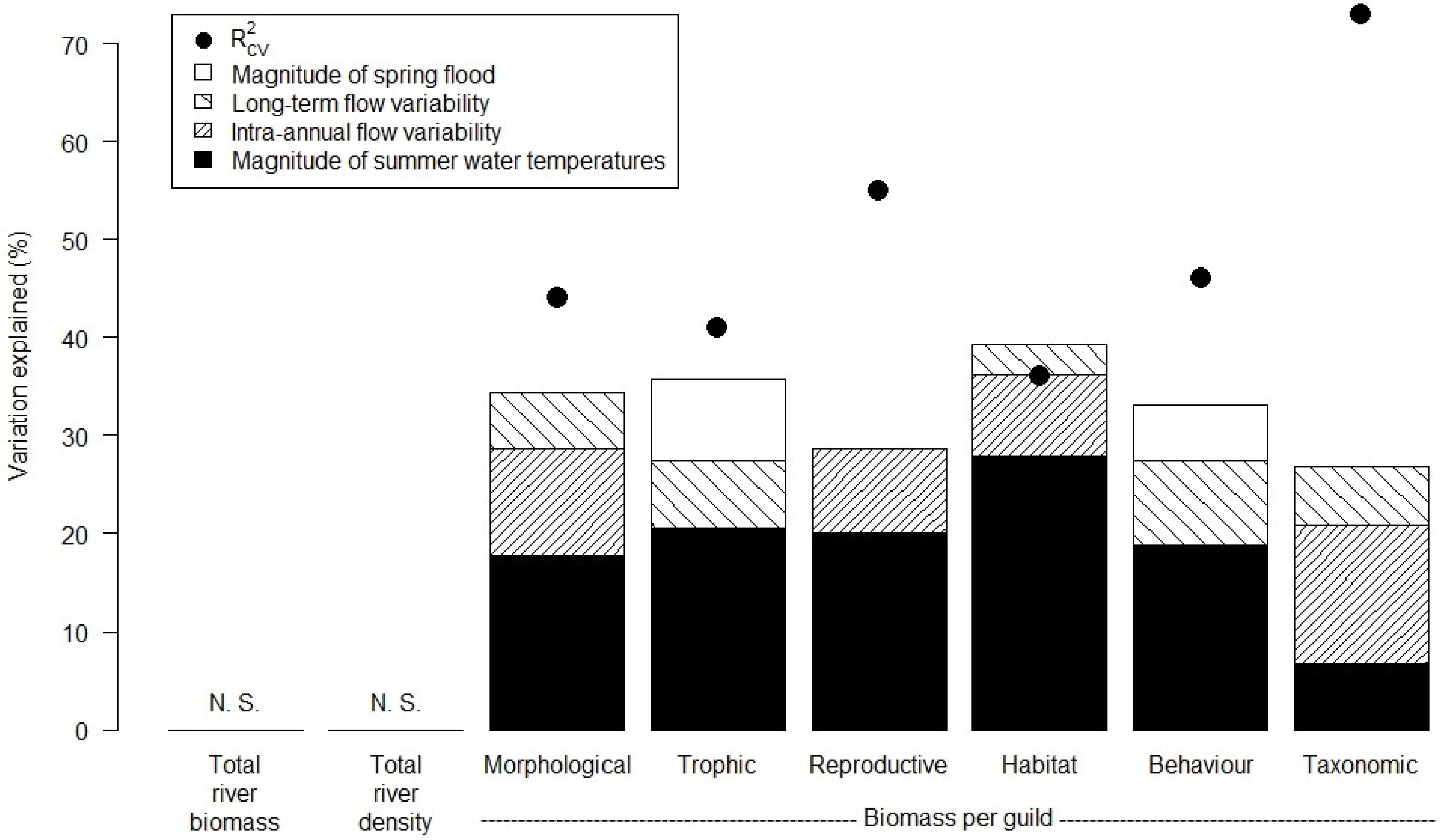
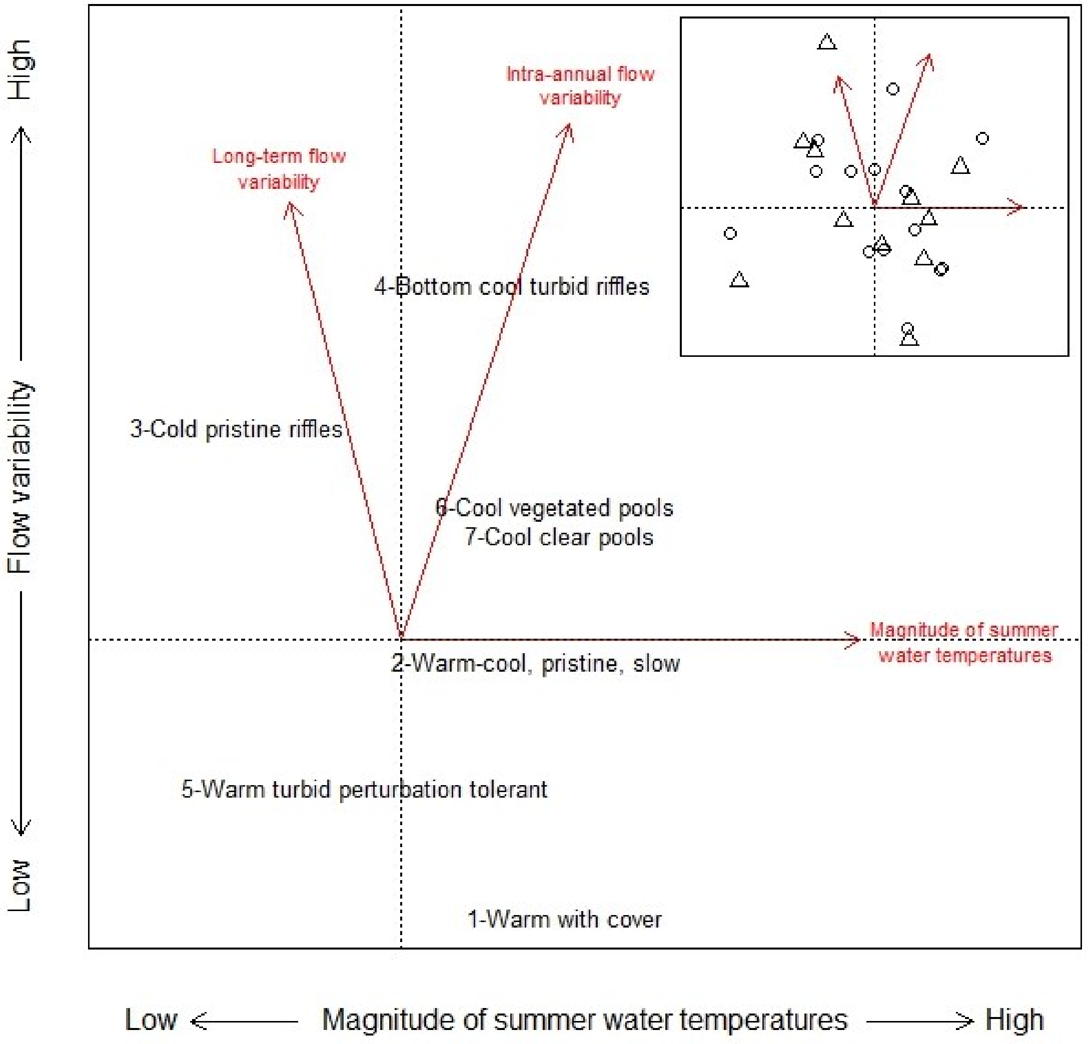
QC
NB
49
48
47
46
−71
−70
−69
−68
−67
−66
−65

Figure 2. Stacked bar plot of the proportion of variation explained by each fish guild explanatory (RDA) and predictive (cross-validation, CV) model, and selected flow and thermal variables. Left: total river density and biomass models as a function of all flow and thermal PC axes are also listed. NS refers to non-significant results.



R^2_{CV}
Magnitude of spring flood
Long-term flow variability
Intra-annual flow variability
Magnitude of summer water temperatures
Variation explained (%)
70
60
50
40
30
20
10
0
N. S.
N. S.
Total river biomass
Total river density
Morphological
Trophic
Reproductive
Habitat
Behaviour
Taxonomic
Biomass per guild

Figure 3. The relative importance (correlation biplot) of the biomass estimates for habitat guilds as a function of selected flow and thermal variables (red arrows). Figure RDA 1 and RDA 2 axes were rotated to display the "magnitude of summer temperature" along the RDA 1 axis. RDA 2 represents the flow variability. Inset represents the relative importance (distance biplot) of rivers with respect to each other and selected flow and thermal variables. Open circles and triangles refer to unregulated and regulated rivers, respectively.



High
Flow variability
Low
Intra-annual flow variability
Long-term flow variability
4-Bottom cool turbid riffles
3-Cold pristine riffles
6-Cool vegetated pools
7-Cool clear pools
Magnitude of summer water temperatures
2-Warm-cool, pristine, slow
5-Warm turbid perturbation tolerant
1-Warm with cover
Low
Magnitude of summer water temperatures
High

Photo: Wapske River, New Brunswick 2013

General Conclusions

"Rather than flowing to the natural rhythms of the hydrologic cycle, rivers are turned on and off like elaborate plumbing works."
– Postel and Richter 2003

Dams and river diversions have undeniably altered the timing and volume of river flows on wide geographic scales. The need to preserve ecosystems services for human gain has placed rivers and their ecological services at the forefront of the cost-benefit equations that determine how rivers get managed. However, this approach has fallen short in delivering holistic solutions to stop or reverse the decline in river health (Postel and Richter 2003). To date, efforts to restore and rehabilitate rivers have focused primarily on improving water quality and establishing minimum flow requirements, without considering the full extent that alterations to flows and thermal regimes may have on fish communities across rivers (Olden and Naiman 2010, Arthington 2012). Focusing on preserving ecological integrity for its own sake, rather than for anthropocentric gains, may therefore provide the framework required to make more comprehensive environmental flow recommendations.

The thesis' main contribution has been to provide a synthesis of the hydrologic and thermal drivers of fish community structure in temperate rivers across Canada. Prior to this work, the literature has yielded disparate findings on the relative role of alterations stemming from river regulation on fish communities. The insight provided here is critical, as it allows river managers to develop more realistic expectations when working to manage river flows with the goal of preserving the ecological integrity of rivers.

Significance of findings and future directions

An important consequence of the observed change of natural river regimes from unregulated reference conditions is the suite of ecological alterations, from differences in species composition to guild representation. Throughout the thesis, we have attempted to quantify dominant patterns in flow and thermal variability across rivers for the purpose of better estimating the degree to which river regulation modifies overall fish community structure.

In a first step to addressing this objective, extensive fish community sampling using electrofishing and visual surveying methods was conducted across targeted rivers. The ability to accurately detect individual fish inhabiting a stream and infer habitat use is of the utmost importance for conservation efforts (Korman et al. 2009, Ellis et al. 2013). Therefore, the findings from this first chapter allowed us to estimate fish richness, density, and biomass per site, combine the best estimates from electrofishing and visual surveys, and scale-up to represent the 'best' river fish estimates. Moreover, we showed evidence for considerable heterogeneity in detection probability driven by fish size for both methods, as was demonstrated by Korman et al. (2010). While not directly involved with the overarching theme of the thesis, this framework was essential for establishing fish response matrices used in other thesis chapters, along with other NSERC HydroNet publications (Boisclair et al. 2015). We acknowledge that in the past, the Catch per Unit Effort (CPUE) may not have been comparable between surveying methods, let alone when compared with snorkelling surveys, where standard parameters (e.g. speed and direction of survey, number of divers) are often inconsistent between studies. Significant surveyor bias or differences in skill level associated with snorkelling surveys (e.g. fish identification, underwater magnification) may also limit the scope of results. Several studies highlighted the strengths and weakness of each of the surveying methods, but very few, if any, compared their relative efficacies at estimating river fish communities over continental scales. Our results are some of the first to quantify the sampling differences in species richness, density, and biomass estimates across these scales and provide a consistent surveying methodology that enables intra- and inter-riverine relationships of fish responses to environmental drivers.

Maintaining flow variability via a dynamic flow regime management approach (Poff 2009) has been advocated by freshwater ecologists to ensure the protection of all biota (Poff and Zimmerman 2010). We adopted a methodology which consists of defining flow variability for all major components of the river flow regime, characterizing dominant flow patterns for all rivers, and quantifying deviations from reference conditions established from unregulated flow regimes within a same flow class, as per the ELOHA concept (Poff et al. 2010). The implicit assumption is that ensuring some threshold value of the selected hydraulic component for regulated rivers will maintain biota and ecosystem integrity. Adapting this concept for multivariate data, our results show a positive linear relationship between biotic and flow alterations and suggest a potential threshold where a certain degree of flow alteration is required to engender significant biotic alterations. We also show that certain biotic attributes deviate significantly from reference conditions, but the direction of these deviations may not be consistent across rivers and regulation practices. However, a greater frequency of biotic deviations from reference conditions across regulated rivers was found to be the result of significant alterations to their respective flow regimes. Moreover, our results suggest a graded biotic response between regulation practices, most notably between ROR and hydro-peaking systems. While these findings limit the direct applicability for fisheries managers, it does allow for a more comprehensive view of the ecological effects of flow alteration occurring across our systems and between regulation practices. The general approach described in this chapter may also be applied to other ecosystems, for which quantified alterations may be used to predict the direction of environmental variable/stressor-community response alteration relationships.

Another significant contribution of the flow alteration science presented in the second chapter centers on the development of hydrologic indices that reflect hourly fluctuations in flow regimes. To date, daily flow indices or averages are used to characterize relationships between flow regimes and ecological functioning. We show however, that these coarser temporal scales miss the more rapidly occurring biological responses to flow changes. For example, repeating the flow alteration calculations excluding dominant hourly flow patterns did not result in a significant biotic-flow alteration relationship. This is in large part due to the flow indices that reflect hourly variations, such as the rate and magnitude of up- and down-ramping of hydro-peaking flows, and their effect on select biotic attributes, notably, decreases of total fish density and biomass. For all other regulated rivers, these flow indices were lower than the mean for unregulated rivers, pointing to more stabilized hourly flows than observed for reference conditions. Furthermore, a study conducted in two of these rivers found that northern pike (*Esox lucius*) possessed the morphological traits (e.g. elongated head, deep body, and long fin insertions) that are thought to lead to improved swimming adaptations for coping with hydro-peaking flows (Senay et al. in review). These results suggest that future hydro-ecological studies need to include hourly flow variation to ensure that short- and long-term fish responses are considered in flow management schemes.

Numerous environmental variables, including water temperature, are known to affect the structure of river fish assemblages (Caissie 2006, McCullough et al. 2009). However, the role of variability of thermal regimes, independent from its interaction with river flows, is understudied (Murchie et al. 2008, Olden and Naiman 2010). Likewise, studies that compare relationships between the different types of guilds and the variables reflecting environmental change are generally lacking. We therefore, assessed long-term fish responses via the range of guild representations (type and density or biomass of guilds), driven by dominant patterns of flow and thermal variation across rivers. Our results are some of the first to consistently point to the importance of summer water temperatures and intra-annual flow variability for explaining and predicting fish guild representation. Not only do we show that integrating thermal regimes is crucial for explaining different types of guild responses, our results demonstrate that other lesser-known guild relationships exist because fish guilds, irrespective of the traits used to group them, are mainly driven by the same environmental variables. A significant contribution of this chapter also involves the development of thermal indices akin to those derived for hydrologic regimes. As awareness of the impact of climate change on ecological systems grows, in addition to the variety of land management effects on water quality and quantity, characterizing thermal regimes for the purpose of quantifying their effect on freshwater fishes will only become more important (Webb et al. 2010, Michel and Knouft 2014).

The concept of environmental filtering refers to the abiotic environment that shapes the distribution of species across the landscape, where abiotic filters prevent the establishment or persistence of biota in the absence of biotic interactions (Kraft et al. 2015). We suggest that flow and thermal variables act, in part, as 'environmental filters', driving community patterns across our rivers and favouring the abundance of certain guilds over others. However, further investigation on the biotic interactions/processes that affect fish community patterns (e.g. competition for resources) and the spatio-temporal scale under investigation (e.g. habitat- or river-scale abiotic variables) are needed to fully understand the mechanism of environmental filtering in our context. The relationship between the abiotic environment and fish assemblages may also be the result of effects on early life history stages beyond what was sampled here (e.g., larvae). Nevertheless, the environmental filtering concept may capture an important process in fish community assembly, where significant fish guild models reflect a tolerance/intolerance of groups of species for abiotic variables, notably, the magnitude of summer thermal regimes and intra-annual flow variability.

We have found that alterations to river and habitat environments are highly variable between rivers and flow regulation practices. The direction and severity of ecological effects are therefore dependent on these contexts, which explain why fish-environmental interaction models are generally developed for a specific river or region. Although many models describing fish-environmental interactions have been proposed, modelling guild responses across global spatial scales and types of regulation practices has been difficult. An intercontinental comparison of fish community interactions with river flows, thermal profiles and habitat features (hydraulic and others) may, therefore, provide the large-scale, transferable models required to predict the ecological consequences of anthropogenic modifications to rivers. Developing general fish-environment models that may assist in predicting the synergistic effects of river regulation and climate change across large spatial scales should be the focus of future research.

Variation in river water temperatures is the result of complex interactions among hydrologic changes, major climate patterns, and increasing anthropogenic impacts stemming from impoundment and dam construction, and other human-related activities (Schindler 2001, Webb et al. 2008). In light of the information provided within the thesis, future work will also center on further exploring the relationship between flow and thermal regimes; in particular, the role of thermal coupling as another driver of fish community response to river regulation. Hydro-peaking river regulation practices often result in intermittent flow peaks or hydropeaks that result from the sudden release of water outflows from the dam or power plant to match the demand for power consumption. As seen, these hydropeaks significantly alter the natural flow regime of rivers, with severe consequences for ecosystem integrity. This type of practice is also known to affect the thermal regime of rivers (Ward 1985), where water releases from reservoirs cause abrupt water temperature variations or thermopeaks associated with hydro-peaking releases from dams or power plants (Toffolon et al. 2010, Zolezzi et al. 2011). The overlap of both peaks, as we have referred to as thermal coupling, has yet to be assessed for the purpose of understanding their implication for fish communities over time and space. Figure 1 illustrates thermal coupling for a hydro-peaking river (A) and contrasts thermal and hydrologic trends for an unregulated river over the same period of time (B). As regulation practices vary greatly, we would hypothesize that thermal coupling patterns would not be carried through across different regulation practices. Future works will, therefore, focus on analyzing the degree of coupling of thermopeaks and hydropeaks, accounting for the time lag between peaks, and their overall ecological effect on fish community organization within hydro peaking-rivers and between different regulation practices.

Implications for river management

Hydropower accounts for 63% of Canada's total electricity generation and is currently the 3rd largest hydropower producer in the world (Canadian Hydropower Association; https://canadahydro.ca). As more rivers and lakes are slated for hydropower development, the conservation of these freshwater systems and the rehabilitation of altered systems will only accrue importance. The key results from the thesis may inform river management by providing the tools and/or models to facilitate the assessment of freshwater systems and the impact of river regulation on ecosystem processes. The reported contributions were summarized as a series of "lessons learned", detailing the important components for developing relationships between proxies of fisheries productivity metrics and environmental conditions, as well as predicting future ecological effects under new environmental conditions (Appendix K; modified from Boisclair et al. 2015). In a nutshell, contributions to this report consist of: 1) establishing a methodology for quantifying fish community structure across rivers, generating reliable site-specific species richness, density, and biomass metrics that combined measures from two commonly used surveying methods; 2) identifying dominant river hydrologic variations among the 105 daily and hourly flow indices calculated (10 PCs across 6 flow components); 3) quantifying multivariate deviations from reference conditions for regulated rivers (alteration scores) and drawing a relationship between biotic and flow alteration scores across regulation practices; and 4) explaining fish guild responses to flow and thermal variations across unregulated and regulated rivers. Specifically, the research presented in the thesis answers methodological and fundamental questions such as, how best to census a river for obtaining proxies of fish production estimates, to what extent are hydrologic and thermal regimes changed in regulated rivers that are managed according to different flow operation strategies, and what are their effects on fish communities. As future research focuses on expanding these relationships to include changes in climatic conditions, we may hope to arrive at informed river management actions that weigh the socio-economic costs/benefits of exploiting rivers for ecosystem services, while preserving the ecological integrity of these systems.

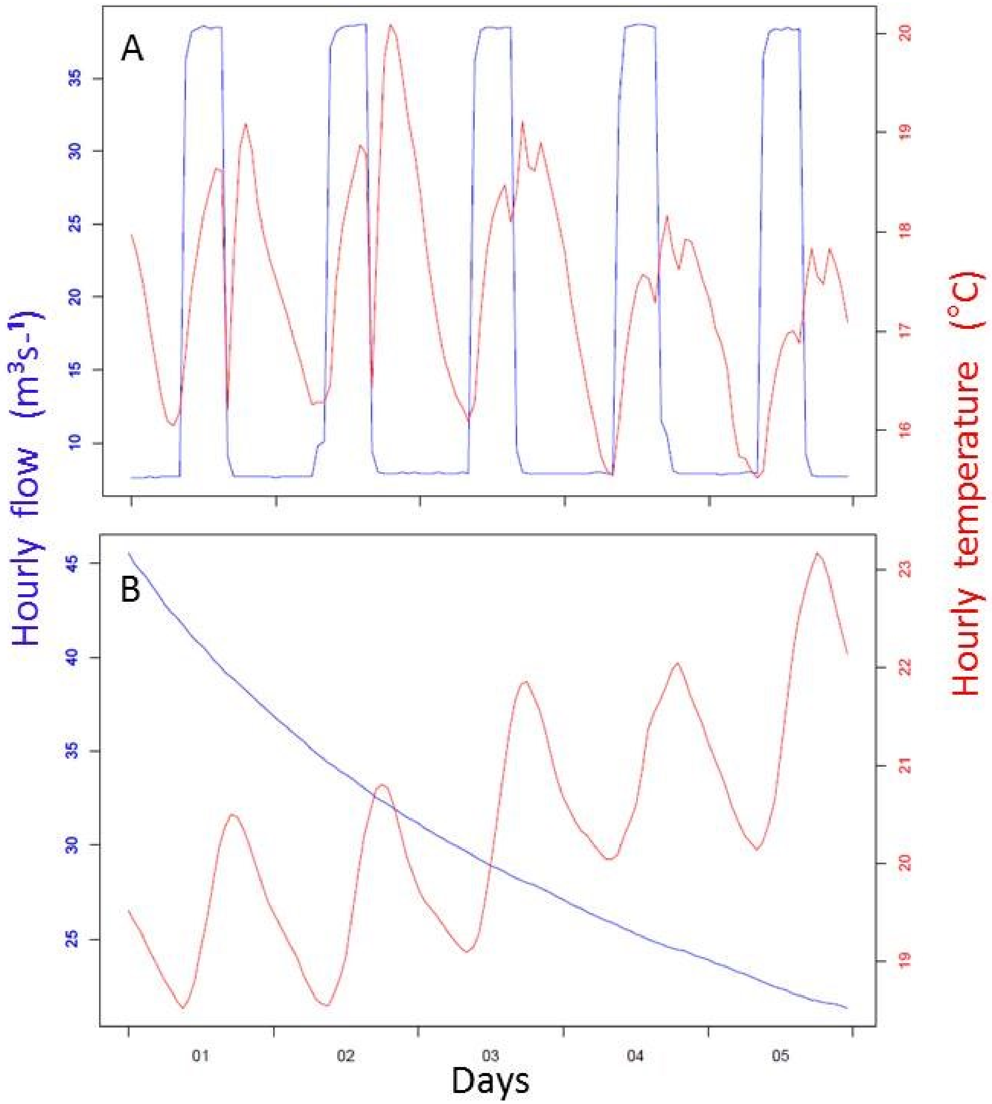


Figure 1. Hydrographs (blue line) and thermographs (red line) for a hydro-peaking (A) and unregulated river (B). Graphs depict the relationship between summer river profiles, hourly flows and water temperatures, over the first week of July, 2013.

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Appendix A Description of the14 unregulated and 10 regulated Canadian river segments surveyed. (CHAPTER 2)

River	Province	Dam name (Regulation type)	Distance from flow gauge (km)	Wetted river width (m)	Length of river sampled (km)	Median daily flows (m^3/s)	Latest stocking programs
Aubinadong	ON	NA	1	40.80	9.80	8.00	brook trout stocking in nearby lakes from 2000-2014 [1]
Au Saumon	QC	NA	0	54.95	8.20	11.09	Unknown
Batchawana	ON	NA	0	50.34	7.80	9.50	no stocking
Beaurivage	QC	NA	3	46.40	5.00	5.98	brook trout last stocked in river in 2007 [2]
Becancour	QC	NA	0	37.25	12.70	12.00	brook trout last stocked in river in 2010 [2]
Coaticook	QC	Penman (ROR)	11	26.60	7.80	5.38	Unknown
Dee	NB	Dee at Trouser lake (storage)	0.2	14.33	13.70	1.68	brook and ounaniche last stocked in upstream lake in 2003 [3]
Du Loup	QC	NA	3	28.46	7.00	4.10	brook trout last stocked in the river in 2002 [2]
Du Sud	QC	Arthurville (ROR)	0.2	60.58	15.40	8.76	brook, brown and rainbow trout last stocked in the river 2009 [2]
Eaton	QC	NA	1.5	36.73	10.20	5.35	Unknown
Etchemin	QC	Jean- Guerin (ROR)	1.7	81.51	6.80	13.10	brook, rainbow and lake trout last stocked in river in 2009 [2]
Goulais	ON	NA	15	34.80	7.20	8.04	no stocking
Gulquac	NB	NA	proxy on Little Tobique	16.80	8.80	3.54	no stocking
Kiamika	QC	Kiamika (storage)	3.3	42.48	14.80	17.84	ouananiche, brook and brown trout last stocked in river in 1999, 2003 and 1994 respectively; lake, brown and brook trout and walleye stocked in upstream lake in 2003 for trout and 2011 for walleye [2]

Magpie	ON	Steephill (hydro-peaking)	8	45.50	10.00	15.73	no stocking
Mississagi	ON	Aubrey Falls (hydro-peaking)	8	89.89	4.90	30.14	yearling rainbow trout stocked in the tributaries of the river (2004-2014); brook trout and splake stocked in watershed lakes [1]
Nicolet	QC	NA	0	88.58	18.80	16.30	rainbow and brown trout last stocked in river in 2014 [2]
Noire	QC	NA	24	46.63	12.90	11.10	walleye and rainbow trout last stocked in river in 2012 and 2010 respectively [2]
Ouelle	QC	NA	3.5	41.38	7.40	5.28	Atlantic salmon last stocked in river in 2000 [2]
Petit Saguenay	QC	NA	0	33.54	6.00	4.75	Atlantic salmon last stocked in river in 2010 [5]
Picanoc	QC	NA	3.1	25.87	9.20	13.16	brook trout last stocked in river in 1999[2]
Serpentine	NB	Snake (storage)	0.2	20.43	18.20	0.76	brook trout and ounaniche last stocked in upstream reservoir in 2012 [4]
Saint-Francois	QC	Weedon (storage)	9	110.37	7.90	57.48	unknown
Saint-Jean	QC	Morin (ROR)	0.3	31.08	9.70	6.15	Atlantic salmon last stocked in river in 2010 [5]

[1]Ontario Ministry of Natural Resources; [2]Ministère des Resources Naturelles et de la Faune; [3]Fisheries and Oceans Canada; [4]Department of Natural Resources; [5]Ministère des Forêts, de la Faune et des Parcs.

Appendix B List of the 25 biotic attributes representing fish groups: fish quantity, diversity, composition, and proportional representation of two habitat guilds. (CHAPTER 2)

Groups	Fish indices	Units	Description
Fish quantity	Total fish density	No. of ind./m²	Density of all fishes per m² for a given river
	Total fish biomass	g/m²	Biomass of all fishes per m² for a given river
	Total biomass of small-sized fishes	g/m²	Biomass of all fishes measuring under 5 cm in total length
	Total biomass of medium-sized fishes	g/m²	Biomass of all fishes measuring between 5 and 20 cm in total length
	Total biomass of large-sized fishes	g/m²	Biomass of all fishes measuring between 20 and 90 cm in total length
Fish diversity	Species richness	No. of species	Number of species sampled in a given river
	Family richness	No. of families	Number of families sampled in a given river
	Hill diversity index N1 (B)	no units	Exponential of the Shannon diversity index that is based on species biomass estimates by river
	Hill diversity index N2 (B)	no units	Inverse of the Simpson's diversity index that is based on species biomass estimates by river
	Shannon diversity index (D)	proportion	Index that considers the number of species and their respective densities per river
	Shannon diversity index (B)	proportion	Index that considers the number of species sampled and their respective biomasses per river
Fish composition	Proportion of Petromyzontidae	proportion	Proportion of the biomass of fishes from the Petromyzontidae family
	Proportion of Anguillidae	proportion	Idem for the Anguillidae family
	Proportion of Salmonidae	proportion	Idem for the Salmonidae family
	Proportion of Cyprinidae	proportion	Idem for the Cyrpinidae family
	Proportion of Ictaluriadae	proportion	Idem for the Ictaluridae family
	Proportion of Lottidae	proportion	Idem for the Lottidae family
	Proportion of Percidae	proportion	Idem for the Percidae family
	Proportion of Catostomidae	proportion	Idem for the Catostomidae family
	Proportion of Cottidae	proportion	Idem for the Cottidae family
	Proportion of Esocidae	proportion	Idem for the Esocidae family
	Proportion of Centrarchidae	proportion	Idem for the Centrarchidae family
	Proportion of Percopsidae	proportion	Idem for the Percopsidae family
Habitat guilds	Proportion of demersal species	proportion	Proportion of species that are listed as demersal species
	Proportion of benthopelagic species	proportion	Proportion of species that are listed as benthopelagic species

Appendix C Description of the flow indices that represent the 25% highest loading on significant principal component axes PC1 and PC2, referenced in chapter 2. (CHAPTER 2)

Flow indices (code)	**Units**	**T**	**D**	**Hydrologic Index**	**Description**	**Source**	**References**
Magnitude of flow events *Average flow conditions* M_A6	NA	D	D	Range in daily flows (10/90)	Range in daily flows is the ratio of the 10 percent to 90 percent exceedence values for the entire flow record.	HIT	8
M_A60	%	H	H	Coefficient of diel variation	Standard deviation of hourly flows divided by mean flow for a 24-h period. Mean of daily coefficients of variation.	Zim	16
Low flow conditions nM_L6	$m^3 s^{-1}$	M	D	Mean minimum monthly flows (Jun)	For each year, compute the minimum flow for the month of June and ML6 is the median of these values.	HIT	12
M_L17	NA	A	D	Base flow index 1	Median of the ratios of the minimum of a 7-day moving average flow for each year divided by the mean annual flow for that year.	HIT	11
High flow conditions M_H15	NA	A	D	High flow discharge (1%)	Compute the 1 percent exceedence value for the entire data record. MH15 is the 1 percent exceedence value divided by the median flow for the entire record.	HIT	3
Frequency of flow events *High flow conditions* F_H1	events/year	A	D	Flood frequency 1 (High flood pulse count)	Median number of events per year for each year the number of flow events with flows above a threshold equal to the 75th percentile value for the entire flow record.	HIT	9,10,11
Duration of flow events *Low flow conditions* D_L12	NA	W	D	Normalized 7-day annual minimum flow	Mean annual minimum of 7-day moving average flow divided by the median for the entire record.	HIT	3

High flow conditions							
D_H6	%	D	D	Variability of annual maximum daily average flow	Coefficient of variation in annual maximum daily average flow.	HIT	9,10,11
Timing of flow events							
Average flow conditions							
T_A1	NA	D	D	Constancy	Constancy is computed via the formulation of Colwell (see example in Colwell, 1974). Using the equations for Shannon information theory parameters, constancy is computed as (using natural logarithms): 1 - ((uncertainty with respect to state) / log (number of state))	HIT	1,2,3,5,6,17
T_A2	NA	D	D	Predictability of flow	Composed of two independent, additive components: constancy (a measure of temporal invariance) and contingency (a measure of periodicity). Predictability is computed from the same matrix as constancy (see TA1; Colwell, 1974).	HIT	5,6,17
High flow conditions							
T_H2	NA	D	D	Variability in Julian date of annual maximum	Circular variance in T_H1. Compute the sum of the cosinus of the difference between each angle (dates on a circular scale) and the circular mean (TH1 before the back-transformation). TH2 is 1 minus the ratio of the sum of cosinus divided by the sample size (number of years).	HIT (Modified by Bourque)	3,9,10,11
Rate of change in flow events							
Average flow conditions							
nR_A1	$m^3\ s^{-1}\ d^{-1}$	D	D	Rise rate	Median of the mean rate of positive changes in flow from one day to the next.	HIT	9,10,11
nR_A7	log of $m^3\ s^{-1}$	D	D	Change of flow (falling)	Median of the change in log of flow for days in which the change is negative for the entire flow record.	HIT	3
Low flow conditions							
R_L2	NA	H	H	Hourly Flash Index 2 (low flow)	Ratio of the minimum hourly flow for each day to the mean hourly flow for this day. Mean of all daily ratios.	Lanthier	

The alphanumeric code refers to the category of the flow regime the hydrologic index was developed to describe; M = Magnitude, F = Frequency, D = Duration, T = Timing & R = Rate of change. Index letters (second letters) refers to: A = Average flow, L = Low flow, H = High flow. Indices used in HIT and in GeoTools are referred to by the same code for compatibility purposes.
The suffix “n” refers to indices that were normalized; daily data were normalized by dividing by MA2 and hourly data by MA61.
“T” refers to the temporal aspect of the hydrograph that the hydrologic index represents: hourly (H), daily (D), weekly (W), monthly (M), seasonal (S), or annual (A). “D” refers to the dataset used to compute the index: D=filtered daily flows, H=filtered hourly flows, HH= unfiltered hourly flows.

Abridged References (including sources): HIT: Calculated with R, See HIT User Manual & Olden and Poff (2003); Zim : Calculated with R (Zimmerman et al. 2010); Steuer : Calculated with R, based on suggestions by Steuer et al. (2010); Lapointe and Bourque: Calculated with R, based on suggestions by M. Lapointe and G. Bourque (personal communication); 1(Clausen and Biggs 1997) ; 2 (Clausen and Biggs 2000) ; 3 (Clausen et al. 2000); 5 (Poff and Ward 1989); 6 (Poff 1996); 8 (Richards 1989); 9 (Richter et al. 1996); 10 (Richter et al. 1997); 11(Richter et al. 1998); 12 (Wood et al. 2000); 16 (McKinney et al. 2001); 17 (Colwell 1974).

Appendix D

S1. Description of common traits ascribed to each of the guilds and taxonomic associations, categories/units and sources. Number of guilds or groups indicated in brackets. (CHAPTER 3)

Guilds	Ecological traits	Units and/or categories
Morphologic (8)	Caudal fin aspect ratio	ratio [8, 17]
	Mouth position	terminal , subterminal [9]
	Visible barbels	presence, absence [5]
	Position of pelvic fin	abdominal, jugular, thoracic [5]
	Pectoral to total length	ratio [5]
	Body height to length	ratio [5]
Trophic (6)	Diet shift	presence, absence [5, 19]
	Trophic level	trophic position ranging from planktivorous (1) to carnivorous (~4) [8]
	Diet	presence, absence : crayfish, annelids, insects, molluscs, fish, fish eggs, small mammals, frogs, salamanders, macrophyte, parasitic, periphyton, birds [6]
Reproductive (8)	Spawning season	spring, summer, fall, winter [5, 19]
	Known guarder of nest or young	presence, absence [1, 20]
	Known builder of nest	presence, absence [1, 20]
	Average fecundity; Egg diameter	eggs (no.) [5, 19]; size (mm) [4, 5, 19]
	Size at 1st reproduction	size (mm) [5, 8, 19]
	Age at 1st reproduction; Maximum age for reproduction; Number of years of reproduction	years (no.) [5, 8, 19, 18] ; years (no.) [5, 8, 19] ; years (no.) [5, 8, 19]
	Spawning water depth	0- 20 ; 21- 60 ; 61- 100 ; 101-200 ; 201+ (cm) [2, 3, 5, 16, 17, 19, 22, 23]
	Spawning substrate	bedrock, boulder, cobble, rubble, gravel, sand, silt or clay, detritus [2, 5, 17, 18]
	Spawning velocities	bays, pools, runs, riffles, rapids [2, 5, 17]
Habitat (7)	Reproductive or spawning habitat	ariadnophils, lithopelagophils, lithophils, pelagophils, phytolithophils, phytophils, polyphils, psammophils, speleophils [1, 20]
	Feeding location	bottom, pelagic, surface [6]
	Thermal preference	cold, cool, warm [6]
	Tolerance to environmental perturbation	intolerant, intermediate, tolerant [10]
	Turbidity tolerance	intolerant, intermediate, tolerant [2, 7, 15, 17, 18, 19, 21]
	Velocity preference	pool, run, riffle, rapids [14, 15, 17, 19]
	Vegetation use	high, medium, low [14, 15, 17, 18, 19]
	Cover use type	algae, substrate, overhead, wood [5, 13, 17, 18, 19]

	Substrate preference	bedrock, boulder, cobble, rubble, gravel, sand, silt or clay, detritus
	Water depth preference	0- 20 ; 21- 60 ; 61- 100 ; 101-200 ; 201+ (cm)
Behavioural (6)	Schooling	presence, absence [5, 19]
	Territorial	presence, absence [5, 19]
	Migratory behavior	anadromous, catadromus, potadromous (migratory), potadromous (non-migratory) [5, 18, 19]
	Feeding behavior	filterer, grazer, pursuit, ambush, sorter, non-feeding [6]
Taxonomic groups (7)	Phylogenetic tree of Canadian freshwater fishes cut at 7 groups	N/A [11]

Abridged References: 1 (Balon 1975); 2 (Becker 1983); 3 (Bradbury et al. 1999); 4 (Minns et al. 1993); 5 (Coad 1995); 6 (Coker et al. 2001); 7 (Danie et al. 1984); 8 (Froese and Pauly 2014); 9 (Goldstein and Simon 1999); 10 (Halliwell et al. 1999); 11(Hubert et al. 2008); 12(Lane et al. 1996)

Appendix E

S2. Morphologic guilds, shared traits and species representing each guild. (CHAPTER 3)

Guilds	Traits	Species
1-Subterminal mouth, cypriniforms	subterminal mouth, cylindrical shape	*Catostomus catostomus, Catostomus platyrhynchus, Cyprinella spiloptera, Exoglossum maxillingua, Hybognathus regius, Moxostoma macrolepidotum, Moxostoma anisurum, Notropis heterodon, Notropis hudsonius, Rhinichthys atratulus, Rhinichthys cataractae, Semotilus corporalis*
2-Soft-dorsal rays, terminal mouth	terminal mouth, abdominal pelvic fins, large caudal fin ratio	*Ameiurus nebulosus, Couesius plumbeus, Cyprinus carpio, Luxilus cornutus, Margariscus margarita, Nocomis biguttatus, Notemigonus crysoleucas, Notropis bifrenatus, Oncorhynchus mykiss, Pimephales promelas, Salmo trutta, Salvelinus confluentus, Salvelinus fontinalis*
3-Discoid	terminal mouth, small caudal fin ratio, large height to length ratio	*Ambloplites rupestris, Lepomis gibbosus*
4-Small bodied and large pectoral fins	large pectoral fins, thoracic pelvic fins	*Ammocrypta pellucida, Cottus bairdi, Cottus cognatus, Cottus ricei, Etheostoma exile, Etheostoma flabellare, Etheostoma nigrum, Etheostoma olmstedi, Percina caprodes, Percina copelandi, Percopsis omiscomaycus*
5-Torpedo	average height to length ratio	*Chrosomus eos, Esox lucius, Fundulus diaphanus diaphanous, Lota lota, Notorus flavus, Notropis rubellus, Notropis stramineus, Phoxinus neogaeus, Pimephales notatus, Semotilus atromaculatus, Umbra limi*
6-High caudal fin	large caudal fin ratio	*Esox masquinongy, Esox niger, Hybognathus argyritis, Hybognathus hankinsoni, Notropis atherinoides, Notropis volucellus, Oncorhynchus clarkii clarkia, Osmerus mordax, Prosopium williamsoni, Salmo salar*
7-Spiny-dorsal rays non discoid	terminal mouth, thoracic pelvic fins, average height to length ratio	*Culaea inconstans, Gasterosteus aculeatus, Gasterosteus wheatlandi, Micropterus dolomieui, Micropterus salmoides, Perca flavescens, Sander vitreus*
8-Eel-like	small caudal fin ratio, small pectoral to total length ratio, small height to length ratio	*Anguilla rostrata, Ichthyomyzon fossor, Lethenteron appendix, Petromyzon marinus*

Appendix F

S3. Trophic guilds shared traits/diet and species representing each guild. (CHAPTER 3)

Guilds	Traits / Diet	Species
1-Invertivores	invertebrates and annelids	*Catostomus commersoni, Etheostoma exile, Etheostoma flabellare, Etheostoma nigrum, Exoglossum maxillingua, Fundulus diaphanus, Gasterosteus wheatlandi, Hybognathus hankinsoni, Moxostoma anisurum, Moxostoma macrolepidotum, Notropis atherinoides, Notropis heterolepis, Percina caprodes, Percina copelandi, Phoxinus neogaeus, Rhinichthys cataractae*
2-Generalists	macrophytes to fish	*Catostomus catostomus, Cottus ricei, Culaea inconstans, Cyprinus carpio, Etheostoma olmstedi, Luxilus cornutus, Margariscus margarita, Notemigonus crysoleucas, Notropis bifrenatus, Notropis hudsonius, Notropis volucellus, Notropis rubellus, Pimephales notatus*
3-Small predators	ontogenetic diet shift	*Salmo trutta, Salvelinus confluentus, Esox niger, Semotilus atromaculatus, Oncorhynchus clarkii, Semotilus corporalis, Couesius plumbeus, Micropterus salmoides, Lepomis gibbosus, Ambloplites rupestris, Micropterus dolomieui, Cyprinella spiloptera, Noturus flavus, Percopsis omiscomaycus, Perca flavescens*
4-Moderate predators	moderate trophic level	*Ameiurus nebulosus, Ammocrypta pellucida, Anguilla rostrata, Cottus bairdi, Cottus cognatus, Gasterosteus aculeatus aculeatus, Nocomis biguttatus, Osmerus mordax, Prosopium williamsoni, Rhinichthys atratulus, Salvelinus fontinalis, Umbra limi*
5-Top-predators	fish, amphibians, small mammals	*Esox lucius, Esox masquinongy, Lota lota, Oncorhynchus mykiss, Petromyzon marinus, Salmo salar, Sander vitreus*
6-Herbivores	phytoplankton and macrophytes, lowest trophic level	*Catostomus platyrhynchus, Chrosomus eos, Hybognathus argyritis, Hybognathus regius, Ichthyomyzon fossor, Lethenteron appendix, Notropis stramineus, Pimephales promelas*

Appendix G

S4. Reproductive guilds, shared traits and species representing each guild. (CHAPTER 3)

Guilds	Traits	Species
1-Marine breeder	fall spawning, large fecundity, deep water spawning	*Anguilla rostrata*
2-Summer-fall spawning nest builders	summer-fall spawning, nest builder, riffle spawning	*Noturus flavus, Oncorhynchus clarkii clarkia, Oncorhynchus mykiss, Salmo salar, Salmo trutta, Salvelinus confluentus, Salvelinus fontinalis*
3-Long-lived riffle spawners	20+ years reproductive years, large eggs, riffle spawning	*Catostomus catostomus, Catostomus commersoni, Moxostoma macrolepidotum, Moxostoma anisurum, Prosopium williamsoni*
4-Small bodied pool spawners	spring-summer spawning, young at maturity (1st year), pool spawning	*Ammocrypta pellucida, Chrosomus eos, Cyprinella spiloptera, Etheostoma exile, Fundulus diaphanus diaphanous, Hybognathus argyritis, Hybognathus hankinsoni, Hybognathus regius, Notemigonus crysoleucas, Notropis atherinoides, Notropis bifrenatus, Notropis heterolepis, Notropis hudsonius, Notropis stramineus, Notropis volucellus, Phoxinus neogaeus, Umbra limi*
5-Low fecundity shallow spawners	15+ years reproductive years, shallow spawners	*Catostomus platyrhynchus, Couesius plumbeus, Luxilus cornutus, Margariscus margarita, Nocomis biguttatus, Notropis rubellus, Osmerus mordax, Percina caprodes, Percina copelandi, Percopsis omiscomaycus, Rhinichthys atratulus, Rhinichthys cataractae, Semotilus atromaculatus, Semotilus corporalis*
6-Late-maturing riffle nesters	nest builder and non-guarding, old at maturity (6+ years), riffle spawning	*Ichthyomyzon fossor, Lethenteron appendix, Petromyzon marinus*
7-Large bodied and long-lived spawners	large fecundity, large at 1st reproduction	*Ameiurus nebulosus, Cyprinus carpio, Esox lucius, Esox masquinongy, Esox niger, Lota lota, Micropterus dolomieui, Micropterus salmoides, Perca flavescens, Sander vitreus*
8-Small nest guarders	nest builder and guarding, small number of eggs, small at 1st reproduction	*Ambloplites rupestris, Cottus bairdi, Cottus cognatus, Cottus ricei, Culaea inconstans, Etheostoma flabellare, Etheostoma nigrum, Etheostoma olmstedi, Exoglossum maxillingua, Gasterosteus wheatlandi, Lepomis gibbosus, Pimephales notatus, Pimephales promelas, Gasterosteus aculeatus*

Appendix H

S5. Habitat guilds, shared traits/preferences and species representing each guild. (CHAPTER 3)

Guilds	Traits / Preferences	Species
1-Warm water with cover	warm and clear water, intermediate perturbation tolerant, uses cover (macrophytes)	*Chrosomus eos, Lepomis gibbosus, Micropterus dolomieui, Micropterus salmoides, Notropis stramineus, Notropis volucellus, Noturus flavus, Percina caprodes*
2-Warm-cool slow-moving pristine water	cool-warm and clear water, intermediate pertubation tolerant, prefer pool-run velocities	*Ammocrypta pellucida, Culaea inconstans, Esox lucius, Esox masquinongy, Exoglossum maxillingua, Hybognathus regius, Hybognathus argyritis Ichthyomyzon fossor, Notropis bifrenatus, Notropis heterolepis, Notropis rubellus, Percina copelandi*
3-Cold pristine riffles	cold water, pertubation intolerant, prefr riffle velocities, uses cover (substrate), lithophiles	*Cottus cognatus, Cottus ricei, Lethenteron appendix, Oncorhynchus clarkii, Oncorhynchus mykiss, Osmerus mordax, Salmo salar, Salmo trutta, Salvelinus confluentus, Salvelinus fontinalis*
4-Riffle bottom dwellers	cool water,turbidity tolerant, intermediate pertubation tolerant, prefer riffle velocities, bottom dwellers	*Catostomus commersoni, Catostomus platyrhynchus, Cottus bairdi, Couesius plumbeus, Etheostoma flabellare, Etheostoma nigrum, Etheostoma olmstedi, Margariscus margarita, Percopsis omiscomaycus, Rhinichthys atratulus, Rhinichthys cataractae*
5-Warm and turbid water	warm and turbid water, pertubation tolerant, bottom dwellers	*Ameiurus nebulosus, Cyprinella spiloptera, Cyprinus carpio, Moxostoma macrolepidotum, Pimephales notatus, Pimephales promelas, Prosopium williamsoni*
6-Cool and slow-moving water with macrophytes	cool water, prefer run-pool habitats with macrophytes, phytophils	*Ambloplites rupestris, Anguilla rostrata, Esox niger, Fundulus diaphanus, Nocomis biguttatus, Notemigonus crysoleucas, Sander vitreus, Semotilus atromaculatus, Umbra limi*
7-Cool and clear pool	cold-cool and clear water, intolerant to perturbation, prefer pool habitats	*Catostomus catostomus, Etheostoma exile, Gasterosteus aculeatus, Gasterosteus wheatlandi, Hybognathus hankinsoni, Lota lota, Luxilus cornutus, Moxostoma anisurum, Notropis atherinoides, Notropis hudsonius, Perca flavescens, Petromyzon marinus, Phoxinus neogaeus, Semotilus corporalis*

Appendix I

S6. Behavioural guilds, shared traits and species representing each guild. (CHAPTER 3)

Guilds	Traits	Species
1-Territorial-grazers	territorial, potadromous, no migration	*Ameiurus nebulosus, Cottus bairdi, Cottus cognatus, Cyprinella spiloptera, Exoglossum maxillingua, Fundulus diaphanus, Lepomis gibbosus, Margariscus margarita, Micropterus salmoides, Nocomis biguttatus, Noturus flavus, Rhinichthys atratulus, Rhinichthys cataractae, Semotilus corporalis*
2-Schooling-sorter	schooling, sort food items	*Catostomus catostomus, Catostomus commersoni, Couesius plumbeus, Culaea inconstans, Cyprinus carpio, Moxostoma anisurum, Moxostoma macrolepidotum, Percopsis omiscomaycus, Phoxinus neogaeus, Pimephales notatus, Pimephales promelas*
3-Territorial-pursuit	territorial, non-schooling, pursue prey items	*Cottus ricei, Esox masquinongy, Esox niger, Etheostoma exile, Etheostoma flabellare, Esox lucius, Etheostoma nigrum, Etheostoma olmstedi, Lota lota, Oncorhynchus clarkii, Percina copelandi, Salmo trutta, Salvelinus fontinalis, Salvelinus confluentus*
4-Schooling-grazers	schooling, graze food items off the substrate	*Ambloplites rupestris, Gasterosteus aculeatus, Gasterosteus wheatlandi, Hybognathus argyritis, Luxilus cornutus, Micropterus dolomieui, Notropis atherinoides, Notropis hudsonius, Notropis stramineus, Perca flavescens, Percina caprodes, Prosopium williamsoni, Sander vitreus, Semotilus atromaculatus, Umbra limi*
5-Anadromous	anadromous, pursue food items, non-feeders	*Anguilla rostrata, Oncorhynchus mykiss, Osmerus mordax, Petromyzon marinus, Salmo salar*
6-Non-territorial-grazers	non-territorial, graze food items off of substrate	*Ammocrypta pellucida, Catostomus platyrhynchus, Chrosomus eos, Hybognathus hankinsoni, Hybognathus regius, Ichthyomyzon fossor, Lethenteron appendix, Notemigonus crysoleucas, Notropis bifrenatus, Notropis heterolepis, Notropis rubellus, Notropis volucellus*

Appendix J

S7. Species representing each taxonomic association. (CHAPTER 3)

Families	Genus	Species
1- Petromoysontids	*Ichthyomyzon*	*fossor*
	Lethenteron	*appendix*
	Petromyzon	*marinus*
2- Umbrid	*Umbra*	*limi*
3- Osmerid	*Osmerus*	*mordax*
Esocids	*Esox*	*lucius, masquinongy, niger*
Anguillid	*Anguilla*	*rostrata*
Ictalurids	*Ameiurus*	*nebulosus*
	Notorus	*flavus*
4- Cyprinids	*Chrosomus*	*eos*
	Cyprinella	*spiloptera*
	Cyprinus	*carpio*
	Exoglossum	*maxillingua*
	Hybognathus	*argyritis, hankinsoni, regius*
	Luxilus	*cornutus*
	Margariscus	*margarita*
	Nocomis	*biguttatus*
	Notemigonus	*crysoleucas*
	Notropis	*atherinoides, bifrenatus, heterolepis, hudsonius, rubellus, stramineus, volucellus*
	Phoxinus	*neogaeus*
	Pimephales	*notatus, promelas*
	Semotilus	*atromaculatus, corporalis*
Catostomids	*Catostomus*	*catostomus, commersonii, platyrhynchus*
	Moxostoma	*anisurum, macrolepidotum*
Lottid	*Lota*	*lota*
5- Fundulid	*Fundulus*	*diaphanus*
6- Gasterosteids	*Culaea*	*inconstans*
	Gasterosteus	*aculeatus, wheatlandi*
Salmonids	*Oncorhynchus*	*clarkii, mykiss*
	Prosopium	*williamsoni*
	Salmo	*salar, trutta*
	Salvelinus	*confluentus, fontinalis*

7- Percids	*Ammocrypta*	*pellucida*
	Etheostoma	*exile, flabellare, nigrum, olmstedi*
	Perca	*flavescens*
	Percina	*caprodes, copelandi*
	Sander	*vitreus*
Centrachids	*Ambloplites*	*rupestris*
	Lepomis	*gibbusos*
	Micropterus	*dolomieu, salmoides*
Cottid	*Cottus*	*bairdii, cognatus, ricei*
Percopsid	*Percopsis*	*omiscomaycus*

Appendix K Summary of specific research contributions rendered to the final report submitted by NSERC HydroNet for Fisheries and Oceans Canada: Canadian Science Advisory Secretariat.

Model	Model power	Comments	"Lessons learned"
Type II linear model (Major Axis) **CHAPTER 2** Biotic anomaly= intercept + coef*Flow anomaly	r= 0.94, p<0.005 (2-tailed)	Alteration indices are calculated for regulated rivers of a specific flow class, therefore flow class analysis must be conducted prior to calculating alteration indices.	· 11 flow indices explained significant portions of the information comprised among the 105 flow indices (~61% to 91%) and these flow PCs may be combined to obtain river-specific alteration indices, resulting in more comprehensive composites of river flow alterations. · The degree of biotic alteration significantly corresponds to the degree of flow alteration in regulated rivers. Thresholds of flow alteration, below which biotic alterations may not occur. · A framework, upon which alterations or deviations from regional references may be estimated and used to predict the direction of environmental variable/ stressor- community response alteration relationships.

RDA (multivariate linear regressions) followed by a forward selection of explanatory variables **CHAPTER 3**			
Biomass of morphological guilds (8 guilds)^0.25 = Intercept + coef^a(Magnitude of summer water temperatures) + coef^b (Intra-annual flow variability) + coef^c (Long-term flow variability)	Adj.R^2= 0.33, p= 0.002; R^2CV= 0.44	The traits/preferences representing each of the guilds were fourth rooted to achieve more normalized distributions, while the explanatory variables were standardized prior to PCA analysis. Explanatory variables are condensed PCs describing flow and thermal indices for the rivers studied. The intercept is a position in multivariate space and coefs in the equation correspond to matrices.	· Fish guild models were significantly explained and predicted by explanatory variables representing river flow and thermal regimes across rivers, whereas total fish density and biomass were not. · All models performed better relative to studying phylogenetic associations. · Flow and thermal variables (the magnitude of summer water temperatures and intra-annual flow variability) were independent drivers of fish guild models. · Combining flow and thermal indices explains >40% of inter-river variations in fish guild densities and biomasses, pointing to the importance of integrating thermal regimes in hydro-ecological studies.
Biomass of trophic guilds (6 guilds)^0.25 = Intercept + coef^a(Magnitude of summer water temperatures) + coef^b (Intra-annual flow variability) + coef^c (Long-term flow variability) +coef^d (Magnitude of spring flood)	Adj.R^2= 0.33, p= 0.003; R^2CV= 0.41		
Biomass of reproductive guilds (8 guilds)^0.25 = Intercept + coef^a(Magnitude of summer water temperatures) + coef^b (Intra-annual flow variability)	Adj.R^2= 0.32, p= 0.003; R^2CV= 0.55		
Biomass of habitat guilds (7 guilds)^0.25 = Intercept + coef^a(Magnitude of summer water temperatures) + coef^b (Intra-annual flow variability)	Adj.R^2= 0.44, p= 0.001; R^2CV= 0.35		
Biomass of behavioural guilds (6 guilds)^0.25 = Intercept + coef^a(Magnitude of summer water temperatures) + coef^b (Long-term flow variability) + coef^c (Magnitude of spring flood)	Adj.R^2= 0.34, p= 0.004; R^2CV= 0.46		

Biomass of phylogenetic groups (7 guilds)^0.25 = Intercept + coef[a](Intra-annual flow variability) + coef[b] (Magnitude of summer water temperatures) + coef[c] (Long-term flow variability)	Adj.R^2= 0.26, p= 0.014; R^2CV= 0.73		