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Modelling the effects of chemical and physical drivers on fisheries productivity metrics across rivers of varying hydrological regimes: lessons learned from NSERC HydroNet 2009-2015

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

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ABSTRACT

Natural Sciences and Engineering Research Council (NSERC) HydroNet is a national research network whose overall objective is to provide government and industry with the knowledge and tools that will improve the capacity of scientists and managers to assess and minimize the effects of hydropower installations and operations on aquatic ecosystems. This project was divided in three components that focused on the existence of significant among-river variations of fisheries productivity metrics, the development of relationships between fisheries productivity metrics and environmental conditions, and the identification of promising new metrics of fisheries productivity. We achieved our objective by estimating fisheries productivity metrics (density [number of fish $\cdot m^{-2}$) and biomass [$g \cdot m^{-2}$] by fish species and size-classes; species richness), nutrient concentrations (total phosphorus, nitrates, nitrites), meso-habitat variables (depth, velocity, substrate composition, macrophyte cover, woody debris, etc), hydrological indices, and thermal indices in 15 unregulated rivers and 13 rivers regulated for hydropower production distributed from Alberta to New Brunswick, Canada. Relationships between fisheries productivity metrics and environmental conditions were assessed with different fisheries productivity metric (e.g. production, catch, recruitment, density, biomass, growth, survival, species richness), organismal scales (e.g. total fish community, guilds, species associations, phylogenetic group, species, life-stages [combinations of species and size-classes]), and spatial scales (e.g. complete river, river segment, meso-habitat, micro-habitat). The explanatory and predictive capacity of fish-environment relationships respond directly to the need of both the proponents and the regulators to:

i)   predict the potential effect of a project on metrics of fisheries productivity;

ii) assess the need for, or the magnitude of, mitigation measures;

iii) identify and measure the relative efficiency of different mitigation strategies;

iv) estimate the existence or the magnitude of residual effects on metrics of fisheries productivity, and;

v)   quantify the need for, or the magnitude of, offsetting.

However, it may be inappropriate to apply the relationships between fisheries productivity metrics and environmental conditions unveiled in this study to rivers, fish communities, or environmental conditions that are outside the range used to develop these relationships. Once these limits are respected, the relationships between fisheries productivity metrics and environmental conditions could be used to predict future river fisheries productivity metrics under a new set of environmental conditions. Knowledge and tools developed by the present project may be useful to inform the decision-making process regarding the development or operation of hydropower facilities, and, if authorities recognize the knowledge and tools developed by the present study, augment the clarity, the consistency, and the certainty of the decision-making process.

Modélisation des effets des facteurs chimiques et physiques sur les paramètres de productivité des pêches dans des rivières ayant des régimes hydrologiques différents : leçons retenues du réseau HydroNet du CRSNG, de 2009 à 2015

RÉSUMÉ

Le réseau HydroNet du conseil de recherches en sciences naturelles et en génie (CRSNG) est un réseau de recherche national dont l'objectif global consiste à fournir au gouvernement et à l'industrie les connaissances et les outils nécessaires pour améliorer la capacité des scientifiques et des gestionnaires à évaluer et à minimiser les effets des installations et des activités hydroélectriques sur les écosystèmes aquatiques. Ce projet a été divisé en trois composantes axées sur l'existence d'importantes variations entre les paramètres de productivité des pêches entre différents cours d'eau, l'établissement de liens entre ces paramètres de productivité et les conditions environnementales et la détermination de nouveaux paramètres prometteurs de productivité des pêches. Nous avons atteint notre objectif en estimant les paramètres de productivité des pêches (densité [nombre de poissons par m^2] et biomasse [grammes par mètre carré] par espèce de poissons et catégorie de tailles; richesse des espèces); les concentrations de nutriments (quantité totale de phosphore, de nitrate et de nitrite); les variables relatives au méso-habitat (profondeur, vitesse, composition du substrat, couverture de macrophytes, débris végétaux, etc.); les indices hydrologiques et les indices thermiques dans 15 cours d'eau dont le débit n'est pas régulé et 13 cours d'eau dont le débit est régulé pour la production d'hydroélectricité distribuée au Canada de l'Alberta jusqu'au Nouveau-Brunswick. Les liens entre les paramètres de productivité des pêches et les conditions environnementales ont été évalués à l'aide de différents paramètres de productivité des pêches (p. ex. production, prises, recrutement, densité, biomasse, croissance, survie, richesse d'espèces); d'échelles biologiques (p. ex. nombre total de communautés de poissons, guildes, associations d'espèces, groupe phylogénétique, espèce, stades biologiques [combinaison d'espèces et de catégories de tailles]) et d'échelles spatiales (p. ex. cours d'eau complets, portion de cours d'eau, méso-habitat et micro-habitat). La capacité d'explication et de prédiction des liens entre le poisson et l'environnement répond directement aux besoins suivants tant des promoteurs que des organismes de réglementation :

i) prévoir les effets possibles d'un projet sur les paramètres de productivité des pêches;

ii) évaluer la nécessité de prendre des mesures d'atténuation et l'ampleur de ces mesures;

iii) déterminer et mesurer l'efficacité relative des différentes stratégies d'atténuation;

iv) estimer l'existence ou l'ampleur des effets résiduels sur les paramètres de productivité des pêches;

v) quantifier le besoin de compensations et leur ampleur.

Toutefois, il pourrait être inapproprié d'appliquer les liens établis entre les paramètres de productivité des pêches et les conditions environnementales dévoilées dans la présente étude aux cours d'eau, aux communautés de poissons ou aux conditions environnementales qui ne font pas partie de la fourchette utilisée pour établir ces liens. Dans le respect de ces limites, on pourrait utiliser les liens entre les paramètres de productivité des pêches et les conditions environnementales pour prédire de futurs paramètres de productivité des pêches en rivière en fonction d'un nouvel ensemble de conditions environnementales. Les connaissances acquises et les outils élaborés dans le cadre du présent projet peuvent être utiles pour orienter la prise de décisions relativement au développement ou à l'exploitation d'installations hydroélectriques et, si les responsables reconnaissent cette utilité, sont susceptibles d'améliorer la clarté, l'uniformité et la certitude du processus décisionnel.

CONTEXT

NSERC HydroNet is a national research network whose overall mission is to provide government and industry with the knowledge and tools that will improve the capacity of scientists and managers to assess and minimize the effects of hydropower installations and operations on aquatic ecosystems. HydroNet intends to inform the decision-making process, and thereby to contribute to the sustainable development of hydropower in Canada. HydroNet is a collaborative research partnership between universities, government agencies, and hydropower companies. In 2009, HydroNet was granted a 5-year research mandate by the Natural Sciences and Engineering Research Council of Canada (NSERC). This mandate was recently extended to 2015 to allow for the completion of papers and reports. The research platform of HydroNet consists in a series of projects that focus on two themes:

1) modelling of fisheries productivity in rivers, and;
2) modelling of fish-habitat interactions in reservoirs.

The theme "modelling of fisheries productivity in rivers" includes projects on metrics of fisheries productivity and their chemical, physical, and biological drivers in rivers. The theme "modelling of fish-habitat interactions in reservoirs" comprises projects on the meso-scale modelling of fisheries productivity metrics in reservoirs and on the prediction of fish entrainment risk in reservoirs. The present report focuses on the modelling of the effects of chemical and physical drivers on fisheries productivity metrics across rivers of varying hydrological regimes.

GENERAL OBJECTIVE

The general objective of the project "Modelling the effects of chemical and physical drivers on fisheries productivity metrics across rivers" is to contribute to the development of knowledge and tools that improve our capacity to predict fisheries productivity metrics in rivers.

STRATEGY

This project was divided in three components that corresponded to the confirmation of the existence of significant among-river variations of fisheries productivity metrics, the development of relationships between fisheries productivity metrics and environmental conditions, and the identification of promising new metrics of fisheries productivity.

INTRODUCTION

Implementation of the new Fisheries Act and Fisheries Protection Policy requires the estimation of the original state of an aquatic ecosystem and the prediction of the effect of a project on fisheries productivity metrics. Explanatory or predictive relationships between fisheries productivity metrics and environmental conditions have long been known to exist in lakes. Fisheries productivity metrics used to develop these relationships range from long-term average catch of commercially important fish species (Rawson 1952, Ryder 1965, Oglesby 1977, Matuszek 1978, Hanson and Leggett 1982) to total fish community annual production (Downing et al. 1990, Downing and Plante 1993). Environmental conditions used to explain variations in fisheries productivity metrics include abiotic (e.g. mean depth, total dissolved solids, total phosphorus, degree-days) and biotic variables (e.g. primary production, biomass of benthic invertebrates). The existence of relationships between fisheries productivity metrics and environmental conditions, and more specifically between total fish community biomass and total phosphorus, has also been explored in rivers (Randall et al. 1995).

The structure of the relationships between fisheries productivity metrics and environmental conditions (hereafter referred to as "fish-environment relationships") implies that scientists and managers can predict the effects of changes in the environmental conditions used as explanatory variables on fisheries productivity metrics. If a project is expected to modify an environmental condition that has been used as an explanatory variable in a fish-environment relationship, expected environmental conditions can be inputted in these relationships, to predict the future state of the fisheries productivity metrics, and by comparison with the initial state, to assess the anticipated effects of the project on this fisheries productivity metric. The main practical limitation of this process is that very few fish-environment relationships have been developed for rivers (Randall et al. 1995). Consequently, the effects of relatively few environmental conditions can be predicted. The main statistical limitation to the development of fish-environment relationships in rivers is that there are hundreds of environmental conditions that have the potential to affect fisheries productivity metrics. This is particularly true if one considers the hundreds of flow and thermal indices that have been proposed to represent the magnitude, frequency, duration, timing and rate of change of flow and water temperature (Richter 1997, Olden and Poff 2003, Olden and Naiman 2010, Arismendi et al. 2013, McLaughlin et al. 2014). Another complicating factor to the development or the use of fish-environment relationships is the multiplicity of the forms that these relationships can take. Relationships between fisheries productivity metrics and environmental conditions may vary in terms of the fisheries productivity metric themselves (e.g. production, catch, recruitment, density, biomass, growth, survival, species richness), the organismal scales (e.g. total fish community, guilds, species associations, phylogenetic group, species, life-stages [combinations of species and size-classes]), and the spatial scales (e.g. complete river, river segment, meso-habitat, micro-habitat). Environmental conditions used as explanatory variables can also vary by their nature (abiotic to biotic) and the spatial scale at which they are expected to operate (landscape to micro-habitat). The overarching objective of this study is to develop explanatory, and eventually predictive, fish-environment relationships that will facilitate the assessment of the effects of hydropower operation or development on fisheries productivity metrics (Figure 1).

		Organismal Scale			
		Species*Size Class	Species	Guilds	Total Community
Spatial Scale	Site		Contribution 2.5		Contribution 1.1 (CV) Contribution 2.6 (CV)
	River Segment	Contribution 2.7 (CV)	Contribution 2.1 Contribution 3.1	Contribution 2.2 (CV)	Contribution 2.3 (CV) Contribution 2.4 (CV)

Figure 1. Illustration of the different contributions, modelling fish-environment relationships, according to organismal and spatial scales. CV indicates that model was cross-validated.

SPECIFIC OBJECTIVES

Objective 1: Assess the statistical significance of among-river variations in various fisheries productivity metrics.

Objective 2: Develop relationships between fisheries productivity metrics and environmental conditions in rivers.

Objective 3: Identify new fisheries productivity metrics that may facilitate the development of fish-environment relationships in rivers.

METHODOLOGY

We achieved our objectives by estimating fisheries productivity metrics (density [number of fish $\cdot m^2$) and biomass [$g \cdot m^{-2}$] by fish species and size-classes; species richness), nutrient concentrations (total phosphorus, nitrates, nitrites), meso-habitat variables (depth, velocity, substrate composition, macrophyte cover, woody debris, etc), hydrological indices, and thermal indices in a series of ecosystems that included unregulated rivers and rivers regulated for hydropower production. This strategy was adopted to increase the range of fisheries productivity metrics and environmental conditions available for modelling purposes.

RIVER SELECTION AND SAMPLING SITES

Study-rivers were selected using four steps meant to maximize the range of variables studied while minimizing the effect of confounding variables. First, the database of the Canadian Dam Association and of provincial governmental agencies were used to assess the distribution of dams over different climatic and eco-regions of Canada; Second, dams installed at least 40 years ago on relatively small (i.e. wadeable) rivers located in southern-central Canadian latitudes, and possessing numerous access points were identified. The focus on relatively old dams was guided by the intent to study rivers in which physical, chemical, and biological variables had been interacting for a long time, while the emphasis on smaller and southern-central rivers was directed by the need for road access downstream of dams and the potential to conduct quantitative fish sampling. Third, regulated rivers for which unregulated rivers that possessed qualitatively similar attributes (watershed area, slope, altitude, proximity to lakes), that had a hydrologic gauge (either from the Canadian Hydrometric Database [HYDAT; Government of Canada 2014] or the Centre d'Expertise Hydrique du Quebec [CEHQ; Government of Québec 2014]]) located at a maximum distance of 15 km from studied sites, and that were located within a distance of 400 km, were retained. Fourth, rivers in which average water transparency (maximum distance at which dark and light quadrants of a Secchi disk could be differentiated) was insufficient (<0.6 m) to conduct electrofishing and snorkelling surveys over multiple km segments were discounted. In situ assessments of the criteria used in steps 1 to 4 were done during pre-sampling surveys held in 2009 and 2010. The selection process led to the identification of 15 unregulated rivers and 13 regulated rivers distributed from Alberta to New Brunswick (Canada; Figure 2).
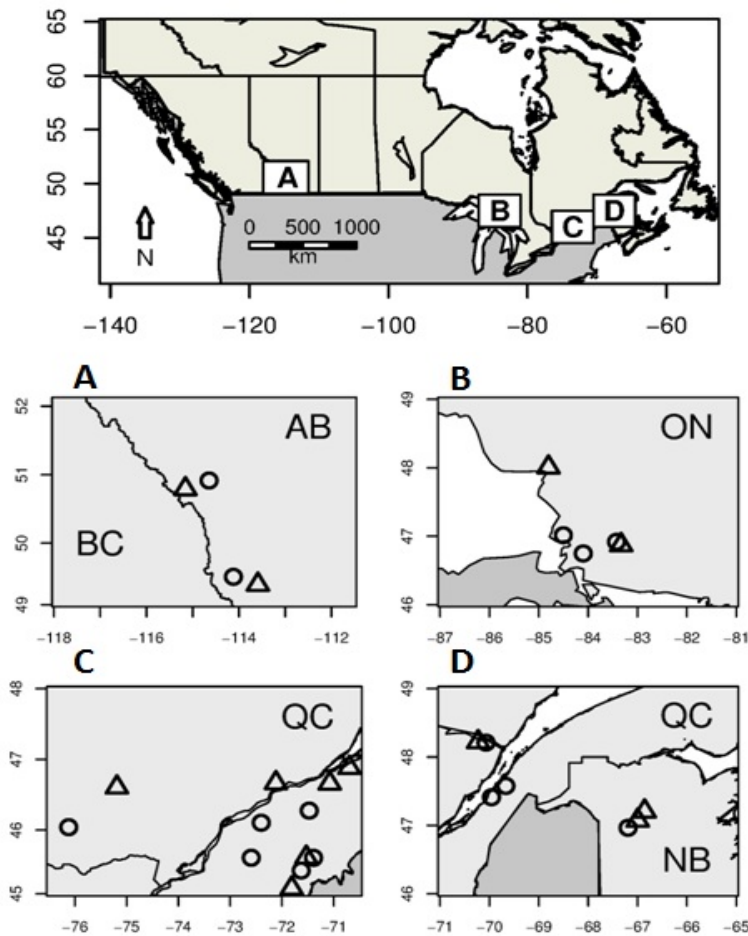
Figure 2. Map of the study area showing the 15 unregulated rivers (circles) and 13 regulated rivers (triangles) distributed across Canada. Sampling was conducted in four provinces: Alberta (AB), Ontario (ON), Québec (QC), and New Brunswick (NB). Specific areas are indicated by boxes labelled from A to D and enlarged views are presented under the principal map.

The 28 rivers selected for study can be categorized with respect to the presence and operation mode of hydroelectric facilities. Unregulated river (hereafter abbreviated "UR") are those without a dam. The presence of a dam involves some sort of regulation, yet not all dams store water. Dams without water storage are categorized as "run-of-the-river" (abbreviated "RR"). Dams that store water may also differ in the way water is released with time. Storage dams may generate power all day long, releasing water gradually (abbreviated "ST", for "storage") or alternate between periods when they generate no electricity and periods of high power generation (abbreviated "PE", for "peaking"), releasing short daily bursts of high flow (Young et al. 2011, McLaughlin et al. 2014). Three rivers were categorized as PE, the Kananaskis, the Magpie, and the Mississagi Rivers. The annual median discharges of these rivers were respectively 6.3 m^3/sec, 16 m^3/sec, and 30 m^3/sec. Water discharge below PE facilities (combination of turbine and spill flow) can vary greatly even through the course of a single hour. On an average day, there is generally one hour when flow is quickly raised, typically from 0.7 to 23 m^3/sec in Kananaskis River, from 8 to 40 m^3/sec in Magpie River and from 0 to 138 m^3/sec in Mississagi River. Flow trough-to-crest amplitude within any single day may be greater than these hourly intervals, but then these trough-to-crest variations would occur over the course of several hours. Across our time series, the largest flow increase within a single hour was an increase

from 0.2 to 28 m^3/sec in Kananaskis River, from 1 to 39 m^3/sec in Magpie River and from 0 to 330 m^3/sec in Mississagi River. In northern latitudes, UR experience flow patterns modulated by climatic processes, showing seasonal periodicity (i.e. spring floods) and occasional random flow peaks after large storms (Young et al. 2011). By contrast, dams may use all the water available for power production or allow the surplus of water flow to spill over the weir. The storage capacity of reservoirs and release of water from dams may also vary greatly from one hydroelectric facility to another, resulting in differences in the magnitude and periodicity of downstream flows. In rivers with RR dams, a small upstream reservoir volume relative to mean flow 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 (Bratrich et al. 2004). In rivers with ST dams, larger storage volumes allow the natural seasonal runoff volumes to shift temporally, resulting in significant seasonal high flow attenuation and enhancement of low flows, especially during the winter months. Rivers with PE dams exhibit frequent periods of significant hourly or daily hydrological fluctuations over a year caused by rapid opening and closing of the dam's sluice gates.

Fish surveys and environmental characterisation were conducted in segments of rivers ranging from 4 km (Ste-Anne River) to 27 km (Kananaskis River) in length (mean = 11 km, standard deviation (sd) = 6 km). For regulated rivers, the upstream limits of each segment were positioned from 200 m (Serpentine and Dee Rivers) to 8 km (Magpie and Mississagi Rivers) downstream of the dam. In each river segment, we sampled 25 to 50 sites (surface: mean=300 m^2, sd=30 m^2, width: mean = 5 m, sd = 1 m; length: mean=60 m, sd=6 m). The position of the first sampling site was selected at random and subsequent sampling sites were positioned, either downstream or upstream (depending on the location of the first sampling site), following a systematic sequence (i.e. left shore, middle, right shore, left shore, etc.). The exact location of sampling sites was adjusted within 5-20 m alongshore to maximize within-site habitat homogeneity (e.g. water depth, water velocity, and sediment size). A distance of 60 to 100 m was maintained between successive sampling sites. This procedure led to the sampling of a total of 989 sites. However, some environmental variables (hydrological or thermal indices) could not be acquired for all rivers (Table 1), and some analyses have been carried on a subset of rivers and sites.

FISH SURVEYS

Fish surveys were conducted at each sampling site using a combination of electrofishing and snorkeling. Fish surveys were conducted during summer months (late-June to September) from 2011 to 2013. Paired single-pass electrofishing and snorkeling surveys were carried out in random order at the same time period between 08:30 and 18:00, and weather permitting, on consecutive days. Although cloud cover may have varied among days, this variable was not expected to affect our fish data (Bourque et al. in preparation[1].). Electrofishing surveys were conducted by teams of three operators, in accordance to Ontario Ministry of Natural Resources (OMNR) policy standards (Jones 2011) using an LR-24 backpack electrofishing unit (Smith-Root®, Vancouver, WA). The electrofishing unit was set to deliver a standardized power of 200 Watts to minimize variations of sampling effectiveness associated to different water conductivities. Captured fish were identified to species, and their lengths (total length, ± 0.1 cm), and masses (wet blotted weight, ± 0.1 g) were measured. Snorkeling surveys were conducted using two divers swimming in a slow upstream fashion (approximately 6 seconds / m^2), covering

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[1] Bourque, G., Lanthier, G., and Boisclair, D. Effect of cloud cover on river fish community descriptors. In preparation.

the same entire site surface area. Fish species and total lengths were recorded into size classes (5 cm increment). 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 snorkeling surveys (Le Cren 1951). The density and biomass of each combination of species and size-classes at each site was estimated independently for both the electrofishing and the snorkeling methods by dividing the total number or mass of any given combination of fish species and size-class by the surface area of the sampling site. As described by Macnaughton et al. (2014) electrofishing may underestimate large fish or schooling species, while snorkeling may underestimate cryptic species. Consequently, the larger of the particular density and biomass estimates between sampling methods for each combination of species and size classes were selected to calculate fish density (number of fish/m^2) and biomass (g/m^2) at each site.

DESCRIPTION OF MESO-HABITAT VARIABLES

Meso-habitat variables (i.e., water velocity, water depth, substrate composition, macrophyte cover within a site) were assessed in a quadrate of 50 x 50 cm replicated 10 times per site following a haphazard design. Water velocity (± 0.01 m/sec) taken at 40% from the bottom of the total depth, and water depth (± 1 cm) were measured using a Marsh-McBirney Flo-Mate 2000 (ACG Technology Ltd and Envirocan Wastewater Treatment Equip. Co. Ltd.; 131 Whitmore Road, Unit 13 Woodbridge, Canada). Water velocity and water depth were each averaged within each site. Substrate composition was also quantified within each quadrate by visually estimating the percent cover (± 5%) of 9 substrate classes: clay, silt, sand, gravel, pebble, cobble, boulder, metric boulder and bedrock (Latulippe et al. 2001; Senay et al. 2015a). Substrate classes were averaged within sites (Table 1).

NUTRIENT SURVEYS

Water samples were taken, on days without rain, in the main flow of the rivers during the low summer flows of 2011 to 2014. Water was collected in 250 ml acid washed high-density polyethylene bottles (Nalgene®, Nalge Nunc International Corporation). One to nine water samples from each of the 28 rivers were obtained. Water samples were kept at 4°C using coolers that were shipped to the University of Alberta's Biogeochemical laboratory for analysis. The mean values of total phosphorus, nitrate, and nitrite concentration were estimated for each river. Individual values that differed from the river-specific mean by more than 15 times the coefficient of variation were excluded from the computations (Table 1).

HYDROLOGICAL INDICES

For 25 of the 28 rivers, daily and hourly flow data were obtained from the Water Survey of Canada (Government of Canada 2013), the Centre d'Expertise Hydrique du Québec (Government of Quebec 2014) and national flow gauge networks, and hydro-electric companies: Trans-Alta, Brookfield Renewable Power and NB Power. Hourly and daily flows were available between 1997 and 2009, during an averaged period of 12 years ranging from 5 to 13 years. These reflected the effects of temporal and climate variability on flow regime and multi-year differences in hydrological indices characterizing river flow regime (Kennard et al. 2010). Hydrological indices representing ecologically relevant components of the flow 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), were calculated for each of the rivers surveyed for a total of 211 flow indices. All flow metrics expressed as discharge units (volume per time) were normalized (n) by dividing these indices by the median flow (daily or

hourly as appropriate) for the available flow records (McManamay et al. 2012). 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. These indices described the magnitude (42), frequency (6), duration (15), timing (4), and rate of change (10) of river flows across all rivers (see Table 2 for description of variables significantly driving fish-environment relationships).

THERMAL INDICES

Summer water temperatures were measured using up to 15 temperature data loggers (Hobo Pendant Temp, precision of ± 0.5°C, ONSET® Computer Corporation) anchored along the river segments. For 22 river segments, temperature data loggers were placed between the most upstream and downstream sites. For the remaining river segments, loggers were located 22 to 69 km away from sites. 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 of any given sampling year. Between 0 and 15 temperature loggers were retrieved and used to calculate summer thermal profiles for each of the rivers studied. Due to atypical flooding events in Alberta in 2013 (Phillips 2013), many loggers were lost, limiting the use of temperature data in rivers to summers in 2006 for the Kananaskis and Elbow Rivers, and in 2014 for the Waterton River. No data could be collected for the Castle River. Water temperature data extracted from loggers were checked for erroneous measurements (i.e., air exposure), which were removed from thermal profiles. Loggers with <5days 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 relevant components of thermal regime (magnitude, variance, frequency, duration, timing and rate of change of daily and hourly temperatures (as described in 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 that reliably represented river average thermal regime from a single summer of temperature data. 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 centered on the warmest week for UR rivers to allow inter-river comparisons (Tables 1 and 2).

Table 1. Description of a subset of river environmental characteristics. For each river, regulation type, province, number of sampled sites, total fish biomass, water depth, water velocity, river width, macrophyte coverage, transparency, habitat heterogeneity, total phosphorus, median daily flow, rise rate, and degree-days are presented. NA indicates that a characteristic could not be quantified (See Table 2 for definitions of variables).

River Name	River Regulation	Province	Site Number	Total Biomass (g/m²)	Depth (cm)	Water Velocity (m/sec)	River Width (m)	Macrophyte (%)	Transparency (m)	Habitat Heterogeneity (HMID)	Total Phosphorus (TP, µg/L)	Median Daily Flow (MA2, m³/sec)	Rise Rate (nRA1, dimensionless)	Degree-Days (DD, °C)
Kananaskis	Peaking	AB	47	0.54	32.71	0.39	25.47	0.15	11.30	6.47	2.50	6.34	0.29	789.45
Magpie	Peaking	ON	26	0.31	40.49	0.32	45.50	3.52	4.70	8.86	6.50	15.73	0.07	1118.00
Mississagi	Peaking	ON	36	0.49	42.19	0.21	89.89	8.74	3.20	12.04	6.13	30.14	0.24	1193.80
Waterton	Storage	AB	47	1.54	40.64	0.37	41.29	0.01	4.56	6.96	4.50	3.85	0.02	1069.53
Dee	Storage	NB	30	1.60	32.44	0.47	14.33	0.05	2.38	5.11	8.00	1.68	0.00	1159.98
Serpentine	Storage	NB	30	4.02	28.19	0.37	20.43	2.48	2.78	5.18	10.30	0.76	0.00	957.83
Kiamika	Storage	QC	30	1.79	47.63	0.18	42.48	20.88	3.33	14.16	4.00	17.84	0.02	1166.91
Saint-François	Storage	QC	30	1.70	35.28	0.23	110.37	1.78	2.16	9.77	10.00	57.48	0.08	1380.29
Coaticook	RunofRiver	QC	30	1.29	35.76	0.29	26.60	0.50	1.77	8.66	9.00	5.38	0.22	1304.85
Du Sud	RunofRiver	QC	30	1.26	42.34	0.35	60.58	0.50	1.33	7.20	6.33	8.76	0.37	1233.31
Etchemin	RunofRiver	QC	40	3.35	36.72	0.27	81.51	0.69	1.90	8.51	12.33	13.10	0.32	1300.26
Sainte-Anne	RunofRiver	QC	30	0.99	40.01	0.24	116.12	0.18	1.45	10.05	16.00	NA	NA	1426.10
Saint-Jean	RunofRiver	QC	49	0.56	45.64	0.56	31.08	0.01	2.64	5.93	5.50	NA	NA	1134.41
Castle	Unregulated	AB	40	1.06	39.39	0.54	46.39	0.00	4.56	6.01	4.00	4.87	0.04	NA
Elbow	Unregulated	AB	46	1.41	37.69	0.60	35.30	0.00	11.97	5.00	1.00	5.30	0.03	367.08
Gulquac	Unregulated	NB	30	1.01	32.81	0.39	16.80	0.02	3.24	7.41	7.67	NA	NA	1066.95
Aubinadong	Unregulated	ON	40	0.37	47.15	0.33	40.80	1.58	5.05	7.42	4.71	8.00	0.05	1234.39
Batchawana	Unregulated	ON	43	0.55	45.60	0.37	50.34	0.34	3.79	6.96	5.00	9.50	0.07	1232.17

River Name	River Regulation	Province	Site Number	Total Biomass (g/m²)	Depth (cm)	Water Velocity (m/sec)	River Width (m)	Macrophyte (%)	Transparency (m)	Habitat Heterogeneity (HMID)	Total Phosphorus (TP, µg/L)	Median Daily Flow (MA2, m³/sec)	Rise Rate (nRA1, dimensionless)	Degree-Days (DD, °C)
Goulais	Unregulated	ON	30	0.38	40.75	0.11	34.80	3.00	2.54	18.20	9.00	8.04	0.08	1230.94
Au Saumon	Unregulated	QC	50	1.09	33.73	0.24	54.95	0.39	2.31	8.69	8.00	11.09	0.28	1297.75
Becancour	Unregulated	QC	50	5.47	46.80	0.26	37.25	2.22	2.89	9.29	9.50	12.00	0.18	1540.18
Du Loup	Unregulated	QC	30	0.83	36.49	0.31	28.46	0.00	2.11	6.81	10.00	4.10	0.17	1234.65
Eaton	Unregulated	QC	30	1.25	30.18	0.19	36.73	0.03	3.15	11.59	7.00	5.35	0.44	1320.16
Nicolet	Unregulated	QC	30	1.26	40.29	0.23	88.58	5.93	1.31	8.90	9.00	16.30	0.36	1439.37
Noire	Unregulated	QC	30	2.11	45.09	0.07	46.63	4.07	1.37	11.16	17.00	11.10	0.35	1467.91
Ouelle	Unregulated	QC	30	3.04	35.33	0.30	41.38	0.00	2.30	8.64	10.00	5.28	0.28	1229.75
Petit-Saguenay	Unregulated	QC	25	0.33	50.57	0.43	33.54	0.02	3.22	6.23	3.83	4.75	0.16	1174.39
Picanoc	Unregulated	QC	30	0.49	57.59	0.19	25.87	4.92	3.70	7.42	3.75	13.16	0.04	1409.19

Table 2. Code, name and descriptions of variables significantly driving fish-environment relationships.

Code	Name	Description
D50	D50	Median substrate size.
HMID	Habitat heterogeneity	The hydro-morphological index of diversity is calculated using the coefficients of spatial variation of water depth and velocity.
TP	Total phosphorus	The mean values of total phosphorus estimated for each river. Values that differed from the river-specific mean by more than 15 times the coefficient of variation were excluded from the computations.
DD	Degree-days	The sum of daily temperatures (°C) over the natural summer period defined as 9 weeks standardized around the warmest week of the summer.
MOmn7	July average in daily mean water temperatures	Monthly average in daily mean water temperature.
MSmn	Summer average in daily mean water temperatures	Average daily mean water temperature during natural summer period defined as 9 weeks standardized around the warmest week of the summer.
DH6	Variability of annual maximum daily average flow	Coefficient of variation in annual maximum daily average flow. Compute the standard deviation for the maximum daily average flow. DH6 is 100 times the standard deviation divided by the mean.
DL12	Normalized 7-day annual minimum flow	Annual minimum of 7-day moving average flow divided by the median for the entire record. Compute the minimum of a 7-day moving average flow for each year. DL12 is the mean of these values divided by the median for the entire record.
FH1	Flood frequency 1 (High flood pulse count)	Compute for each year the number of flow events with flows above a threshold equal to the 75th percentile value for the entire flow record. FH1 is the mean (or median - Use Preference option) number of events per year.
FH5	Flood frequency 2 (1x)	Compute for each year the number of flow events with flows above a threshold equal to the median flow value for the entire flow record. FH5 is the mean (or median - Use Preference option) number of events per year.
FH9	Flood frequency 3 (75%)	Compute for each year the number of flow events with flows above a threshold equal to the 75 percent exceedence value for the entire flow record. FH9 is the mean (or median - Use Preference option) number of events per year.
MA2	Median Daily Flow	Median of the daily mean flow values for the entire flow record.
MA27	Variability in monthly flows (Apr)	Coefficient of variation in monthly flows for April.

Code	Name	Description
MA3	Variability in daily flow	The median of the coefficients of variation (standard deviation/mean) for each year. Compute the coefficient of variation for each year of daily flows and then compute the mean of the annual coefficients of variation.
MA60	Coefficient of diel variation	Standard deviation of hourly flows divided by mean flow for a 24-h period. Mean of daily coefficients of variation.
MH14	Median of annual maximum flows	Compute the annual maximum flows from monthly maximum flows. Compute the ratio of annual maximum flow to median annual flow for each year. MH14 is the median of these ratios.
MH27	High peak flow 2	Compute the daily flow values for flow events above a threshold equal to the 75th percentile value for the entire record. MH27 is the average of all these high flow values divided by the median flow for the entire record.
nML6	Mean minimum monthly flows (Jun)	For each year, compute the minimum flow for the month of June. ML6 is the mean (or median - Use Preference option) of these values. This value is standardized (n) by MA2 (Median Daily Flow).
nRA1	Rise rate	Mean rate of positive changes in flow from one day to the next. Compute the change in flow for days in which the change is positive for the entire flow record. RA1 is the median of these values. This value is standardized (n) by MA2 (Median Daily Flow).
RA5	Proportion of rise days (Number of day rises)	Compute the number of days in which the flow is greater than the previous day. RA5 is the number of positive gain days divided by the total number of days in the flow record.
RA7	Change of flow (falling)	Compute the log10 of the flows for the entire flow record. Compute the change in log of flow for days in which the change is negative for the entire flow record. RA7 is the median of these log values.
RA8	Number of reversals (day-to-day)	Compute the number of days in each year when the change in flow from one day to the next changes direction. RA8 is the average (or median - Use Preference option) of the yearly values.
RH2	Hourly Flash Index 2 (high flow)	Ratio of the maximum hourly flow for each day to the mean hourly flow for this day. Mean of all daily ratios.
RL2	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.

Code	Name	Description
TA1	Constancy	Constancy is computed via the formulation of Colwell. A matrix of values is compiled where the rows are 11 flow categories and the columns are 365 (no February 29th) days of the year. The cell values are the number of times that a flow falls into a category on each day. The categories are (using natural logarithms): log(flow) < .1 x log(mean flow) .1 x log(mean flow) <= log(flow) < .25 x log(mean flow) .25 x log(mean flow) <= log(flow) < .5 x log(mean flow) .5 x log(mean flow) <= log(flow) < .75 x log(mean flow) .75 x log(mean flow) <= log(flow) < 1.0 x log(mean flow) 1.0 x log(mean flow) <= log(flow) < 1.25 x log(mean flow) 1.25 x log(mean flow) <= log(flow) < 1.5 x log(mean flow) 1.5 x log(mean flow) <= log(flow) < 1.75 x log(mean flow) 1.75 x log(mean flow) <= log(flow) < 2.0 x log(mean flow) 2.0 x log(mean flow) <= log(flow) < 2.25 x log(mean flow) log(flow) >= 2.25 x log(mean flow) The row totals, column totals, and grand total are computed. 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)).
TA2	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). It is computed as (using natural logarithms): 1 - ((uncertainty with respect to interaction of time and state - uncertainty with respect to time) / log (number of state)).
TH1	Julian date of annual maximum	Determine the Julian date that the maximum flow occurs for each year. Transform the dates to relative values on a circular scale (radians or degrees). Compute the x and y components for each year and average them across all years. Compute the mean angle as the arc tangent of y-mean divided by x-mean. Transform the resultant angle back to Julian date.
TH2	Variability in Julian date of annual maximum	Circular variance in TH1. 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).

OBJECTIVE 1

Assess the statistical significance of among-river variations in various fisheries productivity metrics.

CONTRIBUTION 1.1

Fisheries productivity metric: Density, Biomass, Richness
Organismal scale: Total community
Spatial scale: Site
Explanatory variable: River regulation and meso-habitat variables

The first step of any attempt to study the determinants of variations among a series of objects (in the present situation, fisheries productivity metrics among river segments or sites) consists in confirming the statistical significance of such variations. The second step of this process consists in modelling this variation. Assessment and modelling of among-river variations in fisheries productivity metrics implies the study of variations in space. Spatial variation stems from the spatially organized nature of the processes shaping the landscape (e.g., the climatic processes influencing rainfalls, the ecological processes whereby species dispersed, the geological processes that distributed minerals in the earth crust). In addition, statistical tests assume that observations are independent of one another (Legendre and Legendre 2012) or, at least, that their dependence to one another is homogeneous. However, because the features and processes in the environment are spatially organized, observations taken at nearby sites (e.g., two consecutive sites) are more dependent of one another than observations taken at a greater distance (e.g., sites 10 km apart): observations are spatially auto-correlated (Legendre 1993, Dormann et al. 2007). Similarly, observations on pairs of rivers located in the same region (e.g., 50 km apart) are expected be more similar than observations on pairs rivers located in different regions (e.g., 1000 km apart). Following that paradigm, the dependence of observations is expected to be some negative function of the distance separating them. Fortunately, methods exist that allow us to use the spatial dependence among observations in a predictive manner and "filter-out" the spatial variation, and its associated autocorrelation to obtain unbiased statistical inference tests. This filtering can be achieved by computing spatial eigenvector maps on the basis of the geodesic distances between pairs of sites within each river; this is the length of the spherical arc between two locations following Earth's curvature. Geodesic distances can be calculated from the geographical coordinates of the sites (in degrees) using the haversine formula (Goodwin 1910). The purpose of this project (Guénard et al., In press) is to analyze the effect of flow management (UR, RR, ST, PE), water depth and velocity as well as median substrate grain size, and spatial eigenvectors on total fish community density, biomass, or species richness in an additive manner (linear model).

Guénard et al. (In Press) analyzed data from 28 rivers, of which 15 are UR and 13 are regulated. Fish were observed in 910 sites (97%), where the range of total fish community density was 0.003-4.57 fish·m^{-2} (median: 0.16 fish·m^{-2}), the range of total fish community biomass was 0.002−66.78 g·m^{-2} (median: 0.67 g·m^{-2}), and the maximum species richness observed per site was 18 (median: 5). All linear models that used spatial eigenvectors as predictors had higher predictive powers (density: 0.47, biomass: 0.26, and species richness: 0.33) than their counterpart without spatial eigenvectors (density: 0.09, biomass: 0.005, and species richness: 0.23).

Table 3. Summary of parameter values, t-test statistics, and p-values for the models describing transformed (log (x+1)) fish density, biomass, and species richness estimates. UR, RR, ST, and PE are respectively unregulated river, run-of-the-river, storage, and peaking dams.

Parameter	Density			Biomass			Species richness		
	Estimate	T	p-value	Estimate	T	p-value	Estimate	T	p-value
RR – UR	0	0	1	-0.03	-0.68	0.5	0.02	0.61	0.5
ST – UR	-0.01	-0.84	0.4	0.35	6.88	<0.0001	-0.09	-2.72	0.007
PE – UR	-0.06	-5.92	<0.0001	-0.27	-10.02	<0.0001	-0.66	-12.74	<0.0001

In the model predicting count density, the effect of water depth and velocity, were retained by the model together with 17% of the 506 spatial eigenfunctions. We found the flow management practices to affect count density, with PE dams having 39% smaller density, on average, than values predicted for UR rivers (a -0.059 fish·m^{-2} difference from a predicted baseline of 0.150 fish m^{-2}; Figure 3A; Table 3). No statistically significant differences in count density were found for RR and ST dams ($p>0.05$). For predicting biomass density, water velocity was the only retained significant predictor and was accompanied by 15% of the spatial eigenfunctions. On average, we found flow management to affect biomass density, with ST dams having 33% higher biomass density (a +0.350 g·m^{-2} difference from a predicted baseline of 0.795 g·m^{-2}) and PE dams to have a 47% lower biomass density (a -0.267 g·m^{-2} from a baseline of 0.566 g·m^{-2}) than that predicted for UR (Figure 3B; Table 3). RR dams were similar to UR conditions in terms of biomass density ($p>0.05$). For predicting species richness, water depth and velocity were selected as predictors together with 10% of the spatial eigenfunctions. As in the two previous analyses, the flow management had an influence on species richness. On average, PE and ST dams had 13% fewer (-0.660 species from the baseline of 5.088) and 1.7% fewer (-0.091 species from the baseline of 5.200 species) fish species, respectively, than predicted for UR (Figure 3C; Table 3). RR dams had similar species richness than for UR ($p>0.05$).
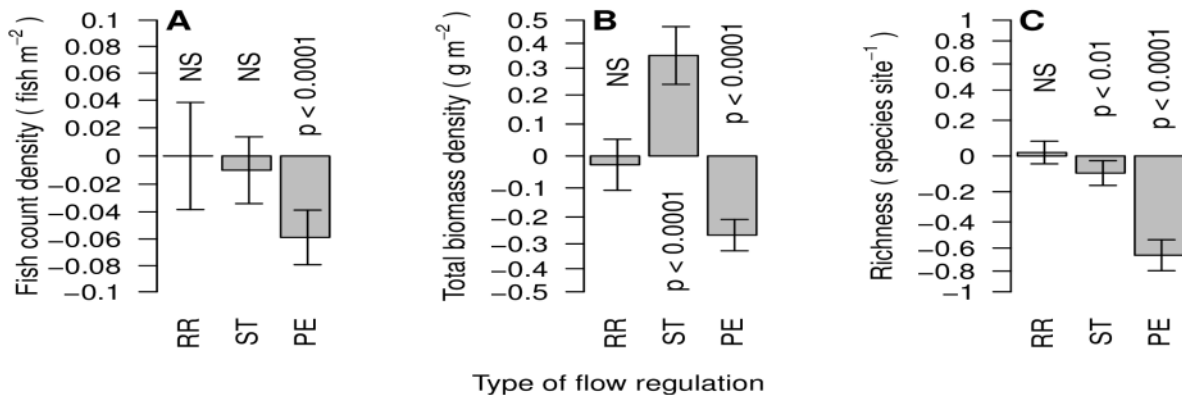
Figure 3. Net effect of flow management strategies on fish: A count density, B biomass density and C species richness compared to that predicted for unregulated rivers (RR: river with run-of-the-river dam, ST: river with a gradual release storage dam, PE: river with a peak release storage dam). Error bars are 95% confidence intervals.

Lessons learned from contribution 1.1

- Rivers located downstream of PE facilities have 39%, 48%, and 13% lower fish densities, biomass, and species richness, respectively, than that predicted for UR rivers.

- Rivers located downstream of ST dams had 33% higher biomass and 1.7% lower species richness than predicted for UR rivers.

- Rivers located downstream of RR dams have similar density, biomass, and species richness than that predicted for an UR rivers.

- The effects of dams may vary, from positive to negative and insignificant, among fisheries productivity metrics (density, biomass, species richness) and flow management practices (ST, PE, but not RR).

- Different models may be needed for density, biomass, and species richness.

OBJECTIVE 2

Develop relationships between fisheries productivity metrics and environmental conditions in rivers.

Fish-environment relationships were developed using different combinations of fisheries productivity metrics (density, biomass, and species richness), organismal scales (total fish community, guilds, phylogenetic group, and combinations of species and size-classes), and spatial scales (river segment, site). Environmental conditions used as explanatory variables encompassed those expected to operate at a spatial scale ranging from the complete river segment (nutrients, and hydrological and thermal indices) to the individual sites (water depth and velocity, substrate composition, macrophyte cover, etc). The projects meant to develop fish-environment relationships were conducted, and are presented below, beginning with combinations of more general fisheries productivity metrics (matrices of various fisheries productivity metrics), organismal scales (total fish community or general guild metrics) and spatial scales (river segment) and, ending with more specific fisheries productivity metrics (density or biomass), organismal scales (species or combinations of species and size-classes), and spatial scales (site). Similarly, projects were conducted, and are presented below, beginning with those that attempted to minimize the number of potential explanatory variables – a process particularly challenging for hydrological and thermal indices.

CONTRIBUTION 2.1

Fisheries productivity metric: Multidimensional biotic anomaly index
Organismal scale: Species
Spatial scale: River segment
Explanatory variable: Multidimensional flow anomaly index

The strategy adopted by Macnaughton et al. (In Press) was to test for the existence of a relationship between "biotic anomaly indices" and "flow anomaly indices" across regulated rivers. This approach is an extension of the Ecological Limit of Hydrologic Alteration concept (ELOHA; Poff et al. 2010), that suggests that there should be a relationship between changes to community descriptors and the extent to which a flow regime has been altered from UR regional conditions. The biotic anomaly index describes the combination of the deviations of various community-scale fish metrics (total abundance, biomass, fish diversity, proportion of small to large fishes) from UR regional conditions. Specifically, we calculated for each river segment, 25 biotic indices representing four groups of fish metrics: fish quantity (total community fish density and biomass, as well as total density and biomass of small, medium and large size classes; N =

5), fish diversity (family and species richness, Hill's H1 and H2 and Shannon's diversity indices; N = 6), fish community composition (proportions of family biomasses; N = 12) and proportional representation of two fish habitat guilds (demersal or benthopelagic fish; N = 2). We then conducted a principal component analysis (PCA) for each of the four groups, allowing us to position all river segments in a multidimensional space. This was done to condense the number of response variables into 5 PC axes that explained dominant patterns of variation for each of the fish groups components (determined via broken stick model). We followed this by calculating the mean and covariance matrix for the UR positions on these 5 PC axes. This then served as our regional biotic reference condition, from which all regulated river positions on these same PC axes were compared. Finally, we estimated a multivariate distance (Mahalanobis 1936), in 5 dimensions, between the coordinates of any given regulated river and this regional reference condition. This distance, which is the biotic anomaly index, was taken as a measure of the multidimensional biotic difference between a regulated river and the UR reference condition. Likewise, the extent to which the flow regime for a given regulated river deviates from reference conditions created by the mean and covariance matrix using only the UR is what we called flow anomaly index. It was estimated using the 105 flow indices calculated for each river segment, representing 6 flow components (flow magnitude, frequency, duration, timing, rate of change and hourly flows). For each of the flow components, PCAs were conducted and significant PC axes (determined via broken stick model) were retained, yielding 10 PC axes in total. The mahalanobis distance between each of the regulated river's location in multivariate space and the UR reference condition was then calculated. This is what we called our flow anomaly index (Figure 4). Hotelling's T² statistic was used to determine whether this distance for each of the regulated rivers differed significantly from reference conditions (Legendre and Legendre 2012). A regulated river was considered flow-altered if the distance from reference conditions of the hydrologic anomaly inferred from flow PCs (anomaly scores) was significantly greater than what can be expected from that of UR rivers. Likewise, a river was considered biotic-altered if biotic anomaly inferred from biotic PCs was significantly greater than expected. To determine whether the degree of biotic anomaly corresponds to the degree of flow anomaly, we ran a Model II linear regression by permutation (N = 999), using the major axis (MA) method and 95% CI for the slope and intercept parameter. 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 anomaly scores calculated (Legendre 2013).
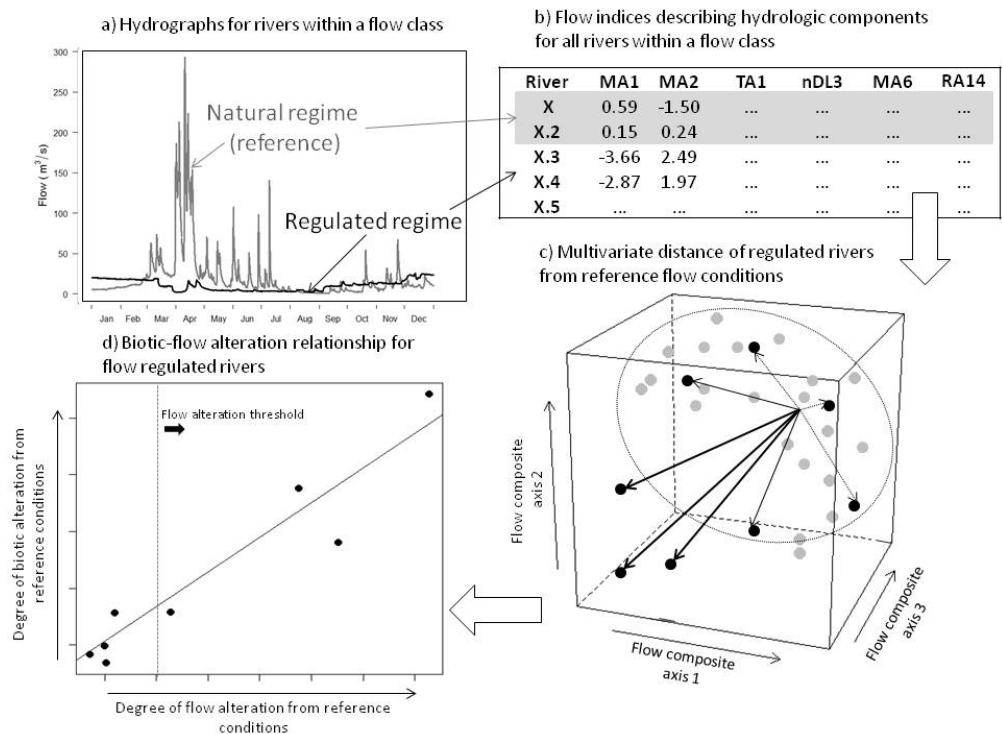
Figure 4. (a) Hydrographs depicting natural (reference) and regulated regimes for rivers belonging to a given flow class. (b) Table of the flow indices that describe each of the flow components by rivers for a given flow class. PCA were conducted for each of the flow components, yielding PC axes representing 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 anomaly score relationship for regulated rivers using the multivariate flow distances previously calculated. Biotic anomaly scores for these same regulated rivers were derived in the same manner as was done for flow anomaly scores. The dashed line refers to the flow anomaly threshold where points to the right of the line are rivers that are significantly altered from the reference flow conditions.

The statistically significant principal component axes explained from 61% to 91% of flow variances. Flow indices that contributed the most (top loaders of principal component analyses) to the inter-river variability for each of the flow components were: MA3 and nML6 (magnitude), FH1 (frequency), DL12 and DH6 (duration), TA2 and TH2 (timing), RA7 and nRA1 (rate of change), and RL2 and MA60 (hourly flows, Table 2). Biotic indices that represented the top loaders for significant principal component axes were fish quantity; total biomass of medium and small-sized fishes; total fish biomasses and densities; fish diversity; Shannon diversity indices derived from both biomass and density estimates; fish composition (the proportion of esocid and lottid families, and the proportion of salmonid, cyprinid, ictalurid and anguillid families); and proportional difference of habitat guilds (demersal or benthopelagic species). Model II regression produced a significant positive linear relationship between biotic and flow anomaly indices ($r = 0.94$, 2-tailed p-value < 0.005), with the PE rivers exhibiting the greatest anomalies overall from UR reference conditions (highest fish and flow indices; Figure 5). Although the overall relationship was driven by one of the PE rivers, the linear relationship between biotic and hydrologic anomaly scores remained marginally significant ($r = 0.65$, 2-tailed p-value $= 0.06$) when the outlier was excluded. Despite significant differences in flow anomaly indices for many of the regulated rivers (7 out of 10 rivers), rivers located downstream of RR and ST dams were

generally not found to have significantly different biotic anomaly indices (cluster in proximity to the UR biotic mean) In fact, only 3 rivers (2 PE and 1 ST river) were significantly different from UR biotic reference conditions. This relationship points to a potential flow anomaly threshold, where any flow anomaly index greater than a threshold value greater than 6 may result in significant biotic anomaly. However, the lack of data points in the moderate to high ranges of flow anomaly indices precluded any true estimation of the potential for establishing a threshold (Figure 5).
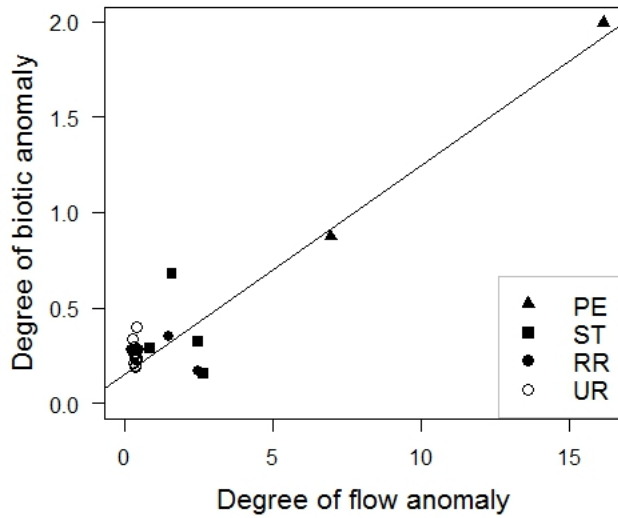
Figure 5. Type II linear regression between biotic and flow anomaly scores (fourth root-transformed) across all 10 regulated rivers, derived from all 105 daily and hourly flow indices. Rivers depicting PE (▲), ST (■), and RR (●) types of regulation regimes as well as UR rivers (○) are illustrated.

Lessons learned from contribution 2.1

- A relatively small number of flow indices (11) can explain a significant portion of the information comprised among the 105 flow indices (~61% to 91%) and these flow PCs may be combined to obtain river-specific anomaly indices, resulting in more comprehensive composites of river flow anomalies.

- The degree of biotic anomaly significantly corresponds to the degree of flow anomaly in regulated rivers. 'Tolerable' thresholds of flow anomaly below which biotic anomalies do not occur can be established when they are informed by regional reference conditions. However, the lack of data points in the moderate to high ranges of flow anomaly scores in our study precludes us from suggesting a generalized threshold.

- An expected flow regime (e.g. post-development) can be transformed into a degree of flow anomaly.

- A framework upon which anomalies or deviations from regional references may be estimated and used to predict the direction of environmental variable/stressor- community response anomaly relationships. The applications of this framework may also extend into other fields concerned with anthropogenic impacts on ecosystem structure and function.

CONTRIBUTION 2.2

Fisheries productivity metric: Fish density and biomass
Organismal scale: Guild
Spatial scale: River segment
Explanatory variable: Hydrological and thermal indices

Building on the previous contribution, Macnaughton et al. (In preparation[2]) uses guilds based on different ecological/functional traits to assess fish community response to flow and thermal regimes across rivers. Numerous environmental attributes are known to affect the structure of river fish assemblages. In particular, the proportion of specific guilds may be affected by variables relating to and including the biogeography, water temperature (Jackson and Harvey 1989), nutrient levels like 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 flow regime 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 certain fish assemblages (Bunn and Arthington 2002, Ibarra et al. 2003, Welcomme et al. 2006, Rolls and Arthington 2014, Taylor et al. 2014).

Guilds have served as the "basic building blocks" of communities, focusing on groups of species with particular trait-environment or functional relationships, which reveal a structure not attributable simply to the abundance of individual species or species composition and taxonomic affiliation (Hawkins and MacMahon 1989, Simberloff and Dayan 1991). They have been developed to describe and predict the community change in response to habitat alteration and environmental perturbation (Frimpong and Angermeier 2010), as they are thought to respond to environmental change in a more predictable manner than individual species (Austen et al. 1994). To date however, across-guild studies comparing the different relationships between the traits that make up each of the guilds and variables reflecting environmental change are lacking. Moreover, the role that changes in thermal regimes stemming from river regulation may have on fish communities is relatively unknown (Murchie et al. 2008). Such an analysis may improve our ability to advance our understanding of trait-environment relationships, and better our capacity to predict the effects of environmental changes on organisms, especially those related to river regulation (Michel and Knouft 2014). Specifically, the objectives of this contribution were to:

1) compare the relationships between guilds based on different types of traits (morphologic, trophic, reproductive, habitat, behavioural) and variables describing flow and thermal regimes in rivers; and,

2) to identify the flow and thermal regime variables that best explain and predict fish density and biomass among guilds.

K-means partitioning analysis based on a range of simple structure indices (SSI criterion; Oksanen et al. 2011) was used to guide the number of ecologically relevant guilds developed with different types of traits. Taxonomic associations were based on phylogenetic distances between the fish species surveyed (Hubert et al. 2008) and served as our null hypothesis.

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[2] Macnaughton, C.J., Senay, C., Dolinsek, I., Bourque, G., Maheu, A., Lanthier, G., Harvey-Lavoie, S., Asselin, J., Legendre, P., and Boisclair, D. Using guilds to assess fish community response to hydrological and thermal regimes across temperate rivers. In preparation.

Hydrological indices representing ecologically relevant components of the flow regime (magnitude, frequency, duration, timing and rate of change of daily flows (IHA; Richter 1997, Olden and Poff 2003, McLaughlin et al. 2014), in addition to those created to capture hourly variations in the flow record (Zimmerman et al. 2010), were calculated for each of the rivers surveyed, for a total of 77 flow indices retained. From the 294 thermal indices, 21 were selected that reliably represented river average thermal regime from a single summer of temperature data. The 77 hydrological indices characterizing the flow regime were summarized by conducting five separate principal component analyses (PCA) for each of the flow regime components (magnitude, frequency, duration, timing and rate of change). For the 21 thermal indices, PCA were conducted for 3 groups: 1- the magnitude, frequency and duration, 2- variance, and 3-rate of change and timing. River scores for PC axes describing a greater fraction of the variation than the broken-stick null model were retained (Legendre and Legendre 2012). Redundancy analyses (RDA) with 999 permutations (Legendre and Legendre 2012) were used to assess the relationships between each response variables, corresponding to river biomass and density estimates for each of the guilds based on morphologic, trophic, reproductive, habitat, behavioural traits and taxonomic associations (response variables) and hydrological and thermal PC axes (explanatory variables).

The PC axes describing the flow and thermal components significantly explained fish density and biomass estimates across guilds per type of traits (a total of 12 models representing densities and biomasses of guilds and taxonomic associations). Our results showed that the best explanatory models (greatest R^2_{Adj}) were found for traits describing habitat and trophic guilds ($R^2_{Adj} = 0.44$ and $R^2_{Adj} = 0.41$, respectively) and that all guild models (R^2_{Adj} and cumulative R^2_{Adj}) outperformed the null hypothesis (taxonomic groups $R^2_{Adj} = 0.26$), which suggests the presence of functional relationships not attributable simply to taxonomic association (Table 4). The explanatory variables most often selected for by fish guild models (>86% of models) were the magnitude of summer water temperatures (PC1 Magnitude of temperatures) followed by the intra-annual flow variability or the difference in the extreme flows within a year (PC1 Magnitude of flows). The magnitude of summer water temperatures combines thermal indices that describe the cumulative degree days (DD), the summer average in daily mean water temperatures (MSmn) and the July average in daily mean water temperatures (MOmn7). The intra-annual flow variability depicts 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; Table 2 and 4). When habitat and trophic guild models were conducted excluding thermal components, flow components significantly explained biomass estimates. However, model strengths based on R^2_{Adj} were 13 and 20% lower, respectively. The same was true when flow PCs were removed from analyses (9 and 10% lower, respectively).

Table 4. *Fish guild explanatory (R^2_{Adj}) and predictive (R^2_{CV}) models as a function of selected flow and thermal Principal Component axes.*

		R^2_{Adj}	p-value	Significant explanatory variables selected for each model (order respected)				R^2_{CV}
Biomass estimates per guild	Morphological	0.33	0.002	Magnitude of summer water temperatures	Intra-annual variability	Long-term variability		0.44
	Trophic	0.41	0.003	Magnitude of summer water temperatures	Intra-annual variability	Long-term variability	Magnitude of spring flood	0.40
	Reproductive	0.32	0.003	Magnitude of summer water temperatures	Intra-annual variability			0.55
	Habitat	0.44	0.001	Magnitude of summer water temperatures	Intra-annual variability			0.35
	Behaviour	0.34	0.007	Magnitude of summer water temperatures	Long-term variability	Magnitude of spring flood		0.46
	Taxonomic	0.26	0.014	Intra-annual flow variability	Magnitude of summer water temperatures	Long-term variability		0.73

Lessons learned from contribution 2.2

- 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 fish guild models performed better relative to studying taxonomic associations, confirming that guild models based on trait-environmental relationships were better than those based on taxonomy.

- Flow and thermal variables depicting the magnitude of summer water temperatures and intra-annual flow variability were independent drivers of fish guild models, pointing to the importance of integrating thermal regimes in hydro-ecological studies.

- Combining flow and thermal indices (more important) can explain a large fraction of inter-river variations in fish guild densities and biomasses (>40%).

- A small number of thermal indices appear particularly important in explaining variations in fish guild density and biomass.

- Both flow and thermal data should be monitored on a regular basis (unregulated as reference + regulated sites).

CONTRIBUTION 2.3

Fisheries productivity metric: Fish biomass
Organismal scale: Total community
Spatial scale: River segment
Explanatory variable: Chemical and physical drivers

Total phosphorus has been shown to affect total fish community biomass in rivers (Randall et al. 1995). However, the effect of other environmental conditions, and particularly those affected by hydropower, is less documented. Lanthier et al. (In preparation[3]) exploited the anticipated effect of phosphorus on riverine fish and the knowledge provided by Guénard et al. (In Press), Macnaughton et al. (In Press), and Macnaughton et al. (In preparation[2]) about the environmental conditions that may (specific flow and thermal indices) explain among-river variations in total fish community biomass to develop a relationship between fish biomass and specific environmental conditions.

The objectives of the project of Lanthier et al. (In preparation[3]) were:

1) to use artificial neural networks to develop explanatory and predictive models of the relationship between total fish biomass (TFB), total phosphorus (TP), water temperature (Degree-days; DD), and flow stability (nRA1) in rivers, and;

2) to assess the shapes of the interactions between fish biomass and key environmental conditions using a new plotting method.

Artificial neural networks (ANN) were selected for analysis because they are powerful and flexible statistical tools that can represent non-linear relationships that often characterize ecological interactions (Lek et al. 1996, Guégan et al. 1998, Chen and Ware 1999). The explanatory power (R^2) of ANN was evaluated by performing a linear regression between observed and fitted values. The predictive power of the ANN was examined using 'leave-one-out' cross-validation runs. Cross-validation corresponds to the procedure of performing multiple comparisons on predetermined subsets of a larger set of observation, each time using all the remaining data for model estimation, and proceeding until all observations had been predicted and predictions compared to their corresponding observations (Guénard et al. 2013). This procedure is appropriate for small data sets (Rumelhart et al. 1988, Kohavi 1995). Predictive power of the model was quantified by calculating the R^2_{cv} (cross-validation R^2; Guénard et al. 2013). The ecological interpretation of relationships between TFB, TP, DD, and nRA1 was first assessed by quantifying the relative importance of environmental conditions on the explanatory power of the ANN using the Connection Weight approach (Olden et al. 2004). Second, a new plotting method was used to provide a visual interpretation of the shape of these relationships and the interactions among the environmental conditions. In this new plotting method, nine panels were generated to illustrate the shape of the relationship between TFB and each

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[3] Lanthier, G., Guénard, G., Bourque, G., Senay, C., Macnaughton, C. J., Harvey-Lavoie, S., Maheu, A., St-Hilaire, A., Rasmussen, J. B., and Boisclair, D. Using artificial neural network (ANN) to model fish biomass among rivers: a new method to identify the interactive effects of explanatory variables. In preparation.

environmental condition. Each panel represented the relationship between the response variable (TFB) and a single descriptor (environmental condition) while the other two descriptors are held constant. The combinations of the 1st, 2nd or 3rd quartiles of the two descriptors that were held constant defined the nine panels. For each river represented in a panel, a Mahalanobis distance (Mahalanobis 1936) was estimated between the values at which descriptors and used to modulate the size of the markers on the plots (i.e., observations with smaller distances have larger markers and vis-versa) and *post-hoc* explorations of linear trends in the ANN model (see below).

TFB in the 25 river segments analyzed ranged from 0.31 (Magpie) to 3.50 g·m^{-2} (Bécancour) and had a mean value of 1.31±0.87 g·m^{-2} (Table 1). Environmental conditions varied 4.2- to 220-fold among river segments (Table 1). DD was the least variable environmental condition with values ranging from 367 (Elbow) to 1540 °C (Bécancour; mean=1194±238°C). In contrast, nRA1 was the most variable environmental condition with values ranging from 0.002 (Serpentine) to 0.44 (Eaton; mean=0.17±0.14).

TFB fitted by ANN ranged from 0.22 g·m^{-2} (Petit-Saguenay) to 3.15 g·m^{-2} (Noire). The R^2 of the linear regression between the fitted and the observed TFB values was 83% while the R^2_{cv} of the relationship between the predicted and the observed TFB values was 67%, suggesting both a good explanatory and predictive power of ANN. There was no relationship between the residuals and the predicted TFB values (r=0.16, *p*=0.44) indicating that ANN did not tend to underestimate or overestimate TFB values over a particular TFB range. The Connection Weight approach revealed that TP, DD, and nRA1 contributed to, respectively, 28%, 53%, and 19% of the explanatory power of ANN. TFB tended to increase as TP and DD increased (Figure 6). However, TFB tended to decrease as nRA1 increased (Figure 6). The graphs generated using the new plotting method suggested that the strength of the relationship between TFB and TP changed with DD values (Figure 6). The R^2_{Adj} of the linear relationship between TFB and TP weighted by inverse Mahalanobis distances ranged from 7% to 12% for DD values of 1160°C (Figure 7 bottom 3 panels). Corresponding values for DD values of 1305 °C were 45% and 48% (Figure 7 top 3 panels). In contrast, the strength of the relationship between TFB and DD changed with both TP and nRA1 values (Figure 8). The R^2_{Adj} of the relationship between TFB and DD weighted by inverse Mahalanobis distances was <1% for TP values of 4 µg·L^{-1} and nRA1 values of 0.04 (Figure 8 bottom left panel). The strength of this relationship increased, to 18% for TP values of 4 µg·L^{-1} and nRA1 values of 0.28 (Figure 8 top left panel), and, to 34% for TP values of 10 µg·L^{-1} and nRA1 values of 0.04 (Figure 8 bottom right panel). When both TP and nRA1 were high (10 µg·L^{-1} and 0.28 respectively, Figure 8 top right panel), the strength of the relationship between TFB and DD increased to 48%. Although TFB globally tended to decrease as nRA1 increased (Figure 6), the relationship between TFB and nRA1 weighted by inverse Mahalanobis distances was never significant (Figure 9).
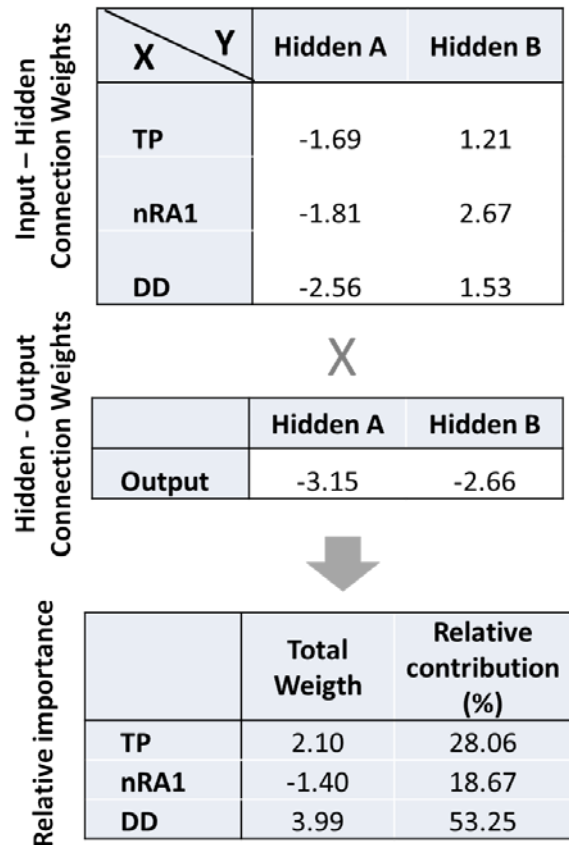
Figure 6. Illustration of the Connection Weight Approach allowing estimating the relative contribution of TP ($\mu g \cdot L^{-1}$), DD (°C) and nRA1 (dimensionless) to explain TFB ($g \cdot m^{-2}$) in the ANN model developed. The Connection Weight Approach uses raw connection weights, which accounts for the direction of the input–hidden–output relationship and results in the correct identification of variable contribution.
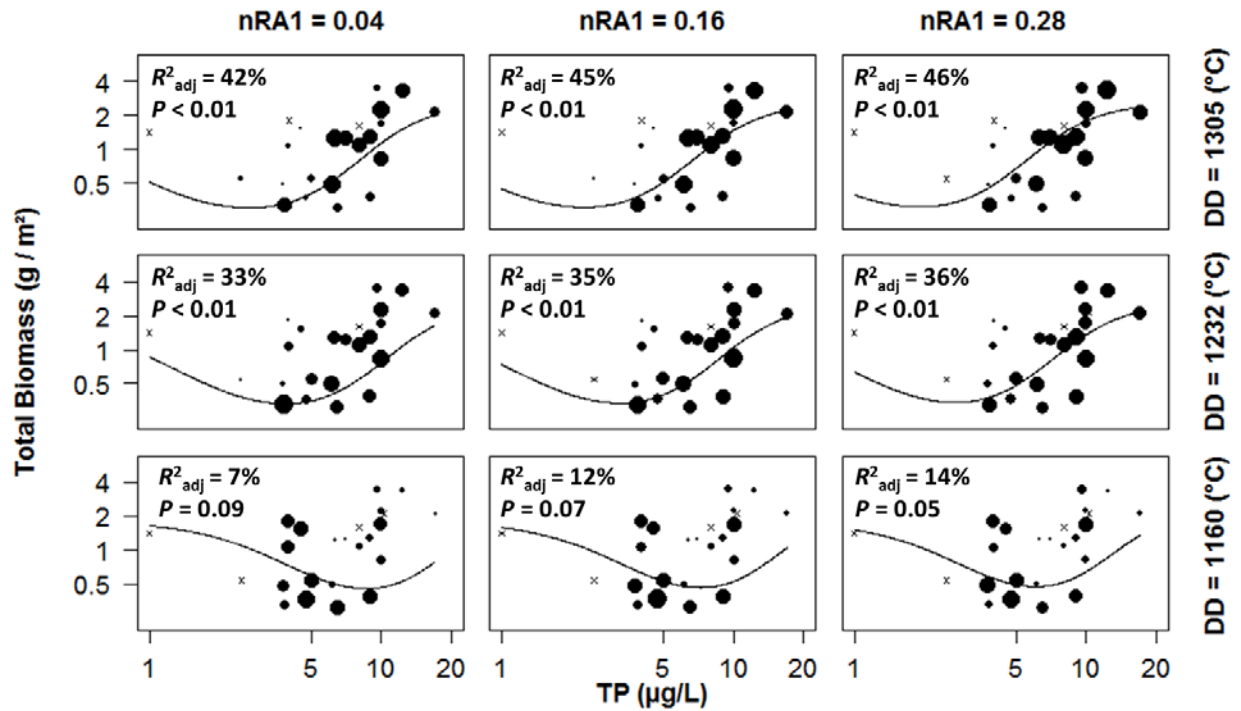
Figure 7. Relationships between TFB ($g·m^{-2}$) and TP ($µg·L^{-1}$) in ANN models. Marker sizes are inversely proportional to the inverse Mahalanobis distance between the values of the two descriptors that were held constant in a panel and the values observed in this river for these descriptors (i.e. rivers represented by small markers are more distant from the values of the conditions held constant in a panel than rivers represented by large markers). For very large distances, small crosses are used as markers instead of circles. Lines represent the relationship between TFB ($g·m^{-2}$) and TP ($µg·L^{-1}$) when ANN is inputted with DD (°C) and nRA1 (dimensionless) that are kept constant at values specified for each panels.
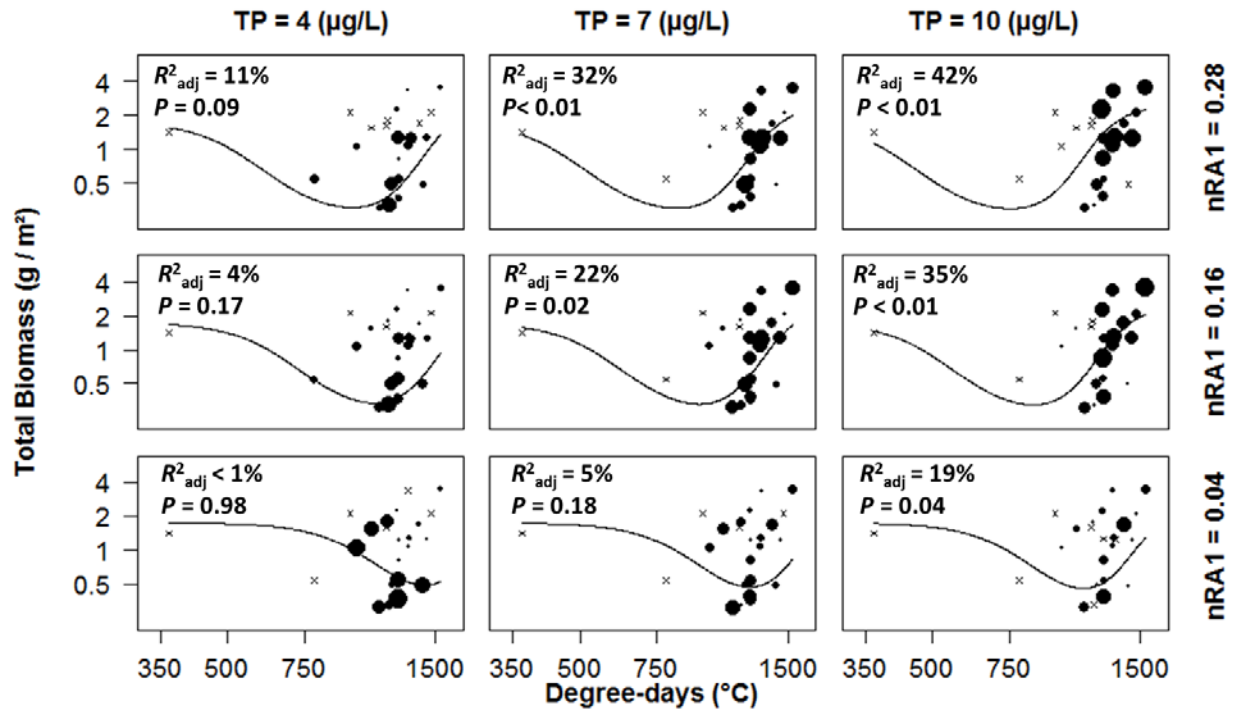
Figure 8. Relationships between TFB ($g·m^{-2}$) and DD (°C) in ANN models. Marker sizes are inversely proportional to the inverse Mahalanobis distance between the values of the two descriptors that were held constant in a panel and the values observed in this river for these descriptors (i.e. rivers represented by small markers are more distant from the values of the conditions held constant in a panel than rivers represented by large markers). For very large distances, small crosses are used as markers instead of circles. Lines represent the relationship between TFB ($g·m^{-2}$) and DD (°C) when ANN is inputted with TP ($µg·L^{-1}$) and nRA1 (dimensionless) that are kept constant at values specified for each panels.
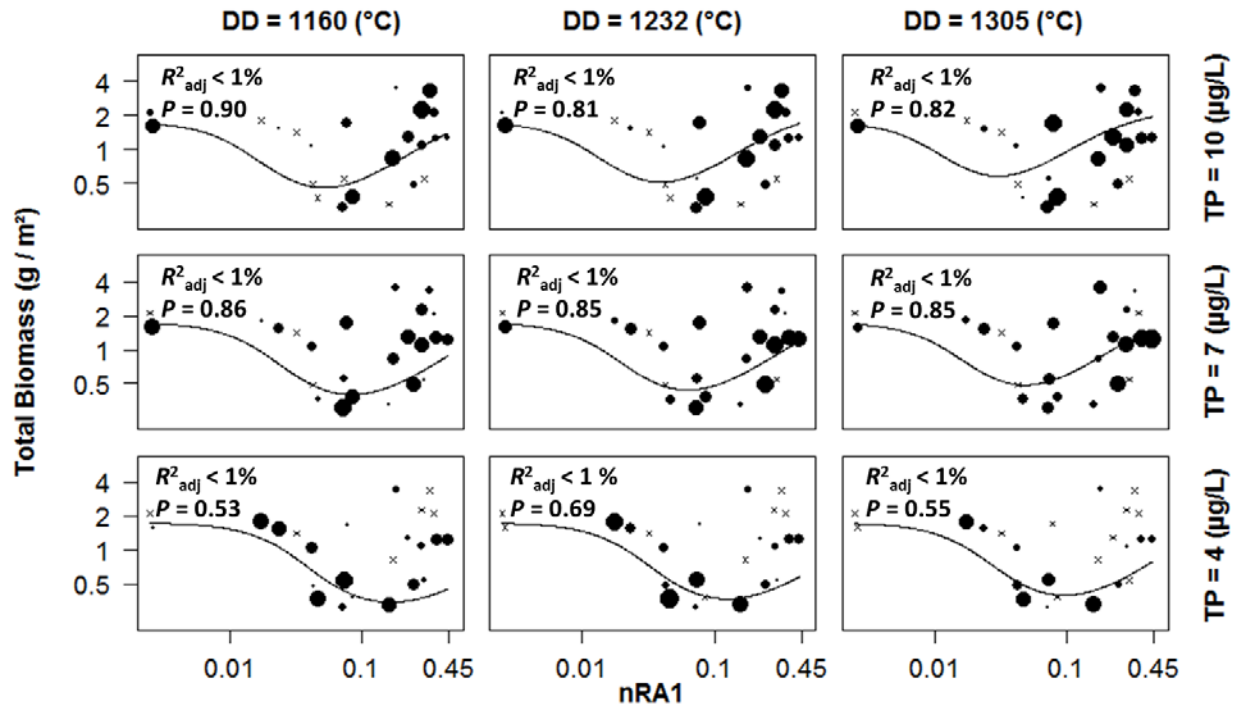
Figure 9. Relationships between TFB (g·m⁻²) and nRA1 (dimensionless) in ANN models. Marker sizes are inversely proportional to the inverse Mahalanobis distance between the values of the two descriptors that were held constant in a panel and the values observed in this river for these descriptors (i.e. rivers represented by small markers are more distant from the values of the conditions held constant in a panel than rivers represented by large markers). For very large distances, small crosses are used as markers instead of circles. Lines represent the relationship between TFB (g·m⁻²) and nRA1 (dimensionless) when ANN is inputted with TP (µg·L⁻¹) and DD (°C) that are kept constant at values specified for each panels.

Lessons learned from contribution 2.3

- Artificial Neural Network allowed the development of a relationship between total fish community biomass, TP (positive effect), DD (positive effect), and flow stability (nRA1; negative effect) that had a strong explanatory (R^2=83%) and predictive (R^2_{CV} = 67%) capacity.

- The flow index had a relatively weak effect on total fish community biomass.

- The strength of the relationship between total fish community biomass and any explanatory variable (TP or DD) depends on the value of the other explanatory variable.

- Expected (e.g. post-development) values for these variables can permit to predict total fish biomass.

CONTRIBUTION 2.4

Fisheries productivity metric: Species richness
Organismal scale: Total community
Spatial scale: River segment
Explanatory variable: Physical drivers

A number of hypotheses have been suggested to explain spatial variations of community diversity (number of species). Such variations are attributed to energy availability (EA; Pianka

1966), habitat heterogeneity (HH; MacArthur and MacArthur 1961), colonisation (Barbour and Brown 1974), competition (Whittaker 1972), and predation (Jackson et al. 2001). EA hypothesis proposes that community diversity increases with energy availability (Currie et al. 2004). EA hypothesis involves two mechanisms (Oberdorff et al. 2011). First, community diversity may be affected by the productivity of potential resources ("resource productivity mechanism"; Wright 1983). Second, community diversity may be affected by the extent to which environmental conditions are within the physiological limits of species ("distributional limits mechanism"; Turner et al. 1987). HH hypothesis states that community diversity increases as the physical heterogeneity of habitats increases (Munguia et al. 2011). For freshwater fish, explaining spatial variations in community diversity has been suggested to require both EA and HH (Guégan et al. 1998). Water temperature, and in particular, the number of degree-days (DD) constitutes a major driver of aquatic productivity (Neuheimer and Taggart 2007). Water temperature impacts productivity of phytoplankton, macrophytes, zooplankton, invertebrates, and fish (Brylinsky and Mann 1973, Benke et al. 1984, Barko et al. 1986, Christie and Regier 1988, Dupuis and Hann 2009) and may be taken as a key determinant of the productivity of potential food resources (basis of the "resource productivity mechanism" of the EA hypothesis). Water temperature also affects the extent to which organisms may use a habitat or an ecosystem (Rooney and Kalff 2000) and therefore also intervenes in the context of the "distributional limits mechanism" of EA hypothesis. Apart from its expected role in the two mechanisms that define EA hypothesis, water temperature is a variable that is easy to measure, and that can modelled or forecasted particularly in rivers (Gostner et al. 2013; Jeong et al. 2013) developed a new method to assess the heterogeneity of aquatic systems: The hydro-morphological index of diversity (HMID). HMID is calculated using the coefficients of spatial variation of water depth and velocity. Gostner et al. (2013) showed that HMID could adequately represent the hydro-morphological heterogeneity in gravel-bed reaches of alpine rivers. The capacity of HMID to represent habitat heterogeneity has not been assessed in sub-alpine or lowland rivers. In addition, the capacity of HMID to explain variations in biological metrics has not been tested, which can be said of an entity (e.g., an individual organism, a parameter value) on which a test had been performed. Potentially advantageous features of HMID are that it can be calculated using simple variables (water depth and velocity) and that it can be modelled or predicted using standard hydrodynamic models (Gostner et al. 2013).

The objective of the project of Lanthier et al. (In preparation)[4] was to quantify the relative importance of EA (represented by DD) and HH (embodied by HMID; Gostner et al. 2013) in explaining among-river variations of fish community diversity (species richness). The relationships between species richness, DD, and HMID were estimated using simple and multiple linear regression models.

Among the 26 river segments used for analysis (13 UR, 13 regulated), a total of 117 144 individual fish, from 63 species belonging to 16 families were observed. Species richness ranged from 6 to 25. The Nicolet (St-Lawrence ecoregion) and Elbow (Alaska and Canada Pacific Coastal ecoregion) rivers had, respectively, the highest and lowest species richness. The number of fish species shared by rivers ranged from 0 to 18 (0% to 100%; mean = 39%). Four pairs of rivers had more than 80% of their fish species in common and 58 pairs of rivers had less than 20% of their fish species in common.

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[4] Lanthier, G., Lafrenaye, A., Maheu, A., Bourque, G., Senay, C., Macnaughton, C. J., Harvey-Lavoie, S., St-Hilaire, A., and Boisclair, D. Relationships between fish community diversity, energy availability, and habitat heterogeneity in rivers. In preparation.

During the standardized summer (9 weeks centered on the warmest week of the summer), the mean water temperature of the 26 river segments ranged from 5.8 to 24.4 °C (mean ± sd = 19.7 ± 3.7 °C). The DD ranged from 367 (Elbow) to 1540 °C·days (Bécancour, St-Lawrence ecoregion; mean ± sd = 1198 ± 235 °C). The mean water depth was 40.37 cm (± 6.79 cm) and ranged from 20.19 (Serpentine, Northeast US and Southeast Canada) to 57.59 cm (Picanoc, St-Lawrence ecoregion, Table 1). The mean water velocity was 0.31 ± 0.12 cm·s^{-1} and ranged from 0.07 cm·s^{-1} (Noire) to 60 cm·s^{-1} (Elbow). The HMID varied 3.6 fold among rivers, and ranged from 5.00 (Elbow) to 18.20 (Goulais, Laurentian Great Lakes; Table 1).

DD and HMID respectively explained 60% ($p< 0.001$) and 48% ($p<0.001$) of the among-river variations in species richness (Figure 10). Species richness increased exponentially with DD and reached a maximum value at intermediate levels of HMID. The unimodal relationship between FCD and HMID remained significant ($R^2_{Adj} = 0.46$, p-value < 0.001) even after removing one river that appeared to drive this relationship (Goulais River; HMID = 18.2, Table 5). Combining both variables permitted to explain 69% ($p<0.001$) of species richness (Table 5). A binary variable 'unregulated' and 'regulated' river had no effect on models. The predictive capacity (R^2_{CV}) of the regression model combining DD and HMID ranged from 0.58 for predictions made on an untransformed basis to 0.64 for predictions made on a logarithmic basis. Neither the number of sites per river ($p>0.49$) nor the length of the river segment surveyed ($p>0.16$) had a statistically significant effect on species richness. Species richness did not vary significantly among ecoregions (p>0.06) or between UR and regulated rivers (p>0.47).
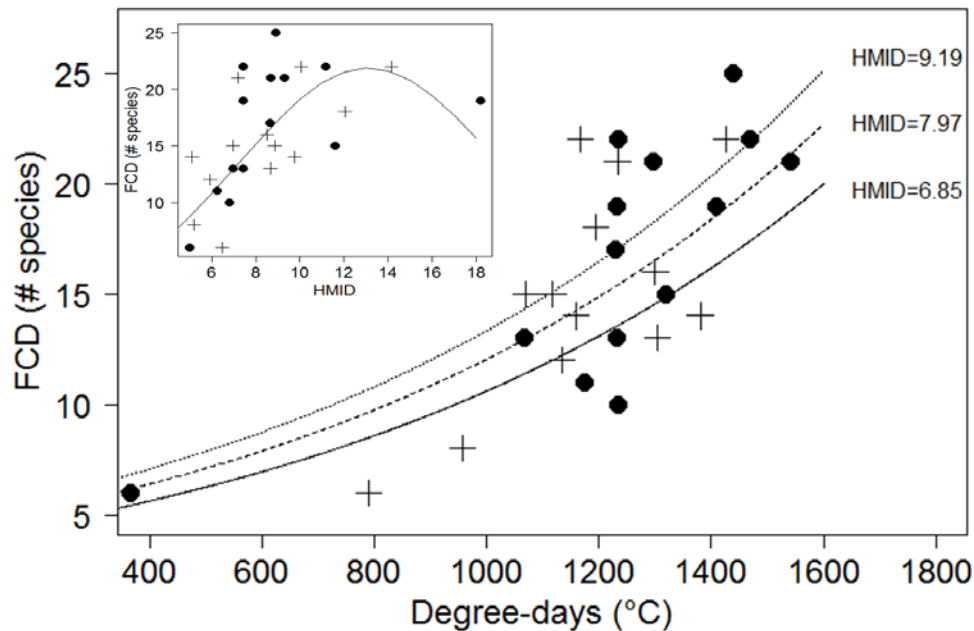
Figure 10. Relationship between FCD and DD ($R^2_{Adj}=60\%$). Lines represent the effect of adding HMID to the model, with the 1st quantile (solid line), 2nd quantile (dashed line) and 3rd quantile (dotted line) of HMID values represented. Unregulated rivers are represented by full circles, and regulated rivers by crosses. Inset: unimodal relationship between FCD and HMID alone.

Table 5. Adjusted R^2 (R^2_{Adj}), p-values (uncorrected and corrected with Šidák correction), and equations representing the relationships between species richness (SR), degree-days (DD), and hydro-morphological index of diversity (HMID). Logarithms (log) are in base e (natural logarithm).

R^2_{Adj} (%)	Uncorrected p-value	Šidák p-value	Equation
60	> 0.001	> 0.001	log(SR) = 1.12 + 0.001• DD
48	> 0.001	> 0.001	log(SR) =0.680 – 0.014 • HMID2 + 0.367 • HMID
69	> 0.001	> 0.001	log(SR) = 0.577 + 0.001• DD+ 0.413 • log(HMID)

Lessons learned from contribution 2.4

- Species richness increased exponentially with DD (R^2=60%) and reached a maximum value at intermediate levels of HMID (R^2=48%).

- DD had a more direct effect on species richness than HMID.

- The relationship between species richness, DD, and HMID had high explanatory (R^2_{Adj} =69%) and predictive (R^2_{CV}= 64%) capacities.

- Thermal data should be monitored on a regular basis.

- Expected (e.g. post-development) values for degree-days and habitat heterogeneity can permit to predict species richness.

CONTRIBUTION 2.5

Fisheries productivity metric: Proportion of species biomass
Organismal scale: Species
Spatial scale: Site
Explanatory variable: Meso-habitat variables

A number of studies have attempted to model within-river species distribution (Austin 2002, Guisan and Thuiller 2005, Sui et al. 2014). The major difficulties associated with the development of within-river species distribution models range from the choice of adequate sampling methodologies (Erős et al. 2009, Lanthier et al. 2013, Macnaughton et al. 2014), suitable temporal and spatial scales (Elith and Leathwick 2009, Sharma et al. 2012), relevant environmental variables (Jackson et al. 2001, Rosenfeld 2003, Bouchard and Boisclair 2008), and statistical tools providing high explanatory or predictive capacity (Guay et al. 2000, Olden and Jackson 2002, Guisan and Thuiller 2005). Within-river species distribution models generally attempt to explain spatial variations of fish presence, density, or biomass among a series of sites using local (attributes observed within sites), lateral (attributes observed on shores adjacent to sites; e.g. riparian characteristics), and/or contextual environmental variables (attributes that refer to the position relative to, or the distance from, landscape characteristics; e.g. distance between a site and the closest confluence). Local environmental variables have been suggested to drive the largest part of within- river species distribution (Bouchard and Boisclair 2008) and may be classified into four groups of environmental features: hydraulic, sediment size, biogenic (i.e. related to biotic processes), and physico-chemical characteristics. Hydraulic features comprise water depth, water velocity, and wetted river width. High water velocities may constrain the distribution of species having low swimming capacities (Jackson et al. 2001, Grossman et al. 2010), while water depth and width may impede fish movement and affect habitat availability (Jackson et al. 2001, Rosenfeld et al. 2011). Sediment size refers to the composition of the substrate that covers riverbeds (e.g. sand, cobble, and boulder). Sediment size may affect fish

distribution by contributing to provide adequate feeding (Mueller and Pyron 2010), refuge (McLaughlin and Noakes 1998) or spawning areas (Talmage et al. 2002). Biogenic features originate from biotic processes and include macrophytes, periphytic algae, and woody debris. Biogenic variables are key components of feeding and sheltering areas (Schlosser 1987, Flebbe and Dolloff 1995, Czarnecka et al. 2014). Physico-chemical features encompass water conductivity, temperature, and transparency. Conductivity has been positively correlated with species density and productivity (da Silva Abes and Agostinho 2001), water temperature may affect fish habitat use (Matthews and Berg 1997, Logez et al. 2012), and high water transparency may favour carnivorous species relying on visual cues (Skov et al. 2002, Pinto and Araújo 2007). Regional variations and river flow regulation may affect the relative contribution of the local variables explaining fish species distribution (Quist et al. 2005, Pont et al. 2006, Haxton and Findlay 2008). Because of such discrepancies, a model developed using specific local variables in a particular river may not be successful in modelling fish distribution in another river (Porter et al. 2000, Guisan and Thuiller 2005, McMillan et al. 2013).

Given the multitude of local environmental variables that have been suggested as explanatory variables, the objectives of the project of Senay et al. (2015b) are:

1) to estimate the relative importance of hydraulic, sediment size, biogenic, and physico-chemical features in within-river species distribution models;

2) to identify the environmental variables having the highest explanatory capacity in within-river species distribution models; and,

3) to assess the effects of physiographic regions and river flow regulation on the relative importance of environmental features contributing to within-river species distribution models.

We addressed our first objective by partitioning the variance of proportion of fish species biomass within each river among the four environmental features (Borcard et al. 1992, Peres-Neto et al. 2006). This method carried multiple partial canonical redundancy analyses (partial RDAs) to quantify the variance explained (R^2_{Adj}, Ezekiel 1930) exclusively and jointly by groups of environmental features. The explained variance of fisheries productivity metrics across sites within each river was partitioned into exclusive and shared fractions associated to four groups of features (i.e. hydraulic, sediment size, biogenic, and physico-chemical). We achieved our second objective using canonical redundancy analyses (RDA) with a forward selection (Blanchet et al. 2008, Dray et al. 2011). This method selected the environmental variables maximizing within-river species distribution models explanatory capacity and quantified the explained variance by each variable. We attained our third objective by conducting a two-way MANOVA that contrasted the exclusive fractions obtained from the variation partitioning (obtained from the first objective) among physiographic regions, and between unregulated and regulated rivers considered as factors (Legendre and Anderson 1999).

A total of 187 044 individual fish, from 62 species belonging to 16 families were observed in the 989 sites distributed among the 28 rivers located from Alberta to New Brunswick. Global within-river species distribution models were significant for 23 of the 28 rivers (2.8 e-6 < p < 0.035). When considering all global within-river species distribution models, environmental features explained between 1% and 60% (mean = 27%) of the within-river variation of proportion of fish species biomass. The exclusive fraction explaining the greatest amount of proportion of fish species biomass variation was related to hydraulic features (mean = 8%, min = 0%, max = 20%), followed by sediment size features (mean = 4%, min = 0%, max = 19%), biogenic (mean = 2%, min = 0%, max = 16%), and physico-chemical features (mean = 2%, min = 0%, max = 19%). We found a non-linear square root relationship between the explanatory capacity of

within-river species distribution models and the total fish biomass in a river ($p = 0.002$, $R^2_{Adj} = 28\%$; Figure 11).
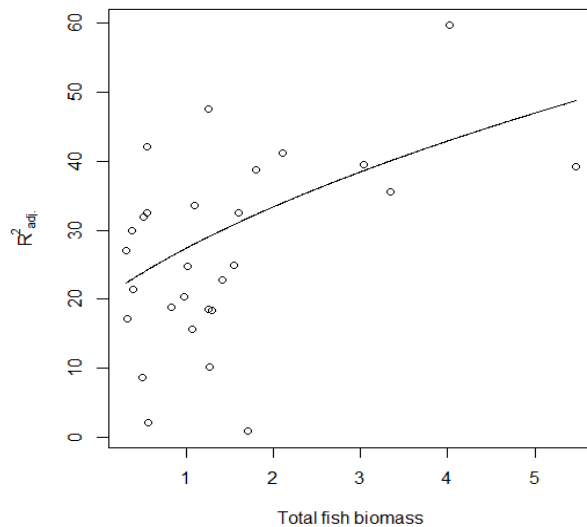
Figure 11. Non-linear square root relationship between within-species distribution models explanatory capacity (R^2_{Adj}) and river total fish biomass (p = 0.002, $R^2_{Adj} = 28\%$).

Identification of key environmental variables with a RDA using a forward selection was conducted for the 23 rivers having significant global within-river species distribution models based on all environmental variables. Within-river species distribution models included 2 to 7 statistically significant environmental variables (mean = 4). Environmental variables most often retained by the forward selection were water velocity (selected in 78% of the models), PC1 (i.e. first principal component representing the greatest proportion of sediment size variability within a river; selected in 57% of the models), water depth (selected in 52% of the models), and PC2 (i.e. second principal component representing sediment size variability within a river; selected in 39% of the models). Environmental variables such as transparency, woody debris, macrophyte, and PC3 (i.e. third principal component representing sediment size variability within a river) were selected in 26% of the models. Temperature, adjusted conductivity, periphyton, and river width were selected in only 9% of the models. Water velocity explained between 0% and 29% (mean = 10%) of the within-river variation in proportion of fish species biomass. Corresponding values for PC1 and water depth were, on average, 6% and 3%. Other environmental variables explained on average 1% of within-river variations in the proportion of fish species biomass.

The MANOVA indicated that physiographic regions ($p = 0.11$), river flow regulation ($p = 0.70$), and the interaction between these two factors ($p = 0.81$) had no statistically significant effect on the relative importance of the environmental features in developing within-river species distribution models.

Lessons learned from contribution 2.5

- Hydraulic conditions at the local scale, and in particular water velocity, were the dominant drivers of daily summer within-river species distribution models.

- Physiographic regions and river flow regulation (or their interaction) have no effect on the relative importance of the environmental features in developing within-river species distribution models.

- The same meso-habitat environmental conditions can be used to develop within-river fish species distribution models across similar rivers located from Alberta to New Brunswick.

- Water velocity, water depth, and sediment size should be prioritized over other environmental features (i.e. river width, macrophyte, periphyton, woody debris, water temperature, conductivity, and transparency) to develop within-river species distribution models.

- It may difficult to develop within-river species distribution models having a relatively high explanatory capacity (~40%) when total fish biomass is < 2 g·m^{-2}.

CONTRIBUTION 2.6

Fisheries productivity metric: Density, biomass, and species richness
Organismal scale: Total community
Spatial scale: Sites
Explanatory variable: Meso-habitat and hydrological variables

Community attributes are expected to result from processes taking place at various spatial scales (Burke and Grime 1996, Tilman 1997, Shurin et al. 2000, Resetarits 2005). Smith and Powell (1971) suggested a conceptual framework whereby lotic fish community attributes at a meso-habitat-scale (~100 m^2) are the result of selective pressures acting sequentially at the scales of continents, regions, watersheds, rivers, and habitats. Tonn et al. (1990) and Poff (1997) further described this series of selective pressures as a hierarchy of filters, from a coarse continental filter to a fine meso-habitat filter, through which species must pass to be part of the community at the meso-habitat-scale. This conceptual framework has been corroborated by studies suggesting that community attributes at a meso-habitat-scale are determined by the shaping of the pool of potential colonizers by climatic, physiological and ecological processes (Keddy 1992, Webb et al. 2010). Quantifying the relative contribution of processes operating at different spatial scales remains challenging because of the difficulties associated with data collection, statistical analyses, and biological interpretation (Ricklefs 1987, Huston 1999, Sharma et al. 2012). The hierarchic organisation of rivers and the prevailing hypotheses about the variables that affect them make lotic ecosystems particularly suitable to study processes taking place at various spatial scales (Fausch et al. 2002). At the river-scale, the natural flow paradigm proposes that flow is the key driver of the chemical, physical, and biological characteristics of these ecosystems (Poff et al. 1997, Gilvear et al. 2002). At the meso-habitat-scale, the river continuum concept proposes that habitat descriptors within a river represent a continuous longitudinal gradient of physical conditions (Vannote et al. 1980). In addition, the serial discontinuity concept suggests that tributaries and hydroelectric facilities may disrupt the river longitudinal gradient (Ward and Stanford 1995, Rice et al. 2001). The river longitudinal gradient may be represented by meso-habitat descriptors, such as water velocity, water depth and substrate composition, which are known to affected fish community attributes (Knouft et al. 2011, Michel and Knouft 2014, Senay et al. 2015b).

The cumulative effects of flow regime and meso-habitat descriptors on fish community attributes, to our knowledge, have never been assessed across multiple regulation types. In addition, most studies that examined the effect of flow regime or meso-habitat descriptors on fish community attributes focussed on relatively few species or rivers (Bradford et al. 1995, Almodovar and Nicola 1999, Flodmark et al. 2004). This impedes the unveiling of generalized trends linking

these variables. The general goal of the project of Senay et al. (Submitted to Aquatic Sciences[5]) is to investigate how flow regime and meso-habitat descriptors explain and predict fish community attributes. The specific objectives of this project are:

1) to identify the hydrological indices that best describe the flow regimes of rivers subjected to different regulation types (i.e. UR and rivers located downstream of RR, ST, and PE facilities); and,

2) to estimate the relative importance of hydrological indices (river-scale variables) and water depth, water velocity and substrate composition (meso-habitat-scale variables) in explaining and predicting fisheries productivity metrics (i.e., total fish community density and biomass and species richness) at sites.

Analyses conducted by Senay et al. (Submitted to Aquatic Sciences[7]) included 880 sites from 25 rivers (14 unregulated; 11 regulated) located in six physiographic regions of Canada. A total of 174 672 individual fish, from 60 species belonging to 16 families, were observed in the 25 river segments. Total community fish density (0 to 11.6 fish·m^{-2}; mean = 0.6, sd = 1), total fish community biomass (0 to 67.2 g·m^{-2}; mean = 1.6, sd = 3.8), and species richness (0 to 7 species; mean = 5, sd = 3), varied widely among the 880 sites and among rivers. For each of the five flow components (magnitude, frequency, duration, timing and rate of change of flow), three flow principal components (PCF) significantly explaining between 72% and 98% (mean = 89%, sd = 10%) of the variance in hydrological indices were used. The resulting 15 PCF (five flow components x three PCF) permitted to develop a statistically significant discriminant function (Wilks' Lambda: 0.0012, F [45,21] = 4.1228, p < 0.0003). This function correctly classified 92% of the rivers to their regulation type. UR rivers were correctly classified in 86% of the cases (two UR rivers, Au Saumon and Nicolet Rivers, were classified as RR). RR, ST and PE rivers were correctly classified in all cases. The first axis of the discriminant function (DF1) explained 78% of the total variance of PCF and differentiated PE rivers from rivers having other regulation types. The second axis of the discriminant function (DF2) explained 20% of the total variance of PCF and contrasted ST from UR and RR rivers. From the 77 hydrological indices, 9 were selected because they were the most correlated (minimum absolute correlation of 0.57) with either DF1 (seven flow indices) or DF2 (two flow indices). UR and RR rivers were mostly characterized by highly variable flow in April (MA27) and high values of hourly low flow flash index (high values of RL2 indicate low flashiness of hourly low flows). ST rivers were particularly associated with high values of flow constancy (TA1) and low variability of April's flow (MA27). PE rivers were more dynamic exhibiting important hourly flow variations (MA60, RH2), more numerous day-to-day flow reversals (RA8), more frequent floods (FH5, FH9) and higher proportions of rise days (RA5). These nine hydrological indices represented 66% of the variation contained in 77 original hydrological indices and were used to describe differences in flow regime among rivers subjected to different regulation types in following analyses.

Relationships between fisheries productivity metrics and environmental conditions were developed using linear mixed-models (LMM) that nested sites within rivers, and within regions. LMM indicated that total fish community density, total fish community biomass, and species richness at sites tended to decrease as water velocity, water depth, substrate size(represented by a principal component axis; PCS), hourly flow variations (MA60) and FH9 (events exceeding the 25th percentile of daily flows) increased. PCS being generally positively associated to smaller particles, their negative effects in LMM indicated that fish community attributes tended to

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[5] Senay, C., Taranu, Z.E., Bourque, G., Macnaughton, C.J., Lanthier, G., Harvey-Lavoie, S., and Boisclair, D. Effects of river-scale flow regimes and local-scale habitat descriptors on fish community attributes. Submitted to Aquatic Sciences.

be higher at sites characterised by large substrate. In contrast, fisheries productivity metrics tended to increase as the flashiness of hourly high flows (RH2) and FH5 (events exceeding the 50th percentile of daily flows) increased. Cross-validation indicated that the three LMM had relatively good predictive capacities. The R^2_{CV} of the relationships between predicted and observed fisheries productivity metrics were, respectively, 66%, 43%, and 51% for total fish community density (Figure 12a), total fish community biomass (Figure 12b), and species richness (Figure 12c). However, the predictions of LMM often tended to underestimate the largest observed fisheries productivity metrics. The largest observed values of total density and biomass were 12.6 fish·m^{-2} and 67.2 g·m^{-2} with corresponding predicted values of 3.6 fish·m^{-2} and 6.6 g·m^{-2}. The largest observed species richness was 17 species, whereas the largest predicted richness was 13 species. It is expected that inclusion in the models of the effects of TP, DD, and HMID, not available at the time of production of this manuscript, will only improve the predictive capacity of LMM for fisheries productivity metrics at the scale of sites.
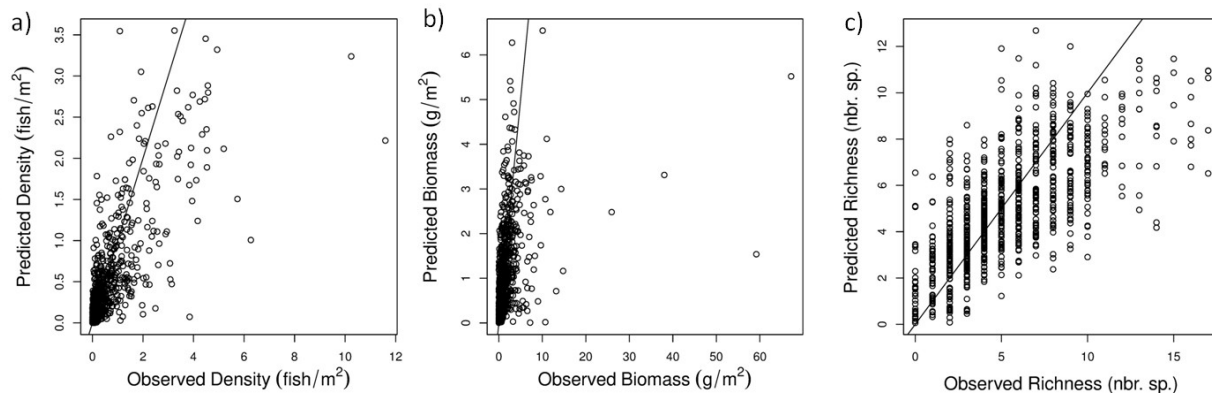
Figure 12. Cross-validation of reduced LMM for each fish community attribute. Relationship between predicted and observed values for total density (a), total biomass (b) and richness (c) as well as a line outlying the 1:1 expected relationship are presented. The R^2_{CV} were 66%, 43% and 51% for total density, total biomass, and richness, respectively.

Lessons learned from contribution 2.6

- Nine hydrological indices represented 66% of the variation contained in 77 original hydrological indices.

- Linear mixed-models that nested sites within rivers and within regions permitted to predict total fish community density (R^2_{CV} =66%), total fish community biomass (R^2_{CV} =43%), and species richness (R^2_{CV} =51%) in response to flow regime at the river-scale and habitat descriptor at the local scale in sites of 300 m^2.

- The model can be used to predict the effects of changing flow and mesohabitat variables in the modelled rivers.

- The model can be expanded to include new rivers.

CONTRIBUTION 2.7

Fisheries productivity metric: Density
Organismal scale: Combinations of species and size classes
Spatial scale: River segment
Explanatory variable: Meso-habitat variables + degree-days + species traits + spatial structure

Fish-environment relationships seek to explain and predict fish distribution as a function of environmental conditions (Guisan and Zimmerman 2000, Boisclair 2001, Guisan and Thuiller 2005). The distribution of any particular fish results from the interaction between fish traits and environmental conditions (Dirnböck and Dullinger 2004, McGill et al. 2006). Conceptually, when a number of different fish species and size classes are studied simultaneously, the relationship between a fisheries productivity metric at a site, fish traits, and environmental conditions, may be written as in matrix notation as follows:

$$Y = X M Z^T$$

Where, Y is a matrix containing a fisheries productivity metric, with as many rows as there are sites, and as many columns as there are combinations of species and size-classes modelled; X is a matrix containing fish descriptors (traits and among-species contrasts based on species phylogeny), with as many rows as there are combinations of species and size-classes modelled, and as many columns as there are fish descriptors; Z is matrix containing environmental conditions, with as many rows as there are sites, and as many columns as there are environmental conditions to describe these sites. M, in this context, is a matrix that contains the model coefficients that describe the relationship between fish traits and environmental conditions.

Guénard et al. (In preparation)[6] tested the predictive capacity of this modelling approach. The strategy used for this purpose consisted in developing matrices Y, X, and Z using the data collected for the 15 UR rivers and in testing the predictions made by the modelling approach for the 13 regulated rivers. Matrix Y contained the density of 143 combinations of species and size classes (48 species, and, on average, 2.6 size-classes per species) as estimated in the 15 rivers. Matrix X contained median fish length (since phylogenetic eigenfunctions do not permit to differentiate conspecific fish of different sizes) (standard length) and 47 among-species contrasts represented by phylogenetic eigenfunctions (number of species estimated using a phylogenetic distance matrix including all species surveyed; Figure 13). Matrix Z contained four descriptors for whole rivers (water depth, water velocity, median substrate grain size, and DD), and 14 spatial eigenfunctions (number of UR rivers describing the potential spatial variation patterns among the the rivers). The use of phylogenetic data to represent species traits is consequent to the expectation that species traits (e.g. physiological, behavioural) are structured with respect to phylogeny and are the result of evolutionary processes (Felsenstein 1985). Consequently, the modelling approach is further referred to as the "Phylogenetic habitat modelling".

Observed fish density by species and size-classes in the sites of the UR rivers ranged from 0 (no fish observed; 1569 observations out of 2145, or 73.1%) to 23 fish·100 m^{-2} (Figure 14a) The fitted fish density values provided by the Phylogenetic habitat model ranged from 7.5×10^{-4} to 8.5 fish·100 m^{-2} (Figure 14b). The model generally fitted the data well (explanatory capacity: likelihood-based $R^2 = 0.53$). It is noteworthy that the highest fish densities are so sparsely observed that they cannot be modelled.

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[6] Guénard, G., Lanthier, G., Harvey-Lavoie, S., Macnaughton, C.J., Senay, C., Lapointe, M., Legendre, P., and Boisclair, D. Phylogenetic habitat modeling. Submitted to Proceeding of the Royal Society B.
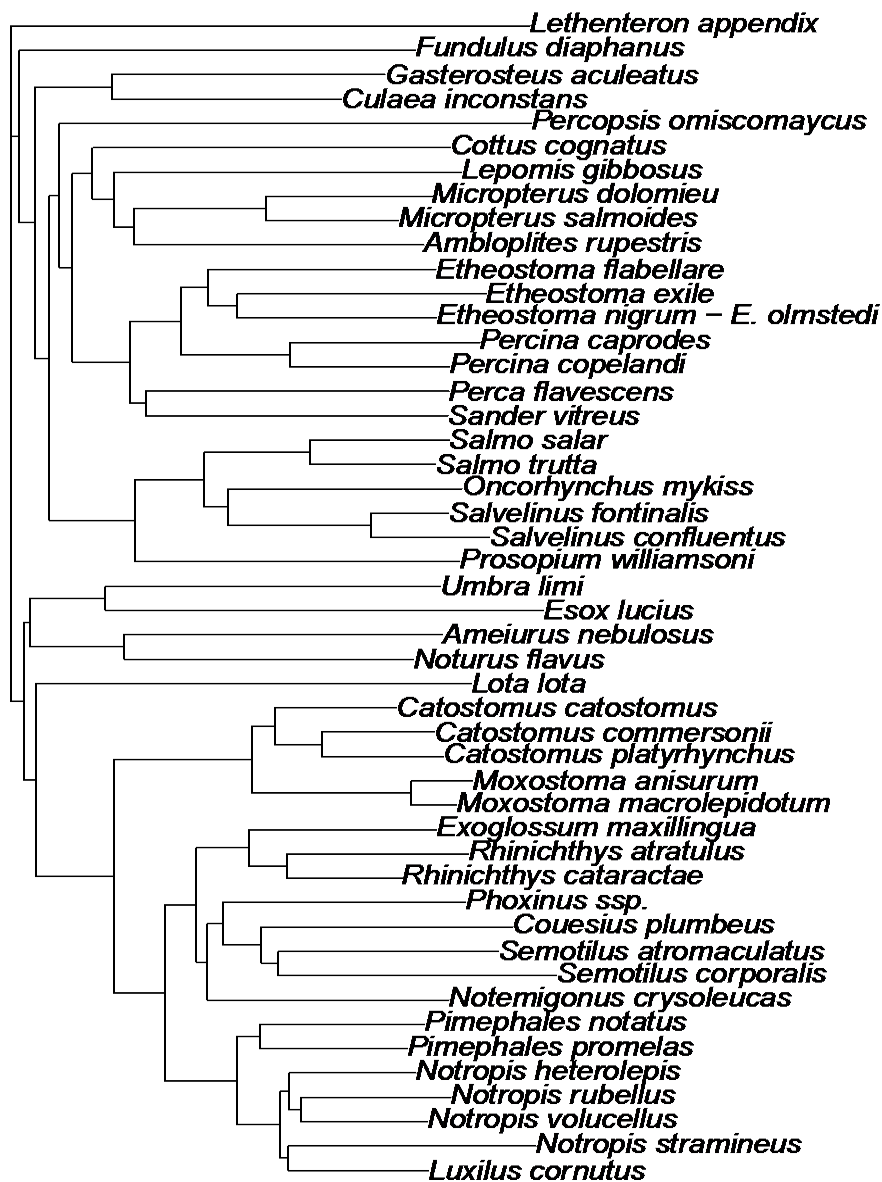
Figure 13. Phylogeny of the fish species observed in the 28 rivers (obtained from Hubert et al. (2008) after removing the species that were not observed during surveys).

Observed fish density by species and size-classes in the sites of the regulated rivers ranged from 0 (1419 observations out of 1859, or 76.3%) to 18.5 fish·100 m^{-2}. The densities predicted by the Phylogenetic-explicit habitat model for the regulated rivers using the information about UR rivers ranged from 2.2 x 10^{-3} to 2.6 fish·100 m^{-2} (Figure 15). On average, the model showed a fair predictive power (likelihood-based cross-validation R^2_{CV} = 0.29) at forecasting the density of fish from 48 species totalling 143 combinations of species and size classes in 13 regulated rivers. When looking down at individual species, few were found to be affected by flow regulation and detected effects were generally positive (higher densities observed than predicted for the same rivers if they were UR).
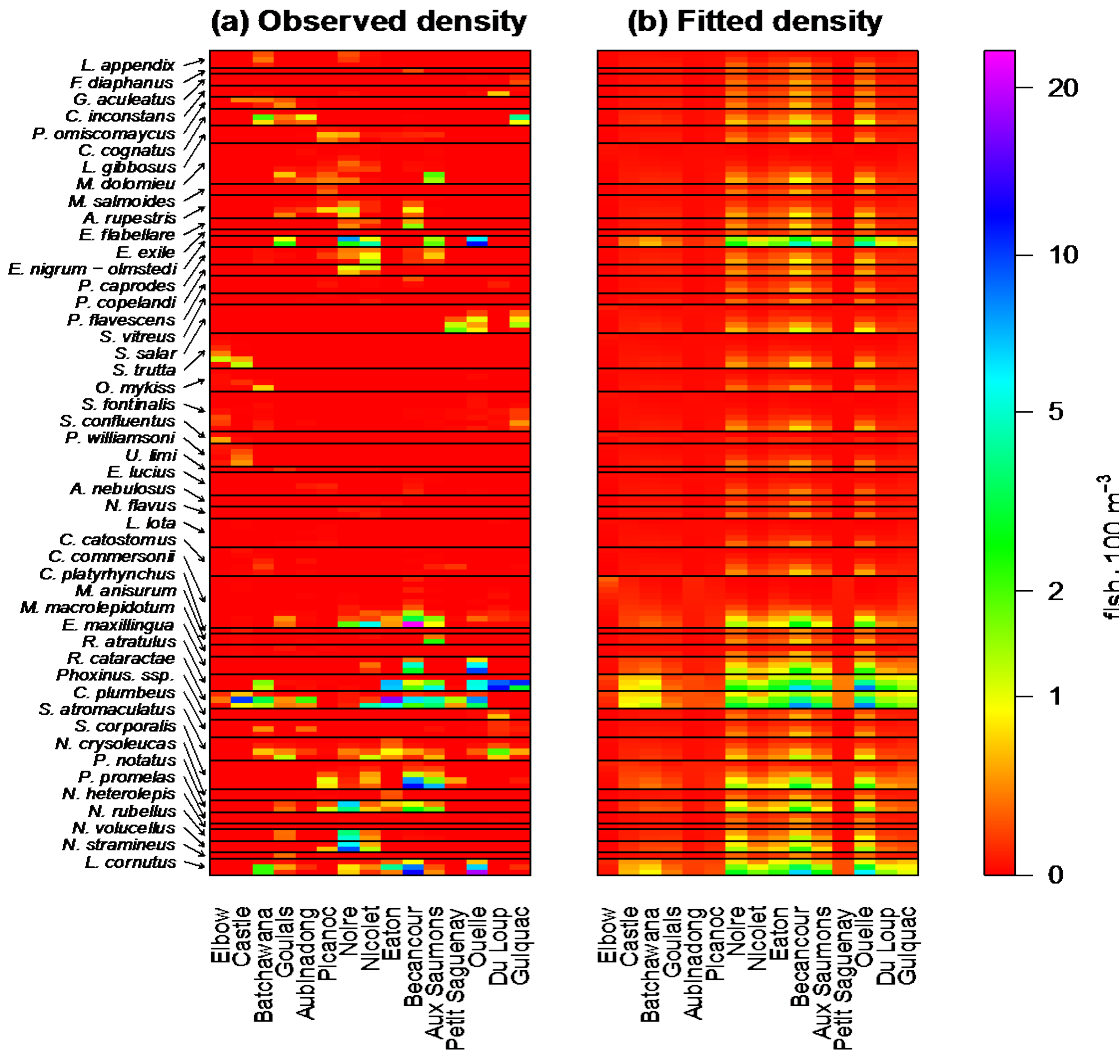
Figure 14. Observed fish density for different species and size classes (in increasing order from the bottom up) in 15 unregulated rivers and corresponding fitted values by the model not including phylogeographic interactions terms.

The results of the analysis performed on the level of the whole rivers show that the Phylogenetic-explicit habitat model represented $Y = X M Z^T$ has the potential to provide statistically defensible predictions. Expectations are that fine-tuning the selection of: the rivers used to develop the model (e.g. a combination of UR and regulated rivers); the organismal scale (e.g. species instead of species and size-classes); the species traits, given the information provided by Macnaughton et al. (In preparation[2]), and; the environmental conditions, given the information provided by many of the projects presented above, may improve both the explanatory and predictive capacity of this modelling approach.

Observed − predicted
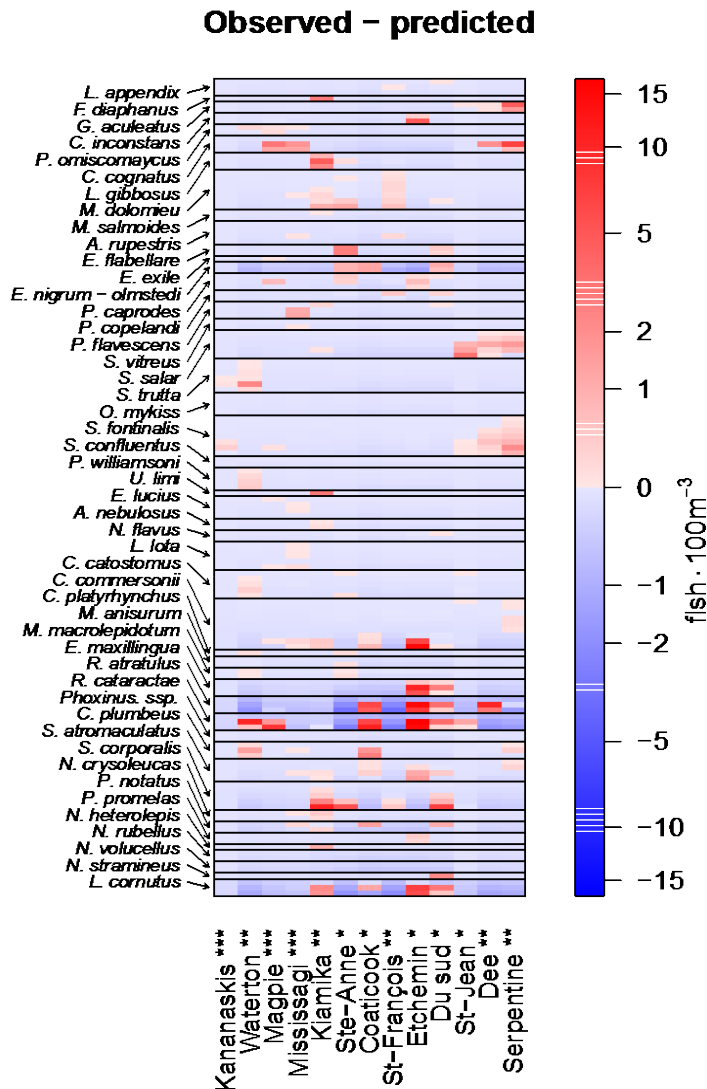
Figure 15. Difference between fish density observed in the 13 regulated rivers for different species and size classes (in increasing order from the bottom up) and baseline values predicted by the model built with information from the unregulated rivers. The dams are categorized with respect to three different types of flow regulation: RR (*), ST (**), and (***) PE. Red rectangles represent densities that are above the baseline, blue rectangles are densities that are below the baseline, and the intensity of the colour represents the absolute value of the difference.

One key feature of Phylogenetic-explicit habitat modelling, not illustrated by the results presented here, is its potential to make 3 kinds of predictions:

a) how a species present in a river (even if rare or endangered) will react to changes in environmental conditions while this river remains within the range of environmental conditions presently found in this river (predicting the effect on a species of a relatively small river alteration),

b) how a species present in a river (even if rare or endangered) will react to changes in environmental conditions that will bring this river outside the range of environmental

conditions presently found in this river (predicting if a species already in the river will augment or disappear), and

c) how will a species not even present in a river may react to the changes in the environmental conditions of a river (predicting the extent to which the changes in environmental conditions will render a river more suitable to a species not present in this river, making it more, or less, susceptible to the invasion by that particular species).

Lessons learned from contribution 2.7

- Relationship between fisheries productivity metrics, species traits, spatial variables, and environmental conditions have the potential to predict how fish species present in a river (even if rare or endangered) may react to changes in environmental conditions that are within or outside the range of environmental conditions initially found in a river.

- Relationship between fisheries productivity metrics, species traits, spatial variables, and environmental conditions have the potential to predict how fish species that are not present in a river may react to changes in environmental conditions that are within or outside the range of environmental conditions initially found in a river (susceptibility of a river to the invasion by particular species).

OBJECTIVE 3

Identify new fisheries productivity metrics that may facilitate the development of fish-environment relationships.

CONTRIBUTION 3.1

Fish typically face temporal and spatial changes in environmental conditions. These changes in environmental conditions can act as stressors. In response to stressors, fish exhibit a neuroendocrine stress response that allows them to cope with the changes happening in their environment (Barton 2002). Fish first activate the hypothalamic–pituitary–interrenal (HPI) axis that leads to the liberation of corticosteroid hormones, mostly cortisol in fish (Donaldson 1981, Randall and Ferry 1992, Romero 2004). Second, individuals proceed to metabolic (e.g. changes in plasma and tissue metabolites, hematocrit levels, protein expression) and behavioural (e.g. feeding, habitat selection, movement) adjustments, allowing them to overcome the effects of the initial stressor (Pickering 1981, Iwama et al. 1997, 1998, Barton et al. 2002). Among other metabolic adjustments, changes in blood glucose and blood lactate concentrations are well established indicators of the degree of stress response by fish (Barton et al. 2002).

The extent to which habitat quality can be measured using physiological indicators of fish stress remains to be explored. Herein, the habitat quality refers to local environmental variables that are affected by flow regimes (mostly flow velocity and depth), which are important characteristics in determining fish habitat use (Jackson et al. 2001; Senay et al. 2015b). It is to be kept in mind that the findings from laboratory studies (e.g. in aquaculture) may not apply to understanding how wild fish distribute spatially in rivers. Wild fish have the inherent capability of selecting a habitat that is not always comprised of the perfect balance of their important needs (feeding, hiding from predators, resting; Godvik et al. 2009). This situation leads to trade-offs between the specific costs and benefits of being at a particular location, which cannot be assessed in laboratory. One key attribute of physiological indicators is that estimating the stress level of fish living in a very large and dynamic river segment may be easier than estimating fish density or biomass in this ecosystem. The first step towards assessing the potential utility of physiological indicators as indicators of habitat quality is to measure the extent to which these stressors vary

within and among ecosystems. The objectives of the project of Harvey-Lavoie et al. (In preparation[7]) is to test the existence of a relationship between blood concentrations of corticosteroid hormones (i.e. cortisol), lactate, glucose in wild fish and flow velocity. This objective was achieved by comparing the physiological response of northern pike (*Esox lucius*) inhabiting two rivers of northeastern Ontario subjected to different flow regimes: Mississagi River, a river subjected to extreme daily flow variations (6 to 307 $m^3 \cdot s^{-1}$ within 3-4 hours) associated to hydro-electric operations (i.e., PE), and Aubinadong River, an UR river.

The objective was assessed by placing each fish separately in a poly-vinyl chloride (PVC; synthetic plastic polymer) cylinder cage. Once placed in the cage, fish were allowed to rest for 24 hours following their capture, in darkness. Resting controls correspond to the fish physiological indicator of stress after having spent 24h in the cage. After the resting period, fish were subjected to two different flow velocity increases: the negative controls correspond to fish subjected to a 0.00 m s^{-1} increase in flow velocity (i.e. stayed in 0.00 m s^{-1}) and the swimming treatments correspond to fish subjected to a fast increase in flow velocity (i.e. from 0.00 m s^{-1} to 0.20 m s^{-1}). We evaluated the stress response to an increase in flow velocity (0.00 m s^{-1} or 0.20 m s^{-1}) by comparing them to the resting controls. Because the stress of teleost fishes is additive and that the cortisol accumulates in fish blood with sequential acute applied stressors (Barton et al. 1986, Schreck 2000), we could assessed the stress response associated to the increase in flow velocity even if resting controls cortisol values were higher than wild fish basal values (Figure 16).

We found that in the Aubinadong pike exposed to a 0.20 m/s increase in flow velocity had significantly higher blood concentrations of glucose and cortisol than fish exposed to a flow velocity of 0.00 m/s (Figure 16). This is totally expected given that flow may provoke a stress response in fish (Jones et al. 1974, Zelnik and Goldspink 1981, Barton et al. 1986, Schreck 2000). However, the response to an increase in flow velocity for fish that originated from Mississagi River, which is subjected to a PE flow regime, was 28% (glucose) to 32% (cortisol) lower than that of fish originating from the Aubinadong River, the UR river. Differences in blood lactate concentrations were also observed, where concentrations for fish from Aubinadong River increased by 247% and 250% when they swam at 0.20 m/s for 20 minutes, compared to the resting and negative controls, respectively. Mississagi River fish did not show an increase in blood lactate concentrations after swimming at 0.20 m/s for 20 minutes. Linear models of the relationship between physiological indicators of stress, rivers, water temperature, flow velocity, fish length, fish sex, and time of day demonstrate that blood glucose and lactate concentrations are better indicators of stress response ($0.37 < R^2_{Adj} < 0.75$) than plasma cortisol concentrations ($0.22 < R^2_{Adj} < 0.46$), which was highly variable between individuals across the same experimental treatment.

The smaller response of fish originating from the Mississagi River may result from the process of habituation or compensation. Habituation is the process by which an applied stressor triggers at first a stress response, but as the stressor is repeated (as in repeated changes in flow in the Mississagi River), fish desensitize to that particular stressor and "learn" that it is not deleterious to his organism (Ladewig 2000). In the case of habituation, a fish would not develop any physiological or behavioural adaptation to overcome the stressor. In contrast, the process of compensation can be thought of as any behavioural or physiological mechanism that a fish mobilizes, thereby extending the organism beyond its homeostasis, which is the steady state or

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[7] Harvey-Lavoie, S., and Boisclair, D. The stress response of a top predator to a flow velocity increase differs between two rivers having contrasting flow regimes. In preparation.

equilibrium (Johnson et al. 1992). Harvey-Lavoie et al. (In review Ecohydrology[8]) used telemetry to assess pike movements in the Aubinadong and Misssissagi Rivers. For a given combination of water temperature, flow, and time of day, pike in the Mississagi and the Aubinadong moved at an average rate of 38.2 m·h^{-1} and 11.7 m·h^{-1} respectively (Figure 17). The longitudinal range of fish (the distance between the most upstream and downstream location where fish were observed), however, was significantly smaller in Mississagi River (mean: 419 m; range: 133-800 m) than in Aubinadong River (mean: 2700 m; range: 136-7939 m). The difference in movements between the pike from the Mississagi and Aubinadong Rivers, along with the smaller stress response to an increase in flow velocity indicates that fish in the regulated river are most likely compensating, rather than habituating, to daily fluctuating flows.
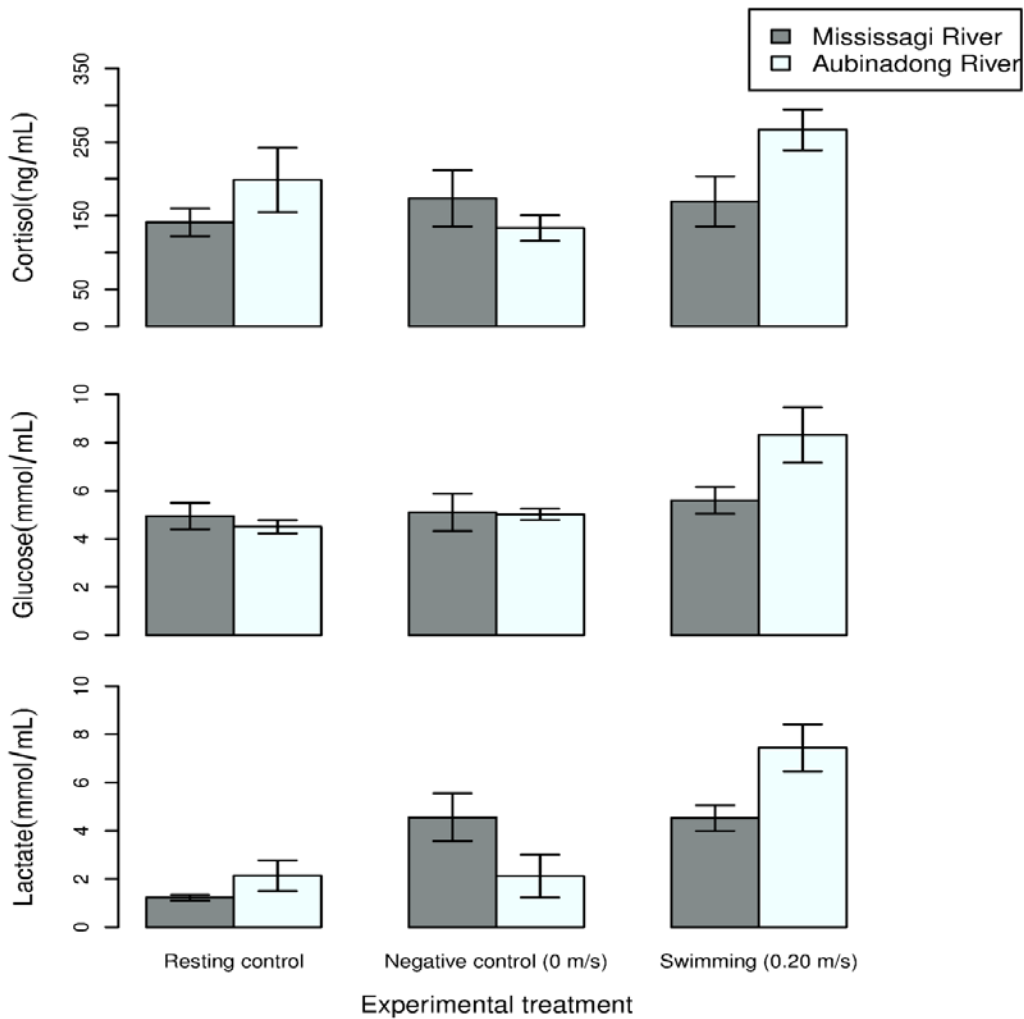
Figure 16. Blood concentrations of cortisol, glucose and lactate (means ± standard errors) of northern pike subjected to the resting control, the negative control or swimming at 0.20 m·s^{-1} for fish originating from Mississagi (PE) and Aubinadong (UR) rivers.

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[8] Harvey-Lavoie, S., Cooke, S.J., Guénard, G., and Boisclair, D. Differences in movements of northern pike inhabiting rivers with contrasting flow regimes. In Review Ecohydrology.

Compensation lead to behavioural and physiological adaptations that allow fish to cope with the prolonged applied stressor. Nonetheless, these adaptations can cause increased energy expenditure in comparison to un-stressed fish. The additional energy expenditures for northern pike inhabiting Mississagi River correspond to their increased mobility and the optimization of their stress response in elevated flow velocities. Therefore, hydropower installation has the potential of decreasing fish productivity by affecting northern pike energy budgets. In contrast, fish that habituate to a stressor do not develop any physiological or behavioural adaptations.
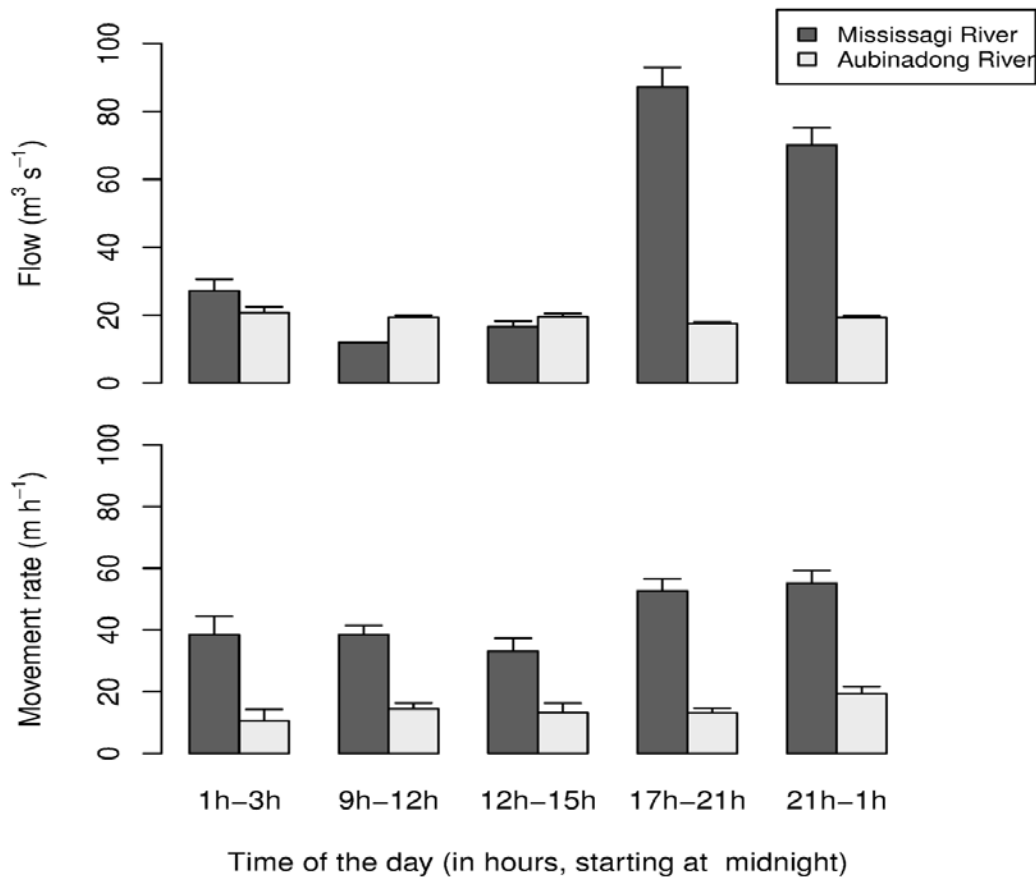
Figure 17. The flow (mean ± standard error; $m^3 \cdot s^{-1}$) and the northern pike movement rate (mean ± standard error; $m \cdot h^{-1}$) in Mississagi River (PE) and Aubinadong River (UR) with respect to the time of the day.

Exercise training is known to promote a higher metabolic response capacity in fish and to significantly increase the intra-specific critical swimming speed (Davison 1989, 1997, McClelland et al. 2006, Zhao et al. 2012, He et al. 2013). For instance, in a study conducted by Young and Cech Jr (1993), the cortisol concentrations, 0.5h after the handling of wild YOY striped bass (*Morone saxatilis*), were significantly reduced by 40% for fish previously exercised (held in 10-19 cm/s) than for unexercised fish (held in 6-12 cm/s) for 30 days. Similarly, lower lactacidemia (i.e. the excess of lactate in blood) has been previously reported by numerous studies on rainbow trout (*Oncorhynchus mykiss*), striped bass and common carp (*Cyprinus carpio*) (Pearson et al. 1990, Young and Cech Jr 1993, Hernández et al. 2002, He et al. 2013). It has been suggested that the increased swimming capacity and lower lactacidemia in exercise-trained fish are

associated to an improvement of the cardio-respiratory capacity (Farrell et al. 1991), to an increase in the activity of muscle enzymes (e.g. creatine kinase, hydroxyacyl CoA dehydrogenase, phosphofructokinase, citrate synthase; Johnston and Moon 1980, He et al. 2013), to an increased capacity in plasma lactate clearance (Pearson et al. 1990), to an increased liver and glycogen storage (Johnston and Moon 1980, He et al. 2013), to an increased myonuclear number and muscle fiber hypertrophy (Hinterleitner et al. 1992, Martin and Johnston 2006) and to an increase in muscle capillaries (Davie et al. 1986). For pike in the present study, it is unknown which of these mechanisms led to the differences in blood lactate concentrations. However, our results are consistent with the possibility that pike from the Mississagi River have compensated and developed swimming abilities slightly different from those of the fish from the Aubinadong River. The hypothesis about the swimming abilities of the fish from the Mississagi River is supported by the work of Senay et al. (Submitted[9]) who found that pike from the Mississagi River had morphological features that were significantly different from those of the Aubinadong River. Pike from the Mississagi River had a longer head (2.8% for females and 3.6% for males), a deeper body (2.5% for females and 9.2% for males), a deeper caudal peduncle (3.5% for female and 3.3% for males), and a larger insertion of the dorsal fin (1.4% for females and 2.2% for males) than fish from the Aubinadong River. Hydrodynamic theory suggests that elongated shapes should reduce the drag and the energy expended while swimming at a given speed, enhancing sustained swimming capacity at high velocities (Webb 1982, 1984). Deeper bodies and larger fins may increase burst swimming capacity, stability, and manoeuvrability (Webb 1984, Standen and Lauder 2005). Taken together, these results suggest that the different environmental conditions found in the two rivers, the most obvious being the differences in flow regime, have modified overall fish morphology, which is related to different aspects of fish swimming capacity like sustained swimming capacity, burst swimming capacity, stability, and manoeuvrability.

LESSONS LEARNED FROM CONTRIBUTION 3.1

- Physiological indicators vary among fish exposed to different flow velocities within rivers suggesting that relationships between indicators of the physiological state of fish and habitat variables may exist.

- The physiological response of fish to stressors may vary between rivers suggesting that physiological indicators may be used to compare the physiological state of fish among rivers.

- Blood glucose and lactate concentrations may be better indicators of stress response than cortisol concentrations.

- Fish exposed to important and frequent flow variations may compensate via changes in their physiology, behaviour, and morphology. The net result of these processes on a metric of fish fitness and fisheries productivity (i.e. growth) is being assessed at the time of the writing of this report.

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[9] Senay, C., Harvey-Lavoie, S., Macnaughton, C.J., Bourque, G., and Boisclair, D. Morphological differentiation in northern pike: The influence of environmental conditions and sex on body shape. Submitted to Journal of Fish Biology.

APPLICATION

The approach used in the present report was to collect data for rivers within a particular range of environmental characteristics (Table 1). These data were used to estimate statistical models, i.e. fitting relationships between the response and the explanatory variables (Table 6). To assess model's predictive power, models were sometime cross-validated. This procedure consist in removing observations from the dataset, calibrating models with the remaining observations, and predicting the removed observations from models that are naive about the removed observations. By comparing the observed values with predicted ones, R^2_{CV}, a metric of the model's predictive power, can be calculated. The R^2_{CV} has a maximum value of one for a perfect model, has not minimum bound, and takes the value 0 for a model no better than taking the mean of the population as a predicted value (Guénard et al. 2013). Models are only expected to provide accurate predictions for rivers within the range of environmental characteristics and located within the spatial extent than the ones in the construction data set, and when the same methodology is used (e.g. fish surveys, environmental characterization). Before applying models to a broad range of new rivers, it would be prudent to first validate them in at least one river, and ideally in many rivers. This would mean to collect data concerning new rivers, totally independent of the present study, in order to assess how the models can accurately predict new systems. Afterwards, the new data should be incorporated into models to improve their capacity to explain and predict an even wider range of rivers as part of an adaptive modelling approach.

All "lessons learned" should be examined in the context that this study was conducted in a series of rivers encompassing a relatively narrow range of environmental conditions (Table 1). Some of the conceptual contributions of this study may be applicable on a broader basis (e.g. the existence of general relationships between fisheries productivity metrics and environmental conditions; the possibility to identify few key flow and thermal indices out of hundreds of potential indices, Table 6). However, it may be inappropriate to apply the relationships between fisheries productivity metrics and environmental conditions unveiled in this study to rivers, fish communities, or environmental conditions that are outside the range used to develop these relationships. Once these limits are respected, the relationships between fisheries productivity metrics and environmental conditions developed by the present study could be used to predict future river fisheries productivity metrics under a new set of environmental conditions. These contributions respond directly to the need of both the proponents and the regulators to:

i)   predict the potential effect of a project on metrics of fisheries productivity;

ii)   assess the need for, or the magnitude of, mitigation measures;

iii)   identify and measure the relative efficiency of different mitigation strategies;

iv)   estimate the existence or the magnitude of residual effects on metrics of fisheries productivity, and;

v)   quantify the need for, or the magnitude of, offsetting.

Knowledge and tools developed by the present project may be useful to inform the decision-making process regarding the development or operation of hydropower facilities, and, if authorities recognize the knowledge and tools developed by the present study, augment the clarity, the consistency, and the certainty of the decision-making process.

Table 6. List of the models provided, model number, model name, contribution, equation, R^2, p-value, and important cautions are presented. See Table 2 for variables definitions.

Model Number	Model Name	Contribution	Equation	R^2	p-value	Important Cautions
1	Multiple regression model Density	1.1	log(Density+1) = 0.3829 - 0.0015 * Depth-0.2194 * Velocity + Sum of 86 coefficients * spatial eigenfunctions	0.47	NA	
2	Multiple regression model Biomass	1.1	log(Biomass+1) = 0.7409 - 0.3605 * Velocity + Sum of 77 coefficients * spatial eigenfunctions	0.26	NA	Spatially-explicit prediction of fish density in 300m² (60m by 5m) river sites for unregulated rivers. Prediction of sites in Alberta, Ontario, Québec, and New Brunswick.
3	Multiple regression model Richness	1.1	log(Richness+1) = 2.3302 - 0.0062 * Depth - 0.8092 * Velocity + Sum of 52 coefficients * spatial eigenfunctions	0.33	NA	
4	Type II linear model (Major Axis)	2.1	Biotic anomaly index^0.25 = 0.15 + 0.11 * (Flow anomaly index^0.25)	r = 0.94	<0.005 (2-tailed)	Biotic and flow anomaly index is fourth rooted. Meet normality and homoscedacity assumptions for flow and biotic anomaly scores and check residuals from the linear regression to assess skewness.
5	Redundancy analyses (RDA) followed by a forward selection	2.2	Biomass of morphological guilds (8 guilds)^0.25 = Intercept + coef[a](Magnitude of summer water temperatures) + coef[b] (Intra-annual flow	0.33	0.002	Guilds were fourth rooted to achieve more normalized distributions, while the explanatory variables were standardized prior to PCA analysis. Explanatory variables are condensed

Model Number	Model Name	Contribution	Equation	R^2	p-value	Important Cautions
			variability) + coef[c] (Long-term flow variability)			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.
6	Redundancy analyses (RDA) followed by a forward selection	2.2	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)	0.33	0.003	
7	Redundancy analyses (RDA) followed by a forward selection	2.2	Biomass of reproductive guilds (8 guilds)^0.25 = Intercept + coef[a](Magnitude of summer water temperatures) + coef[b] (Intra-annual flow variability)	0.32	0.003	
8	Redundancy analyses (RDA) followed by a forward selection	2.2	Biomass of habitat guilds (7 guilds)^0.25 = Intercept + coef[a](Magnitude of summer water temperatures) + coef[b] (Intra-annual flow variability)	0.44	0.001	
9	Redundancy analyses (RDA) followed by a	2.2	Biomass of behavioural guilds (6 guilds)^0.25 = Intercept + coef[a](Magnitude of summer	0.34	0.004	

Model Number	Model Name	Contribution	Equation	R^2	p-value	Important Cautions
	forward selection		water temperatures) + coef[b] (Long-term flow variability) + coef[c] (Magnitude of spring flood)			
10	Redundancy analyses (RDA) followed by a forward selection	2.2	Biomass of taxonomical 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)	0.26	0.014	
11	Artificial Neuronal Networks (ANN)	2.3	log(Biomass) = 3.84 - 3.15 * h1 - 2.66 * h2 where; h1= (1/(1+exp(-(2.12 - 1.69 * TP - 1.81 * nRA1 – 2.56 * DD)))) h2= (1/(1+exp(-(2.17 + 1.21 * TP + 2.67 * nRA1 + 1.53 * DD))))	0.83	0.001	Response variable (TFB) is expressed in natural logarithm. Explanatory variables are standardized. Predictions can be computed for rivers having conditions included in the studied range.
12	Linear multiple regression	2.4	log(Richness) = 0.577 + 0.001 * DD + 0.413 * log(HMID)	0.69	0.001	Species richness and HMID are expressed in natural logarithm. Predictions can be computed for rivers having conditions included in the studied range.
13	Linear mixed-models Richness	2.6	Richness^0.5=RegionIntercept + RiverIntercept + 2.15 - 0.21 * Velocity -2.93 * MA60 + 2.34 * RH2 + 1.23 * FH5 - 0.68 * FH9	0.53	NA	Predictions can be computed for sites having new conditions for rivers included in the model. Explanatory variables are standardized. PC1-3s are

Model Number	Model Name	Contribution	Equation	R^2	p-value	Important Cautions
			- 0.13 * Depth - 0.13 * PC2s - 0.5 * PC3s			principal components computed on substrate classes. No p-values are provided in mixed-models, models calibration is based on AIC.
14	Linear mixed-models Density	2.6	Density^0.25=RegionIntercept + RiverIntercept + 0.65 - 0.08 * Velocity - 0.86 * MA60 + 0.66 * RH2 + 0.19 * FH5 - 0.04 * PC2s - 0.04 * Depth - 0.02 * PC3s	0.64	NA	
15	Linear mixed-models Biomass	2.6	Biomass^0.25=RegionIntercept + RiverIntercept + 0.85 - 0.09 * PC2s - 0.46 * MA60 + 0.41 * RH2 - 0.05 * Velocity - 0.03 * PC1s - 0.04 * PC3s	0.43	NA	
16	Phylogenetically explicit habitat models	2.7	log(Density) = -3.5834 - 8.7911 * V1 + 0.0013 * DD + 1.7891 * log(Total P) + 0.3133 * dbMEM1 + interactions between fish total length and 5 environmental variables + interactions between fish total length and 10 spatial eigenfunctions + 22 interactions between 15 phylogenetic eigenfunctions and 5 environmental variables +	0.52	NA	Species- and size-specific, and spatially-explicit predictions of the distribution of fish among 15 unregulated rivers based on their total length, phylogeny (47 phylogenetic eigenfunctions: V1 - V47), 6 environmental variables and 14 spatial eigenfunctions (dbMEM1 - dbMEM14). Prediction of rivers in Alberta, Ontario, Québec, and New-Brunswick. Prediction possible for other species besides that of the model.

Model Number	Model Name	Contribution	Equation	R^2	p-value	Important Cautions
			1.9881 * interaction V35 * dbMEM1			
17	Multiple linear model Cortisol	3.1	Plasma cortisol= 5.43*ectoparasite load - 64.21 * river of origin + velocity increase + river of origin:velocity increase + 175.96	0.32	< 0.005	The variables river of origin and velocity increase are qualitative. The velocity increase corresponds to the experimental treatments: the resting control (i.e. the basal stress), a negative control (i.e. an increase of 0.00 m/s) and an increase of 0.20 m/s in velocity. The variable ectoparasite load is the number of trematode grubs on the skin on each fish. These are black dots that correspond to *Uvulifer ambloplitis*. The expression ":" denotes an interaction. This is potentially new fisheries productivity metric, the relation was tested in two rivers only: Mississagi River (hydropeaking) and Aubinadong River (unregulated). More work is needed before it can be used as a fisheries productivity metric.
18	Multiple linear model Glucose	3.1	Blood glucose= 0.14*ectoparasite load + 0.27 * river of origin + velocity increase + river of origin:velocity increase + 3.94	0.39	< 0.0001	
19	Multiple linear model Lactate	3.1	Blood lactate= 0.27 * river of origin + velocity increase + river of origin:velocity increase + 2.14	0.50	< 0.0001	

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