

Using fish guilds to assess community responses to temperature and flow regimes in unregulated and regulated Canadian rivers

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SUMMARY

1. Hydropower currently accounts for 63% of Canada's total electricity generation and is bound to increase with the energy demands of a growing population. With damming and flow regulation known as major threats to aquatic biodiversity and river and floodplain habitats, an improved understanding of the specific impacts of river regulation is needed for the proper management of these systems.
2. Although interactions among river flow and thermal regimes have been described in the literature, their concurrent influence on fish guild responses has yet to be analysed for temperate rivers. Such an analysis may be used to identify the ecological traits linked with the flow and thermal variables reflecting river regulation.
3. Extensive field surveys were conducted across 25 unregulated and regulated rivers to estimate fish species density and biomass. Fish guild models were developed to characterise morphologic, trophic, reproductive, habitat preferences and behavioural traits, as well as phylogenetic associations. To characterise ecologically relevant components of the flow and thermal regimes of rivers, we calculated indices based on the magnitude, frequency, duration, timing and rate of change in each driver. Model relationships between fish biomass and density estimates were then run using redundancy analyses (RDA) on each type of guild and dominant patterns of flow and thermal variability.
4. Variables representing the magnitude of summer temperatures and intra-annual flow variability were consistently selected as independent drivers of fish guild responses (>86% of RDA models), clearly showing the importance of integrating thermal regimes in current river hydro-ecological studies.
5. Fish guild density and biomass were significantly explained ($R^2_{Adj} = 25\text{--}44\%$) and predicted ($R^2_{CV} = 35\text{--}76\%$) by flow and thermal variables characterising regimes across unregulated and regulated rivers, whereas total fish density and biomass were not. Fish guild models based on trait–environmental relationships performed better than those based on phylogeny. Our results also showed that the models describing habitat and trophic guilds had the greatest explanatory power ($R^2_{Adj} = 0.44$ and $R^2_{Adj} = 0.41$ respectively).
6. This study identified differences in guild trait–environment relationships across rivers and the guilds most susceptible to changes in flow and temperature conditions resulting from river regulation. In particular, more constant summer temperatures and lower flow variability favoured habitat and trophic guilds over morphologic, reproductive and behavioural guilds.
7. Our results showed that maintaining particular aspects of the flow and thermal regime may be important for ensuring the presence of certain guilds in temperate rivers.

Keywords: ecological traits, flow indices, regulated rivers, thermal indices, trait–environment relationships

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Introduction

Numerous environmental drivers are known to affect the structure of river fish assemblages. However, trait-based approaches that focus on groups of co-occurring species with shared ecological traits, such as fish guilds (Hawkins & MacMahon, 1989; Simberloff & Dayan, 1991), may reveal a unique response of the fish community to environmental perturbation (Poff, 1997; Mathieson *et al.*, 2000; Lamouroux, Poff & Angermeier, 2002; Frimpong & Angermeier, 2010). Indeed, fish guilds have been shown to respond to environmental change in a more predictable manner than individual species (Austin *et al.* 1994). Although phylogenetic associations between species may also be used to describe shared abilities or niche constraints, the notion that they can be used to predict ecological relationships remains unclear (Walter & Ikonen, 1989). As such, guild-based approaches may help improve our inference of causal relationships over that of classifications related to phylogenetic associations.

Fish traits such as trophic position and feeding behaviour (Karr, 1981; Schlosser, 1982), reproductive attributes (Balon, 1975; Aarts & Nienhuis, 2003; Winemiller, 2005) and habitat preferences (Leonard & Orth, 1988; Aadland, 1993; Malavasi *et al.*, 2004; Welcomme, Wine-miller & Cowx, 2006) have, for instance, well-established relationships with river habitat variables, including flow regulation (Vannote & Sweeney, 1980; Lamouroux & Souchon, 2002; Humphries *et al.*, 2008), river biogeography, water temperature (Jackson & Harvey, 1989; Malavasi *et al.*, 2004), nutrient levels (Schlosser, 1982), geomorphology and river flow (Poff & Allan, 1995; Ibarra *et al.*, 2003; Lamouroux & Cattaneo, 2006). Of these, catchment area and flow regimes have often been cited as the most important environmental drivers of guild composition (i.e. the types of traits describing the guilds and proportion of species represented within) in lotic systems (Bunn & Arthington, 2002; Ibarra *et al.*, 2003; Welcomme *et al.*, 2006; Rolls & Arthington, 2014; Taylor, Seilheimer & Fisher, 2014). For example, benthic and pelagic fish guilds were associated with a suite of flow hydrology indices (mean daily flows changes, base flow, number of zero-flow days and high-flow pulses) across 20 catchments where flows were regulated (Arthington *et al.*, 2014).

In contrast to the well-studied effect of flow regulation on guild composition, the extent to which thermal alteration from river regulation has affected fish communities remains poorly described (Murchie *et al.*, 2008; Olden & Naiman, 2010; Arismendi *et al.*, 2013). Although water

temperature and flow regulation have been shown to both shape the progressive replacement of dominant fish species as rivers shift from unregulated to regulated systems (Reyjol *et al.*, 2001), the concurrent influence of flow and thermal regimes on fish guild responses has yet to be analysed for temperate rivers. This represents an important shortcoming given the significance of water temperature in riverine ecosystems (Coutant, 1999; Caissie, 2006; McCullough *et al.*, 2009).

A more comprehensive quantification of thermal regimes, beyond the scope of sampling fish during specific time periods or preferences/tolerances for certain water temperatures, and across a range of rivers remains a major challenge to understanding changes in fish community organisation stemming from river regulation. The limited number of temperature-gauging stations, especially in Canada, has been a substantial impediment to acquiring suitable thermal data across temperate rivers (Guillemette *et al.*, 2011). Integrating thermal regimes is therefore a vital step towards setting more comprehensive environmental flow programs, as flow regimes alone may not provide all the conditions required to understand the complex and interactive influences of flow and thermal regimes (Puckridge *et al.*, 1998; Olden & Naiman, 2010).

Although guilds have long served as the 'basic building blocks' of communities (Simberloff & Dayan, 1991), a broad-scale comparison of the relationships between the different types of guilds and environmental variables reflecting both water quantity and quality are lacking. Such an analysis may serve to better understand these trait-environment relationships and identify the guilds most susceptible to environmental changes related to river regulation and global climate warming (Welcomme *et al.*, 2006; Webb, Stewardson & Koster, 2010; Michel & Knouft, 2014). Here, we examined the relationships between guilds representing different ecological traits, phylogenetic associations and environmental variables, notably those describing temperate river regimes. Specifically, the present objectives are to: (i) characterise flow and thermal regimes across 25 unregulated and regulated rivers; (ii) compare the guild model relationships based on morphologic, trophic, reproductive, habitat and behavioural traits with flow and thermal river variables; (iii) contrast these relationships with those found using either phylogenetic associations or total fish community estimates (i.e. river densities or biomasses); and (iv) identify the flow and thermal variables that best explain and predict fish guild densities and biomasses for each of the fish guild models across unregulated and regulated rivers. By achieving these objectives, we may

identify specific flow and thermal variables that are important to understand and predict how freshwater fish communities respond to environmental changes stemming from river regulation.

Methods

River fish densities and biomasses were measured and flow and thermal regimes were characterised across 25 Canadian unregulated and regulated rivers. We created five fish guild models (each based on morphologic, trophic, reproductive, habitat preferences, behavioural traits) and one model of phylogenetic associations (colated from the literature) to compare the relationships among and within guild models with explanatory variables describing river flow and thermal regimes.

River segments, sites and surveying methodology

A total of 25 river segments were selected based on surveying feasibility (i.e. wadeable stretches of river across the entire wetted width) and road access. Three rivers were situated in the province of Alberta, 5 in Ontario, 14 in Quebec and 3 in New Brunswick (Fig. 1). Of these, 14 rivers were unregulated while the remaining 11 were regulated for hydro-electric purposes (Table 1). Regulated rivers differed according to three flow management practices: run-of-river (ROR), storage with hydro-peaking and storage without hydro-peaking. ROR type rivers generally have a small reservoir, where water flows freely through turbines and has little to no effect on downstream flow regimes (Bratrich *et al.*, 2004). Conversely, storage with and without hydro-peaking practices have large storage reservoirs that allow managers to release water on demand (i.e. for irrigation or for hydropower demands), temporally shifting the natural flow regime and attenuating seasonal high flows. Hydro-peaking rivers additionally provoke frequent and rapid flow peaks that are timed to match daily consumption needs, causing significant flow alteration (Zimmerman *et al.*, 2010) and subsequent ecological impacts (Bond, Jones & Haxton, 2015; Macnaughton *et al.*, 2015b; Senay *et al.*, 2016). All unregulated and regulated rivers segments were analysed together to assess the effect of contrasting river flow and thermal regimes on fish guild models. To ensure that the fish communities surveyed downstream from dams had been interacting over a long period of time, rivers with dams constructed over 40 years ago were selected.

River segments ranged from 5 to 27 km in length (Mississagi and Kananaskis Rivers, respectively;

mean = 12.3 km, standard deviation = 6.1 km), on which total of 870 sites were surveyed, each measuring approximately 300 m² (~5 by 60 m, width and length of a site), with a distance of 60–100 m separating successive surveying sites. The position of the first sampling site was randomly selected prior to field surveying, and subsequent sites were positioned following a systematic design (i.e. left shore, middle, right shore, left shore). Fish community surveys were conducted during the summer months (late June to early September) from 2011 to 2013.

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

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

Fish guild variables

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

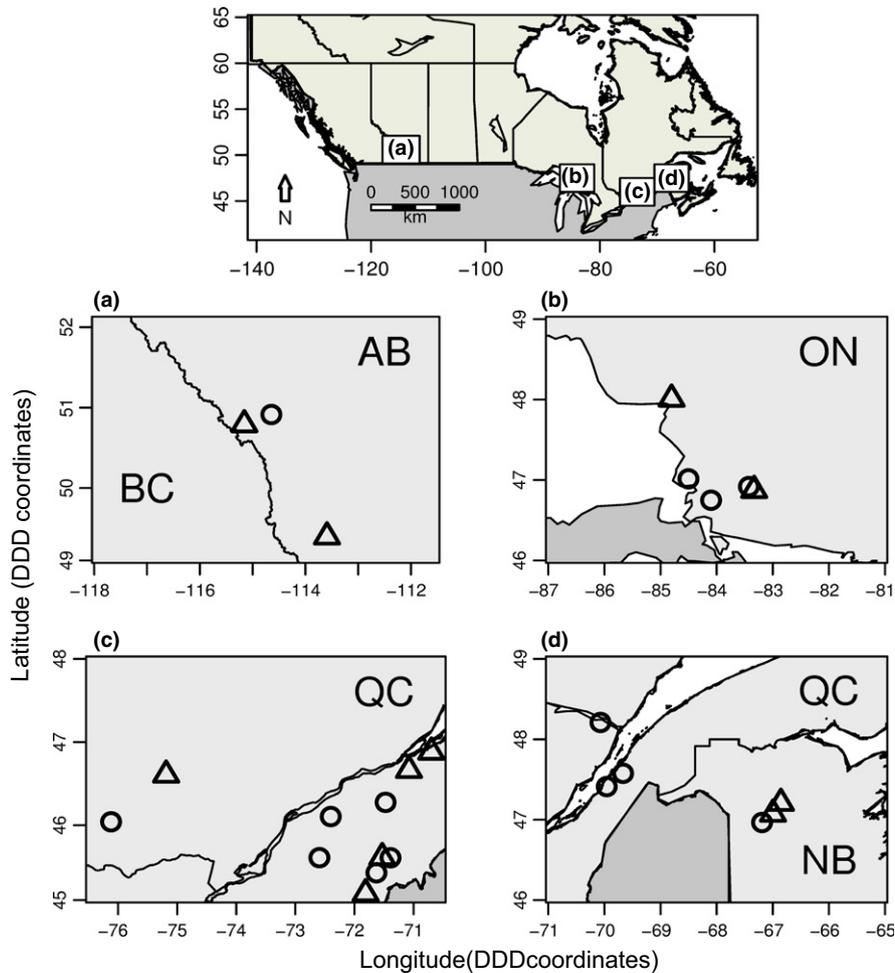


Fig. 1 Map of the study area showing the 25 rivers surveyed in Canada (principal map). Enlarged views depict rivers located in (A) Alberta (AB), (B) Ontario (ON), (C) Quebec (QC) and (D) New Brunswick (NB). Open circles and triangles refer to unregulated and regulated rivers respectively.

occurring in our rivers (Table S1). Quantitative ecological traits (e.g. trophic position ranging from 1 to ~4) were standardised (i.e. centred and reduced) prior to cluster analysis. K-means partitioning was then conducted on species' ecological traits ascribed to each of the type of guilds and a range of simple structure indices (SSI criterion; Oksanen *et al.*, 2011) along with expert knowledge were used to guide the number of ecologically relevant guilds. For example, 10 ecological traits representing fish habitat preferences (e.g. preference for cold, cool and warm water temperatures or tolerance to/for anthropogenic disturbances and turbidity levels) were coded for every species surveyed. K-means partitioning analysis conducted on these traits by species (SSI criterion suggested six groups) along with expert knowledge on the groups of species obtained, resulted in seven habitat guilds (Table S5). Phylogenetic distances between the fish species surveyed were also determined (Hubert *et al.*, 2008) to serve as the 'benchmark' model from which all other models were compared.

Site- and species-specific density and biomass estimates described above were used to derive mean river

densities and biomasses for each of the guilds (e.g. density and biomass for each of the seven habitat guilds). Total fish density and biomass estimates per river were also calculated. Guild density and biomass estimates per river, along with total estimates (i.e. fish densities and biomasses per river segment) were subsequently transformed using the fourth root to achieve more normalised distributions.

Flow indices

Daily and hourly flow data were obtained from the Centre d'Expertise Hydrique du Québec (CEHQ) (2013), the Water Survey of Canada (2013) national flow gauge networks (HYDAT), and hydro-electric companies: Trans-Alta, Brookfield Renewable Power and NB Power. We analysed a 13-year time series (1997–2009) that reflected the effects of temporal and climate variability on the flow regime and the multiyear index differences characterising the 25 rivers (Kennard *et al.*, 2010). Flow indices representing ecologically relevant components of the flow regime (magnitude, frequency, duration, timing and rate

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

River	Province	Regulation type	Catchment area (km ²)	Length of river segments surveyed (km)	Distance of river segment to dam (km)	Distance of river segment to flow gauge (km)	Distance of river segment to thermal logger (km)
Elbow	Alberta	Unregulated	791	22.3	NA	0.0	33.0
Kananaskis	Alberta	Hydro-peaking	362	27.4	3.0	1.0	0.7
Waterton	Alberta	Storage	1631	23.7	0.7	2.4	22.0
Dee	New Brunswick	Storage	141	13.7	0.2	0.2	0.01
Gulquac	New Brunswick	Unregulated	110	8.8	NA	62.0	8.9
Serpentine	New Brunswick	Storage	47	18.2	0.2	0.2	0.0
Aubinadong	Ontario	Unregulated	1440	9.8	NA	1.0	0.05
Batchawana	Ontario	Unregulated	1190	7.8	NA	0.0	0.0
Goulais	Ontario	Unregulated	1637	7.2	NA	15.0	0.0
Magpie	Ontario	Hydro-peaking	1930	10.0	8.0	8.0	4.09
Mississagi	Ontario	Hydro-peaking	4040	4.9	8.0	8.0	5.46
Au Saumon	Quebec	Unregulated	738	8.2	NA	0.0	0.0
Bécancour	Quebec	Unregulated	917	12.7	NA	0.0	69.0
Coaticook	Quebec	ROR	362	7.8	1.0	11.0	0.0
Du Loup	Quebec	Unregulated	515	7.0	NA	3.0	4.46
Du Sud	Quebec	ROR	821	15.4	1.0	0.2	0.0
Eaton	Quebec	Unregulated	646	10.2	NA	1.5	0.0
Etchemin	Quebec	ROR	1160	6.8	3.0	1.7	0.0
Kiamika	Quebec	Storage	702	14.8	0.3	3.3	0.04
Nicolet	Quebec	Unregulated	1550	18.8	NA	0.0	0.0
Noire	Quebec	Unregulated	401	12.9	NA	24.0	0.0
Ouelle	Quebec	Unregulated	796	7.4	NA	3.5	2.83
Petit Saguenay	Quebec	Unregulated	712	6.0	NA	10.0	0.0
Picanoc	Quebec	Unregulated	1290	9.2	NA	3.1	0.6
Saint Francois	Quebec	Storage	2940	7.9	6.0	9.0	3.54

of change in daily and hourly flows) included, among others, the Indicators of Hydrologic Alteration (IHA; Richter, 1997; Olden & Poff, 2003). All flow indices described by McLaughlin *et al.* (2014), in addition to those created to capture hourly variations in the flow record (Zimmerman *et al.*, 2010; Macnaughton *et al.*, 2015b), were calculated for each of the rivers surveyed for a total of 211 flow indices. Flow indices expressed as discharge units (volume per time) were normalised 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. Together, these indices described the magnitude (42), frequency (6), duration (15), timing (4) and rate of change (10) of river flows.

Thermal indices

Summer water temperatures were measured using temperature data loggers (Hobo Pendant Temp, precision of $\pm 0.5^\circ\text{C}$, ONSET[®] Computer Corporation, Onset Head-

quarters, Bourne, MA 02532, USA) anchored along the 25 river segments. For 22 of the 25 river segments, temperature data loggers were placed within river segments. The three remaining river segments loggers were located 22–69 km away from fish survey sites (Table 1). Loggers were deployed in riffle, run or shallow pool river habitats to limit any potential water temperature anomalies that may arise from placing loggers in deep pools, shallow shore habitats and/or tributaries. Loggers were set to record ambient water temperatures every 15 min, from early June to late September in 2013, save for the Elbow, Bécancour and Waterton Rivers, for which loggers were placed in rivers over similar time periods in 2006, 2012 and 2014 respectively. Due to atypical flooding events in Alberta in 2013 (Phillips, 2013), many loggers were lost, limiting the use of temperature data in those rivers. Between 3 and 15 temperature loggers were retrieved and used to calculate summer thermal profiles for each of the rivers studied. Water temperature data extracted from loggers were checked for erroneous measurements (i.e. air exposure), which were removed from thermal profiles. Loggers with <5 days of data removed were kept and data from these

loggers were averaged per day and hour, for each of the loggers, to derive a total of 294 thermal indices describing all components of thermal regime (magnitude, variance, frequency, duration, timing and rate of change in daily and hourly temperatures; Olden & Naiman, 2010). Median values per thermal index were calculated for each river from all retained loggers to further decrease the incidence of local thermal anomalies.

Of the 294 thermal indices calculated, 21 indices were selected to reliably represent general summer thermal trends from a single summer (compared across rivers), their biological relevance and the type of thermal alteration expected for regulated rivers. For example, thermal indices were based on the warmest week rather than on the warmest day because the former is more consistent between years than the warmest day (Maheu *et al.*, 2016). 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 standardised 9-week summer period, which was centred on the warmest week for

unregulated rivers to facilitate inter-river comparisons (Table 2).

Statistical analyses

To reduce the number of explanatory variables chosen to represent flow and thermal regimes across the rivers surveyed, we ran several principal component analyses (PCA), ensuring that the number of observations (i.e. 25 rivers) was greater than the number of explanatory variables included. Specifically, the 77 flow indices characterising the flow regime for the 25 rivers were summarised by conducting five separate PCAs on the correlation matrices for each of the flow regime components (magnitude, frequency, duration, timing and rate of change). River scores for PC axes describing a greater fraction of the variation than the broken-stick null model were retained (Legendre & Legendre, 2012). Performing separate PCAs for each of the flow regime components ensured that indices describing major sources of variation within each component contributed to the retained

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

Component	Name of index	Data	Description	Units	Period of time
Magnitude	MOmn7	Daily	Monthly average in daily mean water temperature	°C	July
	MOmin7	Daily	Monthly average in daily minimum water temperature	°C	July
	MOmax7	Daily	Monthly average in daily maximum water temperature	°C	July
	MSmn	Daily	Average daily mean water temperature	°C	Summer
	MWmax	Daily	Maximum weekly average in daily mean water temperature (during TWmax)	°C	Summer
	DD_midsum	Daily	Cumulative degree-days at mid-summer (week TWmax-4 to TWmax inclusively)	°C-days	Summer
Variance	DD	Daily	Cumulative degree-days	°C-days	Summer
	RNGmn7	Hourly	Monthly average daily range (daily max-daily min)	°C	July
	RNGmax7	Hourly	Monthly maximum daily range (daily max-daily min)	°C	July
	RNGSmn	Hourly	Mean daily range during summer period	°C	Summer
	RNGSmin	Hourly	Minimum daily range during summer period	°C	Summer
	RNGSmax	Hourly	Maximum daily range during summer period	°C	Summer
Timing	AMPLW	Daily	Median of weekly amplitude (max. daily mean water temperature – min. daily mean water temperature)	°C	Summer
	TWmax	Daily	Timing of maximum weekly average in daily mean water temperature (MWmax)	Week number	Summer
Rate of change	RAREv	Hourly	Average number of reversals per day during summer period for upstream-most logger	Number of reversals	Summer
	RAPos	Daily	90th percentile of positive changes in daily mean water temperature	°C	Summer
	RANeg	Daily	90th percentile of absolute negative changes in daily mean water temperature	°C	Summer
Frequency	RARatio	Daily	Absolute value of ratio between RAPos and RANeg	None	Summer
	FDmax25	Daily	Number of days where daily maximum water temperature was above 25°C	Days	Summer
Duration	FDconsmax25	Daily	Maximum number of consecutive days where daily maximum water temperature was above 25°C	Days	Summer
	FDconsmax_min20	Daily	Maximum number of consecutive days where daily minimum water temperature was above 20°C	Days	Summer

PC axes, and that subjectivity associated with the process of selecting individual indices was reduced. Flow indices that contributed the most to the retained PC axes (i.e. top loaders) were identified to explain dominant patterns of flow variation measured in our rivers as described by each of the flow components.

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

Redundancy analyses (RDA) with 9999 permutations (Legendre & Legendre, 2012) were used to assess the relationships between river biomass and density estimates for each type of guild based on morphologic, trophic, reproductive, habitat, behavioural traits and phylogenetic associations (six response matrices), and flow and thermal PC axes (12 explanatory variables). Additional relationships using the total river density and biomass estimates as response variables (two vectors) were also conducted to compare with multivariate fish guild models. A permutational forward selection of explanatory variables was subsequently conducted for significant relationships to identify the best variables for the model describing each response matrix and vector (Blanchet, Legendre & Borcard, 2008; Dray, Legendre & Blanchet, 2011). The proportion of variation explained by selected explanatory variables for each of the response matrices was determined using a cumulative adjusted R^2 ($\text{Cum}R^2_{\text{Adj}}$). Individual canonical axes were also tested for significance to determine whether axes represented variations that were more explained than random (Legendre & Legendre, 2012). For the leading fish guild model (greatest R^2_{Adj}), the response matrix and explanatory variables were plotted in reduced space (correlation biplot), where the focus is on the relationships among habitat guilds, explanatory variables (flow and thermal PCs) and each other. A distance biplot was also illustrated to show the relationships between

explanatory variables and the position of our rivers, as well between unregulated and regulated rivers in reduced space. To facilitate interpretation, RDA 1 and RDA 2 axes were rotated to project the first selected environmental variable on RDA 1. This was done by calculating the angle between RDA 1 and this selected variable and rotating all other points in the figure along this angle.

Each model's ability to predict new responses from selected explanatory variables was quantified using the cross-validation R^2 (R^2_{CV}) via a leave-one-out cross-validation approach (Guénard *et al.*, 2013). R^2_{CV} is bound between $-\infty$ and 1, where $R^2_{\text{CV}} = 1$ when predictions perfectly match the observations and $R^2_{\text{CV}} \leq 0$ when predictions are inaccurate or no better than what would be expected from chance alone. All statistical analyses were performed in R (R Development Core Team, 2014).

Results

Description of fish guilds

The eight morphologic guilds differed from one another with respect to general body shape (discoid, cylindrical or eel-like), the mouth position (subterminal/versusterminal), and fin types, sizes and placements (soft or spiny dorsal rays, large pectoral fins and abdominal pelvic fins respectively; Table S2). The six trophic guilds shared diet preferences and associated trophic level, with a particular distinction between guilds that prey on small to large fishes, amphibians and mammals and shift their diet ontogenetically (Table S3). The eight reproductive guilds shared reproductive behaviours (nest building and/or guarding), spawning time (fall or summer), fecundity level and age of maturity, and spawning habitat preferences (marine, riffles or shallow waters; Table S4). The seven habitat guilds reflected preferences for warm, cool or cold-water temperatures, slow-moving or riffle water velocities and tolerance levels to water turbidity and/or anthropogenic perturbations (Table S5). The six behavioural guilds depicted feeding (grazing, pursuit or sorting), migratory (anadromous) and other (territorial or schooling) behaviours (Table S6). Lastly, the phylogenetic groups were based on the phylogenetic distances between the 57 freshwater species surveyed (Hubert *et al.*, 2008). The phylogenetic tree depicted was then cut at seven groups to ensure that distances between phylogenetic branches were even and the number of groups was similar to the number of guilds representing other guild types (Table S7).

Characterisation of flow and thermal regimes

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

Comparison of fish guild models

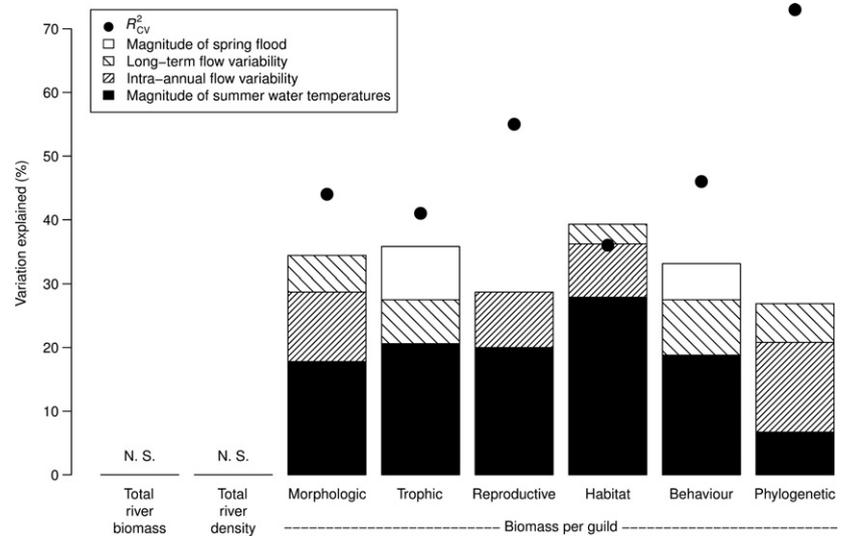
The PC axes describing the flow and thermal components significantly explained fish density and biomass for all guild models (a total of 12 models representing densities and biomasses of guilds and phylogenetic associations). Since the results for fish guild models using biomass were comparable to and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

The explanatory variables most often selected by fish guild models (>86% of models) were the magnitude of summer temperatures (solid black bars, Fig. 2) followed

Table 3 Results of PCAs computed independently on groups of flow and thermal indices; the number of indices per group is shown in brackets. Central columns: the top loaders for the first (1, 2 or 3) axes in each analysis are listed. Right: proportion of variation in the stated group of indices accounted for by 1, 2 or 3 PCA axes. Refer to Table 2 and Macnaughton *et al.* (2015b) for a description of thermal and flow indices mentioned respectively.

Flow and thermal components (no. indices)	Principal component axes			Cumulative variation explained (%)
	PC1 Description (Top loaders)	PC2 Description (Top loaders)	PC3 Description (Top loaders)	
Magnitude of flows (42)	Intra-annual flow variability (MA3, MH14, MH27)	Intra versus inter-year variability in monthly flows (MA31, MA33, MA40)	Long-term flow variability (MH17, MA7, MA8, MH9)	72
Frequency of flows (6)	Flood frequency (FH8, FH1, FH5)	–	–	68
Duration of flows (15)	Magnitude of spring flood (DH13, DH12)	Low exceedence flows (DL14)	–	78
Timing of flows (4)	Predictability of daily flows (TA2, TH2)	–	–	61
Rate of change in flows (10)	Fall rate of flows (RA7, nRA3)	Proportion of rise days (RA5)	–	83
Magnitude of temperatures (10)	Magnitude of summer water temperatures (DD_midsum, MSmn, MOmn7)	–	–	85
Variance of temperatures (6)	Daily range in temperatures over summer (RNGmax7, RNGSmn, RNGmn7, RNGSmax)	–	–	81
Rate of change in temperatures (5)	Flashiness of summer water temperatures (RANeg, RAREv)	–	–	65

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



by the intra-annual flow variability or the difference in the extreme flows within a year (thinly spaced dashed lines, Fig. 2). Highly correlated flow and thermal variables described earlier were not selected in any of the fish guild models. When habitat and trophic guild models were computed without thermal components, the flow components significantly explained biomass estimates. However, model strengths based on R^2_{Adj} were 13 and 20% lower without thermal components respectively. The same was true when flow PCs were removed from the analyses (9 and 10% lower respectively).

Variables selected by forward selection significantly predicted the different types of guild models (R^2_{CV} values; black points, Fig. 2). The best predictive model (largest R^2_{CV}) was found for phylogenetic associations ($R^2_{CV} = 0.73$), but these results were likely driven by the uneven distribution of rare species within groups (e.g. families Fundilidae, Petromyzontidae and Gasterosteidae; Table S7). When phylogenetic predictive models were conducted for groups with >50% presences across rivers, the model's predictive power decreased ($R^2_{CV} = 0.09$). Lastly, explanatory and predictive power results were fairly comparable, suggesting that the models were not overfitted and accurately explained and predicted the effects that selected flow and thermal variables had on different fish guilds.

Habitat guild-environmental relationships

To provide an example of the significant guild-environment relationships identified in our study, we illustrated the association between guild biomasses and flow and thermal PC axes for our strongest model, the habitat guild model (Fig. 3; correlation biplot). The magnitude of

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

Discussion

Characterisation of river regimes

Our study is among the first to show the importance of both the magnitude of summer temperatures and variability of the intra-annual flow on the density and

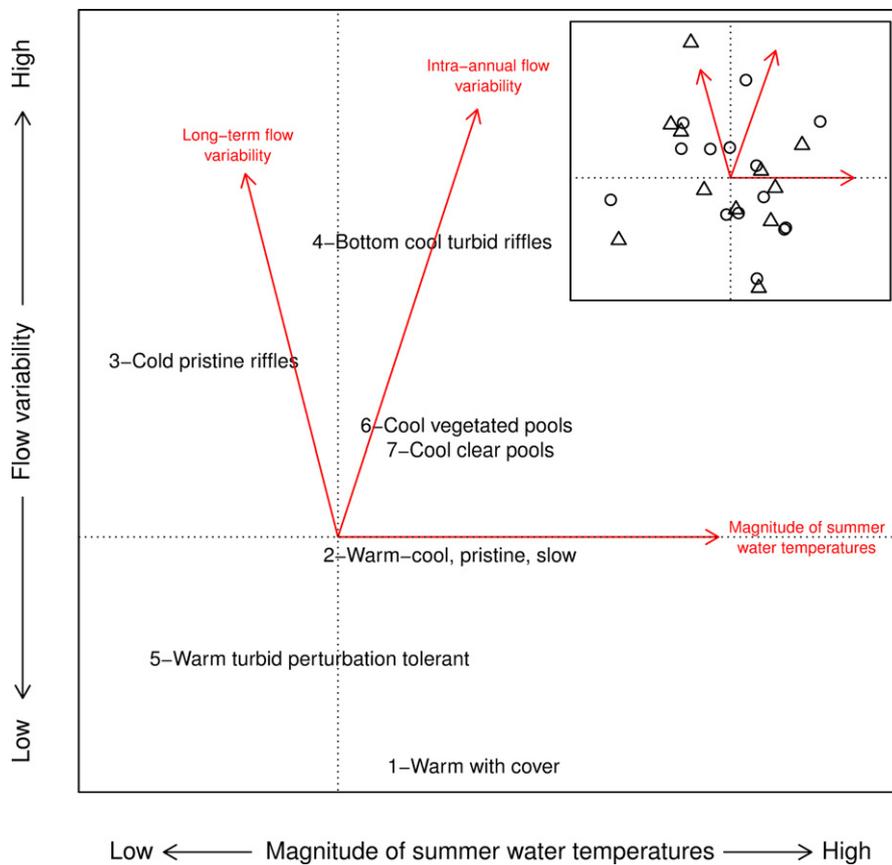


Fig. 3 The relative importance (correlation biplot) of the biomass estimates for habitat guilds as a function of selected flow and thermal variables (red arrows). Figure RDA 1 and RDA 2 axes were rotated to display the 'Magnitude of summer temperature' along the RDA 1 axis. RDA 2 represents the flow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

biomass of different fish guild types. Given that the strength of the habitat guild model decreased when either flow or thermal variables was omitted from analyses and that selected flow and thermal variables were not highly correlated with one another, we demonstrated the importance of integrating thermal regimes in hydro-ecological studies. These findings build on previous work that showed that the interplay of river flow and thermal regimes is crucial in shaping fish community structure (Reyjol *et al.*, 2001; Murchie *et al.*, 2008; Olden & Naiman, 2010).

Our application of the flow index conceptual template (McManamay *et al.*, 2012; Macnaughton *et al.*, 2015b) to river thermal regimes allowed us to depict them as a suite of thermal indices that not only reduced the number of redundant indices but also captured the full range of summer conditions occurring within our river segments. The magnitude of summer temperatures was consistently selected first across guild models, giving importance to thermal indices, notably, those that describe the cumulative degree days at mid-summer, the average daily mean in temperatures, and the July average in daily mean temperatures. We also identified other dominant patterns of temperature variability (i.e. daily

range and flashiness of summer water temperatures) that may have had an effect on fish community organisation. Collectively, these results suggest that thermal regimes are crucial when developing fish guild models.

The importance of summer water temperature regimes for understanding the organisation of different types of guilds has been elucidated here, but year-round thermal regimes are likely important for fish assemblages that rely on different thermal cues for initiating physiological and behavioural activities (e.g. spawning and recruitment of fishes, cold water thermal tolerances; Elliott, 1982; Rolls *et al.*, 2013). Our results also revealed some degree of regional discrimination as glacier-fed rivers located in Alberta (Kananaskis and Elbow Rivers) were strongly associated with low summer temperature variability. This result seems to be an artefact of the absence of large temperature variability during the summer months for these rivers, especially when compared to rivers located in southern Quebec. The study's large spatial scale and short time period (summer months) might also explain why general patterns of water quality and quantity were not observed between regulated and unregulated rivers. A recent investigation of the thermal profiles of regulated rivers in eastern Canada identified

a common pattern of thermal alteration downstream of storage and hydro-peaking dams (i.e. increased temperature magnitude in September and reduced variability), although site-specific impacts were also observed (Maheu *et al.*, 2016). We also found that certain regulated rivers were associated with high flow variability while others were not, suggesting that differences in river regulation practices may have played a role in driving fish guild composition. However, a preliminary analysis assessing the proportions of explained variation from selected environmental variables versus regulation practices (ROR, storage and hydro-peaking) showed that while flow and temperature variables significantly explained fish habitat guilds, regulation practices did not. We suggest that future research considerations should include geographical location of the river and/or headwaters, timing of surveys and an equal representation among regulation practices.

Fish guild models

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

Although habitat guilds had the greatest R^2_{Adj} , all explanatory fish guild models yielded significant results, pointing to the existence of functional relationships between the flow and thermal variables identified and the range of species traits encompassed between the different types of guilds. For example, traits depicting spawning habitat preferences (habitat guilds) and the type of spawning substrata, water velocities and depths (reproductive guilds) may be expected to share similar

relationships with flow and thermal variables. This might explain why differences in model outputs (R^2_{Adj}) were subtle among these guild types. Predictive model results further supported these findings, indicating that fish guild models were accurately predicted by the selected flow and thermal variables across rivers. Although phylogenetic and reproductive fish guild models yielded the largest R^2_{CV} , the models’ predictive power may have been substantially influenced by species prevalence (i.e. the proportion of rivers where a species was surveyed), resulting in poorly performing models that, otherwise, would be viewed as powerful (Olden, Jackson & Peres-Neto, 2002).

Applications of habitat guild–environmental relationships

The guild that responded most strongly to changes in the selected flow and temperature variables was the habitat guild. Specifically, the fish guild that described cold water, riffle-type habitats and fish that were intolerant to environmental perturbations was related to high annual flow variability and low magnitudes of summer temperatures. As such, species that represented this guild, *Cottus cognatus*, *C. ricei*, *Oncorhynchus clarkii*, *Oncorhynchus mykiss*, *Salmo salar*, *S. trutta*, *Salvelinus confluentus* and *Salvelinus fontinalis*, may be more vulnerable to anthropogenic perturbations via significant decreases in indices describing annual flow variability or increases in the cumulative degree days at mid-summer or the summer average in daily mean water temperatures. Planned modifications to unregulated systems may thus severely impact guilds preferring cold and faster moving habitats via the stabilisation of natural flows and increased summer temperatures due to river regulation. Further research, however, is needed to quantify the causal relationships between specific guilds and environmental drivers to better understand the degree to which these guilds may potentially be impacted.

Implications for river management

A key contribution of this study centred on the identification of ecologically relevant thermal indices and the value of both flow and thermal regimes in driving river fish guild responses. The European Water Framework Directive (WFD) outputs have been known to greatly improve the assessment of different stressors including river regulation on the ecological integrity of systems (Hering *et al.*, 2010). The use of trait-based approaches in this study also contributes to developing transferable methods for establishing stressor–trait relationships

across large geographical areas. Potential applications of our results are largely confined to fishes in temperate rivers, although they would likely also have implications for other aquatic taxa (e.g. macroinvertebrates). Broader applications of this study relate to the methodology used for identifying important flow and thermal variables and comparing different trait–environment relationships for a range of guild types. Here, we used empirical fish data to demonstrate the importance of variables depicting water quality and quantity for ensuring the presence of certain guilds in temperate rivers. Our approach, therefore, may be applied to other aquatic data sets assessing the role of flow and thermal drivers on aquatic ecosystems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

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

Table S2. Morphologic guilds, shared traits and species representing each guild.

Table S3. Trophic guilds shared traits/diet and species representing each guild.

Table S4. Reproductive guilds, shared traits and species representing each guild.

Table S5. Habitat guilds, shared traits/preferences and species representing each guild.

Table S6. Behavioural guilds, shared traits and species representing each guild.

Table S7. Species representing each taxonomic association.

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