Freshwater Biology

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

1   **Using guilds to assess fish community response to hydrologic and thermal**

2   **regimes across temperate rivers**

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23   **Key-words:** ecological traits, flow indices, trait-environment relationships, thermal

24   indices, regulated rivers.

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26 **Summary**

27 **1.** Although well-known interactions among river hydrologic and thermal

28 regimes have been described, both have yet to be analysed together for

29 assessing guild responses across temperate rivers. A comparison of the

30 different types of fish guilds responses to environmental variables might

31 highlight the ecological traits most susceptible to current and future

32 environmental change stemming from flow regulation.

33 **2.** Extensive field surveys were conducted across temperate rivers to estimate

34 river species densities and biomasses. Fish estimates were subsequently

35 grouped into type of guilds representing morphologic, trophic, reproductive,

36 habitat, behavioural traits, and phylogenetic associations. River hydrologic

37 data was paired with thermal data derived from *in-situ* water temperature

38 loggers to generate indices characterizing hydrologic and thermal regimes in

39 25 unregulated and regulated rivers across Canada. Redundancy analyses

40 (RDA) served to compare types of guild responses to dominant patterns of

41 varying hydrologic and thermal regimes.

42 **3.** Fish guild data were significantly explained (R^2_{Adj} = 25-44%) and predicted

43 (R^2_{CV}= 35-76%) by explanatory variables representing river hydrologic and

44 thermal regimes across rivers, whereas total fish density and biomass were not.

45 All fish guild models performed better relative to studying phylogenetic

46 associations, confirming that guild models based on trait-environmental

47 relationships were better performing than those based on phylogeny. Results

48 also showed that the best explanatory models were found for traits describing

49 habitat and trophic guilds (R^2_{Adj} = 0.44 and R^2_{Adj} = 0.41, respectively),

50   suggesting that habitat and trophic traits were more closely associated with

51   variables depicting river flow and thermal variability than other guild traits.

4. Flow and thermal variables representing the magnitude of summer water

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53   temperatures and intra-annual flow variability were consistently selected as

54   independent drivers of fish guild models (> 86% of models), pointing to the

55   importance of integrating thermal regimes in hydro-ecological studies.

5. The biomass of guilds representing species' habitat preferences for specific

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57   water velocities and temperatures, tolerance for anthropogenic disturbances,

58   and water clarity were driven by the magnitude of summer water temperatures,

59   and two variables describing river flow variability. Differences between

60   unregulated vs. regulated rivers revealed how more constant summer water

61   temperatures and smaller annual flow variability for downstream regulated

62   river habitats, led to generally warmer and less variable conditions, favouring

63   certain habitat guilds over others.

6. These findings identified the different guild trait-environment relationships

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65   across rivers and highlighted the importance of more comprehensive

66   hydrologic and thermal regime conservation, on which management efforts

67   focused on maintaining the ecological integrity of rivers should rely.

68   **Introduction**

69   Guilds were originally defined as groups of species that exploit the same

70   environmental resources in a similar way (e.g. foliage gleaning guild; Root 1967).

71   Species traits have since been used to establish general rules in community ecology,

72   linking groups of species through shared ecological traits along environmental or

73   landscape gradients (Poff 1997, Lamouroux et al. 2002, Frimpong and Angermeier

74   2010). Though grouping fishes by feeding modes (trophic groups) may be one of the

75   oldest attempted non-taxonomic classification of fishes, guilds have since been

76   expanded to group species that share morphological (Reyjol et al. 2008) and

77   reproductive traits (Balon 1975, Winemiller 2005), or specific river flow or hydraulic

78   preferences (Cattanéo 2005, Lamouroux and Cattanéo 2006, Arthington et al. 2014).

79   As such, guilds have long served as the "basic building blocks" of communities,

80   focusing on groups of co-occurring species with particular trait-environment

81   relationships, which reveal a structure not attributable simply to the abundance of

82   individual species or species composition and phylogeny (Hawkins and MacMahon

83   1989, Simberloff and Dayan 1991). Although phylogenetic relationship may be an

84   indication of shared abilities or constraints, the notion that it can predict ecological

85   function is under debate. Trait-based approaches, however, are independent of

86   phylogenetic associations and may infer causal relationships rather than relying on

87   literature references related to selected fish traits.

88   Recently, guilds have been used to describe the community response to

89   environmental perturbation, as they are thought to respond to environmental change in

90   a more predictable manner than individual species (Austen et al. 1994). Fish traits

91   such as trophic position and feeding behaviour (Karr 1981, Schlosser 1982),

92   reproductive attributes (Balon 1975, Aarts and Nienhuis 2003, Winemiller 2005), and

93   habitat preferences (Leonard and Orth 1988, Aadland 1993, Welcomme et al. 2006)

94   have often been chosen to group species into guilds because of the known

95   community-level relationships between these traits and river habitat variables,

96   including those resulting from flow regulation (Vannote and Sweeney 1980,

97   Lamouroux and Souchon 2002, Humphries et al. 2008). Morphological guilds have

98   also been developed since fish morphology is quite variable and known to reflect

99   aspects of the foraging behaviour and habitat use (Ibañez et al. 2007, Reyjol et al.

100   2008). To date, however, comparing the relationships between the different types

101   guilds and variables reflecting environmental change are lacking. Such an analysis

102   may highlight the guilds most susceptible to environmental change via a better

103   understanding of these trait-environment relationships and increase our capacity to

104   predict the effects of environmental change related to river regulation on these

105   communities (Webb et al. 2010, Michel and Knouft 2014).

106   Numerous environmental attributes are known to affect the structure of river

107   fish assemblages. In particular, specific guilds may be affected by variables relating to

108   and including the biogeography, water temperature (Jackson and Harvey 1989),

109   nutrient levels like the abundance of organic substrates (Schlosser 1982),

110   geomorphology, and river flow (Poff and Allan 1995, Ibarra et al. 2003, Lamouroux

111   and Cattanéo 2006). Of these, catchment area and hydrologic regimes have often been

112   cited as the most important environmental variables driving guild composition (i.e. the

113   types of traits describing the guilds and proportion of species represented within) in

114   lotic systems, implicating anthropogenic influences such as land-use and flow

115   regulation in changing the structure of fish assemblages (Bunn and Arthington 2002,

116   Ibarra et al. 2003, Welcomme et al. 2006, Rolls and Arthington 2014, Taylor et al.

117   2014). For example, benthic or pelagic guilds of fishes were associated with gradients

118   in mean daily flows and their variability, baseflow, number of zero-flow days and

119   high-flow pulses, among many others describing the low-flow hydrology across 20

120   catchments where flows were regulated (Arthington et al. 2014). Reyjol *et al*. (2001)

121   further showed that water temperature and flows (flow regulation) both influenced the

122   progressive replacement of Salmoniforms by Cypriniforms from unregulated to

123   regulated sites.

124   Despite this mounting evidence pointing to changes in guild composition

125   resulting from flow regulation, the role that changes in thermal regimes stemming

126   from river regulation may have on fish communities is relatively unknown (Murchie

127   et al. 2008, Olden and Naiman 2010). A more comprehensive quantification of

128   thermal regimes, beyond the scope of sampling fish during specific time periods or

129   preferences/tolerances for certain water temperatures, and across a range of rivers

130   remains a major challenge to understanding changes in fish community organization

131   stemming from river regulation.

132   Indeed, the significance of water temperature in riverine ecosystems has been

133   widely acknowledged (Coutant 1999, Caissie 2006, McCullough et al. 2009).

134   However, the limited number of temperature gauging stations, especially in Canada,

135   has been a substantial impediment to acquiring suitable thermal data across temperate

136   rivers (Guillemette et al. 2011, Maheu et al. in press). Despite this limitation, a

137   preliminary investigation of thermal profiles across a subset of regulated rivers

138   suggested that the variability in water temperatures was either reduced or increased,

139   depending on the flow management practice adopted. Integrating thermal regimes is

140   therefore a vital step forward into setting more comprehensive environmental flow

141   programs as hydrologic regimes alone may not provide all the conditions required to

142 understand the complex and interactive influences of hydrologic and thermal regimes

143 (Puckridge et al. 1998, Olden and Naiman 2010).

144   This paper examines the relationships between guilds representing different

145 ecological traits, phylogenetic associations, and environmental variables, notably

146 those describing temperate river regimes. Specifically, the present objectives are to: 1)

147 characterize hydrologic and thermal regimes across 25 rivers; 2) compare the

148 relationships between guild models based on morphologic, trophic, reproductive,

149 habitat, and behavioural traits with flow and thermal river variables; 3) contrast these

150 relationships with those found using either phylogenetic associations or total fish

151 community estimates (i.e. river densities or biomasses); and 4) identify the flow and

152 thermal variables that best explain and predict fish guild densities and biomasses for

153 each of the fish guild models across unregulated and regulated rivers. By meeting

154 these objectives, specific flow and thermal variables for understanding how

155 freshwater fish communities respond to environmental changes stemming from river

156 regulation may be inferred.

157

158 **Materials and methods**

159   River fish densities and biomasses were estimated along with flow and thermal

160 regimes across 25 Canadian temperate, unregulated and regulated rivers. Six fish

161 guild models, each based on morphologic, trophic, reproductive, habitat preferences,

162 behavioural traits, and phylogenetic associations were collated from literature to

163 compare the relationships of these guild models and between guilds of a given model

164 with explanatory variables describing river hydrologic and thermal regimes.

165 *River segments, sites, and surveying methodology*

166   A total of 25 river segments were selected based on surveying feasibility (i.e.

167 wadeable stretches of river across the entire wetted width) and road access, across

168 three rivers in the province of Alberta, five in Ontario, 14 in Québec and three in New

169 Brunswick, in Canada (Figure 1). River segments ranged from 5-27 km in length

170 (Mississagi and Kananaskis rivers, respectively; mean = 12.3 km, standard deviation

171 = 6.1 km). Of these, 14 rivers were unregulated while the remaining 11 were

172 regulated for hydro-electric purposes (Table 1). Regulated rivers differed according to

173 three flow management practices: run-of- river (ROR), storage with and without

174 hydro-peaking. ROR type rivers generally have a small reservoir, where water flows

175 freely though turbines and has little to no effect on downstream hydrologic regimes

176 (Bratrich et al. 2004). Conversely, storage with and without hydro-peaking practices

177 have large storage reservoirs that allow managers to release water upon demand (i.e.

178 for irrigation or for hydropower demands), temporally shifting the natural hydrologic

179 regime and attenuating seasonal high flows. Hydro-peaking type rivers additionally

180 provoke frequent and rapid flow peaks that are timed to match daily consumption

181 needs, causing significant flow alteration (Zimmerman et al. 2010) and subsequent

182 ecological impacts (Bond et al. 2015, Macnaughton et al. 2015b, Senay et al. 2016).

183 Despite the variability in hydrologic regimes stemming from regulation, all

184 unregulated and regulated rivers segments were analysed together to assess the overall

185 effect of river hydrologic and thermal regimes on fish guild models. To ensure that the

186 fish communities surveyed downstream from dams had been interacting over a long

187 period of time, rivers with older dams (40+ years) were selected.

188   For the 25 river segments studied, a total of 870 sites were surveyed, each

189 measuring approximately 300 m² (~5 by 60 m, width and length of a site), with a

190 distance of 60 to 100 m separating successive surveying sites. The position of the first

191   sampling site was randomly selected prior to field surveying and subsequent sites

192   were positioned following a systematic design (i.e. left shore, middle, right shore, left

193   shore). Fish community surveys were conducted during the summer months (late June

194   to early September) from 2011 to 2013.

195   Paired single-pass electrofishing and snorkelling surveys were carried out at

196   each site, in random order and at roughly the same time between 08:30 and 18:00 on

197   consecutive days, with a minimum 24-hr recovery interval to allow fish to re-establish

198   themselves after a surveying event. Electrofishing surveys were conducted by teams

199   of three, moving upstream in a zigzag fashion. LR-24 backpack electrofishing units

200   (Smith-Root, Vancouver, WA) were used in accordance with Ontario Ministry of

201   Natural Resources (OMNR) policy standards (Jones 2011). After each survey, fish

202   captured were identified, measured (total length, ±0.1 cm), and weighed (wet blotted

203   weight, ±0.1 g). Visual surveys were conducted using two trained divers, swimming

204   slowly upstream (approximate speed of 6s/m²). Species were identified and lengths

205   estimated by 5 cm-increment size classes throughout each visual survey. Specific

206   information pertaining to electrofishing and snorkelling surveying methods and

207   parameters have been detailed (Macnaughton et al. 2015a, Senay et al. 2016).

208   For both electrofishing and visual surveys, fish density estimates were

209   calculated for every species (fish $\geq$ 3mm in total length) sampled at each site. Site-

210   and species-specific biomass estimates were generated by summing either the masses

211   recorded during the electrofishing surveys or the mass estimates inferred from the

212   observed length-weight relationships applied to the visual survey data (Le Cren 1951).

213   The data for each species collected via the sampling method that yielded larger

214   density or biomass estimates at each site were retained. Fish densities and biomasses

215   per site therefore represented the greatest estimates for each species and likely

216   minimized any species-specific biases of the two sampling methods (Macnaughton et

217   al. 2015a).

218   *Fish guild variables*

219   Considering the large numbers of species present across the rivers (57 species)

220   and the variation of their traits, the guild analyses described below were conducted on

221   an exhaustive list of traits selected to represent the range of fish species occurring in

222   our rivers (Table S1, Supplementary Information). Quantitative ecological traits (e.g.

223   trophic position ranging from 1 to ~4) were standardized (i.e. centred and reduced)

224   prior to cluster analysis. K-means partitioning was then conducted on species'

225   ecological traits ascribed to each of the type of guilds and a range of simple structure

226   indices (SSI criterion; Oksanen et al. 2011) along with expert knowledge were used to

227   guide the number of ecologically relevant guilds. For example, 10 ecological traits

228   representing fish habitat preferences (e.g. preference for cold, cool, and warm water

229   temperatures or tolerance to/for anthropogenic disturbances and turbidity levels) were

230   coded for every species surveyed. K-means partitioning analysis conducted on these

231   traits by species (SSI criterion suggested six groups) along with expert knowledge on

232   the groups of species obtained, resulted in seven habitat guilds (Table S5,

233   Supplementary information). Phylogenetic distances between the fish species

234   surveyed (Hubert et al. 2008) was also established and served as our null hypothesis.

235   Site- and species-specific density and biomass estimates described above were

236   then used to derive mean river densities and biomasses for each of the guilds (e.g.

237   density and biomass for each of the seven habitat guilds). Total fish density and

238   biomass estimates per river were also calculated. Guild density and biomass estimates

239   per river, along with total river estimates (i.e. total fish densities and biomasses) were

240   subsequently transformed using the fourth root to achieve more normalized

241   distributions.

242   *Hydrologic indices*

243   Daily and hourly flow data were obtained from the Centre d'Expertise

244   Hydrique du Québec (CEHQ) and HYDAT from the Water Survey of Canada (2013)

245   national flow gauge networks, and hydro-electric companies: Trans-Alta, Brookfield

246   Renewable Power and NB Power. We analysed a 13-year time series (1997-2009) that

247   reflected the effects of temporal and climate variability on the hydrologic regime and

248   the multi-year index differences characterizing the 25 rivers (Kennard et al. 2010).

249   Flow indices representing ecologically relevant components of the hydrologic regime

250   (magnitude, frequency, duration, timing and rate of change of daily and hourly flows)

251   included, among others, the Indicators of Hydrologic Alteration (IHA; Richter 1997,

252   Olden and Poff 2003). All flow indices described by McLaughlin *et al.* (2014), in

253   addition to those created to capture hourly variations in the flow record (Zimmerman

254   et al. 2010, Macnaughton et al. 2015b), were calculated for each of the rivers

255   surveyed for a total of 211 flow indices. Flow indices expressed as discharge units

256   (volume per time) were normalized by dividing these indices by the median flow

257   (daily or hourly as appropriate) for the available flow records (McManamay et al.

258   2012). A preliminary removal of flow indices that did not exhibit any inter-river

259   variability or had skewed data due to winter ice conditions reduced the number of

260   indices to 77. These indices described the magnitude (42), frequency (6), duration

261   (15), timing (4) and rate of change (10) of river flows.

262   *Thermal indices*

263   Summer water temperatures were measured using temperature data loggers

264   (Hobo Pendant Temp, precision of ± 0.5°C, ONSET[®] Computer Corporation)

265   anchored along the 25 river segments. For 22 of the 25 river segments, temperature

266   data loggers were placed between the most upstream and downstream sites. For the

267   three remaining river segments, loggers were located 22 to 69 km away from sites

268   (Table 1). Loggers were deployed in riffle, run or shallow pool river habitats to limit

269   any potential water temperature anomalies that may arise from placing loggers in deep

270   pools, shallow shore habitats and/or tributaries. Loggers were set to record ambient

271   water temperatures every 15 minutes, from early June to late-September in 2013, save

272   for the Elbow, Bécancour and Waterton rivers, for which loggers were placed in rivers

273   over similar time periods in 2006, 2012 and 2014, respectively. Due to atypical

274   flooding events in Alberta in 2013 (Phillips 2013), many loggers were lost, limiting

275   the use of temperature data in those rivers. Between 3 and 15 temperature loggers

276   were retrieved and used to calculate summer thermal profiles for each of the rivers

277   studied. Water temperature data extracted from loggers were checked for erroneous

278   measurements (i.e. air exposure), which were removed from thermal profiles. Loggers

279   with < 5days of data removed were kept and data from these loggers were averaged

280   per day and hour, for each of the loggers, to derive a total of 294 thermal indices

281   describing all components of thermal regime (magnitude, variance, frequency,

282   duration, timing and rate of change of daily and hourly temperatures (Olden and

283   Naiman 2010). Median values per thermal index were calculated for each river from

284   all retained loggers to further decrease the incidence of local thermal anomalies.

285   Of the 294 thermal indices calculated, 21 indices were selected to reliably

286   represent the river average thermal regime from a single summer, the biological

287   relevance, and the type of thermal alteration expected for regulated rivers. For

288   example, thermal indices were based on the warmest week rather than on the warmest

289   day because the former is more consistent between years than the warmest day. These

290   21 indices described the magnitude (7), variance (6), frequency (1), duration (2),

291   timing (1) and rate of change (4) of water temperatures for the month of July or for a

292   standardized 9-week summer period, which was centred on the warmest week for

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

294   *Statistical analyses*

295   To reduce the number of explanatory variables chosen to represent hydrologic

296   and thermal regimes across the rivers surveyed, we ran several principal component

297   analyses (PCA), ensuring that the number of observations (i.e. 25 rivers) was greater

298   than the number of explanatory variables selected. Specifically, the 77 hydrologic

299   indices characterizing the hydrologic regime for the 25 rivers were summarized by

300   conducting five separate PCAs on the correlation matrices for each of the hydrologic

301   regime components (magnitude, frequency, duration, timing, and rate of change).

302   River scores for PC axes describing a greater fraction of the variation than the broken-

303   stick null model were retained (Legendre and Legendre 2012). Performing separate

304   PCAs for each of the hydrologic regime components ensured that indices describing

305   major sources of variation within each component contributed to the retained PC axes,

306   and that subjectivity associated with the process of selecting individual indices was

307   reduced. Flow indices that contributed the most to the retained PC axes (i.e. top

308   loaders) were identified to explain dominant patterns of flow variation measured in

309   our rivers as described by each of the flow components.

310   Likewise, the 21 thermal indices characterizing each river's thermal regime

311   were subjected to PCAs to identify the main axes of variation within each thermal

312   regime component across all rivers. Due to small number of thermal indices

313   describing the frequency (1), duration (2) and timing (1) of water temperatures, these

314   thermal regime components were grouped with other correlated components and three

315 PCAs on thermal indices were conducted instead of a possible six: 1- magnitude,

316 frequency, and duration (n=10); 2- variance (n=6); and 3- timing and rate of change

317 (n=5). PC axes retained were selected as done for hydrologic indices. Top thermal

318 loaders were identified for each retained thermal PC axis. Correlations between

319 hydrologic and thermal PC axes were computed to assess whether the explanatory

320 variables summarizing hydrologic and thermal regimes were highly correlated with

321 one another ($r > 0.8$).

322 Redundancy analyses (RDA) with 9999 permutations (Legendre and

323 Legendre, 2012) were used to assess the relationships between river biomass and

324 density estimates for each of the types of guilds based on morphologic, trophic,

325 reproductive, habitat, behavioural traits, and phylogenetic associations (6 response

326 matrices), and hydrologic and thermal PC axes (12 explanatory variables). Additional

327 relationships using the total river density and biomass estimates as response variables

328 (2 vectors) were also conducted to compare with multivariate fish guild models. A

329 permutational forward selection of explanatory variables was subsequently conducted

330 for significant relationships to identify the best variables for the model describing

331 each response matrix and vector (Blanchet et al. 2008, Dray et al. 2011). The

332 proportion of variation explained by selected explanatory variables for each of the

333 response matrices was determined using a cumulative adjusted R^2 (CumR$^2_{Adj}$).

334 Individual canonical axes were also tested for significance to determine whether axes

335 represented variations that were more explained than random (Legendre and Legendre

336 2012). For the leading fish guild model (greatest R^2_{Adj}), the response matrix and

337 explanatory variables were plotted in reduced space (correlation biplot), where the

338 focus is on the relationships among habitat guilds, explanatory variables (flow and

339 thermal PCs), and each other. A distance biplot was also illustrated to show the

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340   relationships between explanatory variables and the position of our rivers, as well

341   between unregulated and regulated rivers in reduced space. To facilitate

342   interpretation, RDA 1 and RDA 2 axes were rotated to project the first selected

343   environmental variable on RDA 1. This was done by calculating the angle between

344   RDA 1 and this selected variable and rotating all other points in the figure along this

345   angle.

346   Each model's ability to predict new responses from selected explanatory

347   variables was quantified using the cross-validation R^2 (R^2_{CV}) via a leave-one-out

348   cross-validation approach (Guénard et al. 2013). R^2_{CV} is bound between $-\infty$ and 1,

349   where $R^2_{CV} = 1$ when predictions perfectly match the observations and $R^2_{CV} \leq 0$ when

350   predictions are inaccurate or no better than what would be expected from chance

351   alone. All statistical analyses were performed in R (R Core Team 2014).

352

353   **Results**

354   *Description of fish guilds*

355   The eight morphologic guilds differed from one another with respect to traits

356   describing general body shape (discoid, cylindrical or eel-like), the mouth position

357   (subterminal vs. terminal), and fin types, sizes, and placements (soft or spiny dorsal

358   rays, large pectoral fins and abdominal pelvic fins, respectively; Table S2). The six

359   trophic guilds revealed the shared species diet preferences and associated trophic

360   level, with a particular distinction between guilds that eat small prey and generally

361   shift their diet ontogenetically, have moderate trophic levels, and prey on larger

362   fishes, amphibians and mammals (Table S3). The eight reproductive guilds generally

363   grouped traits that depicted reproductive behaviours (nest building and/or guarding),

364   spawning time (fall or summer), fecundity level and age of maturity, and spawning

365 habitat preferences (marine, riffles or shallow waters; Table S4). The seven habitat

366 guilds differed from one another with respect to preferences for warm, cool or cold

367 water temperatures, slow-moving or riffle water velocities and tolerance levels to

368 water turbidity and/or anthropogenic perturbations (Table S5). The six behavioural

369 guilds depicted fishes that shared similar feeding (grazing, pursuit or sorting),

370 migratory (anadromous), and other (territorial or schooling) behaviours (Table S6).

371 Lastly, the phylogenetic groups were based on the phylogenetic distances between

372 freshwater species in Canada (Hubert et al. 2008) and cut at seven groups to facilitate

373 the comparison of relationships between different types of traits describing guilds

374 (Table S7).

375 *Characterization of hydrologic and thermal regimes*

376   The PCAs conducted separately for each of the flow and thermal components

377 resulted in a total of 12 PC axes (9 and 3 PC axes describing flow and thermal

378 components, respectively) that represented between 61-85% of the variation in the

379 groups of indices (Table 3). The magnitude of summer water temperatures (PC1

380 Magnitude of temperatures) combined thermal indices that described the cumulative

381 degree days at mid-summer (DD_midsum), the summer average in daily mean water

382 temperatures (MSmn), and the July average in daily mean water temperatures

383 (MOmn7). The intra-annual flow variability (PC1 Magnitude of flows) depicted the

384 difference in extreme flows within a year: the variability in daily flows (MA3), the

385 ratio between maximum annual flow and median flow (MH14), and the ratio between

386 the mean of the upper quartile and median flow (MH27). Only 2 pairs of PC axes had

387 correlation coefficients at the $r \geq 0.8$ level, suggesting that explanatory variables were

388 not redundant. Exceptions were found for correlations between variables describing

389 the intra-annual flow variability (PC1 Magnitude of flows) with the proportion of rise

390   days (PC2 Rate of change of flows; r = 0.80), and the flashiness of summer water

391   temperatures (PC1 Rate of change of temperatures) with the fall rate of flows (PC1

392   Rate of change of flows; r = 0.84).

393   *Comparison of fish guild models*

394   The PC axes describing the flow and thermal components significantly

395   explained fish density and biomass estimates for all guild models (a total of 12 models

396   representing densities and biomasses of guilds and phylogenetic associations). Since

397   the results for fish guild models using biomass estimates were comparable to and

398   slightly better than those using density estimates, our results focused on the former

399   fish guild models. Figure 2 showed that the best explanatory guild models (greatest

400   R^2_{Adj}) were found for habitat and trophic types of guilds (R^2_{Adj} = 0.44 and 0.41; p-

401   values = 0.001 and 0.002, respectively). Our results further showed that all guild

402   models outperformed the null hypothesis (phylogenetic groups R^2_{Adj} = 0.26); this

403   suggests the presence of functional relationships not attributable simply to phylogeny.

404   In addition, selected environmental variables did not significantly explain total river

405   density and biomass fish estimates (p-values = 0.22 and 0.69, respectively).

406   Furthermore, fitting non-linear relationships (canonical correlation analysis (CCA) or

407   multivariate regression trees (MRT)) were not as powerful or predictive, suggesting

408   that RDAs were an appropriate tool to investigate the various guild relationships with

409   selected environmental variables.

410   The explanatory variables most often selected by fish guild models (>86% of

411   models) were the magnitude of summer water temperatures (solid black bars, Figure

412   2) followed by the intra-annual flow variability or the difference in the extreme flows

413   within a year (thinly-spaced dashed lines, Figure 2). Highly correlated flow and

414   thermal variables describing the proportion of rise days (PC2 Rate of change of

415   flows), fall rates of flows (PC1 Rate of change of flows) and flashiness of summer

416   water temperatures (PC1 Rate of change of temperatures) were not selected in any of

417   the fish guild models. When habitat and trophic guild models were computed without

418   the thermal components, the flow components significantly explained biomass

419   estimates. However, these model strengths based on R^2_{Adj} were 13 and 20% lower

420   without thermal components, respectively. The same was true when flow PCs were

421   removed from the analyses (9 and 10% lower, respectively).

422   Variables selected by forward selection significantly predicted the different

423   types of guild models (R^2_{CV} values; black points, Figure 2). The best predictive model

424   (largest R^2_{CV}) was found for phylogenetic associations ($R^2_{CV} = 0.73$), but these results

425   were likely driven by the uneven distribution of rare species within a guild (e.g. a

426   single group composed of *Fundulus diaphanus* or a few species belonging to the

427   petromyzontids and gasterosteids groups, respectively). When phylogenetic predictive

428   models were conducted for groups with > 50% presences across rivers, the model's

429   predictive power decreased to $R^2_{CV} = 0.09$. Lastly, explanatory and predictive power

430   results were fairly comparable, suggesting that the models were not overfitted and

431   good at explaining and predicting the effects that selected flow and thermal variables

432   had on different fish guilds.

433   *Habitat guild-environmental relationships*

434   The habitat guild model served as an example to illustrate the relationships

435   between the biomasses of habitat guilds and flow and thermal PC axes (Figure 3;

436   correlation biplot). The magnitude of summer water temperatures, the intra-annual

437   flow variability, and the long-term flow variability explained approximately 39% of

438   the variation of habitat guilds constrained on the first two redundancy axes.

439   Specifically, the biomass of species that preferred habitats with warm to cool water

440   temperatures and macrophyte cover (habitat guild 1) was related with higher

441   magnitude of summer temperatures, whereas the biomass of species that preferred

442   cold water temperatures (habitat guild 3) was negatively related with this same

443   variable. Greater flow variability was also shown to drive guilds of fishes preferring

444   riffle type habitats (habitat guilds 3 and 4), while lower flow variability was related

445   with guilds of fishes preferring warm and turbid habitats with cover and are more

446   tolerant to perturbation (habitat guilds 1 and 5). This suggests that fishes that prefer

447   warm, turbid waters and more tolerant to perturbations are likely to thrive in rivers

448   where flows are more constant and generally warmer during summer months (i.e.

449   regulated rivers). With the exception of two rivers (Kananaskis and Elbow Rivers;

450   triangle and circle icons to the far left of the inset figure), all rivers exhibited

451   moderate to high magnitude of summer temperatures. Despite these findings, no

452   discernible general pattern was observed between regulated and unregulated rivers

453   within the same constrained space (Figure 3; inset).

454

455   **Discussion**

456   *Characterization of river regimes*

457   By quantifying river hydrologic and thermal regimes separately, we were able

458   to show which independent drivers significantly explained and predicted the density

459   and biomass across fish guild types. Specifically, our results are among the first to

460   point to the importance of indices describing the magnitude of summer water

461   temperatures and those depicting the intra-annual variability in flows for driving guild

462   composition. Given that habitat guild model strength was decreased when either

463   selected flow or thermal variables were omitted from the analyses and that selected

464   flow and thermal variables were not highly correlated with one another, we showed

465   the importance of integrating thermal regimes in hydro-ecological studies. These

466   findings align with previous assertions that the interplay of variables describing river

467   hydrologic and thermal regimes is crucial in shaping fish community structure (Reyjol

468   et al. 2001, Murchie et al. 2008, Olden and Naiman 2010).

469   Furthermore, using flow index analyses (McManamay et al. 2012,

470   Macnaughton et al. 2015b) as a conceptual template allowed us to depict river thermal

471   regimes as a suite of thermal indices and reduce the number of redundant indices

472   among them. The magnitude of summer water temperatures was consistently selected

473   first across guild models, giving importance to thermal indices, notably, those that

474   describe the cumulative degree days at mid-summer, the average daily mean in water

475   temperatures, and the July average in daily mean water temperatures. We further

476   identified dominant patterns of water temperature variability (i.e. daily range and

477   flashiness of summer water temperatures) that may have had an effect on fish

478   community organization. Due to the similarity in ecological traits describing types of

479   groupings, such as traits depicting spawning habitat preferences (habitat guilds) and

480   type of spawning substrate, water velocities and depths (reproductive guilds), similar

481   relationships with explanatory variables may have occurred between type of fish

482   guilds. This would suggest that thermal regimes are crucial when developing fish

483   guild models because thermal regime-trait relationships exist between them.

484   *Fish guild models*

485   All fish guild models were significantly explained and predicted by

486   explanatory variables representing river hydrologic and thermal regimes across rivers,

487   whereas total fish density and biomass were not. They also performed better relative

488   to studying phylogenetic associations, suggesting that models based on trait-

489   environmental relationships were better than those based on phylogeny, further

490 supporting the original "basic building blocks" guild concept (Simberloff and Dayan

491 1991). This is to be expected seeing as the distribution of species differed in the rivers

492 surveyed across Canada, while the ecological roles and functional attributes shared by

493 species may not have across this same geographical extent. Furthermore, there is

494 evidence from across the plant and animal kingdoms that ecological traits or

495 functional groupings are better at explaining variation compared to phylogenetic

496 associations, as they are more responsive to proximate environmental factors

497 (Frimpong and Angermeier 2010). Our results were thus in line with much of the

498 guild literature.

499 We had expected that guilds grouping species according to preferences for

500 habitat conditions may be linked to flow and/or thermal variables, as was the case for

501 Lamouroux and Cattanéo (2006), Arthington *et al.* (2014), and Rolls and Arthington

502 (2014). Indeed, habitat guilds did yield the best explanatory model. However, all

503 explanatory fish guild models yielded significant results, pointing to the existence of

504 functional relationships between the flow and thermal variables identified and the

505 range of species traits encompassed between the different types of guilds. Predictive

506 model results further supported these findings, indicating that fish guild models were

507 accurately predicted by selected flow and thermal variables across rivers. Though

508 phylogenetic and reproductive fish guild models yielded the largest R^2_{CV}, we have

509 reason to believe that the models' predictive power may have been substantially

510 influenced by species prevalence (i.e. the proportion of rivers where a species was

511 surveyed), resulting in poorly performing models that, otherwise, would be viewed as

512 powerful (Olden et al. 2002).

513 *Applications of habitat guild-environmental relationships*

514   Our model results pointed to general guild relationships with selected

515 explanatory variables, allowing us to explore the functional relationships that may

516 cause specific fish assemblages to be more vulnerable to variations in hydrologic and

517 thermal regimes, especially those arising from river regulation. For example, the

518 habitat guild that preferred cold water, riffle-type habitats and was intolerant to

519 environmental perturbations was related with high annual flow variability and low

520 magnitudes of summer temperatures. As such, species representing this guild, which

521 included sculpins (*Cottus cognatus, Cottus ricei*) and salmonids (*Oncorhynchus*

522 *clarkii, Oncorhynchus mykiss, Salmo salar, Salmo trutta, Salvelinus confluentus,*

523 *Salvelinus fontinalis*), may be more vulnerable to anthropogenic perturbations, as well

524 as significant decreases in variables describing annual flow variability. Assessments

525 of perturbation tolerance are subjective because for a given species across its

526 geographic range, tolerance may change with respect to the environmental stresses to

527 which the species exhibit tolerance (Frimpong and Angermeier 2010). As river

528 regulation in our systems tends to decrease river flow variability (McLaughlin et al.

529 2014) and contribute to general patterns of thermal alteration, such as reducing water

530 temperature variability and increasing the magnitude in the late summer temperatures

531 (Maheu et al. in press), conservation efforts may begin with the more vulnerable

532 habitat guilds, because intolerance for perturbations may be linked with habitat

533 preferences characteristic of unregulated systems.

534   The importance of summer water temperature regimes for understanding the

535 organization of different types of guilds has been elucidated here, but year-round

536 thermal regimes may be important for fish assemblages that rely on different thermal

537 cues for initiating various activities (e.g. spawning and recruitment of fishes, timing

538 and availability of resources, cold water thermal tolerances; Rolls et al. 2013). Our

539   results also revealed some degree of regional discrimination as glacier-fed rivers

540   located in Alberta (Kananaskis and Elbow rivers) were strongly associated with low

541   summer temperature variability; this result seems to be an artefact resulting from the

542   absence of great temperature variability during the summer months for these rivers,

543   especially when compared to rivers located in southern Quebec. Moreover, a

544   preliminary investigation of thermal profiles across our regulated rivers suggested that

545   the variability in water temperatures was either reduced or increased, depending on

546   the flow management practices adopted: storage or hydro-peaking regulation

547   practices, respectively. In fact, we found that certain regulated rivers were associated

548   with high flow variability, suggesting that differences in river regulation practices

549   may have played a role in driving fish guild composition. Though the habitat guilds

550   that preferred warm water temperatures were associated with regulated rivers, future

551   research considerations should include geographical location of the river and/or

552   headwaters and regulation practices.

553   *Implications for river management*

554   Another important contribution of this study centred on the identification of

555   ecologically relevant thermal indices and the value of both hydrologic and thermal

556   regimes in driving the river fish guild responses. From an applied standpoint, these

557   findings identified the different guild trait-environment relationships across rivers and

558   highlighted the importance of comprehensive hydrologic and thermal regime

559   conservation on which management efforts focused on maintaining the ecological

560   integrity of rivers should rely on. Furthermore, the observed trait-environment

561   relationships may aid in mitigating the effects of modifying hydrologic regimes with

562   selective water release from dam outflows, benefitting to specific guilds via either

563   hypolimnetic (cold) or epilimnetic (warm) water release from reservoirs (Olden and

564 Naiman 2010). Now that we have shown the importance of thermal regimes,

565 quantified separately from hydrologic regimes, we may begin to attempt adaptive

566 flow and thermal management strategies to better conserve ecosystem resources.

567

24

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2
3   **References**
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771

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

River	Province	Regulation type	Watershed area (km²)	Length of river segments surveyed (km)	Distance of river segment to dam (km)	Distance of river segment to flow gauge (km)	Distance of river segment to thermal logger (km)
Elbow	Alberta	unregulated	791	22.3	NA	0.0	33.0
Kananaskis	Alberta	hydro-peaking	362	27.4	3.0	1.0	0.7
Waterton	Alberta	storage	1631	23.7	0.7	2.4	22.0
Dee	New Brunswick	storage	141	13.7	0.2	0.2	0.01
Gulquac	New Brunswick	unregulated	110	8.8	NA	62.0	8.9
Serpentine	New Brunswick	storage	47	18.2	0.2	0.2	0.0
Aubinadong	Ontario	unregulated	1440	9.8	NA	1.0	0.05
Batchawana	Ontario	unregulated	1190	7.8	NA	0.0	0.0
Goulais	Ontario	unregulated	1637	7.2	NA	15.0	0.0
Magpie	Ontario	hydro-peaking	1930	10.0	8.0	8.0	4.09
Mississagi	Ontario	hydro-peaking	4040	4.9	8.0	8.0	5.46
Au Saumon	Québec	unregulated	738	8.2	NA	0.0	0.0
Bécancour	Québec	unregulated	917	12.7	NA	0.0	69.0
Coaticook	Québec	ROR	362	7.8	1.0	11.0	0.0
Du Loup	Québec	unregulated	515	7.0	NA	3.0	4.46
Du Sud	Québec	ROR	821	15.4	1.0	0.2	0.0
Eaton	Québec	unregulated	646	10.2	NA	1.5	0.0
Etchemin	Québec	ROR	1160	6.8	3.0	1.7	0.0
Kiamika	Québec	storage	702	14.8	0.3	3.3	0.04

Nicolet	Québec	unregulated	1550	18.8	NA	0.0	0.0
Noire	Québec	unregulated	401	12.9	NA	24.0	0.0
Ouelle	Québec	unregulated	796	7.4	NA	3.5	2.83
Petit Saguenay	Québec	unregulated	712	6.0	NA	10.0	0.0
Picanoc	Québec	unregulated	1290	9.2	NA	3.1	0.6
St Francois	Québec	storage	2940	7.9	6.0	9.0	3.54

30

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

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

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

775 **Table 3.** Results of PCAs computed independently on groups of flow and thermal indices; the number of indices per group is shown in brackets.
776 Central columns: the top loaders for the first (1, 2 or 3) axes in each analysis are listed. Right: proportion of variation of the stated group of
777 indices accounted for by 1, 2 or 3 PCA axes.
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Flow and thermal components (# indices)	Principal component axes			Cumulative variation explained (%)
	PC1 Description (Top loaders)	**PC2** Description (Top loaders)	**PC3** Description (Top loaders)	
Magnitude of flows (42)	Intra-annual flow variability (MA3, MH14, MH27)	Intra vs. inter- year variability in monthly flows (MA31, MA33, MA40)	Long-term flow variability (MH17, MA7, MA8, MH9)	72
Frequency of flows (6)	Flood frequency (FH8, FH1, FH5)	-	-	68
Duration of flows (15)	Magnitude of spring flood (DH13, DH12)	Low exceedence flows (DL14)	-	78
Timing of flows (4)	Predictability of daily flows (TA2, TH2)	-	-	61
Rate of change of flows (10)	Fall rate of flows (RA7, nRA3)	Proportion of rise days (RA5)	-	83
Magnitude of temperatures (10)	Magnitude of summer water temperatures (DD_midsum, MSmn, MOmn7)	-	-	85
Variance of temperatures (6)	Daily range in temperatures over summer (RNGmax7, RNGSmn, RNGmn7, RNGSmax)	-	-	81
Rate of change of temperatures (5)	Flashiness of summer water temperatures (RANeg, RARev)	-	-	65

779 **Figure captions**

780 **Figure 1.** Map of the study area showing the 25 rivers surveyed in Canada (principal

781 map). Enlarged views depict rivers located in A) Alberta (AB), B) Ontario (ON), C)

782 Québec (QC), and D) New Brunswick (NB). Open circles and triangles refer to

783 unregulated and regulated rivers, respectively.

784

785 **Figure 2.** Stacked bar plot of the proportion of variation explained by each fish guild

786 explanatory (RDA) and predictive (cross-validation, CV) model, and selected flow

787 and thermal variables. Left: total river density and biomass models as a function of all

788 flow and thermal PC axes are also listed. NS refers to non-significant results.

789

790 **Figure 3.** The relative importance (correlation biplot) of the biomass estimates for

791 habitat guilds as a function of selected flow and thermal variables (red arrows). Figure

792 RDA 1 and RDA 2 axes were rotated to display the "magnitude of summer

793 temperature" along the RDA 1 axis. RDA 2 represents the flow variability. Inset

794 represents the relative importance (distance biplot) of rivers with respect to each other

795 and selected flow and thermal variables. Open circles and triangles refer to

796 unregulated and regulated rivers, respectively.

797   **Figure 1.**


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799 **Figure 2.**

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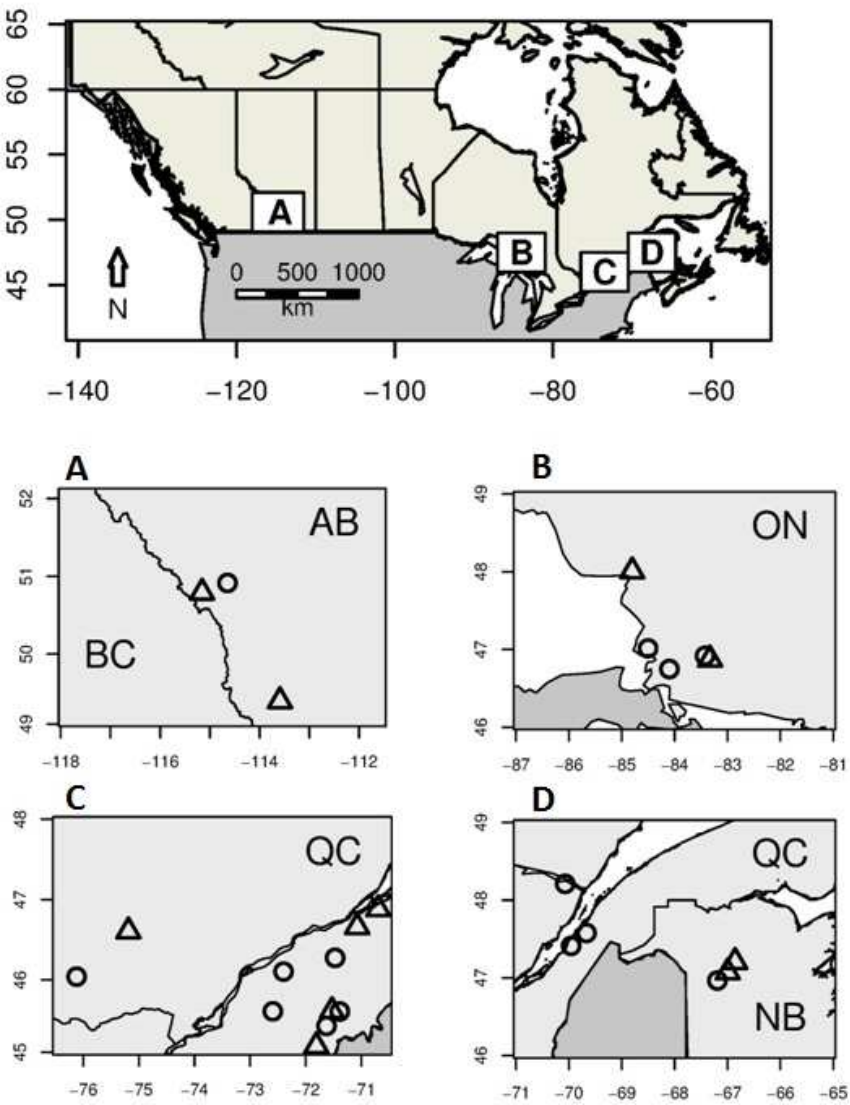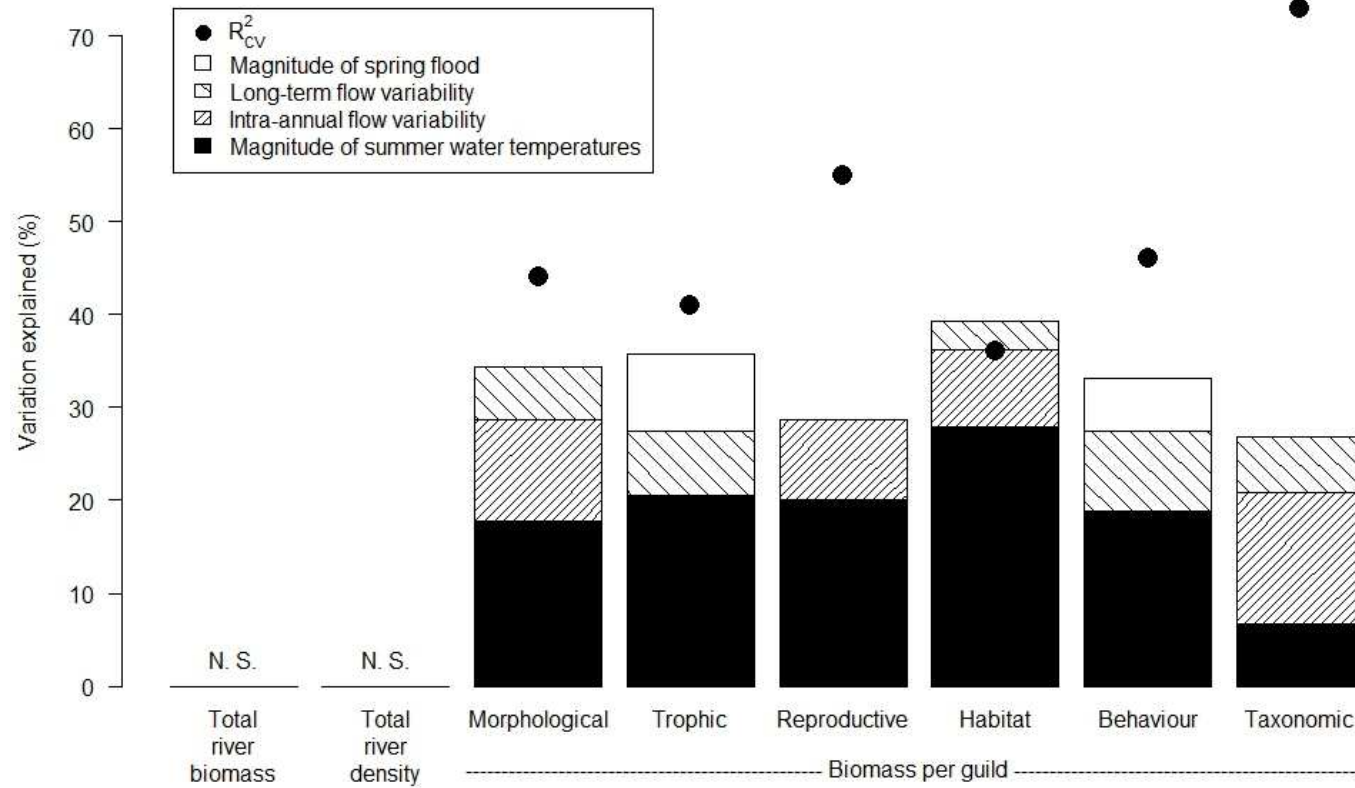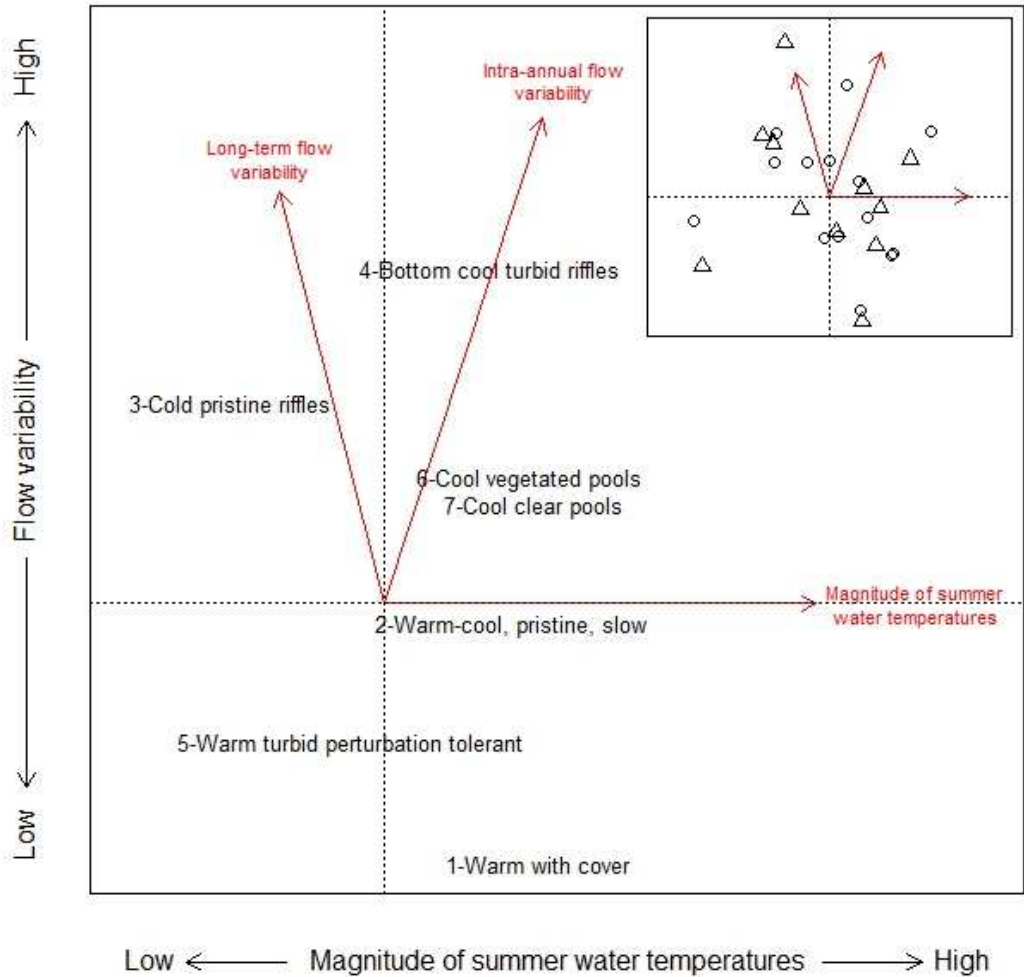
Table S1. Description of common traits ascribed to each of the guilds and taxonomic associations, categories/ units and sources. Number of guilds or groups indicated in brackets.

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

	Schooling	presence, absence [5, 19]
Behavioural (6)	Territorial	presence, absence [5, 19]
	Migratory behaviour	anadromous, catadromus, potadromous (migratory), potadromous (non-migratory) [5, 18, 19]
	Feeding behavior	filterer, grazer, puirsuit, ambush, sorter, non-feeding [6]
Taxonomic groups (7)	Phylogenetic tree of Canadian freshwater fishes cut at 7 groups	N/A [11]

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

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

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

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

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

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

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

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

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

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

Table S7. Species representing each taxomic association.

Families		Genus	Species
1-	Petromoysontids	*Ichthyomyzon*	*fossor*
		Lethenteron	*appendix*
		Petromyzon	*marinus*
2-	Umbrid	*Umbra*	*limi*
3-	Osmerid	*Osmerus*	*mordax*
	Esocids	*Esox*	*lucius, masquinongy, niger*
	Anguillid	*Anguilla*	*rostrata*
	Ictalurids	*Ameiurus*	*nebulosus*
		Notorus	*flavus*
4-	Cyprinids	*Chrosomus*	*eos*
		Cyprinella	*spiloptera*
		Cyprinus	*carpio*
		Exoglossum	*maxillingua*
		Hybognathus	*argyritis, hankinsoni, regius*
		Luxilus	*cornutus*
		Margariscus	*margarita*
		Nocomis	*biguttatus*
		Notemigonus	*crysoleucas*
		Notropis	*atherinoides, bifrenatus, heterolepis, hudsonius, rubellus, stramineus, volucellus*
		Phoxinus	*neogaeus*
		Pimephales	*notatus, promelas*
		Semotilus	*atromaculatus, corporalis*
	Catostomids	*Catostomus*	*catostomus, commersonii, platyrhynchus*
		Moxostoma	*anisurum, macrolepidotum*
	Lottid	*Lota*	*lota*
5-	Fundulid	*Fundulus*	*diaphanus*
6-	Gasterosteids	*Culaea*	*inconstans*
		Gasterosteus	*aculeatus, wheatlandi*
	Salmonids	*Oncorhynchus*	*clarkii, mykiss*
		Prosopium	*williamsoni*
		Salmo	*salar, trutta*
		Salvelinus	*confluentus, fontinalis*
7-	Percids	*Ammocrypta*	*pellucida*
		Etheostoma	*exile, flabellare, nigrum, olmstedi*
		Perca	*flavescens*
		Percina	*caprodes, copelandi*
		Sander	*vitreus*
	Centrachids	*Ambloplites*	*rupestris*
		Lepomis	*gibbusos*
		Micropterus	*dolomieu, salmoides*
	Cottid	*Cottus*	*bairdii, cognatus, ricei*
	Percopsid	*Percopsis*	*omiscomaycus*