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THE EFFECTS OF REGIONAL HYDROLOGIC ALTERATION ON FISH COMMUNITY STRUCTURE IN REGULATED RIVERS

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ABSTRACT

Alterations to temporal patterns of river flow regimes resulting from damming and flow regulation practices may have negative consequences for freshwater communities. However, little has been performed to develop a holistic approach to assess the effects of hydrologic alterations on fish communities across a wide range of rivers and between different regulation strategies. To address this, we used daily and hourly hydrologic data from gauges in 10 regulated and 14 unregulated Canadian rivers. Building on the Ecological Limits of Hydrologic Alteration concept, hydrologic alterations for many ecologically relevant flow indices were combined to obtain river-specific hydrologic alteration scores. Extensive community surveys to estimate fish abundance, biomass, diversity indices and habitat guild representation provided data for the derivation of similar river-specific biotic alteration scores relative to unregulated river conditions. Our results indicate that biological impairment consisting of significant biotic alteration relative to the means from unregulated rivers was directly related to increasing flow alteration scores, with the smallest fish and flow alteration scores observed in run-of-river systems and the greatest alteration scores under hydro-peaking regimes. Our approach not only examined the relationship between river-specific hydrologic alteration scores and the associated biotic responses, but also provided a more comprehensive assessment of the flow-response alteration relationship between regulation practices, which may better inform future environmental flow management guidelines. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS: biotic alteration scores; flow alteration scores; hydrologic indices; natural flow regime; ELOHA framework

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INTRODUCTION

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

The existing literature suggests that dams and associated regulation practices, from run-of-river (ROR) to storage with or without peaking (hydro-peaking or storage) will elicit multiple changes to fish populations (Anderson *et al.*, 2006; Renöfält *et al.*, 2010) via alterations to water quality and hydrologic regimes (Freeman *et al.*, 2001; Dudgeon *et al.*, 2005). ROR-type systems appear to have the least impacts on stream ecology because patterns of water release are designed to optimize power production and inflow, often resulting in flows mimicking natural regimes (Bratrich *et al.*, 2004; Habit *et al.*, 2007). Conversely, hydro-peaking events, typified by the rapid and large release of water from a dam timed to match daily hydropower consumption needs (Cushman, 1985), have been shown to directly impact fish populations through strandings along the changing channel margins (Bradford, 1997; Halleraker *et al.*, 2003), downstream displacements (Scruton *et al.*, 2008), reduced spawning and rearing success because of dewatering of redds (nests), and obstructed migration (Young *et al.*, 2011). Flow alterations may also exert indirect effects through the loss or reduction of suitable habitats (Vehanen, 2000). At the population level, alterations to the flow regime in regulated rivers have been shown to disrupt environmental cues that

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influence the maturation and spawning of riverine fishes, resulting in lower recruitment, and decreases in adult abundance and species richness (Humphries and Lake, 2000; Humphries *et al.*, 2008).

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

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

Our approach is intended to quantify the relationship between fish community, population and flow alteration scores across a range of regulated flow regimes. The extent of regulation practices under consideration, from ROR to hydro-peaking, may also lend support to establishing a more comprehensive assessment of river-specific flow alteration scores and the associated effects on biotic alteration scores. We predict that degrees of fish community alteration will be positively related to the degree of hydrologic alteration, with the greatest alterations occurring under hydro-peaking regulation systems.

MATERIALS AND METHODS

Rivers and sampling protocol

Fish community surveys were conducted during the summer months (late June to August), from 2011 to 2013, in 10 regulated and 14 unregulated Canadian rivers (Appendix 1). Study rivers included five rivers in Ontario, 16 in Québec and 3 in New Brunswick (Figure 1). In each river, 25–50 300 m^2 sites were surveyed, for a total number of sites combining all rivers of $N = 829$. Paired single-pass electrofishing and snorkelling surveys were carried out in random order, at roughly the same time between 08:30 and 18:00 on consecutive days, with a minimum 24 h recovery interval to allow fish to re-establish themselves after a sampling event. Electrofishing surveys were conducted by teams of three using an LR-24 backpack electrofishing unit (Smith-Root®, Vancouver, WA). Captured fish were identified to species, weighed (wet blotted weight, ±0.1 g), measured (total length, ±0.1 cm), and released. Visual surveys were conducted by two observers snorkelling upstream and surveying the sites at a rate of ~6 s/m^2. Species were identified, recorded, and total lengths were estimated in 5 cm increments. Mass-length relationships derived from the electrofishing data were calculated for each species per river and used to estimate the masses of fish recorded during the visual surveys (Le Cren, 1951). Selection of sampling sites and specific details pertaining to surveying methodology is described in Macnaughton *et al.* (2014).

Regulation types

ROR, storage without and with hydro-peaking was treated as three points along a continuous range of flow regulation regimes. We defined these types based on the resultant hydrologic alteration, dam-type, and specific operational characteristics (Appendix 1). In ROR-type systems, a small upstream reservoir volume relative to mean flows may occur, but does not store more water than required for power production for a single day, resulting in downstream flows similar to a natural regime. Conversely, storage-type systems were defined as having larger storage volumes that allow for temporal shifts of the natural seasonal runoff volumes, resulting in significant seasonal high flow attenuation and enhancement of low flows, especially over the winter months. Hydro-peaking type systems were defined

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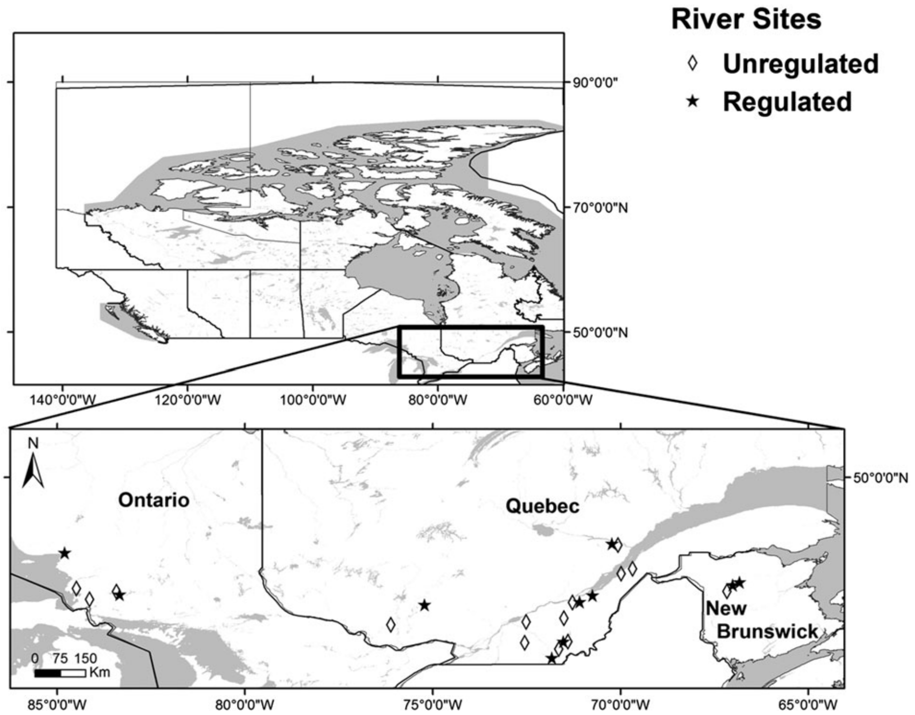

Figure 1. Map of Southeastern Canada featuring the 24 study systems comprising 10 regulated (★) and 14 unregulated (◊) rivers

as exhibiting frequent periods of significant hourly or diel hydrologic fluctuations over a year caused by rapid opening and closing of reservoir release structures (Cushman, 1985; Flodmark *et al.*, 2004). Precise, quantitative thresholds distinguishing these regulation types are not internationally accepted, so we assigned 'types' to our rivers based on preliminary analyses of the regulated hydrographs (after McLaughlin *et al.*, 2014).

Hydrologic Indices

Daily and hourly flow data were obtained from the Centre de l'Expertise Hydrique du Québec (CEHQ) (http://www.cehq.gouv.qc.ca) and the Water Survey of Canada (Canadian Hydrometric Database or HYDAT) (http://ec.gc.ca/rhc-wsc) national flow gauge networks, and industry partners. We analysed a 12-year time series (1997–2009) to control for the effects of temporal and climate variability on subsequent analyses and to detect differences in indices summarized across flow records (Kennard *et al.*, 2010). Flow indices representing ecologically relevant components of the hydrographs for our rivers included among others, the Indicators of Hydrologic Alteration (IHA; Richter, 1997). All flow indices described by Olden and Poff (2003), in addition to those created to capture hourly variations in the flow record, were calculated for each of the rivers surveyed for a total of 211 flow indices. Prior to analysis, flow indices were evaluated for indetermination (e.g. index calculating the number of days above 7× median flows when a river never reached this threshold), computational and mathematical errors (e.g. coefficient of variation for circular data). In general, all flow indices were assessed for aberrant values (outliers) across all rivers, and those that exhibited any type of problem, computationally or other, were deemed lower quality and not included in further analyses. A preliminary removal of low quality flow indices (i.e. indices that did not exhibit any inter-river variability or had skewed data because of winter ice conditions) reduced the number of indices to 105, with 101 derived from daily flows (D) and the remaining 4 from hourly flows (H). The inclusion of hourly flow indices captures the extent of hydrologic alteration resulting from hydro-peaking practices, which often alter flows on an hourly basis to meet energy demands. All flow metrics expressed as discharge units (volume per time) were normalized by dividing these indices by the median flow (daily or hourly, as appropriate) for the available flow records (McManamay *et al.*, 2012c).

Hydrologic class analysis was initially carried out on data from 96 unregulated rivers across Canada representing five regional flow classes, comprised of three western and two eastern regions. The 14 unregulated rivers selected for the present study belonged to these east flow classes. When grouping all of the East1 ($N = 27$) and East2 ($N = 18$) unregulated rivers described in McLaughlin *et al.* (2014), the pooled flow distributions (principal component scores) were not bimodal and were therefore combined into one regional

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reference flow class. In our opinion, the unregulated flow class analysis carried out on the 14 unregulated rivers represents a broader and more conservative range of flow characteristics against which indices from regulated rivers may be compared. As more unregulated rivers contribute to the general pool, we are thereby increasing the range of natural flow regime variability within the given flow class and bettering our chances of capturing the range of natural flow regimes for this regional flow class. Altered flows for regulated rivers are thus more conservatively and reliably detected when they are defined against a broader, rather than narrower reference flow class. As we did not have an even representation of regulated rivers by regulation type, all regulated rivers were treated equally and compared within the same multivariate space.

Biotic attributes

For the electrofishing and visual surveys, density estimates were calculated for the species sampled at each site. All individuals recorded were also assigned to a size category (small: <5 cm; medium: 5 to 20 cm; large: 20 to 90 cm) for each river. Site-, species- and size category-specific biomass estimates were generated by summing either the masses recorded during the electrofishing surveys or the mass estimates inferred from the observed length-weight relationships applied to the visual survey data. The data collected via the sampling method that yielded larger density or biomass estimates for each species, and size category at each site were used to calculate the total species densities and biomasses in each of the rivers studied. These total river fish density and biomass attributes therefore, represented the greatest estimates for each species and likely minimized any biases from the two sampling methods (Macnaughton *et al.*, 2014). Species and family richness were estimated by counting the numbers of species and families detected in each river. Shannon's (H) and Simpson's (D) diversity indices were derived from the estimated species biomass and densities using the *vegan* package (Oksanen *et al.*, 2011) for R (R Development Core Team, 2014). In addition, Hill's $N1$ and $N2$ indices describing the effective number of species (Hill, 1973) were calculated for each river as:

$$N1 = \exp(\mathrm{H}) \text{ and}$$

$$N2 = 1/\mathrm{D}$$

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

Statistical analysis

Characterizing flow alteration for our regulated systems first involved identifying the range observed for hydrologic indices across each of the six flow components (daily flow magnitude, frequency, duration, timing, rate, and hourly flows), done by river. This was performed by conducting six separate principal component analyses (PCA) on the correlation matrices for each of the components characterizing the flow regime across all 24 rivers. For each flow component, river PC scores along significant PC axes (PC1 or both PC1and PC2) evaluated using the broken-stick rule (Legendre and Legendre, 2012) were retained for a total of 10 PC axes. Performing separate PCAs for each of the flow components ensured that indices describing major sources of variation within each hydrologic subset, contributed to the retained PCs and that subjectivity associated with the process of selecting the indices was reduced. Flow indices that contributed the most to the significant PC axes (i.e. top loaders) were also identified to explain dominant patterns of variation for each of the flow components measured in our rivers (Appendix 3). Likewise, the correlation matrices of each of the four groups of fish community attributes were subjected to PCA to identify the greatest portion of variation within each of the groups of fish attributes across all rivers. All significant PCs for each of the groups of fish attributes were retained for a total of 5 axes, and fish community attributes contributing significantly to each of these axes were identified.

Reference conditions describing natural hydrologic variability and fish community structure were established by calculating the means and covariance matrices separately for the flow components (10 PC axes), and fish groups (5 PC axes), for the 14 unregulated rivers. Mahalanobis (1936) generalized distances were calculated for each of the rivers (Legendre and Legendre, 2012). This distance computes the deviation between two points in multivariate space whose axes are not orthogonal, thereby taking into account the correlations among indices (Legendre and Legendre, 2012). Hotelling's T^2 statistic was used to determine whether this distance for each of the regulated rivers differed significantly from reference conditions. A regulated river was considered flow-altered if the distance of the hydrologic alteration inferred from flow PCs from reference conditions (alteration scores) was significantly greater than what can be expected

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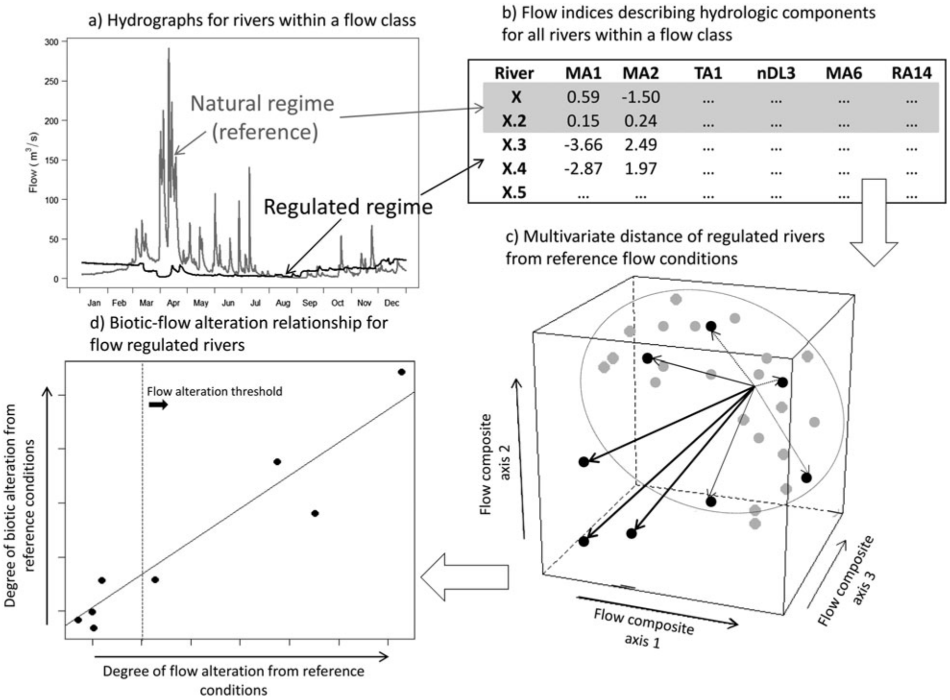
from that of unregulated rivers. Likewise, a river was considered biotic-altered if biotic alteration inferred from biotic PCs was significantly greater than expected. A schematic of how the alteration scores were calculated is provided in Figure 2. A Model II linear regression was computed by permutation ($N = 999$) using the major axis (MA) method and 95% CI for the slope and intercept parameters to compare the biotic and hydrologic alteration scores of all regulated rivers (Legendre, 2013). Model II regressions are generally used when the two variables in the regression equation are not controlled by the researcher and errors on the x and y axes are relatively important, as is the case for the flow and biotic alteration scores calculated (Legendre, 2013). Assuming that the relationship is linear, it may be possible to establish a flow alteration score threshold above which significant biotic alteration may occur. All statistical analyses were performed in R Language (R Core Team 2014).

RESULTS

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

Several regulated rivers were significantly different from hydrologic and/or biotic reference conditions. Significant hydrologic alteration scores were found for hydro-peaking rivers



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

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

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

Across the significantly flow-altered rivers, general patterns of attenuation of the natural flow regime were observed. In particular, daily flow magnitudes representing the variability in daily flows (MA3) and high flow discharge (MH15), the top loadings on PC1, were greatly decreased from flow reference conditions for all regulated rivers, with hydro-peaking and storage rivers exhibiting up to a four-fold decrease in high flows. Slightly higher indices characterizing baseflows (ML17) and mean minimum monthly flows for the month of June (nML6) were also seen in several regulated rivers, most notably hydro-peaking systems. Across our regulated rivers, the predictability (TA2) and constancy (TA1) of flows were both increased relative to means for unregulated rivers. For the hydro-peaking rivers, the number of day-to-day changes in daily flows (RA8) more than doubled, but for storage-type rivers Dee and Serpentine, this index decreased five-fold. Particular to hydro-peaking rivers were indices describing hourly flow fluctuations, namely the coefficient of hourly variation (MA60), which was 24 and over three-times greater for the Mississagi and Magpie Rivers, respectively. For all other regulated rivers, this index was lower than the mean for unregulated rivers. In addition, the Mississagi River had a significantly smaller hourly low flow flashy index (RL2) than the regional average, which indicated that minimum hourly flows for this river were much less than in the unregulated rivers. Lastly, storage systems demonstrated decreases in negative change (nRA7) or in the rise rates in flows (nRA1), both indicated some degree of flow stabilization.

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

Model II regression produced a significant positive linear relationship between biotic and flow alteration scores ($r = 0.94$, two-tailed p-value = 0.007), with the two hydro-peaking rivers exhibiting the greatest alterations overall (Figure 3). Despite significant differences in flow alteration scores for many of the regulated rivers independent of regulation type, ROR and storage systems tended to cluster in close proximity to the biotic mean for unregulated rivers. Although the overall relationship was driven by one of the hydro-peaking rivers, the linear relationship between biotic and hydrologic alteration scores remained marginally significant when the outlier was excluded ($r = 0.65$, two-tailed p-value = 0.06). These findings suggest a potential flow alteration threshold, where any alteration scores associated with a threshold value of approximately 6 (Figure 3) may bring about significant biotic alterations.

DISCUSSION

Our results indicate that for a given regional reference flow class, regulated rivers generally exhibit flow indices that suggest that flows are altered well beyond their natural

Table I. Flow and fish alteration scores and associated p-values for the 10 regulated rivers

River	Regulation type	Flow alteration score	p-value	Fish alteration score	p-value
Magpie	Peaking	55.66	**<0.001**	7.00	**0.01**
Mississagi	Peaking	129.34	**<0.001**	15.95	**<0.001**
Coaticook	ROR	20.06	**0.01**	1.35	0.94
Du Sud	ROR	1.94	0.99	2.24	0.67
Etchemin	ROR	3.97	0.72	2.22	0.68
St Jean	ROR	12.19	**0.04**	2.81	0.46
Dee	Storage	21.44	**0.01**	1.24	0.96
Kiamika	Storage	6.94	0.25	2.30	0.65
Serpentine	Storage	19.90	**0.01**	2.58	0.54
St Francois	Storage	12.93	**0.04**	5.42	**0.04**

Significant differences between flow and fish alteration scores and the reference conditions are given in bold. Flow and fish means and SD for unregulated rivers are 3.03 ± SD 0.34 and 2.11 ± SD 0.45 respectively.

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

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

parameters. Both hydrologic and biotic alteration scores for hydro-peaking systems in particular differed significantly from means for unregulated rivers, while most ROR and certain storage regulation practices were not associated with significant alterations. These findings suggest that 'tolerable' thresholds of flow alteration below which biotic alterations do not occur may be established when they are informed by regional reference conditions. However, the lack of data points in the moderate to high ranges of flow alteration scores in our study precludes us from suggesting a generalized threshold at this time.

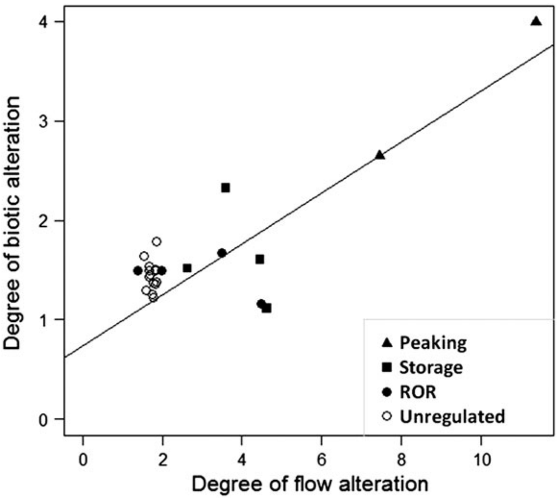

Figure 3. Major axis regression relationships between biotic and flow alteration scores (fourth root-transformed) across all 10 regulated rivers, derived from all 105 daily and hourly flow indices. Rivers depicting Peaking (▲), Storage (■), ROR (●) types of regulation regimes as well as unregulated rivers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

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

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well as hourly low flashy floods over 24-h periods in hydropeaking rivers.

The flow in the Saint-Francois River, like most of the storage systems in our data set, was significantly altered but the inconsistency with which significant biotic alterations are observed across storage systems point to factors other than flow regulation influencing fish community structure. In fact, the Saint-Francois River is dammed at several different points, which may alter the fish community attributes as much as the regulation type. Despite demonstrating biotic alterations, the attributes we used may not capture the full extent of community responses to low and moderate levels of hydrologic alteration. The potential value of larger datasets spanning broader ranges of biotic responses and hydrologic alterations to understanding the ecological effects of flow alterations has previously been identified (Lloyd *et al.*, 2003).

The effects of altered flow regimes on fish species are likely confounded by other factors comprising both the physical environment and the ecological traits of individual species (e.g. migratory patterns/behaviours) (Poff and Zimmerman, 2010). In the Dee and Serpentine Rivers (storage), the observed increases in the proportion of salmonids relative to the reference condition may be attributed to several factors, both anthropogenic and environmental. On the one hand, the occurrence of large fishes (between 20 and 30 cm standard length) detected downstream of the dams may be the result of periodic ‘flushing’ of water from the reservoirs to increase the downstream potential for generating hydropower. In this scenario, the larger salmonids such as landlocked Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) sampled are assumed to have been entrained downstream. This idea is supported by increases in indices representing the magnitudes of high flow volumes in the Dee and Serpentine Rivers. On the other hand, the prevalence of suitable salmonid habitats (i.e. habitats characterized by cold, clear and moderately fast waters; Bjornn and Reiser, 1991) and stocking programmes in these rivers (see Appendix 1) may also explain the increases in relative proportions of salmonids.

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

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