Fisheries and Oceans Canada
Pêches et Océans Canada

Ecosystems and Oceans Science
Sciences des écosystèmes et des océans

Canadian Science Advisory Secretariat (CSAS)

Research Document 2016/047

National Capital Region

Key physical and chemical drivers of fisheries productivity (flow, nutrient and thermal regimes) across rivers in various Canadian regions: lessons learned from NSERC's HydroNet 2010-2015

Michel Lapointe[1], Joseph B. Rasmussen[2], Maheu, A.[3], Kwak, J.A.[3], Beaupré, L.[3] and, St-Hilaire, A.[3]

[1] McGill University
805 Sherbrooke St. W.
Montreal, QC H3A 2K6

[2] University of Lethbridge
4401 University Drive
Lethbridge, Alberta T1K 3M4

[3] Centre Eau-Terre-Environnement (Research Centre)
490, rue de la Couronne
Québec, Québec G1K 9A9

June 2016

Foreword

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

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

Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

ISSN 1919-5044

Lapointe, M., Rasmussen, J.B., Maheu, A., Kwak, J.A., Beaupré, L., St-Hilaire, A. 2016. Key physical and chemical drivers of fisheries productivity (flow, nutrient and thermal regimes) across rivers in various Canadian regions: lessons learned from NSERC's HydroNet 2010-2015. DFO Can. Sci. Advis. Sec. Res. Doc. 2016/047. vi + 55 p.

TABLE OF CONTENTS

ABSTRACT

This report summarizes findings of general interest under the physical habitat research theme of NSERC-HydroNet (2010-2015). The report addresses 3 key, physico-chemical determinants of fish habitat productivity below hydro dams: the degree of alteration of the natural flow regime (Section A of this report); the river's nutrient regime (Section B) and the alteration of its thermal regime (Section C). Each of the three self-contained sections briefly reviews key literature and then identifies the specific objectives of HydroNet work on the particular set of determinants of habitat productivity that it addresses. Then each section describes some low cost multi-site field sampling and statistical modelling approaches that were used to efficiently monitor the effects of regulation, in turn, on a particular river system's flow regime, nutrient regime and thermal regime. Following this, each section presents significant patterns that emerged from comparatively analyzing aspects of the large data sets collected under HydroNet, covering a wide range of regulated and reference river systems across Canada. In particular, some specific effects of Run of the River, Peaking and Storage type hydro systems on both flow and thermal regimes are illustrated. Finally, the analysis demonstrates the important roles played by variations in riverine nutrient levels and species richness in determining total fish biomass, a useful index of habitat productivity in each system.

Principaux facteurs physiques et chimiques de la productivité des pêches (débit, nutriments et régimes thermiques) dans des cours d'eau de diverses régions canadiennes : leçons tirées du réseau HydroNet du CRSNG 2010-2015

RÉSUMÉ

Le présent rapport résume les constatations d'intérêt général associées au thème de recherche de l'habitat physique du réseau HydroNet du Conseil de recherches en sciences naturelles et en génie du Canada (CRSNG) 2010-2015. Le rapport porte sur trois principaux facteurs physico-chimiques déterminants de la productivité de l'habitat du poisson en aval des barrages hydroélectriques : le degré de modification du régime d'écoulement naturel (section A du présent rapport); le régime nutritif du cours d'eau (section B), et la modification de son régime thermique (section C). Chacune des trois sections autonomes examine brièvement les principales publications scientifiques, puis détermine les objectifs particuliers des travaux sur le réseau HydroNet en ce qui concerne l'ensemble précis de facteurs déterminants visés de productivité de l'habitat. Ensuite, chaque section décrit certains des échantillonnages à faible coût sur le terrain à plusieurs endroits et des approches de modélisation statistique qui ont servi à surveiller efficacement les effets de la régulation sur le régime d'écoulement, le régime de nutriments et le régime thermique d'un réseau de cours d'eau en particulier. Par la suite, chaque section présente les tendances importantes qui ont ressorti de l'analyse comparative des aspects des grands ensembles de données recueillis par le réseau HydroNet, couvrant un large éventail de systèmes de cours d'eau réglementés et de référence au Canada. Plus particulièrement, certains effets précis des systèmes de dérivation de cours d'eau, de demande hydroélectrique de pointe et de stockage de l'eau sur les régimes d'écoulement et thermique sont illustrés. Enfin, l'analyse démontre le rôle important joué par les variations de l'apport en nutriments et la richesse des espèces fluviales pour déterminer la biomasse totale du poisson, qui constitue un indice utile de la productivité de l'habitat dans chaque système.

SECTION A - FLOW REGIMES: A tool to assess the types and relative severity of flow regime anomalies associated with particular hydro dams

Michel Lapointe
McGill University

OUTLINE: WHAT IS THE TOOL AND WHAT IS IT USEFUL FOR?

When regulators analyze new hydro projects (or recertify existing installations), they need to assess the possible severity of the project's flow regime modification, among other 'pathways of effects' on fish populations. To this end, an "ideal" (but data expensive) approach would involve the use of empirical relations specifying Ecological Limits of Hydrological Alteration (ELOHA), calibrated to the particular region and its aquatic fauna (Poff et al. 2010). Empirical ELOHA relations are based on detailed, multi-site data on both altered flow regimes and biota. They aim to quantify, for various geographic classes of river ecosystems, the thresholds of flow alteration leading to unacceptably altered levels of biotic metrics of interest, including measures of fish population health (Acreman and Dunbar 2004; Arthington et al. 2006). Unfortunately, the data gathering in Canada remains to this day insufficient to populate and evaluate such ELOHA models. However, the HydroNet 2010-15 data base on fish communities and flow regimes provides a pilot feasibility demonstration in this direction (Boisclair et al. 2016. Smokorowski et al. 2011).

In the current absence of fully tested ELOHA rules, less powerful approaches are available to assess flow regime alteration. Building on previous work of McManamay et al. (2012 a, b,c), HydroNet 2010-2015 developed one such approach for Canadian conditions. Illustrations of its use (along with key methodological details) are given in this section of the report. Further details are given in McLaughlin et al. (2014). In contrast to ELOHA, the approach presented here does not identify ecological thresholds of allowable alteration; however it can yield a ranking of regulated systems in terms of both the type and the relative severity of their flow regime **anomalies** compared to unregulated norms. These data can be used to rank the severity of flow regime alterations across a set of projects (past and proposed) and to prioritize particular regulated systems for more detailed impact studies. The office based method presented here can be applied, simply using readily available hydrometric data sets, to any regulated site of interest, in any region, and at any level of detail justified by the project.

The main aim of this section (A) of the report is to demonstrate some potential uses of this practical approach to quantifying regulation effects on natural flow regimes.

DEFINITIONS: FLOW REGIME ALTERATIONS AND FLOW REGIME ANOMALIES: DIFFERENT CONCEPTS FOR DIFFERENT USES

1. Here we define a **flow regime "alteration"** as the change of various aspects of the flow regime caused by hydro operations. The degree **of flow regime alteration** can thus be quantified by directly comparing on the given system various "flow metrics" (such as mean annual flood, mean January flow, etc.) computed over pre- and post- damming flow periods (Richter et al. 1996, 1997). This requires that multi-decade long flow records exist for both pre- and post- regulation. It also assumes that climate and watershed hydrology both remained stationary (unchanged) over both pre and post regulation periods (or alternatively that we can identify and remove longer term climatic and land use trends modifying flow regimes). Unfortunately, for many existing hydro-sites in Canada, pre-regulation flow

records are often too short to carry out the required Before-After comparison (this indeed was the case at most selected HydroNet regulated study sites).

More importantly, even when sufficient historical flow records exist, this technique does not, on its own, clarify to what extent the altered (After) flow regime is anomalous compared to the range of natural regimes to which are exposed fish populations in other watersheds in the region, which is the main application of the alternate approach proposed here.

2. The calculation of scores of **flow regime anomaly**, presented in this report, avoids these data gap problems and provides an alternate and conceptually distinct approach to assess the degree of severity of flow regime alteration at a regulated site. Anomalies are quantified ("scores" are generated) by comparing the post-damming regulated regime to a range of flow regime "normals" observed at unregulated sites with broadly comparable watershed character, located in the same hydrological region (McManamay et al. 2012 a,b,c, McLaughlin et al. 2014). This approach does not require pre-regulation flow data. Instead it only requires analyses of 2-3 decades of recent hydrometric records, at a set of regulated and otherwise broadly comparable unregulated sites in the study region. This analysis can be conducted with existing data (or in the case of proposed developments using simulated future hydrographs), at practically all existing or proposed hydro sites in any region of Canada.

3. We illustrate below how the **anomaly scores** generated here are a practical way of detecting and quantifying various types of regime anomalies. We first illustrate how simple visual inspection of hydrographs is a poor tool to detect subtle but potentially important features of the regulated flow regimes. In contrast, the statistical method presented here yield scores for various **anomalous** features of the studied flow regime (i.e. individual anomaly scores for various metrics of flow magnitudes, durations, timing, etc.). Combined with expert knowledge on fish ecology, the size of anomaly scores can then provide a simple 'heuristic' to estimate the probability of significant ecosystem impacts at regulated sites.

   Specifically, the tool can identify those regulated systems with the strongest anomaly scores and thus help prioritize these sites for more detailed monitoring of possible faunal impacts. The analysis can also disclose where potentially altered flow regime conditions at some regulated sites remain well within the normal range of variability for unregulated (reference) sites in the region. In such cases, if healthy fish populations are documented at unregulated sites with a comparable set of flow metrics as those computed at a given regulated site, this finding can support claims that the flow regime alteration caused by regulation may be, in itself, too minor to produce negative impacts on fish fauna.

4. It is important to note that regime **anomaly** and regime **alteration** as used in this report are different concepts that serve different purposes. A regime "anomaly" as defined here, in theory, does not always represent a flow regime alteration due to regulation. Some other highly anomalous watershed characteristic of the regulated system, atypical for its geographical location and flow class (such as unusually large lakes or expansive urban areas) could also be at play, irrespective of regulation. Conversely, regime alteration by hydro damming does not always produce a clearly anomalous regime (for example, weakly regulated systems with little hydro-reservoir storage and no peaking activity may behave quite similarly to unregulated systems draining small, upstream lakes). However, all regime anomalies detected by the proposed method across the set of 16 HydroNet regulated sites analyzed here were related to hydro-regulation effects.

INTRODUCTION

Each riverine ecosystem is unique and dynamic. First, a river's flow regime is known to affect the ecosystem's physical structure (channel widths, depths, bed sediment sizes and seasonal sediment stability, water turbidity and temperatures, etc. (Church 2002; Caissie 2006). By controlling bioenergetics as well as spawning, feeding and refugia habitat conditions, the flow regime is also an important driver of the river system's ecological integrity (Booker et al. 2007; Bunn and Artington 2002; Lytle and Poff 2004; Pluckridge, et al. 1998; Poff et al. 1997; Poff and Zimmerman 2010; Mims and Olden 2012). The ecologically important features of a river's flow regime are summarized by sets of hydrologic indices (or "metrics") that describe the magnitude, frequency, duration, timing and rate-of-change of flow events (Poff et al. 1997). The most widely used sets of indices are the Nature Conservancy's Indicators of Hydrologic Alteration (IHA) (Richter et al. 1996) and the United States Geological Survey's (USGS) Hydrologic Index Toolkit (HIT) (Olden and Poff 2003), which includes the IHA.

After construction of a storage reservoir, downstream river flows can be artificially modified by dam operators, within project design limits. The degree of flow alteration that occurs is quite variable however, as it depends on the physical characteristics of the impoundment (reservoir volume and outlet structures can limit the amount of water that can be retained or quickly released) and its mode of operation (e.g. number of turbine units used in peaking and their flow capacities, environmental release rules set by regulators, etc.). To generalize, research shows that hydro dams with significant storage volume (or water residence time) tend to be used in ways that reduce maximum flows, reduce overall flow variability and rise rates (excepting peaking systems which increase hourly change rates), while very often increasing minimum flows and the number of flow reversals per year (Magilligan and Nislow 2005; McManamay et al. 2012a; Poff et al. 2007). However, specific alterations to the natural regime are quite variable across dammed river systems. Various approaches can be used to quantify the type and intensity of regime modification at a particular site.

Regime alterations (cf definition 1 above) are conventionally identified by comparing flow indices calculated from pre-dam flow records to indices calculated from the post-dam, regulated records (Richter et al. 1996). However, where pre-regulation flow records are too short (under 2 decades) for minimal statistical validity, this analysis can become complex and imprecise. Given insufficient pre-regulation records, alteration estimates may require hind-casting of pre-dam discharges using complex runoff hydrology and flow routing models, possibly requiring pre-damming weather and land use data to account for climate and land use changes pre vs post regulation.

However, scientists and managers can be interested in comparing the degree and type of flow regime characteristics across numerous dammed systems, even in the absence of historical flow data. Thus a need for an alternate methodology focusing on the detection of **flow regime anomalies** (cf. definition 2, above) has been proposed (McManamay et al. 2012 c). This approach first requires identifying classes of unregulated rivers that share broad hydrologic properties with the pre-regulated state of the dammed system. McManamay et al. (2012a) describes flow classes as "groups of streams that share similar natural hydrology; thus, they provide a stratified approach to evaluate hydrologic alterations or departures from natural baseline conditions." Analyzing the range of flow regime traits within each reference flow class, the natural **range of variability** of various hydrograph components can be determined, and significant deviations in regulated systems can be identified by comparison (Poff 1996; Poff et al. 2006; McManamay et al. 2012a). Such an approach is illustrated here with application to Canada.

Our specific objectives under the Flow Regimes component of the HydroNet 2010-2015 NSERC-SNG Program were:

1. to classify 98 unregulated rivers (proximal to 16 regulated HydroNet rivers) for which high quality daily flow records were available into "flow classes" representative of regional flow regime norms, and to evaluate the main qualitative differences between these flow classes;
2. to assign each of the 16 HydroNet regulated rivers spread across Canada to the appropriate flow class based on geographic location and physical watershed characteristics (pre-impoundment);
3. to compute metrics of flow regime anomalies for each regulated system (evaluated by comparison with the range of metric values normally observed in comparable unregulated systems in the appropriate flow class);
4. to describe the main types of observed regime anomalies across our Canadian study set, as a function of regulation type (large storage dams versus run of the river, vs peaking systems).

A sample of results that illustrate the method are given here (more detail is given in McLaughlin et al. 2014, and in McLaughlin 2014).

STUDY SITES

For logistical and budget reasons, HydroNet targeted its data gathering on a subset of small-medium sized southern Canadian rivers dammed for hydropower, with watershed areas mostly in the range 500-2000 km^2 (median value, approx. 1000 km^2). Site selection was strongly conditioned by cost of river site access and feasibility of accurate fish sampling by electrofishing and seining. (The fish sampling methods and resultant data are summarized in other CSAS 2015 HydroNet reports, specifically see Boisclair et al. 2016 and publications references therein). HydroNet site selection was also stratified by region (with a cluster of sites in the Western Cordillera of Eastern BC and western Alberta, a second in Ontario and Quebec Shield regions, and a third in southern Quebec and New Brunswick Appalachian geological regions). Finally HydroNet sought to include sites with various types of regulation (larger storage dams, with or without peaking operations as well as Run of River or ROR). Based on quality of flow records, 16 regulated rivers across these regions were finally selected to study impacts of hydro operations on flow regimes. All were dammed for hydro-power production between four decades and a century ago.

In the next step, we identified as potential reference sites in each region, the largest possible number of nearby river gauges located on unregulated watersheds within a range of half to twice the watershed size of each regulated site. For this comparative analysis, the distance required in general to secure a sufficient number of reference sites (of similar drainage area) will depend on the watershed size at the regulated sites being studied. In this study, with regulated sites of drainage area 500-2000 km^2, all possible reference gauges within a radius of about 400-500 km from the regulated site were identified. This yielded in the range of 5-20 reference sites per regulated site from which we could establish regional, flow class unregulated "normals". 96 reference gauges were identified this way, to contextualize natural flow regimes relevant for comparisons with the 16 regulated sites located in the various sub-regions studied.

Other than discarding gauges identified as draining regulated watersheds or watersheds incorporating large cities, no attempt was made to target in reference sets only so called "pristine" watersheds (inexistent in too many regions). Nor could we target for reference sets specific, narrow ranges of watershed relief, % lake cover, or % forested lands, closely matching conditions at specific regulated sites. Thus the range of flow regimes observed in each reference class include the effects of existing variability in all these runoff generation factors (except for the presence of large cities) across unregulated watersheds of similar size in the given region. To skip methodological details, go to **Results.**

STATISTICAL METHODS

The statistical procedures used follow the general approach and guidelines presented by McManamay et al. (2012a, 2012b and 2012c). Specific details are given in McLaughlin et al. 2014 and McLaughlin 2014. Daily discharge data was obtained for the 96 unregulated rivers and 16 regulated rivers over a common 20-year time span across the study regions. It is well know that heightened hourly flow change rates due to hydro peaking have effects on fish at individual and population levels (Zimmerman et al. 2010). However, because hourly data were readily available only at a small subset of HydroNet sites, these data are not discussed here (but see McLaughlin 2014). Flow indices (predominately drawn from the HIT toolkit (Olden and Poff 2003)) were calculated using the statistical software package R and subsets of highly correlated flow indices were permanently removed from the analysis. 150+ commonly cited flow indices were pared down to 70 indices representative of the main index groups that describe flow magnitude, frequency, duration, timing and rate of change.

Defining flow class reference groups across HydroNet study regions

From the set of 96 reference (unregulated) rivers distributed over two distinct regions (in Western and in Eastern Canada), we identified five broad flow regime classes. The classification was based on a simple K-Means clustering applied to observed discharge regime characteristics, defined by 70 flow regime metrics computed for each of 96 reference river hydrographs (Figure A1). Since HydroNet reference rivers cover only limited sub-regions in southern Canada, here the resultant 5 flow classes were chosen only to provide context for the 16 HydroNet regulated sites. **In no way are they proposed as a general classification of Canadian river flow regimes.** One example of a broader based, Canadian river regime classification, but based on somewhat different criteria, is given in Monk et al. 2011.

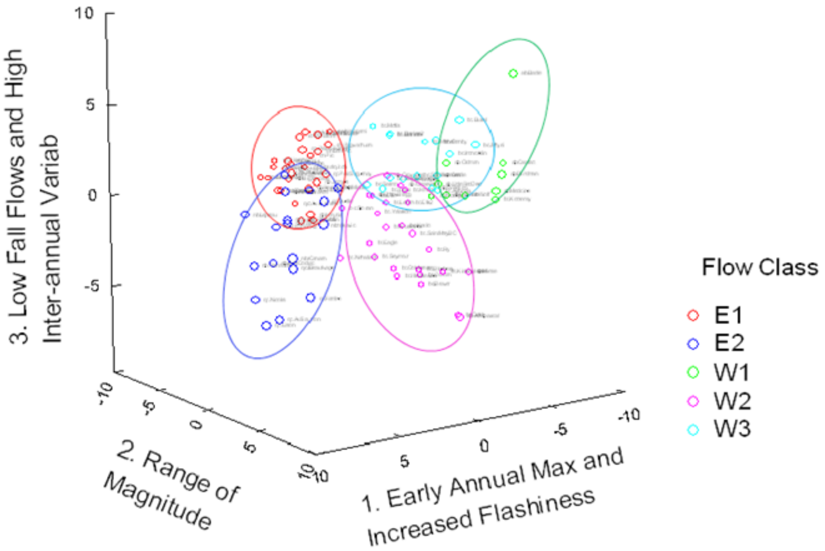


Figure A1. Five flow classes in PCA space. PC1, 2 and 3 explain 23.9%, 15.6% and 10.5% of the total index variance. The K-means process appears to have effectively clustered the sites based on similar flow regimes since the classes are grouped together in PC space. Some transitional sites are expected.

The 5 resultant flow classes largely track east-west location as this factor is associated with well-known variations in precipitation and runoff patterns across the southern zone of Canada (McLaughlin 2014). The contrasting regime behavior between our Eastern and Western river sets is obvious on the plot. Note however that the classification distinguished 3 distinct flow classes (W1-3) located within a few hundred kilometers in the western Rocky Mountain region. Here these 3 flow classes reflect differences in headwater elevations (and presence of glaciers) and differences in topographic effects on precipitation regime (reflecting watershed location east or west of the Rockies). Other distinguishing characteristics of each of these flow classes are discussed more fully in McLaughlin (2014).

In the next step of this approach, the 16 selected regulated rivers were each assigned to an appropriate regional flow class for flow regime comparison. These assignments are based on the watershed's location and physical characteristics. Specifically, Discriminant Function Analysis (DFA) was used to predict the appropriate natural flow classes as reference, based on latitude and longitude, watershed size, relief and % of pre-reservoir lake area.

Quantifying anomalies in regulated flow metrics using z-scores

For each of the 5 regional flow classes, we extract "normal" ranges for each of the 70 flow regime index values. These ranges reflect for example the effects on runoff timing of observed variations in % lake cover, watershed relief or % forested lands within a regional set of unregulated gauges of broadly similar watershed areas. These references provide observed ranges of flow metric values **prior to regulation** for HydroNet rivers. From these values, we were able to identify the features of the flow regimes at each of the HydroNet regulated sites that are most **anomalous** compared to the "norms" for its regional reference class.

To quantify the strength of index anomalies at any regulated site, we calculate standardized scores (or "Z-scores") for all flow indices, based on the mean and standard deviation for that metric, within the unregulated reference class. (The Z-score for a regulated site metric is therefore the number of reference class standard deviations for the same index above or below its class mean). Where normality assumptions were satisfied, we estimated p values for the null hypothesis that the metric value is not atypical, i.e. that the given flow metric at the regulated site is drawn from the same statistical distribution as found across the set of unregulated sites in the appropriate reference class.

Note that the exact Z-score values obtained using this method depend of course on the narrowness or breadth of conditions captured in the regional reference set selected. The wider the variability in metrics accepted with a given flow class (in effect the larger the size of the class ellipses on Figure A1), the more **conservative** will be the attribution of an anomalous status to a regulated site, based high Z-scores of a flow regime. This was felt to be desirable here, to minimize false positives in anomaly. Here, wider reference classes with greater "within class" variability yield more conservative estimates of anomalies (with fewer false positives).Thus, in the eternal classification dilemma, we aimed in this case for broader grouping rather than finer splitting across natural gradients in flow regimes. To increase reference sample sizes, we have in general included in reference groups for this study all roughly comparably sized unregulated, gauged watersheds located within 400-500 km of regulated sites.

RESULTS

To illustrate the usefulness of the method and its possible application, we present here results of the analysis for one regulated system in Eastern Canada, chosen from the 16 HydroNet regulated rivers. (A more complete and formal discussion of results across all regions and regulated sites can be found in McLaughlin et al. 2014).

Figure A3 presents an 8-year long hydrograph of the regulated Saint-François River (below site 2), a tributary of the Saint Lawrence River located in southern Quebec. Based on its watershed characteristics, this site was assigned with high statistical confidence by Discriminant Function Analysis (DFA) to regional flow class E2. Reference class E2 encompasses 18 broadly comparable sized reference watersheds in the Appalachian physiographic province across southern Qc and southern NB, cf Figure A2). The mean distance from the Saint-François site 2 to the 18 reference rivers in E2 is 280 km.

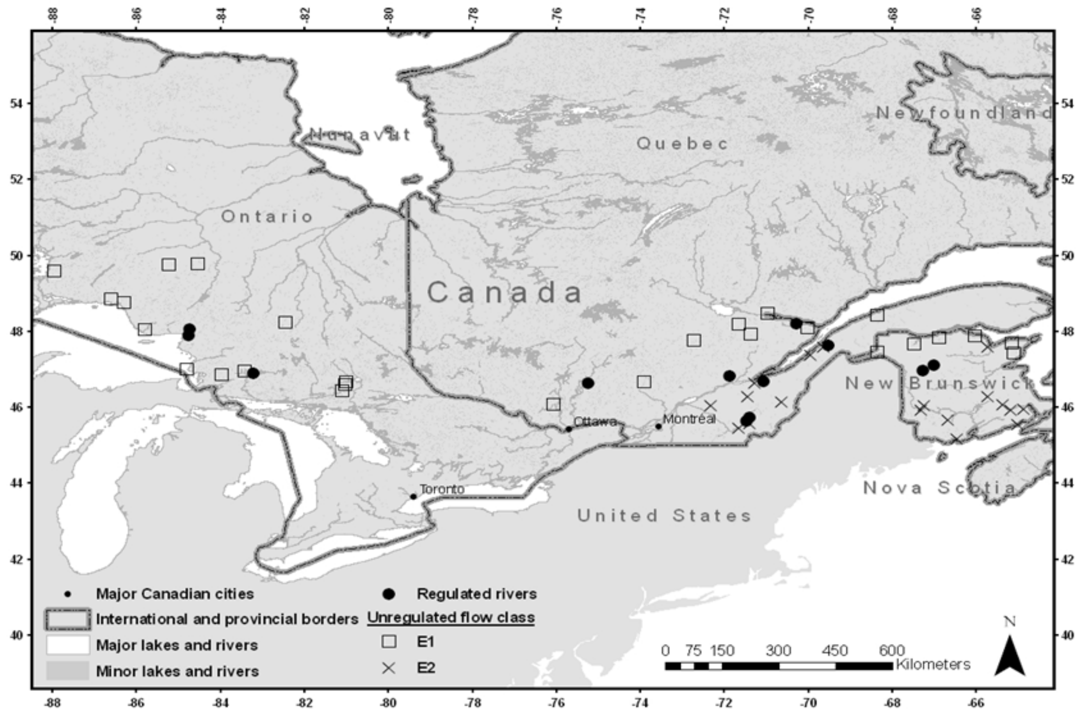


Figure A2. Location across Eastern Canada of regulated gauges (solid circles) studied under HydroNet , along with reference gauges belong to flow classes E1 (open squares) and E2 (x). See Figure A1 for some flow regimes characteristics distinguishing these 2 "natural flow classes" (and see McLaughlin 2014)

Visual hydrograph comparisons

We next illustrate how difficult it is to identify and quantify the precise nature of flow regime anomalies at a regulated site (see Figure A3) by visual hydrograph comparisons. Figure A4 presents a sample of multi-year hydrographs from two unregulated rivers in the appropriate reference group E2. For all hydrographs shown, daily discharge values are normalized by the median Q for each site, to better control for variations in watershed size. The range of discharges on the Saint-François River (Figure A3) does appear somewhat smaller than that observed at the two reference rivers (Figure A4). However, beyond this observation, no statistical inference can be made concerning this effect with such a small comparison pool (N=2), nor can one disentangle from such casual hydrograph inspection possible effects of regulation on timing of high and low flows, rates of change, number of rises and falls per year, etc. More formal statistical analysis of flow metrics comparing with the full E2 set of 18 rivers is thus required to clarify possible flow regime anomalies caused by regulation in Figure A3. This is the essence of the method proposed here.

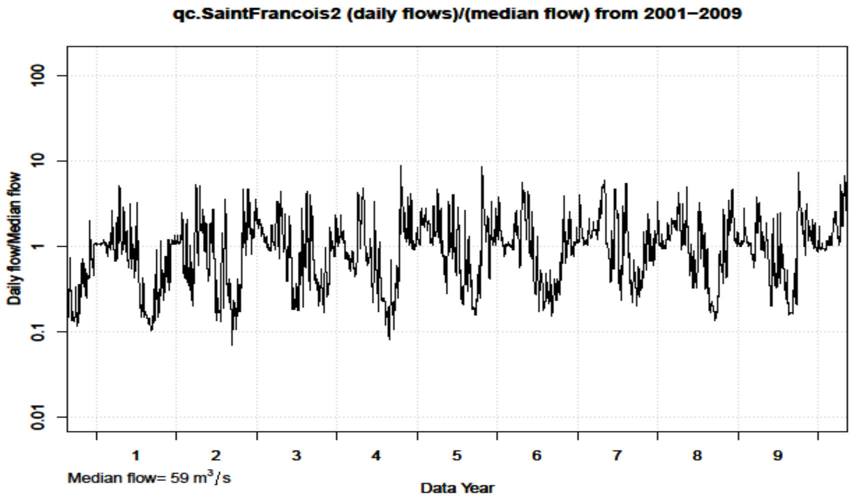


Figure A3. Nine recent years of hydrographs at Saint-François River site 2, a regulated site.

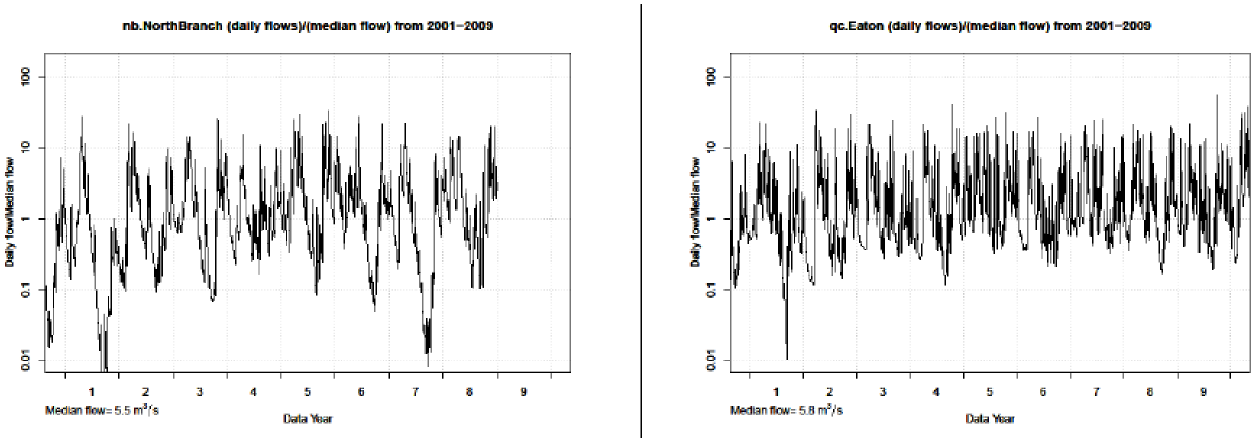


Figure A4. To illustrate the difficulty of visual comparisons, the same nine years of hydrographs at 2 reference sites from class E2, the regime class to which the unregulated Saint-François River was assigned. All discharge values are normalized by the median daily discharge at each gauge. The quantitative anomaly comparisons conducted next compare metrics at Saint-François site2 to those extracted over 18 such reference hydrographs, all belong to class E2 (cf Figure A5).

Figure A5 illustrates the basic idea behind anomaly detection. It plots the values of only 2 metrics (shown on the axes) for three regulated systems (red dots) belonging to E2, including the Saint-François 2 site shown in Figure A3, against the same metrics for the 18 unregulated, reference systems in E2 (blue dots). The plots reveal that the Saint-François 1 and 2 sites have a much lower values of flow volumes during high runoff season (on X axis, 3 month scale mean discharge values, here again scaled as multiples of median daily flow) than are observed among the entire E2 flow class in southern Quebec and northern NB. They also have much lower values of the coefficient of variation of daily flows (shown on Y axis).

Figure A5 further shows that both Saint-François regulated sites have broadly similar degrees of anomaly on these metrics, measured by a distance to the centroid of the metric values across the 18 reference rivers (which are the blue dots). The 2 same metrics for the regulated Etchemin River (red dot in center of group) are seen to be non-anomalous, compared to the mean and variability within the reference group. The Etchemin was classified for the purpose of HydroNet as a Run of the River (ROR) system: its storage volume is quite small relative to mean annual flow and all its metrics show values that are within the normal range of variability for the set of E2 reference flow regimes.

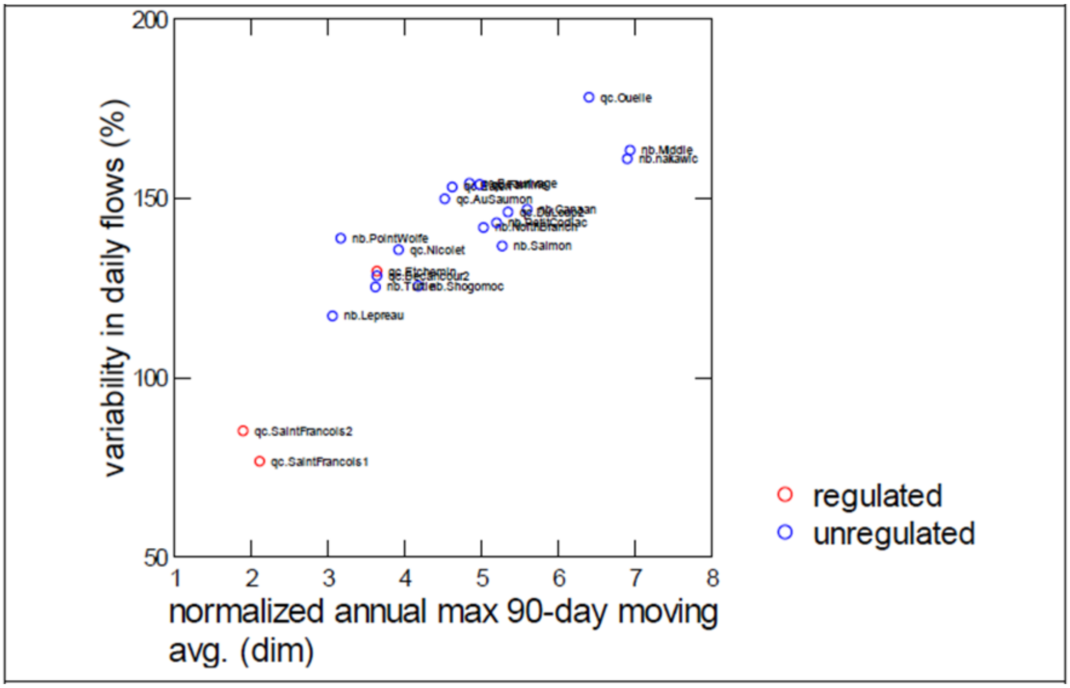


Figure A5. This plot displays 2 (nDH5 vs. MA3) of the top 4 loading indices on PC2 across flow class E2, the gradient of range of variability on which the two Saint-François sites display most anomalous behavior It is apparent from this plot (and also true for the other high loading PC2 Indices that we explored) that the Saint-François has systematically reduced index scores for the indices that highly influence PC2.

We next generalize to all 70 metrics retained in this study the comparisons shown in Figure A5. This is done by calculating Z-scores of degree of anomaly (Z-scores) for all 70 metrics for the Saint-François regulated site (recall from Methods that the Z-score for a regulated site metric represent the number of reference class (E2 here) standard deviations that its value lies above or below the reference class mean for that same metric). For the regulated and reference rivers in class E2, Principal Component Analysis of all 70 Z-scores can then be used to visualize (Figure A6) the distribution of regulated versus reference score values, by projecting them on the main axes of variability across the reference rivers of the set of 70 metrics.

This plot confirms that while the Etchemin river has similar scores to unregulated rivers on the two main PC axes of metric variability among reference rivers, the Saint-François sites plot unusually low (i.e. display regime **anomalies**) on PC2 (Y axis) a combination of various metrics describing high flow, spring time runoff volumes, one of the main axes of variability across E2 unregulated sites. Figure A6 also shows however that the Saint-François sites do not display anomalous behavior in terms of metrics of frequency of low flows nor flashiness (on PC1, X axis, the other main axis of natural variability among E2 class rivers).

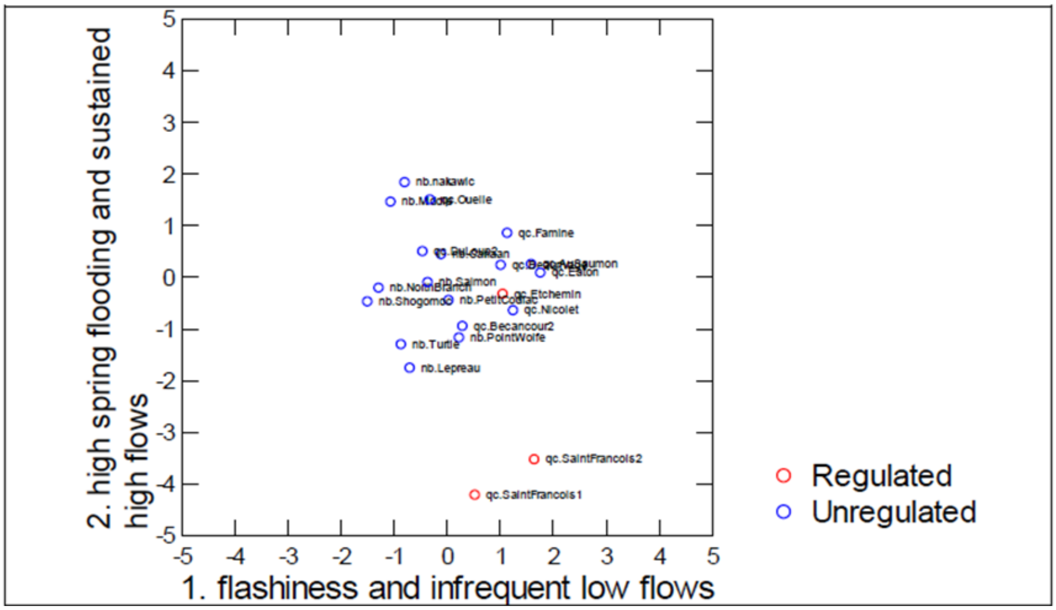


Figure A6. Regulated and unregulated flow class E2 rivers in multivariate PCA space based on all unregulated rivers of this class. PC1 explains 29.5% of the total variance within E2 reference sites. PC2 explains 19.2% of the total variance. Here PC1 and PC2 scores have been standardized based on the reference set means and SD. If regulated rivers plot well outside the cluster of unregulated reference systems along a PC axis, certain flow indices loading this axis are highly anomalous. As conventional, axes are named based on an evaluation of the top loading indices. For details see McLaughlin et al 2014. Note that the Saint-François River plots outside the range of reference scores on PC2 while the Etchemin River falls within the reference range on both PC1 and PC2.

Pinpointing the most anomalous particular features of the flow regime at a regulated site.

For any given regulated system, anomaly scores can be used to identify, and target for further enquiry, particular features of a regulated flow regime that are the most anomalous (highest Z-scores) and thus possibly most likely to be limiting for particular species within the regional fish fauna (or, in some cases, most likely to favor invasive fish species). This information can then be interpreted through the lens of the expert judgment of fish population biologists with knowledge of regional fauna.

Table A1 presents a subset of the 70 flow regime metrics at the Saint-François 2 site that are most highly anomalous (absolute Z-score greater than 3.5, that is the regulated metric is more than 3.5 times the standard deviation away from the reference mean for that same metric). Similar tables have been generated and discussed for the 16 regulated HydroNet study rivers (McLaughlin, 2014). For each metric listed here, the third column gives its anomaly score (Z-score). In the cases where the reference metric distributions are normal, the second column also gives the probability that such a Z-score at the regulated site is consistent with the null hypothesis (i.e. the metric value remains consistent with the range of normal variability observed within its reference class).

Table A1. The most anomalous flow metric values observed at the regulated Saint-François River site 2. Column 3 gives the metric's Z-score (i.e. the number of standard deviations above or below the class mean for the given metric within reference class E2). The name and a definition of each metric are given in columns 6 and 7. Means and standard deviation values for each metric across the reference set of unregulated rivers in flow class E2 are given in last 2 columns.

Index Code	p-val	z-score	load1	load2	Index Name	Description	Units	Raw Value	Class Mean	Class SD
RAS	0.000	**8.54**	0.54	0.40	Proportion of rise days (Number of day rises)	Compute the number of days in which the flow is greater than the previous day. RA5 is the number of positive gain days divided by the total number of days in the flow record.	dim	0.42	0.28	0.02
MA41	0.000	**7.41**	0.41	-0.23	Specific mean annual runoff	Compute the annual mean daily flows. MA41 is the mean of the annual means divided by the drainage area.	m^3s^1/km^2	0.10	0.03	0.01
nML1	0.000	**5.98**	-0.45	-0.51	Mean minimum monthly flows (Jan)	For each year, compute the minimum flow for the month on January. ML1 is the mean (or median – Use Preference option) of these values.	dim	1.01	0.47	0.09
DA4	0.000	**-4.48**	-0.65	-0.32	Median fall period	Median duration of consecutive periods of falling values.	days	2.00	4.11	0.47
MA6	0.002	**4.13**	0.41	-0.50	Ratio of low flow (Q90) to high (Q10) quantiles	Range in daily flows is the ratio of the 90 percent to 10 percent exceedance values for the entire flow record (low flow/ high flow). Compute the 90 percent and 10 percent exceedance values for the entire flow record. Exceedance is computed by interpolating between the ordered (descending) flow values. Divide the 90 percent exceedance value by the 10 percent value.	dim	0.12	0.04	0.02
FH3	0.003	**-4.04**	-0.01	0.81	Days per year above 3x flow median	Compute the number of days each year that the flow is above a threshold equal to three times the median flow for the entire record. FH3 is the mean (or median – Use Preference option) of the annual number of days for all years.	days/year	17.00	73.36	13.97
nML3	0.004	**3.99**	0.31	-0.68	Mean minimum monthly flows (Mar)	For each year, compute the minimum flow for the month of March. ML3 is the mean (or median – Use Preference option) of these values.	dim	1.01	0.56	0.11
MA3	0.006	**3.88**	0.20	0.90	Annual Variability in daily flows 1	Mean (or median – Use Preference option) of the coefficients of variation (standard deviation/ mean) for each year. Compute the coefficient of variation for each year of daily flows and then compute the mean of the annual coefficients of variation.	%	84.99	144.24	15.28
ML17	0.006	**3.87**	0.37	-0.46	7-day minimum baseflow	Compute the mean annual flows. Compute the minimum of a 7-day moving average flow for each year and divide them by the mean annual flow for that year. ML17 is the mean (or median – Use Preference option) of those ratios.	dim	0.16	0.06	0.03
RAS	0.021	**3.57**	0.59	-0.32	Number of reversals (day-to-day)	Compute the number of days in each year when the change in flow from one day to the next changes direction. RAS is the average (or median – Use Preference option) of the yearly values.	events/year	128.50	88.94	11.09

Generating hypotheses concerning "pathways of effects" on fish, based on anomalous Z-scores.

Useful insights on potential fish population impacts can be generated from these statistical analyses. Resulting impact hypotheses need then to be further investigated by project biologists. Some possible effects are described next for the case of the regulated Saint-François River.

It was observed above (Figure A5) that 3-month spring high flow volumes on this system are unusually low compared to its reference group E2. This might have effects on the duration of pike spawning in the riparian vegetation along the Saint-François river floodplain. Table A1 also shows that the strongest absolute anomalies on the Saint-François compared to its regional references (Z-scores over 4 in Table A1) relate to the constancy and high level of both early and late winter discharges. The January minimum daily flow (in row 3, scaled to median flow always) is almost 6 standard deviations greater than the mean for the reference set E2. This is a typical effect for a base load generating system with large storage dam in Quebec. Such a regime anomaly may have effects on mid-winter ice cover formation in steeper river reaches and thus possible effects for winter habitat conditions of some fish. Note also that the March minimal flow levels are also 4 standard deviations higher than normal for the reference E2 group, possibly accelerating breakup in lower gradient river reaches where an ice cover has been able to form. Also notable (last 2 rows of Table A1) are the 7 day minimum flow in summer which has a Z-score of 3.9 ($p= 0.006$), likely implying (compared to reference group conditions) more moderate water temperatures during heat waves and less thermal stress for cool water species. Finally, the number of days with flow reversals (likely caused by release operations) at 128 (Table A1), is 3.6 SD higher than expected among the 18 reference rivers (which has mean of 89, SD of 11 days, Table A1).

Some general trends on the effects of mode of regulation, observed from pooling all HydroNet study sites across Canada

The analyses presented above allow the comparison, within one region and flow class, of the mode and intensity of regime "anomalies" across various regulated sites. This general approach can also be used to compare regime anomalies across a larger set of regulated rivers, pooling sites across different regions and different reference classes.

Figure A7 presents an ordination of anomaly (Z) scores for all 70 studied metrics across all 16 HydroNet regulated sites, distributed from BC to New Brunswick. (Each regulated site's Z-scores are computed with respect to its own appropriate reference flow class, as the basis for anomaly determination). This analysis reveals the qualitatively different effects of various types of regulation across the HydroNet sample. As expected, peaking systems (in red) tend to strongly increase the strength of day-to-day flow variations (flashiness) compared to relevant regional norms. In contrast, storage systems (in green) mostly tend to increase baseflow related metrics. Finally, ROR systems (in blue) have low Z-scores (behaviors similar to applicable reference class norms). In this ordination space, ROR scores lie within the cloud of scores (blue ellipse) for the unregulated references. The 2 New Brunswick sites (in purple) have unusual regimes compared to the rest of the study set. They appear to be operated to store headwater runoff for occasional but irregular rapid ramping of releases, lasting many days or weeks, to supply hydro dams further downstream. The differences in resulting flow regime when compared across all 70 selected metrics to more typical daily peaking regimes (red dots) stand out clearly in the anomalies analysis.

Figure A7 also illustrates how this approach can be used to rank regulated systems across Canada in terms of the overall type and degree of regime anomaly, expressed as the 2D distance and direction of a site scores on such PC plots distance from those of unregulated references (blue ellipse here). Using this metric, it can be noted that among the small sample (5) of peaking sites (in red) studied under HydroNet, one site, the Kananaskis River site 2 in Alberta (below Pocaterra Dam), displays the most anomalous regime. Compared to Kananaskis 2, the peaking regime observed on the Magpie and Michipicoten Rivers in Ontario, when compared to the norms of its local reference class, is relatively more benign in terms of flashiness (PC1) although it has a greater homogenization effect (PC2) on seasonal flows (smaller range of magnitude and higher baseflows).

Across HydroNet study storage sites (in green), the Saint-François 1 site (bottom right on Figure A7) is seen to display the strongest degree of seasonal homogenization of regime (the lowest range of magnitude on PC2 axis, compared to its regional references) while the much smaller reservoir at Sugar Lake on the Shuswap River in BC produces much a weaker homogenization anomaly. (This type of ranking information, across any regime axis, may be useful for site selection towards further studies aiming to establish thresholds of flow anomalies compatible with acceptable impacts on fish populations. Note that such “euclidian distances” from class means can alternatively be computed using z-scores across all 70 anomaly metrics, instead of just using summary PC scores as illustrated on Figure A7).

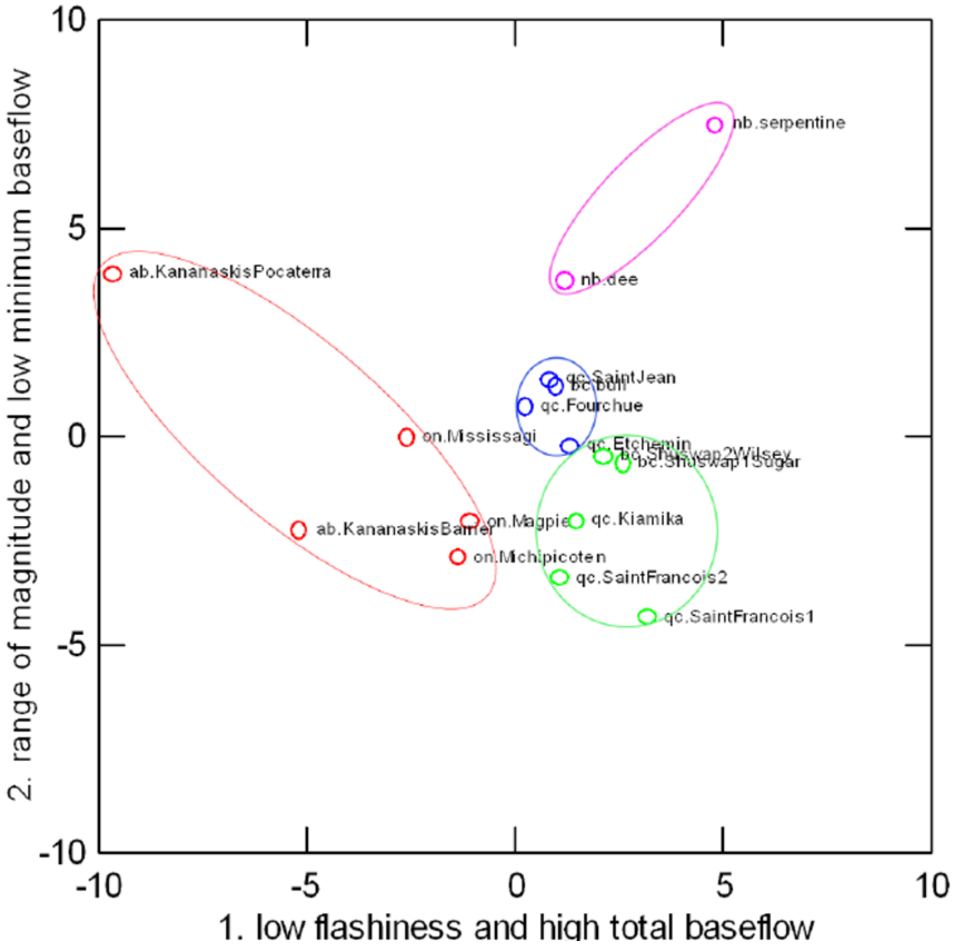


Figure A7. Principal Component analysis of Z-scores for all 70 studies metrics across all 16 regulated study sites in Canada (here each Z score is computed against the mean and SD of the given metric for the appropriate reference flow class at each site). Color codes refer to types of regulation: red for peaking sites, purple for atypical sudden release modes, green for mainly storage effects and blue for Run of the River sites (see discussion in text).

Finally, pooling across all 16 HydroNet regulated sites, Figure A8 presents histograms of anomaly scores (Z-scores) for all 70 flow regime metrics, grouped by regulation type, each overlain on Z-score distributions for all relevant reference (unregulated) sites. In aggregate, Figure A8 shows that peaking systems in the HydroNet sample display the largest proportion of the highest anomaly metrics (with Z-scores indicating values of particular metrics in some cases more than 10 or even 20 reference group standard deviations away from class means), followed by storage systems. See McLaughlin 2014 for more detail on the nature of these various types of regime anomalies and a discussion of possible effects on fish populations of various types of regime anomalies, based on literature reviews.

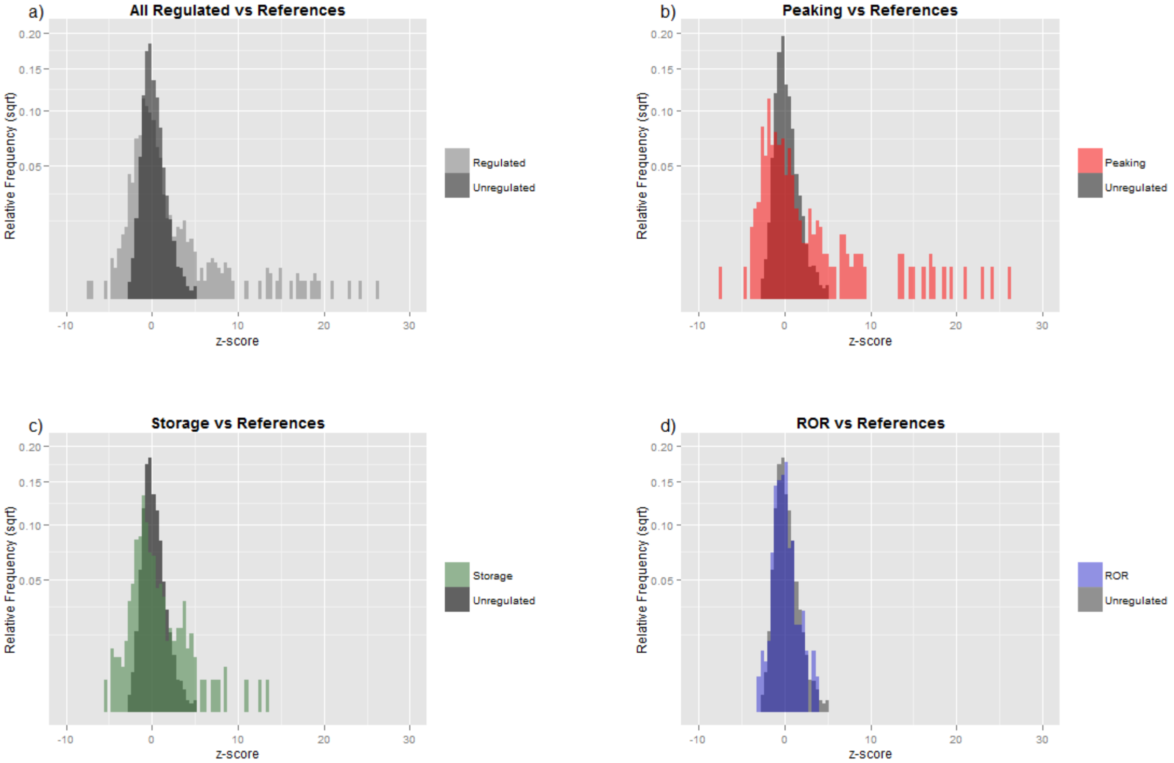


Figure A8. Histograms of all 70 anomaly scores observed over the 16 regulates sites studied across Canada, compared to histograms of reference site scores (i.e. scores at unregulated sites). Colored plots are histograms for subsets of the 16 sites classified by regulation type, overlain on these sites reference scores: b) peaking sites, c) storage sites and d) ROR sites.

CONCLUSIONS

It is important to recall that the purpose of the approach presented here is not to quantify the precise degree of **alteration** (see definition 1 given in this section's Outline) of the flow regime following damming (Richter et al. 1996 describe approaches to this end). Rather the aim is to clarify the degree of **anomaly** (cf. def. 2) of any regulated regime with respect to the range of unregulated regimes to which the regional fauna may be adapted. The approach presented here provides a tool to identify (and if needed rank) strongly anomalous flow regimes on dammed systems. It is assumed here that, in many cases, identifying anomalous regime at hydro sites (compared to regional norms) is simpler and possibly more relevant to managers than quantifying the precise degree of regime alteration, pre- versus post- damming. For example, when an altered flow regime due to hydro regulation remains well within the range of regimes observed in comparable unregulated rivers with healthy fish populations, the potential for negative effects on similar fish populations at the hydro site may be assumed to lower.

Note however that analyses of regime alteration (comparing pre- versus post- damming periods) are still useful and in some contexts may even be required to understand damming impacts on some key habitat types. Two examples of possible pathways of effects on fish populations of modest flow regime alterations are given next: these involve possibly significant changes to bed sediment composition in some reaches triggered by modest changes to high flows, or changes to summer thermal regimes triggered by modest changes in low flow regimes.

The details of natural bed sediment transport patterns and local grain size composition along alluvial rivers are well known to be highly sensitive to the particular high flow regime of each river. Sand, gravel, cobble bed composition and transport levels can be strongly modified after only minor reductions in mean annual flood levels and in ways that can affect fish habitat. In particular, in geomorphologically sensitive reaches along the newly regulated system (for example in non-bedrock reaches located close downstream of unregulated tributaries carrying high sand or silt loads), even a minor alteration of the regulated mainstem flow regime can have significant long-term impacts on post regulation wetted channel widths and bed sediment composition. The resultant long-term geomorphic changes to such sensitive reaches often take decades to become manifest, usually as an increase of sand encroachment within and/or the eventual burial of prior river bed gravels. These changes can significantly affect key fish spawning or invertebrate prey habitats. Interesting examples of various impacts to the geomorphic structure of fish habitats following regulation are given in Ligon et al (1995). However, because of the sensitivity of bed sediment transport patterns to flow levels, in some cases minor alterations in mean flood levels that can have significant impacts on fish habitats in some reaches of the regulated river may not be large enough to show up as a clear, regional scale anomaly in flood levels. Thus precise analyses of flow regime alteration (pre versus post), focusing on mean annual flood metrics, may remain important to predict such effects.

Similarly, estimates of degree of **alteration** (pre vs. post) of extreme, summer low flow levels (e.g. the 7day duration low flow of a few year recurrence, etc.) may be needed to predict regulation effects on summertime wetted habitat area, water temperatures and associated thermal stress levels affecting fish populations, particularly at the southern limit of their range. Here again, regional anomaly estimates of such low flow metrics may not be sensitive enough to detect regime alterations with significant effects on summer thermal stresses in some reaches.

LITERATURE CITED

Acreman, M. C., & Dunbar, M. J. 2004. Defining Environmental River Flow Requirements – a review. Hydrology and Earth System Sciences, 8(5), 861-876.

Arthington, A. H., Bunn, S. E., Poff, N. L., & Naiman, R. J. 2006. The Challenge of Providing Environmental Flow Rules to Sustain River Ecosystems. Ecological Applications, 16(4), 1311-1318.

Boisclair, D., Lapointe, M., Saint-Hilaire, A., Rasmussen, J.B., Senay, C., Lanthier, G., Bourque, G., Guénard, G., Macnaughton, C.J., Harvey-Lavoie, S. 2016. Modelling the effects of chemical and physical drivers on fisheries productivity metrics across rivers of varying hydrological regimes: lessons learned from NSERC HydroNet 2009-2015. DFO Can. Sci. Advis. Sec. Res. Doc. 2016/033. viii + 62 p.

Caissie, D. 2006. The thermal regime of rivers: a review. Freshwater Biology 51: 1389–1406.

Church, M. 2002. Geomorphic Thresholds in Riverine Landscapes. Freshwater Biology, 47(4), 541-557.

Daigle, A., St-Hilaire, A., Beveridge, D., Caissie, D., & Benyahya, L. 2011. Multivariate Analysis of the Low-Flow Regimes in Eastern Canadian Rivers. Hydrological Sciences Journal, 56(1), 51-67.

Fausch, K. D., Taniguchi, Y., Nakano, S., Grossman, G. D., & Townsend, C. R. 2001. Flood Disturbance Regimes Influence Rainbow Trout Invasion Success Among Five Holarctic Regions. Ecological Applications, 11(5), 1438-1455.

Junk, W. J., Bayley, P. B., & Sparks, R. E. 1989. The Flood Pulse Concept in River-Floodplain Systems. Canadian Special Publication of Fisheries and Aquatic Sciences, 106, 110-127.

Kennard, M. J., Pusey, B. J., Olden, J. D., Mackay, S. J., Stein, J. L., & Marsh, N. 2010. Classification of natural flow regimes in Australia to support environmental flow management. Freshwater Biology, 55(1), 171-193.

Ligon, F. K., Dietrich, W. E., & Trush, W. J. 1995. Downstream Ecological Effects of Dams: A geomorphic perspective. BioScience, 45(3), 183-192.

Magilligan, F. J., & Nislow, K. H. 2005. Changes in hydrologic regime by dams. Geomorphology, 71, 61- 78.

McLaughlin, F., Lapointe, M., Bourque, G., Boisclair, D. 2014. Using regional flow classes as references to analyse flow regime anomalies across a set of Canadian rivers regulated for hydro-electric production. Journal of Hydrology, 519: 307-28

McLaughlin, Fraser W.R. 2014. McGill University, (available online). Using Regional Flow Regime Classes to Identify Flow Anomalies in a Set of Canadian Rivers Regulated by Dams.

McManamay, R. A., Orth, D. J., & Dolloff, C. A. 2012a. Revisiting the Homogenization of Dammed Rivers in the Southeastern US. Journal of Hydrology, 424-425, 217-237.

McManamay, R. A., Orth, D. J., Dolloff, C. A., & Frimpong, E. A. 2012b. A Regional Classification of Unregulated Stream Flows: Spatial Resolution and Hierarchical Frameworks. River Research and Applications, 28, 1019-1033.

McManamay, R. A., Orth, D. J., Dolloff, C. A., & Frimpong, E. A. 2012c. Regional Frameworks Applied to Hydrology: Can Landscape-Based Frameworks Capture the Hydrologic Variability? River Research and Applications, 28, 1325-1339.

Mims, M. C., & Olden, J. D. 2012. Life History Theory Predicts Fish Assemblage Response to Hydrologic Regimes. Ecology, 93(1), 35-45.

Monk, W. a., Peters, D. L., Allen Curry, R., & Baird, D. J. 2011. Quantifying Trends in Indicator Hydroecological Variables for Regime-Based Groups of Canadian Rivers. Hydrological Processes, 25, 3086 - 3100.

Pluckridge, J. T., Sheldon, F., Walker, K. F., & Boulton, A. J. 1998. FloVariability and the Ecology of Large Rivers. Marine And Freshwater Research, 49, 55-72.

Olden, J. D., & Poff, N. L. 2003. Redundancy and the Choice of Hydrologic Indices for Characterizing Streamflow Regimes. River Research and Applications, 19, 101-121.

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., Sparks, R. E. 1997. The Natural Flow Regime. BioScience, 47(11), 769-784.

Poff, N. L., Olden, J. D., Merritt, D. M., & Pepin, D. M. 2007. Homogenization of Regional River Dynamics by Dams and Global Biodiversity Implications. Proceedings of the National Academy of Sciences of the United States of America, 104(14), 5732-5737.

Poff, N. L., Olden, J. D., Pepin, D. M., & Bledsoe, B. P. 2006. Placing Global Stream Flow Variability in Geographic and Geomorphic Contexts. River Research and Applications, 22, 149-166.

Poff, N. L. 1996. A Hydrogeography of Unregulated Streams in the United States and an Examination of Scale-Dependence in some Hydrological Descriptors. Freshwater Biology, 36, 71-79.

Poff, N. L., Richter, B. D., Arthington, A. H., Bunn, S. E., Naiman, R. J., Kendy, E., Acreman, M. 2010. The Ecological Limits of Hydrologic Alteration (ELOHA): A New Framework for Developing Regional Environmental Flow Standards. Freshwater Biology, 55, 147-170.

Poff, N. L., & Zimmerman, J. K. H. 2010. Ecological Responses to Altered Flow Regimes: A Literature Review to Inform the Science and Management of Environmental Flows. Freshwater Biology, 55(1), 194-205.

Richter, B. D., Baumgartner, J. V., Powell, J., & Braun, D. P. 1996. A Method for Assessing Hydrologic Alteration within Ecosystems. Conservation Biology, 10(4), 1163-1174.

Richter, B. D., Baumgartner, J., Wigington, R., & Braun, D. P. 1997. How Much Water does a River Need? Freshwater Biology, 37, 231-249.

Smokorowski, K. E., Bergeron, N., Boisclair, D., Clarke, K., Cooke, S., Cunjak, R., Dawson, J. 2011. NSERC 's HydroNet: A National Research Network to Promote Sustainable Hydropower and Healthy Aquatic Ecosystems. Fisheries, 36(10), 480-488.

Steuer, J. J., Stensvold, K. a., & Gregory, M. B. 2010. Determination of Biologically Significant Hydrologic Condition Metrics in Urbanizing Watersheds: An Empirical Analysis over a Range of Environmental Settings. Hydrobiologia, 654, 27-55.

Stromberg, J. C., Beauchamp, V. B., Dixon, M. D., Lite, S. J., & Paradzick, C. 2007. Importance of Low-Flow and High-Flow Characteristics to Restoration of Riparian Vegetation along Rivers in Arid South-Western United States. Freshwater Biology, 52(4), 651-679.

Whitfield, P. H., & Cannon, A. J. 2000. Recent Variations in Climate and Hydrology in Canada. Canadian Water Resources Journal, 25(1), 19-65.

Wooton, J. T., Parker, M. S., & Power, M. E. 1996. Effects of Disturbance on River Food Webs. Science, 273(5281), 1558-1561.

Zimmerman, J. K. H., Letcher, B. H., Nislow, K. H., Lutz, K. A., & Magilligan, F. J. 2010. Determining the Effects of Dams on Subdaily Variation in River Flows at a Whole-Basin Scale. River Research and Applications, 26, 1246-1260.

SECTION B - CHEMICAL DRIVERS: Nutrients as chemical drivers of fish biomass: empirical models of the relationship between the nutrient regime and fish biomass, and the effect of impoundment on river nutrient regimes

Rasmussen, Joseph B.
University of Lethbridge

PART I: Modelling fish biomass as a function of nutrient richness

Fish biomass (FB) can be used as an estimate of the productivity of an ecosystem, and the relationship between the fish biomass and the concentration of chemical nutrients in the water can be used to evaluate the importance of nutrients as drivers of fish productivity. Since nutrients are well known to drive both primary productivity and primary producers in both lakes (Dillon and Rigler 1974, Bachmann and Jones 1974) and rivers (Stockner and Shortreed 1978, Peterson et al. 1993) it is reasonable to expect that energy flow from primary producers to the “food base” that supports fish (secondary productivity), would be similarly dependent on the nutrient regime (Deegan and Peterson 1992, Hyatt et al. 2004).

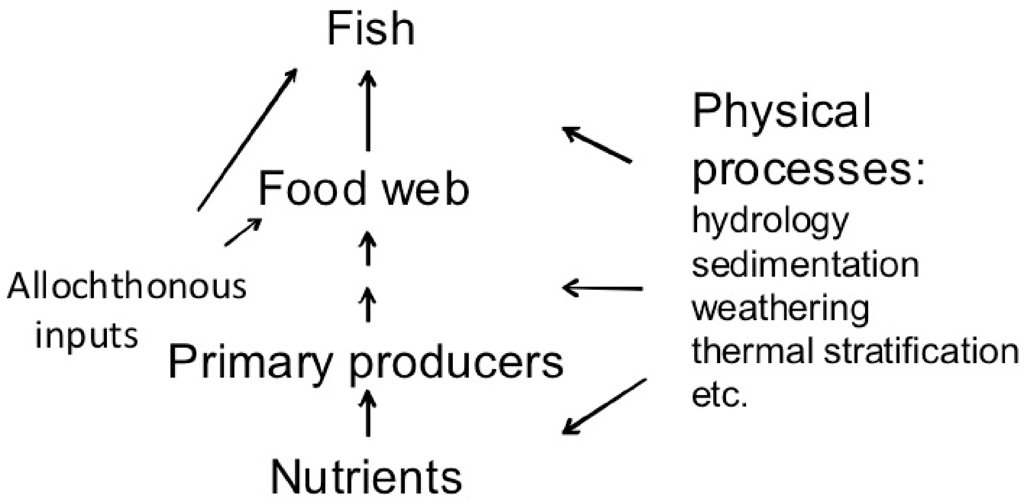


Figure B1. The dependence of fish abundance and productivity on the underlying trophic regime, and ultimately the nutrient regime, and the impact of physical factors that shape fish habitat.

Physical factors can modify the pathway through which nutrients cycle and energy flow; thus hydrology (flow regime, thermal stratification, wave action, etc.) and the climatic regime will influence the rates of all chemical and biological processes. Such factors can shape the habitat and thus affect fish directly, or indirectly, via their effect on intra and inter-specific interactions among fish, and on the distribution and renewal rate of food.

Effects of the nutrient regime can arise through geographic (regional or geomorphological) differences in nutrient export capacity of watersheds, through factors that affect the fate and distribution of nutrients within the drainage network, or through anthropogenic inputs (i.e. eutrophication) or land use differences. Regardless of the source of nutrient variability trophic status is among the most pervasive contributors to system variability, and needs to be factored into any comparisons of productivity, no matter what the trophic level of interest.

Aquatic ecosystems, even in species poor glaciated regions like Canada, can often support a very wide variety of species or ecotypes and life history stages, each of which can differ in their resource requirements, and thus the pathway through which they are affected by the underlying ‘food regime’ (Chu et al. 2003). Thus the complexity of the energy flow path shown in Figure B1 is not only a considerable underestimation of reality, but since the species and functional groups present in different aquatic habitats differ greatly from region to region within Canada, reflecting both large-scale historical zoogeographical factors, local colonization and extirpation process, human introductions and removals, and pure chance as well (Mandrak and Crossman 1992).

Objective

To establish a relationship between productive capacity for fish and the nutrient regime: TP (total phosphorus concentration in water), and TN (total nitrogen concentration).

Hypotheses

1. The working hypothesis was that the total phosphorus concentration in the water (TP) will be the best overall predictor of fish biomass (Downing and Plante 1993; Hyatt et al. 2004; Deegan and Peterson 1992). While we did not expect to see significant links between fish biomass and TN, we were open to the possibility that the TN:TP ratio might play a role in situations where the ratio is low (Downing and McCauley 1992).
2. Based on previous studies by Randall et al. (1995), a second hypothesis was that aquatic ecosystems with different flow regimes would have different relationships between Fish Biomass (FB) and nutrients, and that flowing water systems would in general be richer in terms of FB than lakes. It was also expected that since primary producers in littoral systems have access to a greater range of nutrient sources including benthic sources, that this would result in greater fish abundance, and that FB may be a negative function of depth.
3. Since fish communities with different species composition and food web structure differ in regard to the types of resources and food web paths that lead to fish, a third hypothesis was that systems that supported a wider range of species and functional groups would, by virtue of having a broader spectrum of basal trophic resources (e.g. sediment, benthic microflora and fauna, macrophytes and detritus, phyto-and zooplankton) have more FB (Hooper et al. 2005; Carey and Wahl 2011). While fish species richness may not necessarily be the best metric for comparing such trophic richness, it was expected that for systems with similar nutrient richness and physical habitat factors, would be an increasing function of fish species richness. Moreover, it was expected that regions with greater species richness e.g. Central Canada (Chu et al. 2003), would have greater FB than for example coastal islands (e.g. Newfoundland or Vancouver Island) where zoogeographical limitations have restricted post-glacial access of many fish families such as catostomids, cyprinids, coregonids, esocids, siluriids and cottids which play a significant trophic role in continental fish communities.

Methods

The relationship between fish biomass FB ($g \cdot m^{-2}$) and the total phosphorus (TP) and total nitrogen (TN) concentration of the water ($mg \cdot m^{-3}$) was determined empirically by comparing FB estimates from a wide range of published and unpublished studies to estimates of TP concentration. Estimates were obtained from a wide range of different types of fish habitats representing both flowing and standing water environments, ranging widely in depth, from shallow littoral systems to deep thermally stratified lakes, and from systems regulated by dams and other impoundments to free-flowing systems, where fish can enter or leave freely.

Estimates of fish biomass were obtained from published and unpublished sources, and were based on a wide variety of methods. Most estimates for rivers and streams were based on electrofishing, either backpack methods for small streams, or boat-based protocols for larger rivers. Some were based on mark and recapture methods, and in some cases a combination of these methods. Estimates for small lakes and ponds were obtained by a wide variety of methods, including index gill netting, mark and recapture, beach or purse seining, or a combination of these. Estimates for large lakes and reservoirs were obtained from hydroacoustics, usually dual-beam methodologies, often in combination with information on the relative abundance of species obtained from mid or deep-water trawls, gill-netting or purse seining. For some large lakes, estimates were based on quantitative surveys of salmon smolt migrating from the lake, or other types of fisheries surveys on target species, combined with information on community make-up based on trawls, seines or gill-nets. In this way estimates of the impact of nutrient fertilization on fish abundance could be obtained for a wide range of west coast sockeye salmon lakes.

Nutrient data were obtained either from the same published or unpublished reports as the fish data, however, often this information had to be retrieved from other publications or reports on the respective water bodies, published at a similar time. In some cases, the information was obtained from large-scale studies of nutrient export trends, either published or available on government websites, for whole river systems or regions, where GIS as well as historical information allowed good estimates for the appropriate portion of the river, lakes or reservoirs.

Results and Discussion

Comparison of fish biomass, nutrient richness and species richness among regions and ecosystem types

Significant and important differences among regions and ecosystem types can be seen in Figure B2 and Table B1. Fish Biomass estimates for river and stream sites were on average significantly higher than those of lakes, ponds and reservoirs, which is consistent with Randall et al. (1995) and Hypothesis 2. Total P and N levels in rivers and streams were also on average higher than those of lakes, reflecting the fact that lakes most commonly occur in the headwater portions of drainage systems, where nutrient levels tend to be lowest. Mean species richness did not differ between lakes and rivers.

Regions also differed significantly with regard to fish biomass for both lakes and rivers, with the Western/Cordillera and Newfoundland < Central Canada, USA & Europe in support of Hypothesis 3. Trophic richness also differed among regions, with Western/Cordillera < Newfoundland, Central Canada, USA & Europe.

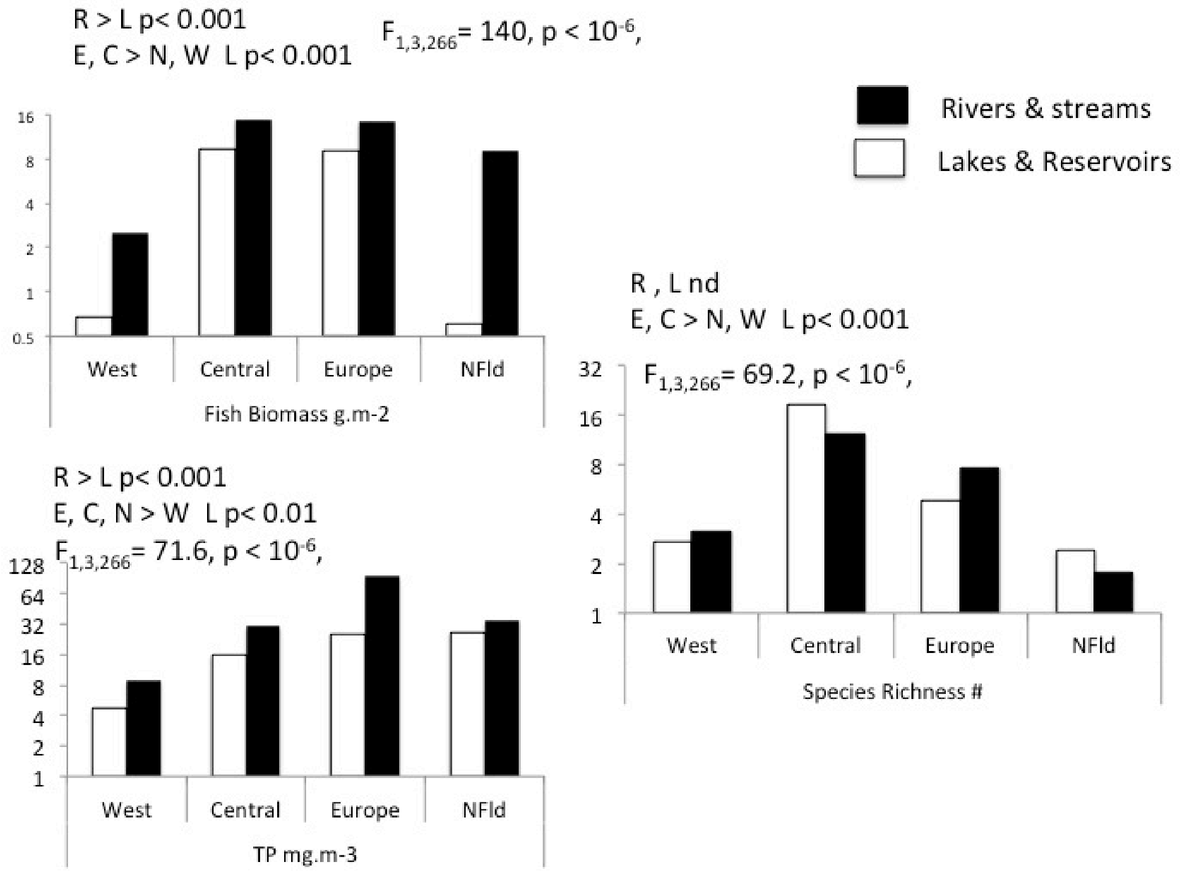


Figure B2. Summary comparison of fish biomass (a), total phosphorus concentration (b), and fish species richness (c), between rivers (filled bars) and lakes (open bars), across geographical regions. West = West coast of North America and associated cordillera; Central = Central Canada, Appalachia, and northern USA, Europe = north and central Europe, Nfld = Newfoundland and Labrador. Axes are $\log_2$ transformed. 2-way ANOVA, on Log transformed variables with Tukey post hoc comparisons.

Species richness was also very different among regions with Central Canada & USA, and Europe all significantly richer than Newfoundland and the West/Cordillera. The lake/river difference in mean fish biomass (per unit area), was strongest in the species poor regions (2-way ANOVA, FB X TP interaction, $p < 0.001$, Figure 2) with FB more than 4-fold lower in lakes than rivers in the West and NFLD. By contrast, lake fish biomass in the more species rich regions (Central North America and Europe), was only 30-50% lower than rivers.

Why are lakes in species poor regions prone to ‘under-produce’?

The faunas of these two species poor regions, for the most part, lack true lacustrine specialists, i.e. fish species that complete their entire life-cycles, from spawning to the adult stage, within the lakes (2007; Cote 2007; Cote et al. 2011; Clarke and Scruton 1999). The fishes that comprise the limnetic faunas in these regions are primarily salmonids that spawn in rivers and streams, producing young that migrate to the lakes for a portion of their juvenile life, before leaving again and to mature elsewhere, either at sea or in larger lakes or rivers. As a result, any factor that leads to a bottleneck in recruitment, e.g. limited availability or access to good spawning or nursery habitat, or barriers that restrict movement of either outgoing juveniles or returning adults, whether they be natural or man-made, will limit populations to a fraction of the lake’s productive capacity. Since the regional fish faunas are so species poor due to zoogeographical barriers that have limited post-glacial access from major refugia (Van Zyll de Jong et al. 2005; McPhail and Lindsey 1970), there are rarely other species present that are capable of compensating for such recruitment limitations, and as a result total fish biomass of such systems can be far below what the lakes could support. Recruitment limitations of this kind are not limited to lakes, but can of course occur in rivers and streams as well especially upstream of waterfalls or other barriers, but the generally greater availability of salmonid spawning and habitat, and the overall higher connectivity of rivers, makes rivers more likely to approach their productive capacity than lakes in species poor regions.

Recruitment limitation limits lake fish biomass in differently in these two species poor regions. The lakes in the Cordillera are much larger and deeper, their watersheds are steeper, and their oligotrophy is much more extreme than in Newfoundland. Moreover, the salmonids that use the lakes are different, and the role of lakes in their life-history is also different. In the West, the main species utilizing the large, deep fjord lakes is the Sockeye Salmon (*Oncorhynchus nerka*) and their land-locked counterpart the Kokanee salmon. Both spawn primarily in streams, usually inflows, and migrate to the lakes as fry, and spend one or more years as pelagic zooplanktivores, before migrating out, either as smolts going to sea for one or more years, or as adults migrating to spawn.

Hydroacoustic fish surveys were found for 46 such ‘sockeye’ lakes, and of these, only 16 were considered to have fish communities that approached productive capacity as judged by primary productivity, zooplankton biomass and nutrient richness (Shortreed et al. 2001; Hyatt et al. 2004). The remainder often had fish populations as much as 10-fold lower than the trophic regime was estimated to be able to support, and were considered unlikely to respond to nutrient fertilizations. For these lakes FB was uncorrelated with TP, and the mean size of fry or outmigrating smolts was uncorrelated to abundance (Hyatt and Stockner 1985). The most common reason cited for sockeye and kokanee populations being below capacity was limited access to good spawning habitat, with migration barriers also an often-cited factor (Shortreed et al 2001). Restricted access to suitable spawning gravels is greatly exacerbated by the steep terrain leading to washout of fine gravels, and waterfalls and impassible ‘chutes’ near the lakes on most inflow streams. In only one case was the presence of another species, the Three-Spined Stickleback *Gasterosteus aculeatus*, listed as a factor limiting sockeye abundance (Shortreed et al. 2001). While there are some other salmonids that do sometimes use these lakes, none are efficient pelagic zooplanktivores or lake spawners (McPhail 2007). As a result, poor species richness in the regional fauna of the Cordilleran region of Western North America makes the probability of ‘under saturation’ due to recruitment limitation greater, and this factor has its greatest impact on fish biomass in the large deep fjord lakes.

The lakes of Newfoundland are much shallower and less oligotrophic than the western fjord lakes, and while the geography of the landscape is much less steep, fine gravel can still be limiting in some areas because most glacial outwash is below sea level due to post glacial subsidence and increases in marine sea level (Batterson and Liverman 2010). Many of the lakes appear as widenings along relatively low-gradient rivers to which riverine fish have ready access (Cote et al 2011).

The main fishes that use the lakes are Atlantic Salmon parr (*Salmo salar*) and juvenile Brook Trout (*Salvelinus fontinalis*) (Clarke and Scruton 1999). Both are generalist feeders, utilizing mainly littoral benthic macroinvertbrates and neither are effective zooplanktivores. The Arctic Charr (*Salvelinus alpinus*) is present in Newfoundland, and its juvenile stages are efficient zooplanktivores, but the species is found in very few of the lakes (Van Zyll de Jong et al. 2005). The Three-Spined Stickleback is also found in some of the lakes but its contribution biomass is small (Ryan 1984). Newfoundland Atlantic Salmon are atypical in that they often move from rivers into lakes and feed on littoral macroinvertebrates (Ryan 1986). This likely reflects the fact that Newfoundland lakes lack the diverse array littoral zone competitors found in most continental lakes (Ekinaro and Gibson 1999). Similarly, the Brook Trout found in Newfoundland lakes are also juveniles that have moved from stream nursery habitats to lakes as larger juveniles. Neither species spends more than a fraction of its lifecycle in the lakes; the salmon smolt and migrate to sea following their lacustrine phase, and the brook trout move to streams and spawn.

The extremely low biomass in many of the Newfoundland lakes relative to their associated rivers and to their nutrient levels, is an indication of under-saturation. Moreover, the biomass of fish in these lakes is uncorrelated to nutrient richness, despite considerable range in trophic richness (Cote et al. 2011) and size of parr is not correlated with density (Ryan 1986). The abundance of both salmonid species within river systems is likely determined by the capacity of the spawning and nursery habitat in the streams and rivers, and the abundance of fish in the larger lakes appears to bear little relation to what the lake resources could support, since the lacustrine phase of the salmon and Brook Trout in Newfoundland is only a minor portion of their overall life-history. Thus the recruitment limitation leading to under-saturation in Newfoundland lakes likely results from lake habitat being available in higher proportion than spawning and rearing habitats for the two main salmonids that use the river systems. Just as on the west coast, the poor species richness in the Newfoundland fish fauna makes the probability of ‘under saturation’ due to recruitment limitation greater, since there is a lack of lacustrine specialists, especially zooplanktivores, whose abundance would be limited by the lake resources rather than the recruitment capacity of associated rivers and streams.

Interestingly, species-poor systems are not confined to salmonid dominated coastal regions. In Central North America and Europe, there are species poor headwater systems where the one or two species present are either Yellow Perch (*Perca flavescens* or *P. fluviatilis*), cyprinids (often the Roach *Rutilus rutilus*, but Northern Red-Belly Dace and Golden Shiner lakes are also found), centrarchids (usually Bluegill or Pumpkinseed Sunfish) or catostomids (usually White Sucker) (Horppila et al. 2010; Kelso and Johnson 1991).

While biomass in these lakes is invariably low compared to similar multi-species lakes where these same species are found in communities of 5-10 species, there are no cases of extreme under production, where biomass is over an order of magnitude deficient relative to trophic resources, such as the cases described in coastal salmonid lakes. The likely reason for this is that recruitment limitation is much less likely to occur in perch, minnow or sucker lakes, since these species are capable of spawning and completing their life cycles in lakes or slow moving streams, and do not have specialized requirements such as clean fine gravels. As a result bottlenecks related to access to spawning grounds and/or habitat fragmentation are not likely to occur in species poor perch, minnow or sucker systems.

*Table B1. Comparison of mean values (arithmetic mean ± SE, geometric mean ×,÷ error factor, and median and 25th & 75th %iles) of FB, TP, Sp and N within and among regions and ecosystem types. Geometric mean = 10^mean log10, and error factor (%) = [1 - 10^(SE of log10 values) * 100].*

	Fish Biomass (FB) g$\cdot$m^{-2}	**Total Phosphorus (TP) mg$\cdot$m^{-3}**	**Total Nitrogen (TN) g$\cdot$m^{-3}**	**Species Richness (#Sp)**	**N**
General	7.57 ± 3.9 3.47, 9.6% 3.88, 1.23, 9.5	30.0 ±1 3.0 16.3, 33% 15, 6.1,27.6	0.59 ± 0.12 0.28, 13% 0.21,0.12, 0.56	6.7 ± 3.5 3.72, 32% 3, 2, 8	235
Rivers and streams	10.2 ± 2.8 5.03, 28% 5.5, 2.4, 12.5	41.9 ± 11.2 22.4, 20% 22.5, 10.5,110	0.82 ± 0.16 0.51, 18% 0.43,0.22, 1.90	6.2 ± 3.4 3.9, 16% 3, 2, 8	84
Lakes and Reservoirs	4.9 ± 2.1 1.4, 31% 1.7, 0.6, 5.5	13.8 ± 1.6 8.9, 10% 7.9, 5.0, 20	0.22 ± 0.05 0.19, 13% 0.15,0.10, 0.42	7.1 ± 2.5 3.7, 15% 3, 2, 8	151
Newfoundland Labrador	4.9 ± 2.5; 2.2, 19% 2.1, 0.8, 3.7	30.3 ± 6.0; 24.2, 15% 22, 10.7,32.5	0.48 ± 0.10; 0.30, 23% 0.30,0.20, 0.54	2.1 ± 0.09; 1.9, 20% 2, 1, 3	34
Central Canada and USA	12.1±2.5; 6.9±24% 5.1,2.1, 12.5	22.9±6.5; 16.4±16% 13, 7.5,21.5	0.35±0.10; 0.26±21% 0.27,0.14, 0.45	15.5 ±1.5; 9.5±13% 8, 5, 12	78
Western Cordillera	1.61±0.6; 0.62±25% 0.61,0.39,1.08	6.62±1.25; 5.21±13% 5.1, 3.2,7.0	0.12±0.0.02; 0.0.07±18% 0.10,0.06, 0.13	.9 ±0.7; 2.4±16% 2, 2, 4	95
Europe	11.7 ± 2.8 7.4, 16% 8.5,4.1, 17.2	60.1 ± 11.3 35.4, 20% 49, 29.5,105	1.31 ± 0.25 0.85, 22% 0.82,0.35, 1.92	6.3 ± 1.2 4.3, 16% 5, 3, 10	28

The relationship between trophic richness and fish biomass

As is the case for other components of aquatic ecosystems such as phytoplankton (Dillon and Rigler 1974; Bachmann and Jones 1974) and zooplankton, and zoobenthos (Hanson and Peters 1984; Rasmussen 1988), by far the best statistical measure of nutrient richness for assessing the trophic richness of systems for fish is the total phosphorus (TP) concentration of the water (Hanson and Leggett 1982; Ney et al. 1990; Randall et al. 1995)—as predicted by Hypothesis 1. While total nitrogen (TN) is generally correlated with total phosphorus, and can sometimes provide reasonable predictions of trophic richness, TN is usually present in excess of the Redfield ratio, and more variable than TP, and as a result is a much weaker predictor, except in cases of severe N-limitation (Dillon and Rigler 1974).

Since nutrient-based models of fish productive capacity are intended to estimate the potential biomass that a given trophic regime can support, systems that exhibited ‘under-saturation’ due to recruitment limitation, as outlined previously were excluded from the regression analyses. Thus of the 235 estimates listed in Table B1, 201 (84 rivers, 117 lakes) from the four geographic regions were included in the log-log regressions (Tables B2-B4).

Log TP was a highly significant predictor of Log FB in all regions; moreover rivers and lakes did not differ in these FB vs TP models indicating that the main driver of higher fish biomass in rivers (Table B1) was their overall greater nutrient richness.

Although Log TP was a significant predictor in all regions, both intercept and slope varied significantly among regions; intercepts (Table B2) varied by more than an order of magnitude (-0.83 to 0.24), and slopes also varied significantly from 0.63 to 1.26. Intercept and slope estimates were not correlated to each other, but intercepts were highly correlated to mean species richness of the data set (r=0.95, n=6, p=0.003), with the highest value in the species rich Appalachian reservoirs, and lowest values in the West and Newfoundland. Intercepts were also negatively correlated with the precision of the model (R^2), with the strongest regressions tending to have higher intercepts (r=0.69, n=6, p=0.05). While slope was not significantly correlated with either R^2 or species richness, the data sets with the greatest range of species richness tended to have the lowest R^2 values.

The close relationship between intercept and species richness implied that much of the residual variability in these FB vs. TP relationships is related to species richness, and when Log S was tested it was highly significant in the overall model (Figure B4) and in all but the smallest of the regional data sets (Table B3). Thus even in regions such as Newfoundland and the West, where species richness was low and did not vary over a broad range, it still made a statistically significant contribution to the models. Besides the overall model, Log S made the strongest contribution in the Central region, where species richness was overall highest, and also exhibited the greatest range of variation (Table B1). Predictions were also improved slightly by the addition of Log mean depth, which was a significant (-) factor in the overall model and in all but one of the regions (Table B3).

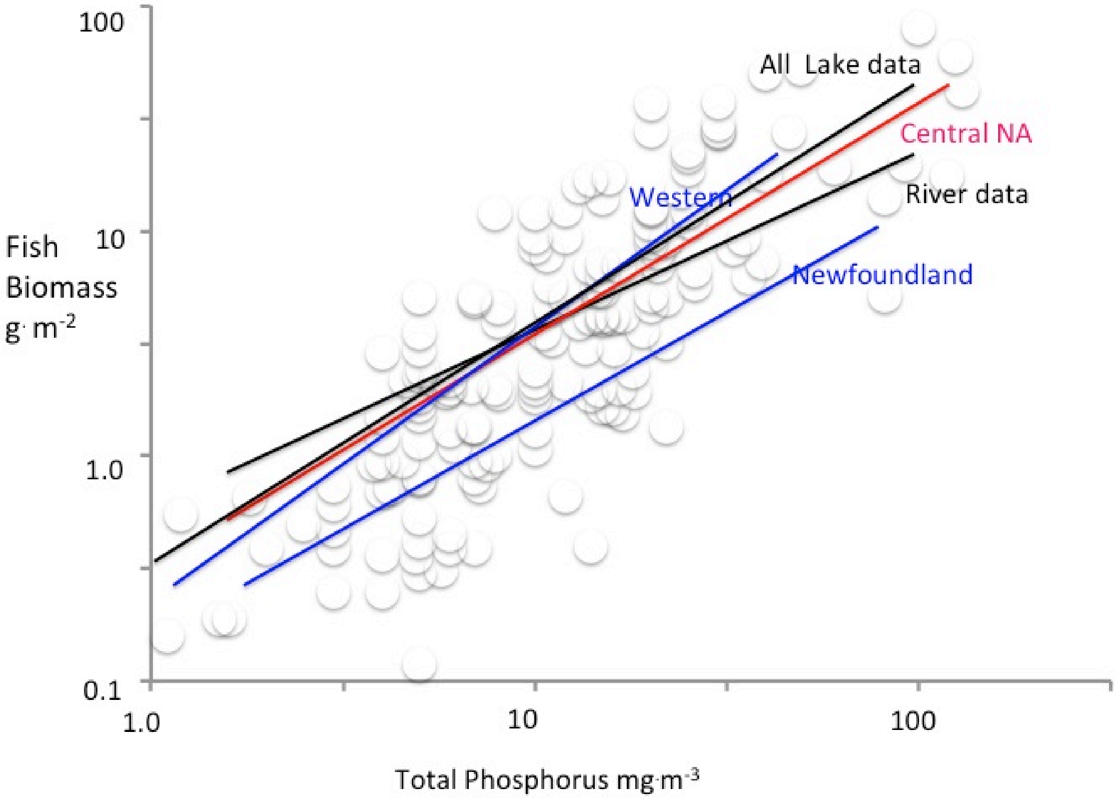


Figure B3. Log FB vs Log TP Relationships for different regions, compared to previously published relationships.

These multiple regression models retain the predictive effect of log TP, which was strong in all regions and no longer significantly variable among regions. They incorporate the predictive power of species richness, which captured all of the significant regional differences of the previous model, and the effect of mean depth (Log Dm t=-3.0). This variable captured both the difference between shallow and deep lakes, and also helped capture the effect of flowing versus standing water. While rivers, in general, had higher fish biomass than lakes (Table B1), they also had higher TP concentrations on average than lakes, and thus the predictive power of TP, combined with mean depth captures the main differences both within and among lakes and rivers, and the regional differences as well, to the extent no region had significant residuals, and in addition there were no significant interaction terms between region and the slope of either LogTP, Log S or Log Dm.

Table B2. Comparison of Intercepts and Slopes among regions, and with previously published studies.

Log$_{10}$ FB = Intercept + slope * Log$_{10}$ TP	**Intercept ± SE**	**Slope ± SE**	**RMS, R^2**	**Log S # species**	**N**
Central NA	$-0.50_{\pm 0.13}$	$+1.11_{\pm 0.11}$	0.36, 0.56	1.18	77 lakes, rivers
Western NA	$-0.63_{\pm 0.10}$	$+0.91_{\pm 0.13}$	0.30, 0.44	0.46	64 lakes, rivers
Newfoundland	$-0.78_{\pm 0.30}$	$1.01_{\pm 0.23}$	0.41, 0.45	0.30	34 lakes, rivers
Europe	$-0.69_{\pm 0.24}$	$+0.95_{\pm 0.18}$	0.33, 0.69	0.80	26 lakes, rivers
All lake data	$-0.46_{\pm 0.07}$	$+1.14_{\pm 0.06}$	0.26, 0.59	0.42	151
All river data	$-0.21_{\pm 0.08}$	$+0.70_{\pm 0.07}$	0.36, 0.45	0.45	78
Hanson & Leggett 1982	-0.23	0.71	MSE =?, 0.75	---	18 Central lakes
Ney et al. 1990	0.24	1.02	MSE =?, 0.84	1.70	N=21 Appalachian Reservoirs
Randall et al. 1995	$-0.29_{\pm 0.16}$	$0.63_{\pm 0.11}$	0.28, 0.65	---	18 Global lakes & rivers

Why is species richness such a strong predictor?

The power of fish species richness to influence the relationship between trophic richness and fish biomass has been little studied, and in fact, has been generally ignored by aquatic ecologists. Since species differ in life history, habitat requirements, and sensitivity to environmental risks, species richness can potentially buffer systems against recruitment limitation, thus providing redundancy by hedging against risks. However, this is not likely an important factor here since the sites that were considered to be strongly undersaturated were removed *a priori* from the data set. The contribution of species richness in the multiple regression models (Table B3) likely reflects functional diversity among species in trophic ecology. Thus the differences among species in food resources that they use, and the associated food web pathways and production sources that drive energy flow within the community likely means communities with greater species richness have access to a broader range of energy and nutrient sources (Carey and Wahl 2011). Although most species overlap trophically to some extent, and many are ‘trophic generalists,’ the extent to which they differ can lead to additive effects on community biomass. For example, the food chain in a lake that lacks pelagic zooplanktivores would make far less efficient use of plankton productivity than one that contained efficient zooplanktivores, and fish biomass, in the latter system should be higher. Similarly, efficient microbenthivores, herbivores, detritivores, deposit feeders, and periphyton feeders should all expand the trophic spectrum of the community significantly. This principle, the combination of redundancy and functional complementarity, has been shown to explain the observed increases in the productivity, biomass and stability of grasslands (Tilman and Downing 1994; Hooper et al 2005) and other plant communities; however, the significance of fish biodiversity for productivity has received little consideration.

Table B3. Comparison of multiple regressions predicting Log FB in different regions.

Log FB = A + B*Log TP+ C*logS+ D*log Dm	**A ± SE**	**B ± SE**	**C ± SE**	**D ± SE**	**RMS, R^2**	**N**
Central NA	$-.65_{\pm0.11}$	$0.82_{\pm0.10}$	$0.60_{\pm0.08}$	$-0.21_{\pm0.06}$	0.30, 0.74	77 lakes, rivers
Western NA	$-.59_{\pm0.14}$	$0.72_{\pm0.16}$	$0.37_{\pm0.16}$	$-0.07_{\pm0.03}$	0.28, 0.75	64 lakes, rivers
Newfoundland	$-.32_{\pm0.21}$	$0.89_{\pm0.16}$	$1.26_{\pm0.33}$	$-52_{\pm0.27}$	0.27, 0.76	34 lakes, rivers
Europe	$-.64_{\pm0.23}$	$0.81_{\pm0.16}$	$0.52_{\pm0.32}$	$0.05_{\pm0.20}$	0.30, 0.75	26 lakes, rivers
General Model	$-.89_{\pm0.07}$	$1.03_{\pm0.06}$	$0.59_{\pm0.05}$	$-0.09_{\pm0.03}$	0.28, 0.82	201 lakes, rivers

Species richness is likely only a crude metric by which to represent a potentially complex effect, and further research may show that indices that quantify both redundancy and complementarity among species, will provide more powerful predictions. Log S is, however, a simple and reasonable proxy, whose predictive strength seems compelling (Table B3). The fact that species richness contributes almost as strongly to biomass prediction in some of the regional submodels as it does in the integrated data set that spans across region (Table B3) is potentially very important. This is so because species richness varies greatly across regions, and models that incorporate this variable might thus be prone to confounding regional differences. However, species richness also varies considerably within regions, as headwater lakes and streams, even in species rich areas such as Central Canada, often have very few species, due to dispersal barriers and other factors (Jackson et al. 2001). Thus although species richness varies considerably less within than across regions, the fact that it makes a strong contribution within regions, as well as among, weakens any argument that its effects simply result from spurious correlations with other regional differences. Moreover, the fact that adding Log S to the models succeeded in removing all significant residual regional differences between the regional submodels further supports its significance.

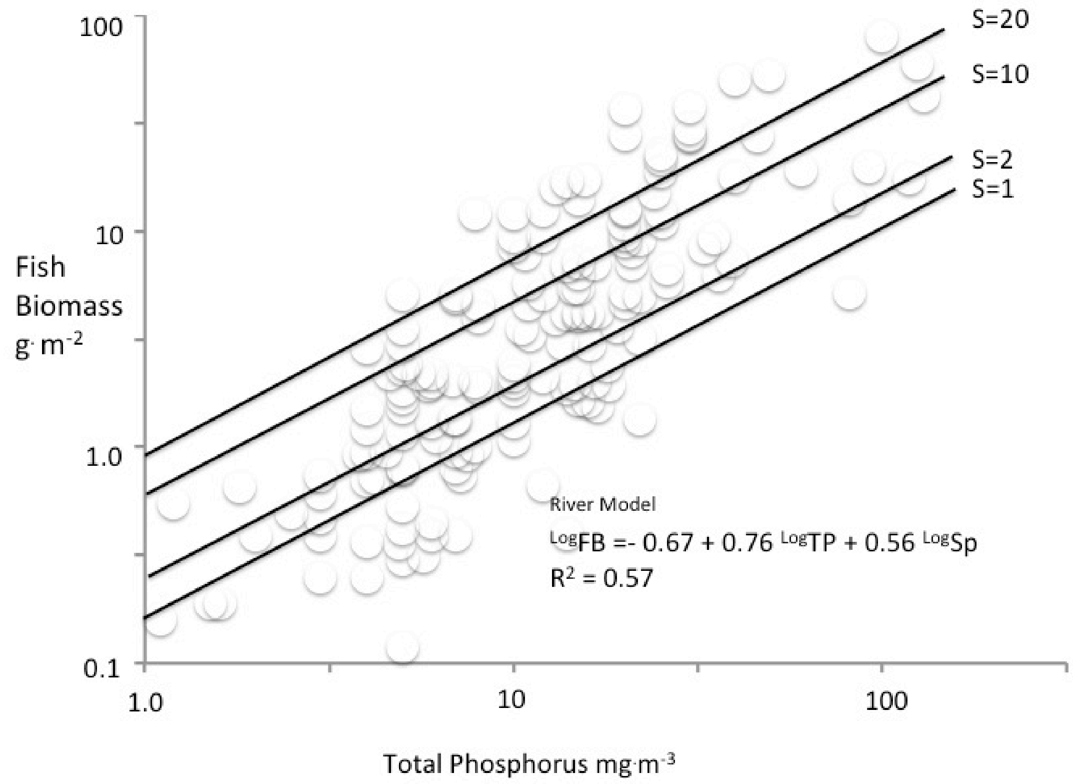


Figure B4. The combined influence fish of trophic richness (total phosphorus) and fish species richness on fish biomass. The plots are based upon the General model in Table B3 with mean depth set to 1m.

Lakes vs. Rivers

Although the previous analyses yielded models wherein rivers and lakes did not differ significantly, further analysis of the effect of depth for lakes showed that the slope of the Log FB vs Log TP relationship was increased significantly with lake depth. Thus shallow lakes had FB/TP slopes much less than 1, whereas the slope for deep lakes was close to 1.0. Thus the interaction between the two variables, Log TP* Log Dm was highly significant yielding the following multiple regression model for lakes and reservoirs.

$$^{Log}FB = -0.21_{\pm 0.09} + 0.34_{\pm 0.07}\,^{Log}TP + 0.68_{\pm 0.04}\,^{Log}Sp - 0.46_{\pm 0.07}\,^{Log}Dm + 0.38_{\pm 0.06}\,^{Log}Dm{*}^{Log}TP;$$

$R^2 = 0.85$, RMS=0.26.

The interaction between TP and Dm is shown in Figure B5. Thus the effect of water column richness increases with depth of the water column, which likely reflects the increasing importance of water richness with increasing depth. The low FB vs TP slope for shallow lakes is reasonable given the potential for increased influences of benthic and allochthonous resources to productivity.

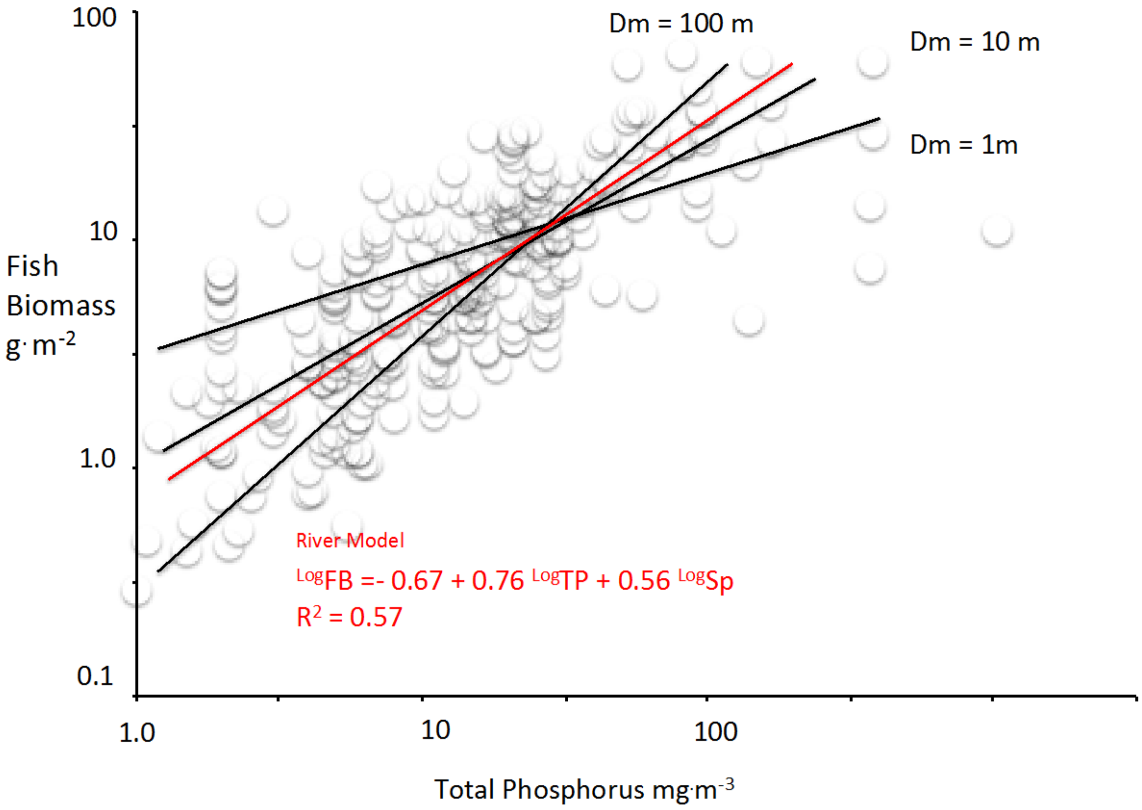


*Figure B5. The effect of lake depth on the relationship between Log FB and TP; a graphical representation of the TP * Dm interaction term in the multiple regression model shown. The general river model is shown for comparison (red).*

No interaction between TP and depth could be detected for rivers, and the slope of the FP vs TP relationship for rivers was intermediate between the values obtained for deep and shallow lakes.

$$^{\text{Log}}\text{FB} = -\ 0.67_{\pm 0.09} + 0.76_{\pm 0.08}\ ^{\text{Log}}\text{TP} + 0.56_{\pm 0.06}\ ^{\text{Log}}\text{Sp};\ R^2 = 0.57,\ \text{RMS} = 0.30$$

The coefficient for species richness was similar in magnitude and predictive power to that obtained in the lake model, but the overall precision of the river model was considerably lower than that obtained for lakes.

Using Production-Biomass models to estimate renewal rate of a fishery: a worked example based on Williston Reservoir

While TP has been used to predict commercial fish yields (Hanson and Leggett 1982) as well as sportfish yields (Jones and Hoyer 1982), the precision with which this can be done is limited, since the proportion of the total fish community that actually contributes to the fishery will depend on many factors, both ecological and social. The proportion of community biomass targeted by a fishery is usually very high in boreal lakes (Rawson 1951) whose communities contain whitefish, ciscoes, perch, walleye and lake trout of targetable size to commercial and recreational fisheries. While sockeye salmon smolts are not directly targeted by fisheries, they are of course a highly valued fisheries resource, and that can constitute as much as 90% of the biomass in many west coast lakes (Hyatt et al. 2004). Alternatively, many lakes may contain significant biomass of large carp, chubs, shiners, bullheads and suckers (Carlander 1955) that are often not targeted by fisheries, and in such situations only a few percent of community biomass may be contributing to fisheries. Clearly, the proportion of the community biomass targeted by a fishery is highly variable, and will depend on the types of fish species present in a region, the structure of the food web, and to a very large extent on social factors such as which fish species are ‘desirable’ and which are not. None of these factors are direct or predictable functions of the nutrient regime, at least not on a broad scale across regions that differ broadly in their faunas and in their culture.

If however, from the fisheries management perspective a list of target species and their size ranges can be decided on and the proportion to which these fishes contribute to the total biomass of the community, this proportion can then be used as a weighting factor by which to multiply a community biomass prediction from models such as those described in Tables B3 & B4. The productivity/biomass (P/B) ratio (specific productivity) of these fish will be a function of climate/latitude and body size and can be predicted by models that relate P/B to latitude, mean annual temperature and body size (Randall 1992; Downing and Plante 1993), or from tabulated measurements of P/B for various species adjusted for latitude (e.g. Carlander 1969), and averaged across the species and sizes targeted by the fishery. These estimates of P/B can then be multiplied by the weighted biomass estimate to yield an estimate of the productive capacity of the fishery. Such an approach can either be conducted on a species by species basis, or averaged across the fishery.

To illustrate the use of P/B models to evaluate the productive capacity of a fishery, I will use a pertinent example of Williston Reservoir on the Peace River in north-eastern BC. Williston Reservoir has a mean TP value of 5.8 mg.m^{-3}, mean depth of 42 m, a fish community of 5 species, and its mean fish biomass based on hydroacoustic surveys is 1.6 g.m^{-2}. This mean biomass falls somewhat below the expected value from the general standing water model (1.8 g. m^{-2}).

$$^{Log}FB = -0.21_{\pm 0.09} + 0.34_{\pm 0.07}\,^{Log}TP + 0.68_{\pm 0.04}\,^{Log}Sp - 0.46_{\pm 0.07}\,^{Log}Dm + 0.38_{\pm 0.06}\,^{Log}Dm{*}^{Log}TP;\quad R^2 = 0.85,\ RMS = 0.26.$$

Since the RMS of this log-log model = 0.26, the error factor associated with this estimate is 1.82, and thus the fish biomass estimate for Williston Reservoir is well within the error bounds of the model.

The general river model predicts a fish biomass value of 2.0 g.m^{-2} for a river with TP 5.8 and 5 species. This log-log model (Figure B5)

$$^{Log}FB = -0.67_{\pm 0.09} + 0.76_{\pm 0.08}\,^{Log}TP + 0.56_{\pm 0.06}\,^{Log}Sp;\quad R^2 = 0.57,\ RMS = 0.30$$

has an RMS value of 0.30 (error factor = 2.0), and thus the observed estimate is also well within the error bounds of this model, although the observation is consistent with the pattern that deep oligotrophic standing waters have fish biomass estimates that fall below rivers of the same trophic status (Figure B5).

The gill net samples taken in Williston Reservoir to compare with the hydroacoustic survey studies recorded 5 species of fish; however, lake whitefish were by far the most abundant, and constituted the only significant targetable species from a fisheries perspective. Lake Whitefish from 0.5 – 1.5 kg, (35-45 cm) was the range of targetable fish sizes in Williston Reservoir. Although this group made up > 85% of the biomass of fish from the gill net catches, the hydroacoustic analyses showed that this group in fact made up on average around 20% of the biomass of the Williston Reservoir fish community. This is consistent with other studies that have shown that gill net samples often overestimate the proportion of the community made up by large fish and underestimate the proportion made up by small fish (MacLellan and Hume

2011; Prchalova et al. 2008, 2009, 2010). While this may partly reflect mesh size biases, it mostly reflects the greater range of mobility of larger fish compared to small ones, which is a major contributing factor in determining the catch of gill nets and other passive gear (Prchalova et al. 2010).

In order to estimate the productive capacity of a fishery targeting the 0.5-1.5 kg whitefish which made up 20% of the total biomass of the reservoir, it is possible to first estimate the P/B ratio of these fish using a model of Downing and Plante (1993)

^{Log} Productivity (kg/ha) = 0.20 +0.93 * ^{Log} Biomass (kg/ha) - 0.19 * ^{Log} W(g) + 0.02 * MAT(^{o}C)

For a fishery targeting a biomass of 3.2 kg.ha^{-1} (20% of total biomass of 1.6 g. m^{-2} or 16 kg ha^{-1}), made up of fish maximum size 1.5 kg fish such as in the Williston example (mean annual temperature: MAT = -2^{o}C), the model predicts productivity of 1.07 kg.ha^{-1}. This implies a P/B ratio of 1.07/3.2 of 0.33, which is somewhat lower than the values for lake whitefish in the Downing and Plante (1993) data set. Alternatively, the average of eighty lake whitefish P/B ratios for the populations in their data set was 0.21. Applying this value (i.e. 3.2 * 0.21) yields a productivity estimate of 0.67 kg.ha^{-1}.

If one then makes the assumption that a sustainable harvest should be no greater than 10 % of potential productivity (Downing and Plante 1993), then a reasonable estimate for the potential sustainable yield of such a whitefish fishery on Williston Reservoir would be somewhere between 0.07 and 0.11 kg ha^{-1}.

There are some potential issues with this approach that are difficult to assess, since the estimates of P and B upon which the Downing and Plante model was based include all age classes for a given species rather than just older larger sized individuals that would be targeted by the fishery. Thus specific productivity of these larger fish would be expected to be lower than that of the overall population. Part of the reason for the ‘10% assumption’ mentioned above is to allow for the fact that the renewal rate of the biomass actually targeted by the fishery will be lower than that estimated for the whole population. Thus adherence to this fairly conservative rule of thumb should protect the fishery against overexploitation.

This worked example demonstrates that while fish biomass estimates are applicable to whole communities, and not just the portion of the community target by fisheries, fish biomass estimates such as those provided by biomass models can be used as the starting point to estimate the sustainable yield of a fishery.

PART II: Effects of river impoundment/regulation on nutrient regimes and downstream fish biomass

In standing water, biological cycling of nutrients by plankton can produce both sinks, due to sedimentation (Stanley and Doyle 2002; Bosch 2008), and sources, due to internal loading (Nurnburg 2007), in standing water. Impoundment of waterways by dams, therefore, has the potential to influence downstream nutrient regimes by disrupting the hydrological flow regimes, damping seasonal variability by trapping nutrient pulses (Power et al. 1996: Bunn and Arthington 2002), and in this way influence potential productivity for fish (Friedl and Wuest 2002; Poff and Ward 1989). Alternatively, a run-of-the-river facility may exhibit minimal upstream ponding, and thus have minimal downstream impact on nutrient regimes.

The extent to which the nutrient regimes of downstream receiving waters in regulated rivers are affected by impoundment would be expected to increase with biological productivity, the degree of thermal stratification and the extent to which down stream flows are hypolimnetic (Nurnburg 2007). Modified temperature regimes in stratified reservoirs can cause oxygen depletion in hypolimnetic waters and stimulate internal loading if organic sedimentation rates are high; this would make the reservoir a source of enrichment for downstream waters. Alternatively, pulses of sediment bound nutrients might be permanently trapped within the reservoir, making the impoundment an effective sink, at least seasonally (Stanley and Doyle 2002). Thus downstream waters may be enriched, impoverished, or alternatively, unaffected depending on the types of physical and biological processes taking place within the reservoir.

Specific Objectives

1. Compare the nutrient regimes in regulated and nearby unregulated (reference) rivers across diverse ecoregions of Canada,
2. Evaluate the extent to which Canadian hydroelectric reservoirs affect the nutrient regimes of downstream rivers, and,
3. Estimate the potential impact on fish biomass associated with the nutrient variability within and among regions, and that associated with downstream effects of impoundments, using predictions from the models generated in the previous section.

Hypotheses

1. It was expected that regulated rivers might exhibit different nutrient regimes from unregulated rivers due to the possible effects of impoundment on sedimentation nutrient transport (Bosch and Allan 2008; Bosch et al 2009), and that this difference would increase with nutrient richness since effects of sedimentation nutrient transport and shifts in biogeochemical processes would be expected to be greater in nutrient-rich rivers (Nurnburg 2007; Friedl and Wuest 2002).
2. It was expected that rivers downstream of reservoirs might exhibit nutrient regimes that differ from those found upstream, and that the downstream nutrient levels might be higher in some cases (reflecting internal loading processes within the reservoir) and lower in other cases reflecting the importance of sedimentation within the reservoirs. The shifts in nutrient concentration (both positive and negative) downstream relative to upstream would likely increases in magnitude with nutrient loads, as both sedimentation (Bosch et al 2009; Friedl and Wuest 2002) and internal loading (Nurnberg and Peters 1984; Gomez et al. 1999) might be expected to increase.

Methods

The HydroNet sampling program developed across Canada identified paired regulated (Hydropower) vs unregulated systems in BC, AB, ON, QC, NB and NL in 2011 and 2012 (Figure B5). Reference rivers are chosen as the closest regional representative of the corresponding regulated system (Verdonschot 2000), having comparable climate and geomorphology as outlined in Smokorowski et al. (2011). Sites range from BC to NL in the Cordillera, Prairies, Boreal Shield and Atlantic Maritime ecozones. Nutrients were analyzed for 16 regulated and 16 reference sites with 175 grab samples collected across the six provinces.

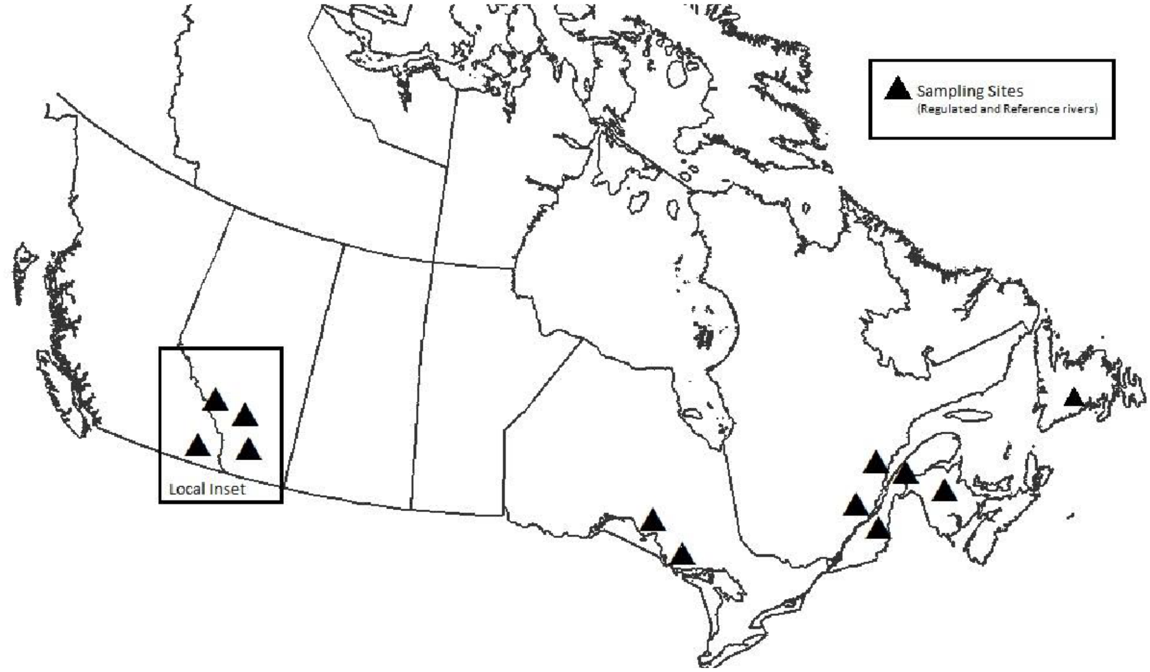


Figure B6. Regional distribution of Canadian sampling sites: triangle refers to location of multiple reference and regulated sites it each region, N= 33.

Table B4. Regulated and reference sites sampled by HydroNet in different ecoprovinces of Canada.

Province	River	Latitude	Longitude	Regulated/ NonRegulated	Ecoprovince
NFL	West Salmon R.[1]	48.1728	-56.2309	R	Boreal Shield
Ontario	Magpie R.[2]	48.0217	-84.8122	R	Boreal Shield
Ontario	Mississagi R.[3]	46.8747	-83.3193	R	Boreal Shield
Quebec	Saint Jean R.[4]	48.1978	-70.2533	R	Boreal Shield
Quebec	Etchemin R.[5]	46.6674	-71.0856	R	Atlantic Maritime
Quebec	Fourchue R.[6]	47.6506	-69.5123	R	Atlantic Maritime
NB	Dee R.[7]	-67.0062	47.1218	R	Atlantic Maritime
NB	Serpentine R.[7]	-66.9924	47.1960	R	Atlantic Maritime
BC/Montana	Kootenay (below Libby)[8]	48.3669	-115.3198	R	Montane Cordillera
BC	Elk R. (below Elko)[9]	49.2797	-115.0998	R	Montane Cordillera
BC	Bull R. (below Aberfeldie)[10]	49.4927	-115.3618	R	Montane Cordillera
Alberta	Kananaskis R. (below Pocaterra)[11]	50.7023	-115.1183	R	Montane Cordillera
Alberta	Kananaskis R. (below Barrier)[14]	51.0442	-115.0298	R	Montane Cordillera
Alberta	Elbow R. (below Glenmore)[13]	51.0089	-114.0862	R	Prairies
Alberta	Old Man R.[12]	49.5591	-113.8758	R	Prairies
Alberta	Waterton R.[15]	49.3331	-113.6664	R	Prairies
Alberta	St. Mary's R.[16]	49.3613	-113.0624	R	Prairies
NFL	Twillick Br.[1]	48.1155	-55.57.66	NR	Boreal Shield
Ontario	Batchawena R.[2]	46.9980	-84.5230	NR	Boreal Shield
Ontario	Aubinadong R.[3]	46.8944	-83.4129	NR	Boreal Shield
Quebec	Petite Saguenay R.[4]	48.1977	-70.0579	NR	Boreal Shield

Rivers up and downstream of 15 reservoirs were also sampled in the Kootenay region of southeastern BC and east of the Rocky Mountains in southern Alberta in the Cordillera and Prairie ecozones. The sampling design focused on comparison of inflows and outflow to identify upstream/downstream differences in nutrient concentrations within the same system on both run-of-the-river and peaking systems. Nutrient concentrations for systems with several major inputs to the reservoir were weighted by averaged discharge for the sampling month, to produce the estimate of upstream nutrient concentrations. The reservoirs chosen were mixed-use water bodies, managed for hydropower generation, recreation, drinking water supply, irrigation and flood control (Table B5-B6). To provide the simplest possible basis for the upstream/downstream comparison avoiding the complexity associated with flood pulses, sampling was done at baseflows. To provide an upstream/downstream comparison for a similar scale reach on a free-flowing river, we sampled the Belly River upstream of its diversion structures.

To ensure sampling consistency, clean technique and simplicity for HydroNet participants to follow, samples were collected in standard 500 ml acid-washed polyethylene Nalgene bottles supplied to participating partners across Canada prior to field sampling. All water samples were kept cool (4^{o}C) and shipped to the University of Alberta Biogeochemical lab for TN and TP analysis.

TN, TP, DIC analyses (Biogeochemical Analytical Laboratory University of Alberta) were carried out as follows. Total nitrogen (TN) (= DIN minus N_2 gas + DON + PON) was analyzed as an aggregate with an in-line digestion and oxidization method using ultraviolet light and heated alkaline persulfate. NO_3^- was reduced to NO_2^- by a Cd column, which was measured colorimetrically as a diazonium ion (APHA 2004-4500-N). Total phosphorus (TP) (= ortho, poly, + organic PO_4 (diss + part) was measured colorimetrically as ortho- PO_4 by ascorbic acid reduction (APHA 2004-4500-P), after online digestion (heat, ultraviolet and persulfate) to oxidize organic - PO_4. Dissolved inorganic carbon (DIC) was analyzed as an aggregate using a Shimadzu Model TOC-5000A carbon analyzer.

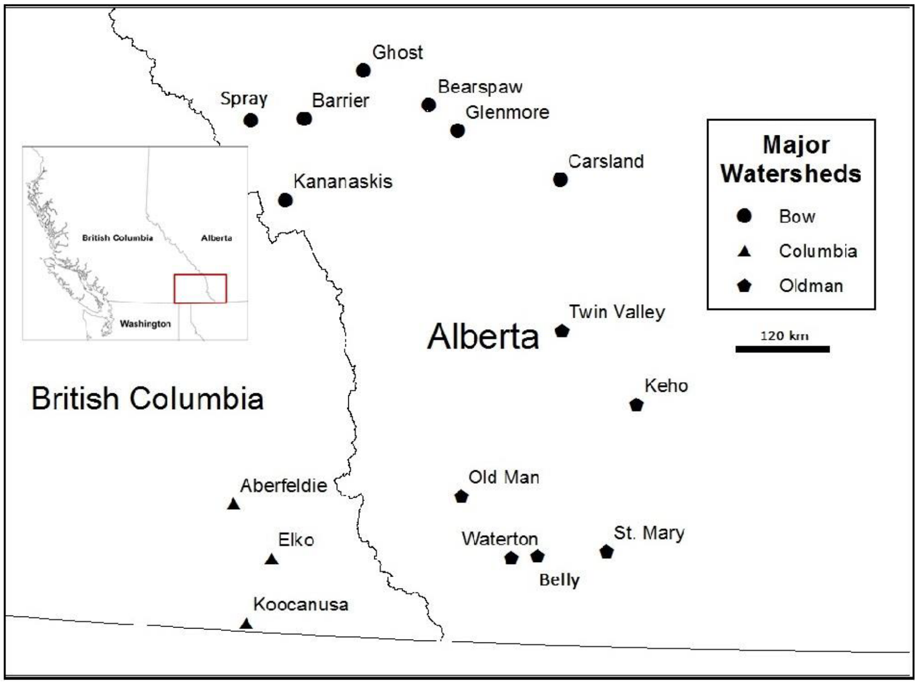


Figure B7. Reservoirs in BC and AB sampled in riverine habitat upstream and downstream of impoundment.

Table B5. Reservoirs sampled in BC and Alberta for upstream/downstream comparison of nutrient regime.

Dam	Reservoir	Year built	Purpose	Type
Glenmore	Glenmore	1932	WS	Run-of-river
Carsland	Carsland	1973	I/R	Weir
Bearspaw	Bearspaw	1954	H/C	Peaking
Ghost	Ghost	1929	H/R	Run-of-river
Spray	Spray Lakes Lower	1951	H/R	Peaking
Pocaterra	Kananaskis	1955	H/R	Peaking
St. Mary	St. Mary	1951	I/H	Run-of-river
Twin Valley	Twin Valley	2004	I/R/C	Irrigation storage
Keho	Keho	1923	I/R	Irrigation storage
Waterton	Waterton	1963	I/H/R	Run-of-river
Barrier	Barrier	1947	H/R	Peaking
Oldman	Oldman	1990	I/H/R/C	Run-of-river
Aberfeldie	Aberfeldie	1922	H	Run-of-river
Elko	Elko	1924	H	Run-of-river
Libby	Koocanusa	1973	H/R/C	Run-of-river
Belly (control)	Belly (control)	n/a	Weir d/s	Control section

I= irrigation, H= hydropower, R= recreation, C= flood control, WS= water supply

Results

It was expected (Hypothesis II-1) that regulated rivers might exhibit different nutrient regimes from unregulated rivers due to the possible effects of impoundment on sedimentation nutrient transport (Bosch and Allan 2008; Bosch et al 2009). However, no significant difference was found between nutrient regimes in regulated and reference rivers, using two sample paired t-tests for TP (t_{30}= 0.55, p = 0.58) or TN (t_{30}= 0.29, p = 0.77). Note that no detailed land use data were available to control in the comparison for the effect of this potential co-variable (as it affects soil and urban nutrient budgets). Data were also compared across 2011 and 2012 and no significant differences were found. HydroNet sites all exhibited consistently low TP values (2-12 $mg^{\cdot} m^{3}$) mostly within the oligotrophic trigger range developed by the CCME guidelines (Environment Canada 2004). These values were thus in the lower half of the overall log TP range used in modeling Fish Biomass (Figure B3; Table B1), both quite close to the distribution of values found in the Western Cordillera and Newfoundland fish data sets (Table B1). The N:P ratios were very similar in mean and range to those obtained for the fish biomass sites, ranging from 12->100. Only 3 of the 33 sites fell below the Redfield Ratio of 16 (Redfield 1958), indicating possible N limitation. Although TP values were consistently within the oligotrophic range, just as in the fish biomass modeling data set TN values were much more variable, ranging from 64 - 1300 $mg^{\cdot} m^{3}$. Thus, at this level of oligotrophy, the degree to which sedimentation, nutrient transport and other biogeochemical changes associated with impoundment was likely too low to result in significant effects of river regulation on the nutrient regime.

The range of mean TP values found across the HydroNet data set of paired regulated and unregulated rivers was 2-12 $mg^{\cdot} m^{-3}$. The lower boundary of 2 $mg^{\cdot} m^{-3}$ predicts a range of 0.3 - 0.6 $g^{\cdot} m^{-2}$ of fish biomass from the general models given in Table B2, depending on which of the regional models is used, and the upper boundary of 2 mg$\cdot$m^{-3} predicts a range of 2.0 – 5.0 g$\cdot$ m^{-2} (Figure B7).

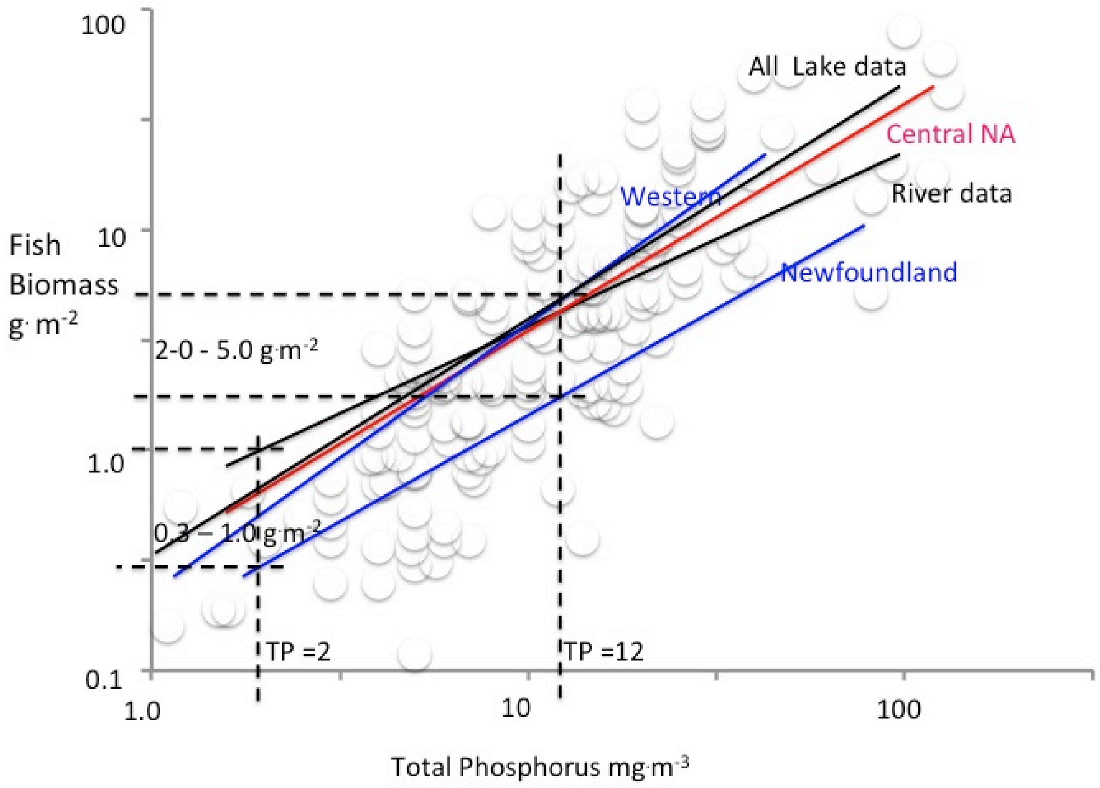


Figure B8. The range of Fish Biomass values predicted for a range of TP values from 2 - 12 mg.m-3 for communities of 2, and 10 species, using the general multiple regression model shown in Table B3, Figure B4.

If values of species richness can be specified, then the models in Table B3, can be used, and the general model (Figure B4) would apply to all regions. For a fish community with 2 species, the TP range of 2-12 mg$\cdot$ m^{-3} would predict a range of 0.4 -2.5 g$\cdot$ m^{-2}, and for a fish community with 10 species, the TP range of 2-12 mg$\cdot$ m^{-3} would predict a range of 1.1 -6.5 g$\cdot$ m^{-2} (Figure B8). Thus the six-fold range of TP values found at the HydroNet sites across Canada, translate to approximately a six-fold range in fish biomass, but the magnitude of the values will depend on the species richness of the community in question.

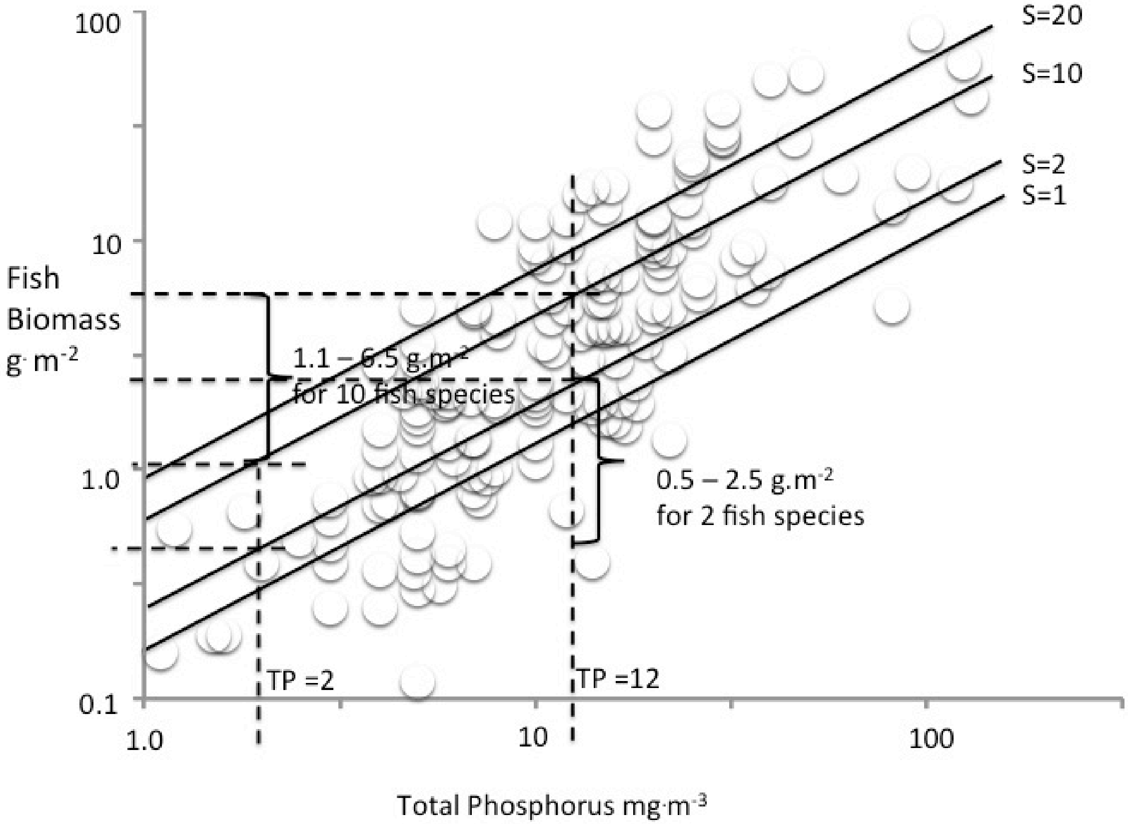


Figure B9. The predicted effect of the TP range found in HydroNet rivers for different levels of species richness, based on the river model shown in Figure B4.

Nutrient regimes upstream vs downstream of Reservoirs

It was expected (Hypothesis II-2) that processes such as sedimentation and internal loading might lead to significant impoundment effects leading downstream differences in levels of N and P. However, most reservoirs had downstream TP values that were within 20 % of their upstream values and there was no significant directional bias to the upstream/downstream difference for either TP (paired $t_{15} = 1.74$, $p = 0.10$) or TN (paired $t_{15} = 0.82$, $p = 0.43$). Of the 4 reservoirs where large upstream/downstream differences in TP were found, two had higher values downstream indicating that internal loading within the reservoir was leading to downstream enrichment, and two had lower values, indicating that the reservoir was acting as a nutrient sink. The greatest nutrient sinks were Glenmore (run-of-the-river) and Spray Reservoirs (peaking). The two greatest nutrient sources were Twin Valley (irrigation storage) and Bearspaw (peaking). Although there was no directional bias, the % difference between downstream and upstream (root mean square difference) was an increasing function of TP (Figure B9) as hypothesized (II-2).

Thus it appears that whether the reservoir is a source or a sink, the larger the phosphorus load the greater the downstream effect is likely to be. Nutrients settle out in reservoirs as plankton develop and take up nutrients that enter from upstream sources (Finger et al. 2007), and oligotrophic reservoirs produce very low plankton crops (Friedl and Wuest 2002; Kennedy 2001). It is therefore reasonable to expect plankton sedimentation to trap a larger fraction of a richer load. Internal loading of nutrients from accumulated sediment is more likely to occur in thermally stratified water bodies that experience hypoxia or anoxia in the bottom waters, a condition that is strongly associated with eutrophication (Nurnberg 2007).

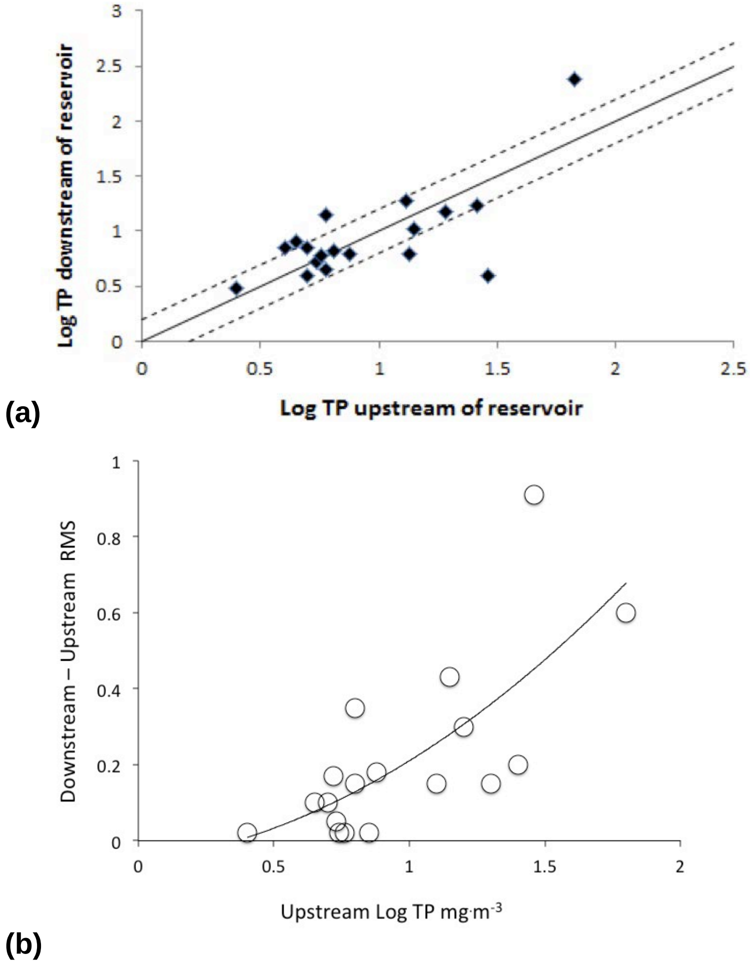


Figure B10. TP sampling upstream and downstream of reservoirs in BC and Alberta. (a) Solid line indicates no change in TP up and downstream of reservoirs. Dashed lines indicate a 20% difference between up and downstream values, where the reservoir was acting as a sink (trapping) or source (releasing) nutrients downstream. (b) Root mean square (RMS) of downstream TP deviation relative to upstream TP; RMS = 0.18 Log TP2 + 0.088 Log TP -0.056 R2 = 0.53

Most of the BC and Alberta reservoirs in this study receive their runoff from mountain watersheds and are thus little influenced by agriculture in their watersheds. Prairie reservoirs situated along small streams with low discharge that receive little mountain runoff, can be greatly impacted by upstream agricultural inputs leading to cyanobacterial blooms (Mitchell and Prepas 1990). Twin Valley Reservoir situated along the Little Bow River is not only an example of this, but also a fairly young reservoir (built in 2004, Brinkmann and Rasmussen 2010). It experiences significant mid-summer *Aphanizomen* blooms that settle, decompose and deplete hypolimnetic oxygen leading to downstream enrichment. Thus nutrient levels along stream/reservoir watercourses will exhibit little longitudinal change if biological nutrient demand is minimal, however, when metabolism increases, both sedimentation and internal loading will increase making reservoirs greater sinks and/or sources, depending on their internal oxygen regimes.

The regulated hydroelectric rivers and their corresponding reference systems, although not free of agricultural influences are situated primarily in the boreal zone where such influences are minimal. Thus TP values were within the oligotrophic range (2 – 12 $mg.m^{-3}$, log TP = 0.3 -1.1) which places them at the low end of the trophic spectrum in Figure B9, and thus unlikely to experience significant longitudinal shift in nutrient concentration from upstream to downstream of reservoirs.

Fundamental/Scientific relevance

Establishing links between trophic richness, and the capacity of systems to support diverse and productive fish communities, and developing models that predict the standing crops that can be expected as a function of nutrient metrics and biodiversity are important goals for aquatic ecology and fisheries science.

The relationship between trophic richness and nutrient trapping and release to downstream sections of rivers by reservoirs is not well known, and to establish models that can predict longitudinal shifts in nutrient concentrations and productivity at all levels along regulated river courses is important for aquatic ecology and fisheries science.

Benefits to Industry and Government

Since nutrients are strongly related to productivity at all levels, it is important for industries, managers and regulators to have quantitative metrics of nutrient abundance and fish biomass. and good predictive models that can provide clear benchmarks of the amount of fish that a system can be expected to support, for a given level of richness, biodiversity and in different geographic regions.

Nutrient regimes differ within and among regions and assessing the impact of environmental disturbances on fish productive capacity will depend on understanding the baseline productivity that can be expected from a given type of community.

Literature Cited

Bachmann, R.W., Jones, J.R. 1974. Phosphorus inputs and algal blooms in lakes. Iowa State Journal of Research 49: 155-160.

Batterson, M., Liverman, D. 2010. Past and future sea level change in Newfoundland and Labrador: guidelines for policy and planning. Newfoundland and Labrador Dept of Natural Resources Geological Survey Report 10-1 pp 129-141.

Bosch, N.S. 2008. The influence of impoundments on riverine nutrient transport: An evaluation using the Soil and Water Assessment Tool. Journal of Hydrology 355: 131-147.

Bosch, N.S., Allan, J.D. 2008. The influence of impoundments on nutrient budgets in two catchments of Southeastern Michigan. Biogeochemistry 87:325-338.

Bosch, N.S., Johengen, T.H., Allan, J.D., Kling G.W. 2009. Nutrient fluxes across reaches and impoundments in two southeastern Michigan watersheds. Lake and Reservoir Management 25: 389-400.

Brinkmann, L., Rasmussen, J.B. 2010. High levels of mercury in biota of a new prairie irrigation reservoir with a simplified food web in Southern Alberta, Canada. Hydrobiologia 79**:** 393-402.

Bunn, S.E., Arthington, A.H. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30: 492-507.

Carey, M.P., Wahl, D.H. 2011. Determining the mechanism by which fish diversity influences production. Oecologia 167: 189-198.

Carlander, K.D. 1955. The standing crop of fish in lakes. Journal of the Fisheries Research Board of Canada. 12: 543-570

Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.

Chu, C., Minns, C.K., Mandrak, N.E. 2003. Comparative regional assessment of factors impacting freshwater fish biodiversity in Canada. Canadian Journal of Fisheries and Aquatic Sciences. 60: 624-634.

Clarke, K.D., Scruton, D.A. 1999. Brook trout production dynamics in the streams of a low fertility Newfoundland watershed. Transactions of the American Fisheries Society. 128:1222-1229.

Cote, D. 2007. Measurements of salmonid population performance in relation to habitat in eastern Newfoundland streams. Journal of Fish Biology. 70: 1134-1147.

Cote, D., Adams, B.K., Clarke, K.D., Langdon, M. 2011. Salmonid biomass and habitat relationships for small lakes. Environmental Biology of Fishes. 92: 351-360.

Deegan, L.A., Peterson, B.J. 1992. Whole river fertilization stimulates fish production in an Arctic tundra river. Canadian Journal of Fisheries and Aquatic Sciences. 49: 1890-1901.

Dillon, P.J., Rigler, F.H. 1974. The phosphorus-chlorophyll relationship in lakes. Limnology and Oceanography 19:767-763.

Downing, J.A., McCauley, E. 1992. The nitrogen-phosphorus relationship in lakes. Limnology and Oceanography. 37: 936-945.

Downing, J.A., Plante, C. 1993. Production of fish populations in lakes. Canadian Journal of Fisheries and Aquatic Sciences 50: 110-120.

Ekinaro, J., Gibson, R.J. 1999. Interhabitat migration of juvenile Atlantic salmon in a Newfoundland River system. Journal of Fish Biology. 51: 373-388.

Environment Canada. 2004. Canadian guidance framework for the management of phosphorus in freshwater ecosystems. Ottawa, Canada.

Finger, D.P., Bossard, P., Schmid, M., Jaun, L., Müller, B., Steiner, D. 2007. Effects of alpine hydropower operations on primary production in a downstream lake. Aquatic Sciences. 69: 240-256.

Friedl, G., Wuest, A. 2002. Disrupting biogeochemical cycles—consequences of damming. Aquatic Sciences 64: 55-65.

Gomez, E., Durillon, C., Rofes, G., Picot, B. 1999. Phosphate adsorption and release from sediments of brackish lagoons: pH, O_2 and loading influence. Water Research 33: 2437-2447.

Hanson JM, Leggett WC. 1982. Empirical prediction of fish biomass and yield. Canadian Journal of Fisheries and Aquatic Sciences 39:257-263.Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J. and Wardle, D. A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs. 75: 3-35.

Horppila, J., Olin, M., Vinni, M., Estlander S, Nurminen L, Rask M, Ruuhijärvi J, Lehtonen H. 2010. Perch production in forest lakes: the contribution of abiotic and biotic factors. Ecology of Freshwater Fish 19: 257-266.

Hyatt, K.D., McQueen, D.J., Shortreed, K.S., Rankin, D.P. 2004. Sockeye salmon nursery lake fertilization: review and summary of results. Environmental Reviews 12: 133-162.

Hyatt, K.D., Stockner, J.G. 1985. Responses of sockeye salmon to fertilization of coastal lakes. Canadian Journal of Fisheries and Aquatic Sciences 42: 320-331.

Jackson, D.A., Peres-Neto, P.R., Olden, J.D. 2001. What controls who is where in freshwater fish communities—the role of biotic, abiotic and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences 58: 157-170.

Jones, J.R., and Hoyer, M.V. 1982. Sportfish harvest predicted by summer chlorophyll a concentration in midwestern lakes and reservoirs. Trans. Am. Fish. Soc. 111: 176–179.

Kelso, J.R.M, Johnson, M.G. 1991. Factors related to the biomass and production of fish communities in small oligotrophic lakes vulnerable to acidification. Canadian Journal of Fisheries and Aquatic Sciences 48: 2523-2532.

Kennedy, R.H. 2001. Considerations for establishing nutrient criteria for reservoirs. Journal of Lake and Reservoir Management 17: 175-187.

MacLellan, S.G., Hume, J.M.B. 2011. Pelagic Fish Surveys of 20 Lakes in Northern British Columbia From 2006 to 2009. Canadian Technical Report of Fisheries and Aquatic Sciences 2950. 139 pp. Appendix 1-6.

McPhail, J.D., Lindsey, C.C. 1970. Freshwater Fished of Northwestern Canada and Alaska. Fish. Res. Board Can. Bull. 173, Ottawa.

Mandrak, N.E., Crossman, E.J. 1992. Postglacial dispersal of freshwater fishes into Ontario. Canadian Journal of Zoology 70: 2247-2259.

McPhail, J.D. 2007. Freshwater Fishes of British Columbia. University of Alberta Press. Edmonton, Alberta.

Mitchell, P., Prepas, E.E. 1990. Atlas of Alberta Lakes. University of Alberta Press, Edmonton

Ney, J.J., Moore, C.M., Tisa, M.S., Yurk, J.J. and Neves, R.J. 1990. Factors affecting the sport fishery in a multiple-use Virginia reservoir. Lake and Reservoir Management 6:21-32.

Nurnberg, G.K., Peters, R.H. 1984. Biological availability of soluble reactive phosphorus in anoxic and oxic fresh-waters. Canadian Journal of Fisheries and Aquatic Sciences 4: 757-765.

Nurnberg, G.K. 2007. Lake responses to long-term hypolimnetic withdrawal treatments. Lake and Reservoir Management 23: 388-409.

Peterson, B.J., Deegan, L., J. Helfrich. J. Hobbie, M. Hullar, B. Moller, T. E. Ford, A. Hershey, A. Hiltner, G. Kipphut, M. A. Lock, D. M. Fiebig, V. McKinley, M. C. Miller, J. R. Vestal, R. Ventullo and G. Volk . 1993. Biological responses of a tundra river to fertilization. Ecology 74: 653-672.

Poff, N.L., Ward, J.V. 1989. Implications of streaflow variability and predictability for lotic community structure –a regional analysis of stream flow patterns. Canadian Journal of Fisheries and Aquatic Sciences 55: 201-217.

Power, M.E., Dietrich, W.E., Finlay, J.C. 1996. Dams and downstream aquatic biodiversity: potential food web consequences of hydrologic and geomorphic change. Environmental Management 20: 887-895.

Prchalova, M., Kubecka, J., Riha, M., Litvin, R., Cech, M., Frouzov, J., Hladik, M., Hohausova, E., Peterka, J., Vaskek, M. 2008. Overestimation of percid fishes (Percidae) in gillnet sampling. Fisheries Research 91:79–87.

Prchalova, M., Kubecka, J., Riha, M., Mrkvicka, T., Vasek, M., Juza, T., Kratochvil, M., Peterka, J., Drastik, V., Krizek, J. 2009. Size selectivity of standardized multimesh gillnets in sampling coarse European species. Fisheries Research 96: 51–57

Prchalova, M., Mrkvicka, T., Kubecka, J., Peterka, J., Cech, M., Muska, M., Kratochvil, M., Vasek, M. 2010. Fish activity as determined by gillnet catch: A comparison of two reservoirs of different turbidity. Fisheries Research 102: 291–296.

Randall, R.G. 1992. Using allometry with fish size to estimate production and biomass (P/B) ratios of salmonid populations Ecology of Freshwater Fish 11: 196-202.

Randall, R.G., Kelso, J.R.M, Minns, C.K. 1995. Fish production in freshwaters: are rivers more productive than lakes. Canadian Journal of Fisheries and Aquatic Sciences 52: 631-643.

Rasmussen, J.B. 1988. Littoral zoobenthic biomass in lakes, and its relationship to physical, chemical, and trophic factors. Canadian Journal of Fisheries and Aquatic Sciences 45:1436-1447.

Rawson, D.S. 1951. Studies of the Fishes of Great Slave Lake. J. Fish. Res. Board Can. 8: 207-240.

Redfield, A.C. 1958. The biological control of chemical factors in the environment. American Scientist 46: 205-221.

Ryan, P.M. 1984. Age and growth and food of threespine stickleback in three lakes of central Newfoundland, Canada. Canadian Technical Report Fisheries and Aquatic Sciences 1325 iv + 16 p.

Ryan, P.M. 1986. Lake use by wild anadromous atlantic salmon as an index of subsequent adult abundance. Canadian Journal of Fisheries and Aquatic Sciences 43: 2-11.

Shortreed, K.S., Morton, K.F., Malange, K., Hume, J.M.B. 2001. Factors limiting juvenile sockeye production and enhancement potential for selected B.C. nursery lakes. Canadian Science Advisory Secretariat Research Document 2001/098. 54 pp.

Smokorowski, K. E., Bergeron, N., Boisclair, D., Clarke, K., Cooke, S., Cunjak, R., Dawson, J. 2011. NSERC 's HydroNet: A National Research Network to Promote Sustainable Hydropower and Healthy Aquatic Ecosystems. Fisheries, 36(10), 480-488.

Stanley, E.H., Doyle, M.W. 2002. A geomorphic perspective on nutrient retention following dam removal. BioScience 52: 693-701.

Stockner, J.G., Shortreed, K. 1978. Enhancement of autotrophic production by nutrient addition in a coastal rainforest stream on Vancouver Island. Journal of the Fisheries Research Board of Canada. 35: 28-34.

Stockner, J., Langston, A., Sebastian, D., Wilson, G. 2005. The Limnology of Williston Reservoir: British Columbia's largest lacustrine Ecosystem. Water Quality Res. Journal of Canada. 40: 28-50.

Tilman, D., Downing, J.A. 1994. Biodiversity and stability of grasslands. Nature 367:363-65.

Van Zyll de Jong, I.C., Cowx, I.G., Scruton, D.A. 2005. Association between biogeographic factors and boreal lake fish assemblages. Fisheries Management and Ecology 12: 189-199.

Verdonschot, P.F.M. 2000. Integrated ecological assessment methods as a basis for sustainable catchment. Hydrobiologia 422: 389-412.

SECTION C - THERMAL REGIMES: Modelling water temperatures in regulated rivers

Maheu, A., Kwak, J.A., Beaupré, L., St-Hilaire, A.
Centre Eau-Terre-Environnement, Institut national de la recherche scientifique

DESCRIBING THE THERMAL REGIME OF RIVERS

Water temperature plays an important role in freshwater ecology and changes in temperature can significantly impact fish distribution, growth, mortality, production, habitat use and community dynamics (Caissie 2006). Most aquatic organisms are adapted to a certain range of temperature and organisms undergo thermal stress above a certain physiological tolerance threshold. For example, salmonids are particularly sensitive to warm water temperatures and considerable work has been done to determine upper thermal tolerance limit for salmonid species (Wehrly et al. 2007; Elliott and Elliott 2010; Breau 2013). In addition, seasonal and daily variations in water temperature are also important to consider given organisms have specific temperature requirements throughout their life history (Ward and Stanford, 1982; McCullough, 1999). Overall, the thermal regime of a river, which can be defined as the water temperature conditions in a river and how these vary through time, is of critical importance to maintain the ecological integrity of aquatic ecosystems (Olden and Naiman 2010). Accordingly, the characterization of the thermal regime of rivers is important in order to describe desirable conditions over time, compare different systems and assess anthropogenic impacts. Different conceptual frameworks have been proposed to describe the thermal regime of rivers.

Inspired from the natural flow regime paradigm (Poff et al. 1997), Olden and Naiman (2010) proposed to describe the thermal regime of a river by characterizing its five constituting components: magnitude, frequency, duration, timing and rate of change. Figure C1 provides examples of the five components of the thermal regime for a typical annual time series. The thermal regime can be summarized by using descriptive statistics which measure the central tendency or dispersion of each of its five components. Different series of descriptive metrics have been proposed to quantify the thermal regime of rivers (Chu et al. 2010; Guillemette et al. 2011; Arismendi et al. 2013; Rivers-Moore et al. 2013). In the context of impact assessments, this approach has the advantage of being able to target the specific components of the thermal regime that could be modified by the presence of a dam on the river and develop a management response accordingly. Although this approach allows for a comprehensive characterization of the thermal regime, it requires numerous metrics to capture the multivariate properties of water temperature variability and faces the inherent difficulty of selecting the most relevant and informative ones.

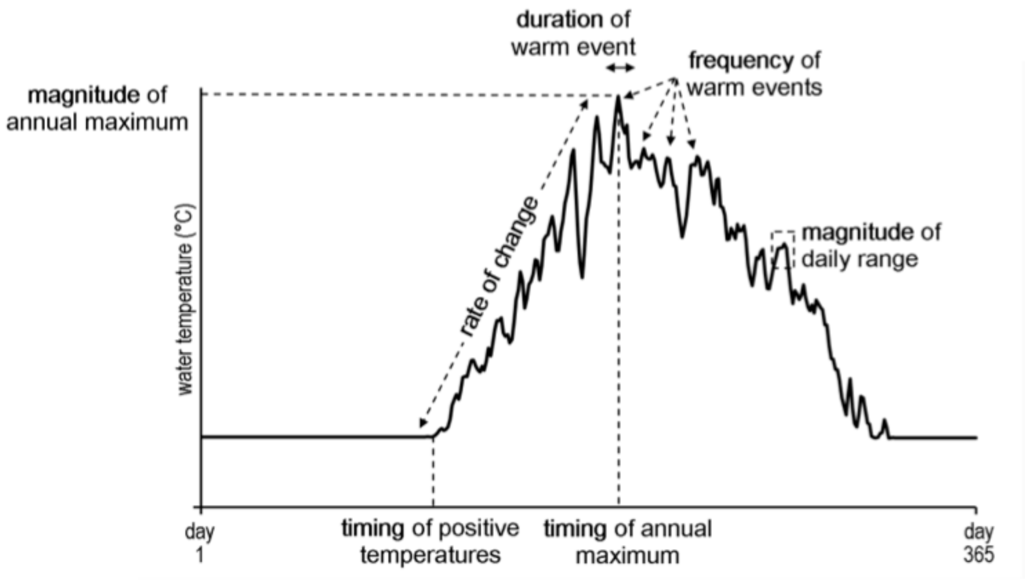


Figure C1. Examples of the five components (magnitude, frequency, duration, timing and rate of change) of a typical annual time series of river water temperature.

In the natural thermal regime approach described above, a large number of metrics are dedicated to describing the annual cycle in water temperature, although metrics have also been proposed to describe variations at other time scales (e.g. daily, interannual). At northern latitudes, river water temperature generally follows a truncated sinusoidal function during the open water period. As such, another approach to the characterization of the thermal regime of rivers is to describe the annual water temperature cycle with a cosine function (Maheu et al., submitted). The annual cycle can then be described by three parameters describing its magnitude (a_0), amplitude (A) and timing (ϕ):

$$T_w(t) = a_0 + A\cos\frac{2\pi}{365}(t-\phi) \qquad (1)$$

where t is the day of the year, a_0 is the annual average of the time series (°C), A is the amplitude of the signal (°C) and ϕ is the phase of the signal which correspond to day of the year of the annual maximum. This approach offers an alternative to the characterization of the thermal regime with numerous and often redundant metrics by providing a parsimonious description of the annual water temperature cycle river using only three parameters. This approach can also be used to assess and describe the alteration of the annual water temperature cycle by dams or other anthropogenic activities by comparing the annual cycle, as described by the magnitude (a_0), amplitude (A) and timing (ϕ) parameters, between regulated and reference sites. For example, deviation of the magnitude parameter from reference conditions would result in a vertical translation of the annual signal of water temperature while deviation in the timing parameter would result in a horizontal translation of the annual signal (Figure C2). A difference in the amplitude parameters would lead to different warming/cooling rates in the spring/autumn as well as a difference in peak temperatures in the summer (Figure C2).

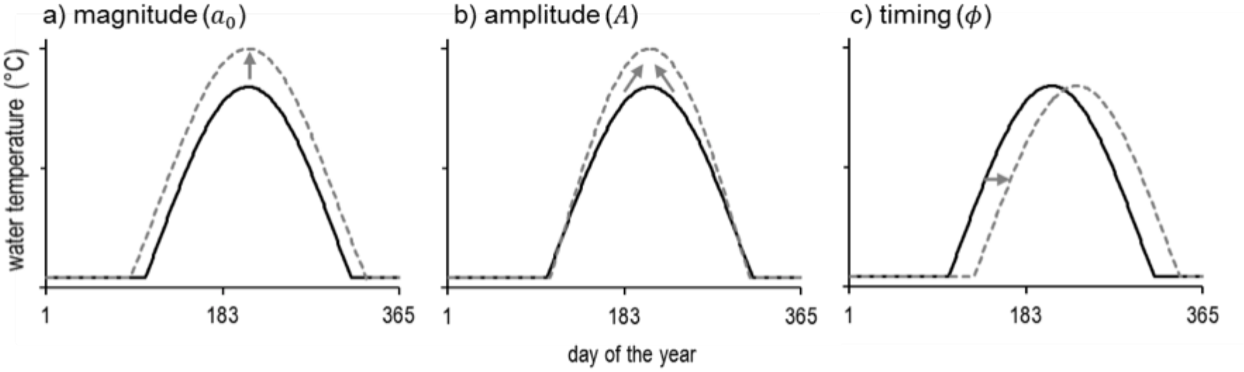


Figure C2. Schematic representation of changes in of a) magnitude; b) amplitude and c) timing parameters describing the annual water temperature cycle in rivers

OBSERVED IMPACTS OF DAMS ON THE THERMAL REGIME OF RIVERS

The two approaches for the characterization of the thermal regime have been used to compare the thermal regime of regulated and natural rivers. Using a series of metrics describing the magnitude, frequency, duration, timing and rate of change in summer water temperature conditions, a regional comparison of the summer thermal regime of natural versus regulated rivers has been performed for medium-sized rivers (drainage area at most upstream location between 4766 and 4040 km^2) in Eastern Canada (Ontario, Quebec and New Brunswick). Regulated rivers represented three different operational types (run-of-river, storage and peaking). This regional analysis provides a practical approach to qualitatively prognosticate the impact of dams on the thermal regime of rivers according to their operational type.

Water temperature was monitored by deploying two to ten thermal loggers along a river reach. In regulated rivers, thermal loggers were deployed as close to the dam as possible (within 0.1 to 1.5 km of the dam, with the exception of two sites where loggers were at 8.2 km and 9.7 km from the dam) and covered a distance ranging between 4 and 25 km (mean = 10 km) downstream of the dam. In natural rivers, thermal loggers covered a longitudinal distance ranging between 3 and 45 km (mean = 14 km). Metrics describing the magnitude, frequency, duration, timing and rate of change in summer water temperature were computed for each logger and the median value of the monitored reach was used to make comparisons among rivers. To allow comparison of thermal regimes at a regional scale and for different years, air temperature conditions were taken into consideration when describing the magnitude and timing of water temperature regimes. Figure C3 shows the relationship between air and water temperature metrics for 29 rivers (17 natural and 12 regulated rivers) for the summers of 2011 to 2013. Each point on the figure represents conditions in one river in a given year and the dotted line in panels a, b and c represents the 90% confidence interval of the linear model between air and water temperature metrics for natural rivers. As illustrated in Figure C3, the presence of a reservoir (i.e. storage and peaking dams) led to considerable differences in the thermal regime of rivers, particularly regarding the magnitude of the thermal regime in September and the timing of the weekly maximum water temperature in the summer. For example, water temperatures were generally warmer in September in impounded rivers with storage or peaking operations (Figure C3c). This warming effect of storage and peaking dams was observed throughout the entire monitored reach of the regulated rivers (4.3 to 13.4 km). In fact, these distances should be considered as the minimum distance impacted and it is likely that the warming effect extended over greater distances downstream, but data were not available further away from the dam. The magnitude of the thermal regime of storage and peaking systems was influenced to a lesser extent in July and August, although storage reservoirs sometimes led to cooler (i.e. July) or warmer (i.e. August) conditions than in natural rivers (Figure C3a-b). Similar to what was observed in September, the effect of storage and peaking dams in July and August generally extended over the entire monitored reach (4.3 and 13.4 km). In addition, the presence of a reservoir generally delayed the timing of the weekly maximum water temperature whereas in natural rivers, the weekly maximum occurred simultaneously for air and water temperature (Figure C3d). While dams with deep reservoirs generally modified the thermal regime of rivers in the summer, run-of-river dams in the HydroNet study set only had a minimal impact on the magnitude and timing of summer water temperature conditions (Figure C3). Note however that the designation “run of the river” is is very often used very loosely by operators and in ways that include, arguably misleadingly, systems with regular but non daily peaking; or with peaking discharges that are a relatively low multiple of non peaking discharges; or with day-time peaking using storage shifts limited purely to previous night time flows; or systems with larger reservoirs that are not used every year to store and dampen high flow releases. None of these modes of operation strictly fully preserve the systems natural flow regime, the technical definition of “run of the river”.

Using a multivariate analysis (Daigle et al., 2011), two components of the thermal regime of rivers were identified as presenting important differences between regulated and natural rivers: the summer mean daily range (daily maximum minus daily minimum) and the mean number of reversals per day (Figure C4). The mean number of reversals per day represents the number of changes of direction in one day. For example, the water temperature cycle in an unregulated river is typically characterized by two changes of direction during the day: water temperature decreases from midnight to early morning, then increases in the afternoon and then start to decline again in the evening (Caissie et al., 2012). The two selected aspects of the thermal regime of rivers (i.e. mean daily range and mean number of reversals per day) were not correlated with air temperature but natural rivers presented a distinct range of values when compared to managed water courses. The summer mean daily range varied between 2.0 and 6.1 °C in natural rivers while it was under 2 °C for many storage and peaking systems. The mean number of reversals per day ranged between 2.1 and 3.0 for natural rivers, while it often exceeded three reversals per day for storage and peaking systems as well as for certain run-of-river systems. Although rivers regulated by storage dams were characterized by a greater number of reversals per day than natural rivers, the magnitude of these diel variations was generally small. For example, at the site closest to the dam, the mean diel range during the summer varied between 0.5 and 1.3 °C for storage systems while the mean diel range in natural rivers varied between 2.0 and 6.1 °C.

As illustrated by these two metrics, regulated rivers appear to have a distinctive pattern of water temperature variation at the sub-daily scale compared to natural rivers. This finding highlights the importance of considering sub-daily scales in thermal assessments.

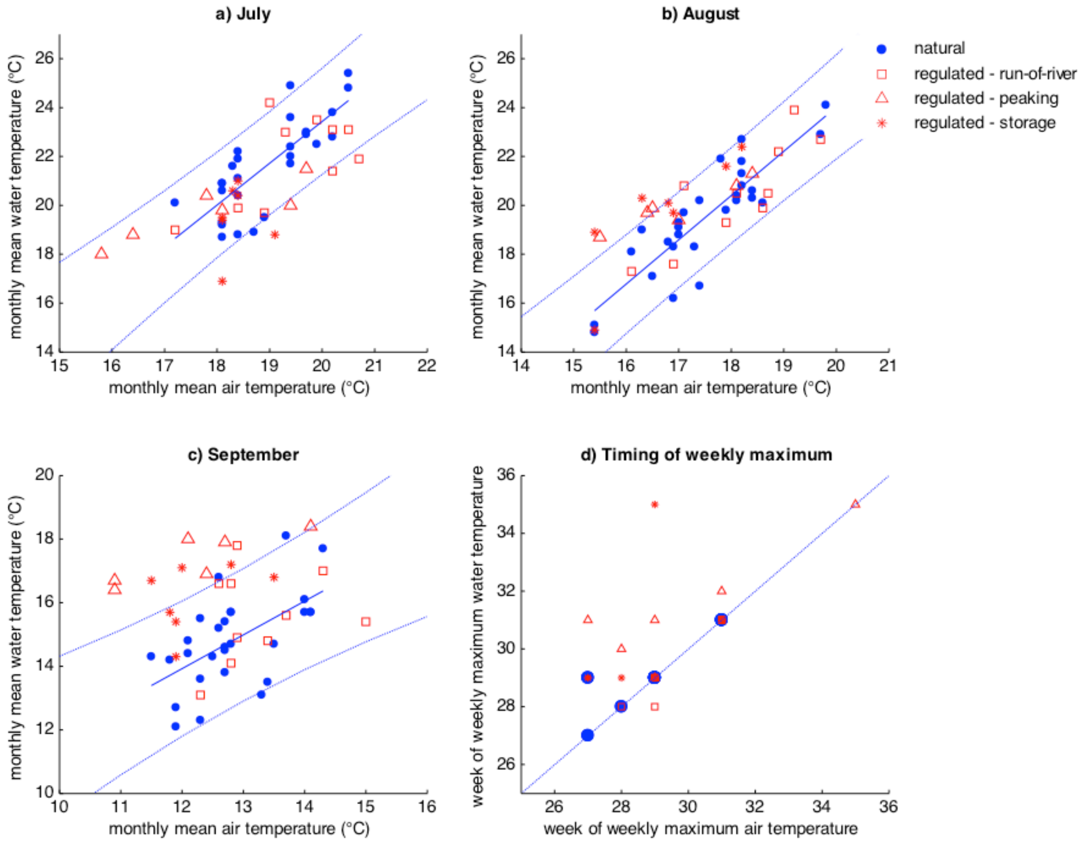


Figure C3. Magnitude and timing of the summer thermal regime of natural (blue) and regulated (red) rivers in relation to air temperature conditions in Eastern Canada. Water temperature was monitored over river reaches of 4 to 25 km (mean = 10 km) in regulated rivers and over river reaches of 3 to 45 km (mean = 14 km) in natural rivers. Metrics correspond to the median of the river reach.

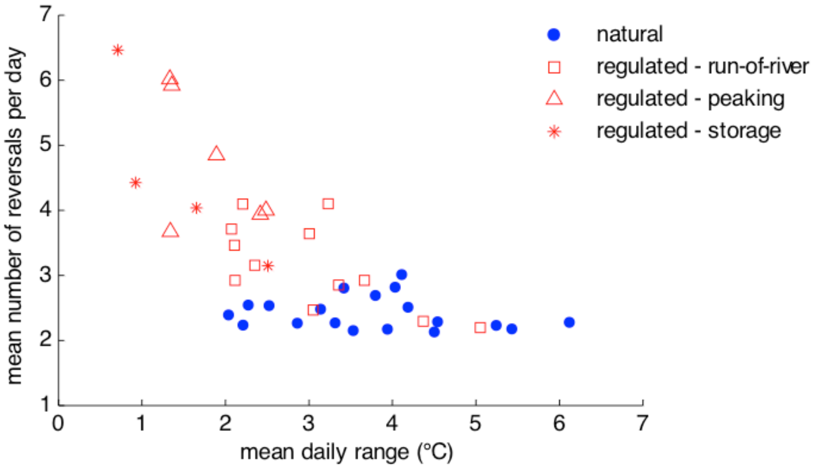
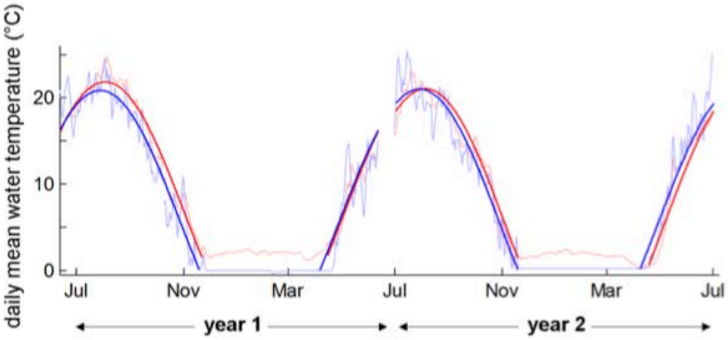


Figure C4. Water temperature characteristics of natural (blue) versus regulated (red) rivers in Eastern Canada. Water temperature was monitored over river reaches of 4 to 25 km (mean = 10 km) in regulated rivers and over river reaches of 3 to 45 km (mean = 14 km) in natural rivers. Metrics correspond to the median of the river reach.

In addition to a regional comparison of the summer thermal regime of natural and regulated rivers (Figures C3 and C4), a year-around comparison was also performed for two regulated rivers in Quebec with different operational types (run of river and storage). For these systems, the annual water temperature cycle of regulated rivers was compared with the annual cycle of a similar and nearby natural river. The annual cycle of the St-Jean River (run-of-river) was not significantly different from the reference natural river. On the other hand, the Fourchue River (storage) had a delayed timing compared to the reference natural river, in addition to having a greater magnitude in one of the two years of the study (Figure C5). In the Fourchue River, the water intake is located near the bottom of the reservoir and the warming effect of the dam can rather be related to the reservoir being relatively shallow (mean depth of 5.7 m). This finding highlights the importance of considering morphometric characteristics of reservoirs when assessing the impacts of dams on the thermal regime of rivers. In addition to modifying the thermal regime during the open water period, the storage dam also significantly increased water temperature during the winter. In fact, mean daily water temperature remained above 1 °C at the foot of the dam throughout the winter (Figure C5) and the warming effect of the reservoir prevented the formation of an ice cover over the river for at least 2.5 km downstream of the dam. The absence of an ice cover warrants attention given the influence of ice on hydrological and ecological processes. For example, the absence of ice cover in regulated rivers can create favorable conditions for frazil production which may cause deleterious effects to fish habitat (Simpkins et al. 2000).



	year 1		year 2	
	regulated	reference	regulated	reference
a_0 (°C)	**6.6**	5.7	5.4	5.6
A (°C)	15.2	15.1	15.7	15.4
ϕ (day of year)	**216**	211	**217**	210

Figure C5. Annual cycle in daily mean water temperature for the Fourchue River, a regulated river with a storage reservoir (red) and a reference natural river (blue) for two years (2012-2014). Equation 1 provides a description of the parameters in the figure legend. For the regulated river, the site closest to the dam (300 m) is shown and for the reference river, the mean annual cycle over a 2.5-km (year 1) and 3.6-km (year 2) river reach is shown.

MODELLING RIVER WATER TEMPERATURE IN REGULATED RIVERS

Although water temperature monitoring does not necessarily require expensive equipment, it can prove to be logistically challenging in some instances. Moreover, in the context of the study of the impact of dams on the thermal regime of rivers, this challenge is exacerbated by the fact that there are different types of dams and water management schemes. It becomes very difficult to monitor all possible impacted rivers. For this reason, modelling is often considered as a viable alternative to extensive monitoring.

There is a plethora of existing water temperature models (see Benyahya et al. 2007 for a partial review). Most of the models used to study the thermal impact of dams are deterministic (i.e. based on a more or less complex conceptualization of the physical processes). However, there are very few examples of such applications in Eastern Canada.

One such exercise was recently conducted on the Fourchue River (Quebec). In the first phase of the project, two models, one deterministic and one statistical, were compared (Beaupré, 2014). The deterministic model used was SNTEMP (Bartholow, 1995), a simulation tool that has often been used in the United States, to investigate the impacts of impoundments on river temperature. The statistical model is based on an interpolation method implemented in a multivariate space created using canonical correlation analysis (Guillemette et al. 2011). Both models were calibrated on two reaches of the Fourchue River, upstream and downstream of the reservoir. SNTEMP was used to simulate mean water temperatures time series using meteorological inputs and discharge. The statistical model was used to directly estimate thermal indices (descriptive statistics of the thermal regime). The two models were compared based on their efficiency to estimate thermal indices such as mean and maximum monthly water temperature. Temperature was monitored at 18 locations in the Fourchue River during the summers of 2011 and 12 locations in 2012 to describe the thermal regime and calibrate the models. Both models were able to simulate mean monthly thermal indices adequately (e.g. Figure C6). However, the statistical model achieved better results than SNTEMP in estimating some of the thermal indices (Figure C7), especially the mean and maximum daily ranges with Root Mean Square Errors (RMSE) of 4.1 °C and 4.9 °C respectively for SNTEMP as compared to 0.6 °C and 1.4 °C for the statistical model.

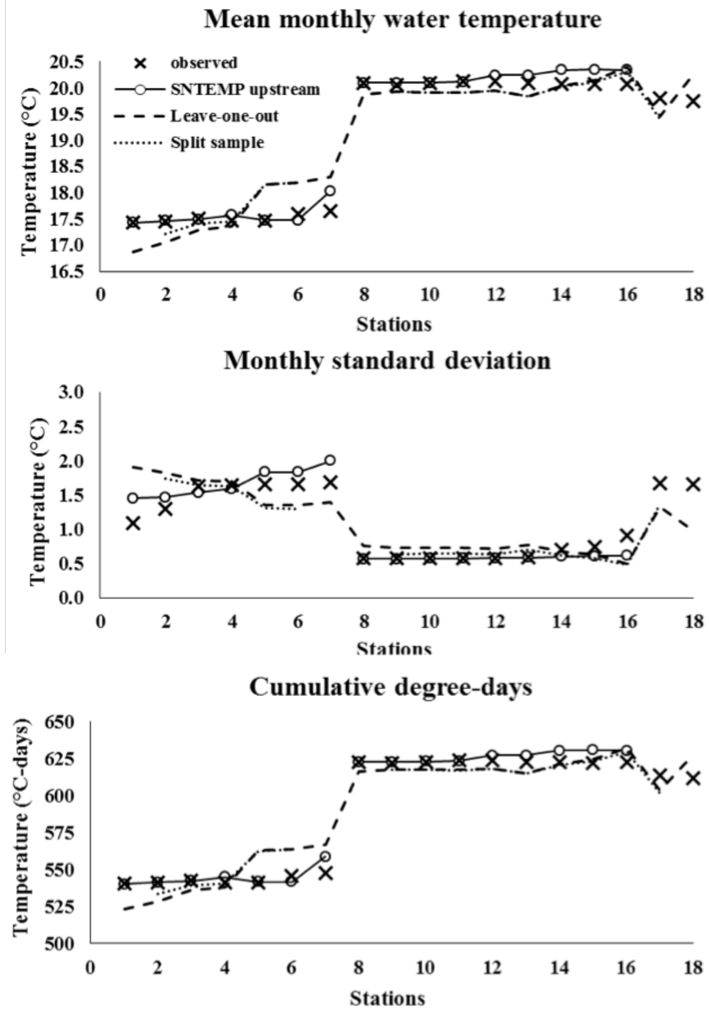


Figure C6. Observed and simulated mean monthly water temperatures, standard deviation and cumulative degree-days for August 2011, using SNTEMP and the statistical model in Leave-one-out and split-sample modes. Stations 1 to 18 are from upstream to downstream (from Beaupré, 2014).

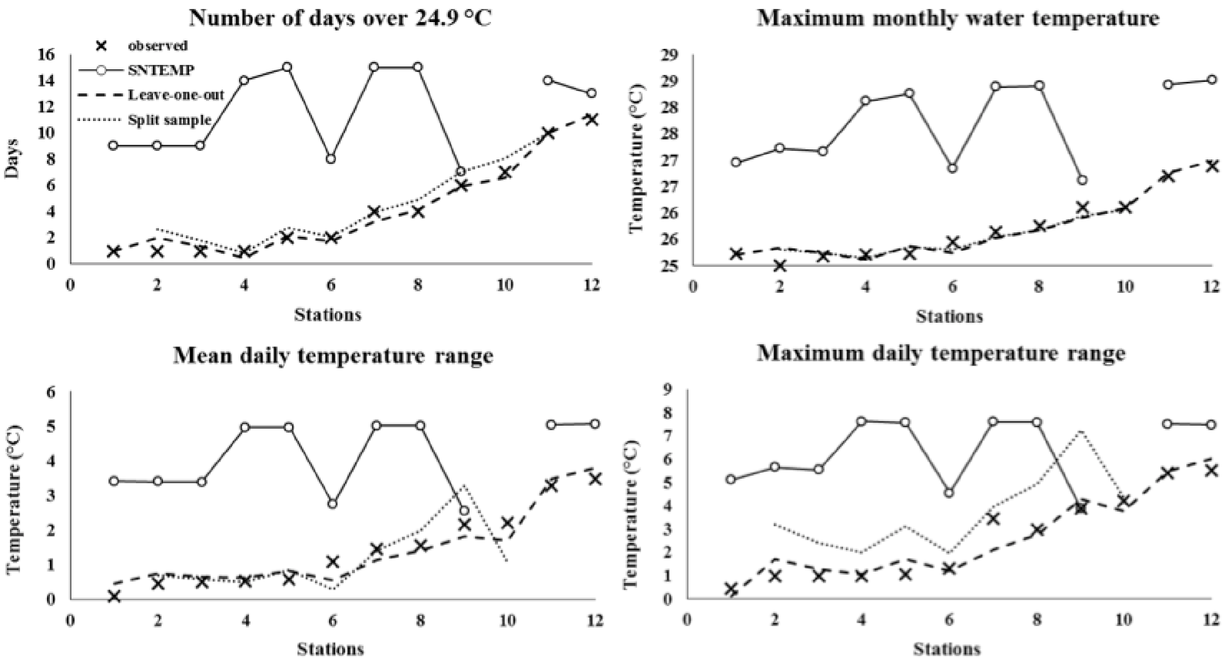


Figure C7. Observed and simulated monthly maximum water temperatures, mean and maximum temperature ranges and the number of days over 24.9 °C for August 2012, using SNTEMP and the statistical model in Leave-one-out and split-sample modes. Stations 1 to 12 are from upstream to downstream (from Beaupré, 2014).

Subsequently, additional models were added to the comparative study, with the condition that they all use at least both air temperature and flow as input data. The inclusion of flow as a required input ensured that all models could be used in the context of the presence of a dam, to study different flow management scenarios. In the deterministic category, the CEQUEAU hydrological and water temperature model was used (Morin and Couillard, 1990). Three statistical models were also implemented: an Artificial Neural Network (ANN), an Auto-regressive Moving Average with eXogenous variables model (ARMAX) and a Nonlinear Autoregressive with eXogenous variables model (NARX). The CEQUEAU model is a semi-distributed model that has been recently re-programmed by Rio-Tinto Alcan. The hydrological component of CEQUEAU takes into account the physical characteristics of the watershed by decomposing it in Elementary Representative Areas (ERA) of equal surface for which the altitude, percentage of forest cover and the percentage covered by lakes and wetlands are defined. On each ERA, vertical routing of water is simulated daily, starting with meteorological inputs (total daily rain and/or snow), and through reservoirs representing the upper and lower soil horizons. Detailed description of both vertical and upstream-downstream routing of water by CEQUEAU was given by Morin and Couillard (1990). The water temperature module was described by St-Hilaire et al. (2000). Water temperature is defined by calculating the ratio of enthalpy (H) over the product of water volume (V, as simulated by the hydrological module) and water specific heat capacity (θ). Changes in the enthalpy are calculated for each ERA, and each day using a heat budget approach. The semi-empirical relations used in the heat budget were all described by Morin and Couillard (1990).

A comparison of these models was completed for the ice-free periods of 2011 to 2014. Calibration of the deterministic model was done by hand, with a split sample approach. Table C1 summarizes the performance statistics of the four models. Except for the ANN, all models performed relatively well, with RMSE of the order of or less than 1°C. The CEQUEAU model showed a relatively strong negative bias for the calibration phase, caused by the fact that it was not as efficient as the statistical models to reproduce higher water temperatures. Given its autoregressive nature, the ARMAX model outperformed the other statistical approaches, while the ANN performed more poorly, most likely because more data would be required for the learning phase of this non-parametric approach.

Table C1. Root Mean Square Error (RMSE) and bias calculated between observed and simulated water temperatures at a station located 7 km downstream of the Morin Dam on the Fourchue River (From Kwak et al., 2016).

Model	Calibration phase		Validation phase	
	RMSE (°C)	BIAS (°C)	RMSE (°C)	BIAS (°C)
CEQUEAU	1.03	-1.17	1.05	-0.74
ANN	1.86	0.54	2.53	7.14
ARMAX	0.62	0.02	0.96	1.28
NARX	0.71	0.26	1.05	0.94

All models used in this comparative study could potentially be used to study the impact of the management of water releases associated with dam operations on a river if difficulties in the calibration process are overcome. Large data requirement is often stated to be an impediment to the implementation of deterministic models. Both SNTEMP and CEQUEAU require information about basin physiography and land use. In addition, SNTEMP requires information about canopy closure above the stream. However, both deterministic models allow for simulation of temperatures at different locations of the river reach, and for different dam water release scenarios. The only tested statistical model that is not local (i.e. limited to one station) is the geostatistical model of Beaupré (2014). While the other statistical models are 0-D (i.e. only provide simulated water temperatures at one point on the river). The geostatistical approach used by Beaupré (2014) can provide estimates anywhere along the river, provided that there is a sufficient number of monitoring stations to perform the initial interpolation in multivariate space.

Hence, it can be seen that there are some alternatives to deterministic approaches to simulate the impact of dams on the thermal regime. Model selection should be based on the following criteria:

1) data availability;
2) model capacity to account for flow variability;
3) the requirement to simulate water temperature at different locations; and
4) the relative ease of calibration and validation.

MANAGING THE THERMAL REGIME OF REGULATED RIVERS

The natural dynamics of water temperature are important to maintain the integrity of rivers. Yet, seasonal and daily patterns of variations in water temperature previous to dam construction are often unknown given the common absence of pre-dam data. In the absence of information on the thermal regime of a river previous to dam construction, different approaches are available to determine the desirable natural thermal regime template. Empirical or statistical models based on unregulated rivers can be used to estimate the natural thermal regime and help set management goals in regards to water temperature. For example, the magnitude and timing of the natural thermal regime of a river can be broadly estimated from air temperature measurements (Figure C3). Care should be taken when using regional models given the relation between air and water temperature conditions varies according to the size and position of the river in the watershed. Our ability to model regional patterns of sub-daily variations in water temperature remains limited, although a good understanding of the range of values observed in natural rivers can help define a range of acceptable values in regulated rivers (Figure C4).

Various statistical and deterministic models are also available to simulate water temperature in regulated rivers. As shown in Section 3, many of these models can be adapted to account for flow variability and as such can be used to study different flow management scenarios. In addition, statistical and deterministic models can be used to study the spatial extent of a dam’s impact on the thermal regime of rivers.

In addition to considering a natural regime template, water temperature in regulated rivers can also be managed according to life history requirements of species of interest. Through the characterization of the annual water temperature cycle, the full life cycle needs of a species can be assessed. For example, the thermal regime of the Fourchue River (storage dam) would not provide optimal growth conditions for brook trout given daily mean water temperature would exceed 19°C for more than 60 days according to the estimated annual water temperature cycle (Figure C8). In addition, a year-around perspective on river water temperature also highlights the early accumulation of thermal units in the Fourchue River as a result of the warming effect of the dam during the winter (Figure C6). For example, mean daily water temperature ranged between 1.2 and 3.3°C during the winter and as such, the thermal assessment would suggest further investigation into a potentially accelerated development of aquatic organisms in the warmer regulated river.

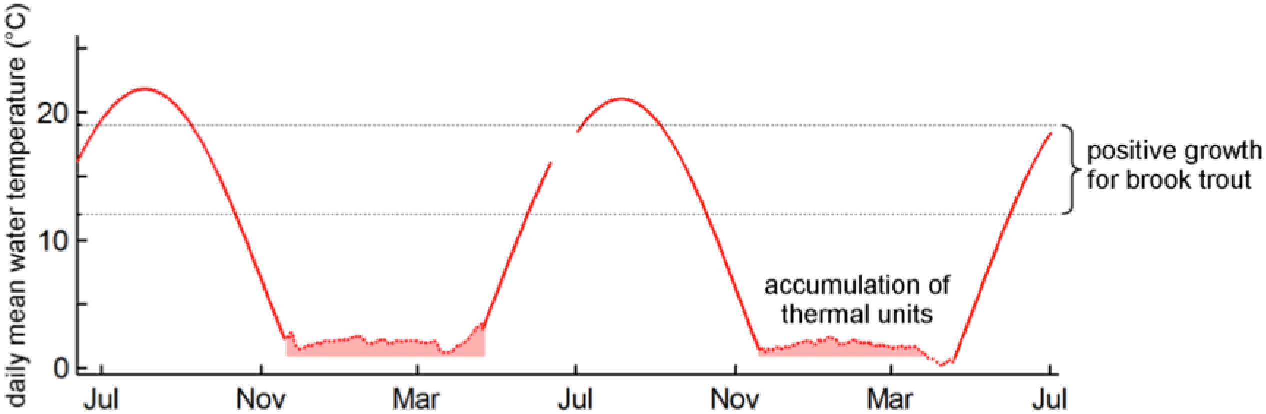


Figure C8. Annual cycle in daily mean water temperature for the Fourchue River (storage dam) and potential influence on life history and bioenergetics.

LITERATURE CITED

Arismendi I, Johnson SL, Dunham JB, Haggerty R. 2013. Descriptors of natural thermal regimes in streams and their responsiveness to change in the Pacific Northwest of North America. Freshwater Biology: 58(5):880-894.

Bartholow, JM. 1995. The stream network temperature model (SNTEMP): A decade of results. Workshop on Computer Application in Water Management. Fort Collins, CO: Water Resources Research Institute, CSU. p. 57-60.

Beaupré, L. 2014. Comparaison de modèles thermiques statistique et déterministe pour l'estimation d'indices thermiques sur les portions aménagées et naturelles de la rivière Fourchue (Québec, Canada). M. Sc. Thesis, INRS-ETE. 61 p.¸

Benyahya L, Caissie D, St-Hilaire A, Ouarda TBMJ. 2007. A review of statistical water temperature models. Canadian Water Resources Journal, 32(3):179-192.

Breau, C. 2013. Knowledge of fish physiology used to set water temperature thresholds for in-season closures of Atlantic salmon (*Salmo salar*) recreational fisheries. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/163.

Caissie D. 2006. The thermal regime of rivers: a review. Freshwater Biology 51: 1389–1406.

Caissie, D., Breau, C., Hayward, J., and Cameron, P. 2013. Water temperature characteristics within the Miramichi and Restigouche rivers. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/165.

Chu C, Jones E, Allin L. 2010. Linking the thermal regimes of streams in the Great Lakes Basin, Ontario, to landscape and climate variables. River Research and Applications 26: 221–241.

Daigle A, St-Hilaire A, Beveridge D, Caissie D, Benyahya L. 2011. Multivariate analysis of the low-flow regimes in eastern Canadian rivers. Hydrological Sciences Journal 56: 51–67.

Elliott JM, Elliott J a. 2010. Temperature requirements of Atlantic salmon Salmo salar, brown trout Salmo trutta and Arctic charr Salvelinus alpinus: predicting the effects of climate change. Journal of fish biology 77: 1793–817.

Guillemette N, St-Hilaire A, Ouarda TBMJ, Bergeron N. 2011. Statistical tools for thermal regime characterization at segment river scale: Case study of the Ste-Marguerite River. River Research and Applications 27: 1058–1071.

Kwak, J. A. St-Hilaire, F. Chebana. 2016. A comparative study for water temperature modelling in small basin, the Fourchue River, Quebec, Canada. Hydrological Sciences Journal. (in press)

Maheu A, Poff NL, St-Hilaire A. 2015. A classification of stream water temperature regimes in the conterminous United States. River Research and Applications. DOI: 10.1002/rra.2906

McCullough DA. 1999. A review and synthesis of effects of alterations to the water temperature regime on freshwater life stages of salmonids. : 279.

Morin G, Couillard D. 1990. Predicting river temperatures with a hydrological model. In Chereminisoff NP. (ed) Encyclopedia pf fluid mechanics, surface and groundwater flow phenomena (pp.171-209). Gulf Publishing Company: Huston, USA.

Olden JD, Naiman RJ. 2010. Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. Freshwater Biology 55: 86–107.

Poff NL, Allan JD, Bain MMB, Karr JJR, Prestegaard KL, Richter BDB, Sparks RE, Stromberg JJC, KL P, RE S. 1997. The Natural Flow Regime. Bioscience: 769–784.

Rivers-Moore N a, Dallas HF, Morris C. 2013. Towards setting environmental water temperature guidelines: a South African example. Journal of environmental management 128: 380–92.

Simpkins DG, Hubert WA, Wesche TA. 2000. Effects of fall-to-winter changes in habitat and frazil ice on the movements and habitat use of juvenile rainbow trout in a Wyoming tailwater. Transactions of the American Fisheries Society 129: 101–118.

St-Hilaire A, Morin G, El-Jabi N, Caissie D. 2000. Water temperature modelling in a small forested stream: implication of forest canopy and soil temperature. Canadian Journal of Civil Engineering, 27:1095-1108.

Ward J V, Stanford JA. 1982. Thermal responses in the evolutionary ecology of aquatic insects. Annual Reviews in Entomology 27: 97–117.

Wehrly KE, Wang L, Mitro M. 2007. Field-Based Estimates of Thermal Tolerance Limits for Trout: Incorporating Exposure Time and Temperature Fluctuation. Transactions of the American Fisheries Society 136: 365–374.