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Mesoscale modelling of fisheries productivity metrics in reservoirs: lessons learned from NSERC's HydroNet 2010-2015

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Foreword

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

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ABSTRACT

The general objective of the NSERC HydroNet project “mesoscale modelling of fisheries productivity metrics in reservoirs” is to contribute to the development of knowledge and tools that improve our capacity to estimate and predict metrics of fisheries productivity in reservoirs. This project was conducted on Lac du Bonnet, Manitoba, a hydropower reservoir on the Winnipeg River. This project was divided in two components that correspond to different types of methodologies and logistical challenges: a pelagic zone component (> 3 m deep) and a littoral zone component (< 3 m).

The pelagic zone component used hydroacoustic surveys to develop fish size spectra. Hydroacoustic survey data accuracy can be improved easily by correcting for boat avoidance. Hydroacoustic is a consistent and repeatable method to describe size spectra in freshwater bodies. Size spectra derived in this reservoir are consistent with theoretical expectations of aquatic ecosystem size structure and provide description of intra- and inter-annual changes in the state of aquatic communities.

The littoral zone component used a range of sampling techniques (seine, gill nets, boat electrofishing) to compare models of diverse fisheries productivity metrics (abundance, biomass, richness), taken at different times (2012-2013, day and night), as a function of a variety of habitat variables (local, e.g. macrophyte cover; lateral, e.g. shore use; contextual, e.g. distance to major tributary). A number of conclusions were derived from these analyses on how best to sample fish communities in a reservoir with the purpose of developing fish-environment relationships. Sampling more sites within a year may be preferable than repeatedly sampling fewer sites within this year. Modelling (or validating) fish-environment relationships in reservoirs may require more than a single year of sampling. Seining may be superior at estimating species richness than other sampling gears. Electrofishing may be the best sampling gear to develop fish-environment relationships in the littoral zone of reservoirs. A combination of local and contextual habitat variables should be used to explain variation in fisheries productivity metrics in the littoral zone of reservoirs and to identify important productivity areas of reservoirs. The explanatory capacity of relationships between total fish abundance and environmental conditions is higher when sampling fish at night than at day. A series of predictive relationships between fisheries productivity metrics and environmental conditions was also provided.

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

Modélisation à moyenne échelle des mesures de la productivité des pêches dans les réservoirs : enseignements tirés du réseau HydroNet du Conseil de recherches en sciences naturelles et en génie du Canada (CRSNG) 2010-2015

RÉSUMÉ

L'objectif global du projet de « modélisation à moyenne échelle des mesures de la productivité des pêches dans les réservoirs » du réseau HydroNet du CRSNG consiste à contribuer à l'acquisition de connaissances et à l'élaboration d'outils pour améliorer notre capacité à estimer et à prévoir les paramètres de la productivité des pêches dans les réservoirs. Ce projet a été mené sur le lac du Bonnet (Manitoba), un réservoir hydroélectrique sur la rivière Winnipeg. Ce projet a été divisé en deux composantes qui correspondent à différents types de méthodes et de défis logistiques : une composante pour la zone pélagique (> 3 m de profondeur) et une composante pour la zone littorale (< 3 m).

La composante de la zone pélagique a utilisé des relevés hydroacoustiques pour établir des spectres des tailles du poisson. L'exactitude des données des relevés hydroacoustiques peut être améliorée facilement en apportant des corrections pour compenser les modifications de la trajectoire du bateau visant à éviter d'autres embarcations. Les relevés hydroacoustiques constituent une méthode uniforme et reproductible servant à décrire les spectres des tailles dans des cours d'eau douce. Les spectres des tailles obtenus dans ce réservoir sont conformes aux attentes théoriques relatives à la structure par taille de l'écosystème aquatique, et fournissent une description des changements de l'état des communautés aquatiques au cours d'une année et d'une année à l'autre.

La composante de la zone littorale a utilisé toute une gamme de techniques d'échantillonnage (pêche à la senne, au filet maillant, à l'électricité en bateau) pour comparer les tendances des diverses mesures de la productivité des pêches (abondance, biomasse, richesse), prises à différents moments (2012-2013, de jour et de nuit), en tant que fonction d'un éventail de variables relatives à l'habitat (locale, p. ex., macrophytes; latérale, p. ex., utilisation du rivage; contextuelle, p. ex., distance par rapport aux principaux affluents). Un certain nombre de conclusions ont été tirées de ces analyses sur la meilleure façon d'échantillonner les communautés de poissons dans un réservoir, dans le but de déterminer les relations entre le poisson et l'environnement. L'échantillonnage d'un plus grand nombre de sites en une année serait préférable à l'échantillonnage répété d'un plus petit nombre de sites dans la même année. La modélisation (ou validation) des relations entre le poisson et l'environnement dans les réservoirs pourrait nécessiter plus qu'une seule année d'échantillonnage. La pêche à la senne est susceptible de donner de meilleurs résultats que d'autres engins d'échantillonnage aux fins de l'estimation de la richesse des espèces. La pêche à l'électricité serait peut-être le meilleur mode d'échantillonnage pour établir les relations entre le poisson et l'environnement dans la zone littorale des réservoirs. Une combinaison de variables locales et contextuelles de l'habitat devrait servir à expliquer la variation des mesures de la productivité des pêches dans la zone littorale des réservoirs et à désigner les principales zones de productivité des réservoirs. La capacité d'expliquer les relations entre l'abondance totale de poissons et les conditions environnementales est meilleure lorsque l'échantillonnage des poissons est réalisé la nuit plutôt que le jour. Une série de relations prédictives entre les mesures de la productivité des pêches et les conditions environnementales est également fournie.

Les connaissances acquises et les outils élaborés dans le cadre du présent projet peuvent être utiles pour orienter la prise de décisions relatives au développement ou à l'exploitation d'installations hydroélectriques et, si les responsables reconnaissent cette utilité, sont susceptibles d'améliorer la clarté, l'uniformité et la certitude du processus décisionnel.

CONTEXT

NSERC HydroNet is a national research network whose overall mission is to provide government and industry with the knowledge and tools that will improve the capacity of scientists and managers to assess and minimize the effects of hydropower installations and operations on aquatic ecosystems. HydroNet intends to inform the decision-making process, and thereby to contribute to the sustainable development of hydropower in Canada. HydroNet is a collaborative research partnership between universities, government agencies, and hydropower companies. In 2009, HydroNet was granted a 5-year research mandate by the Natural Sciences and Engineering Research Council of Canada (NSERC). This mandate was recently extended to 2015 to allow for the completion of papers and reports. The research platform of HydroNet consists in a series of projects that focus on two themes: 1) modelling of fisheries productivity in rivers, and; 2) modelling of fish-habitat interactions in reservoirs. The theme “modelling of fisheries productivity in rivers” includes projects on the productivity of fisheries and its chemical, physical, and biological drivers in rivers. The theme “modelling of fish-habitat interactions in reservoirs” comprises projects on the mesoscale modelling of fisheries productivity metrics in reservoirs and on the prediction of fish entrainment risk in reservoirs. The present report focuses on the mesoscale modelling of fisheries productivity metrics in reservoirs.

GENERAL OBJECTIVE

The general objective of the project “mesoscale modelling of fisheries productivity metrics in reservoirs” is to contribute to the development of knowledge and tools that improve our capacity to estimate and predict metrics of fisheries productivity in reservoirs.

STRATEGY

This project was divided in two components that correspond to different types of methodologies and logistical challenges: a pelagic zone component (> 3 m deep) and a littoral zone component (< 3 m).

PELAGIC ZONE COMPONENT

INTRODUCTION

Estimating the original state of an aquatic ecosystem and predicting impacts of hydro development within reservoirs on fish productivity in a cost-effective and timely manner requires rapid assessment of a wide range of organisms across an even wider size range. This is not easily accomplished – a reason why it has seldom been done. Key problems include logistical and cost issues of conducting surveys with various fishing gear and gear selectivity with no known netting device capable of unbiased sampling across species and sizes (see additional details with respect to the littoral zone below). This problem is acute in the pelagic zone of aquatic environments. In this project, in an exploratory attempt to address these problems, high-resolution acoustics capable of yielding echo levels (backscatter) from single organisms ranging from plankton to large fish were used to conduct repeated surveys of the Lac du Bonnet reservoir in Manitoba. Initially, the focus has been on fish (>4 cm in length) as it was thought to be the most direct and useful way to assess the productivity of freshwater lakes and reservoirs. If successful, it was postulated that such surveys could provide a relatively fast and cost-effective means of assessing the abundance of organisms and with repeated surveys changes in abundance over time and hence productivity.

Three major issues facing acoustic surveys in unknown environments are the potential for what is generally termed “boat avoidance”, especially of large mobile fish, species identification and the conversion of echo strength to a biological metric. The metric is typically biomass or echo “size” which can be converted to fish size with experimentally determined models. In most deep-water marine environments where acoustic surveys are routinely run worldwide, avoidance of “quiet” acoustic research vessels (ICES 209 Report) is typically not great, but fish densities are too high to allow measures of individual fish, as they cannot be consistently isolated in the acoustic beam (there are exceptions to this – see Rose 2009). In some freshwater environments, however, especially those in shallow waters, boat avoidance may be substantial. On the other hand, in waters in which there are only a few species and densities are relatively low at all spatial scales, it may be feasible to consistently isolate fish within the narrow acoustic beam (ca. 70) of most modern split beam transducers and by doing so assess the size structure of fish by species within this environment. This proved to be the case in several freshwater reservoirs initially surveyed in Newfoundland (G.A. Rose, unpublished).

In reservoirs and lakes containing many species of a wide size range, the problem of species identification in an unfamiliar environment is very difficult to resolve (perhaps it could be done with multi-frequency and other techniques but it would involve a great deal of research with no guarantee of success). On the other hand, initial surveys in Lac du Bonnet (reservoir) and Manigotagan Lake (natural) in Manitoba indicated that densities did not preclude the measurement of individual organisms during trial daytime surveys (at night the presence of dense plankton clouds obscured many small targets, especially in Lac du Bonnet). As a consequence of these initial investigations, it was decided to pursue a size-based acoustic approach to the assessing the state of these ecosystems, with particular focus on Lac du Bonnet. The approach proved sufficiently promising that repeated surveys in 2 years were conducted to assess both inter-annual and intra-annual dynamics of the size structure of the pelagic zone of this reservoir ecosystem.

Body size is a fundamental property of all organisms, being linked to life history traits and physiological properties, including production (Sheldon et al. 1972), metabolic rate (Gillooly et al. 2001), reproductive efficiency (Fenchel 1974), and trophic interactions (Thiebaut and Dickie 1993; Yvon-Durocher et al. 2011; Giacomini et al. 2013). As a consequence of these links, the abundance of organisms varies predictably with body size in aquatic ecosystems, generally decreasing with increasing size (Kerr 1974; Boudreau et al. 1991; Thiebaut and Dickie 1993).

Community size spectra, describing the relative abundance of organisms by size, provide a useful method for evaluating the status of aquatic ecosystems (Petchey and Belgrano 2010; Emmrich et al. 2011; Murry and Farrell 2014). Spectra provide information on underlying size-based mechanisms in communities (Boudreau et al. 1991) and create a link between traits at the individual and population levels with the structure and dynamics of the community (White et al. 2007). In general, the slope of size spectra is indicative of the relative abundance of fish by size, whereas spectral height indexes overall community abundance (Daan et al. 2005; Yemane et al. 2005; Sweeting et al. 2009). An examination of changes in size spectra over time can be used to investigate systematic shifts in fish communities (Emmrich et al. 2011) and assess the impact of environmental changes on aquatic communities (Rice and Gislason 1996; Duplisea and Castonguay 2006; Petchey and Belgrano 2010). Comparisons of spectra among and within systems may be used to assess spatial differences in productivity (Sprules and Munawar 1986; Macpherson et al. 2002).

Following these initial trials, several objectives were formulated:

- 1) to assess and quantify the avoidance of the specially built acoustic survey vessel
- 2) to assess if acoustic size-based methods could capture the size structure of the pelagic zone of the Lac du Bonnet ecosystem

-
- 3) to assess if inter-annual and intra-annual dynamics of size structure could be captured by repeated acoustic surveys, indicative of variable recruitment and mortality over the size spectrum

METHODS

Detailed methods of this study have been published in Stern (2012), Pollom and Rose (2015) and Wheeland and Rose (2015a, 2015b). Here are given some general descriptions only.

This study was conducted in July and August of 2011 and 2012 at Lac du Bonnet (50°22'27" N, 95°53'48"W; surface area, 84 km², maximum depth, 26 m), a hydropower reservoir in southeastern Manitoba (Figure 1). Lac du Bonnet has been dammed since the construction of the MacArthur Falls generating station in 1952 (Manitoba Hydro 2013a).

Lac du Bonnet contains a diverse fish community consisting largely of percids (e.g., walleye (*Sander vitreus*), sauger (*Sander canadensis*), yellow perch (*Perca flavescens*)), cyprinids, coregonids, catostomids (e.g., white sucker (*Catostomus commersonii*)), burbot (*Lota lota*), smallmouth bass (*Micropterus dolomieu*), mooneye (*Hiodon tergisus*), northern pike (*Esox lucius*), and lake sturgeon (*Acipenser fulvescens*) (Coordinated Aquatic Monitoring Program (CAMP) 2013; HydroNet, unpublished data).

A 5.5 m Boston Whaler boat was specially modified for hydroacoustic work and powered by a relatively quiet 90-hp Honda. An example of a survey track (survey 10) is shown here (Figure 1), indicated by parallel solid black lines. Dashed lines indicate basin boundaries. Grey hatched areas were not sampled.

Georeferenced acoustic data were collected with a BioSonics DTX echosounder (BioSonics Inc., Seattle, Washington, USA) transmitting to two calibrated splitbeam transducers (200 and 430 kHz), both downward facing. The echosounder was powered by rechargeable battery packs, being electrically isolated from the engine and other electronics to reduce the potential for electrical interference. Acoustic data were recorded at a threshold of -130 dB.

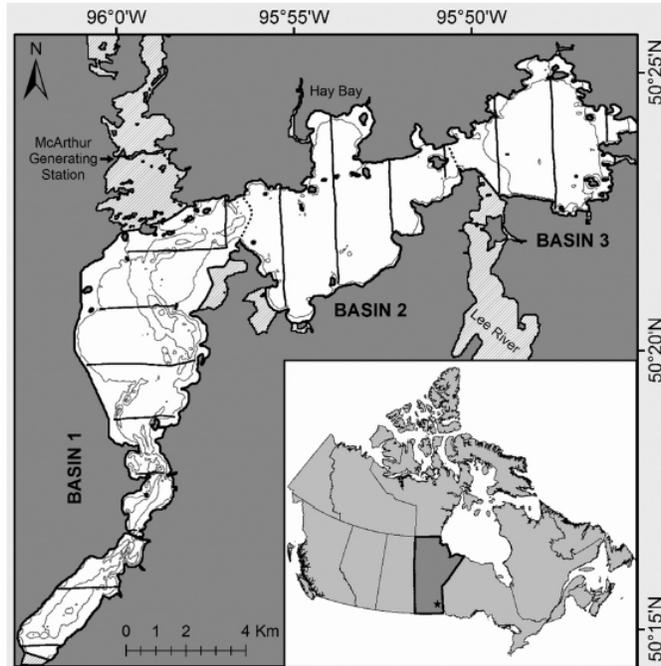


Figure 1. Bathymetry (5 m contours) of Lac du Bonnet, Manitoba, Canada, as determined from hydroacoustic data. An example survey track (survey 10) is shown here, indicated by parallel solid black lines. Dashed lines indicate basin boundaries. Grey hatched areas were not sampled.

All 11 surveys (Table 1) were completed during daylight hours, beginning at least 30 min after sunrise. Data (e.g., see Figure 2) were edited and analyzed using Echoview 5.0 software (Myriax, Hobart, Tasmania, Australia). Single-target detection and tracking parameters were derived empirically and kept consistent for all surveys, with a lower target strength (TS) limit corresponding to approximately 4 cm length. Total lengths of individual fish were estimated from the mean TS of its track at 200 kHz using the equation derived by Love (1971).

Table 1. Hydroacoustic surveys conducted over the study period at Lac du Bonnet.

Survey Number	Date
1	July 26 th , 2011
2	August 2 nd , 2011
3	August 3 rd , 2011
4	August 15 th , 2011
5	August 18 th , 2011
6	August 27 th , 2011
7	July 28 th , 2012
8	August 2 nd , 2012
9	August 8 th , 2012
10	August 11 th , 2012
11	August 24 th , 2012

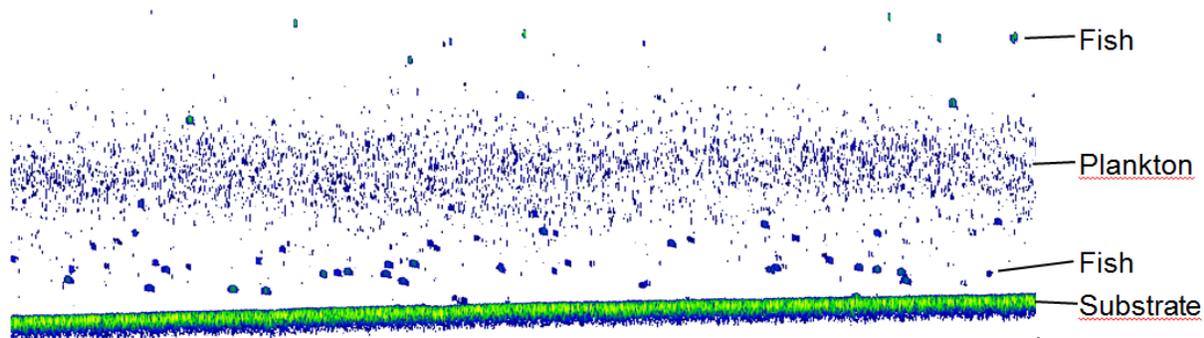


Figure 2. Example of hydroacoustic data for part of a survey.

Fish community size spectra were constructed using normalized logarithmic binning (White et al. 2008) with the normalized natural logarithm of fish abundance per length interval plotted against the midpoint of each logarithmic size class. Normalized fish counts within each size interval were adjusted for the volume sampled during each acoustic survey to standardize for sampling effort.

General linear models (GLM) were used to test for variation in spectral parameters over time (between years, within the season). ANOVAs were used to test for variation in spectral parameters among lake basins, with Tukey HSD tests used to compare means of all possible pairs. Statistical analyses were done in R version 3.1.0 ([R Foundation for Statistical Computation](http://www.R-project.org/), Vienna, Austria), Systat (San Jose, CA, USA) and XLStat (Addinsoft, International).

RESULTS

Objective 1) Assess and quantify the avoidance of the specially built acoustic survey vessel (from Wheeland and Rose 2015a)

Pairs of transects (mean length 576 m) were utilized to assess avoidance (A_c), the first drifting over a set course, then repeated either drifting or motoring at specific speeds ($1.03\text{-}3.70\text{ m}\cdot\text{s}^{-1}$) meant to mimic survey conditions. A total of 50 transect pairs were completed, 13 at Manigotagan and 37 at Lac du Bonnet. All pairs at Manigotagan were drift:motor (D:M) pairs, while both D:M ($n = 31$) and D:D ($n = 6$) pairs were completed at Lac du Bonnet. Avoidance coefficients (A_c) were computed by dividing the fish density (fish counts/sampled volume) of the first transect of each pair by the fish density of the second transect. An A_c value ≥ 1.0 indicates no avoidance, whereas a value approaching $A_c = 0$ is considered to indicate near complete avoidance. Transects pairs at Manigotagan were characterised by deeper waters (ANOVA: $F_{1,42} = 41.08$, $P < 0.01$), fish deeper in the water column (ANOVA: $F_{1,42} = 32.84$, $P < 0.01$) and fish of larger TS (Wilcoxon; $W = 42.5$, $P < 0.01$) than those at Lac du Bonnet. Study site had a significant influence on A_c of D:M pairs (GLM: $\chi^2 = 4.42$, $P = 0.04$). We detected no significant influence of fish depth or survey speed on A_c (Figure 3). Transects at Manigotagan did not show significant avoidance, with median A_c not different from one (Wilcoxon: $V = 50.5$, $P = 0.75$; $n = 13$, median = 0.81, 95% CI = 0.69, 1.48). At Manigotagan, A_c values ranged from 0.52 to 2.31, with $A_c < 1$ in 61% of transect pairs. In contrast, avoidance was apparent at Lac du Bonnet, with a median A_c value significantly less than one ($V = 64.0$, $P < 0.01$; $n = 31$, median = 0.51, 95% CI = 0.45, 0.79). A_c values at Lac du Bonnet ranged from 0 to 1.95, with $A_c < 1$ in 81% of transect pairs. There was no significant difference in A_c between years (GLM: $\chi^2 = 0.07$, d.f. = 1, 29, $P = 0.79$) for D:M pairs at Lac du Bonnet in 2011 ($n = 15$, median = 0.53, Q1 = 0.47, Q3 = 0.96) and 2012 ($n = 16$, median = 0.37, Q1 = 0.14, Q3 = 0.85). An A_c value of 0.5

indicates that only half the fish observed during drifting were subsequently observed during motoring.

Quantification of the avoidance coefficient enables survey measures of organism density to be corrected for avoidance of the survey vessel when appropriate.

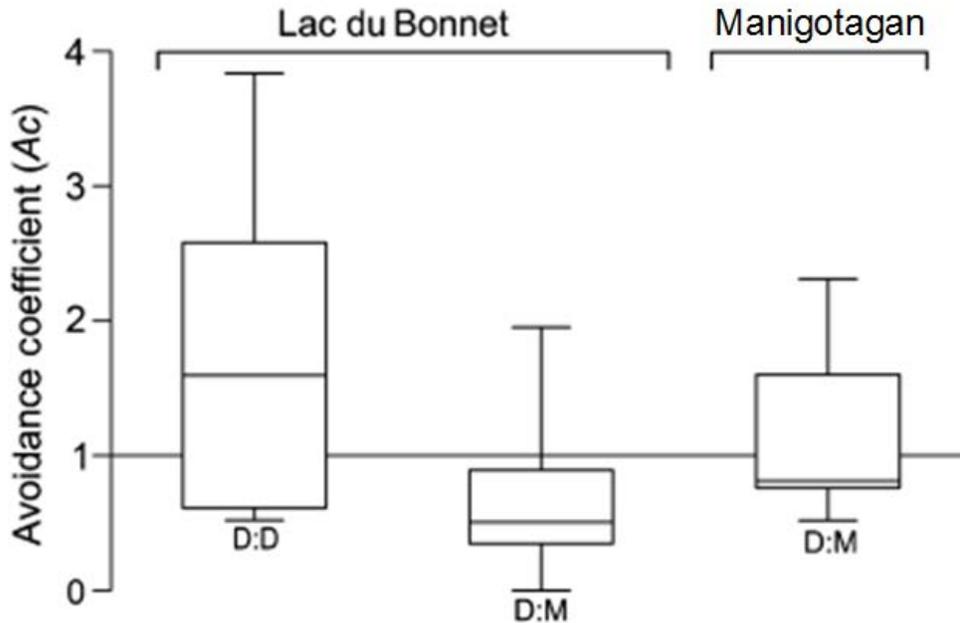


Figure 3. Avoidance coefficients (Ac) of paired drift:motor ($D:M$) transects differed significantly among study sites, Lac du Bonnet and Manigotagan, with significant avoidance ($P < 0.05$) occurring at Lac du Bonnet. Avoidance was not detected in drift:drift ($D:D$) transect pairs at Lac du Bonnet (figure from Wheeland and Rose 2015a).

Objective 2) Assess if acoustic size-based methods could capture the size structure of the pelagic zone of the Lac du Bonnet ecosystem (from Wheeland and Rose 2015b)

Six surveys were completed in 2011 and five were completed in 2012, with size spectra computed for the reservoir as a whole (Figure 4). Overall fish densities were low ($0.0031 \text{ fish} \cdot \text{m}^{-3}$, $SD = 0.0019$). Data formed significant size spectra in all cases (linear model, $p < 0.05$), with R^2 values ranging from 0.87 to 0.99. All slopes were negative. Spectral height for Lac du Bonnet was significantly influenced by year and day of the year (GLM: year (categorical), $p < 0.01$, $F_{[1,8]} = 48.12$; day of year (continuous), $p < 0.01$, $F_{[1,8]} = 23.79$). Height was greater in 2011 (mean \pm $SD = 0.19 \pm 0.15$) than in 2012 (-0.19 ± 0.20) and declined as the summer progressed (Figure 4). Spectral slopes did not change significantly between the two years surveyed (2011, -1.29 ± 0.15 ; 2012, -1.39 ± 0.12) or within each sampling season (GLM: year (categorical), $p = 0.24$, $F_{[1,8]} = 1.62$; day of year (continuous), $p = 0.09$, $F_{[1,8]} = 3.86$).

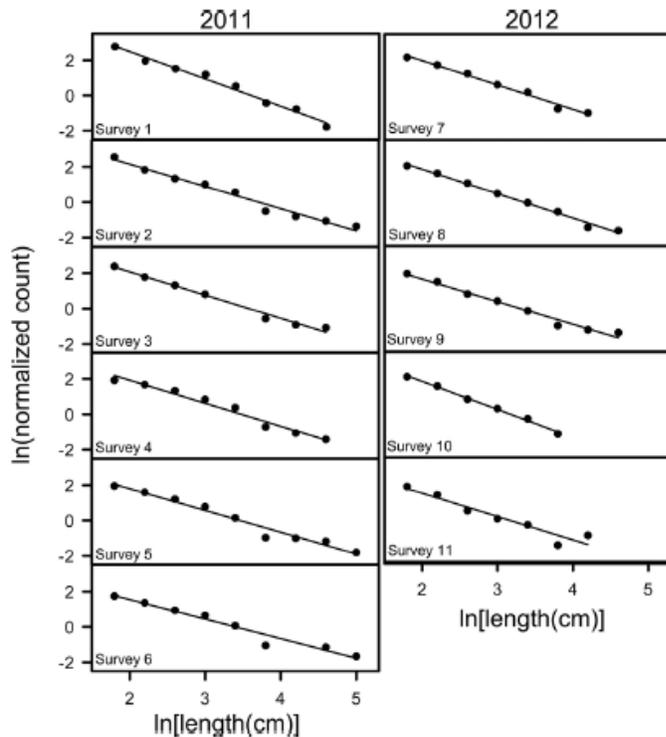


Figure 4. Individual spectral regressions for the whole reservoir for each survey completed (see Table 1 for survey dates; figure from Wheeland and Rose 2015b; for more detail see that paper).

Objective 3) Assess if inter-annual and intra-annual dynamics of size structure could be captured by repeated acoustic surveys, indicative of variable recruitment and mortality over the size spectrum (from Pollom and Rose 2015)

In order to assess before and after states of aquatic ecosystems a method must be robust and sufficiently sensitive to detect even small changes in size structure as compared to longer term averages. The next phase of this study was to test if size structure varied between years and within the summer season. Validation of interannual variation would be difficult because only 2 years of data would be available and there would be no absolute knowledge of the strength of recruiting year-classes. Nevertheless, a limited test could be made by comparing advancing size classes from year to year (similar to comparing advancing cohorts). Testing of intra-annual variation was thought to be more straightforward, against a priori expectations that all size classes would decline over the summer season, the smaller classes with a higher rate of decline as a result of natural mortality and larger classes a lesser but measureable rate during the main fishing season.

The data in arithmetic format are shown in Figure 5 (Pollom and Rose 2015). Natural log-transformed counts of all size classes of fishes declined linearly throughout the summer season (Figure 6). All surveys showed abundance declining between adjacent size classes by approximately 1 natural logarithm unit or a factor of approximately 3 (e.g., size 4 cm fish were on average approximately 3 times as abundant as size 8 cm fish). Day of year explained between 74.7 and 97.4% of variation in seasonal abundance declines for the 5 size classes with the exception of the largest size class in 2012 which declined over the season but with greater variability among surveys.

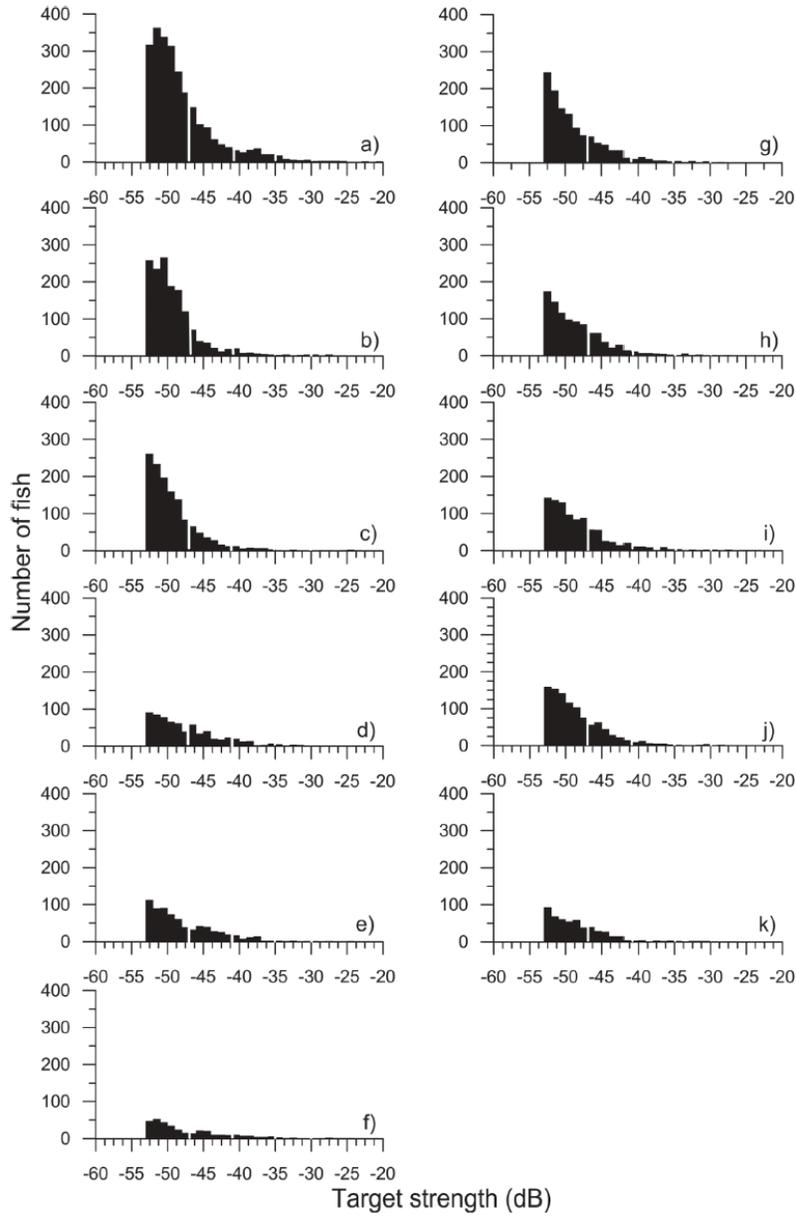


Figure 5. Acoustic target strength (dB) counts of fish tracks. Counts of fish tracks for the different size classes obtained during the 11 surveys of Lac du Bonnet in 2011 and 2012 (see Table 1 for survey dates). The white dividing lines represent the breaks among assigned size classes (figure from Pollom and Rose 2015).

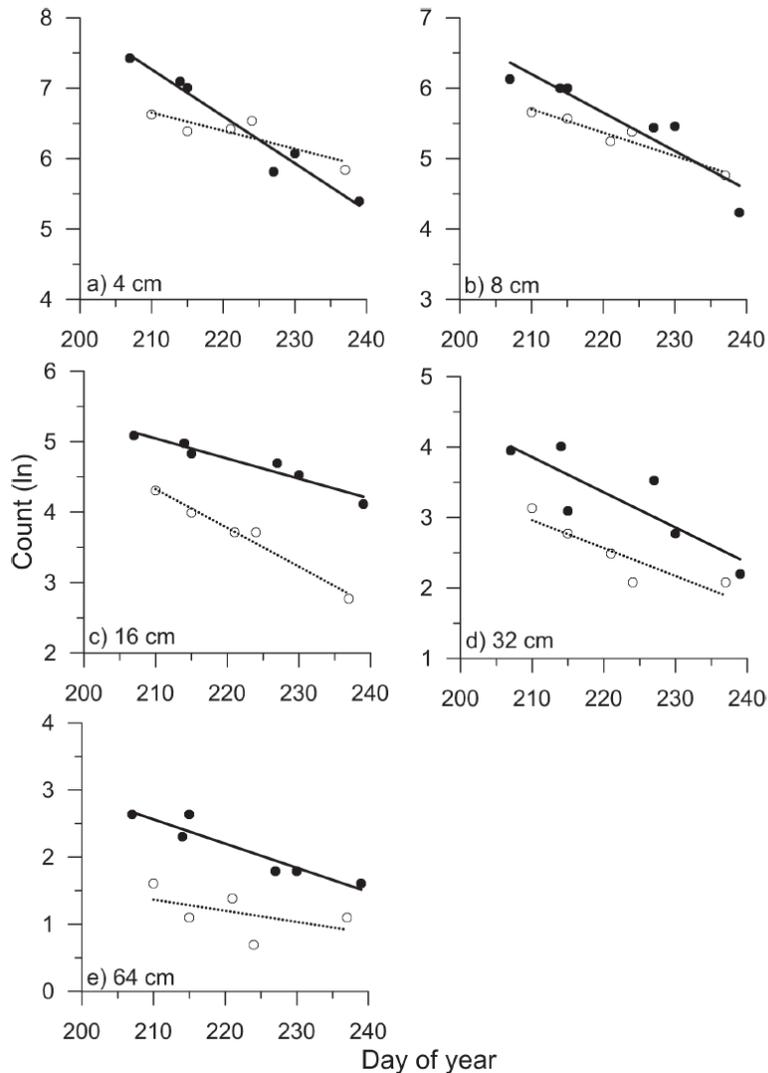


Figure 6. Counts of fish from acoustic surveys. Natural logarithmic counts of 5 target strength size classes (a-e representing size groups 4, 8, 16, 32 and 64 cm, respectively) from the 11 acoustic surveys carried out on Lac du Bonnet in 2011 (closed circles) and 2012 (open circles; figure from Pollom and Rose 2015).

Instantaneous loss rates in the counts over both study periods were variable but generally lower with increasing fish size (Figure 7). Decline rates over the approximately 30-day study periods in both years ranged from -0.067 to $-0.016 \cdot \text{day}^{-1}$. From the end of surveys in 2011 to the first survey in 2012, for the largest 3 size classes, loss rates ranged from approximately -0.0026 to near $0 \cdot \text{day}^{-1}$, an order or magnitude lower than during the summer study period. The smallest size classes were not considered because recruitment, not growth, was almost certainly the main factor in their abundance dynamics from year to year. Based on these data, the mean instantaneous loss in size classes ($> 16 \text{ cm}$) was approximately $0.001 \cdot \text{day}^{-1}$ over the approximately 11 months that were not surveyed, or a fall to summer survival of 71%. In contrast, summer survival during the present study period averaged 33% for the same large size classes. Loss rates of the largest 2 size classes of fish were considerably higher during the summer fishery than during the rest of the year (Figure 7).

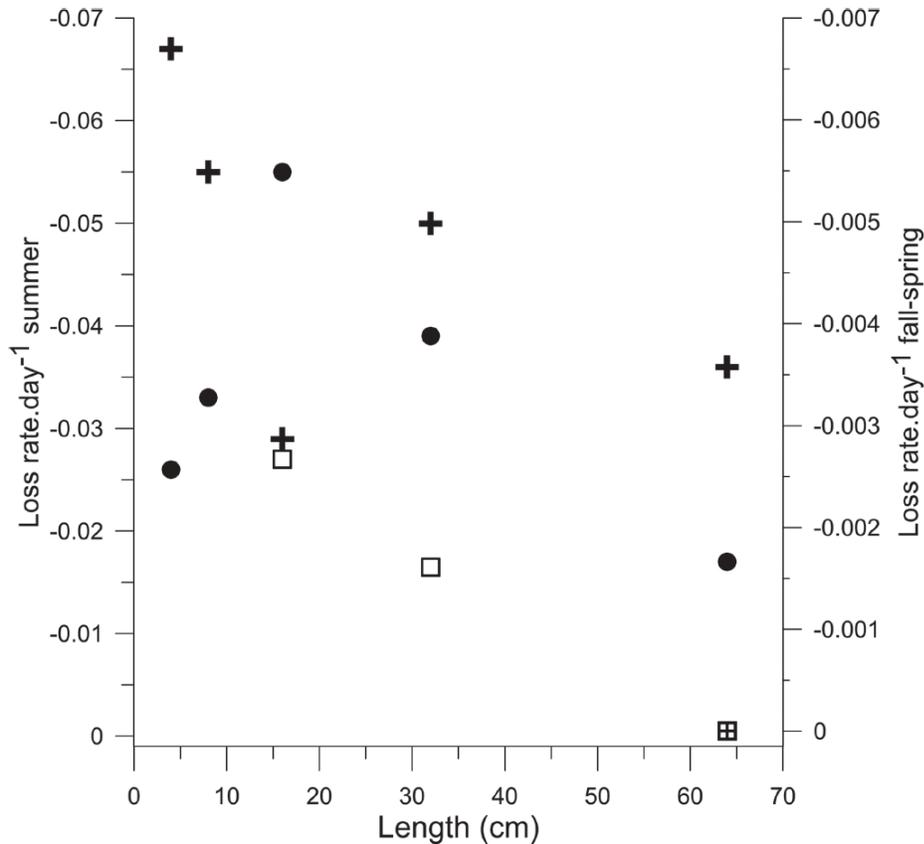


Figure 7. Daily declines in fish abundance. Daily loss rates (declines in counts) within the summer study periods for the 5 size classes in 2011 (crosses) and 2012 (circles), scale on left axis. Inter-annual loss rates from the last survey in 2011 to first survey of 2012 (squares) for size classes (>16 cm) (64 cm class to same class) (crossed square), scale on right axis (figure from Pollom and Rose 2015).

LESSONS LEARNED BY THE MESOSCALE MODELLING OF FISHERIES PRODUCTIVITY METRICS IN THE PELAGIC ZONE OF RESERVOIRS

- It is important and feasible to estimate boat avoidance using the methods of Wheeland and Rose (2015a) if survey indices of abundance are to be used as absolute values of fish abundance or biomass.
- Acoustic methods could be used to describe size spectra in this aquatic reservoir and also in other more natural freshwater bodies (e.g., Newfoundland ponds, Lake Manigotagan, Manitoba – although these were not quantified). The results were consistent and repeatable.
- The derived spectra “fit” theoretical expectations of aquatic ecosystem size structure.
- Fish of all size classes declined as measured acoustically over the summer season, with the highest rates of decline in the smallest size class and the lowest in the largest.
- The rates of decline varied between years, especially for the smaller size classes.
- Limited inter-annual comparisons of advancing size classes were consistent with expectations and supported the integrity of the surveys.
- Loss rates were higher in summer than in winter.

APPLICATION

The methods and research results described here are thought to form the basis for relatively fast, cost-effective and repeatable measures of the size distribution of fishes in the pelagic zones of lakes and reservoirs. They form a basis for assessing change, both natural and human-caused, in the state and productivity of aquatic ecosystems. They are backed by substantial ecological theory. For example, recruitment dynamics would show as changes in the slope and intercept of size-based spectra, and as in traditional catch curve analyses, shunting of the spectra to the left would indicate fewer large fish. The worst-case scenario for productivity would be indicated by a reduction in spectra height and a increase in slope, the best an increase in height and decrease in slope. In other words, the worst-case scenario would be an overall reduction in the number of individuals (decreased height), particularly for larger size classes (increased slope) and the best case is an overall higher count (increased height) with a greater proportion of those being larger individuals (decreased slope).

The major disadvantage of these methods is that species are not identified. In terms of understanding ecosystem productivity, however, this may not be a major impediment. They could be used as a sole measure of ecosystem state employing the size of fish within a community as the metric, or in combination with other metrics from the littoral zone. Longer time series of size spectra would enable description and prediction of ecosystem state – the most straightforward means to do this is to assess the fish.

LITTORAL ZONE COMPONENT

INTRODUCTION

Implementation of the new Fisheries Act and Fisheries Protection Policy requires the estimation of the original state (e.g., pre-development) of an aquatic ecosystem and the prediction of the effect of a project on fisheries productivity metrics. The development of predictive relationships between fisheries productivity metrics and environmental conditions faces numerous difficulties.

Studies that attempt to develop fish-environment relationships often maximize spatial replication (the number of sites sampled) but minimize temporal replication (the number of surveys per site; Lanthier et al. 2013). Lanthier et al. (2013) suggested that for some fish species, like schooling species, increasing the number of surveys per site is advantageous compared to maximizing the number of sites with only one survey per site. However, it has long been recognized that increasing sample size leads to better models (Peterman 1990, Stockwell and Peterson 2002). Metrics of fisheries productivity vary from one year to the next depending on several factors including recruitment success and overwintering and spring conditions (Górski et al. 2011, Moyle and Vondracek 1985). Inter-annual variations in fisheries productivity metrics complicate the development of reliable fish-environment relationships (Rose 2000). It has been suggested that developing fish-environment relationships for management purposes using only one year of data is inadequate (Van Horne 1983), but still this is a common practice due to budgetary and logistical limitations. Yet, the utility to sample fish over multiple years remains poorly documented.

All fish sampling gears are selective and have strengths and weaknesses under specific environmental conditions. Several studies have compared the relative capacity of different sampling gears to estimate community composition (Clement et al. 2014, Dembkowski et al. 2012, Jurajda et al. 2009) and catch per unit effort (CPUE; Chamberland et al. 2014, Götz et al. 2014, Lapointe et al. 2006). Few studies however have assessed which gear, or combination of gears, provides fish data that may maximize the capacity to develop relationships between fisheries productivity metrics and environmental conditions (Eggleton et al. 2010, Lubinski et al. 2008). There is no consensus as to the value of combining data across gears in order to

estimate fisheries productivity metrics and develop fish-environment relationships with high predictive power (Eggleton et al. 2010, Fago 1998, Lubinski et al. 2008).

Littoral-based fish-environment relationships generally use local environmental conditions (i.e. within site) as explanatory variables (e.g. Bryan and Scarnecchia 1992, Gamboa-Pérez and Schmitter-Soto 1999). However, it has been suggested that using contextual environmental conditions (i.e. position of a site relative to landscape attributes) may improve the explanatory or predictive capacity of fish-environment relationships (Porter et al. 2000). Other studies have used a combination of environmental conditions observed at a number of spatial scales to model metrics of fisheries productivity. Brind'Amour et al. (2005) suggested that interactions between littoral fish communities and their habitat occur at multiple spatial scales, and therefore, that environmental conditions observable at different spatial scales may influence fisheries productivity metrics.

Freshwater fish distribution patterns have long been known to vary within a day (Lucas and Baras 2001). Emery (1973) observed a marked increase in apparent fish abundance at night in shallow waters of Ontario Lakes; nearly half the species were encountered more frequently at night than during the day. These observations were attributed in-part to vertical migrations. Similarly, Sanders (1992) observed significantly greater abundance, biomass and richness of most species at night in near-shore waters of the Ohio and Muskingum rivers; catch differences were primarily attributed to diel movements off-shore to in-shore during the evening-twilight period. Two consequences of this situation are that fisheries productivity metrics noted at a site may differ dramatically between days and nights, and that relationships between fish productivity metrics and environmental conditions may vary between days and nights (Bédard et al. 2005; Imre and Boisclair 2005). The effect of day-night variations in fish distribution patterns in reservoirs has rarely been assessed.

Four specific objectives were developed to reduce the difficulties associated to the development of predictive relationships between fisheries productivity metrics and environmental conditions in reservoirs:

- 1) Measure the effect of sample size, and of within-year or between-year replication, on the capacity to develop relationships between metrics of fisheries productivity and environmental conditions.
- 2) Identify the sampling method/combinations of sampling methods that may be best to estimate/predict metrics of fisheries productivity in the littoral zone of reservoirs.
- 3) Assess the relative roles of local, lateral, and contextual environmental conditions in models aimed at modelling/predicting metrics of fisheries productivity in the littoral zone of reservoirs.
- 4) Evaluate the difference between daytime and nighttime estimates/models of metrics of fisheries productivity in the littoral zone of reservoirs.

METHODS

This project was conducted in Lac du Bonnet, a reservoir formed circa 1951 by damming of the Winnipeg River, and since then operated by Manitoba Hydro to generate hydropower. This reservoir can be characterized as turbid, mesotrophic and windswept with a mean depth of 7.7 m. Lac du Bonnet can be divided into three basins from west to east: the west basin includes the main channel (Winnipeg River) and can be defined as lotic; the central and east basins can be defined as lentic (Figure 8). We achieved the objectives by establishing 43 sampling sites (Figure 8) each measuring 200 m (alongshore and extending, perpendicularly to shore, to the 3 m depth isobath) around the 121 km perimeter of Lac du Bonnet. Sites could not

be randomly allocated over the entire perimeter as steep littoral zone (e.g. dike, outcrops) prevented sampling, and locations facing cottages were avoided.

In 2012, the sampling sites were surveyed for fish using a seine (35 m long x 3 m wide, ½" mesh; July 7th to August 23rd), gangs of experimental gill nets (four nets 20 m long x 1.8 m wide with five mesh sizes: one dual mesh net, 5/8" and 1", and 3 single mesh nets: 2", 3" and 4.25"; July 8th to August 20th), and boat electrofishing (Smith-Root SR20 with 5.0 GPP; August 14th to August 15th). Sampling in 2012 took place only during the day (2.5 hours after sunrise to 2.5 hours before sunset). In 2013, the sampling sites were surveyed twice by seining for fish during the day (first day survey from July 1st to July 23rd and second day survey from July 20th to August 4th) and 30 randomly selected sampling sites were surveyed once by seining during the night (end of evening nautical twilight to start of morning nautical twilight; August 9th to August 19th). Electrofishing at night was conducted between August 14th and August 21st 2013. Surveys were conducted 13 to 20 weeks after ice melt in 2012 and 7 to 15 weeks after ice melt in 2013. A total of 22 physical (e.g. shore use, shore slope, substrate composition) and biological (e.g. macrophyte cover) environmental conditions were described for each sampling site (Table 2).

Total fish abundance (fish/100m² or Catch Per Unit Effort [CPUE] depending on the sampling gear) and biomass (g wet/100m² or Mass Per Unit Effort [MPUE] depending on the sampling gear) at a site were obtained by dividing the number or the mass of fish collected by the surface area sampled (m²) or the effort (fishing hours or shocking seconds). Fish abundance and biomass were estimated at each site by species and size-classes (0-20, 20-50, 50-125, 125-316, 316-794, and 794-1995 mm total length). Fish 0-20 mm were too small to be effectively captured with our mesh sizes and were excluded from subsequent analyses. All fish abundance and biomass data were log-transformed to improve data normality. Fish abundance and biomass were estimated at each site for individual surveys, for combinations of seine surveys (the sum of fish collected divided by the sum of surface area sampled, both within and inter-years), and for combinations of surveys from different sampling methods (the sum of standardized fish data, i.e. fish abundance and biomass were translated to a mean of 0 and scaled to a standard deviation of 1 before being summed across sampling methods). Standardized fish data has the advantage of being unitless, describing fish abundance and biomass as relative to other site values, which makes it an appropriate way to combine information from different sampling methods (Götz et al. 2014, Stergiou et al. 2002). Relationships between fish variables (abundance, biomass, presence-absence, by species and combinations of species and size-classes; species richness) and environmental conditions were assessed using multiple regression analyses. In objective 4, 5 and 7, the 12 environmental conditions identified in objective 6 were used without further selection (Table 2). The explanatory power of these relationships was estimated (R^2_{adj}). The predictive power of these models (R^2_{cv} ; Guénard et al. 2013) was quantified using a leave-one out cross validation procedure.

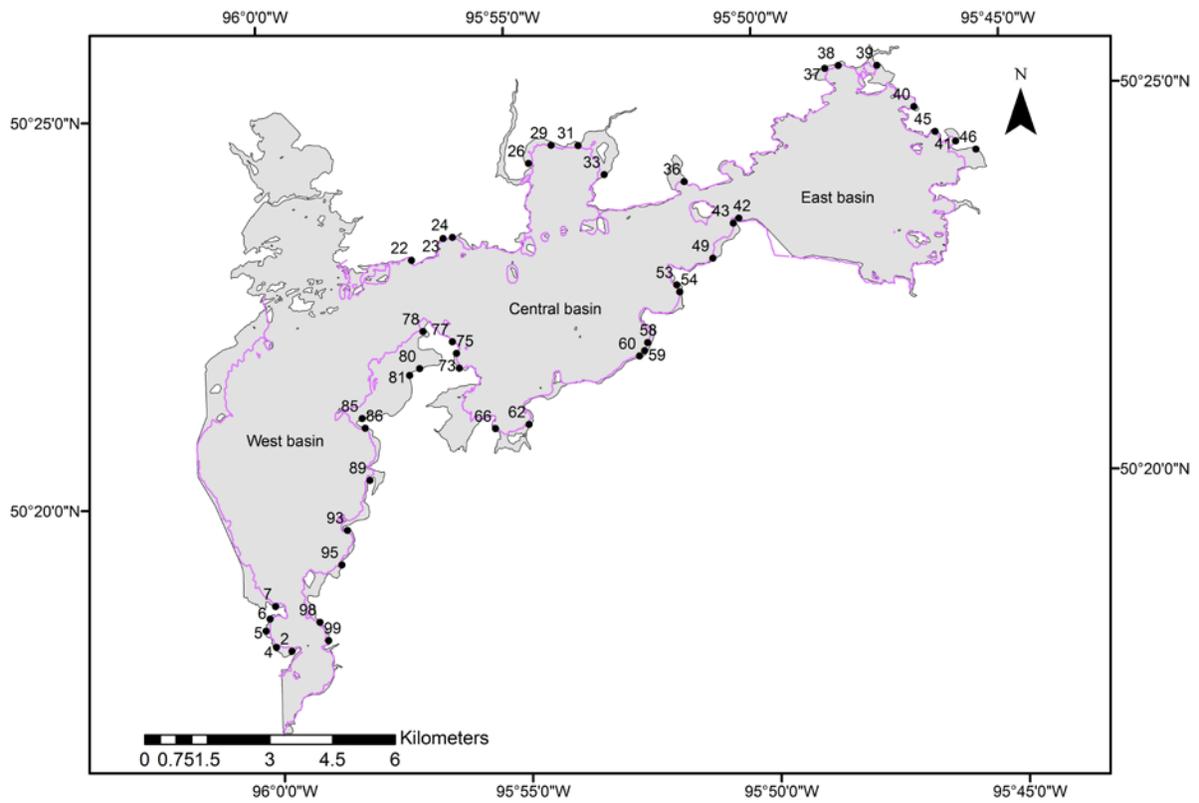


Figure 8. Map detailing the 43 sampling sites established in the littoral zone of Lac du Bonnet. Purple line represents 3 m depth contour.

Table 2. Habitat variables used to explain variation in fisheries productive metrics (FPM) and their potential effects.

Habitat variable	Unit	Potential effects	Reference(s)
Local			
Slope*	%	Influences biomass of submerged macrophyte communities	(Duarte and Kalff 1986)
Macrophyte coverage*	%	Productive feeding environment; refuge from predators; reproductive environment for phytophilic fish species	(Randall et al. 1996) (Bolding et al. 2004) (Dibble et al. 1997)
Substrate			
Substrate particles strongly influence fish assemblages			(Wang et al. 2006)
Compacted fine*	%		
Loose fine*	%		
Small coarse†	%		
Large coarse†	%		
Mean depth	m	Among most important variables in explaining variability in relative fish biomass in Argentina lakes and reservoirs	(Quiros 1990)
Lateral			
Bog	P/A	Low pH often cited as limiting fish species richness	(Rahel 1984)
Grassland*	P/A	Presence or absence of trees cited as important driver of fish abundance in streams	(Inoue and Nakano 2001)
Road	P/A	Associated with negative effects on biotic integrity in aquatic ecosystems	(Trombulak and Frissell 2000)
Golf course	P/A	Associated with heavy pesticide and fertilizer use that may pollute runoff	(Watschke et al. 1989)
Contextual			
Distance to			
Big tributaries*	m	Defines the proximity to complementary resources such as thermal refuge or alternate food source	(Bruns et al. 1984)
Permanent tributaries*	m		(Dunning et al. 1992)
All tributaries	m	Used preferentially for spawning and nursery habitat by the majority of the Great Lakes fish community	(Wei et al. 2004)
Big marshes*	m		
All marshes	m		
Artificial reef*	m	Area of increased habitat heterogeneity may favour increased species richness	(Guegan et al. 1998)
Main channel	m	Fish communities are linked to flow regimes	(Pegg and Pierce 2002)
Average fetch*	km	Significant predictor of physical habitat conditions and fish abundance in the Great Lakes; significant predictor of biomass for three Great Lakes fish species	(Randall et al. 1996) (Randall et al. 1998) (Randall et al. 2004)
Geographical classification			
West basin	P/A	Lotic to lentic transition observed in basins moving west to east	
East basin*	P/A		
Northwest shore*	P/A	Contrast in local habitat composition and fish community observed among northwest and southeast shores, presumably a factor of fetch exposure (mean wind angle 286°)	

* denotes variables selected in objective 6 and used in objective 4, 5 and 7

† denotes variable was log10 transformed to improve distribution normality.

RESULTS

A total of 30 fish species and 71 combinations of species and size-classes were collected on the littoral zone of Lac du Bonnet. No more than 13 of these species (only fish species for which abundance or biomass showed no temporal trend were used for analyses), and 15 of these combinations of species and size-classes, were collected in a sufficient number of sites (threshold of 15 sites) to permit the development of relationships between fish variables and environmental conditions. These numbers varied among surveys (e.g. first or second day survey; night survey). Given this situation, for any given survey, 48-87 potential relationships could be developed between fish variables (total fish abundance, total fish biomass, species richness, and abundance, biomass or presence-absence by species or by combinations of species and size-classes) and environmental conditions.

Objective 4) Measure the effect of sample size, and of within-year or between-year replication on the capacity to develop relationships between metrics of fisheries productivity and environmental conditions.

The effect of sample size and of within-year replication on the capacity to develop relationships between metrics of fisheries productivity and environmental conditions was assessed using the seine data collected in 2013 (only gear and year for which sufficient replication was available). Multiple regression analyses indicated that, when using 43 sites surveyed during the day, 15 to 38 % of potential fish-environment relationships have a positive predictive power ($R^2_{CV} > 0$; Table 3; for examples of these relationships, see Figures 9 and 10). There were notable between-day differences, not only in the number of relationships developed, but also in the mean predictive power ($0.15 < R^2_{CV} < 0.38$) and the maximum predictive power ($0.42 < R^2_{CV} < 0.60$) of these relationships. The low predictive power of the fish-environment relationships developed using the data collected during the first day survey may be attributable to the fact that fish may still have been moving from spawning to feeding sites at that time because of late ice melt in 2013 (Stewart and Watkinson 2004). Combining the two daytime surveys that included 43 sites did not markedly improve the predictive power of the fish-environment relationships. The range of the % of potential fish-environment relationships with positive predictive power (1 to 15%), the mean predictive power ($0.02 < R^2_{CV} < 0.28$), and the maximum predictive power ($0.02 < R^2_{CV} < 0.45$) of fish-environment relationships developed using 30 sites surveyed during the day were lower than corresponding values with 43 sites. Combining the two 30-sites daytime surveys markedly decreased the % of the potential fish-environment relationships with positive predictive power (5%; Table 3). Using an equal number of sites (30), night surveys permitted to develop a relatively good number of models (19% of potential models) compared to day surveys (1 to 15% of potential models) but these possessed a low mean predictive power ($R^2_{CV} = 0.09$).

Table 3. Percentage (% Models) of potential relationships (#Models) developed between fish variables and environmental conditions using seine data of 2013 that performed better than the null hypothesis. Mean predictive power (Mean R^2_{CV}) and maximum predictive power (Max R^2_{CV}) are presented for relationships developed using a single daytime survey, a single nighttime survey, or combinations of surveys.

Surveys	N	#Models	% Models	Mean R^2_{CV}	Max R^2_{CV}
First day survey	30	75	1	0.02	0.02
Second day survey	30	84	15	0.28	0.45
First and second day survey	30	87	5	0.26	0.61
Night survey	30	81	19	0.09	0.24
All three surveys	30	86	15	0.24	0.47
First day survey	43	84	15	0.15	0.42
Second day survey	43	84	38	0.38	0.60
First + Second day survey	43	87	32	0.25	0.61

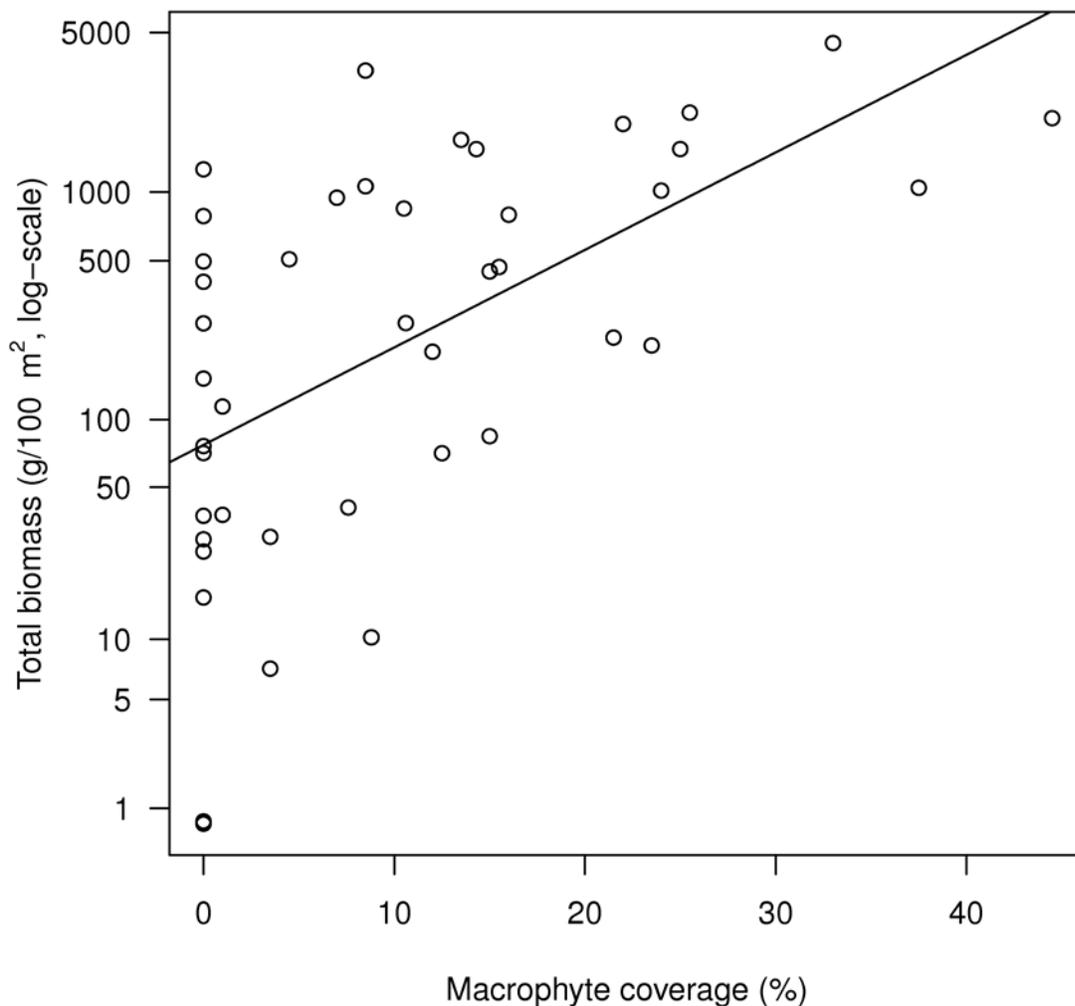


Figure 9. Fish total biomass (TB) captured during the 2013 seine second day survey as a function of macrophyte coverage (MC). The significant linear relationship (p -value < 0.0001; $R^2_{adj} = 0.31$; $R^2_{CV} = 0.28$) equation is $\log_{10}(1+TB) = 0.043*MC + 1.89$

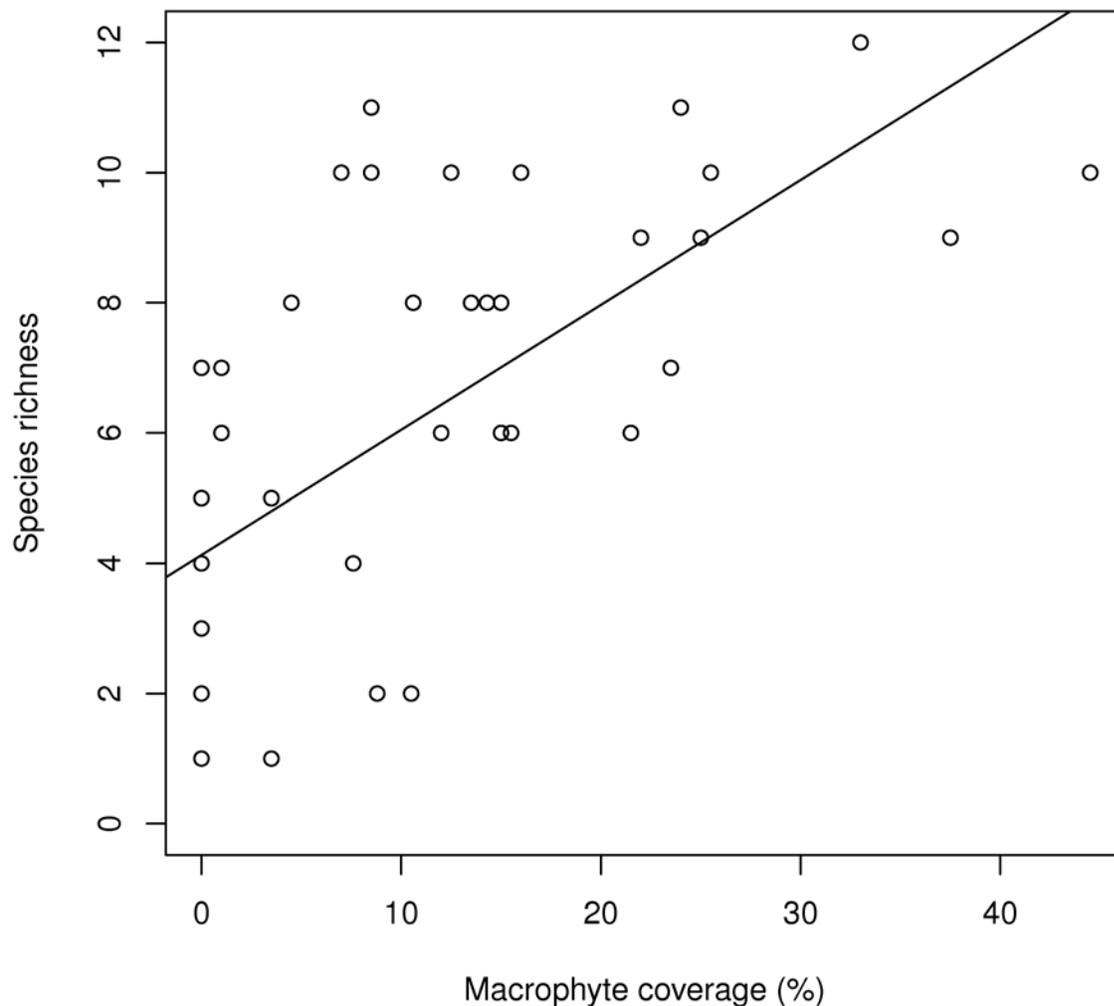


Figure 10. Fish species richness (SR) captured during the 2013 seine second day survey as a function of macrophyte coverage (MC). The significant linear relationship (p -value < 0.0001; $R^2_{adj} = 0.43$; $R^2_{CV} = 0.41$) equation is $SR = 0.19 * MC + 4.13$

The effect of between-year replication on the capacity to develop relationships between metrics of fisheries productivity and environmental conditions was assessed using the seine data (only gear for which sufficient samples were available) collected in 2012 and 2013. For 2013, only the fish data from the second day survey were used for analyses (fish data from the first day survey of this year may be affected by fish movements between spawning and feeding habitats). Total fish abundance, biomass, and species richness were 1.4 to 2.8-fold higher in 2012 than in 2013 (Table 4). Total fish abundance, biomass, and species richness did not permit the development of statistically significant fish-environment relationships in 2012 (Table 5). However, relationships with relatively high explanatory ($R^2_{adj} = 42$ -59%) and predictive power ($R^2_{CV} = 4$ -36%; Table 5) were developed using the fish data of 2013 (e.g., Figures 9 and 10). Across all fish variables (abundance, biomass, presence-absence, by species and combinations of species and size-classes), the data collected in 2012 permitted the development of fewer fish-environment relationships than the data collected in 2013. The 2012 relationships also had a lower mean R^2_{CV} than the 2013 relationships (Table 6). Combining the data collected in 2012 to those of 2013 provided fish-environment relationships that had statistical significance, explanatory power, and predictive power similar to, or lower than, relationships developed using

only the data collected in 2013 (Tables 5 and 6). These results are consistent with the expectation that fish abundance may affect habitat selection patterns (McMillan et al. 2013). During years of high abundance, even less preferred/suitable habitats (sink habitats) can be used by a large number of individuals (Van Horne 1983), decreasing the contrast between high value habitats and low value habitats (Gibson et al. 2008), and impairing the capacity to develop fish-environment relationships.

Table 4. Statistics of total fish abundance, biomass, and species richness estimated using the 43 sites sampled by seining in 2012 and 2013 (only second day survey).

Fish variable	Year	Minimum	Median	Mean	Maximum	Standard deviation
Total fish abundance (fish/100 m ²)	2012	3.6	152.9	305.0	1893.1	390.4
	2013	0.7	69.6	109.3	659.6	140.4
Total fish biomass (g/100 m ²)	2012	14.5	606.7	1314.2	8430.1	1755.9
	2013	0.7	266.0	721.9	4495.0	969.4
Species richness (#species)	2012	3	9	8.5	15	2.4
	2013	1	6	6.1	12	3.3

Table 5. Statistics of fish-environment relationships developed for total fish abundance, biomass and species richness when using the seine data of a single year (2012 or 2013) or of a combination of years (2012 and 2013).

Fish variable	Year	P.value	R ² _{adj}	R ² _{CV}
Total abundance (fish/100 m ²)	2012	0.07	0.021	-0.15
	2013	0.0004	0.54	0.29
	2012 and 2013	0.004	0.40	0.14
Total biomass (g/100 m ²)	2012	0.14	0.15	-0.19
	2013	0.002	0.42	0.04
	2012 and 2013	0.003	0.44	0.14
Species richness (#species)	2012	0.9	-0.17	-0.66
	2013	0.0001	0.59	0.36
	2012 and 2013	0.27	0.08	-0.32

Table 6. Percentage (% Models) of potential relationships (#Models) developed between fish variables (total fish abundance, total fish biomass, species richness, and abundance, biomass or presence-absence by species or by combinations of species and size-classes) and environmental conditions using daytime seine data of 2012, 2013 (second day survey), and a combination of the seine data of 2012 and 2013. Mean (Mean R²_{CV}) and maximum predictive power (Max R²_{CV}) of fish-environment relationships are presented.

Year	#Models	% Models	Mean R ² _{CV}	Max R ² _{CV}
2012	87	20	0.18	0.38
2013	87	37	0.38	0.60
2012 and 2013	87	37	0.20	0.59

Objective 5) Identify the sampling method/combinations of sampling methods that may be best to estimate/predict metrics of fisheries productivity in the littoral zone of reservoirs.

The comparative analysis of the capacity of different sampling gears to develop fish-environment relationships was conducted using fish data collected at 43 sites during the day in 2012 using the seine, the electrofishing boat, and the set of gill nets (Table 7). While different fish abundance and biomass data collected using different sampling gears may be difficult to compare, it can only be noted that species richness values obtained using 43 seine hauls were consistently higher than values obtained using 43 electrofishing transects. Electrofishing was the sampling gear that permitted to obtain the highest percentage of potential fish-environment relationships (31%; Table 8; for an example, see Figure 11). This sampling gear also provided relationships with the highest mean (0.24) and maximum (0.49) predictive power. Combining sampling gears improved the development of fish-environment relationships only when seine and electrofishing boat data were merged but this improvement was relatively minor increasing the percentage of potential fish-environment relationships by 2% and the mean predictive power by 0.04 (Table 8). This result confirms the applicability, in reservoirs, of the findings of Lubinski et al. (2008) and Eggleton et al. (2010), which suggest that combining sampling gears may not improve habitat use models in lakes. Given that it took 2 days to complete the sampling of 43 sites with the electrofishing boat, and that it took 25 days with the seine, it is obviously more efficient, to develop fish-environment relationships, to further increase the number of sites sampled using the electrofishing boat than to conduct seine surveys.

Table 7. Minimum, median, mean, maximum, and standard deviation of total fish abundance, biomass, and species richness estimated at 43 sites surveyed during the day in 2012 using three sampling gears.

Fish variable	Sampling gear	Minimum	Median	Mean	Maximum	Standard deviation
Total abundance (fish)	Seining	7	248	474	3210	626
	Electrofishing	0	47	93	453	114
	Gillnetting	3	47	78	361	85
Total biomass (g)	Seining	29	932	2063	14295	2838
	Electrofishing	0	877	1310	6351	1489
	Gillnetting	359	3670	4629	18856	3818
Species richness (#species)	Seining	3	9	9	15	2
	Electrofishing	0	4	5	8	2
	Gillnetting	2	6	6	9	2

Table 8. Percentage (% Models) of potential relationships (#Models) developed between standardized fish variables and environmental conditions using seine, electrofishing boat, gillnets data collected in 2012. Mean predictive power (Mean R^2_{CV}) and maximum predictive power (Max R^2_{CV}) are presented for relationships developed using a single daytime survey.

Sampling gear	#Models	% Models	Mean R^2_{CV}	Max R^2_{CV}
Seine	82	21	0.18	0.38
Electrofishing boat	72	31	0.24	0.49
Gillnets	48	15	0.10	0.19
Seine and Electrofishing boat	75	33	0.28	0.49
Seine and Gillnets	59	19	0.15	0.38
Electrofishing boat and Gillnets	53	17	0.19	0.28
Seine, Electrofishing boat, and Gillnets	56	23	0.20	0.33

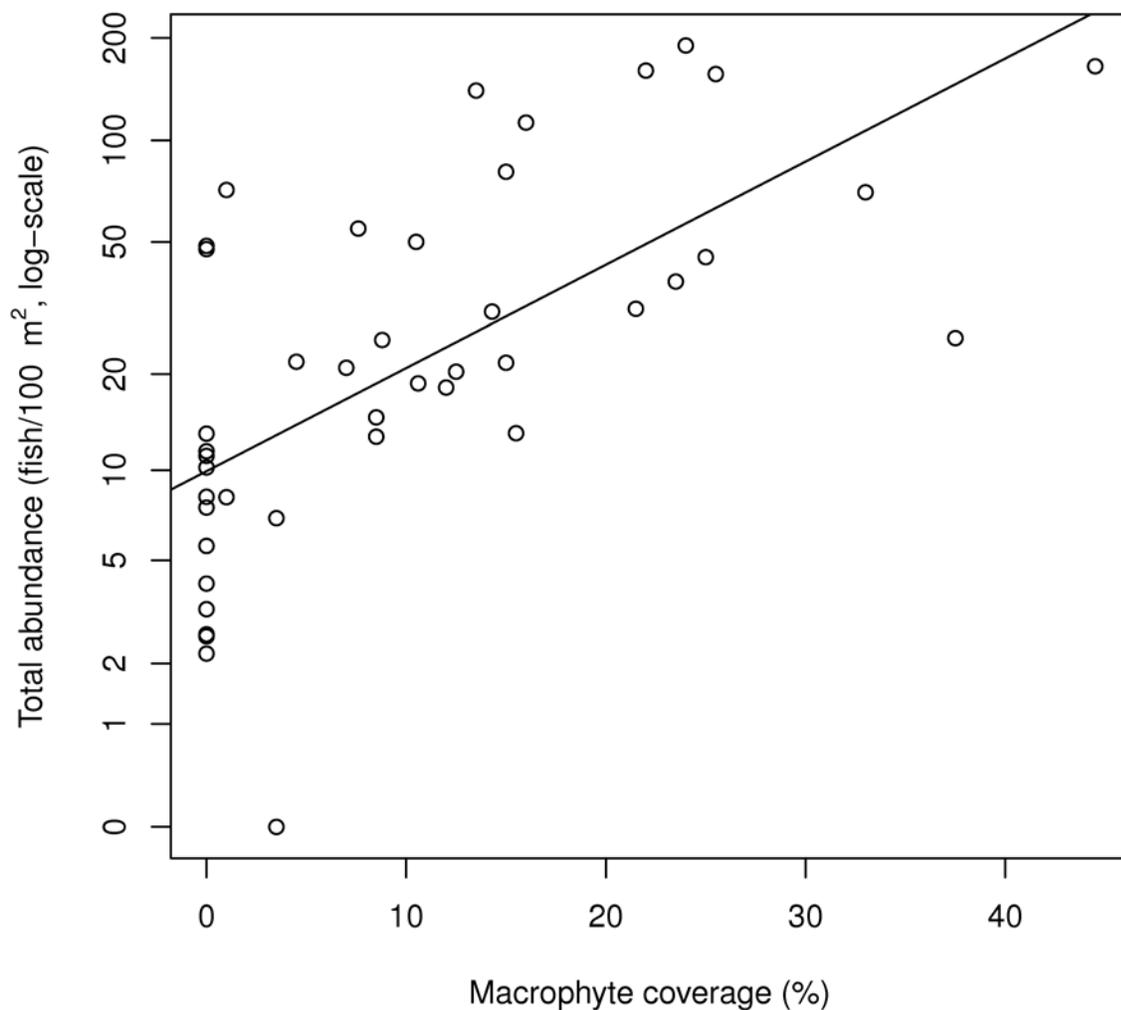


Figure 11. Fish total abundance (TA) captured during the 2012 electrofishing day survey as a function of macrophyte coverage (MC). The significant linear relationship (p -value < 0.0001; $R^2_{adj} = 0.40$; $R^2_{CV} = 0.37$) equation is $\log_{10}(1+TA) = 0.030*MC + 1.04$

Objective 6) Assess the relative roles of local, lateral, and contextual environmental conditions in models aimed at modelling/predicting metrics of fisheries productivity in the littoral zone of reservoirs (from Satre et al., unpublished manuscript).

Assessment of the relative roles of local, lateral, and contextual environmental conditions (see Table 2) on fish-environment relationships was done using seven fish sampling scenarios, consisting of different combinations of sampling methods (seining, boat electrofishing, and gillnetting), years (2012 and 2013) and time periods (day and night), and using three fisheries productivity metrics (total fish abundance, total fish biomass and fish species richness). This led to the formation of 21 univariate fish datasets (three fisheries productivity metrics x seven sampling scenarios). Multiple regressions were used to assess the relative roles of three environment datasets (local, lateral, and contextual variables; Table 2) in explaining variations of fisheries productivity metrics observed in the 21 fish datasets. Only 12 of the 21 fish datasets were retained for detailed analyses, having exhibited significant correlation with the sets of environmental conditions. Starting with the 22 environmental conditions measured (Table 2), forward selections were conducted and only the 12 environmental conditions significantly related to at least one fish dataset was retained. These 12 environmental conditions are the ones used in objectives 4, 5 and 7 (see Table 2). Selection criteria in forward selection included p -value < 0.05 and $R^2_{adj} > 10\%$; selection was stopped if the cumulative R^2_{adj} reached the R^2_{adj} of a global model including all environmental conditions (Blanchet et al. 2008). Variation partitioning was conducted using these 12 environmental conditions divided into three categories (local, lateral and contextual) to assess the relative explanatory power of each category. Further forward selections (same criteria as above) were conducted to identify key environmental conditions explaining fish distribution.

Local habitat variables explained on average 21% (R^2_{adj}) of the variation within the reduced fish datasets, while lateral and contextual habitat variables explained on average 2% and 14% respectively (Table 9, Figure 12). The portion of variation explained by local habitat variables was statistically significant in 10 out of 12 fish datasets, while the portion explained by lateral variables was significant in 3 out of 12 fish datasets. The portion of variation explained by contextual habitat variables was significant in 7 out of 12 fish datasets. Using only local and contextual habitat variables, 20% to 64% (on average 44%) of the variation within the 12 reduced fish datasets was explained. Key variable assessment showed that among local habitat variables, macrophyte coverage, compacted fine substrate and loose fine substrate explained the most variation in fisheries production metrics having been selected in 75%, 33%, and 42% of reduced fish datasets, respectively (Table 10). In their respective datasets, fisheries productivity metrics were positively correlated to macrophyte coverage (e.g., Figures 9, 10 and 11) and loose fine substrate, but negatively correlated to compacted fine substrate. Among contextual habitat variables, distance to big marshes and distance to big tributaries explained the most variation having been selected in 42% and 33% of reduced fish datasets, respectively (Table 10). In their respective datasets, fisheries productivity metrics were negatively correlated to the distance to big marshes and to big tributaries (e.g., Figure 13).

These findings are similar to those of Wang et al. (2003) who found that local (reach-scale) variables explained the most inter-river variation in abundance ($R^2=21\%$), succeeded by contextual (watershed-scale) variables ($R^2=11\%$); lateral (riparian-scale) variables explained the least variation ($R^2=5\%$). Bouchard and Boisclair (2008) also observed that local habitat variables explained most variation in intra-river abundance ($R^2_{adj}=31\%$), succeeded by contextual (longitudinal) variables ($R^2_{adj}=1\%$); lateral variables failed to explain any variation. In both studies, including local and contextual variables increased explanatory power of models, as opposed to using only local variables to explain variation. Brind'Amour et al. (2005) also

observed that fetch (contextual variable) and to a lesser degree macrophytes (local variable) best explained variation in fish community composition in the littoral zone of a Québec lake.

The present study reinforces these findings previously made in inter- and intra-river and lake studies, broadening them to intra-reservoir studies. Macrophyte coverage (local) was selected most often (75% of the models; Table 10; e.g., Figures 9, 10 and 11) across metrics as statistically and biologically significant. Compacted fine substrate and loose fine substrate (local) were highly correlated ($|r|=73\%$) with macrophyte coverage; because these variables were highly correlated and selected less often across metrics, these two variables may be redundant given macrophyte coverage. Numerous studies have noted macrophytes provide productive feeding environments, refuge from predators, and reproductive environments for phytophilic fish species (Bolding et al. 2004, Dibble et al. 1997, Randall et al. 1996). Effective contextual habitat variables included distance to big marshes (42% of the models) and distance to big tributaries (33% of the models; Table 10; e.g., Figure 13). Marshes have been cited to provide spawning and nursery habitat for a majority of a fish community (Wei et al. 2004), while tributaries may provide complementary resources such as thermal refuge or alternate food sources (Bruns et al. 1984, Dunning et al. 1992).

Table 9. The percentage of variation explained (R^2_{adj}) by type of environmental conditions (local, lateral, contextual) for a given fish dataset, bold values indicating statistical significance.

Fish variable	Fish dataset	Local	Lateral	Contextual
Total abundance	Gillnets-day	0.004	-0.020	0.234
	Electrofishing-day	0.608	0.027	0.110
	Seine-day 2	0.145	-0.015	0.166
	Seine-day 3	0.128	0.037	0.159
	Seine-night	0.289	-0.033	0.083
	Electrofishing-night	0.093	0.086	0.211
Total biomass	Seine-day 2	0.293	0.091	0.074
Species richness	Electrofishing-day	0.240	-0.020	0.141
	Seine-day 2	0.246	-0.015	0.058
	Seine-day 3	0.184	-0.020	-0.030
	Seine-night	0.112	0.004	0.276
	Electrofishing-night	0.216	0.141	0.196
Average		0.213	0.022	0.140

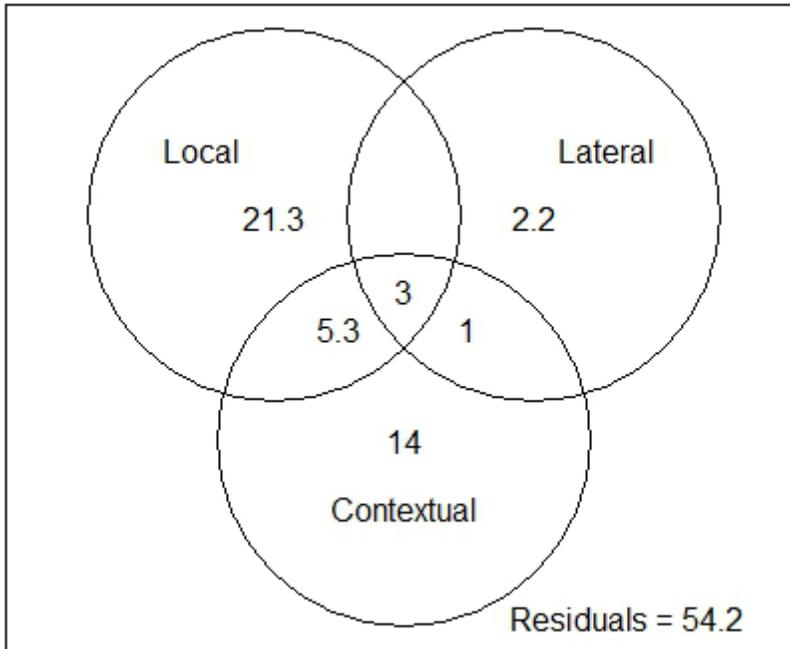


Figure 12. Average percentage of variation explained (R^2_{adj}) by type of environmental conditions (local, lateral, contextual). Shared parts represent joint explanation.

Table 10. Key variable assessment results where “X” denotes statistically significant environmental variables within a given fish dataset in at least one forward selection, and the percent row indicates the percentage of fish datasets for which a variable was selected at least one time.

Fish variable	Fish data set	Local	Lateral	Contextual
		slope	Macrophyte coverage	Compacted fine sub.
			Loose fine sub.	Grassland
			East basin	Northwest shore
			Average fetch	Dist. to big trib.
			Dist. to permanent trib.	Dist. to big marsh
			Dist. to fish sanctuary	
Total abundance	Gillnets-day			X
	Electrofishing-day	X	X	X
	Seine-day 2		X	X
	Seine-day 3		X	X
	Seine-night		X	X
Total biomass	Electrofishing-night		X	X
	Seine-day 2	X	X	X
Species richness	Electrofishing-day		X	
	Seine-day 2		X	X
	Seine-day 3		X	X
	Seine-night			
	Electrofishing-night			X
%		17	75	33
		42	8	8
		0	25	33
		17	42	25

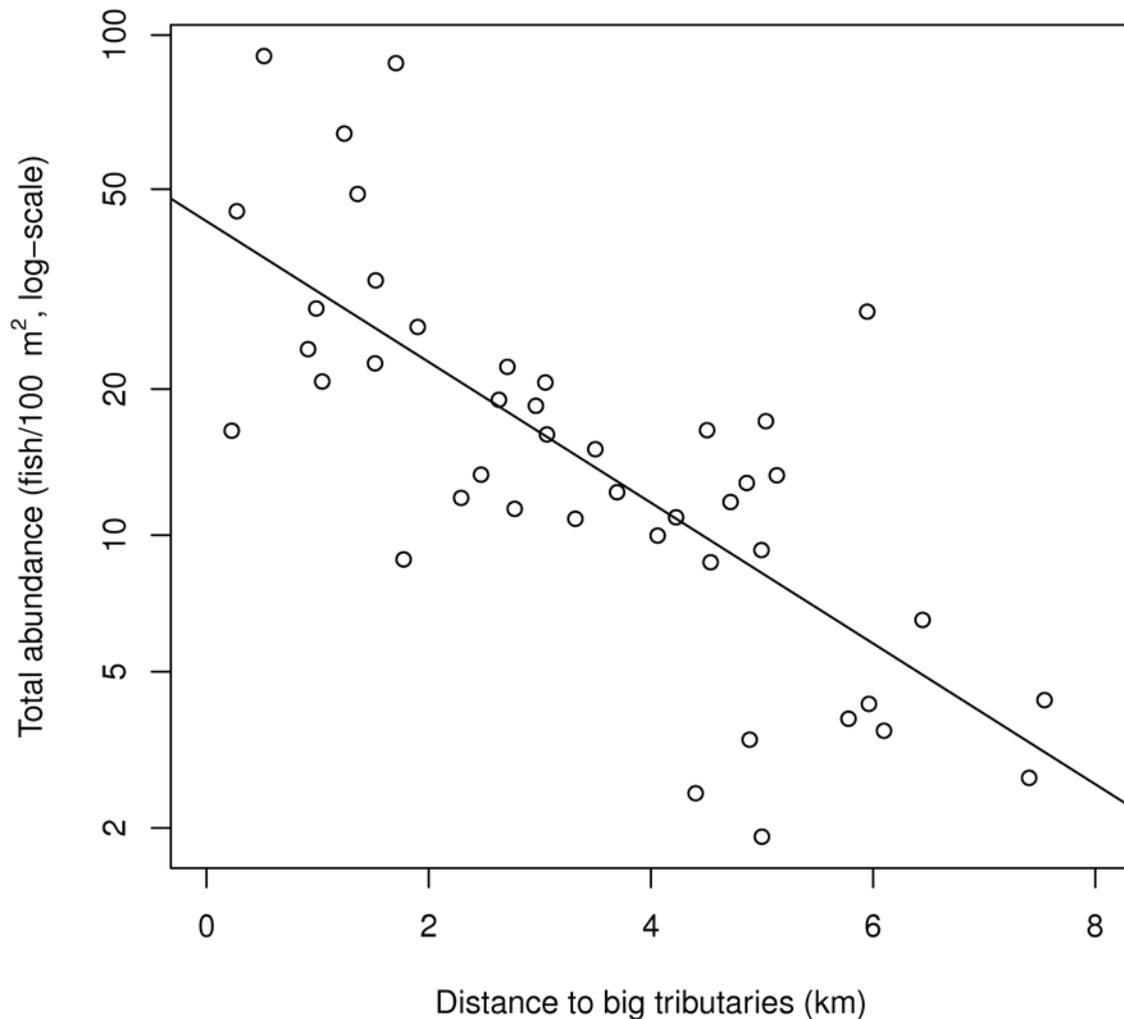


Figure 13. Fish total abundance (TA) captured during the 2013 electrofishing night survey as a function of the distance to the nearest big tributary (DBT). The significant linear relationship (p -value < 0.0001; $R^2_{adj} = 0.54$; $R^2_{CV} = 0.51$) equation is $\log_{10}(1+TA) = -0.14*DBT + 1.65$

Objective 7) Evaluate the difference between daytime and nighttime estimates/models of metrics of fisheries productivity in the littoral zone of reservoirs.

The difference between daytime and nighttime estimates/models of metrics of fisheries productivity in the littoral zone was assessed using the paired seining data collected at 30 sites in 2013 (only gear for which sampling was done during the day and the night of a same year). Comparisons of estimates and models were conducted using total community metrics (total abundance and biomass; species richness) and fish species. Mean, median, range, standard deviation and paired t-tests by permutation (comparing paired day and night data) were estimated for each total community metric. No statistically significant difference in total abundance or total biomass was noted between day and night (Table 11). Species richness was significantly higher when seining was done at night. Community-level fish-environment relationships were assessed using a combination of local (i.e. within site), lateral (i.e. shore characterization) and contextual (i.e. position relative to landscape attributes) environmental conditions (see Table 2). Statistically significant relationships between total fish abundance or

species richness and environmental conditions were found only for nighttime data (Table 12). No significant relationship was found for total fish biomass.

Table 11. Comparison of total abundance (TA), total biomass (TB) and species richness (SR) values during the day and at night. * Denotes permutational paired t-test statistical significance (p -value ≤ 0.05).

Fish variable /day period	Mean	Median	Minimum	Maximum	Standard deviation	Mean difference	p-value
TA/Day	104.7	60.5	0	744.0	140.5	-98.0	0.07
TA/Night	202.7	87.0	4.3	1079.2	136.9		
TB/Day	725.1	378.7	0	4989.6	138.8	-53.43	0.83
TB/Night	778.5	635.3	60.9	2341.7	76.7		
SR/Day	5.6	5.5	0	10	50.2	-2.7	0.0003*
SR/Night	8.3	8	3	15	33.4		

Table 12. Statistics of the relationships between fish community variables (TA=total abundance; TB=total biomass; SR=Species richness) and environmental conditions during the day and at night. * Denotes statistically significant multiple linear models (p -value ≤ 0.05).

Fish variable /day period	p-value	R ² _{adj}
TA/Day	0.10	0.27
TA/Night	0.034*	0.39
TB/Day	0.14	0.24
TB/Night	0.11	0.27
SR/Day	0.09	0.29
SR/Night	0.02*	0.44

Species estimates included the abundance and the biomass of 13 fish species (only fish species for which abundance or biomass showed no temporal trend were used for analyses). Paired t-tests by permutation were run for each species using day and nighttime data from 30 sites. The abundance of Rock bass (*Ambloplites rupestris*), Sauger (*Sander canadensis*), Troutperch (*Percopsis omiscomaycus*) and Walleye (*Sander vitreus*) were higher at night than during the day, while the biomass of Spottail shiner (*Notropis hudsonius*), Troutperch, Walleye, and Yellow perch (*Perca flavescens*) were higher at night. Statistically significant models could be developed for Logperch (*Percina caprodes*), Mimic shiner (*Notropis volucellus*), Rock bass and Yellow perch abundance and Johnny darter (*Etheostoma nigrum*), Logperch, Mimic shiner and Rock bass biomass at night, and Northern pike (*Esox lucius*) and Weed shiner (*Notropis texanus*) abundance and Weed shiner and Yellow perch biomass during the day. Across all fish metrics, more models could be developed from night surveys, but day surveys could produce better models (Table 3).

Seining at night provided higher values of total fish abundance and species richness than daytime sampling. Seining at night also permitted to increase the explanatory power of relationships between total abundance or species richness and environmental conditions. These findings are similar to those obtained by Emery (1973). He observed a marked increase in apparent fish abundance at night in shallow waters of Ontario lakes. In this study, nearly half the species were encountered more frequently at night than during the day. These observations were attributed in-part to vertical migrations. Similarly, Sanders (1992) observed significantly higher abundance, biomass and richness of most species at night in near-shore waters of the Ohio and Muskingum rivers; catch differences were primarily attributed to diel movements off-

shore to in-shore during the evening-twilight period. Midwood et al. (2015) observed higher catch per unit effort and richness at night with boat electrofishing in coastal wetlands of the St. Lawrence river.

Relationships between electrofishing boat fish data at 43 sites and environmental conditions were also compared between the 2012 day survey and the 2013 night survey. Electrofishing at night in 2013 produced better models of total fish abundance but subperforming models of species richness, compared to the 2012 day survey (Table 13; e.g., Figures 11 and 13). Both surveys were unsuccessful to model total fish biomass. Across all fish metrics, the 2012 day electrofishing survey produced more models but the 2013 night survey produced models with higher R^2_{CV} (Table 14; e.g., Figure 14). However, these results are less straightforward to interpret than the above seining results as electrofishing day and night surveys were conducted on different years and are consequently subject to notable inter-year differences (see objective 4).

Table 13. Statistics of fish-environment relationships developed for total fish abundance, biomass and species richness when using 2012 daytime and 2013 nighttime electrofishing data.

Fish variable	Year-time period	p-value	R^2_{adj}	R^2_{CV}
Total abundance (fish/100 m ²)	2012-day	0.0001	0.60	0.42
	2013-night	0.0001	0.73	0.56
Total biomass (g/100 m ²)	2012-day	0.45	0.01	-0.50
	2013-night	0.40	0.03	-0.53
Species richness (#species)	2012-day	0.008	0.36	0.09
	2013-night	0.009	0.34	-0.19

Table 14. Percentage (% Models) of potential relationships (#Models) developed between fish variables (total fish abundance, total fish biomass, species richness, and abundance, biomass or presence-absence by species or by combinations of species and size-classes) and environmental conditions using 2012 daytime and 2013 nighttime electrofishing data. Mean (Mean R^2_{CV}) and maximum predictive power (Max R^2_{CV}) of fish-environment relationships are presented.

Year-time period	#Models	% Models	Mean R^2_{CV}	Max R^2_{CV}
2012-day	87	25	0.24	0.49
2013-night	87	9	0.37	0.56

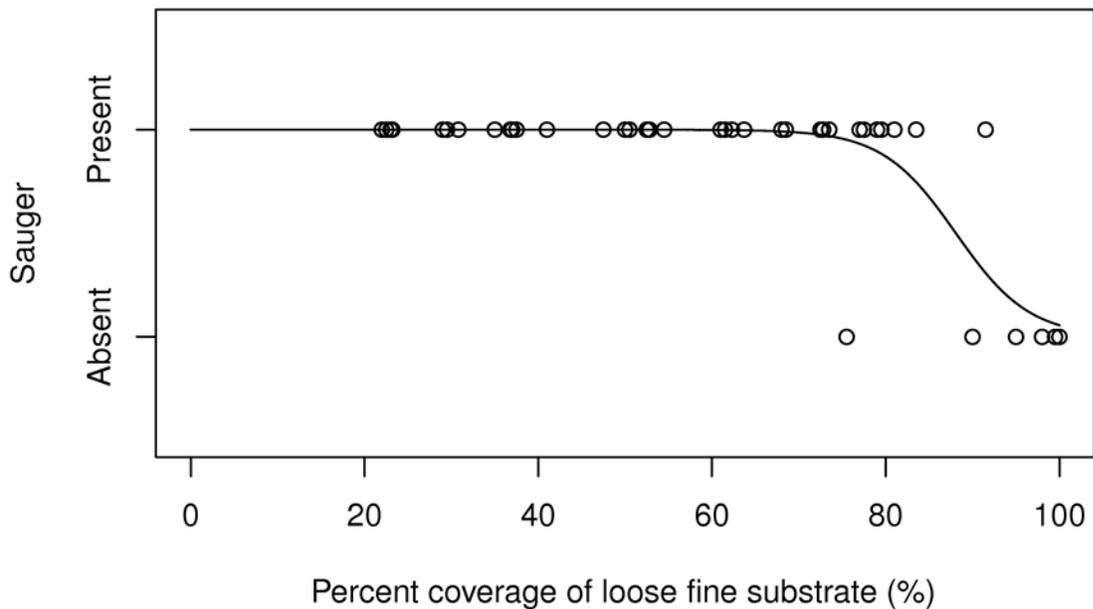


Figure 14. Sauger (*Sander canadensis*) presence or absence (PA) during the 2013 electrofishing night survey as a function of the percent coverage of loose fine substrate (mixture of clay, silt and sand; LFS). The significant logistic relationship (p -value = 0.0071; $R^2_{adj} = 0.73$; $R^2_{CV} = 0.67$) equation is $PA = 1/(1 + e^{-(0.236 \cdot LFS + 20.81)})$

Total fish abundance model using 2013 night electrofishing survey data was among the top performing models (Table 13). This model involves 12 habitat variables (see Table 2), but as shown in Objective 6 some habitat variables performed as a whole better than others (Table 9 and 10, Figure 12). A forward selection (same criteria as in objective 6) was conducted to identify a parsimonious model of 2013 night electrofishing total fish abundance (Figure 15), as an example of a practical tool to explain and predict changes in fish abundance from changes in environmental conditions.

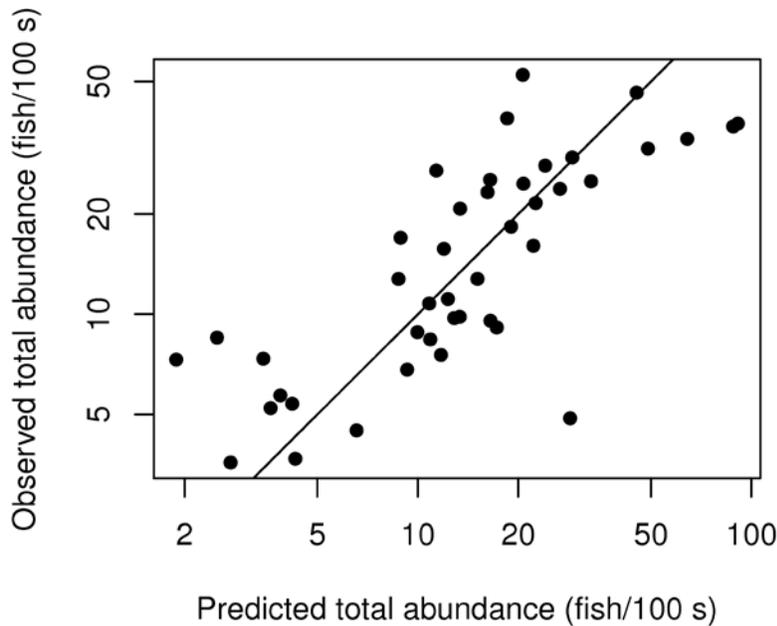


Figure 15. Relationship between observed and predicted 2013 electrofishing night survey fish total abundance (TA), representing the performance of a parsimonious model of macrophyte coverage (MC) and the distance to the nearest big tributary (DBT). Black line represents a 1:1 expected relationship between observations and predictions. The significant linear relationship (not shown; p -value $\ll 0.0001$; $R^2_{adj} = 0.63$; $R^2_{CV} = 0.60$) equation is $\log_{10}(1+TA) = 0.13*MC - 0.20*DBT + 1.18$

LESSONS LEARNED BY THE MESOSCALE MODELLING OF FISHERIES PRODUCTIVITY METRICS IN THE LITTORAL ZONE OF RESERVOIRS

All “lessons learned” should be examined in the context that this study was conducted in single reservoir sampled over 2 summers.

Objective 4): Measure the effect of sample size, and of within-year or between-year replication on the capacity to develop relationships between metrics of fisheries productivity and environmental conditions.

- Sampling fish on the littoral zone 10-12 weeks after ice melt may improve the capacity to develop fish-environment relationships in reservoirs.
- The mean (and often the maximum) predictive power of fish-environment relationships is frequently low suggesting that fish may not have very strict habitat requirements in reservoirs.
- Sampling more sites within a year may be preferable to develop fish-environment relationships in reservoirs than repeatedly sampling fewer sites within this year.
- There are large between-year differences in the number and the explanatory or predictive power of fish-environment relationships. These differences may be attributable to between-year variations in fish abundance. Modelling (or validating) fish-environment relationships in reservoirs may require more than a single year of sampling.

Objective 5): Identify the sampling method/combinations of sampling methods that may be best to estimate/predict metrics of fisheries productivity in the littoral zone of reservoirs.

- Seining may be superior at estimating species richness in the littoral zone of reservoirs than other sampling gears.
- Electrofishing may be the best sampling gear to develop fish-environment relationships in the littoral zone of reservoirs.

Objective 6): Assess the relative roles of local, lateral, and contextual environmental conditions in models aimed at modelling/predicting metrics of fisheries productivity in the littoral zone of reservoirs.

- Local and contextual scale environmental conditions contributed similarly to explaining variation across abundance, biomass and richness metrics, whereas lateral scale contributed minimally.
- A combination of local and contextual habitat variables should be used to explain variation in fisheries productivity metrics in the littoral zone of reservoirs and to identify important productivity areas of reservoirs.

Objective 7): Evaluate the difference between daytime and nighttime estimates/models of metrics of fisheries productivity in the littoral zone of reservoirs.

- The explanatory capacity of relationships between total fish abundance and environmental conditions is higher when sampling fish at night than during the day.
- The capacity to develop relationships between species richness and environmental conditions is higher during the day than at night when collecting fish with an electrofishing boat and is higher at night than during the day when collecting fish with a seine.

APPLICATION

The littoral zone component of this study identified how sampling should be done to better estimate or model fisheries productivity metrics on the littoral zone of a reservoir. It also provided a series of predictive relationships between fisheries productivity metrics and environmental conditions (e.g., Figure 15). We contend that these may have direct practical and management implications. For instance, if Manitoba Hydro were to plan to modify the water level in Lac du Bonnet, or to develop a new reservoir on the Winnipeg River, the findings of the present study could serve to justify the sampling methods used to monitor the effects of such endeavours on littoral zone fish. In addition, the relationships between fisheries productivity metrics and environmental conditions developed by the present study could be used to predict future littoral fisheries productivity metrics under a new set of environmental conditions. These contributions respond directly to the need of both the proponents and the regulators to: i) adequately measure the initial state of fisheries productivity metrics; ii) predict the potential effect of a project on metrics of fisheries productivity; iii) assess the need for, or the magnitude of, mitigation measures; iv) identify and measure the relative efficiency of different mitigation strategies; v) estimate the existence or the magnitude of residual effects on metrics of fisheries productivity, and; vi) quantify the need for, or the magnitude of, offsetting. Knowledge and tools developed by the present project may be useful to inform the decision-making process regarding the development or operation of hydropower facilities, and, if authorities recognize the knowledge and tools developed by the present study, augment the clarity, the consistency, and the certainty of the decision-making process.

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