

PERSPECTIVE / PERSPECTIVE

A preliminary national analysis of some key characteristics of Canadian lakes

Charles K. Minns, James E. Moore, Brian J. Shuter, and Nicholas E. Mandrak

Abstract: Knowledge of Canada's lakes is needed to manage environmental stresses. Lake inventory and lake feature databases were used to build a national impact assessment template and assess regional typology. There are ~910 400 lakes with area $\geq 0.1 \text{ km}^2$ (10 ha), 37% of the Earth's total. Lake features (number of lakes by size class, maximum depth, mean–maximum depth ratio, Secchi depth, pH, and total dissolved solids) were modeled regionally by secondary watershed (SWS) using linear regression models. Lake trout (*Salvelinus namaycush*) occurrence was analyzed as a cofactor to highlight regional links between lake characteristics and aquatic biota. Significant (R^2 from 0.231 to 0.492) regional models were obtained using area or maximum depth, lake trout occurrence, and their cross products as covariates. Analyses of fitted SWS coefficients showed that ecozones were a better predictor of lake characteristics than primary watersheds. The national typology was consistent with previous regional assessments. The regional models were used to estimate the number, area, and volume of lake trout lakes by size class and ecozone. There are ~66 500 lake trout lakes covering ~3 510 000 km^2 primarily on Boreal and Taiga Shield areas. Regional lake resource models will enable national assessment of stresses such as climate change and invasive species.

Résumé : Il est essentiel de connaître les lacs canadiens afin de pouvoir gérer les stress de l'environnement. Nous avons utilisé des banques de données d'inventaire des lacs et des caractéristiques lacustres afin de bâtir une matrice nationale d'évaluation des impacts et d'évaluer la typologie régionale. Il y a ~910 400 lacs à superficie $\geq 0,1 \text{ km}^2$ (10 ha), soit 37 % du total mondial. Nous avons modélisé les caractéristiques lacustres (nombre de lacs par classe de taille, profondeur maximale, rapport des profondeurs moyenne–maximale, profondeur de Secchi, pH et solides dissous totaux) par région en fonction des bassins versants secondaires (SWS) à l'aide de modèles de régression linéaire. Nous avons analysé la présence du touladi (*Salvelinus namaycush*) comme co-facteur pour souligner les liens régionaux entre les caractéristiques lacustres et les organismes. Nous avons obtenu des modèles régionaux significatifs (R^2 de 0,231 à 0,492) en utilisant la superficie, ou la profondeur maximale, la présence du touladi et leurs produits croisés comme covariables. Des analyses des coefficients SWS ajustés montrent que les écozones sont de meilleures variables prédictives des caractéristiques lacustres que les bassins versants primaires. La typologie nationale s'accorde aux évaluations régionales antérieures. Les modèles régionaux ont servi à estimer le nombre, la superficie et le volume des lacs à touladis par classe de taille et par zone. Il y a ~66 500 lacs à touladis couvrant ~3 510 000 km^2 , principalement dans les régions boréales et la taïga sur le bouclier canadien. Les modèles régionaux de ressources lacustres permettront une évaluation nationale des stress, tels que le changement climatique et les espèces envahissantes.

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Introduction

Canada has a great abundance of lakes, representing the largest national share of the Earth's readily accessible freshwater resources (Minns and Moore 1995; Downing et al. 2006); however, Schindler (2001) has pointed to the growing realization that much of Canada's freshwater resources are under pressure from a multitude of stressors. Chu et al. (2003) presented a national assessment of stressors affecting Canada's freshwater fishes showing a clash of human-driven development pressures and conservation needs mainly along the southern margin of the country, whereas climate change is already impacting the northern regions of Canada (Reist et al. 2006). Minns (2001), reporting on the science of freshwater fish habitat management in Canada, noted the poor state of knowledge of our freshwater ecosystems. Among eight priorities for the future, Minns identified the need for increased efforts on pattern recognition and inventory to "address the longer-term need for documentation of resource properties and change over the vast areas of freshwater habitat in Canada." To expand the scope for assessing the existing and potential cumulative impacts of human stresses on freshwater fishes and their ecosystems, there is a need to deploy all available information to characterize our freshwater ecosystems. Lakes, which account for the majority of freshwater resources and fisheries production, are impacted by many human activities and are the focus of this study. This characterization of lakes must span large regions as the spatial scale of threatening environmental disturbances like climate change and invasive species (Jensen et al. 1996) and of resource management challenges like eutrophication and overfishing (Carpenter et al. 1999; Post et al. 2002; Lester et al. 2003) increases.

Regional, or synoptic, limnology has a long history. Early in the 20th century, Naumann (1929) explored the imprint of landscape on Swedish lakes following ideas laid down earlier (cf. Rawson 1939). Most synoptic studies of lakes have concentrated on small localities, although more recently, larger lake districts have been gaining more attention (Kratz and Frost 2000). Again in Sweden, Hakanson (1996) advanced an approach and techniques for modelling key lake variables from map-based information. Since 2000, several European countries have been working to develop a lake typology in response to a European Union directive on water policy (Moss et al. 2003). In addition to developing a pan-European typology, individual countries have been developing national typologies, e.g., Poland (Kolada et al. 2005) and Finland (Nykänen et al. 2005).

In Canada, localized synoptic limnology might be exemplified by the studies at the Experimental Lakes Area in northwestern Ontario and in the Laurentian region of Quebec (cf. Minns 2001). Contributed papers in Frey (1963) provide much of the history of regional lake typology in Canada. Regional efforts are exemplified by the early classification work of Northcote and Larkin (1956) in British Columbia, by the assessments in the 1980s of the impacts of acidic deposition on lakes east of the Ontario–Manitoba border and south of latitude 52° (Kelso et al. 1990), and more recently, the surveys of lakes by John Smol and his associates across the Taiga and Arctic regions of Canada and elsewhere (cf. Ruhland and Smol 1998). There have been no

previous attempts to study synoptic limnology across the whole of Canada.

This study has three components: (i) a statistical representation of Canada's lake resources for use as a template in a national-scale impact assessment model; (ii) an assessment of regional typology for Canadian lakes; and (iii) a pilot demonstration of the potential use of the regional lake characteristic models for assessment and management. Although the lakes were the primary focus, lake trout (*Salvelinus namaycush*) occurrences by region and lake were examined as an example of how biota might be incorporated into models of lake characteristics. The first component addresses the need to characterize Canada's lake resources with approaches advocated by Minns (2001) and outlined by Hakanson (1996). The numerical models will subsequently be used to facilitate national assessments of the likely impacts of climate change on fishery resources. The second component lays the foundation for an aquatic ecological classification system for Canada's freshwater lake resources. The third component provides first-order estimates of the extent of lake trout resources in Canada.

Materials and methods

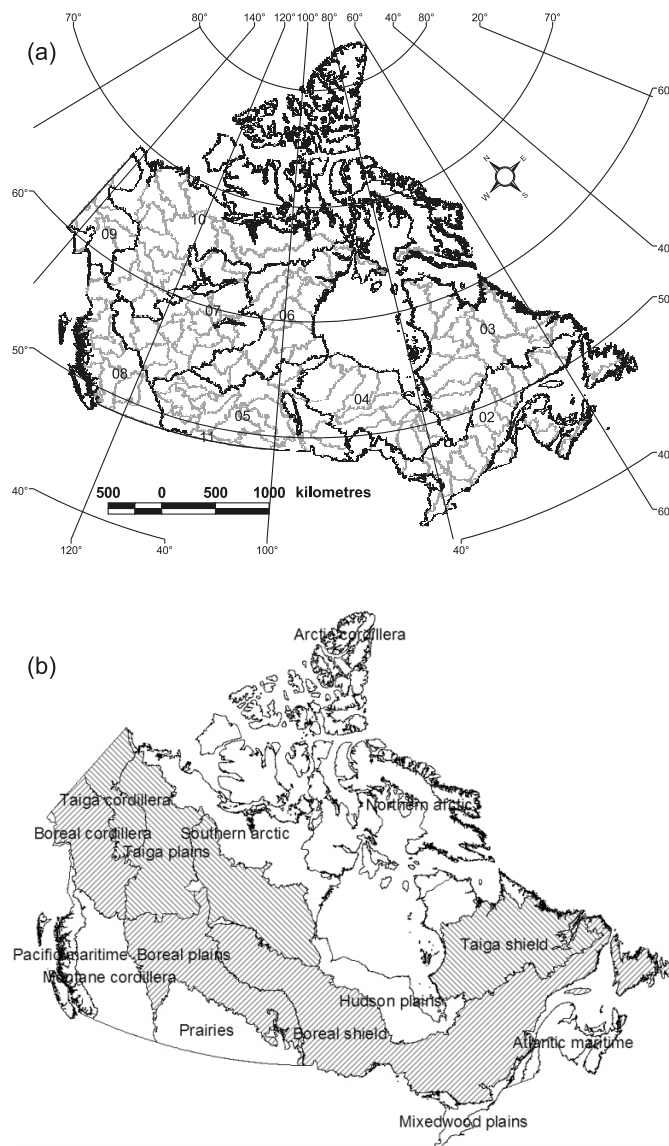
Canadian secondary watersheds and ecozones

Watershed units are the preferred basis for organizing regional data on freshwater ecosystems as it is through the drainage networks of watersheds that freshwaters are connected and flow and, thereby, energy and nutrients move. Watersheds also helped establish the distributions of many freshwater biota. Canada has a hierarchical scheme of watersheds with 11 primary, 164 secondary, and 953 tertiary units. The primary watersheds are determined by which ocean the largest rivers drain toward, and the secondary and tertiary watersheds represent sub- and sub-sub-drainages of the primary river systems. We chose the secondary watershed (SWS) as the basic unit for aggregation and analysis of lake patterns (Fig. 1a). They provide a readily manageable number of units while providing broad representative coverage of watersheds and landscape features, e.g., ecozones, that vary across Canada. Canada has a terrestrial ecological classification system (Ecological Stratification Working Group 1996) that is based on landscape features (geology, soils, terrestrial vegetation, and climate). There are 15 ecozones (Fig. 1b), and most SWS lie predominantly within a single ecozone (mean percentage of any SWS in one ecozone is 83.1%, the minimum is 45.7%, and 31.7% of SWS lie wholly in a single ecozone). Most of the SWS with lower dominant percentages straddle the Northern Arctic and Arctic Cordillera ecozones. We examine to what extent a regional lake typology was consistent with the terrestrial ecozonation.

Number of lakes

There are an estimated 90 358 lakes with area ≥ 1 km² (100 ha) in Canada in the Global Lakes and Wetlands Database (GLWD; www.wwfus.org/science/data.cfm). Lehner and Doll (2004) showed that lakes with area < 1 km² have not been completely inventoried, primarily because of the limited resolution of available maps. Our first objective was to estimate, by secondary watershed (SWS), the numbers of

Fig. 1. Maps of Canada showing (a) primary (PWS) and secondary (SWS) watersheds and (b) terrestrial ecoregions (in a, PWS are outlined in black lines and SWS are outlined in shaded lines; in b, Taiga and Boreal regions are cross hatched NW–SE and SW–NE, respectively).



lakes in a semilogarithmic series of size classes starting at 0.1 km² and with boundary limits at 0.2, 0.5, 1.0, 2.0, 5.0, 10.0, 20.0, 50.0, and 100.0 km².

In their global analysis of aggregated lake size data, Lehner and Doll (2004) showed that observed distributions followed the function, $N_{a \geq A} = \alpha A^\beta$, where N is the number of lakes with area (a) greater than or equal to a threshold area (A). This function approximates the Pareto distribution, which has been shown to be useful in many fields (Vidondo et al. 1997). Downing et al. (2006) used the Pareto distribution model to estimate the global abundance and size distribution of lakes. Here, a similar approach is used to estimate, by secondary watershed, the numbers of lakes in the smaller lake size classes that are underassessed in available estimates of the numbers of lakes in Canada.

The GLWD data for Canada were used to estimate the

Pareto distribution parameters using the logarithmic version of the equation: $\text{Ln}(N) = \text{Ln}(\alpha) + \beta \text{Ln}(A)$ with a common slope, β , and categorical variables for SWS units. The lake data were attributed with secondary watershed identifiers using ESRI's Arcview 3.3 GIS, and the data were grouped into a semilogarithmic series of lake-area size classes delimited by 1, 2, 5, 10, 20, 50, and 100 km². Lehner and Doll showed that counts below 1 km² were incomplete.

Estimates of the numbers and size distribution of Canadian lakes by SWS were derived by combination of estimation for smaller lakes and summary for larger lakes. The regression equations obtained with the Pareto distribution analysis were used to estimate numbers of lakes in the area size intervals 0.1–0.2, 0.2–0.5, and 0.5–1.0 km² for all secondary watersheds. A bias correction ($\exp(\text{EMS}/2)$, where EMS is the error mean square from the Ln–Ln regression) was applied to adjust for the data transformation effect (Sprugel 1983). The average lake area in each size class was estimated using eq. 8 in Downing et al. (2006). For the size-class intervals 1.0–2.0, 2.0–5.0, 5.0–10.0, 10.0–20.0, 20.0–50.0, and 50.0–100.0 km², the numbers and areas of lakes used were those reported in the GLWD data. By size class and secondary watershed, an average lake area was computed as the ratio of total area and number. For lakes with area ≥ 100.0 km², individual lakes with areas reported by S. Wang and A. Davidson (Canada Centre for Remote Sensing, Ottawa, Ontario, Canada, unpublished data) were assigned by secondary watershed.

National lakes database

Data about lakes, including name and identification data, latitude and longitude (or northing and easting), lake area, elevation above sea level, maximum and mean depth, Secchi depth, pH, conductivity, and total dissolved solids (TDS), were gathered from a wide range of government agency sources and supplemented by published material (Appendix A, Table A1 and references therein). These lake characteristics are ones that have been frequently included in models of lake productivity (Hakanson 1996). Records of the presence of lake trout (*S. namaycush*) were also summarized by tertiary watershed from a national fish distribution database (N.E. Mandrak, unpublished data). These sources were supplemented with data from published literature, particularly for larger lakes. Nicholson and Moore's (1988) bibliography of Canadian freshwater limnology and fisheries was especially useful for locating older sources of lake data.

As any single source of data rarely included all parameters of interest, we attempted to use lake name, geographic coordinates, and any identification information to match data from multiple sources by lake. Where multiple values of particular parameters were obtained for a single lake, we established a hierarchy for valuing data sources when choosing a value. Generally, we ranked the larger, more established, data sets more highly than smaller ones and ranked more recent data more highly than older data. The source data sets were assembled in a Microsoft Access database and procedures were written to implement the matching and selection process. This meant that the software remained open-ended, allowing the addition of new data sets and parameters in the future. As a minimum requirement, we specified that every lake selected must have a lake area and

geographic coordinates. Once a composite lake data set had been assembled, the records were attributed with tertiary watershed, ecozone, and province or territory membership. The reduced data set was then screened for inconsistencies such as mean–maximum depth ratios ≥ 1 or Secchi depth that exceeded maximum depth. Such data entries were deleted. Although the record of lake trout occurrences was clearly incomplete, lakes without a recorded occurrence were treated as denoting an absence in the analyses reported here.

As of 30 January 2007, there were 50 262 individual lake data records with one or more selected parameters in the database. After selection and consolidation of that information, there was a reduced data set of 16 950 lake data records with one or more of the selected parameters. The level of matching success was relatively low, reflecting the lack of standardization of lake names, the inconsistent application of identification systems, and inaccuracies and imprecision in geographic coordinates. Existing naming conventions for Canadian topographical features such as lakes do not cover all sizes of lakes. Often different agencies within, and between, levels of government have established independent identification systems that cannot be cross-matched. Much of the data were gathered and recorded before the advent of more recent global positioning system (GPS) and geographic information system (GIS) technologies with the result that locations are often only recorded by degrees and minutes of latitude and longitude, leaving a wide margin for error both in location of the sites and in matching data from multiple sources. Resource limitations meant that not all identifiable data could be included in the current version of the database.

Modelling lake morphometry and water quality characteristics

Regional patterns in lake parameters (maximum depth (Z_{\max}), mean to maximum depth ratio (Z_{ratio}), Secchi depth (Secchi), pH, and total dissolved solids (TDS)) were modeled via least-squares regression equations. To reduce the size-related dispersion of points in some lake parameters lake area (Area), Z_{\max} , Z_{ratio} , Secchi, and TDS were transformed to natural logarithms (Ln). Z_{ratio} was modeled rather than mean depth, as it is a key parameter in a model of hypsometric curves linking area to depth in lakes (Lester et al. 2004). The approach was to model each dependent lake parameter as a function of Area (or Z_{\max}), the presence (1) or absence (0) of lake trout, and the cross product of Area or Z_{\max} with lake trout presence or absence as the independent variables. This approach allowed for the possibility that both the intercept and slope might provide information about differences between lakes with, and without, lake trout. Lake size characteristics like Area and Z_{\max} are involved in many predictive models for lakes (Leach and Herron 1992). The basic models were then extended to consider regional variation by inclusion of primary (PWS) or secondary (SWS) watershed membership as dummy variables; an overall intercept was included in the regression model along with coefficients for all but one of the dummy variables.

The models were fitted using linear least-squares regression. Final model selection was based on consideration of R^2 , the minimization of the EMS and the residual sum-of-

squares, the significance of the constituent parameters, and the corrected Akaike information criterion (AIC_c) (Hurvich and Tsai 1989; Burnham and Anderson 2004), with watersheds or ecozones being taken altogether in a single step. The emphasis in model selection was on parsimony, recognizing that regional models must often rely on a minimal number of input parameters as many are rarely available extensively. Posteriori testing of differences among fitted primary or secondary watershed, or ecozone coefficients, was not undertaken as the intent of the modelling was to characterize regional variables in lake characteristics and not to generate a minimal set of regional groups.

As there were a number of SWS with no data for each key parameter, a method of estimating missing SWS values in the lake parameter models was devised. The available estimated SWS coefficients for each parameter were grouped by either PWS or ecozone, and an analysis of variance was performed. In one instance, pH was modeled with the TDS coefficient as a covariate as the pH coverage was much less than that of other parameters. AIC_c was used to choose between the PWS and ecozone models. The selected model was used to estimate the missing SWS values and generate an overall picture of how each parameter varied across Canada.

Lake trout distribution

Lake trout were chosen as a working example of an aquatic species of interest because this study was part of ongoing work to examine the potential impact of climate change and other stressors on key fishery species in Canadian lakes. The occurrence of lake trout in lakes was examined in three ways. First, a national distribution database (N.E. Mandrak, unpublished data) was used to determine the occurrence by tertiary watershed (TWS) using all available records from lakes and rivers. Occurrence was summarized by secondary watershed as the percentage of TWS units with lake trout present (WS%). Second, all lakes within TWS with one or more occurrences of lake trout were selected as a subset of the national lakes database. Using that subset, the percentage of lakes with lake trout present (LK%) was estimated by SWS. Not all SWS had a sample size of lakes (N_{SWS}) sufficient to produce a reliable estimate of LK%. Where WS% was greater than 0.0 and $N_{\text{SWS}} < 10$, a composite estimate of LK% was obtained from the available data and used to fill SWS gaps. The product of WS% and LK% provided an overall estimate of the percentage of all lakes with lake trout present by secondary watershed.

Third, as the percent occurrence of lake trout varies with lake size, an independent analysis was performed to derive a means of scaling the overall SWS occurrences (WS%·LK%) by lake size class. There were insufficient data across the species range to support any analysis supporting both location and lake size simultaneously. The analysis here assumed that all the subset of the database could be used to estimate the variation in occurrence by size class as an odds ratio applied to the SWS mean (WS%·LK%). By size class, we estimated the percentage of lakes with lake trout (SZ%) and expressed the SZ% values as odds ratios (SZ_{ratio}) against the overall value obtained. Then adjusted LK% (size class) values were computed as $(LK\% \cdot SZ_{\text{ratio}}) / (LK\% \cdot SZ_{\text{ratio}} + (1 - LK\%)1)$. Then WS%·LK% (size class) gives the estimated

proportion of lake trout lakes by SWS and size class. Lakes with area $\geq 100 \text{ km}^2$ were assumed to be completely enumerated with respect to lake trout occurrence.

Lake and lake trout resources

The models obtained in the previous sections were used in combination to estimate the number, area, and for lake trout lakes, volume of lakes by secondary watershed and size class. Bias corrections were applied where the equations involved Ln transformations (Sprugel 1983). These values were summarized across all size classes and across all ecozones. By size class, the extent of lake trout resources was also tallied for Boreal and Taiga Shield ecozones to assess the contribution of the Shield to the total. By ecozone, the extent of lake trout resources was summed both above and below the 100 km^2 area threshold.

Results

Numbers of lakes

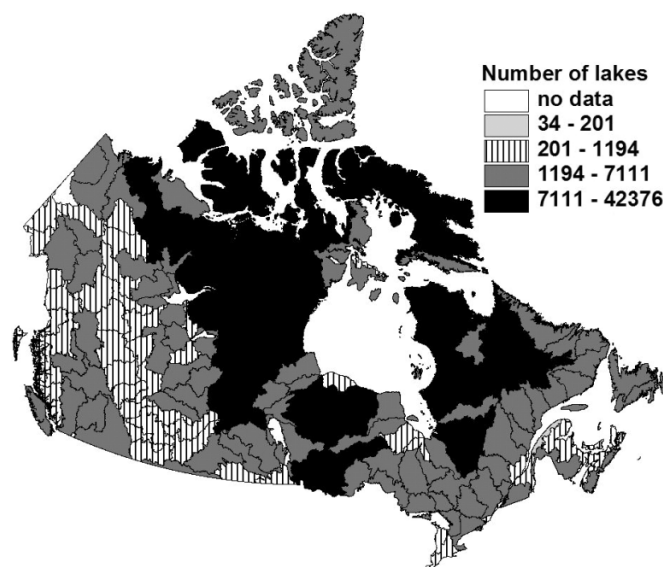
Three (8P, 9E, and 9M) of 164 secondary watersheds (SWS) had no lakes according to the GLWD database. The largest portions of these watersheds are outside of Canada. Analysis of covariance of the regression model of $\text{Ln}(N)$ with $\text{Ln}(A)$ as a covariate and SWS as a categorical variable produced the following results: $F_{\text{Ln}(A)} = 13425.7$ (df = 1,880) and $F_{\text{SWS}} = 59.7$ (df = 160,880), both significant at $P < 0.001$. (EMS = 0.17884, giving a bias correction of $\exp(\text{EMS}/2) = 1.094$ when detransforming and estimating numbers of lakes.) The slope was -1.032 , with SWS intercept values ranging between 1.051 (~34 lakes $> 0.1 \text{ km}^2$) and 8.188 (~42375 lakes $> 0.1 \text{ km}^2$), with a mean of 5.245 (~2674 lakes $> 0.1 \text{ km}^2$) (Fig. 2). The slope lies above the mean value, -0.89 , reported for regional estimates (Downing et al. 2006) but very close to the global value, -1.06 , obtained by Lehner and Doll (2004). Applying the resulting equations across all Canadian secondary watershed and summing the results, the numbers of lakes are 910371 with area $\geq 0.1 \text{ km}^2$ (10 ha) and 84516 with area $> 1.0 \text{ km}^2$. Using Downing et al.'s (2006) global estimate of the number of lakes, Canada holds 36.8% of the Earth's total.

The area with the highest number of lakes is on the Canadian Shield centered on Hudson's Bay (Fig. 2). The lowest number of lakes is mainly found in the Plains region between the Shield and the mountain ranges between Alberta and British Columbia in the west and in the Maritime regions on both coasts.

National lakes database

The number of data values varied from a low of 8741 for pH to 16949 for Area (Table 1). All parameters had considerable ranges. Depending on the lake parameter, there were data in 106 to 138 of 164 SWS, although there were from 10 to 20 with a single value. All lake parameters spanned considerable ranges, as expected for a national data set covering from the smallest to largest lakes across the regions of Canada. All but one ($\text{Ln}(Z_{\text{max}})$ vs. pH) of the pairwise Pearson correlations were highly significant at $P < 0.001$ (Table 2). The highest correlations were between $\text{Ln}(Z_{\text{max}})$ and $\text{Ln}(Z_{\text{mean}})$ (0.924), followed by pH and $\text{Ln}(\text{TDS})$ (0.694), and those of $\text{Ln}(Z_{\text{max}})$ and $\text{Ln}(Z_{\text{mean}})$ with $\text{Ln}(\text{Sec-})$

Fig. 2. Estimated number of lakes, with area $> 0.1 \text{ km}^2$, by secondary watershed based on the intercept of the Pareto model of lake frequency ($\text{Ln}(N_{\geq A})$) versus area ($\text{Ln}(A)$) for Canadian lakes.



chi) (> 0.57). Correlations of pH and $\text{Ln}(\text{TDS})$ with lake dimensions were lower than those among lake metrics.

Lake morphometry and water quality models

In many instances, there were obvious variations in the distributions of lake variables both regionally, using primary watersheds to illustrate, and with or without the presence of lake trout (Fig. 3). Lake area, maximum depth, and Secchi depth were consistently greater when lake trout were present (Figs. 3a, 3b, and 3d). There was also much regional variation in some variables, notably pH, $\text{Ln}(\text{TDS})$, and mean-maximum depth ratio (Figs. 3c, 3e, and 3f). pH values were markedly lower in primary watersheds 01 and 02 in the southeastern quadrant of Canada, the area most impacted by acidic deposition (Kelso et al. 1990). TDS distributions included much higher values in primary watersheds 05 and 08 in the central Canadian Prairies and Plains where saline lakes are most prevalent.

Predictive models were developed for all lake characteristics (Table 3). AIC_c was used to guide selection of the simplest regional model using covariates. For Z_{max} , Z_{ratio} , and Secchi, the parameters included produced large increases in the R^2 and noticeable reductions in EMS. For pH, addition of parameters beyond Area made little difference to R^2 and EMS. For TDS, all covariate models explained very little of the variance and so no covariate was included. All covariates included and secondary watershed (SWS) factors were significant at $P < 0.001$. In every case, comparison of model fits without watersheds, with primary watersheds (PWS), or with SWS showed that with SWS produced the best fit (R^2 , EMS) and improved fit (AIC_c) compared with the other choices (Table 4). Not all covariates were included in every model. Lake trout presence or absence (LTPA) was included in the models of Z_{max} , Z_{ratio} , and Secchi; Area was included for Z_{max} and pH; and Z_{max} was used for Z_{ratio} and Secchi. Area was a good predictor of Z_{max} , but Z_{max} was the better predictor for other important depth-related parameters. The

Table 1. Summary statistics for Canadian lake characteristics indicating the number of SWS with data ($n > 0$) and with a single value ($n = 1$).

Parameter	<i>N</i>	Minimum	Maximum	Mean	SD	No. of SWS with data ($n > 0$)	No. of SWS with a single value ($n = 1$)
Area (km ²)	16 949	0.001	82 900.000	27.749	909.376		
Z_{\max} (m)	16 605	0.200	614.000	18.276	23.045	138	10
Z_{mean} (m)	14 059	0.100	172.000	6.589	8.827		
Z_{ratio}	13 767	0.005	1.000	0.374	0.126	113	13
Ln(Area)	16 949	-11.859	11.325	-0.464	2.022		
Ln(Z_{\max})	16 605	-1.609	6.420	2.467	0.957		
Ln(Z_{mean})	14 059	-2.303	5.147	1.482	0.877		
Secchi (m)	14 348	0.100	41.050	3.857	2.348	129	19
Ln(Secchi)	14 348	-2.303	3.715	1.176	0.619		
pH	8 741	3.030	11.000	7.063	0.956	106	20
TDS (mg·L ⁻¹)	12 858	1.000	84 314.000	100.628	966.395	126	13
Ln(TDS)	12 858	0.000	11.342	3.882	0.926		

Table 2. Pearson correlations among pairs of parameters in Canadian lakes.

Parameter	Ln(Area)	Ln(Z_{\max})	Ln(Z_{mean})	Z_{ratio}	Ln(Secchi)	pH	Ln(TDS)
Ln(Area)		0.458	0.405	-0.162	0.052	0.085	-0.047
Ln(Z_{\max})	16 605		0.924	-0.334	0.576	0.024	-0.146
Ln(Z_{mean})	14 059	13 767		0.035	0.579	0.121	-0.138
Z_{ratio}	13 767	13 767	13 767		-0.098	0.067	0.091
Ln(Secchi)	14 348	14 234	12 589	12 480		0.036	-0.118
pH	8 741	8 729	7 368	7 357	7 646		0.694
Ln(TDS)	12 858	12 745	11 788	11 681	12 219	6 350	

Note: Upper right matrix is the correlation; lower left matrix is the number of data pairs; Bonferroni-corrected significance at $P < 0.001$ is presented in bold.

cross-product term Z_{\max} ·LTPA was only retained in the Secchi model. No covariates were included in the TDS model. The lake size coefficients were positive in the Z_{\max} , Secchi, and pH models. The coefficients for LTPA were positive, indicating higher values with lake trout present. In the Secchi model, the cross-product term indicated that although Secchi depths were generally higher in lake trout lakes, the slope of the relationship with Z_{\max} was lower. This indicates that Secchi values are higher in shallower lake trout lakes but converge to similar values regardless of lake trout presence in deeper lakes.

The available estimated SWS coefficients were grouped by both primary watershed (PWS) and ecozone. Analysis of variance models examined as a basis for completing the mapped coverage of each lake parameter showed that ecozone was a better predictor than primary watershed membership (Table 5). This was also true for the Pareto intercept coefficients in the model of lake numbers by SWS. The ecozone models were used to estimate missing values for five lake characteristics.

Overall, data for the five lake parameters were most available along the southern parts of Canada (Figs. 4a, 4c, 5a, 5c, and 5e) with the greatest abundance in Ontario and British Columbia. The areas with the least data were concentrated in northern Quebec and Labrador and in the eastern Arctic. Those areas with the least or no data, and hence with estimated SWS coefficients, will be the most unreliable. However, there are discernible patterns across the country.

The spread of SWS coefficient means across ecozones re-

veals much of the spatial structure of lake characteristics in Canada (Fig. 6). Allowing for Area via the covariate fitting, there are three main areas of lakes with greater Z_{\max} : along the edge of the St. Lawrence drainage (PWS 02), in the west in British Columbia and Yukon (Pacific-Maritime and Montane Cordillera ecozones), and in the northern mainland areas of the western Arctic (Taiga Cordillera and Southern Arctic ecozones) (Fig. 4b). Allowing for Z_{\max} , the lower Z_{ratio} values are concentrated on the Canadian Shield south of Hudson's Bay and the higher values are concentrated in the west and north of the country, particularly in the Taiga Cordillera and Plains (Fig. 4b). Higher Secchi depths are more prominent in the far northern regions, whereas lower values are more common on the Prairies and through Boreal and Taiga Plains (Fig. 5b). pH values were generally lower on the Canadian Shield, with the lowest values occurring in those areas most affected by acidic deposition in southern Newfoundland and Nova Scotia and south-central Ontario (Fig. 5d). The higher pH values were found in the Prairies and Boreal and Taiga Plains. TDS values were higher on the Prairies and Boreal Plains and lower in eastern parts of Canada, particularly in Quebec and Labrador on the Canadian Shield (Fig. 5f).

Lake trout distribution

The distribution records for lake trout, and many other fish species, in Canada were insufficient to allow a definitive mapping of occurrence at this time. In the more remote regions of the country, considerable effort would be required

Fig. 3. Box plots showing the distributions of lake characteristics by primary watershed (PWS) and absence–presence of lake trout: (a) Ln(lake area, km²), (b) Ln(maximum depth, m), (c) mean–maximum depth ratio, (d) Ln(Secchi depth, m), (e) pH, and (f) Ln(TDS, mg·L⁻¹). (Lake trout absence on the left and presence on the right of each PWS marker.)

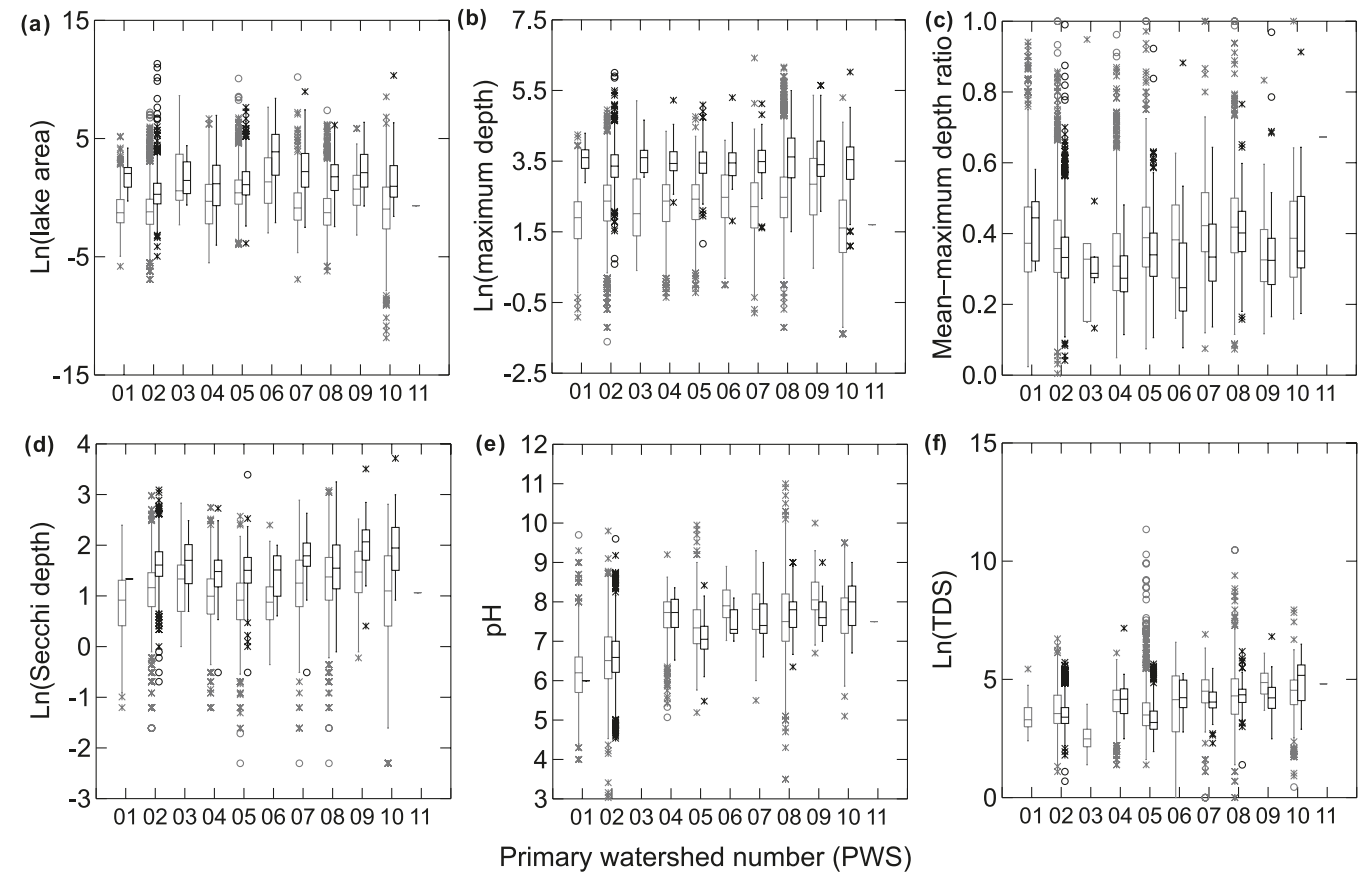


Table 3. Linear regression models of key lake characteristics, maximum depth (Z_{\max}), mean to maximum depth ratio (Z_{ratio}), Secchi depth (Secchi), pH, and total dissolved solids (TDS), by secondary watershed (SWS) with covariates (lake area (Area), lake trout presence or absence (LTPA), Z_{\max}).

Dependent	Source	Coefficient	<i>N</i>	df	Mean-square	<i>F</i> ratio	Probability	<i>R</i> ²
Ln(Z_{\max})	SWS	*		137	14.438	28.51	<0.001	
	Ln(Area)	0.1949		1	1587.716	3135.23	<0.001	
	LTPA	0.7765		1	1044.438	2061.61	<0.001	
	Error		16 605	16 465	0.506			0.4519
Z_{ratio}	SWS	*		112	0.228	18.63	<0.001	
	Ln(Z_{\max})	−0.0570		1	24.532	2005.57	<0.001	
	LTPA	0.0253		1	0.862	70.50	<0.001	
	Error		13 767	13 652	0.012			0.2310
Ln(Secchi)	SWS	*		128	3.509	15.72	<0.001	
	Ln(Z_{\max})	0.3617		1	925.188	4145.32	<0.001	
	LTPA	0.5826		1	18.774	84.12	<0.001	
	Cross [†]	−0.1368		1	11.879	53.23	<0.001	
	Error		14 234	14 102	0.223			0.4215
pH	SWS	*		105	36.943	78.59	<0.001	
	Ln(Area)	0.0528		1	57.989	123.36	<0.001	
	Error		8 741	8 634	0.470			0.4924
Ln(TDS)	SWS	*		125	35.021	67.66	<0.001	
	Error		12 858	12 732	0.523			0.3969

*See Figs. 4 and 5 for maps showing the distributions of fitted SWS coefficients.

[†]Cross product of Ln(Z_{\max}) and LTPA.

Table 4. Comparison of fit statistics for models of lake characteristics without or with primary (PWS) or secondary (SWS) watershed coefficients.

Modeled character	Covariates	Watershed variables*	AIC _c [†]	Error mean square	R ²
Z _{max}	Area	None	-7 896.1	0.621	0.3219
	LTPA	PWS	-9 183.6	0.575	0.3732
		SWS	-11 154.3	0.506	0.4519
Z _{ratio}	Z _{max}	None	-58 775.5	0.0140	0.1135
	LTPA	PWS	-60 189.2	0.0126	0.2012
		SWS	-60 507.3	0.0122	0.2310
Secchi	Z _{max}	None	-19 571.2	0.253	0.3389
	LTPA	PWS	-20 161.3	0.242	0.3667
	Z _{max} ·LTPA	SWS	-21 211.4	0.223	0.4215
pH	Area	None	-836.8	0.908	0.0070
		PWS	-4 754.7	0.580	0.3672
		SWS	-6 487.2	0.470	0.4924
TDS	None	PWS	-3 348.0	0.770	0.1031
		SWS	-8 217.9	0.522	0.3969

*None, model with covariates but no watershed variables.

[†]AIC_c = AIC + 2K(K + 1)/(N - K - 1) and AIC = N·Ln(RSS/N) + 2K, where RSS is residual sum of squares, N is sample size, and K is the number of parameters fitted (Hurvich and Tsai 1989; Burnham and Anderson 2004).

Table 5. Model selection results for estimating missing secondary watershed values for key lake characteristics based on regression models with primary watersheds (PWS) or ecozones as the determining factor.

Lake character	N	PWS			Ecozone		
		R ²	K	AIC _c	R ²	K	AIC _c
Pareto lake numbers	161	0.332	12	56.10	0.591	15	-15.79
Maximum depth (Z _{max})	138	0.330	12	-151.82	0.372	15	-153.43
Mean-maximum depth ratio (Z _{ratio})	113	0.226	12	-522.10	0.280	15	-527.69
Secchi depth (Secchi)	129	0.167	12	-175.81	0.236	15	-179.49
pH	106	0.323	11	-123.27	0.473	15	-139.17
pH (with TDS as a covariate)	96	0.526	12	-137.81	0.584	16	-139.24
TDS	126	0.456	12	-2.71	0.673	15	-59.27

Note: N is number of SWS and K is the number of parameters.

to delimit lake trout distribution by tertiary watershed and to determine the proportion of lakes with the species present. The available occurrence records by TWS indicated that lake trout are widely distributed on the Boreal Shield and Taiga Shield and on the Montane and Boreal Cordillera (Fig. 7a). The greatest recorded numbers of lake trout lakes were found on the southern Boreal Shield (Ontario and Quebec) (Fig. 7b). The overall proportion of lakes with lake trout in TWS with the species present and with a lake sample of 10 or more was 0.23 (Fig. 7c). This proportion was used to fill missing LK% gaps where presence was noted by SWS (WS% > 0). This proportion is probably an underestimate as lake trout are expected to occur more often in the northern parts of their range where lower surface water temperatures should allow it to succeed in a wider range of lakes. Hershey et al. (2006) showed that 44.6% of 158 Arctic Alaskan lakes supported lake trout. The product of WS% and LS% gave an estimate of the proportion of lakes in each SWS with lake trout (Fig. 7d). There are three main concentrations of lake trout lakes on the southern Boreal Shield, on the Taiga Shield west of Hudson Bay, and in the Boreal Cordillera. Those areas of highest occurrence are consistent

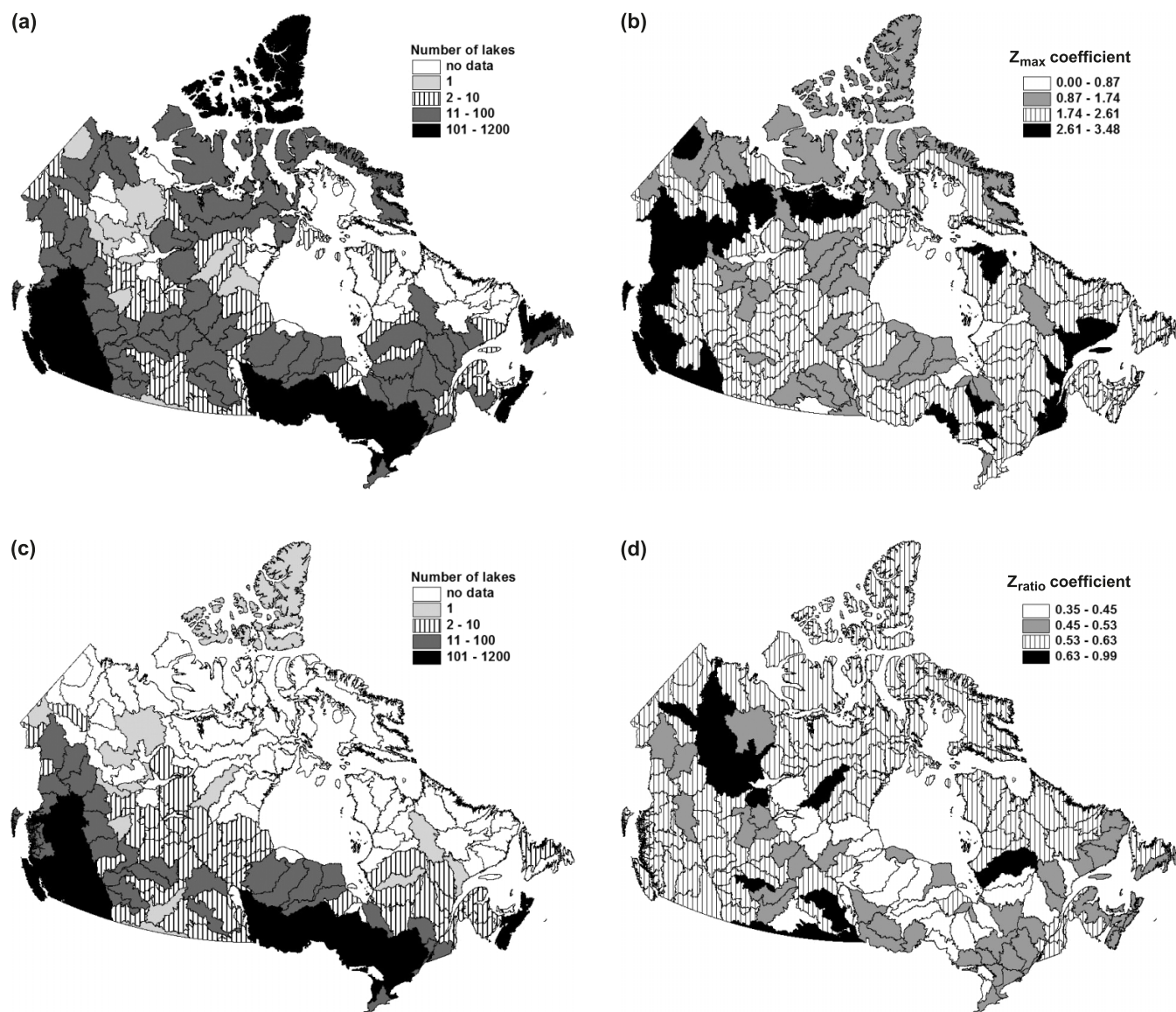
with the patterns of glacial refugia and postglacial dispersal identified via genetic markers by Wilson and Hebert (1998).

The analysis of lake trout occurrence by size class showed that the proportion of lakes with lake trout (SZ%) was 0.210 overall and varied from 0.038 in the 0.1–0.2 km² size class to 0.389 in the 10.0–20.0 size class (Table 6). The overall value here differed slightly from the values used to fill LK% gaps in SWS (0.21 vs. 0.23) because of the sample size restriction used for the latter. The SZ% values rose with increasing lake size. The resulting odds ratios, SZ_{ratio}, ranged from 0.179 to 1.853.

Lake and lake trout resources

Combining the results given above, the size of total and lake trout resources in Canada were estimated by lake size class and by ecozone (Table 7). There are an estimated 910 132 lakes with area > 0.1 km² in Canada, with an estimated total area of 1 028 151 km². Lakes larger than 100 km² account for 44.5% of the total area, and other size classes contribute 4.5%–8.5% of the total. The majority of lakes (number, 53.7%; area, 54.7%) are on the Canadian Shield (Boreal and Taiga). The Arctic zone contains the

Fig. 4. The distributions for maximum depth (Z_{\max}) and mean–maximum depth ratio (Z_{ratio}), respectively, of (a, c) sample size and (b, d) regression-fitted watershed coefficients by secondary watershed.



next largest share (number, 29.5%; area, 20.1%). There are an estimated 66 500 lake trout lakes in Canada, with 50% on the Boreal Shield, 29% on the Taiga Shield, and 8% in the Southern Arctic. By number, the largest percentage of lake trout lakes (38%) are estimated to be in the 0.2–0.5 km² area size class, with 25% in the 0.1–0.2 size class and 17% in the 0.5–1.0 size class. The lakes larger than 100.0 km² dominated by area and volume, 76.6% and 95.6%, respectively. The St. Lawrence – Great Lakes account for much of the area and volume in the >100.0 km² size class. The next highest area contribution was in the 2.0–5.0 interval (4.36%), and the next volume contribution was in the 20.0–50.0 interval (0.86%). Most of the lake trout resource is on the Shield (Boreal and Taiga combined), with 79% by number, 65.2% by area, and 74.8% by volume.

Discussion

Although the country-wide lake database described here is

undoubtedly incomplete, there were sufficient data to successfully fit predictive models and to discern regional patterns in the characteristics of Canada's lakes. To evaluate the results obtained here, there are four areas to consider: the database; the regional models and typology; the potential uses of these models; and the direction of future studies.

The Canada lakes database analyzed here has several shortcomings. The data collection is incomplete, but moving beyond the more readily accessible assemblages of data would require considerable person power and time. Some areas such as British Columbia, Ontario, Quebec, and Nova Scotia have undertaken extensive inventories of lake resources in the past. Our data coverage was weakest on the Taiga Shield, especially in northern Quebec and Labrador and in the eastern Arctic.

The set of lake characteristics examined here is limited compared with the many identified by Leach and Herron (1992). Chemical parameters such as total phosphorus, chlorophyll *a*, dissolved organic matter, and alkalinity that

Fig. 5. The distributions for Secchi depth (Secchi), pH, and total dissolved solids (TDS), respectively, of (a, c, e) sample size and (b, d, f) regression-fitted watershed coefficients by secondary watershed.

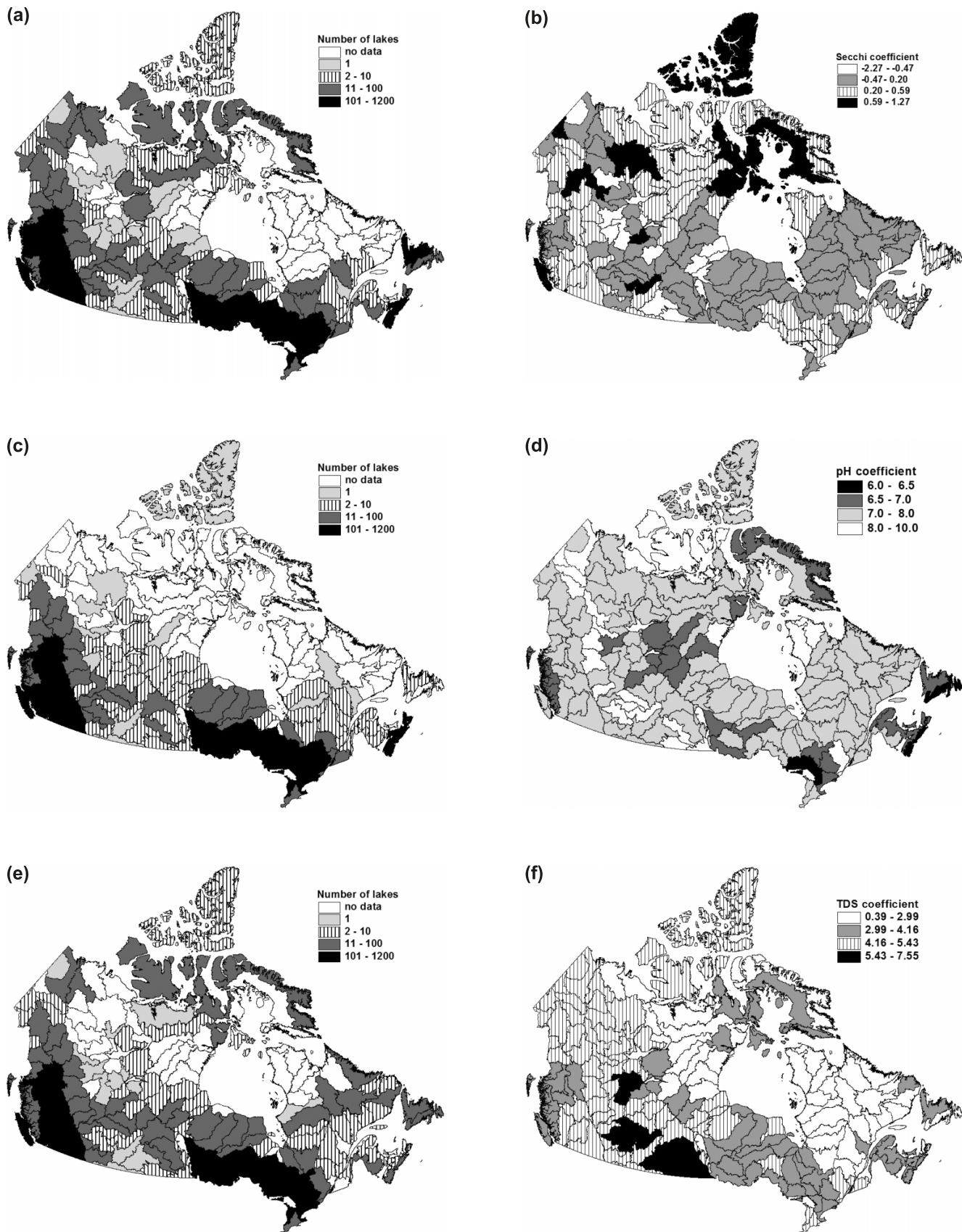
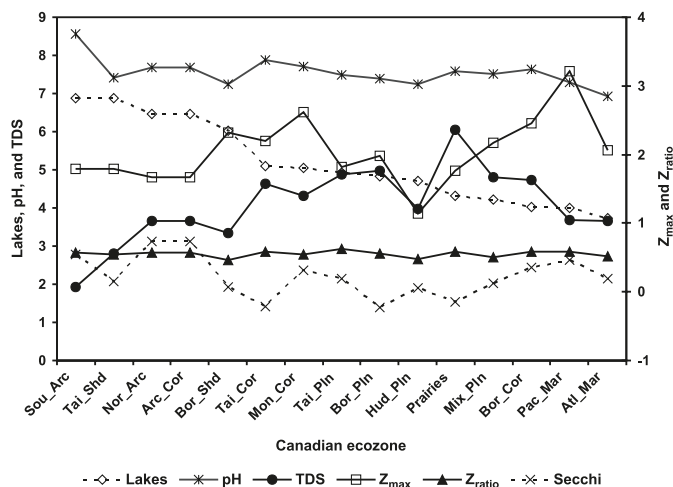


Fig. 6. Mean regression coefficients by ecozone for the lake characteristic SWS coefficients: numbers of lakes, Z_{\max} , Z_{ratio} , Secchi, pH, and TDS. (Lakes, pH and TDS on the left y axis scale and the rest on the right y axis scale).



have been shown to be more immediate factors in lake productivity would be valuable additions to a lakes database. However, the current parameters Secchi depth, pH, and TDS are often highly correlated with those potential additions. For example, total phosphorus in lake water is an important predictor of components of biomass and production in lakes (Hakanson 1996), but in earlier studies, TDS was often the parameter cited as a good predictor (Leach and Herron 1992). The regional pattern in Secchi depth is inversely similar to the regional variation in dissolved organic matter (DOM) levels (Molot et al. 2004); DOM is a primary determinant of light attenuation in lakes and hence higher levels lead to lower Secchi values.

The temperature and oxygen regimes are important factors in shaping the levels and forms of productivity in lakes, especially for cold stenotherms like lake trout (Ryan and Marshall 1994), although those regimes are formed through the interaction of morphometric (e.g., area, depth), edaphic (e.g., total phosphorus, TDS), and climatic (e.g., air temperature and precipitation) factors as described by Rawson (1939) and many others (cf. Leach and Herron 1992) during the evolution of limnology. Temperature and oxygen were not added to the present framework as representing the seasonal and spatial dynamics with individual lakes would require much more complexity in the database.

The regional models obtained here have a predictive power greater than we expected a priori. The use of secondary watershed membership as a dummy variable provided a convenient means of bypassing the potential complexities inherent in Canada's terrestrial ecoclassification system with all the detail of soil types, surficial and bedrock geology, permafrost status, landform types, land use, etc. (Ecological Stratification Working Group 1996). The models presented here assumed that the variables operate independently. It is likely that compound variables based on the variables assessed here and additional ones such as light, temperature, and nutrient levels would further improve the performance of the predictive models. Examples include the simple models of lake fishery productivity of Schlesinger

and Regier (1982) based on climate and the morphoedaphic index of Ryder (1965) and the more complex multifactor model of lake trout productivity (Shuter et al. 1998) where life history features are linked to lake characters.

Regional lakes studies have shown how landscape factors influence lake attributes (Stendera and Johnson (2006) in Sweden; Martin and Soranno (2006) in Michigan). The post hoc analyses of secondary watershed coefficients by primary watershed and ecozone to find a method for estimating missing values showed that ecozone was a better predictor of regional variation in lake characteristics, which is in line with expectations from landscape studies. The results suggest that there is scope for further investigation of the links between landscape and lake features on a Canada-wide scale. Because the primary objective was to obtain models representing lake attributes for use in large-scale assessment studies, the secondary watersheds provided a convenient and acceptable resolution for capturing regional variation in lake attributes.

The preliminary ecozone typology of Canadian lakes obtained here is consistent with that from earlier regional studies. Northcote and Larkin (1956) indicated that TDS and mean depth were important parameters in lake typology for British Columbia lakes in the Pacific-Maritime and Montane Cordillera ecozones. The Schlesinger and Regier (1982) model of fish yield in lakes brings together the three main elements of regional limnology (morphometric, edaphic, and climatic) as described by Rawson (1939). These elements parallel the features that are overlain in terrestrial ecozone classifications. Therefore, it should not be surprising that ecozones explained much of the regional variation evident in lake attributes assessed by secondary watershed. Those aspects of the lake characteristic models related to lake trout occurrence, taken here as a sample biotic component, are consistent with other efforts that have sought to integrate abiotic and biotic elements in lake typologies. Johnson et al. (1977) presented a typology for Ontario lakes based on similar lake characteristics and the occurrences of several top predators. Hershey et al. (2006) developed a similar typology for Alaskan lakes. The results obtained here indicate that in future, it should be feasible to derive a more sophisticated national lake classification and assessment tool similar to that developed for shallow European lakes (Moss et al. 2003).

Those components of the regional lake feature models tied to lake trout occurrence were consistent with previously reported patterns (Ryan and Marshall 1994; Marshall 1996; Gunn et al. 2003). Lake trout occur more frequently in larger lakes than in smaller ones, in deeper ones, with greater Secchi depths. It was expected that the proportion of lakes with lake trout would be lower in the smaller lake size classes. Smaller lakes are less likely to have sufficient maximum depth to allow either thermal stratification, thereby ensuring suitable thermal habitat is available during summer in the southern reaches of the species range, or winter refuge from freeze-out with greater ice thicknesses during winter in the northern reaches of the range. Depth and Secchi depth, an inverse indicator of productivity, also interact in shaping oxygen levels below the thermocline in the cooler waters preferred by lake trout, thereby affecting the suitability of lakes for lake trout (Ryan and Marshall 1994). The absence

Fig. 7. Lake trout occurrence by secondary watershed (SWS): (a) percentage of tertiary watersheds (TWS) with lake trout present (WS%); (b) number of lakes with lake trout by SWS; (c) percentage with lake trout (LK%) from TWS with lake trout; and (d) percentage of lakes (WS%·LK%).

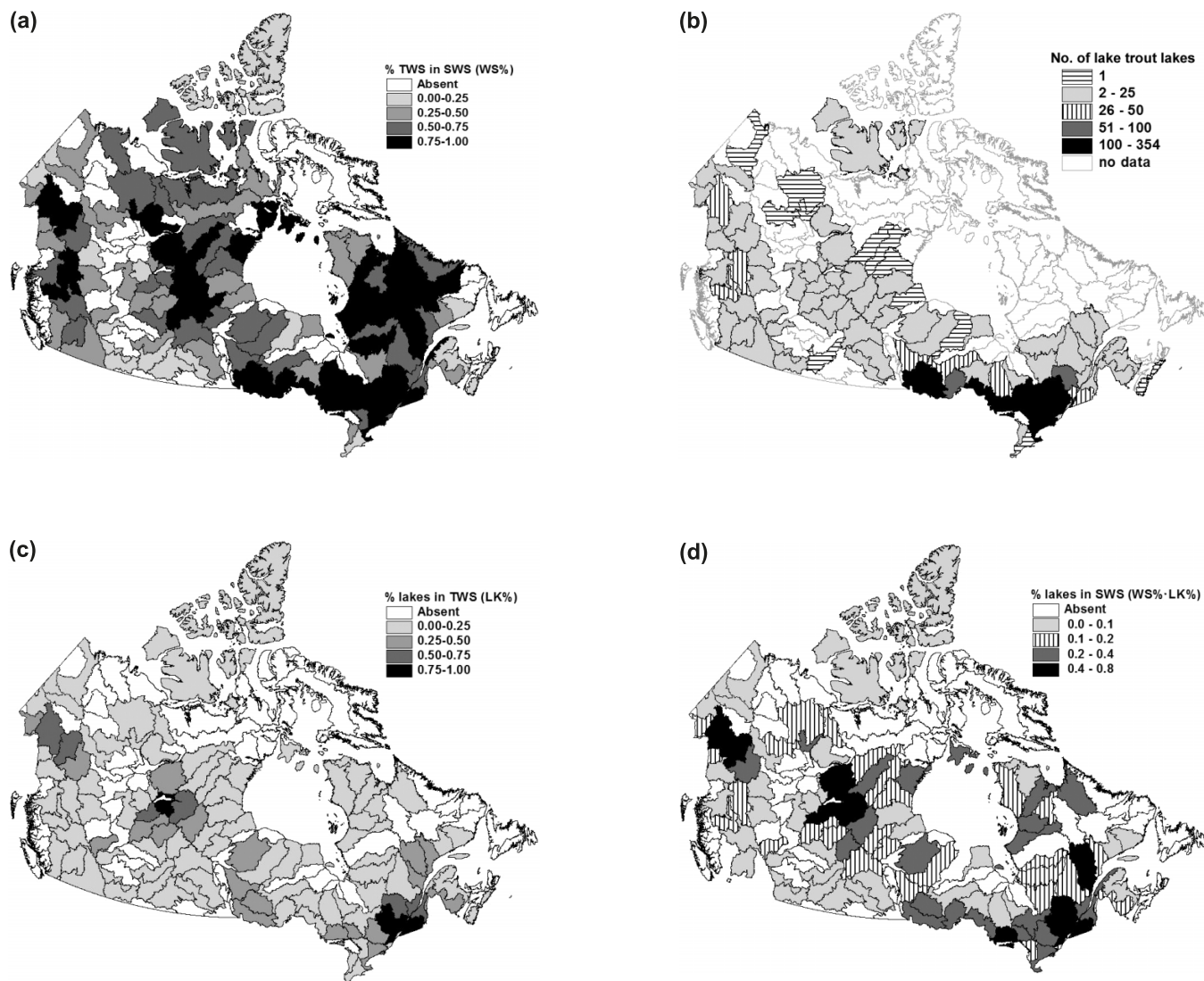


Table 6. Numbers of lakes by size class in the national lakes database and the proportion with lake trout present (SZ_{perc}) and the odds ratio (SZ_{ratio}) by size class to the overall proportion.

Size class (km ²)	No. of lakes	SZ_{perc}	SZ_{ratio}
0.1 to 0.2	2 017	0.038	0.179
0.2 to 0.5	3 011	0.122	0.579
0.5 to 1	2 490	0.198	0.945
1 to 2	2 159	0.258	1.229
2 to 5	1 990	0.305	1.453
5 to 10	863	0.352	1.677
10 to 20	573	0.389	1.853
20 to 50	404	0.366	1.744
50 to 100	192	0.344	1.637
100 plus	282	0.340	1.621
Total	13 981	0.210	

of lake trout effects in the pH and TDS models was consistent with the regional patterns of occurrence of lake trout. Although TDS is an indicator of lake trout carrying capacity (Shuter et al. 1998), lake trout distribution predominantly covers areas with moderate to low TDS levels. The pH levels, although lower in those eastern areas of Canada affected by acidic deposition, are mainly above extirpation thresholds for lake trout (Schindler 1988), and lower values typically occur in smaller lakes that are less suited to lake trout for reasons already given.

The total lake counts and area are derived primarily by direct counts and measures from extensive mapping of Canada's landscape, but the estimates for the lake trout resource are limited by the incomplete coverage of distribution data and the lack of adequate lake inventory data in the more remote regions of the country. Although the more southerly estimates of occurrence by watersheds and lake size draw on relatively large samples of data, the northerly estimates may well be underestimates as limited surveys such as that

Table 7. Total and lake trout lake resources (number, area (km²), and for lake trout, volume (km³)) in Canada by (a) area size class (km²) and (b) ecozone.

(a) Size class.								
Category	All lakes		Lake trout lakes (all ecozones)			Lake trout lakes (Shield)		
	Number	Area	Number	Area	Volume	Number	Area	Volume
0.1–<0.2	465 256	64 415.5	16 489	2 282.9	15.2	13 367	1 850.8	11.5
0.2–<0.5	272 256	82 970.2	25 051	7 634.3	58.0	19 866	6 054.2	42.9
0.5–<1.0	88 341	61 154.8	11 573	8 011.3	69.4	9 056	6 269.1	50.4
1.0–<2.0	39 195	54 052.7	5 323	7 339.3	68.8	4 028	5 567.5	48.1
2.0–<5.0	29 094	87 239.8	656	15 305.5	163.5	504	11 860.9	117.9
5.0–<10.0	8 898	60 757.8	5 067	11 382.9	141.4	3 922	8 917.4	103.0
10.0–<20.0	3 855	52 761.4	403	9 006.1	125.4	316	6 928.5	89.6
20.0–<50.0	1 994	60 267.3	1 668	12 196.1	193.1	1 312	9 502.8	140.9
50.0–<100.0	681	46 624.4	132	9 062.3	162.1	100	6 872.8	110.6
≥100.0	562	457 907.2	119	269 056.3	21 443.1	69	165 372.8	16 062.7
Total	910 132	1 028 151.1	66 479	351 277.0	22 440.0	52 540	229 196.7	16 777.5

(b) Ecozone.								
Category	All lakes		Lake trout lakes < 100 km ²			Lake trout lakes ≥ 100 km ²		
	Number	Area	Number	Area	Volume	Number	Area	Volume
Northern Arctic*	125 433	103 013.3	846	1 296.8	11.0	2	719.0	1.3
Southern Arctic	142 737	114 259.9	5 041	7 237.1	90.3	10	5 175.6	256.6
Taiga Cordillera	4 215	2 590.7	60	74.8	0.6	0	0.0	0.0
Taiga Shield	249 587	246 645.1	19 436	26 386.5	273.9	27	41 033.3	2 131.4
Taiga Plains	42 194	64 024.6	2 051	2 818.6	65.4	12	34 222.5	2 318.3
Boreal Cordillera	11 241	8 580.6	1 824	1 958.2	38.9	5	1 728.0	105.9
Hudson Plains	15 889	12 068.0	120	186.7	0.9	0	0.0	0.0
Boreal Plains	40 266	74 834.6	2 389	2 962.5	39.9	14	8 133.2	111.5
Boreal Shield	238 950	315 375.2	33 036	37 437.3	440.9	42	124 339.5	1 3931.4
Montane Cordillera	13 559	14 010.4	404	536.7	11.1	4	1 220.8	51.3
Prairies	12 464	8 903.3	139	209.8	2.1	0	0.0	0.0
Atlantic Maritime	4 874	3 382.4	165	201.3	2.6	0	0.0	0.0
Pacific Maritime	4 030	2 791.0	0	0.0	0.0	0	0.0	0.0
Mixedwood Plains	4 693	57 672.0	850	914.7	19.2	3	52 484.3	2 535.4
Total	910 132	1 028 151.1	66 360	82 220.8	997.0	119	269 056.3	21 443.1

Note: The lake trout resources on the Boreal Shield and Taiga Shield are shown by size class. The ecozones are ordered by mean annual air temperature (1961–1990 norms), and the lake trout resource by ecozone is divided at the 100 km² size boundary.

*Northern Arctic and Arctic Cordillera were combined within secondary watershed units.

of Hershey et al. (2006) suggest that lake trout are more common, especially in smaller lakes in regions with colder climates.

The simple application of a model of species occurrence with regional lake character models to estimate the extent of lake trout lake resources readily demonstrates how such models can be used for large-scale environmental assessments. Similar assessments were made for the impacts of acidic deposition on lake biotic resources in eastern Canada (Jones et al. 1990) and for a national mass balance of contaminants (Woodfine et al. 2002). Such large-scale assessment tools are necessary to gauge long-term and cumulative impacts and to weigh them against social and economic constraints if we are to move beyond limitations that currently render most cumulative effects assessment futile (Duinker and Grieg 2007). Assessing potential large-scale impacts of stressors, such as climate change, land use change, and invasive species, is a critical precursor to identification of vulnerabilities and the formulation of mitigation and adaptation

strategies (Metzger and Schröter 2006). These assessments need to be spatially explicit and quantitative to compete with social and economic imperatives that inevitably impact many ecosystems.

The increasing geographic scope of environment stresses requires a broader canvas both for inventory and characterization of lake resources and for the development of management and adaptation strategies. This study has demonstrated that a national synoptic limnology of Canada is within reach and that such a framework can be usefully applied. The next steps should include expanding the spatial coverage by assembling existing information sources, and where gaps still remain, new inventory work will be needed. The range of parameters assessed on a national scale should be expanded, especially with respect to those such as temperature, oxygen, total phosphorus, and DOM where more localized studies have demonstrated their importance to understanding lake processes and productivity. As this national lake assessment capability increases, so the ability to

evaluate large-scale environmental stresses will be enhanced, bringing us closer to a more useful assessment of cumulative impacts.

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References

- Burnham, K.P., and Anderson, D.R. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociol. Methods Res.* **33**: 261–304. doi:10.1177/0049124104268644.
- Carpenter, S.R., Ludwig, D., and Brock, W.A. 1999. Management of eutrophication for lakes subject to potentially irreversible change. *Ecol. Appl.* **9**: 751–771. doi:10.1890/1051-0761(1999)009[0751:MOEFLS]2.0.CO;2.
- Chu, C., Minns, C.K., and Mandrak, N.E. 2003. Comparative regional assessment of factors impacting freshwater fish biodiversity in Canada. *Can. J. Fish. Aquat. Sci.* **60**: 624–634. doi:10.1139/f03-048.
- Downing, J.A., Prairie, Y.T., Cole, J.J., Duarte, C.M., Tranvik, L.J., Striegl, R.G., McDowell, W.H., Kortelainen, P., Caraco, N.F., Melack, J.M., and Middelburg, J.J. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. *Limnol. Oceanogr.* **51**: 2388–2397.
- Duinker, P.N., and Grieg, L.A. 2007. Scenario analysis in environmental impact assessment: improving explorations of the future. *Environ. Impact. Assess. Rev.* **27**: 206–219. doi:10.1016/j.eiar.2006.11.001.
- Ecological Stratification Working Group. 1996. A national ecological framework for Canada. Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research, and Environment Canada, State of Environment Directorate, Ottawa. Map at scale 1:7.5 million. Available online at <http://www.ec.gc.ca/soer-ree/English/Framework/default.cfm>. Pdf copy available from <http://res.agr.ca/cansis/publications/ecostrat/intro.html>.
- Frey, D.G. (Editor). 1963. *Limnology in North America*. University of Wisconsin Press, Madison, Wis.
- Gunn, J.M., Steedman, R.J., and Ryder, R.A. (Editors). 2003. *Boreal shield watersheds: lake trout ecosystems in a changing environment*. Lewis Publishers, Boca Raton, Florida.
- Hakanson, L. 1996. Predicting important lake habitat variables from maps using modern modelling tools. *Can. J. Fish. Aquat. Sci.* **53**(Suppl. 1): 364–382. doi:10.1139/cjfas-53-S1-364.
- Hershey, A.E., Beaty, S., Fortino, K., Keyse, M., Mou, P.P., O'Brien, W.J., Ulseth, A.J., Gettel, G.A., Lienesch, P.W., Luecke, C., McDonald, M.E., Mayer, C.H., Miller, M.C., Richards, C., Schuldt, J.A., and Whalen, S.C. 2006. Effects of landscape factors on fish distribution in arctic Alaskan lakes. *Freshw. Biol.* **51**: 39–55. doi:10.1111/j.1365-2427.2005.01474.x.
- Hurvich, C.M., and Tsai, C.-L. 1989. Regression and time series model selection in small samples. *Biometrika*, **76**: 297–307. doi:10.1093/biomet/76.2.297.
- Jensen, M.E., Bourgeron, P., Everett, R., and Goodman, I. 1996. Ecosystem management: a landscape ecology perspective. *Water Resour. Bull.* **32**: 203–215.
- Johnson, M.G., Leach, J.H., Minns, C.K., and Olver, C.H. 1977. Limnological characteristics of Ontario lakes in relation to associations of walleye (*Stizostedion vitreum vitreum*), northern pike (*Esox lucius*), lake trout (*Salvelinus namaycush*), and small-mouth bass (*Micropterus dolomieu*). *J. Fish. Res. Board Can.* **34**: 1592–1601.
- Jones, M.L., Minns, C.K., Marmorek, D.M., and Elder, F.C. 1990. Assessing the potential extent of damage to inland lakes in eastern Canada due to acidic deposition: II. Application of the regional model. *Can. J. Fish. Aquat. Sci.* **47**: 67–80. doi:10.1139/f90-007.
- Kelso, J.R.M., Shaw, M.A., Minns, C.K., and Mills, K.H. 1990. An evaluation of the effects of atmospheric acidic deposition on fish and fishery resource of Canada. *Can. J. Fish. Aquat. Sci.* **47**: 644–655. doi:10.1139/f90-072.
- Kolada, A., Soszka, H., Cydzik, D., and Golub, M. 2005. Abiotic typology of Polish lakes. *Limnologica*, **35**: 145–150.
- Kratz, T.K., and Frost, T.M. 2000. The ecological organization of lake districts: general introduction. *Freshw. Biol.* **43**: 297–299. doi:10.1046/j.1365-2427.2000.00568.x.
- Leach, J.H., and Herron, R.C. 1992. A review of lake habitat classification. In *The development of an aquatic habitat classification system for lakes*. Edited by W.D.N. Busch and P.G. Sly. CRC Press, Boca Raton, Fla. pp. 27–72.
- Lehner, B., and Doll, P. 2004. Development and validation of a global database of lakes, reservoirs, and wetlands. *J. Hydrol. (Amst.)*, **296**: 1–22. doi:10.1016/j.jhydrol.2004.03.028.
- Lester, N.P., Marshall, T.R., Armstrong, K., Dunlop, W.I., and Ritchie, B. 2003. A broad-scale approach to management of Ontario's recreational fisheries. *N. Am. J. Fish. Manage.* **23**: 1312–1328. doi:10.1577/M01-230AM.
- Lester, N.P., Dextrase, A.J., Kushneriuk, R.S., Rawson, M.R., and Ryan, P.A. 2004. Light and temperature: key factors affecting walleye abundance and production. *Trans. Am. Fish. Soc.* **133**: 588–605. doi:10.1577/T02-111.1.
- Marshall, T.R. 1996. A hierarchical approach to assessing habitat suitability and yield potential of lake trout. *Can. J. Fish. Aquat. Sci.* **53**(Suppl. 1): 332–341. doi:10.1139/cjfas-53-S1-332.
- Martin, S.L., and Soranno, P.A. 2006. Lake landscape position: relationships to hydrologic connectivity and landscape features. *Limnol. Oceanogr.* **51**: 801–814.
- Metzger, M.J., and Schröter, D. 2006. Towards a spatially explicit and quantitative vulnerability assessment of environmental change in Europe. *Reg. Environ. Change*, **6**: 201–216. doi:10.1007/s10113-006-0020-2.
- Minns, C.K. 2001. Science for freshwater fish habitat management in Canada: current status and future prospects. *Aquat. Ecosyst. Health Manage.* **4**: 423–436. doi:10.1080/146349801317276099.
- Minns, C.K., and Moore, J.E. 1995. Factors limiting the distributions of Ontario's freshwater fishes: the role of climate and other variables, and the potential impacts of climate change. *Can. Spec. Publ. Fish. Aquat. Sci.* No. 121. pp. 137–160.
- Molot, L.A., Keller, W., Leavitt, P.R., Robarts, R.D., Waiser, M.J., Arts, M.T., Clair, T.A., Pienitz, R., Yan, N.D., McNicol, D.K., Prairie, Y.T., Dillon, P.J., Macrae, M., Bello, R., Nordin, R.N., Curtis, P.J., Smol, J.P., and Douglas, M.S.V. 2004. Risk analysis of dissolved organic matter-mediated ultraviolet B exposure in Canadian inland waters. *Can. J. Fish. Aquat. Sci.* **61**: 2511–2521. doi:10.1139/f04-165.
- Moss, B., Stephen, D., Alvarez, C., Becares, E., Van De Bund, W., Collings, S.E., Van Donk, E., De Eyto, E., Feldmann, T., Fernández-Aláez, C., Margarita Fernández-Aláez, M., Franken, R.J.M., García-Criado, F., Gross, E.M., Gyllström, M., Hansson, L.-A., Irvine, K., Järvä, A., Jensen, J.-P., Jeppesen, E., Kairesalo, T., Kornijów, R., Krause, T., Künnap, H., Laas, A., Lill, E., Lorens,

- B., Luup, H., Miracle, M.R., Nöges, P., Nöges, T., Nykänen, M., Ott, I., Peczula, W., Peeters, E.T.H.M., Phillips, G., Romo, S., Russell, V., Salujõe, J., Scheffer, M., Siewertsen, K., Smal, H., Tesch, C., Timm, H., Tuvikene, L., Tonno, I., Virro, T., Vicente, E., and Wilson, D. 2003. The determination of ecological quality in shallow lakes — a tested system (ECOFRAME) for implementation of the European Water Framework Directive. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* **13**: 507–549. doi:10.1002/aqc.592.
- Naumann, E. 1929. The scope and chief problems of regional limnology. *Int. Rev. Hydrobiol.* **22**: 423–444. doi:10.1002/iroh.19290220128.
- Nicholson, H.F., and Moore, J.E. 1988. Bibliography on the limnology and fisheries of Canadian freshwaters. No. 10. (Final cumulative edition.) Vols. 1, 2, and 3. *Can. Tech. Rep. Fish. Aquat. Sci.* No. 1600.
- Northcote, T.G., and Larkin, P.A. 1956. Indices of productivity in British Columbia lakes. *J. Fish. Res. Board Can.* **13**: 515–540.
- Nykänen, M., Kairesalo, T., Mäkelä, S., Huitu, E., Ala-Opas, P., and Mannio, J. 2005. A typology and ecological classification system for Finnish lakes: applicability of the ECOFRAME scheme. *Boreal Environ. Res.* **10**: 159–179.
- Post, J.R., Sullivan, M., Cox, S., Lester, N.P., Walters, C.J., Parkinson, E.A., Paul, A.J., Jackson, L., and Shuter, B.J. 2002. Canada's recreational fisheries: the invisible collapse. *Fisheries*, **27**: 6–17. doi:10.1577/1548-8446(2002)027<0006:CRF>2.0.CO;2.
- Rawson, D.S. 1939. Some physical and chemical factors in the metabolism of lakes. *Am. Assoc. Adv. Sci.* **10**: 9–26.
- Reist, J.D., Wrona, F.J., Prowse, T.D., Power, M., Dempson, J.B., Beamish, R.J., King, J.R., Carmichael, T.J., and Sawatzky, C.D. 2006. General effects of climate change on arctic fishes and fish populations. *Ambio*, **35**: 370–380. doi:10.1579/0044-7447(2006)35[370:GEOCCO]2.0.CO;2. PMID:17256641.
- Ruhland, K., and Smol, J.P. 1998. Limnological characteristics of 70 lakes spanning Arctic treeline from Coronation Gulf to Great Slave Lake in the central Northwest Territories, Canada. *Int. Rev. Hydrobiol.* **83**: 183–203. doi:10.1002/iroh.19980830302.
- Ryan, P.A., and Marshall, T.R. 1994. A niche definition for lake trout (*Salvelinus namaycush*) and its use to identify populations at risk. *Can. J. Fish. Aquat. Sci.* **51**: 2513–2519. doi:10.1139/f94-250.
- Ryder, R.A. 1965. A method for estimating the potential fish production of north-temperate lakes. *Trans. Am. Fish. Soc.* **94**: 214–218. doi:10.1577/1548-8659(1965)94[214:AMFETP]2.0.CO;2.
- Schindler, D.W. 1988. Effects of acid rain on freshwater ecosystems. *Science (Washington, D.C.)*, **239**: 149–157. doi:10.1126/science.239.4836.149.
- Schindler, D.W. 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. *Can. J. Fish. Aquat. Sci.* **58**: 18–29. doi:10.1139/cjfas-58-1-18.
- Schlesinger, D.A., and Regier, H.A. 1982. Climatic and morpho-edaphic indices of fish yields from natural lakes. *Trans. Am. Fish. Soc.* **111**: 141–150. doi:10.1577/1548-8659(1982)111<141:CAMIOF>2.0.CO;2.
- Shuter, B.J., Jones, M.L., Korver, R.M., and Lester, N.P. 1998. A general, life history based model of regional management of fish stocks: the inland lake trout (*Salvelinus namaycush*) fisheries of Ontario. *Can. J. Fish. Aquat. Sci.* **55**: 2161–2177. doi:10.1139/cjfas-55-9-2161.
- Sprugel, D.G. 1983. Correcting for bias in log-transformed allometric equations. *Ecology*, **64**: 209–210. doi:10.2307/1937343.
- Stendera, S., and Johnson, R.K. 2006. Multiscale drivers of water chemistry of boreal lakes and streams. *Environ. Manage.* **38**: 760–770. doi:10.1007/s00267-005-0180-8. PMID:16955233.
- Vidondo, B., Prairie, Y.T., Blanco, J.M., and Duarte, C.M. 1997. Some aspects of the analysis of size spectra in aquatic ecology. *Limnol. Oceanogr.* **42**: 184–192.
- Wilson, C.C., and Hebert, P.D.N. 1998. Phylogeography and post-glacial dispersal of lake trout (*Salvelinus namaycush*) in North America. *Can. J. Fish. Aquat. Sci.* **55**: 1010–1024. doi:10.1139/cjfas-55-4-1010.
- Woodfine, D., MacLeod, M., and Mackay, D. 2002. A regionally segmented national scale multimedia contaminant fate model for Canada with GIS data input and display. *Environ. Pollut.* **119**: 341–355. doi:10.1016/S0269-7491(01)00344-X. PMID:12166668.

Appendix A

Table A1 appears on the next page.

Table A1. List of main lake data sources and contacts by province or territory.

	Source	Contact
Canada	Evans 2000 ^a	
Newfoundland and Labrador	Van Zyll De Jong and Cowx 2005 ^b LRTAP NIS Lake Database	Michael van Zyll De Jong
Nova Scotia	Lake Inventory Database Alexander et al. 1986 ^c	John MacMillan
Prince Edward Island	No data	
New Brunswick	Environment Canada Pilgrim et al. 2003 ^d	Tom Clair, Ian Dennis
Quebec	Ministère du Développement Durable de l'Environnement et des Parcs Hydro-Quebec Fallu et al. 2000 ^e	Diane Morin, Daniel Blais, Mario Bérubé, Marc Simmoneau, Pierre Levasseur, Jacques Dupont Richard Verdon, Jean-Louis Fréchette Marie-Andrée Fallu
Ontario	Lake Inventory Database, Ontario Ministry of Natural Resources	Brian Shuter, Nigel Lester
Manitoba	Ontario Environment Water Quality Database DFO Fish Habitat Management GIS	William Franzin, DFO Winnipeg Walt Lysack
Saskatchewan	Manitoba Conservation/Water Stewardship DFO Fish Habitat Management GIS	William Franzin, DFO Winnipeg Kevin Murphy, Mark Duffy, Ken Scott
Alberta	Saskatchewan Environment Alberta Environment Sustainable Resource Development Atlas of Alberta Lakes	Bridgette Helbig, Ron Tchir, Thai Nguyen Huu Ken Crutchfield, Stuart Nadeau http://alberta-lakes.sunsite.ualberta.ca/
British Columbia	BC Ministry of Sustainable Resource Development online databases	http://srmapps.gov.bc.ca/apps/fidq/ Rick Nordin
Yukon, NWT, and Nunavut	Hamilton et al. 2001 ^f Antoniades et al. 2003a, ^g 2003b ^h Bouchard et al. 2004 ⁱ Falk 1979 ^j Lindsey et al. 1981 ^k Pienitz et al. 1997a, ^l 1997b ^m Ruhland et al. 2003 ⁿ Shortreed and Stockner 1986 ^o Wilson and Gajewski 2002 ^p	P.K. Hamilton, Kathleen Ruhland, Darlene Lim, John Smol, Dermot Antoniades

^aEvans, M.S. 2000. The large lake ecosystems of northern Canada. *Aquat. Ecosyst. Health Manage.* 3: 65–79. doi:10.1016/S1463-4988(99)00071-8.

^bVan Zyll De Jong, M.C., and Cowx, I.G. 2005. Association between biogeographical factors and boreal lake fish assemblages. *Fish. Manag. Ecol.* 12: 189–199. doi:10.1111/j.1365-2400.2005.00442.x.

^cAlexander, D.R., Kerekes, J.J., and Sabean, B.C. 1986. Description of selected lake characteristics and occurrence of fish species in 781 Nova Scotia lakes. *Proc. N.S. Inst. Sci.* 36: 63–106.

^dPilgrim, W., Clair, T.A., Choate, J., Hughes, R. 2003. Changes in acid precipitation-related water chemistry of lakes from southwestern New Brunswick, Canada, 1986–2001. *Environ. Monit. Assess.* 88: 39–52. doi:10.1023/A:1025592202153. PMID:14570410.

^eFallu, M.-A., Allaire, N., and Pienitz, R. 2000. Freshwater diatoms from northern Québec and Labrador (Canada): species–environment relationships in lakes of boreal forest, forest–tundra and tundra regions. *Bibliotheca Diatomologica*, Vol. 45. J. Cramer, Berlin/Stuttgart.

^fHamilton, P., Gajewski, K., Atkinson, D., and Lean, D. 2001. Physical and chemical limnology of lakes from the Canadian Arctic Archipelago. *Hydrobiologia*, 457: 133–148. doi:10.1023/A:1012275316543.

^gAntoniades, D., Douglas, M.S.V., and Smol, J.P. 2003a. The physical and chemical limnology of 24 ponds and one lake from Isachsen, Ellef Ringnes Island, Canadian High Arctic. *Int. Rev. Hydrobiol.* 88: 519–538. doi:10.1002/iroh.200310665.

^hAntoniades, D., Douglas, M.S.V., and Smol, J.P. 2003b. Comparative physical and chemical limnology of two Canadian High Arctic regions: Alert (Ellesmere Island, NU) and Mould Bay (Prince Patrick Island, NWT). *Arch. Hydrobiol.* 158: 485–516. doi:10.1127/0003-9136/2003/0158-0485

ⁱBouchard, G., Gajewski, K., and Hamilton, P. 2004. Biogeography of diatoms from the Canadian Arctic Archipelago. *J. Biogeogr.* 31: 1955–1973. doi:10.1111/j.1365-2699.2004.01143.x.

^jFalk, M.R. 1979. Biological and limnological data on ten lakes surveyed in the Northwest Territories, 1971–72. *Environ. Can. Fish. Mar. Serv. Data Rep.* No. 129.

^kLindsey, C.C., Patalas, K., Bodaly, R.A., and Archibald, C.P. 1981. Glaciation and the physical, chemical and biological limnology of Yukon lakes. *Can. Tech. Rep. Fish. Aquat. Sci.* No. 966.

^lPienitz, R., Smol, J.P., and Lean, D.R.S. 1997a. Physical and chemical limnology of 59 lakes located between southern Yukon and the Tuktoyaktuk Peninsula, Northwest Territories (Canada). *Can. J. Fish. Aquat. Sci.* 54: 330–346. doi:10.1139/cjfas-54-2-330.

^mPienitz, R., Smol, J.P., and Lean, D.R.S. 1997b. Physical and chemical limnology of 24 lakes located between Yellowknife and Contwoyto Lake, Northwest Territories (Canada). *Can. J. Fish. Aquat. Sci.* 54: 347–358. doi:10.1139/cjfas-54-2-347.

ⁿRuhland, K.M., Smol, J.P., Wang, X., and Muir, D.C.G. 2003. Limnological characteristics of 56 lakes in the central Canadian Arctic treeline region. *J. Limnol.* 62: 9–27.

^oShortreed, K.S., and Stockner, J.G. 1986. Trophic status of 19 subarctic lakes in the Yukon Territory. *Can. J. Fish. Aquat. Sci.* 43: 797–805. doi:10.1139/f86-098.

^pWilson, S.E., and Gajewski, K. 2002. Surface-sediment diatom assemblages and water chemistry from 42 subarctic lakes in the southwestern Yukon and northern British Columbia, Canada. *Ecoscience*, 9: 256–270.