Limnol. Oceanogr., 48(6), 2003, 2321–2334

Regional comparisons of watershed determinants of dissolved organic carbon in temperate lakes from the Upper Great Lakes region and selected regions globally

Marguerite A. Xenopoulos,[1] *David M. Lodge, Jason Frentress, Timothy A. Kreps, Scott D. Bridgham,*[2] *Elizabeth Grossman, and Caryn J. Jackson*
Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana 46556

Abstract

We analyzed how dissolved organic carbon (DOC) concentration in lakes of the North American temperate forest (Upper Great Lakes region) is related to nine catchment characteristics (lake area, lake perimeter, drainage area, ratio of drainage area to lake area, proportion of watershed occupied by wetlands, proportion of lake perimeter in wetlands, shoreline development, elevation, and watershed slope) and compared selected relationships to those from other regions across the globe. For the temperate lakes, the proportion of the lake perimeter and the proportion of the watershed occupied by wetlands were the best predictors of DOC in both univariate ($r^2 = 0.34$ and 0.30, respectively) and multivariate regression models. Forested wetlands, in particular those with coniferous vegetation, explained the largest proportion of lake DOC variability. Wetlands with scrub-shrubs and emergent vegetation explained very little or no variability. Secondary to wetlands, lake DOC decreased with lake area and watershed slope. When we combined the temperate lake data set with that of 10 other geographical regions of the world (ranging from subtropical to tundra), the only two variables significant in predicting DOC were proportion of wetlands in the watershed ($r^2 = 0.36$) and lake elevation ($r^2 = 0.34$). We conclude that regional or small-scale DOC models likely have limited applicability in predicting DOC in other geographical areas of the world.

One important link between terrestrial and aquatic systems is the supply to lakes of terrestrial dissolved organic matter (DOC; generally measured as dissolved organic carbon). DOC affects many physical, chemical, and biological processes and thus plays a central role in lakes. For instance, DOC affects secondary production, provides important substrates to the microbial food web (Wetzel 1992), and can affect the mobility and toxicity of metals (Thurman 1985). DOC also attenuates visible and ultraviolet light (Morris et al. 1995; Xenopoulos and Schindler 2001*a*), both of which strongly affect ecological processes (e.g., Xenopoulos et al. 2000, 2002). In addition, DOC affects the mixing depth and the development of seasonal/diurnal thermoclines in lakes (Fee et al. 1996; Snucins and Gunn 2000; Xenopoulos and Schindler 2001*b*). Given its importance to these diverse processes in lakes, it is important to quantify the factors that control the concentration of lake DOC.

In general, much is already known about DOC export from the terrestrial ecosystems. Watershed sources of DOC are related to landscape, hydrology, and anthropogenic factors. Allochthonous DOC (organic carbon produced on land and released to waterways) can be delivered to lakes via stream inflows (Schindler et al. 1996*a*), groundwater (Schiff et al. 1997), and shallow subsurface runoff from wetlands (Gergel et al. 1999) and uplands (Schindler et al. 1996*a*). In some regions, a large amount of DOC originates in the upper soil horizons from decomposing vegetation and is flushed from the watersheds into streams and lakes, primarily during spring snowmelt (McKnight et al. 1993) or major precipitation events (Hinton et al. 1997). However, we know little about how these processes might differ in importance in different regions worldwide.

DOC production in the soil varies across a range of vegetation communities and soil types, but the consequences for lake DOC are only partly known. For example, in North American montane and boreal regions, watersheds with high coverage of wetlands contain lakes with higher DOC concentrations relative to lakes in high elevation or polar catchments with little vegetation and poor soil development (McKnight et al. 1997; Xenopoulos and Schindler 2001*a*). Similar positive relationships between the proportion of wetland cover and DOC in lakes exist in a number of regions globally (e.g., Engstrom 1987; Kortelainen 1993; Gergel et al. 1999). Despite these many studies, little is known about how differences in the dominant type of vegetation in wetlands (e.g., forested, emergent, scrub-shrub) affect the quantity of DOC export into lakes. Differences in the dominant plant species in the wetlands and their location within the catchment likely determine the amount of terrestrial DOC exported to lakes. For example, in uplands, soils derived from coniferous forests are much richer in DOC than those from hardwood stands (Cronan and Aiken 1985) or grass-

---

[1] Corresponding author (max@ualberta.net).

[2] Present address: Center for Ecology and Evolutionary Biology, P.O. Box 5289, University of Oregon, Eugene, Oregon 97403.

Acknowledgments

We thank the Ottawa National Forest for assisting our initial efforts to select lakes for sampling and for facilitating our project. Our Notre Dame colleagues—Gary Lamberti, Ron Hellenthal, P. Weishampel, and Sean Dunlap—contributed to initial planning for this project. We thank M. L. Pace (Institute for Ecosystem Studies) for allowing us the use of a portion of his DOC data. We also thank M. Arts, R. Sommaruga, I. Laurion, M. Ventura, E. Prepas, P. Kortelainen, R. Rae, and W. Vincent for their help by providing us with information or additional data for the global data set. The Notre Dame Center for Environmental Science and Technology paid for the lake sampling. M. A. Xenopoulos acknowledges support by a National Sciences and Engineering Research Council of Canada (NSERC) postdoctoral fellowship, by the University of Notre Dame, and by a grant from the U.S. EPA.

lands (Rae et al. 2001). Here, we report on the effects of wetland type on DOC in lakes from the Upper Great Lakes region.

Recently, Pace and Cole (2002) observed synchronous behavior of DOC concentration over multiple years in temperate lakes of the Upper Midwest region in the United States, which suggests strong climatic control of DOC. In fact, there was a positive relationship between precipitation events and DOC in the study lakes. This synchronous behavior was particularly pronounced in lakes directly connected to the landscape with a stream. However, the effects of other catchment characteristics (watershed area, wetlands), which might explain the ~20-fold difference in DOC among the analyzed lakes, were not addressed in that study.

The following sets of parameters were correlated to DOC concentration in North Temperate lakes of the Upper Great Lakes region: drainage basin morphometry, wetland type and abundance, and vegetation location within the drainage basin. Lake DOC was also related to some previously studied parameters, including the ratio of the watershed drainage area to lake surface area (drainage ratio: A_d/A_0) (Schindler 1971), lake area, and watershed slope (Rasmussen et al. 1989; Kortelainen 1993; Houle et al. 1995).

Finally, these empirical relationships from the Upper Great Lakes region were compared to previously published relationships for lakes in other regions, ranging from subtropical to tundra ecosystems. Except for a study by Rasmussen et al. (1989) that compared lakes from seven regions of the northern United States and Canada, no other study has described multiregional relationships between lake DOC and catchment properties. In addition, the Rasmussen et al. (1989) study did not quantify wetlands, which are now known to be among the more important contributors of DOC to lakes.

Methods

Upper Great Lakes forest area description—We sampled lakes from the Ottawa National Forest located in the Upper Peninsula of Michigan and northeastern Wisconsin. All the study lakes are located in Michigan except for 10, which are located along the Michigan–Wisconsin border. The deglaciated terrain contains a high density and diversity of lakes situated in glacial till deposits and receiving water from precipitation and surface and subsurface flows. The region is composed of a mosaic of different geology, soils, hydrology, wetland types, lake hydrological types (seepage, drainage, etc.) and terrestrial vegetation (hardwoods and conifers), all experiencing similar climate. Wetlands are common in the area and generally constitute a significant proportion (average ~30%) of the catchments, and many of the wetlands contain significant amounts of peat (notably in the bogs and fens).

DOC sampling and measurements—DOC was sampled in 100 lakes in July and August 1997 and 1998. For 88 lakes, surface water at midlake was collected by plunging an acid-rinsed 500-ml Nalgene bottle to a depth of about 30 cm. Samples were kept cold until analysis. Water was passed through a Whatman GF/F glass fiber filter (0.6-μm pore size), and organic carbon concentration was measured by combustion on a Shimadzu TOC 5000 Analyzer (Sharp et al. 1993). Prior to analysis, samples were acidified with distilled nitric acid and purged for 2 min with CO_2-free air to remove inorganic carbon. Twelve additional lakes were sampled in 1998 for DOC by researchers from the Institute of Ecosystem Studies (Millbrook, New York). Those lakes were sampled and analyzed for DOC as described in Pace and Cole (2002).

Watershed and lake morphometric characteristics—Lake surface area (A_0), watershed (catchment = drainage area + lake area = A_d) area, and lake perimeter (PER) were measured with a geographic information system (GIS) using ArcView 3.2 with Hydro and Spatial Analyst extensions and digital elevation models (DEM, http://data.geocomm.com/dem/). Digitized topographic maps were obtained from Michigan and Wisconsin Departments of Natural Resources (http://www.state.mi.us/webapp/cgi/mgdl/, http://www.dnr.state.wi.us/org/at/et/geo/). Watersheds were delineated after the procedure developed by Environmental Systems Research Institute, Inc. (ESRI), and the University of Texas Center for Research of Water Resources with an avenue script developed by F. Olivera (http://www.crwr.utexas.edu/gis/gishyd98/atlas/EXERCISE/URUBAMBA/peru.htm).

Watershed slope (WSS) was calculated as in Rasmussen et al. (1989) using the average watershed boundary elevation and lake elevation (ELEV) data obtained from GIS. Watershed boundary elevations were estimated by combining watershed perimeters and the elevations from the DEM. The elevation values were then averaged in an ArcView table. Shoreline development (SD) was estimated as in Wetzel and Likens (1991).

For each lake, wetland spatial coverage was calculated in the drainage basin from: (1) the proportion of watershed area that was occupied by wetland (= WATWET) and (2) the proportion of the lake perimeter that was wetland (= PERWET). The proportion of the catchment and lake perimeter in wetlands was quantified using ArcView GIS as above by overlaying the watershed polygons on the digitized wetland maps. Digitized wetland maps were obtained from the Michigan Department of Natural Resources (www.state.mi.us/webapp/cgi/mgdl/) and Wisconsin Department of Natural Resources (www.dnr.state.wi.us/org/at/et/geo/datasharing/custodia/wwi_1.htm). Percent contribution of different wetland types (*see below*) was also recorded from these maps in relation to total wetland area within each lake watershed (98 lakes) and for each lake perimeter (65 lakes). Michigan digitized wetlands were classified into types according to the Cowardin et al. (1979) classification systems, as coded by the National Wetlands Inventory (NWI). Wisconsin digitized wetlands were classified following the Wisconsin Wetlands Inventory (WWI; WDNR 1991). For analytical consistency, WWI codes were converted into the national (NWI) codes following the protocol of Johnston and Meysembourg (2002). For our study lakes, the watersheds contained a total of 55 different NWI wetland types, whereas lake perimeters included 23 types. To simplify analysis, wetland categories were reduced to 12 types for ordination and multiple regression analysis and further reduced to 4 types

Table 1. Summary of NWI wetland codes that were recorded in the Ottawa National Forest combined for analysis (1) PCA and multiple regressions and (2) univariate regressions. NWI codes and associated vegetation are described in detail in Cowardin et al. (1979; or download the data from http://wetlands.fws.gov/Pubs_Reports/Class_Manual/class_titlepg.htm) and on the NWI Web site (http://wetlands.fws.gov/; http://www.nwi.fws.gov/atx/atx.html).

NWI codes	Code 1	Code 2	Characteristic
L1OWH*, L1OWHh*, L2ABHh*, POWF*, POWFb*, POWH*, POWHb*, POWU*, POWZ*, POWZb*, PABH*	LLPOW	LLPOW	Lacustrine limnetic and palustrine open water†
PEM/ABZ*, PEM/OWF*, PEM/OWH*, PEM/OWZ*, PEM/OWZh*, PEMB, PEMC*, PEME, PEMF, PEMFh*, PEMG*, PEMY, PEMZ	PE	PE	Palustrine emergent
PFO/1B*, PFO1Y*	PFBLD	CPF	Palustrine forested broad-leaved deciduous
PFO/SS3B*, PFO/SSB, PFO/SSY	PFSS	CPF	Palustrine forested scrub-shrub
PFO2B*	PFNLD	CPF	Palustrine forested needle-leaved deciduous
PVO4/1B, PFO4/1Y*, PFO4B, PFO4Y*	PFNLE	CPF	Palustrine forested needle-leaved evergreen
PFOB, PFOC*, PFOY	PF	CPF	Palustrine forested (no specified subclass)
PSS/EMB, PSS/EMC*, PSS/EMFb, PSS/EMY	PSSE	CPSS	Palustrine scrub-shrub emergent
PSS1B, PSS1F*, PSS1Y	PSSBLD	CPSS	Palustrine scrub-shrub broad-leaved deciduous
PSS2/3B*, PSS2/EME*	PSSNLD	CPSS	Palustrine scrub-shrub needle-leaved deciduous
PSS3/EMB, PSS3B	PSSBLE	CPSS	Palustrine scrub-shrub broad-leaved evergreen
PSS5F*, PSSB, PSSF, PSSY, PSSY/EMY	PSS	CPSS	Palustrine scrub-shrub (no specified subclass)

* NWI code that was not found directly on the lake perimeter.

† According to NWI, this category includes deep and shallow open-water habitats and thus includes the study lake and other lakes and ponds or bogs present in the watershed.

for univariate regression analysis (Table 1). NWI codes were combined on the basis of the major vegetation type in the wetland (Table 1).

Lakes were also classified by hydrological type into four groups: seepage (no apparent surface inlet or outlets); seepage-inlet (inlets, no apparent surface outlets, but likely water loss through subsurface seepage); headwater (outlets, no apparent surface inlets); and drainage lakes (inlets and outlets).

Statistical analysis of DOC in northern temperate lakes—Pearson product–moment correlation coefficients with Bonferroni-adjusted probabilities were used to detect significant independent covariables. All variables (except for ELEV, PERWET, WATWET, and WSS) were $\log_{10}$ transformed to stabilize the variance, normalize the residuals (for regression analysis, *see below*), and normalize their distribution. As an exploratory analysis, univariate linear regressions were used initially to detect which of nine independent variables (A_0, PER, A_d, A_d/A_0, WATWET, PERWET, SD, ELEV, and WSS) best predicted DOC concentrations in lakes with a Bonferroni-adjusted alpha value of 0.005 (adjusted for nine regressions). Ordinary least square and stepwise forward multiple regressions were subsequently used to model the relationship between DOC and watershed variables in the Upper Great Lakes region. For the multiple regression models, not all the variables were tested simultaneously because of collinearity. We used the condition index (CI; Belsley et al. 1980) to detect collinearity in the models. In cases where CI was >30 (indicating high collinearity), we selected the independent variable (from two that were highly correlated) with the highest coefficient of determination (r^2) from the univariate analysis above to be used in the multiple regression models. Although many of the variables used in the final regression models were weakly correlated ($r < 0.5$), the collinearities that resulted were low, as estimated by the condition index (CI < 30) or the variance inflation factor (VIF $\ll 10$), and the variance decomposition criterion did not destabilize the regression coefficients (Belsley et al. 1980). All regression models (univariate and multivariate) produced satisfactory plots of residuals.

An ordination analysis (principal components analysis, PCA) identified the relation of each wetland type to the direction and magnitude of lake DOC concentration. Wetland types were also related to DOC using univariate and multiple regressions as described above. All statistical analyses were done using SAS (SAS Institute 2001).

Global comparisons—To determine how patterns from the Michigan lakes relate to patterns in other areas of the world, published values of DOC were compiled in relation to six catchment characteristics (A_0, A_d, A_d/A_0, SD, ELEV, and WATWET where available) if data from 10 or more lakes were reported. Published data were obtained from 10 geographical areas of the world (Table 2). These areas comprised a variety of ecoregions and include the central boreal Shield (Curtis and Schindler 1997; Kelly et al. 2001), eastern boreal Shield (D'Arcy and Carignan 1997), boreal plains (Prepas et al. 2001), and northern Great Plains (Mitchell and Prepas 1990; Arts et al. 2000) of Canada; alpine and prealpine (Laurion et al. 2000) in the Alps and Pyrenees; boreal forest (Kortelainen 1993; Subregion 1) in Finland; tundra (Kling et al. 2000) in Alaska; southeastern conifer forest and sand pine scrub (Kanciruk et al. 1986) in Florida; the central U.S. Rockies (Eilers et al. 1986; Subregions 1 and 2); and grasslands and croplands (Rae et al. 2001) in New Zealand (Table 2). If two or more DOC data points were published for one

Table 2. Comparison table for global DOC analysis of vegetation, wetlands, and groundwater flow in the 11 different ecoregions.

	Vegetation	Wetlands	Groundwater flow	Ecoregion*	No. of lakes
Temperate forest†	Hardwood/coniferous	Common	Important	Western Great Lakes forests	100
Central boreal Precambrian Shield‡	Coniferous/hardwood	Few	Absent	Central Canadian Shield forests	22
Boreal plain§	Coniferous	Common	Important	Mid-continental Canadian forests	26
New Zealand‖	Grassland/cropland/forested	Few	Unknown	Southland montane grasslands and Fiordland temperate forests	11
Alaska¶	Tundra: sedges and grasses	Few	Not important	Arctic foothills tundra	10
Alps and Pyrenees#	Prealpine and alpine	Rare	Not important	Alps conifer and mixed forests	26
Northern Great Plains**	Prairie grass	Common	Important	Northern mixed grasslands and northern short grass	53
Eastern boreal shield††	Hardwood/coniferous	Few	Not important	Eastern Canadian forests	32
Finland‡‡	Coniferous	Common	Not important	Scandinavian and Russian taiga and Scandinavian montane birch forest and grasslands	189
Florida§§	Hardwood/coniferous	Common	Important	Southeastern conifer forests and flooded grasslands and savannas	42
U.S. Rockies‖‖	Alpine	Few	Important	Colorado Plateau shrublands and Wasatch and Uinta montane forests	34

* Olson et al. (2001). Data also available on www.worldwildlife.org/science.
† This study.
‡ NOLSS data, including Lake Superior and Lake Nipigon from Kelly et al. (2001); ELA data from Curtis and Schindler (1997).
§ Prepas et al. (2001). Digitized DOC data courtesy of E. E. Prepas (Laurentian University, Canada).
‖ Rae et al. (2001).
¶ Kling et al. (2000).
\# Laurion et al. (2000).
** Mitchell and Prepas (1990) for Alberta, Canada, and Arts et al. (2000) for Saskatchewan, Canada.
†† D'Arcy and Carignan (1997).
‡‡ Kortelainen (1993). Digitized data courtesy of P. Kortelainen (Water and Environment Research Institute, Finland).
§§ Kanciruk et al. (1986).
‖‖ Eilers et al. (1986).

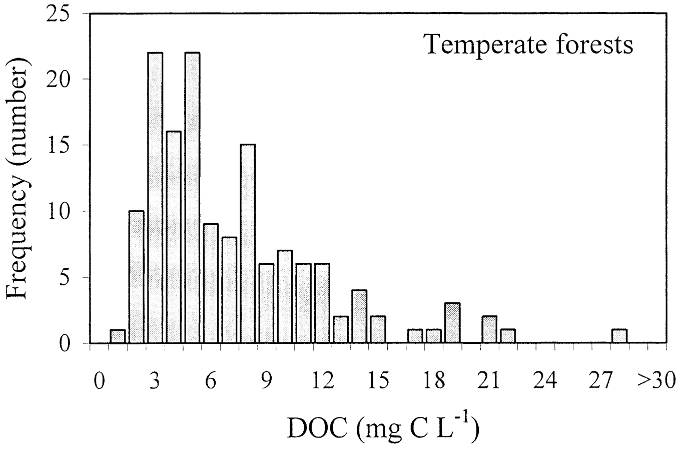

Fig. 1. Frequency distribution of DOC in North Temperate lakes of the Upper Great Lakes region.

site, then the average of the values was recorded for our regressions. Data from Kortelainen (1993) were transformed from total organic carbon (TOC) to DOC as outlined by Wetzel (1983; TOC is ~10% higher than DOC). DOC and all independent variables were obtained from published tables or reports, with two exceptions. From two authors (E. E. Prepas, Laurentian University, Canada; P. Kortelainen, Water and Environment Research Institute, Finland), we obtained data in electronic format. The data were analyzed using ordinary least squares univariate and multiple regressions as described above.

Results

Watershed characteristics related to DOC in the Upper Great Lakes forest—In the Ottawa National Forest lakes we sampled, DOC levels ranged from 1.6 to 29 mg C L^{-1} (Fig. 1). Several independent variables were cross-correlated (Table 3). In particular, lake area was highly correlated with lake perimeter and watershed area (Table 3; $r = 0.95$ and $r = 0.72$, respectively), and watershed wetland area was sig-

Table 3. Correlation matrix for the watershed variables measured in the North Temperate forest.

	A_0 (ha)	A_d (ha)	PERWET	WATWET	ELEV (m)	WSS (%)	SD (km)	PER (km)
Lake area (A_0)								
Watershed area (A_d)	0.73***							
Perimeter wetland (PERWET)	−0.39***	-0.12^{NS}						
Watershed wetland (WATWET)	−0.26*	0.06^{NS}	0.58***					
Lake elevation (ELEV)	-0.04^{NS}	-0.17^{NS}	0.04^{NS}	0.29*				
Watershed slope (WSS)	−0.24*	−0.52**	−0.28*	−0.45***	-0.02^{NS}			
Shoreline development (SD)	0.38***	0.31**	-0.094^{NS}	0.08^{NS}	0.04^{NS}	-0.21^{NS}		
Lake perimeter (PER)	0.95***	0.68***	−0.46***	−0.24*	0.01^{NS}	-0.21^{NS}	0.49***	
Drainage ratio (A_d/A_0)	−0.43***	0.27**	0.40***	0.44***	-0.12^{NS}	−0.33***	-0.12^{NS}	−0.40***

Correlations were significant at the * $P<0.05$, ** $P<0.01$, and *** $P<0.0001$ levels; NS, not significant.

nificantly correlated with perimeter wetland area, although the coefficient for this correlation was not as high ($r = 0.58$; Table 3).

Correlation of each of nine independent variables against DOC concentration in the 100-lake data set showed six significant univariate relationships (Bonferroni corrected, $P < 0.005$) between the catchment variables and DOC in lakes (Fig. 2). The best predictor of lake DOC was perimeter wetland area, which explained 34% of the variability but was followed closely by watershed wetland area ($r^2 = 0.30$). Lake area, drainage ratio, and watershed slope explained 10, 13, and 13% of the variability, respectively, in univariate regressions (Fig. 2).

On reanalysis of the above relationships by separation into each of the four assumed hydrological lake types, the watershed lake DOC relationship differed among lake types (Table 4). No significant differences were found in mean DOC concentration and WATWET or PERWET among lakes types ($P = 0.22$). For headwater lakes, no significant relationships between watershed variables and DOC existed, although this may be because of the low sample size. For seepage lakes, however, all watershed variables (except SD, not shown) related significantly to DOC (Table 4). WSS explained 14% of the variance in DOC in seepage lakes and 29% in seepage inlet lakes. PERWET and WATWET explained a greater proportion of DOC variability in seepage (55% vs. 40%, respectively) and seepage inlet (36% vs. 40%) compared to drainage lakes (18% vs. 17%). Only for seepage lakes were catchment area, lake size, and drainage ratio related to lake DOC (Table 4). Our results suggest very different landscape controls over DOC among the four hydrological types of lakes, and variation in the proportion of these lake types could partially explain regional differences in watershed correlates with lake DOC concentrations.

Analyzing all 100 lakes together, forward stepwise regressions produced a model where PERWET had a positive effect and WSS and A_0 had a negative effect on DOC concentration (Eq. 1).

$$\begin{aligned}\text{Log DOC} &= 0.396 + 0.291(\text{PERWET}) - 0.039(\text{WSS}) \\ &\quad - 0.084(\log \mathrm{A}_0) \\ &\qquad p < 0.0001, \qquad r^2 = 0.43 \qquad (1)\end{aligned}$$

The final variables tested in this model were A_0, PERWET, WSS, ELEV, SD, and A_d/A_0 to insure low CI numbers and, thus, low collinearity. Perimeter wetlands always entered first in the stepwise regression and were the strongest variable in the model, followed by watershed slope and lake area. Drainage ratio was not a significant variable and did not enter into stepwise models when lake area was excluded. WATWET was not included in the final model because of its strong correlation with PERWET. However, in a post hoc analysis (best model techniques, SAS Institute 2001) only 1% of additional variation was explained by the model when PERWET and WATWET were used as independent variables together or separately in multiple regressions ($r^2 = 0.44$ when WATWET is included in models). In other words, both PERWET and WATWET explained nearly the same amount of variability in lake DOC. Finally, in a backward elimination regression model (all nine variables tested), only PERWET and WATWET remained as significant variables ($r^2 = 0.44$).

Wetlands and their correlation to lake DOC in lakes from the Upper Great Lakes region—Before examining the effect of different kinds of watershed vegetation on lake DOC, the independence of abundance of one type of wetland in the watershed was tested against that of other wetland types. No significant correlations between the proportions of the 12 different wetland types were found (not shown), and we concluded that wetland types were independently distributed among watersheds in the Ottawa National Forest.

PCA of wetland types in the watershed and DOC showed that 14% of the variation was explained by the first axis and 11% by the second axis (Fig. 3A). In general, forested wetlands, especially those with coniferous trees (PFNLE and PFNLD), were positively related to lake DOC, whereas open-water wetlands (including lakes; LLPOW) were inversely related to DOC (Fig. 3A). Scrub-shrub and emergent wetlands (PSSBLD, PSS, PSSNLD, PE) were not related to DOC (Fig. 3A).

In the PCA of perimeter wetland types and DOC, the first axis explained 15% of the variation and the second axis an additional 12% (Fig. 3B). Forested wetlands (PFNLE, PF) around the lake perimeter were again most positively correlated with DOC concentrations, with a negative effect of some scrub-shrub wetland types (PFSS, PSSBLE).

In univariate regression analysis using the four major wetland types in the watersheds (open water, LLPOW; all for-

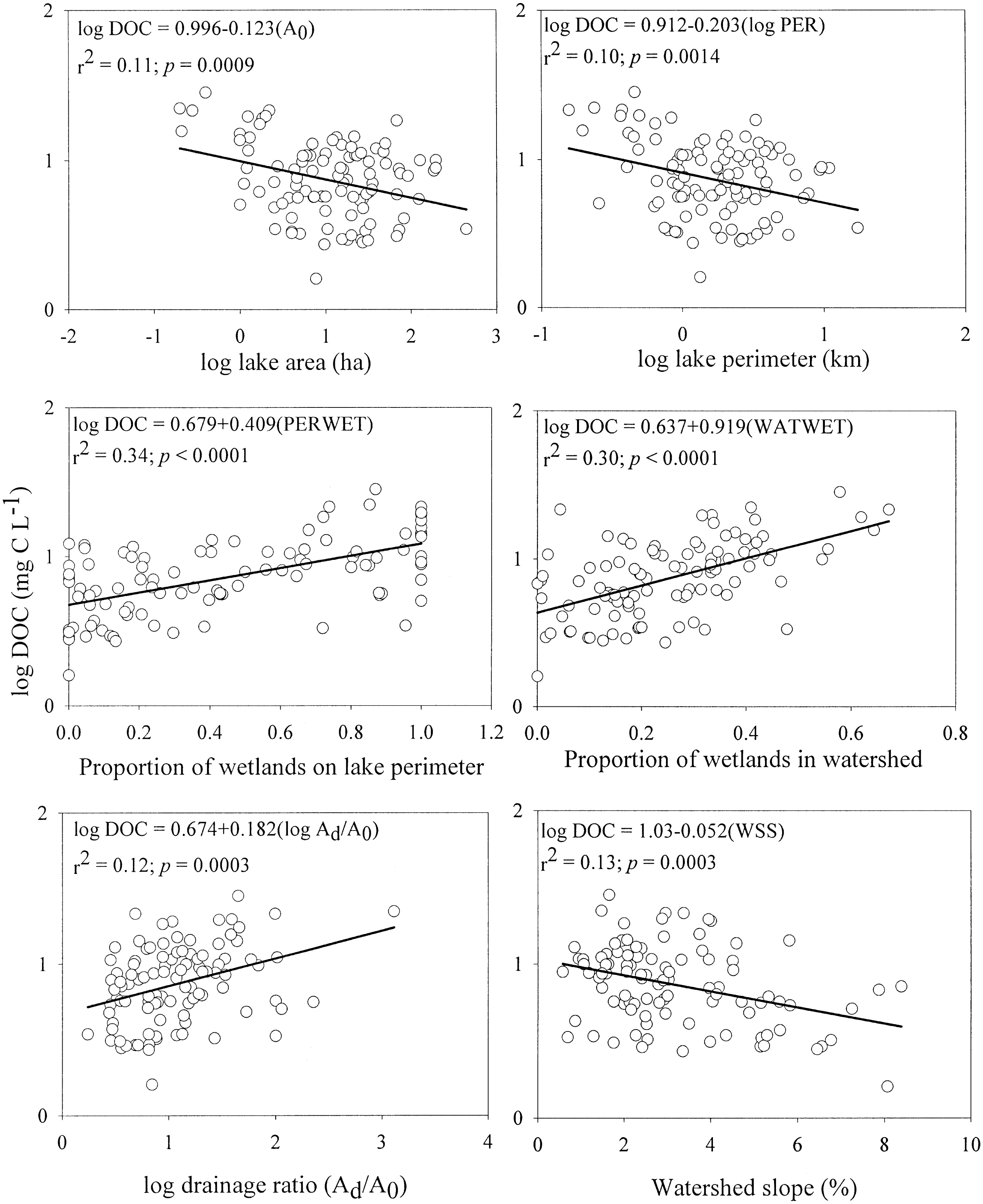

Fig. 2. Relationships between DOC and six catchment characteristics in North Temperate lakes. Not shown are the relationships between DOC and watershed area, elevation, and shoreline development, which were not significant.

Table 4. Univariate coefficient of determination and associated probability for watershed variable relationships with DOC in the different hydrological types.

	Seepage-inlet (n=18)	Seepage (n=43)	Drainage (n=29)	Headwater (n=10)
A_0	NS	r^2=0.40 P<0.0001	NS	NS
A_d	NS	r^2=0.11 P=0.0319	NS	NS
A_d/A_0	NS	r^2=0.29 P=0.0002	NS	NS
PERWET	r^2=0.36 P=0.0090	r^2=0.55 P<0.0001	r^2=0.18 P=0.0211	NS
WATWET	r^2=0.40 P=0.0049	r^2=0.40 P<0.0001	r^2=0.17 P=0.0255	NS
WSS	r^2=0.29 P=0.0215	r^2=0.14 P=0.0189	NS	NS

NS, not significant.

ested, CPF; all scrub-shrub, CPSS; and emergent, PE), all forested, open water, and scrub-shrub significantly explained a proportion of lake DOC variability (Fig. 4). Forested wetlands were positively correlated with DOC, whereas open-water wetlands were negatively related. The proportion of CPSS wetlands in the watershed was also significantly positively related to DOC, but the variation explained by this relationship was very low. The same relationships occurred with the proportion of the different wetland types around the lake perimeter (Fig. 4).

Forward stepwise regression relating DOC and the proportion of each 12 wetland types within the watershed yielded the following model (in order of entry).

$$\begin{aligned}\text{Log DOC} &= 0.736 - 0.0048(\text{LLPOW}) + 0.0104(\text{PFNLE}) \\ &\quad + 0.0292(\text{PF}) + 0.00845(\text{PSSE}) \\ &\quad + 0.0135(\text{PSSNLD}) + 0.0126(\text{PSS}) \\ &\qquad p < 0.0001, \qquad r^2 = 0.44 \qquad (2)\end{aligned}$$

The variation explained by this model is a significant improvement over that with the simple (i.e., undifferentiated by type) proportion of wetlands in the watershed (Fig. 2) and is similar to the multiple regression model above, which used the catchment morphometric variables (Eq. 1).

The proportion of the 12 wetland types, together with the 6 catchment variables versus any additional variation in DOC concentration, showed that 6 variables (from 18) entered the forward stepwise regression, of which the first 5 variables were related to wetlands, and the r^2 increased to 0.57 (in order of entry).

$$\begin{aligned}\text{Log DOC} &= 0.644 + 0.386(\text{PERWET}) + 0.0064(\text{PF}) \\ &\quad + 0.0061(\text{PFNLE}) + 0.790(\text{PFNLD}) \\ &\quad + 0.644(\text{PFBLD}) - 0.064(\log \text{A}_0) \\ &\qquad p < 0.0001, \qquad r^2 = 0.57 \qquad (3)\end{aligned}$$

Only forested wetlands (in particular those with coniferous trees) entered into this model.

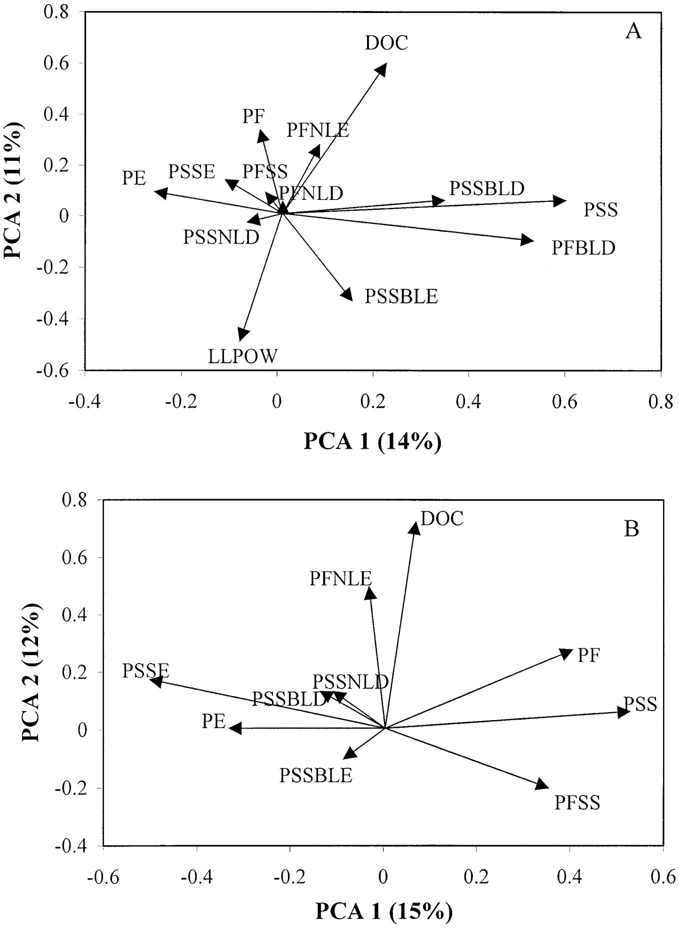

Fig. 3. PCA scores of each wetland type and DOC for (A) within the watershed and (B) around the lake perimeter. Codes are as in Table 1.

Catchment characteristics related to DOC in regions across the globe—Lake DOC concentrations differed considerably among regions globally (Fig. 5). Lakes from high altitude and latitude (Alps, Pyrenees, central U.S. Rockies, and Alaska) had substantially less DOC than those from other geographical areas. The highest DOC concentrations occurred in lakes from the northern Great Plains and boreal plains (Fig. 5).

For this global data set, we examined the relationship of six independent variables (A_0, A_d, WATWET, ELEV, SD, A_d/A_0) to DOC concentration in lakes. In univariate regressions using data from all regions, lake elevation and proportion of wetlands in the watershed explained significant proportions of DOC variation (Fig. 6). Because the Finnish data set from Kortelainen (1993) was much larger than the other global DOC data, a second regression analyses without these data showed no differences existed between results with and without the Finnish data (ANCOVA, $P > 0.05$).

A multiple regression analysis using lakes from all regions yielded a significant model in which WATWET had a positive effect on DOC, whereas SD and ELEV had a negative effect.

$$\begin{aligned}\text{Log DOC} &= 0.61 + 1.092(\text{WATWET}) - 0.202(\text{ELEV}) \\ &\quad - 0.00036(\log \text{SD}) \\ &\qquad p < 0.0001, \qquad r^2 = 0.45 \qquad (4)\end{aligned}$$

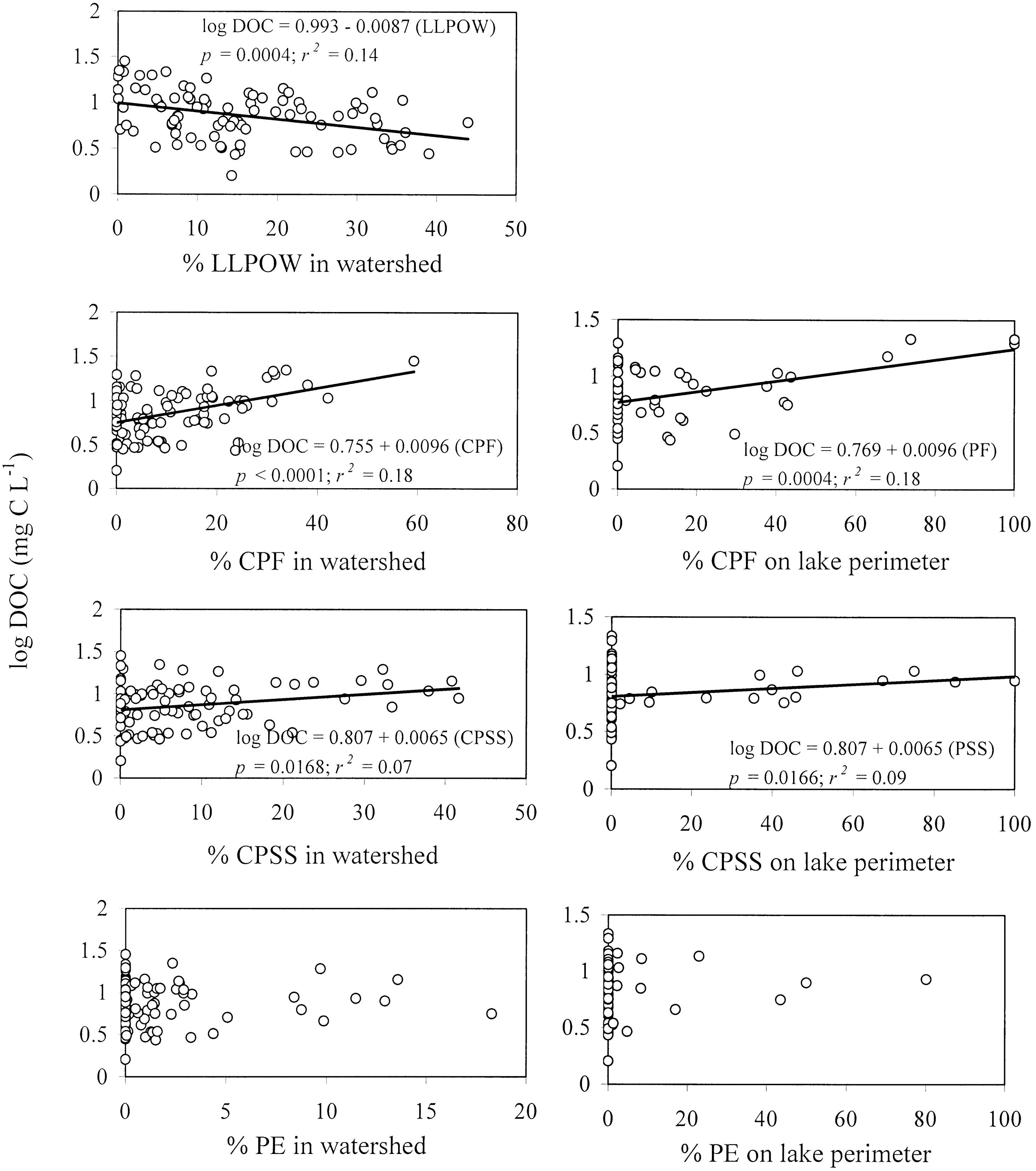

Fig. 4. Relationships between DOC and proportion of major wetland types. On the left are wetlands within the watershed, and on the right are wetlands around the lake perimeter.

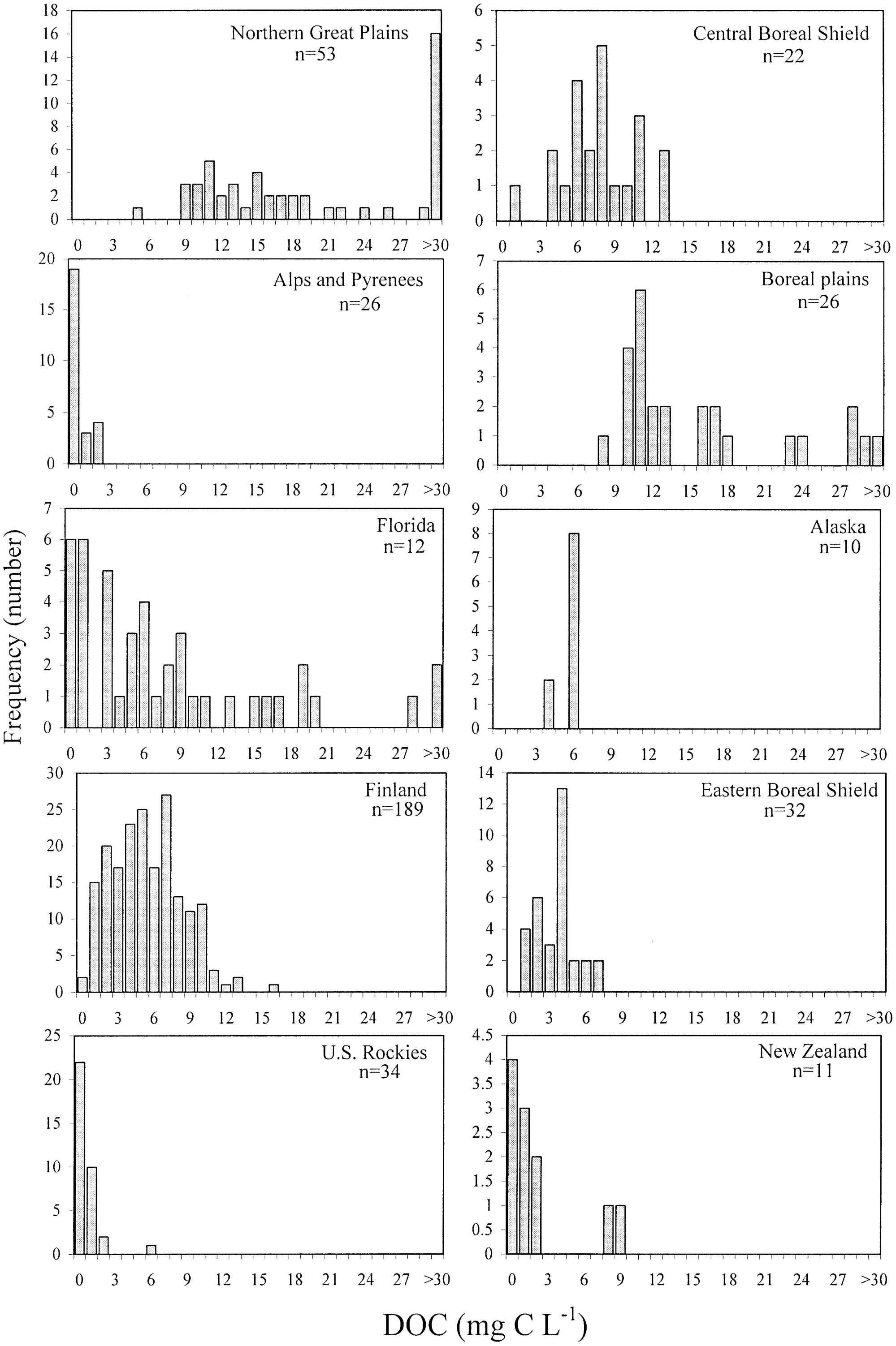

Fig. 5. Global frequency distribution of DOC in 10 geographical regions.

The final variables tested in this model to insure no collinearity was present were A_d, WATWET, ELEV, and SD. In a stepwise forward regression for global DOC, proportion of wetlands in the catchment entered first followed by lake elevation.

Simple univariate linear regression models were used to compare patterns across global regions, and results were reported for parameters in each region (Table 5). Where significant relationships were found, coefficients of determination were low ($r^2 < 0.5$) except for the relationships between lake area, watershed area, and DOC in the central Canadian Shield ($r^2 = 0.65$, 0.57, respectively) and New Zealand (r^2

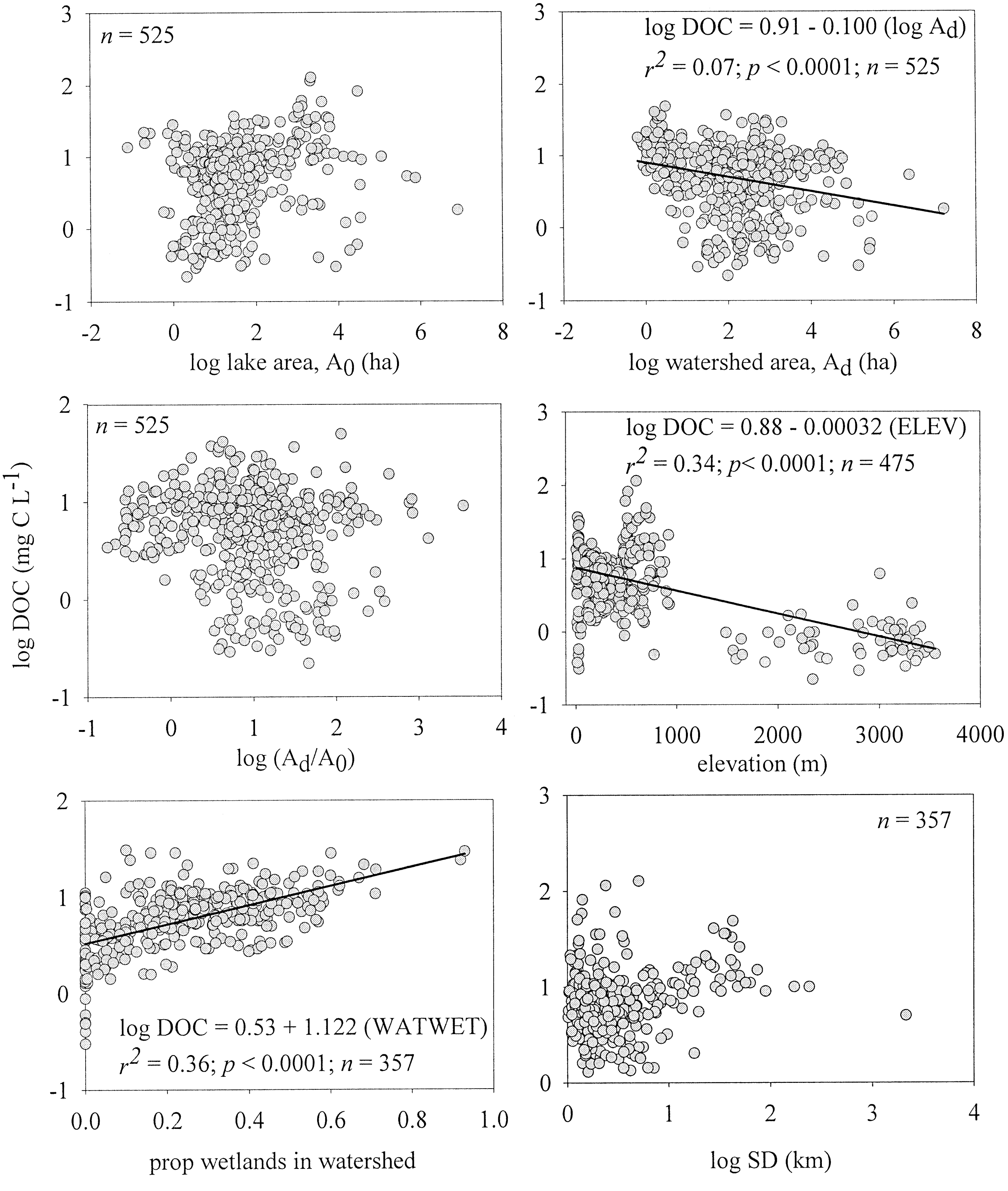

Fig. 6. Global univariate regressions between DOC and six catchment characteristics.

= 0.53, 0.56, respectively). For regions such as Florida, Alaska, the eastern boreal Shield, and the U.S. Rockies, no relationships between DOC and available morphometric variables were found (Table 5). In the Alps and Pyrenees, the DOC was positively related to A_0 ($r^2 = 0.29$), opposite to all other documented DOC and lake area relationships. However, this is a result of the direct relationship between A_0 and elevation ($P < 0.0001$; $r^2 = 0.64$).

Table 5. Summary of relationships between DOC and six catchment variables in 11 geographical regions. Where relationships were significant ($P<0.05$), r^2, P value, and (in parentheses) the direction of the relationship ($+$ = positive, and $-$ = negative) are shown.

	A_0	A_d	A_d/A_0	WATWET	ELEV	SD
North Temperate	$r^2=0.11$ $(-)$ $P=0.0009$	NS	$r^2=0.12$ $(+)$ $P=0.0003$	$r^2=0.30$ $(+)$ $P<0.0001$	NS	NS
Central boreal Shield	$r^2=0.65$ $(-)$ $P<0.0001$	$r^2=0.57$ $(-)$ $p<0.0001$	$r^2=0.38$ $(+)$ $P=0.002$	ND	ND	ND
Eastern boreal Shield	NS	NS	NS	NS	NS	ND
Alaska	NS	NS	NS	ND	NS	ND
Alps and Pyrenees	$r^2=0.29$ $(+)$ $p<0.0001$	$r^2=0.16$ $(+)$ $p=0.0489$	NS	ND	$r^2=0.29$ $(-)$ $P<0.001$	ND
Boreal Plains	NS	NS	NS	$r^2=0.10$ $(+)$ $P=0.0182$	ND	ND
Northern Great Plains	NS	$r^2=0.12$ $(-)$ $P=0.0333$	NS	ND	NS	$r^2=0.42$ $(-)$ $P<0.0001$
New Zealand	$r^2=0.53$ $(-)$ $P<0.0109$	$r^2=0.56$ $(-)$ $p=0.0081$	NS	ND	ND	ND
Florida	NS	NS	NS	ND	NS	ND
U.S. Rockies	NS	NS	NS	ND	NS	ND
Finland	NS	NS	$r^2=0.05$ $(+)$ $P=0.0030$	$r^2=0.48$ $(+)$ $P<0.0001$	$r^2=0.22$ $(-)$ $P<0.0001$	NS

NS, not significant; ND, data not available.

Discussion

Many ecological processes in aquatic ecosystems are tightly linked to terrestrial systems by the flow of water through the environment. Spatial scale was particularly important when examining lake DOC–watershed relationships. At a global scale, lake elevation and the amount of wetlands were the most important predictors of DOC concentration in lakes. However, landscape controls over DOC concentrations varied regionally, with no single catchment variable being significant in all regions.

Wetland control of DOC concentration—Wetlands were the best predictor of DOC in lakes from the Upper Great Lakes region and globally. Given their importance, it is reasonable to assume that wetlands connected to lakes, either directly or by a stream, will contribute more DOC to those lakes than wetlands that are higher up in the watershed with correspondingly weaker hydrological connections to the lakes (e.g., Amoros and Bornette 2002). However, we did not find that this was the case for our study lakes because both PERWET and WATWET explained equal amounts of variation in lake DOC. This result was also found by Gergel et al. (1999) for northern Wisconsin lakes. In the latter study, the area of wetlands within a watershed explained the same amount of variation in lake DOC as wetlands within 25 m of a lake perimeter. We show here that even when wetlands are directly on the lake perimeter, no additional variation in DOC is explained.

Our results suggest that this lack of connectiveness results from differences between wetland types that are found around the lake perimeter and in the watershed (Table 1). Forested wetlands were most strongly positively correlated with lake DOC concentrations but are typically not found around lake perimeters; therefore, wetlands in the watershed explain similar variation in DOC concentration, even though they are not directly hydrologically connected. In fact, open-water wetlands (LLPOW) with the most intimate hydrological contact with lakes were negatively correlated with lake DOC concentrations.

The type of wetland is as important as the total area of wetlands in predicting lake DOC concentrations. In particular, the proportion of forested wetlands, especially those having coniferous vegetation, is positively and significantly related to DOC in Michigan lakes, whereas other types are only weakly related or not related at all. In fact, the model explaining the highest variability between DOC and watershed variables (Eq. 3) was dominated by parameters associated with wetlands, particularly forested and coniferous ones (e.g., PFNLE). Such relationships likely reflect the high rates of humic and fulvic acid production from litter from coniferous vegetation. Coniferous wetland trees in this region are predominantly black spruce (*Picea mariana*), white cedar (*Thuja occidentalis*), and tamarack (*Larix laricina*), with the former two being evergreen and the latter deciduous.

The effect of wetland type on DOC concentrations in lakes might be even stronger than indicated by our analysis because there are distinct limitations to the NWI data that were available to us. For example, sites were typically not classified to sufficient detail to determine whether coniferous, needle-leaved, evergreen forests (PFNLE) were predominantly white cedar or black spruce, despite the fact that the two wetland types have opposite hydrogeomorphic positions in the watershed (cedar swamps are minerotrophic or groundwater fed, whereas black spruce stands are typically ombrotrophic bogs with only precipitation inputs), soil pH and alkalinity, peat depth, carbon quality, decomposability, and presumably DOC production rates (Bridgham et al. 1998, 2001). Many other sites were even more grossly defined as simply forested (PF), and similar difficulties existed in other NWI classifications. Additionally, it was impractical to use all 55 different NWI wetland types that occurred in the Michigan study region, so we had to reduce these to higher order groupings.

Quantification of upland vegetation types also might have improved the predictive capabilities of watershed controls over lake DOC. In forested catchments lacking wetlands, DOC exported into lakes is largely derived from leaf litter and organic matter transported from uplands. Unfortunately, the proportion of the uplands area in the catchment covered by coniferous and hardwood forests was not calculated in the present study; therefore, this possibility could not be assessed. Future work could examine the role that upland vegetation in the catchment plays in the DOC dynamics of lake ecosystems.

Watershed morphometry—DOC was not strongly related to watershed morphometry in northern Michigan lakes. In contrast, Rasmussen et al. (1989) (which included northern Wisconsin) found variability in lake DOC to be explained by catchment morphometry, perhaps because WSS, an important predictor in the Rasmussen et al. (1989) model, acts as a surrogate for the proportion of wetlands in the watershed. Flat terrain or basins with low slopes (thus, low WSS) would be expected to contain more wetlands than watersheds with high relief (Winter 1992; Kortelainen 1993). In fact, watershed slope was negatively correlated with wetlands ($r = -0.45$) in the watersheds that we examined. We also expected the drainage ratio to be an important predictor of DOC (equal to wetlands), as previously shown in boreal Shield lakes and other North American lakes (Schindler 1971; Rasmussen et al. 1989). The poor relationship between DOC and the drainage ratio in our results might not be surprising because others also failed to find a significant relationship between these two variables (e.g., Houle et al. 1995). Engstrom (1987) proposed that only drainage ratio values of $<$6–10 (e.g., small catchment relative to the lake area) should be correlated to DOC. The strong correlation shown in Schindler (1971) was for a lake region where $>$90% of the lakes had a drainage ratio $<$10. In the Michigan lakes, the average drainage ratio was 33, and only 48% of these lakes had a drainage ratio $<$10. The differences in catchment areas relative to lake areas in northern temperate lakes of the Great Lakes region versus Precambrian Shield lakes is also likely a function of watershed slope because low-relief catchments tend to be larger.

Scale matters—When relationships between DOC and catchment-related variables are examined at a global scale, factors such as drainage ratio and lake size are not significant predictors of DOC (despite their importance at smaller regional scales). At this larger scale, the proportion of wetlands in the catchment remains the best predictor of lake DOC, followed closely by lake elevation. Although elevation and wetlands are correlated (lakes higher in elevation contain fewer wetlands in their catchment), lower DOC in high-altitude lakes is also likely a result of less soil development and reduced or altered vegetation (Xenopoulos and Schindler 2001*a*). Nevertheless, regional or small-scale DOC models likely have limited applicability to predict DOC in other geographical areas of the world. Others have also shown that separating lakes regionally improves the predictive power of regression models (Rasmussen et al. 1989; Kortelainen 1993).

This limited applicability is illustrated by comparing the results from lakes in the Upper Great Lakes region with those in the relatively proximate Canadian Shield. There was a stronger correlation between watershed morphometry (A_0, A_d/A_0, etc.) and DOC in Precambrian Shield bedrock–dominated regions than in the North Temperate forests. Large geological differences between the two regions might explain this discrepancy. For one, boreal Shield lakes are nutrient-poor, with a low ratio of catchment to lake area, and are steep and well drained. North Temperate lakes are relatively nutrient-rich, their watersheds have less relief, and they are poorly drained. North Temperate lakes also have more than twice the wetland coverage of the Canadian Shield on average. Similar geological differences between the Canadian Shield, the boreal plains of Florida, and the northern Great Plains were also found. In the Finnish boreal forest, low relief is also characteristic of the region, along with a high proportion of wetlands in the region (Kortelainen 1993). Only New Zealand lakes appear to be similar to Precambrian Shield lakes with respect to the relationships between DOC and lake and watershed areas. The New Zealand lakes are mostly dominated by grasslands and alpine vegetation in their catchment (although some are forested), contain less humic material, and are more transparent. These lakes are found in similarly sloped terrain, with a small proportion of wetlands in their catchment. It is nevertheless surprising that eastern boreal Shield lakes (eastern Quebec; D’Arcy and Carignan 1997) are not related to any of the catchment variables in our analysis and do not fit the usual patterns with catchment area and drainage ratio of the Precambrian Shield lakes in the Experimental Lakes Area (northwestern Ontario). In their analysis, D’Arcy and Carignan (1997) did find a relationship between DOC and catchment slope and total open lake area (the study lake and other lakes in the catchment, equal to LLPOW in Fig. 4). However, these variables were not included in the global data set.

Climate and other factors—The best regression model (Eq. 4) used multiple landscape variables and explained only 57% of the variability in lake DOC. This unexplained variation might be a function of other important factors that alter DOC concentration in lakes that we did not account for. These factors include water residence times (Curtis and Schindler 1997) and anthropogenic factors such as land use, deforestation, climate change, and acid rain (e.g., Schindler et al. 1996*b*). Water residence time is relatively easy to estimate in bedrock lakes, but harder in groundwater-connected lakes. The amount of photo- and biological degradation of DOC depends partly on the amount of time that DOC remains in a lake. Long water residence times, such as those typically found in closed-basin lakes (e.g., saline lakes with residence times over multiple decades), result in greater photobleaching, degradation, or sedimentation of DOC, which reduces its concentration (Curtis and Adams 1995). The residence times in North Temperate lakes were not measured but are shorter (less than ~10 yr). Thus, this factor would likely explain little additional variability in lake DOC.

Drought and acid rain also can affect DOC concentrations in lakes (Schindler et al. 1996*b*). Because DOC depends on water for transport, drought conditions can reduce DOC export from the watershed, change flow paths of DOC through upland soils, and lower DOC concentrations in lakes. In an experimental climate change experiment, DOC export from peatlands was found to depend primarily on the hydrologic flux through the system and not climate-induced changes in DOC concentrations (Pastor et al. 2003). Additionally, DOC export as a function of hydrologic flux was different in a bog and a fen, reinforcing the correlation of type of wetland as a potential determinant of DOC. As for acidification, acid deposition is relatively low in the Upper Peninsula of Michigan (http://nadp.sws.uiuc.edu), and the well-buffered soils would mitigate any acid rain effects.

Lakes within a geographical region are known to exhibit similar physical, chemical, and biological characteristics (to varying degrees; Pace and Cole 2002). The extent that individual lakes diverge from the regional average depends, in part, on processes governing the flux of materials across the landscape. Our results show that although watershed controls over DOC concentrations can often be identified at a regional scale, these controls vary significantly across regions and among different lakes with different hydrological settings within a region. Given the considerable roles that DOC maintains in aquatic systems, identifying the mechanisms that control DOC and how they relate to an ever-changing landscape should be regarded as a high priority in future research.

References

AMOROS, C., AND G. BORNETTE. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. Freshw. Biol. **47:** 761–776.

ARTS, M. T., AND OTHERS. 2000. The attenuation of ultraviolet radiation in high dissolved organic carbon waters of wetlands and lakes on the northern Great Plains. Limnol. Oceanogr. **45:** 292–299.

BELSLEY, D. A., E. KUH, AND R. E. WELSCH. 1980. Regression diagnostics: Identifying influential data and sources of collinearity. Wiley Series in Probability and Mathematical Statistics, John Wiley and Sons.

BRIDGHAM, S. D., K. UPDEGRAFF, AND J. PASTOR. 1998. Carbon, nitrogen, and phosphorus mineralization in northern wetlands. Ecology **79:** 1545–1561.

———, C.-L. PING, J. L. RICHARDSON, AND K. UPDEGRAFF. 2001. Soils of northern peatlands: Histosols and gelisols, p. 343–370. *In* J. L. Richardson and M. J. Vepraskas [eds], Wetland soils: Genesis, hydrology, landscapes, and classification. CRC Press.

COWARDIN, L. M., V. CARTER, F. C. GOLET, AND E. T. LAROE. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Fish and Wildlife Service.

CRONAN, C. S., AND G. R. AIKEN. 1985. Chemistry and transport of soluble humic substances in forested watersheds of the Adirondack Park, New York. Geochim. Cosmochim. Acta **49:** 1697–1705.

CURTIS, P. J., AND H. E. ADAMS. 1995. Dissolved organic matter quantity and quality from freshwater and saline lakes in east central Alberta (Canada). Biogeochemistry **30:** 59–76.

———, AND D. W. SCHINDLER. 1997. Hydrologic control of dissolved organic matter in low-Precambrian Shield lakes. Biogeochemistry **36:** 125–138.

D'ARCY, P., AND R. CARIGNAN. 1997. Influence of catchment topography on water chemistry in southeastern Québec Shield lakes. Can. J. Fish. Aquat. Sci. **54:** 2215–2227.

EILERS, J. M., AND OTHERS. 1986. Western lake survey phase 1. Characteristics of lakes in the Western United States. V 2. Data compendium for selected physical and chemical variables. U.S. Environmental Protection Agency.

ENGSTROM, D. R. 1987. Influence of vegetation and hydrology on the humus budgets of Labrador lakes. Can. J. Fish. Aquat. Sci. **44:** 1306–1314.

FEE, E. J., R. E. HECKY, S. E. M. KASIAN, AND D. R. CRUIKSHANK. 1996. Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield lakes. Limnol. Oceanogr. **41:** 912–920.

GERGEL, S. E., M. G. TURNER, AND T. K. KRATZ. 1999. Dissolved organic carbon as an indicator of the scale of watershed influence on lakes and rivers. Ecol. Appl. **9:** 1377–1390.

HINTON, M. J., S. L. SCHIFF, AND M. C. ENGLISH. 1997. The significance of storms for the concentration and export of dissolved organic carbon from two Precambrian Shield catchments. Biogeochemistry **36:** 147–165.

HOULE, D., R. CARIGNAN, M. LACHANCE, AND J. DUPONT. 1995. Dissolved organic carbon and sulfur in southwestern Québec lakes: Relationships with catchment and lake properties. Limnol. Oceanogr. **40:** 710–717.

JOHNSTON, C. A., AND P. MEYSEMBOURG. 2002. Comparison of the Wisconsin and National wetlands inventory. Wetlands **22:** 386–405.

KANCIRUK, P., J. M. EILERS, R. A. MCCORD, D. H. LANDERS, D. F. BRAKKE, AND R. A. LINTHURST. 1986. Characteristics of lakes in eastern United States. V 3. Data compendium of site characteristics and chemical variables. U.S. Environmental Protection Agency EPA/600/4-86/007c.

KELLY, C. A., E. FEE, P. S. RAMLAL, J. W. M. RUDD, R. H. HESSLEIN, C. ANEMA, AND E. U. SCHINDLER. 2001. Natural variability of carbon dioxide and net eplimnetic production in the surface waters of boreal lakes of different sizes. Limnol. Oceanogr. **46:** 1054–1064.

KLING, G. W., G. W. KIPPHUT, M. M. MILLER, AND W. J. O'BRIEN. 2000. Integration of lakes and streams in a landscape perspective: The importance of material processing on spatial patterns and temporal coherence. Freshw. Biol. **43:** 477–497.

KORTELAINEN, P. 1993. Content of total organic carbon in Finnish lakes and its relationship to catchment characteristics. Can. J. Fish. Aquat. Sci. **50:** 1477–1483.

LAURION, I., M. VENTURA, J. CATALAN, R. PSENNER, AND R. SOMMARUGA. 2000. Attenuation of ultraviolet radiation in mountain lakes: Factors controlling the among- and within-lake variability. Limnol. Oceanogr. **45:** 1274–1288.

MCKNIGHT, D. M., R. L. SMITH, R. A. HARNISH, C. L. MILLER, AND K. E. BENCALA. 1993. Seasonal relationships between planktonic microorganisms and dissolved organic material in an alpine stream. Biogeochemistry **21:** 39–59.

———, R. Harnish, R. L. Wershaw, J. S. Baron, and S. Schiff. 1997. Chemical characteristics of particulate, colloidal, and dissolved organic material in Loch Vale Watershed, Rocky Mountain National Park. Biogeochemistry **36:** 99–124.

Mitchell, P., and E. E. Prepas. 1990. Atlas of Alberta lakes. Univ. of Alberta Press.

Morris, D. P., and others. 1995. The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. Limnol. Oceanogr. **40:** 1381–1391.

Olson, D. M., and others. 2001. Terrestrial ecoregions of the world: A new map of life on earth. Bioscience **51:** 933–938.

Pace, M. L., and J. J. Cole. 2002. Synchronous variation of dissolved organic carbon and color in lakes. Limnol. Oceanogr. **47:** 333–342.

Pastor, J., J. Solin, S. D. Bridgham, K. Updegraff, C. Harth, P. Weishampel, and B. Dewey. 2003. Global warming and the export of dissolved organic carbon from boreal peatlands. Oikos **100:** 380–386.

Prepas, E. E., and others. 2001. Landscape variables influencing nutrients and phytoplankton communities in boreal plain lakes of northern Alberta: A comparison of wetland- and upland-dominated catchments. Can. J. Fish. Aquat. Sci. **58:** 1286–1299.

Rae, R., C. Howard-Williams, I. Hawes, A.-M. Schwarz, and W. F. Vincent. 2001. Penetration of solar ultraviolet radiation into New Zealand lakes: Influence of dissolved organic carbon and catchment vegetation. Limnology **2:** 79–89.

Rasmussen, J. B., L. Godbout, and M. Schallenberg. 1989. The humic content of lake water and its relationship to watershed and lake morphometry. Limnol. Oceanogr. **34:** 1336–1343.

SAS Institute. 2001. SAS version 8.2 for Windows. Statistical Analysis Systems Institute.

Schiff, S. L., R. Aravena, S. E. Trumbore, M. J. Hinton, R. Elgood, and P. J. Dillon. 1997. Export of DOC from forested catchments on the Precambrian Shield of central Ontario: Clues from ^{13}C and ^{14}C. Biogeochemistry **36:** 43–65.

Schindler, D. W. 1971. A hypothesis to explain differences and similarities among lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. **28:** 295–301.

———, and others. 1996*a.* The effects of climatic warming on the properties of boreal lakes and streams at the Experimental Lakes Area, northwestern Ontario. Limnol. Oceanogr. **41:** 1004–1017.

———, P. J. Curtis, B. R. Parker, and M. P. Stainton. 1996*b.* Consequences of climate warming and lake acidification for UV-B penetration in North American boreal lakes. Nature **379:** 705–708.

Sharp, J. H., R. Benner, L. Bennet, C. A. Carlson, R. Dow, and S. E. Fitzwater. 1993. Reevaluation of high-temperature combustion and chemical oxidation measurements of dissolved organic carbon in seawater. Limnol. Oceanogr. **38:** 1774–1782.

Snucins, E., and J. Gunn. 2000. Interannual variation in the thermal structure of clear and coloured lakes. Limnol. Oceanogr. **45:** 1639–1646.

Thurman, E. M. 1985. Organic geochemistry of natural waters. Dr W. Junk Publishers.

WDNR. 1991. A user's guide to the Wisconsin Wetland Inventory. Wisconsin Department of Natural Resources PUBL.-WZ022-92.

Wetzel, R. G. 1983. Limnology, 2nd ed. Saunders College Publishing.

———. 1992. Gradient-dominated ecosystems—sources and regulatory functions of dissolved organic matter in fresh water ecosystems. Hydrobiologia **229:** 181–198.

———, and G. E. Likens. 1991. Limnological analyses, 2nd ed. Springer-Verlag.

Winter, T. C. 1992. A physiographic and climatic framework for hydrologic studies of wetlands, p. 127–148. *In* R. D. Robarts and M. L. Bothwell [eds], Aquatic ecosystems in semi-arid regions: Implications for resource management. Environment Canada.

Xenopoulos, M. A., and D. W. Schindler. 2001*a.* Physical factors determining ultraviolet radiation flux into ecosystems, p. 36–62. *In* C. S. Cockell and A. R. Blaustein [eds], Ecosystems, evolution and ultraviolet radiation. Springer.

———, and ———. 2001*b.* The environmental control of near-surface thermoclines in boreal lakes. Ecosystems **4:** 699–707.

———, Y. T. Prairie, and D. F. Bird. 2000. Influence of ultraviolet-B radiation, stratospheric ozone variability, and thermal stratification on the phytoplankton biomass dynamics in a mesohumic lake. Can. J. Fish. Aquat. Sci. **57:** 600–609.

———, P. C. Frost, and J. J. Elser. 2002. Joint effects of ultraviolet radiation and phosphorus supply on phytoplankton growth rate and elemental composition. Ecology **83:** 423–435.

Received: 4 December 2002
Accepted: 13 May 2003
Amended: 19 June 2003