Small lakes dominate a random sample of regional lake characteristics

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SUMMARY

1. Lakes are a prominent feature of the Northern Highland Lake District (NHLD) of Wisconsin, covering 13% of the landscape. Summarising the physical, chemical, or biological nature of NHLD lakes at a regional scale requires a representative sample of the full size distributions of lakes. In this study, we selected at random 168 lakes from the full size distribution of lakes in the NHLD and sampled each lake for a broad suite of limnological variables.
2. Most lakes were small. The median lake area was 1.1 ha, however, half of the surface area of water was in a relatively small number of lakes larger than 162 ha. Smaller lakes tended to be low in dissolved inorganic carbon (DIC) and high in dissolved organic carbon (DOC). Inclusion of small lakes (<4 ha) in the survey resulted in an acid neutralising capacity (ANC) median (76.5 μEq L^{-1}) much lower than previous estimates, and a DOC median (10.1 mg L^{-1}) about 50% higher than it would have been without the smaller lakes. Unlike DOC, total P tended to be evenly distributed across lake sizes.
3. The implications of these findings are that regional summaries of lake characteristics for the NHLD are influenced by the inclusion of small lakes in the sample, even though most of the water surface area is in lakes larger than 162 ha. Excluding small lakes introduces bias in the estimates of organic carbon and inorganic carbon values, for example. Similar biases may be introduced for lake characteristics at the global scale if small lakes are not sampled, because the size distribution of lakes globally is dominated in number by small lakes.

Keywords: carbon, lake, regional survey, size distribution

Introduction

Small water bodies are abundant (Downing *et al*., 2006) and have disproportionately high hydrologic and nutrient processing rates (Smith *et al*., 2002). The Northern Highland Lake District (NHLD) of northern Wisconsin has more than 7500 lakes, most of which are smaller than 20 ha, coloured with dissolved organic carbon (DOC), and moderately acidic (Black, Andrews & Threinen, 1963). High organic carbon concentrations are associated with important ecosystem processes, such as the regulation of bacterial growth (Del Giorgio, Cole & Cimbleris, 1997), productivity (Jansson *et al*., 2000), and the efflux of carbon dioxide to the atmosphere (Hope, Kratz & Riera, 1996, Riera, Schindler & Kratz, 1999). Although

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most lakes in the NHLD are small, most of the surface area is contained in the larger lakes (Black *et al.*, 1963). Because physical, chemical and biological characteristics of lakes are related to their sizes (Riera *et al.*, 2000; Kalff, 2002), and because the NHLD has a large gradient in lake sizes, characterising the regional limnological conditions requires data from the full size distribution of lakes.

Surveys from the full size distribution of lakes that include a broad range of limnological variables have rarely been conducted. However, an exemplar is the assessment of lake trophic status in the northeastern U.S. (Peterson *et al.*, 1998). In the NHLD, an impressive survey of the region's navigable waters was conducted in the 1960s (Black *et al.*, 1963), but the data included only a few variables and did not include carbon species. Eilers, Brakke & Landers (1988) selected, at random, 153 lakes from northern Wisconsin for a regional acid deposition study, but the minimum lake size selected was 4 ha. Given the difficulty in gaining access to remote lakes of the region, which often are surrounded by private property, it is not surprising that data from small lakes are sparse. Because surface waters are a prominent feature of the NHLD landscape, covering 13% of its surface (Peterson *et al.*, 2003), and because aquatic systems are important sites for material processing in a landscape perspective (Kling *et al.*, 2000), obtaining data from the full distribution of lake sizes is a necessary step in modelling important regional ecosystems processes.

In this study, we conduct the first survey of lakes selected at random from the full size distribution in the NHLD. We describe the distributions of a suite of limnological variables important to the ecology and carbon cycling of lakes, and demonstrate that inclusion of small lakes influences the distributions of most limnological variables.

Methods

Study site

The survey was conducted during the summer of 2004 in the Northern Highland Lake District (NHLD, ca. 5000 km^2) of northern Wisconsin, U.S.A. (Fig. 1). The NHLD's more than 7500 lakes include a variety of hydrological, morphological and trophic regimes (Black *et al.*, 1963). Lakes range in size from small ponds and bogs to large lakes well over 2500 ha in size. Lake depths range from less than one to more than 30 m. The land cover is a mix of deciduous and coniferous forest (62%), wetlands (25%), and lakes (13%). The retreat of the last glaciers ca. 12 000 years ago (Martin, 1932) left glacial till to a depth of about 30 m. The relatively porous nature of the soils promotes groundwater flow, which is an important hydrologic source for many of these low conductivity, moderate alkalinity and low productivity lakes. However, hydrological regimes include perched, seepage and drainage lakes. Precipitation (0.8 m annually; National Atmospheric Deposition Program) is an important water source for lakes in the region.

Lake selection and sampling

Lakes were selected from unique Water Body Identification Codes (WBICs). Linear features and water bodies identified as impoundments or stream openings were identified from maps digitised by the Departments of Natural Resources of Michigan and Wisconsin (1 : 24 000 USGS 7.5′ topographic quadrangles) and were excluded. More than 7500 lakes ranging in size from about 0.01 to over 2800 ha remained in the data set. We used a stratified random survey, an approach consistent with the Environmental Monitoring and Assessment Program (EMAP) guidelines (Larsen *et al.*, 1994) of the U.S. Environ-

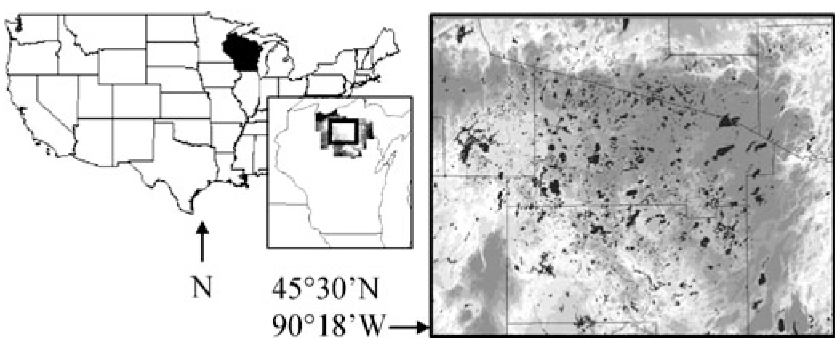

Fig. 1 The Northern Highlands Lake District of Northern Wisconsin.

mental Protection Agency, to select and sample 300 lakes from the data set as follows. All lakes were ordered by area and divided into 20 bins of equal population. From each bin, 15 lakes were chosen at random. Because of logistical issues in travelling to many lakes scattered over a wide geographical region, we clustered lakes into 31 geographically small regions of about 150 km^2 each. The order of regions sampled was randomised to reduce correlation of geographic region with time. For any one sampling date we visited only one region, although not all lakes in a region could be visited on a single trip. After all 31 regions were visited, the regions were again selected at random, and lakes previously not visited were sampled. There were 45 sampling days spread between May 20 and August 19. Some lakes that were chosen for sampling could not be visited. Difficulty portaging the sampling gear to a lake or failure to gain access to a lake through private property were reasons for abandoning a sampling effort.

Lakes were sampled at their approximate geographic centre. Lake depth and water clarity were measured with a Secchi disk. Our measurement of lake depth was neither a measurement of the maximum nor the mean depth. Because the measurement was made in the middle of the lake and most lakes in the region tend to be bowl shaped, our measurement was probably between mean and maximum depth. Dissolved oxygen (DO) and thermal profiles were obtained from a YSI Model 58 (YSI, Inc., Yellow Springs, OH, U.S.A.) metre (DO air calibrated; temperature calibrated in the laboratory), and the approximate middle of the epilimnion was estimated from the profile. Thermal stratification was calculated from the thermal profile according to the methods listed on the Internet at the North Temperate Lakes Long Term Ecological Research (NTL-LTER) program Web site (http://lter.limnology.wisc.edu). Water samples for later analyses (Table 1, chemical variables) were obtained from the middle of the epilimnion, using a peristaltic pump. For samples that required filtration [dissolved inorganic carbon (DIC), DOC, cations and anions], a 0.45 μm filter was attached inline. All samples were refrigerated upon returning to the vehicle, and samples for total nitrogen (TN) and total phosphorus (TP) were preserved by acidification. Acid neutralizing capacity (ANC) and pH were determined the day of sampling by Gran alkalinity titration (for ANC) and measurement by pH probe (Accumet 950; Fisher Scientific, Hanover Park, IL U.S.A.). pH was not air equilibrated. DIC and DOC were measured with a carbon analyzer (TOC-V; Shimadzu Scientific Instruments, Columbia, MD, U.S.A.). TN and TP were measured with a segmented flow auto-analyzer (Astoria-Pacific, Inc., Clackamas, OR, U.S.A.). Anions were measured using an ion chromatograph (DX500; Dionex Corporation, Sunnyvale, CA, U.S.A.), and cations using mass spectrometry (ICP-MS; PerkinElmer Life and Analytical Sciences, Shelton, CT, U.S.A.). Details of chemical analyses are available on the Internet at the NTL-LTER Web site listed above.

Data analyses

To correct for bias introduced by not sampling all 300 lakes, we replaced missing data using multiple imputation (Levy, 1999). Multiple imputation is a technique for estimating the uncertainty of imputed variables. For each variable for each lake not sampled in a given bin, we chose at random (with replacement) a value from lakes sampled in that bin. We repeated the imputation 1000 times to provide a distribution of estimates for each variable in the lakes not sampled. The distribution mean for each variable in each lake was used in the calculation of the median for the regional lake population. We chose to present the median for the 300 lakes because distributions tended to be highly skewed. For comparison purposes, we also calculated the median from sampled lakes only (i.e. excluding imputed data). The mean cumulative distributions for some variables, including 95% confidence intervals, were plotted from the 1000 cumulative distributions generated by multiple imputation.

We fit a Pareto distribution to the regional lake area data set to compare the size distribution of NHLD lakes with those of other regions. We used the maximum likelihood estimator for parameter estimates (Bernardo & Smith, 2000). Of particular interest is the parameter (β) that describes the logarithmic decline in number of lakes with lake area, because this parameter has been used previously (Downing *et al.*, 2006, Table 1) to compare lake area distributions among regions and to estimate the global abundance of lakes.

Where indicated, results have been area weighted to reflect the influence of lake size. For correlations, data were transformed ($\log_{10}$) to normalise distributions and linearise relationships. Shoreline develop-

Table 1. Median values for unweighted and area-weighted variables. Imputed medians were calculated from imputed data, except for lake area and perimeter, which were calculated from the GIS coverage.

Variable	Lake distribution		Area weighted distribution	
	Imputed median	Median of lakes visited	Imputed median	Median of lakes visited
Lake physical variables				
Lake area (m^2)	1.09×10^4	5.36×10^4	–	–
Lake perimeter (m)	488	1.06×10^3	–	–
Secchi (m)	1.43	1.63	3.10	3.18
Depth (m)	3.90	4.00	9.00	9.00
Hypolimnetic depth (m)	–	5.50	–	12.0
Lake chemical variables				
Epilimnetic DO (mg L^{-1})	7.49	7.64	9.27	9.27
Epilimnetic DO saturation (%)	82.9	86.2	92.7	92.7
Metalimnetic DO (mg L^{-1})	4.70	6.11	8.94	8.94
Metalimnetic DO saturation (%)	50.1	66.1	84.9	85.3
Hypolimnetic DO (mg L^{-1})	–	0.50	–	4.50
Hypolimnetic DO saturation (%)	–	4.08	–	40.4
ANC (μEq L^{-1})	76.5	46.0	604	664
pH (non-equilibrated)	5.84	6.26	7.68	7.68
DIC (mg L^{-1})	1.91	1.56	8.12	8.27
DOC (mg L^{-1})	10.1	7.74	3.88	3.82
Total N unfiltered (μg L^{-1})	550	474	384	309
Total P unfiltered (μg L^{-1})	12.9	10.0	9.00	8.00
Cl (mg L^{-1})	0.470	0.350	1.55	1.55
SO_4 (mg L^{-1})	1.29	1.50	2.47	2.54
Ca (mg L^{-1})	1.90	1.46	9.30	10.3
Mg (mg L^{-1})	0.648	0.509	2.68	2.95
Na (mg L^{-1})	0.598	0.488	1.65	2.23
K (mg L^{-1})	0.504	0.464	0.642	0.647
Fe (mg L^{-1})	0.215	0.102	0.020	0.007
Mn (mg L^{-1})	0.025	0.016	0.003	0.003

DO, dissolved oxygen; ANC, acid neutralising capacity; DIC, dissolved inorganic carbon; DOC, dissolved organic carbon.

ment factor (SDF), an index of the irregular shape of lakes, was calculated for each lake according to Kalff (2002). The minimum SDF, 1, indicates a lake is a perfect circle.

Results

Of the 300 lakes chosen, we sampled 168. The 132 lakes not sampled tended to be small with a mean lake area of 8.37 ha (median = 1.20 ha). This shifted the size distribution of lakes visited upward from the regional mean area of 15.0 ha (median = 1.09 ha) to a mean area of 37.3 ha in the sample (median = 5.36 ha) (Table 1). Imputing missing data tended to change median values for most variables in a direction consistent with characteristics of small lakes. For example, median DOC increased from 7.74 to 10.10 mg L^{-1}, whereas median Secchi depth decreased from 1.63 to 1.43 m. Missing data for hypolimnetic depth were not imputed, because relatively few lakes were fully stratified.

Most lakes in the NHLD are small. However, large lakes account for most of the region's water surface area (Fig. 2). Lakes smaller than the median accounted for only 2% of the water surface area in the region. Lakes 20 ha and larger accounted for 90% of the lake surface area for the region, and the largest six lakes sampled, which ranged from 330 to 1170 ha, had half of the surface area. When the Pareto distribution was fit to all lakes in the region, β was estimated to be −0.19. This value was substantially lower than the minimum (−0.66) found in Downing *et al.* (2006). Because the minimum lake area in our study was lower than other surveys, we recalculated β after excluding lakes smaller than 10 ha and obtained an estimate of −0.52. The lower limit was chosen to be consistent with the lower limit of the Eastern Lakes Survey, which had an estimated β of −0.76 (Downing

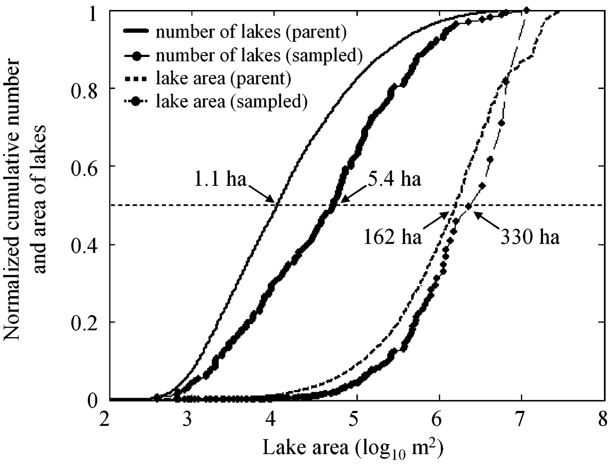

Fig. 2 Cumulative frequency of number of lakes and area of lakes versus lake size in area. Data are plotted for both the parent distribution (parent) obtained from GIS coverages and the sampled distribution (sampled). Median values intersect the horizontal line.

et al., 2006, Table 1), and which included some lakes from the NHLD.

Lakes tended to be irregularly shaped, with large perimeters given their areas. SDF ranged from just over one to 10.9, with a mean of 1.42. SDF tended to increase with lake area. Like area, lake perimeter can be used to weight distributions of variables. Perimeters of lakes less than or equal to the median lake area (5.4 ha) account for 10% of the total perimeters, which is greater than the 2% of total area they represent.

Stratification and DO saturation were related to lake area and depth. Larger, deeper lakes tended to have deeper thermoclines. Of the 168 lakes sampled, 162 had a thermocline, but only 47 had distinct hypolimnia. About 90% of the lakes had undersaturated DO in the epilimnia, and about 75% of the regional epilimnetic surface area was undersaturated (Fig. 3). Although most lakes had lower DO saturation in their metalimnia relative to their epilimnia (Fig. 3b, Table 1), some larger lakes had metalimnetic DO peaks, resulting in a similar proportion (~0.1) of lakes being at or above DO saturation. Most of the hypolimnetic waters were undersaturated (Fig. 3c). However, some larger lakes had supersaturated hypolimnia leading to 20% of the area weighted hypolimnia being at or above DO saturation. DO saturation was also related to sample day, with negative correlations in the epilimnion ($r = -0.22$, $P < 0.01$), metalimnion ($r = -0.31$, $P < 0.001$) and hypolimnion ($r = -0.45$, $P < 0.001$), indicating that lakes sampled later in the summer tended to have lower DO saturation.

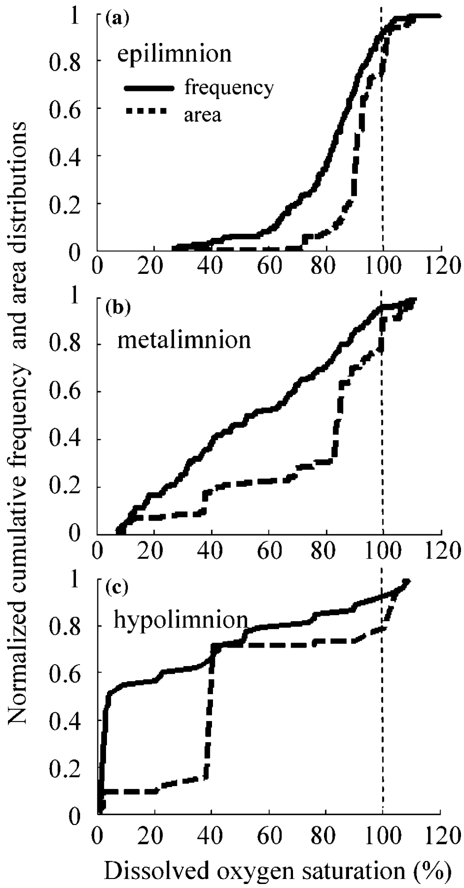

Fig. 3 Cumulative frequency and area distributions for (a) epilimnetic, (b) metalimnetic, and (c) hypolimnetic dissolved oxygen (DO) saturation. Vertical dashed lines indicate saturation points. The line thicknesses are greater than the 95% confidence intervals of imputed data.

Lake chemical characteristics covered broad ranges, and patterns often related to lake area. ANC ranged from zero to 1912 μEq L^{-1}, with the median being 76 μEq L^{-1} (Table 1). Larger lakes tended to have higher ANC (Fig. 4c), and the area weighted median for ANC was 604 μEq L^{-1}. DIC and DOC spanned similar ranges in concentrations and were related to lake area, but in opposite ways. DOC ranged from 0.80 to 32.1 mg L^{-1}, with a median of 10.1 mg L^{-1}. DIC ranged from 0.43 to 26.1 mg L^{-1}, with a median of 1.91 mg L^{-1} (Table 1, Fig. 4a,b). Area weighted DOC (median of 3.88 mg L^{-1}) was lower than unweighted DOC, and area weighted DIC (median of 8.12 mg L^{-1}) was higher than the unweighted DIC.

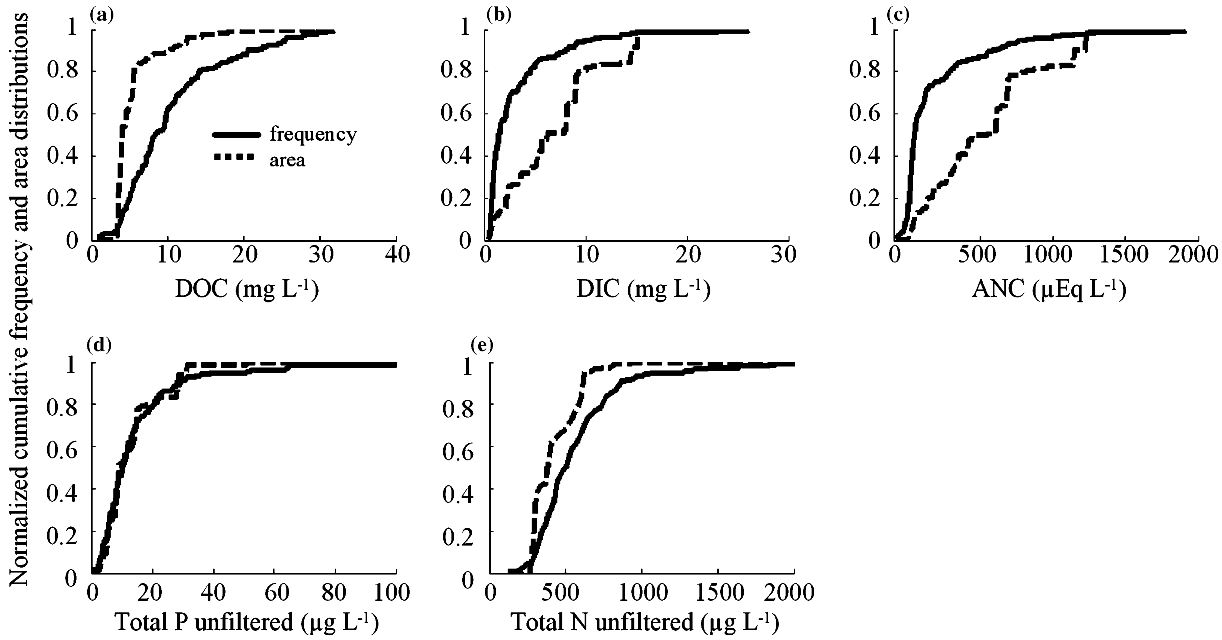

Fig. 4 Cumulative frequency and area distributions for (a) dissolved organic carbon (DOC), (b) dissolved inorganic carbon (DIC), (c) acid neutralising capacity (ANC), (d) total phosphorus, and (e) total nitrogen. The line thicknesses are greater than the 95% confidence intervals of imputed data.

Total phosphorus spanned three orders of magnitude, ranging from 1.0 to 180 μg L^{-1}, although half the lakes were under 13 μg L^{-1}, and only eight lakes were above 50 μg L^{-1}. The median for the unweighted and weighted samples (12.9 and 9.00 μg L^{-1} respectively) indicated slightly lower TP in larger lakes (Fig. 4d). TN also spanned a large gradient, ranging from 124 to 6112 μg L^{-1}. The median values for unweighted and area-weighted samples (550 and 384 μg L^{-1} respectively) indicated that smaller lakes had higher TN (Fig. 4e).

The distribution of cations across lake sizes was similar to that of ANC. Across the full range of lakes, the decreasing rank order of cations (by median concentrations) was Ca, Mg, Na, K, Fe, and Mn (Table 1). Cations other than Fe and Mn tended to have higher concentrations in larger lakes. Area-weighted medians for the two most prevalent anions, SO_4 and Cl (2.47, 1.55 mg L^{-1} respectively), tended to be higher than unweighted medians (1.29 and 0.47 mg L^{-1} respectively), indicating that larger lakes had higher concentrations.

Many variables had positive correlations ($P < 0.05$) with lake area, including pH ($r = 0.72$), Secchi depth ($r = 0.63$), SO_4 ($r = 0.44$), ANC ($r = 0.37$), and Ca ($r = 0.28$). Some variables had negative correlations with lake area, DOC ($r = -0.61$), Fe ($r = -0.33$), TN ($r = -0.47$), and TP ($r = -0.47$). SDF was directly related to lake area ($r = 0.60$) and correlated with variables in ways similar to lake area. For the variables listed above, SDF correlations were generally lower, except for ANC ($r = 0.43$) and Ca ($r = 0.42$). Although lake area is an important correlate of many variables for the region, it explains only part of the variation in lake characteristics. For example not all small lakes are low in ANC and high in colour. For many variables, removing the lake area correlation shows their relationship with other variables. DOC is related to TN ($r = 0.53$), Fe ($r = 0.45$), and SO_4 ($r = -0.23$). TP is correlated with TN ($r = 0.57$) and Fe ($r = 0.43$). ANC is related to cations and DIC as expected, but also to TP ($r = 0.25$) and DOC ($r = -0.12$). DIC is strongly related to ANC and cations, but also to TP ($r = 0.37$), secchi depth ($r = -0.22$) and TN ($r = 0.20$). TN is related to other variables, as mentioned above, and also to SO_4 ($r = -0.25$). Correlation with sample day was tested for variables to see whether lakes sampled later in the season had characteristics differing from those sampled earlier. The correlation with lake area was first removed because the largest six lakes were sampled in the first half of the survey, resulting in a negative correlation

(r = −0.26) between lake area and time. In addition to DO (described above), TP (r = −0.30) and SO_4 (r = −0.19) were significantly correlated with sample day.

Discussion

Lake size is known to be correlated with hydrology, productivity and conductivity (Kalff, 2002). In our study, we found many variables to be correlated with lake area. Had we restricted sampling to larger lakes, our view of the NHLD would be biased toward the clear, low productivity, moderate ANC characteristics of larger lakes. Correcting for sampling bias through imputation changes the results for most variables and emphasises the importance of including small lakes in the regional analysis (Table 1). We illustrate, using ANC, how inclusion of the full distribution of lake areas leads to an interpretation differing from previous studies. A previous survey (Eilers *et al.*, 1988) of lakes larger than 4 ha found ANC to be about 50, 250 and 600 μEq L^{-1} along points of 0.2, 0.4 and 0.8 in the cumulative frequency distribution. In our study, the same points in the distribution had ANC less than half those, with values of 18, 55 and 265 μEq L^{-1} (Fig. 4c). When weighted by lake area, however, the ANC we measured was considerably higher at about 242, 580, and 850 μEq L^{-1} for the same points in the distribution. Previous characterisations of the region as having moderate ANC (Stoddard *et al.*, 1999) may be true when lakes are weighted by area, but the unweighted median ANC (76.5 μEq L^{-1}) is much lower.

Sampling the full size distribution of lakes provides a more complete representation of both inorganic and organic carbon for the region. When only lakes >4 ha are considered, DIC appears to be the dominant carbon form in the region. DIC relates directly with lake area in this study (Fig. 4b), presumably because larger lakes tend to have a larger proportion of their hydrologic load from deep groundwater, and most DIC in non-bog lakes in the region is bicarbonate (HCO_3^-) derived from mineral weathering in groundwater (Magnuson, Kratz & Benson, 2006). In contrast, DOC relates inversely with lake area, and its loading is associated with wetlands in the watershed (Gergel, Turner & Kratz, 1999; Xenopoulos *et al.*, 2003) and aerial inputs from surrounding vegetation (Gasith & Hasler, 1976). The inclusion of smaller lakes in the sample shifts the regional C balance toward higher DOC values. For example, if we had sampled only lakes >4 ha, the median DOC would have been 6.1 mg L^{-1}, a value considerably lower than the median (10.1 mg L^{-1}) for the full distribution. The implications of higher DOC for lake physical and biological processes include shallower surface mixed layers (Snucins & Gunn, 2000), reduced planktonic production and increased planktonic respiration (Del Giorgio & Peters, 1994), and increased ecosystem respiration through mineralisation of allochthonous organic carbon (Hanson *et al.*, 2003).

Small lakes can play an important role in terrestrial organic carbon mineralisation (Hanson *et al.*, 2004) and burial (Einsele, Yan & Hinderer, 2001), and may be particularly important to carbon cycling in the NHLD. The high perimeter to area ratio for smaller lakes results in high contact surface with surrounding vegetation. Coupled with short water residence times and high DOC retention (Curtis & Schindler, 1997), the high carbon load may lead to a condition of elevated carbon mineralisation and net efflux of CO_2 to the atmosphere. Although carbon flux was not measured in this study, the median DOC and TP concentrations (Table 1) were consistent with lakes that are net sources of carbon to the atmosphere (Hanson *et al.*, 2004). Furthermore, most of the lake surface area was undersaturated in DO during the season when productivity and DO saturation are at their highest annual values (Hanson *et al.*, 2006). Undersaturated surface water DO is associated with net heterotrophy in temperate lakes (Prairie, Bird & Cole, 2002) and has been found to be strongly correlated with supersaturated CO_2 concentrations, which are indicative of annual CO_2 evasion in other regions (Kortelainen *et al.*, 2006).

The importance of SDF in explaining variability in other data in this study was difficult to gauge. Because SDF is calculated from both lake area and lake perimeter, it is highly correlated with both, confounding our ability to discriminate its unique contribution to variance in other lake variables. For example, we might expect SDF and DOC to be positively correlated, because aerial input of organic carbon occurs primarily at the lake's shore (Gasith & Hasler, 1976). However, they are negatively correlated (r = −0.34), suggesting that lake area may be masking any SDF relationship due to this mechanism. Lake area tended to be more highly correlated with other variables. Exceptions were SDF's higher correlations with two variables related to groundwater loading, ANC and

Ca. An obvious, though speculative, explanation for this relationship could be that higher SDF equates to higher groundwater loading.

Nutrient stoichiometry tended to depart from the classic Redfield ratios (C : N: $P = 106 : 16 : 1$; Redfield, Ketchum & Richards, 1963). The mean of the DOC:TN ratio was about 18, and the mean of the TN : TP ratio was about 54 across all lakes. The ratios tended to be higher in smaller lakes, because DOC and TN concentrations were higher, whereas TP was more evenly distributed across lake sizes (Fig. 4). While pelagic feedback systems tend to stabilise plankton stoichiometry (Klausmeier *et al*., 2004), terrestrial inputs may drive stoichiometry away from the classic Redfield ratios, and this effect may be stronger in small lakes with higher perimeter : area ratios. The high C : P ratio in allochthonous loads, which is typical of terrigenous vegetation, leads to a condition of heightened heterotrophy in lakes (Hanson *et al*., 2003) without stimulating an increase in aquatic primary or secondary production (Elser *et al*., 2000).

Sampling lakes across their full size distributions in a variety of regions may prove to be important for characterising lakes at the global scale. Recent work by Downing *et al*. (2006) estimated that 99% of the world's lakes are smaller than 10 ha, and that these lakes account for 31% of the total lake surface area. They derived their estimate of the global size distribution from Pareto distributions fit to a number of regional lake surveys. Our estimate of the β parameter for the Pareto distribution was less negative than theirs, suggesting fewer small lakes in the NHLD than would have been predicted by their results. The differences in estimates of the lake size distributions could be due to a number of factors, including our inclusion of very small lakes, our use of maximum likelihood in fitting the parameters, or possibly unique characteristics of lakes in the NHLD, a region not fully represented in their study. Differences aside, both studies emphasise the abundance of small lakes. The characteristics of small lakes in our study are sufficiently different from larger lakes to alter estimates for limnological variables at the regional scale.

Considering that representative surveys of small lakes are rare, estimating lake solute concentrations at a global scale would be problematic. Furthermore, results from this study probably would not generalise well to other regions, because of regional differences in factors controlling lake solutes, such as lake morphometry, watershed characteristics, hydrology, and climate. For example, Xenopoulos *et al.* (2003) found large regional differences in factors controlling lake DOC concentrations, suggesting that DOC models developed for one region are not applicable to other regions. Without further study of small lakes around the world, we are left to speculate on the limnological characteristics of the majority of the world's lakes.

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