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A geomorphic template for the analysis of lake districts applied to the Northern Highland Lake District, Wisconsin, U.S.A.

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SUMMARY

1. We tested the degree to which a lake's landscape position constrains the expression of limnological features and imposes a characteristic spatial pattern in a glacial lake district, the Northern Highland Lake District in north-central Wisconsin.
2. We defined lake order as a metric to analyze the effect of landscape position on limnological features. Lake order, analogous to stream order, is based solely on geographical information and is simple to measure.
3. We examined the strength of the relationship between lake order and a set of 25 variables, which included measures of lake morphometry, water optical properties, major ions, nutrients, biology, and human settlement patterns.
4. Lake order explained a significant fraction of the variance of 21 of the 25 variables tested with ANOVA. The fraction of variance explained varied from 12% (maximum depth) to 56% (calcium concentration). The variables most strongly related to lake order were: measures of lake size and shape, concentrations of major ions (except sulfate) and silica, biological variables (chlorophyll concentration, crayfish abundance, and fish species richness), and human-use variables (density of cottages and resorts). Lake depth, water optical properties, and nutrient concentrations (other than silica) were poorly associated with lake order.
5. Potential explanations for a relationship with lake order differed among variables. In some cases, we could hypothesize a direct link. For example, major ion concentration is a function of groundwater input, which is directly related to lake order. We see these as a direct influence of the geomorphic template left by the retreat of the glacier that led to the formation of this lake district.
6. In other cases, a set of indirect links was hypothesized. For example, the effect of lake order on lake size, water chemistry, and lake connectivity may ultimately explain the relation between lake order and fish species richness. We interpret these relationships as the result of constraints imposed by the geomorphic template on lake development over the last 12 000 years.
7. By identifying relationships between lake characteristics and a measure of landscape position, and by identifying geomorphologic constraints on lake features and lake evolution, our analysis explains an important aspect of the spatial organization of a lake district.

Keywords: constraint, geomorphology, lake, lake district, landscape, legacy, spatial pattern

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Introduction

A lake district is a landscape rich in lakes that share origin, climate and catchment geology. Despite these common traits, lakes within a lake district vary considerably in their physical, chemical and biological characteristics. Understanding the underlying causes of this heterogeneity has been a recurrent theme of regional limnology (Birge & Juday, 1911; Thienemann, 1925; Naumann, 1932; Hutchinson, 1957; Margalef, 1983; Allan & Johnson, 1997). Lake features ranging from internal features such as food web structure and nutrient cycling to morphometry and interaction between a lake and its catchment have been invoked as explanatory factors. Major ion chemistry, for example, is best predicted by hydrogeochemical models of ion weathering and transport in the catchment (Likens, 1985). Water chemistry, nutrient concentrations and food–web interactions (Harris, 1986) best explain phytoplankton biomass and composition. Finally, fish species richness and composition are best explained by multiple variables including extinction and isolation (Tonn & Magnuson, 1982; Rahel, 1986; Tonn *et al*., 1990; Magnuson *et al*., 1998b).

Efforts to select the best predictors and to identify proximate causes, however, have tended to obscure the spatial linkages among lakes in the landscape and have thus hampered a landscape perspective on lake districts. Here we propose a new perspective on regional limnology that explicitly takes into account spatial patterning in lake districts. We elaborate on the concept of landscape position as developed by Kratz & Medland (1989); Webster *et al*., (1996); Kratz *et al*., (1997) and Magnuson & Kratz (2000). These papers provide a set of observations and a conceptual framework for evaluating how lakes interact with neighbouring lakes, with the hydrology of the region, and with the terrestrial landscape. A key premise of this concept is that a lake's position relative to other features of the landscape constrains the expression of a wide range of limnological properties and processes. Kratz *et al*. (1997) discuss several examples of the relationship between landscape position and properties ranging from lake morphometry to fish richness. Webster *et al*. (1996) discuss how landscape position influences the response of a lake's water chemistry to drought episodes. The wide range of variables that were found to be related to landscape position in those analyses suggests that the geomorphologic configuration of this landscape by glacial forces over 10 000 years ago has imposed constraints which have yielded spatial patterning in lake characteristics across the landscape.

From the analysis of past work, we derive two major conclusions. First, we conclude that lake features in a lake district are not randomly distributed in space, but reflect a spatial pattern. Choosing an appropriate metric describing the spatial location of the lake, i.e. its position in the landscape, can help describe this pattern. Kratz *et al*. (1997), for example, found that the position of a lake within the groundwater flow system was a useful descriptor of landscape position (i.e. a descriptor that revealed spatial patterning) in the Northern Highland Lake District. We posit that each lake district displays a characteristic spatial organization, and that different metrics of landscape position can reveal different aspects of this spatial pattern within a lake district, or among lake districts (e.g. Soranno *et al*., 1999)

Second, we conclude that disparate lake features, apparently unrelated to each other, are nonetheless related to a lake's landscape position. For example, Kratz *et al*. (1997) found that lake area, water specific conductance, and fish species richness all increased with landscape position, with landscape position defined by the location of lakes within the local groundwater flow system. More generally, regional limnological studies often find a large degree of redundancy among variables (e.g. Riera *et al*., 1992), with significant correlation among apparently unrelated properties. We hypothesize that this redundancy is brought about by landscape constraints on lake features.

The purpose of our analysis here is two-fold. To begin, we expand on the analysis of lake landscape position in the Northern Highland Lake District. Landscape position was defined in previous studies as the position of a lake in the groundwater flow system. Because this property is difficult to measure, those analyses were restricted to a small number of lakes. We expand on previous studies by analyzing relationships between lake position and limnological properties in a large set of lakes in the same region. To do this, we first define lake order, a new metric of landscape position that is related to stream order and is easy to measure using only geographic information. We then test the presence and strength of relationships between limnological properties and lake order. The limnological properties we analyzed are compiled from published surveys and include morphological variables, variables related to water optical properties, major ions, nutrients, biological variables, and human-use variables.

Finally, we provide refinements to the theoretical framework elaborated by Kratz *et al*. (1997) and Magnuson & Kratz (2000). We posit that the spatial organization of a lake district is the result of the historical processes that led to the formation of the lake district. We view this influence of historical geomorphologic processes on present-day lake characteristics as a legacy of the past. In our study landscape, it was the retreat of the glaciers that left an imprint, a *geomorphic template*, on the landscape that directly determined lake morphometry and, through the development of hydrologic flowpaths, landscape position. Furthermore, we allege that the relationships observed between disparate lake features and metrics of landscape position were not just directly conditioned by the geomorphic template but, perhaps more importantly, were the result of the constraints imposed by that template on the process of lake ontogeny since the time of the formation of the lake district.

Methods

Study area

The Northern Highland Lake District, situated in north-central Wisconsin and the Upper Peninsula of Michigan, contains more than 2500 lakes in an area of $\approx 3500\ km^2$. In the present landscape, which was formed 10 000–13 000 years ago during the Wisconsin glaciation, 30–50 m of sandy, noncalcareous glacial outwash overlie granitic Precambrian bedrock (Okwueze, 1983; Attig, 1984). Elevation ranges from 470 to ≈ 550 meters above sea level. Despite the generally low relief, an uplands region is in the north-east, and lowlands are in the south. The north-west has lower relief and extensive wetlands. The lake district is high in elevation relative to the rest of Wisconsin. It is the headwaters for several large rivers that flow to the Mississippi River, and several small streams that flow north to Lake Superior.

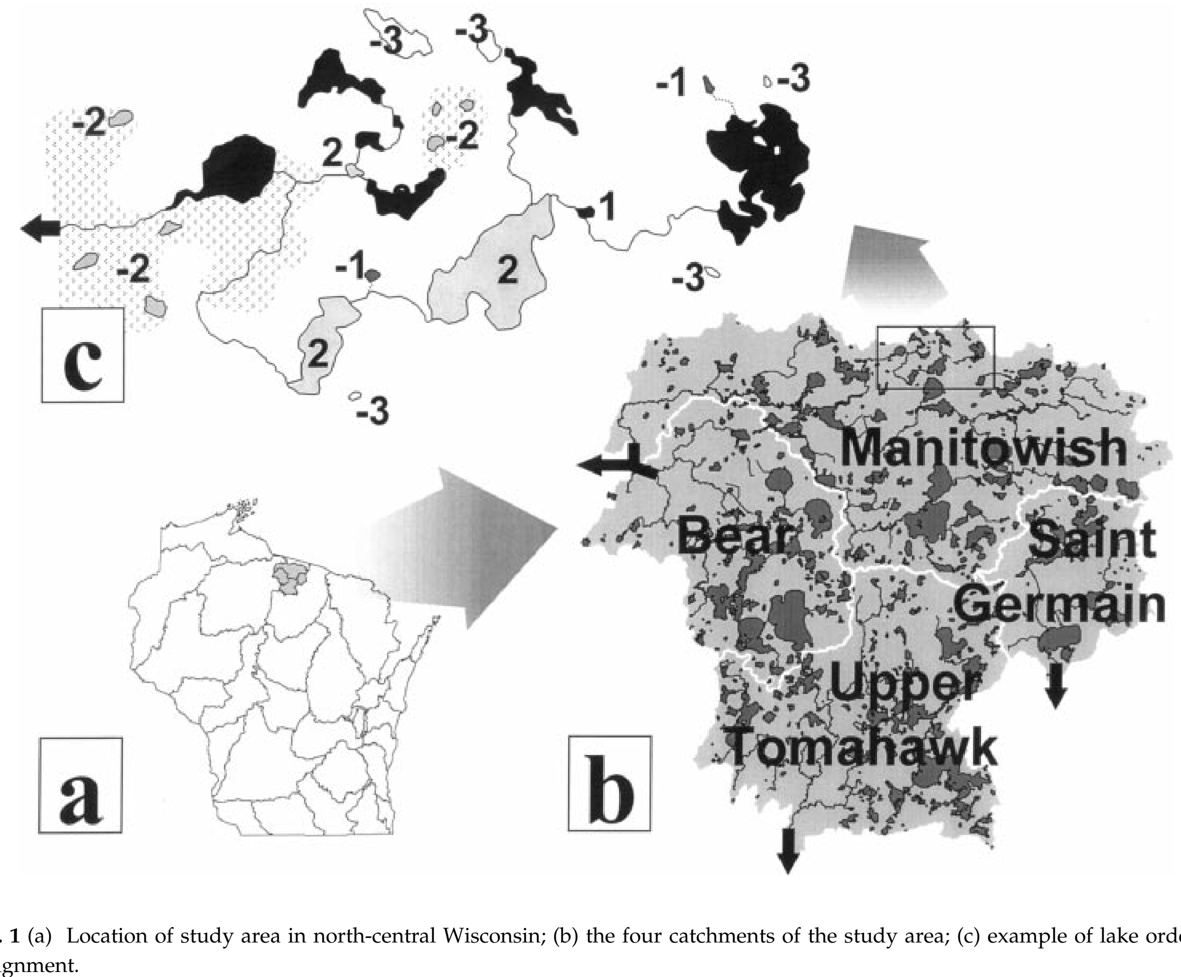

Fig. 1 (a) Location of study area in north-central Wisconsin; (b) the four catchments of the study area; (c) example of lake order assignment.

We selected four major catchments for analysis (Fig. 1a). The Manitowish and Bear catchments drain into the Chippewa-Flambeau River system, which flows south-west to the Mississippi. The Lower Tomahawk and Saint Germain catchments are drained by the Wisconsin River, which flows south to the Mississippi River. Altogether, these four catchments are 1741 km^2 in area and contain over 550 lakes constituting 216 km^2 or 15% of the area (Fig. 1b). These four catchments are centered around the Trout Lake Station, which has been the base facility for numerous lake surveys, including those carried out by E. A. Birge and C. Juday from 1924 through 1941 (Beckel, 1987) and by the North Temperate Lakes Long-term Ecological Research program (Magnuson *et al.*, 1998a). Limnological research in this region spans most of the century, making this lake district one of the best studied in the world (Beckel 1987).

The strong linkage between many limnological properties and lake hydrology in this region has been recognized since the pioneering work of Birge, Juday, and collaborators (e.g. Juday & Birge, 1933). More recently, Eilers *et al.* (1983) concluded that chemical susceptibility to lake acidification in 275 lakes in north-central Wisconsin was determined most strongly by hydrology, that is, whether a lake's water budget was dominated by direct precipitation, groundwater flow, or surface runoff. More generally, groundwater input has been recognized as a good predictor of major ion chemistry (Hurley *et al.*, 1985; Kenoyer & Anderson, 1989; Michaels, 1995), because the flowpaths of groundwater allow weathering of the sparingly soluble glacial outwash that dominate the geology of this region (Kenoyer & Bowser, 1992a, 1992b). In contrast, precipitation and surface runoff supply more dilute water. The proportion of groundwater input to a lake depends on its position in the landscape. Lakes that are high in the landscape tend to be precipitation-dominated lakes that recharge aquifers, whereas lakes lower in the landscape tend to be in closer contact with aquifers and are either groundwater flow-through lakes or lakes that receive groundwater discharge (Anderson & Munter, 1981; Cheng & Anderson, 1994).

Lake order

Our definition of lake order is based on the type and strength of the connections between a lake and the surface drainage network. We used a numbering system to clearly differentiate those lakes without permanent inlets or outlets (seepage lakes, negative lake order), from those having inlets and outlets (drainage lakes, positive lake order). For lakes with both surface inlets and outlet, lake order was defined as the order of the stream that drains the lake. Stream order was measured following Strahler (1964) using 1 : 100 000 scale maps (Wisconsin Department of Natural Resources, 1994). Thus, a lake whose outlet was a stream of order 3 would be assigned a lake order of 3, whether its inlets were of order 3 and below, or two or more inlets were of order 2. Likewise, a lake drained by an order 1 stream would be assigned a lake order of 1. Headwater lakes (i.e. lakes with no inlets but with a surface outlet), were differentiated from order 1 lakes and assigned lake order 0. Headwater lakes tend to be spring-fed and to have smaller catchment areas than order 1 lakes.

Lakes without any permanent drainage by streams were assigned negative lake orders. Lakes connected to the surface drainage network only by temporary streams or streams of very low flow were assigned lake order – 1. These were operationally identified as streams marked as temporary on 1 : 24 000 USGS (U.S. Geologic Survey) topographic sheets, or as streams that were displayed on 1 : 24 000 scale maps, but not on 1 : 100 000 scale maps. Lake order – 2 was assigned to lakes connected to the drainage system by a wetland where channelized flow was absent. Finally, lake order – 3 was assigned to closed-basin lakes hydrologically unconnected to the drainage network by surface water.

Just like stream order, lake order is sensitive to map scale and accuracy. The use of smaller scale maps could have resulted in a slightly different lake order assignment.

Data sources

We tested the following published data for a relationship with lake position: lake morphometry, geographic position, optical properties, major dissolved ions, major nutrients, biological variables, and human variables. Table 1 summarizes data sources and provides references to methods. Variables selected for this study are in Table 2, together with descriptive statistics and data sources.

Table 1 Description of data sets. The acronym is used to identify each data set in Table 2

Data set	Acronym	Comments	References
USGS 1 : 24 000 topographic maps	TOPO	Mostly 1981; some quads from early 1970s	U.S. Geological Survey
GIS hydrography coverage	HYDRO	Produced by Wisconsin Department of Natural Resources (WDNR); based on 1 : 100 000 maps	Wisconsin Department of Natural Resources (1994)
Wisconsin Department of Natural Resources	WDNR	Lake morphometry data produced by WDNR	Wisconsin Department of Natural Resources (1995)
Birge and Juday Data Set	BJ	Data collected 1920–41. Lakes sampled once during summer, some lakes sampled more than one year	Johnson (1984)
Surface Water Resources	SWR	Survey conducted between 1963 and 1969 by the Wisconsin Conservation Department (Wisconsin Department of Natural Resources) for statewide lake inventory. Lakes sampled once. All named lakes and numerous unnamed lakes sampled	Andrews & Threinen (1966, 1970) Black *et al.* (1963)
Eastern Lake Survey	ELS	Data collected for acid rain sensitivity study; lakes sampled once in autumn	Overton *et al.* (1986)
EPA Environmental Research Laboratory in Duluth and University of Minnesota at Duluth	ERLD	Chemical surveys of over 275 lakes in Wisconsin conducted between 1979 and 1982 for evaluation of trophic state and sensitivity to acid deposition	Eilers *et al.* (1983); Glass & Sorenson (1994)
Capelli & Magnuson (1983)	CM	Survey (1982) of crayfish species and abundance in north-central Wisconsin	Capelli & Magnuson (1983)
Fish community analysis study	FISH	A series of surveys (1978–81) of fish species presence–absence in north-central Wisconsin	Rahel (1984, 1986), Tonn & Magnuson (1982)

Table 2 List of variables used in this study, with descriptive statistics and data sources (see Table 1 for meaning of acronyms)

Variable	Units	*N*	Min	Max	Mean	SD	Data sources
Lake location							
Lake elevation	m.a.s.l.*	556	457	538	493	10.5	TOPO
Total catchment area	ha	314	26	63450	2190	9070	SWR
Lake morphometry							
Lake area (*A*)	ha	556	0.3	1568	46.7	140.1	HYDRO
Lake perimeter (*P*)	m	556	201	49927	2767	4512	HYDRO
SDF†	Unitless	556	1.01	4.21	1.39	0.45	Calculated from HYDRO
Maximum depth	m	314	0.3	35.1	8.8	5.2	WDNR
Mean depth	m	59	1.8	15	5.6	2.6	WDNR
Variables related to water optical properties							
Secchi depth	m	268	0.6	10.1	3.4	1.6	BJ, ELS, SWR
Turbidity	NTU	70	0	7	1.0	1.3	ERLD
Water color	PCU	213	0	192.5	27.7	27.6	BJ, ELS
DOC‡	mg L^{-1}	70	1.9	12.5	5.2	2.3	ELS, LTER
Major ions							
Conductivity	μS cm^{-1}	365	6	250	42.1	35.8	BJ, ELS, SWR, ERLD
pH	– log(mol H L–1)	396	4.3	8.5	6.6	0.8	BJ, ELS, SWR, ERLD
ANC§	μeq L^{-1}	386	10	2420	345.9	363.4	BJ, ELS, ERLD
Calcium	mg L^{-1}	190	0.13	21.68	5.08	4.63	BJ, ELS, SWR, ERLD
Magnesium	mg L^{-1}	173	0.09	9.22	2.11	1.72	BJ, ELS, ERLD
Chloride	mg L^{-1}	97	0.15	5.19	0.86	1.05	ELS, ERLD
Sulfate	mg L^{-1}	102	0.61	6.56	3.08	0.95	ELS, ERLD
Nutrients							
Total phosphorus	μg L^{-1}	92	2	62	16	11	ELS, ERLD
Kjeldahl nitrogen	μg L^{-1}	160	150	940	400	130	BJ, ERLD
Dissolved silica	mg SiO_2 L^{-1}	181	0	15.9	2.1	2.7	BJ
Biological variables							
Chlorophyll *a*	mg L^{-1}	78	0.70	33.3	5.04	5.80	ERLD
Dry weight of plankton	mg L^{-1}	196	0.40	5.51	1.26	0.75	BJ
Crayfish abundance	No. males/trap	50	0	36.9	4.70	7.25	CM
Fish richness	No. species	66	0	33	9.4	8.4	FISH
Human-use variables							
Density of cottages¶	No. per km shoreline	179	0	12.40	1.75	2.35	SWR
Density of resorts¶	No. per km shoreline	179	0	2.49	0.29	0.44	SWR

*m.a.s.l., meters above sea level.
†shoreline development factor, calculated as **SDF=P/[2√(πA)]**, where *P* is lake perimeter, and *A* is lake area.
‡Dissolved Organic Carbon.
§Acid Neutralizing Capacity.
¶Cottages are small housing units, or cabins, commonly used as second residence or rented to tourists. Resorts are large tourism complexes. We collated these data for a subset of the entire lakes set, selecting lakes randomly and stratifying based on lake order. Calculating the number of cottages or resorts per kilometer of shoreline controlled for the effect of shoreline length.

For many variables, we combined data from multiple sources (Table 1). Where values for a given lake were available in two or more data sets, an average was used in the analysis. Variables common to multiple data sets were scrutinized using 1 : 1 plots to ensure the quality of our aggregated data set. We pooled and averaged variables only if their correlation was greater that 0.7 and the slope from a geometric regression was between 0.8 and 1.2.

When variables from different data sets were incongruous, only the 'better' data set (usually the more recent) was used. The 'better' data set was selected based on an evaluation of sampling and analytical methodology (precision, accuracy, and reported detection limit) and on the comprehensiveness of the data sets. Data sets spanned more than 60 years, and some lakes may have changed. Where this was suspected (notably, the concentration of chloride; Bowser, 1992), only the most recent data were used. Once the data sources for each variable were selected, pairwise scatterplots were used to detect outliers; these were excluded from further analyses.

Statistical analyses

To quantify the strength of the relationship between each variable and lake order, we used three analytical devices. First, we inspected relations with lake order on box-and-whisker plots and symmetrical dot plots. Box-and-whisker plots give a visual representation of the distribution properties of a sample based on nonparametric measures of central tendency, dispersion, and skewness. Symmetrical dot plots represent the distribution of data points using all cases. Together, these plots give information about the number of cases in each lake order category and their statistical distribution, as well as about the presence, strength, and shape of the relationship between the variable and lake order (Jacoby, 1997). Second, we tested for differences among lake orders using one-way analysis of variance (ANOVA) with lake order as a categorical variable. Finally, if an ANOVA suggested that lake orders differed significantly, we used multiple means comparisons with the Bonferroni correction to test for differences among individual lake orders.

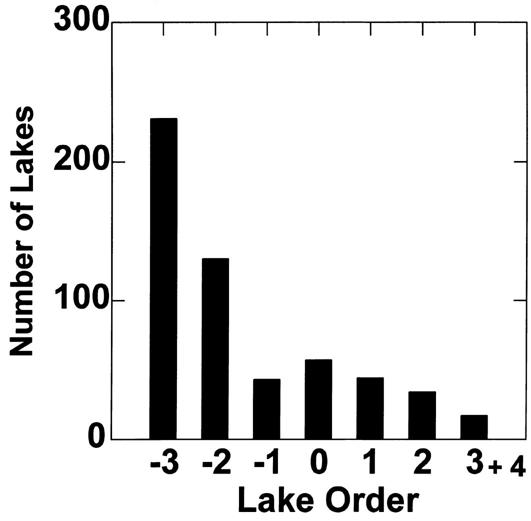

Fig. 2 Distribution of lakes by lake order.

We decided not to use linear regression analysis because lake order, the predictor variable, is not continuous, but ordinal. In addition, inspection of plots revealed that not all relationships were linear.

Results

Lake order compared to other measures of landscape position

Because lake order is based on position along a drainage network, the number of lakes in each class decreased as order increased (Fig. 2). Out of 556 lakes, 231 lakes (42%) were isolated, closed-basin lakes (lake order – 3), whereas there were only 11 lakes of order 3 and six of order 4. Because of the small number of order 4 lakes, we merged them with order 3 for all further analysis.

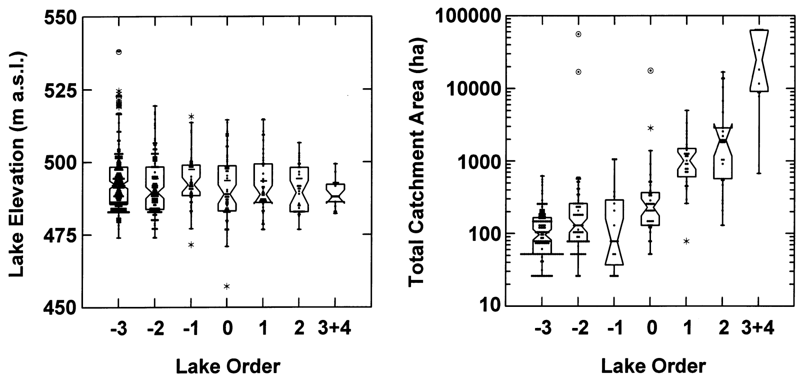

Fig. 3 Box plots for lake elevation (in meters above sea level), and total catchment area vs. lake order.

We found that lake order was associated to some extent with two other metrics of landscape position. Lake elevation ranged from 457 to 538 m above sea level. Lake order was unrelated to lake elevation, except that lakes at a high elevation tended to be of order – 3 (Fig. 3a). Total catchment area increased sharply with lake order, but only for drainage lakes of order 0 or greater. Lakes of lower order consistently had small catchments (Fig. 3b).

Lake features and lake order

Of the 25 lake variables, only four (DOC, sulfate, total phosphorus, and dry weight of plankton) did not differ significantly among lake orders. One variable (crayfish abundance) was marginally significant ($P = 0.06$) and the rest differed significantly based on one-way ANOVA (Table 3). Among the variables with a significant ANOVA, the percentage of the

Table 3 Results of analysis of variance. Unless otherwise noted, all models are one-way ANOVA to test for differences among lake order classes

Variable	Transformation	*N*	MSE	R^2	*P*-value
(a) Morphometric variables					
Lake area	log	556	0.38	0.24	< 0.0001
Lake perimeter	log	556	0.14	0.27	< 0.0001
SDF*	log	556	0.01	0.26	< 0.0001
Maximum depth	None	205	33.87	0.12	< 0.0001
Mean depth	None	114	4.97	0.17	0.002
(b) Variables related to water optical properties					
Secchi depth	None	268	2.20	0.12	< 0.0001
Turbidity	log	70	0.03	0.29	< 0.0001
Water color	log	213	0.19	0.16	< 0.0001
DOC†)	log	70	0.03	0.16	0.09
(c) Major ions					
Conductivity	log	365	0.06	0.54	< 0.0001
pH	None	396	0.46	0.36	< 0.0001
ANC‡)	log	386	0.14	0.50	< 0.0001
Calcium	log	190	0.11	0.57	< 0.0001
Magnesium	log	173	0.08	0.51	< 0.0001
Chloride	log	97	0.12	0.35	< 0.0001
Sulfate	None	102	0.90	0.06	0.4
(d) Nutrients					
Total phosphorus	log	92	0.07	0.07	0.42
Kjeldahl nitrogen	None	160	0.15	0.15	0.0003
Dissolved silica	log(x + 0.05)	181	0.19	0.46	< 0.0001
(e) Biological variables					
Chlorophyll *a*§	log	78	0.12	0.28	0.0002
Chlorophyll *a*¶	log	76	0.10	0.37	< 0.0001
Dry weight of plankton	log	196	0.05	0.04	0,22
Crayfish abundance	log (x + 1)	50	0.20	0.23	0.06
Fish richness	sqr (x + 0.5)	66	1.12	0.41	< 0.0001
(f) Human-use variables					
Density of cottages	None	179	4.9	0.14	0.0002
Density of resorts	None	179	0.15	0.25	< 0.0001

*Shoreline development factor.
†Dissolved organic carbon.
‡Acid neutralizing capacity.
§Including all data.
¶Excluding two outliers of lake order 2.

variance accounted for by lake order (as measured by R^2) varied from 12% (maximum depth), to 56% (calcium concentration).

ANOVA tests are sensitive to small differences among classes (especially in our highly unbalanced models), tend to have low *P*-values when the degrees of freedom are high, and do not provide information about the presence or absence of a trend with lake order. Observation of a trend with lake order would increase our confidence that lake order is related systematically to a variable. Below, we discuss the relations between each group of variables and lake order taking into account the visual inspection of graphs and multiple mean comparisons among lake orders (Figs 4–10).

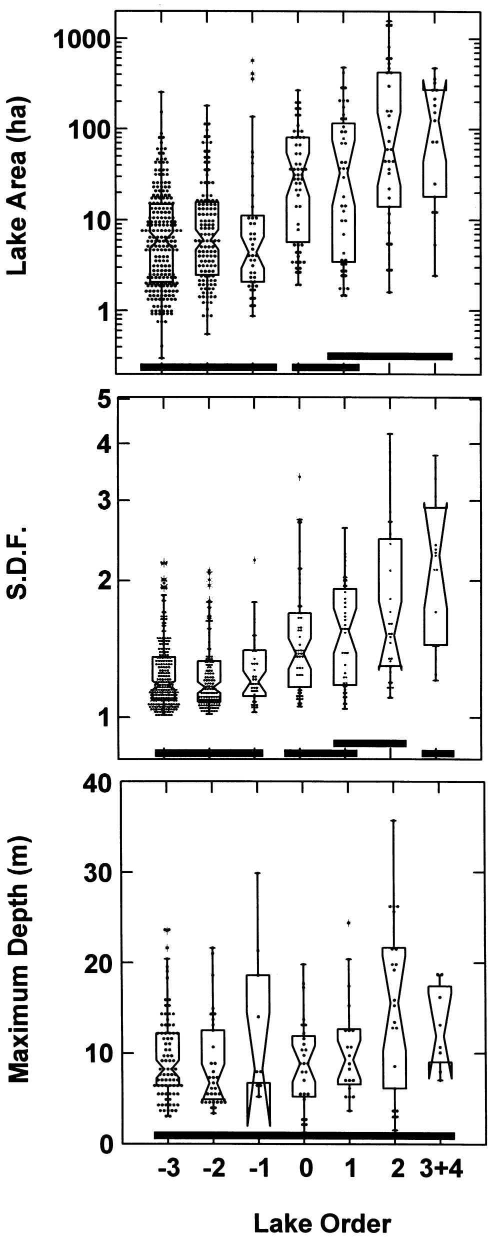

Fig. 4 Box plots for lake area, shoreline development factor (SDF), and maximum depth vs. lake order. Thick lines at the base of each graph group lake orders not significantly different according to multiple means comparison tests.

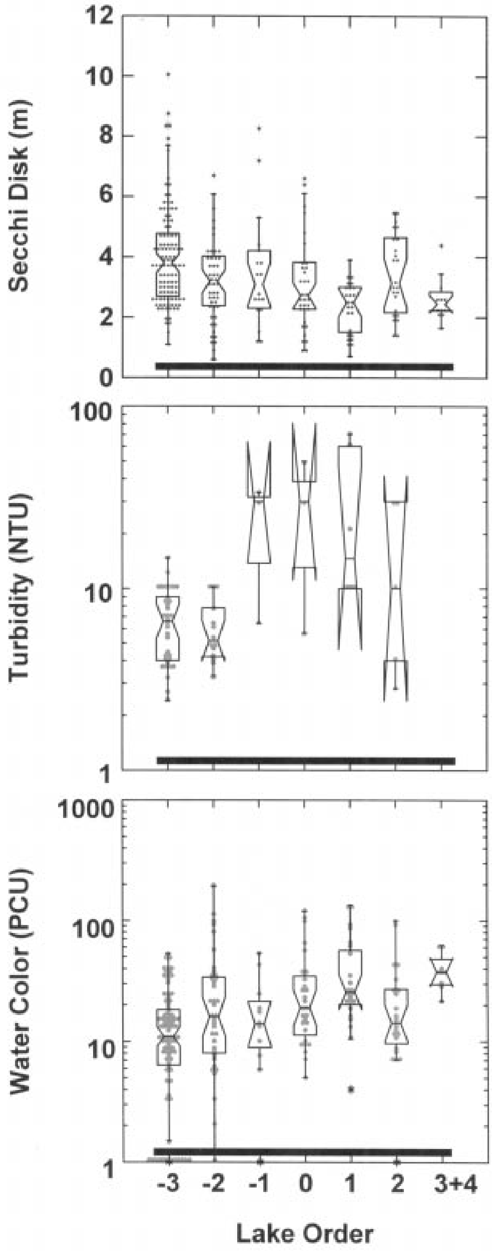

Fig. 5 Box plots for Secchi disk depth, water turbidity, and water color vs. lake order. Thick lines at the base of each graph group lake orders not significantly different according to multiple means comparison tests.

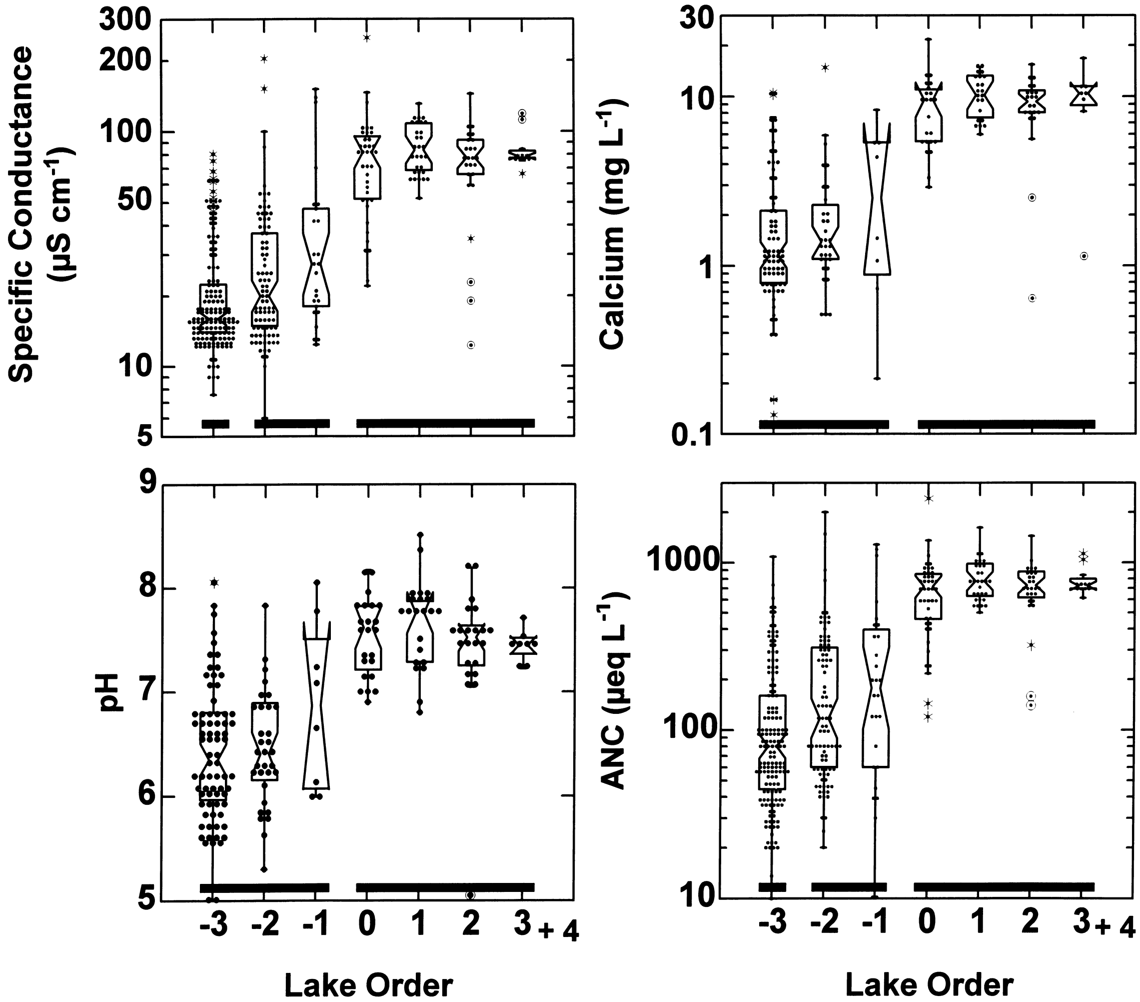

Fig. 6 Box plots for specific conductance, calcium concentration, pH, and Acid Neutralizing Capacity (ANC) vs. lake order. Thick lines at the base of each graph group lake orders not significantly different according to multiple means comparison tests.

Lake area (Fig. 4a), shoreline length, and the shoreline development factor (Fig. 4b) increased with lake order. Lakes high in the landscape tended to be numerous, small, and circular in shape, while lowland lakes were less common, large, and tended to have convoluted shorelines. Both maximum depth (Fig. 4c) and mean depth (not shown) differed significantly among lake orders (ANOVA, Table 3), with a slight tendency to increase with lake order (Fig. 4), but multiple mean comparisons detected no significant differences. In this district, lake depth is limited by the 30 meter thickness of the layer of glacial sediments over bedrock.

Optical properties of water were weakly related to lake order. Secchi depth, turbidity, and water color differed significantly among orders (Table 3), but differences among orders were small (Fig. 5), and multiple means comparison tests did not detect significant differences for any pairing. Nonetheless, Secchi depth, turbidity and water color changed in directions that were consistent with each other, i.e. water color and turbidity increased, and Secchi depth decreased with lake order. DOC, which influences water color and, thus, clarity, did not differ significantly with lake order (Table 3).

Water chemistry variables were strongly related to lake order. Specific conductance, pH, acid neutralizing capacity (ANC), and the concentrations of calcium and magnesium (Fig. 6 and Table 3) increased markedly with lake order. Differences were highest between seepage lakes (classes – 3, – 2 and – 1) and drainage lakes (classes 0 and higher).

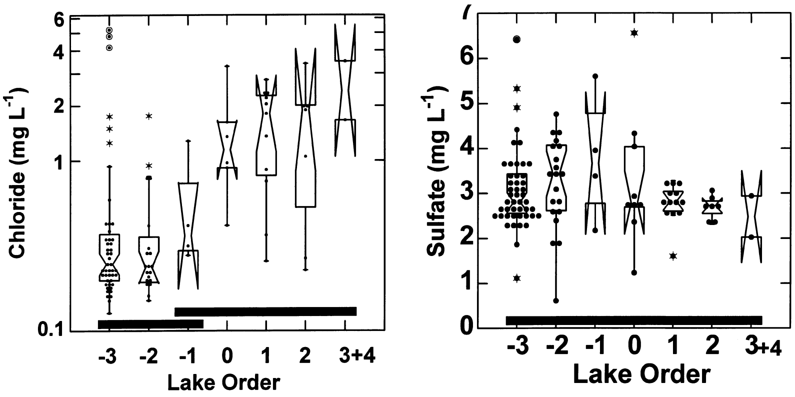

Fig. 7 Box plots for chloride concentration, and sulfate concentration vs. lake order. Thick lines at the base of each graph group lake orders not significantly different according to multiple means comparison tests.

These properties tended to increase with lake order for seepage lakes, but not among drainage lakes. Several studies point to the controlling influence of weathering reactions and groundwater transport for these chemical species. Groundwater is much more concentrated in dissolved ions than precipitation and surface runoff water (Hurley *et al.*, 1985; Kenoyer & Anderson, 1989).

For the major anions, sulfate was unrelated to lake order, while chloride patterns were similar to the weathering variables (Fig. 7). Weathering of salts is unlikely to be a significant source of chloride in this area; however, road salting in the winter was significant enough to increase the concentration of chloride in some lakes during the last two decades (Bowser, 1992). If proximity to roads were related to lake order, then a positive relation between chloride and lake order would be expected. Our data, while consistent with this explanation, are not adequate to determine the mechanism. It suggests an example of how the physical and social landscape interact to affect lake characteristics in relation to position in the landscape.

Among nutrients, only silica presents a clear relationship with lake order (Fig. 8). Like calcium, magnesium and carbonates, silica concentrations are directly associated with weathering reactions and thus groundwater inputs to lakes (Hurley *et al.*, 1985). By contrast, phosphorus and nitrogen concentrations are typically low in groundwater, and catchment sources are likely low as well in this predominantly forested region. Atmospheric inputs are a major source of nitrogen (Wentz *et al.*, 1995) and may also be significant for phosphorus, as they are in other nutrient poor areas (Cole *et al.*, 1990). Thus, a larger catchment area should mean larger inputs, and we therefore expected a positive relationship between phosphorus and nitrogen concentrations and lake order. Uptake processes in the catchment and in-lake processes, however, could induce considerable variability into the relationship.

Even though we expected biological variables would be farther removed from geomorphologic constraints compared to morphometric, physical and chemical variables, three out of four biological variables analyzed were related to lake order (Fig. 9). Only dry weight of plankton, measured by Birge and Juday (by evaporation and loss on ignition), showed no relation to lake order. This variable is at best a crude estimate of plankton biomass (both phytoplankton and zooplankton), and is probably closer to organic seston, which includes dead particulate organic matter. In contrast, chlorophyll *a* concentration increased with lake order, even though data were sparser and included two outliers (two lakes of order 2 with extremely low chlorophyll). Crayfish abundance and fish richness were strongly related to lake order.

Land and water use by humans is superimposed on and interacts with the natural landscape. We included two human-use variables in our analysis to explore whether the influence of a lake's landscape position extended to influence the social landscape. Both the number of resorts per unit shoreline and cottages per unit shoreline increased with lake order (Fig. 10). A similar relationship is evident for the number of boats in lakes (Reed-Anderson *et al.* 2000). Lakes low in the landscape are better suited for recreational activities:

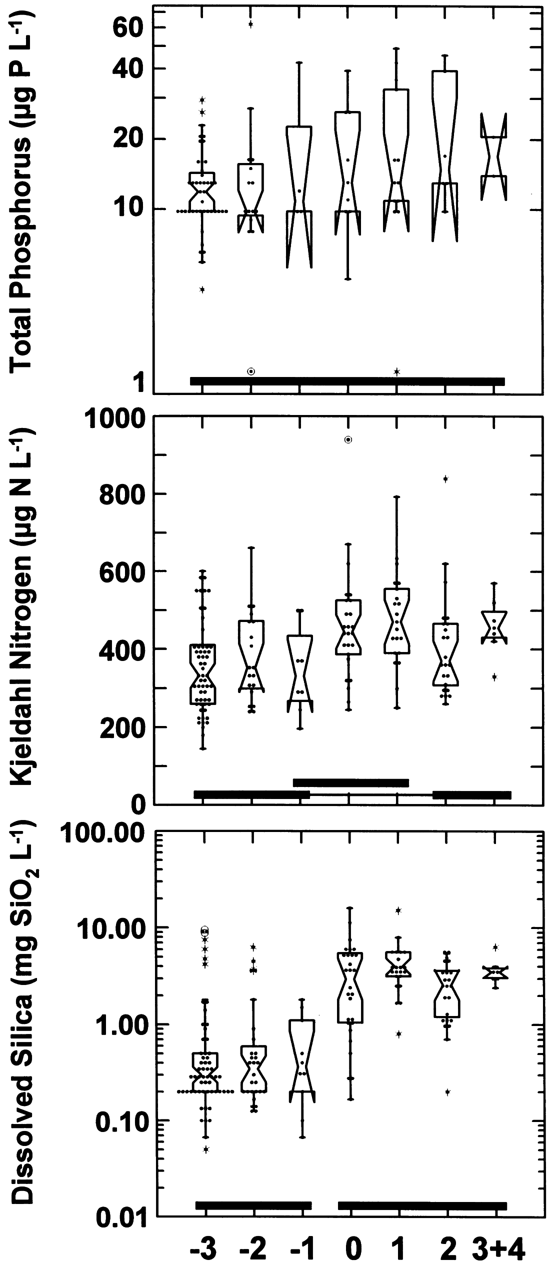

Fig. 8 Box plots for total phosphorus, Kjeldahl nitrogen, and dissolved silica vs. lake order. Thick lines at the bottom of each graph group lake orders not significantly different according to multiple means comparison tests. Thin lines linking two thick lines indicate noncontiguous lake orders that are not significantly different.

they tend to be more accessible, larger, more productive, and offer better fishing. In contrast, lakes high in the landscape tend to be smaller, less accessible, and are often stained and offer poorer fishing.

Discussion

Our purpose has been to determine the extent to which lake districts are spatially organized with repeatable patterns among lakes. Despite the simplicity of lake order as a measure of a lake's landscape position, it explained variability in several disparate variables in this analysis. Of 25 lake variables examined, 21 differed significantly among lake orders based on ANOVA tests. When we used a more stringent test (i.e. multiple mean comparisons), the number of variables that showed differences among lake orders decreased to 13. Yet among these 13 variables were lake properties as disparate as lake area, fish richness, and cottage density around lakes. This speaks strongly in support of our hypothesis that landscape position should be related to a broad array of lake properties. Since lake order is a spatial property, our analysis reveals the presence of spatial organization in the Northern Highland Lake District.

Lake order as a measure of landscape position

Lake order is a useful measure of a lake's landscape position. It is simple, easy to measure from maps, and provides a proxy for mechanisms that are of importance to physical, chemical and biological features of lakes in our study area: hydrologic inputs through groundwater, terrestrial inputs through surface waters, and connections among lakes via surface streams.

Lake order is related to the proportion of groundwater input in a lake's water budget. High order lakes, those that are low in the drainage network, tend to receive a larger proportion of groundwater than low order lakes. This is because groundwater flow tends to follow surface water drainage (Coates, 1990; Brown, 1995), although this relationship is probably scale-dependent and breaks down at small scales (e.g. Hunt *et al.*, 1998), and because in this headwater region streams tend to discharge groundwater. Thus, groundwater input to lakes and lake landscape position are positively related (Cheng & Anderson, 1994; Michaels, 1995; Kratz *et al.*, 1997). Since the concentration of certain ions (i.e. calcium, magnesium, carbonates and silica) is a direct function of groundwater input (Hurley *et al.*, 1985; Kenoyer & Anderson, 1989; Michaels, 1995), the concentration of those ions should increase with lake order, as is the case (Figs 6 and 8c).

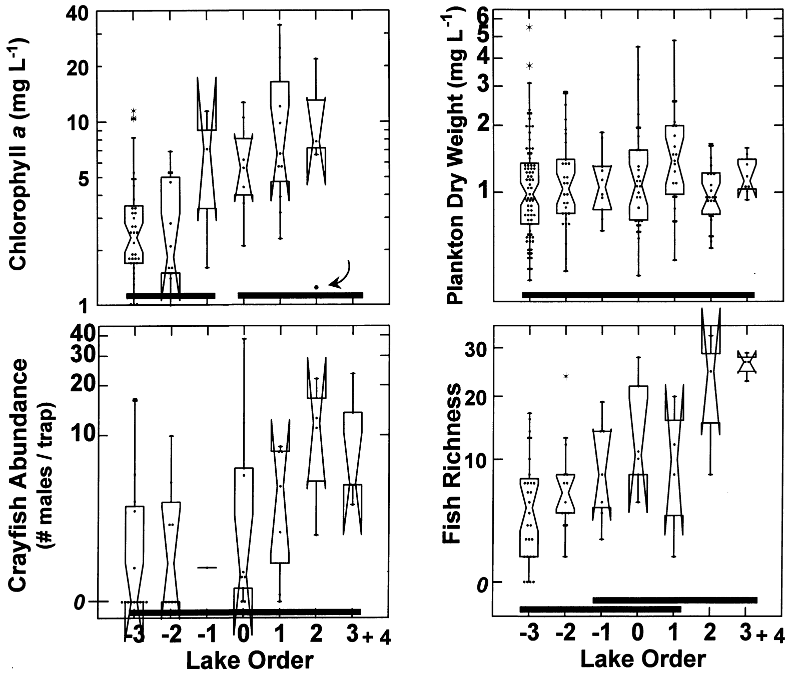

Fig. 9 Box plots for chlorophyll *a* concentration, plankton dry weight, crayfish abundance, and fish species richness vs. lake order. Thick lines at the base of each graph group lake orders not significantly different according to multiple means comparison tests.

Lake order is related to total catchment area (Fig. 3) and to the catchment to lake area ratio. These are measures of the significance of terrestrial inputs to lakes, which increase with stream order (Vanotte *et al.*, 1980) and hence with lake order for drainage lakes.

Finally, lake order is a proxy for lake connectivity through surface water, a property of biogeographic significance. Colonization via surface waters from downstream sources decreases from order 3 + 4 lakes to isolated order – 3 lakes.

We compared lake order to two other metrics of landscape position that could serve as alternatives to lake order: lake elevation and total catchment area. Lake elevation was not related to lake order (ANOVA $R^2 = 0.02$, $n = 556$, $P = 0.16$), and was a poor predictor of lake features in this lake district. For example, fish species richness was related more

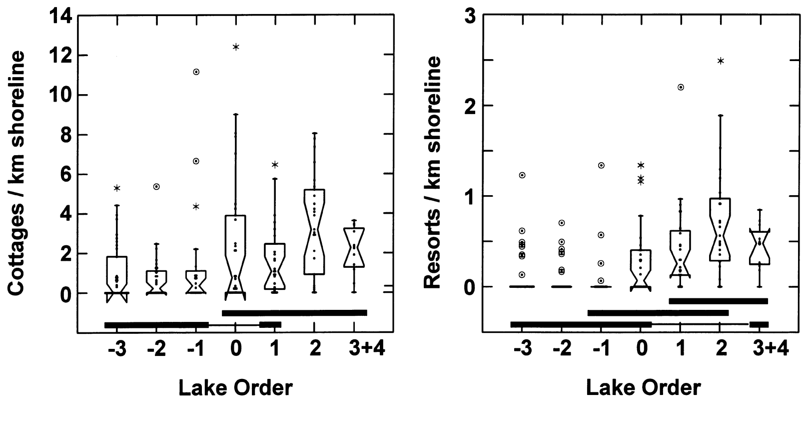

Fig. 10 Box plots for density of cottages, and density of resorts vs. lake order. Thick lines at the bottom of each graph group lake orders not significantly different according to multiple means comparison tests. Thin lines linking two thick lines indicate noncontiguous lake orders that are not significantly different.

strongly to lake order ($R^2 = 0.38$, $n = 66$, $P < 0.001$) than to elevation ($R^2 = 0.12$, $n = 66$, $P = 0.04$). Furthermore, the lack or loss of explanatory power from elevation was apparent even when we performed separate regressions for each catchment. The contrast between strong relationships of lake characteristics with lake order and weak relationships with elevation suggests that the relative, not the absolute, landscape position of lakes is important, and that this relationship operates at a spatial scale smaller than the entire lake district.

Total catchment area has been used frequently in regional limnology as an indicator of terrestrial inputs to lakes. In our analysis it was related strongly to lake order, plus it has the advantage of being a continuous variable. Why then use lake order? We think lake order is conceptually superior in the context of our question. Lake order reflects the geomorphology and the legacy of the geomorphic template and constrained processes that structured the landscape and the characteristics of the lakes, including their catchment area. Thus, total catchment area can be considered an attribute constrained by landscape position. Moreover, connectivity between lakes is conceptually related to lake order, but unrelated to total catchment area. The merit of the concept of landscape position lies as much in its heuristic value as in its predictive power.

Lake order and the legacy of the last glaciation

We argued in the introduction that the spatial pattern of a lake district originated in the geomorphologic processes that generates a landscape. In the case of the Northern Highland Lake District, the origin of the landscape can be traced back to the end of the Wisconsin glaciation, about 13 000 years ago. Some of the features we investigated (i.e. morphometric features) can be directly linked to those processes. Others (e.g. biological variables) were strongly related to lake order not through a single and direct causal link, but through a multivariate set of causal variables linking the property of interest to lake position. Still other features were unrelated to lake order; they may still reveal spatial patterning, but it is unrelated to the particular geographic metric that we chose for this analysis. In the following discussion, we provide examples of all three cases.

Direct links, the influence of the geomorphic template

We observed that, as one moves down the landscape, lakes were more likely to be larger and to have a more complex shape. This pattern probably reflects the geomorphologic processes that formed the lake district. During the retreat of the Wisconsin glaciation, blocks of ice detached from the glaciers and melted to form numerous small, isolated circular lakes. Large lakes, in contrast, were formed when the incipient surface drainage system filled end moraines, or when two or more simple basins coalesced to form a larger lake, perhaps because of increases in lake level occasioned by larger discharge of groundwater or surface inputs. In both cases, larger lakes would tend to be more complex in shape and to be part of the surface drainage system. Thus geomorphology acted as a constraint, favoring the formation of one type of lake over another depending on its location in the landscape. Still, there are large variations in size and shape within each lake order. In low elevation, low relief areas covered by extensive wetlands, such as the north-west section of our study area, some seepage lakes are large, although still nearly circular in shape. Conversely, some lakes low in the drainage system are small, with relatively large streams flowing through them.

Indirect links, the legacy of the geomorphic template

Three of the four biological variables we evaluated were related to lake order, but explaining these relationships requires invoking intervening explanatory variables. Consider the case of the concentration of chlorophyll. In our data set, chlorophyll is best predicted by the concentrations of total phosphorus and silica ($R^2 = 0.61$, $n = 58$, $P < 0.001$; ERLD data). The concentration of silica is clearly related to lake order. If lake order is introduced as a covariate in an ANCOVA model, the most terse model includes lake order and total phosphorus ($R^2 = 0.65$, $n = 65$, $P < 0.001$). Other factors that might affect chlorophyll concentrations, such as lake area, mean depth or water renewal time, are also related to lake order. Thus, environmental constraints on chlorophyll concentration can be traced back to a lake's position in the landscape.

Similar arguments can be used to explain the stronger relationships between lake order and crayfish abundance and fish species richness. Crayfish abundance in this lake district is best predicted by calcium concentration, the quality of the littoral substrate, and lake size (Capelli & Magnuson, 1983; Lodge *et al*., 1998). Calcium is necessary for growth and structure, and lakes with a calcium concentration below ≈ 4 mg/L do not sustain crayfish populations. The quality of the bottom substrate is another important habitat requirement. Silt and muck, common in seepage lakes, are not suitable for crayfish, whereas cobbles and pebbles are most suitable (Capelli & Magnuson, 1983). Lake size is important because larger lakes are more likely to provide patches of suitable habitat. All three variables (calcium concentration, bottom materials, and lake size) are related to lake order, explaining its relationship with crayfish abundance. Analogous explanations account for the relationship between fish species richness and lake order. Fish species richness is well predicted by lake area in our data set ($R^2 = 0.74$, $n = 66$, $P < 0.0001$). This alone could statistically explain the relationship between fish species richness and lake order, but lake area is highly correlated with other causal factors important to fish such as lake connection by streams for invasions, the probability of severe winter oxygen, and low pH (Tonn & Magnuson, 1982; Rahel, 1984, 1986; Tonn *et al*., 1990; Magnuson *et al*., 1994, 1998b).

No relation to lake order, Would other metrics do it?

Lake water optical properties were unrelated to lake order. Water color in these lakes is related to humic and fulvic components of dissolved organic carbon concentration (DOC). Lake DOC concentrations are correlated with the presence and extent of wetlands in the catchment area (Hope *et al*., 1996; Gergel *et al*. 1999). This suggests that DOC and water color may be more related to inputs from the immediate catchment than to a lake's position in the drainage system. Thus the spatial patterning of lake water color should be related to the distribution of wetlands, and this, in turn, is potentially related to geomorphology and may therefore be also related to the legacy of the glacial processes that shaped the landscape. It is just not related to the hydrologic measure of landscape position that we have focused on for this analysis.

Lake order and the organization of lake districts

Lake order was capable of explaining a significant fraction of among-lake variability in a broad selection of variables in the Northern Highland Lake District. In some cases (morphometry, water chemistry), the relationship was explained directly by geomorphological or hydrological considerations; in other cases (biological variables, human-use variables), the 'response' variable was indirectly influenced by the lake's landscape position. However, in all cases, lake order could be viewed as integrating a multiplicity of covarying mechanisms to explain the observed relationship.

Taken individually, none of the relationships reported here will strike any limnologist as new. Even if not reported, they belong to the expert knowledge of many local scientists. Taken together, however, they compose a powerful view of how the legacy of the glacial processes that acted during the genesis of the lake district, impinges on a broad range of lake features, and ultimately defines the spatial character of a lake district.

Lake order in particular and landscape position in general are best seen as constraints (*sensu* Allen & Starr, 1982; Pickett *et al*., 1994) based on lake origin and development, rather than as ultimate causes. It is an expression of the spatial organization of a lake district. Lakes that are high in the landscape are not determined to be small or to have species-poor fish communities. The geomorphic template laid down by the glaciers caused these lakes to be more likely to have these features through the way that processes are constrained during lake development. The position they happen to occupy was constrained by their genesis and, as well, constrained their subsequent ontogeny.

The analysis of lake order is important, not because we may gain more insight on proximate mechanisms, or because we may improve our predictions of any individual lake's features, but because it reveals how lakes are related to each other across the landscape now, and how they may respond to external forces in the future. Moreover, it provides a framework for regionalization, allowing us to make better predictions and better management decisions with scant data. It also provides a mechanism to compare across lake districts (Soranno *et al*., in 1999). Finally, it provides a framework for the synthesis of regional analyses of lakes, streams, and the terrestrial landscape. Terrestrial ecologists have embraced landscape perspectives (Turner, 1989). Stream ecologists have long incorporated a landscape and geomorphological perspective (Vanotte *et al.*, 1980). The lake order concept can help to develop such a spatially explicit landscape perspective for lakes.

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