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Lake landscape position: Relationships to hydrologic connectivity and landscape features

Sherry L. Martin and Patricia A. Soranno
Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan 48824

Abstract

To improve our understanding of lake landscape position, we compared four metrics based on different aspects of lake surface hydrologic connections: (1) ''lake hydrology,'' which is a general measure of lake surface hydrologic position, (2) ''lake order,'' which measures connections to streams by stream order, (3) ''lake network number,'' which measures connections to other lakes, and (4) ''lake network complexity,'' which measures the complexity of connections to other lakes (in a chain or branched). We sampled 71 lakes in northern Michigan, U.S.A. and measured lake landscape position and landscape characteristics around each lake (e.g., land use/cover and geology) to answer two questions: (1) which metric of landscape position explains the most variation in lake water chemistry/clarity? and (2) what landscape and physical features are also related to landscape position? All four landscape position metrics explained significant variation in some water chemistry/clarity variables. However, lake order, the metric based on stream order, consistently explained the most variation, ranging from 22% (dissolved organic carbon) to 53% (conductivity and calcium), with lake hydrology, the metric based on both streams and lakes, explaining similar amounts of variation to lake order, but less overall. Landscape position was also significantly related to both lake morphometry and the proportion of wetland types in buffer areas, which may help explain why landscape position is related to lake water chemistry and clarity variables.

Introduction

The study of stream ecosystems has benefited tremendously from being viewed from a landscape perspective (Hynes 1975; Vannote et al. 1980; Fisher et al. 2001). In contrast, only recently have lakes been viewed along a spatial gradient, interconnected through groundwater and/or surface water pathways (Kratz et al. 1997; Riera et al. 2000; Quinlan et al. 2003). By identifying and evaluating the importance of spatial structure across lakes, these studies have found that variability of some lake features follows a pattern consistent with the position of the lake within the landscape. The concept of lake landscape position provides a general framework to explicitly investigate spatial patterning of lake characteristics and to identify mechanisms driving variation of ecological processes in lakes. For example, in northern Wisconsin, precipitation is the dominant source of water to lakes positioned high in the landscape, whereas surface and groundwater input are the dominant source of water to lakes lower in the landscape (Kratz et al. 1997). This is one feature that explains why lakes higher in the landscape respond more strongly and recover more slowly to drought than lakes lower in the landscape (Webster et al. 2000).

Kratz et al. (1997) define the landscape position of a lake as a ''combination of the hydrologic description with information on the spatial placement of a lake within a lake district.'' Partially because of the complex nature of defining a lake's hydrology, lake landscape position has been measured in three different ways to date, each metric addressing a distinct aspect of a lake's hydrologic connectivity. The first metric is based on the relative position of a lake within a groundwater flow system (Kratz et al. 1997). This metric was developed and tested specifically in the groundwater-dominated Northern Highland Lake District of northern Wisconsin. In this district, lakes higher in the landscape have relatively lower groundwater inputs, and therefore, lower calcium and magnesium concentrations, derived from groundwater sources, than lakes lower in the landscape. Expanding upon this groundwater-based system, lake chain number measures lake landscape position with regard to

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lakes connected along a linear chain through primarily surface-flow systems (Soranno et al. 1999). This metric was tested in six surface flow–dominated lake districts representing a wide range of hydrogeomorphic settings. In general, similar to the groundwater metric, as lake chain number increased, loading of nonreactive weathering products (such as alkalinity, calcium, and magnesium) increased. In contrast, lake chain number was also related to increased concentrations of total nutrients and chlorophyll *a* (Chl *a*) along the lake chain. Finally, landscape position has been measured using lake order (LO) (Riera et al. 2000). Lake order is determined primarily by the stream order of the outlet stream connection. As with lake chain number, LO also explains significant variability in alkalinity, conductivity, calcium, and Chl *a* (Riera et al. 2000; Quinlan et al. 2003). However, LO was only weakly related to concentrations of total nutrients.

Although these studies have found each of these individual metrics of landscape position to successfully quantify some aspect of lake landscape position, each one has done so without incorporating the hydrologic connections that the other metrics emphasized. In addition, some metrics of landscape position explained significant variation in lake productivity variables whereas others did not. Thus, it is unclear which metric of landscape position explains the most variation in lake water chemistry/clarity. Furthermore, few studies have analyzed other features of the landscape, which may be related to landscape position, as possible explanatory factors for why landscape position has such a strong relationship with some lake water chemistry/clarity variables. For example, some studies have found that heterogeneity of geology regulates patterns of some lake response variables along a landscape position gradient (Soranno et al. 1999; Quinlan et al. 2003). However, these features have not been specifically incorporated into studies of landscape position.

The goal of our study is to improve the understanding of lake variability and spatial patterns in lake districts by considering both hydrologic connectivity as well as other landscape features (Fig. 1). We ask two questions: (1) which metric of landscape position is most strongly related to lake water chemistry/clarity? and (2) what landscape and physical features are related to landscape position? First, we compare four landscape position metrics, each based on different aspects of surface hydrologic connections of a lake (stream and lake combined, stream-only, lake-only, and lake network complexity [LNC]). Because of the difficulty of obtaining groundwater data for all of our lakes, we did not collect these data and therefore were not able to compare landscape position based on groundwater connections. We hypothesize that a metric of landscape position that combines both types of surface hydrologic connections (lakes and streams) will explain the most variability in lake water chemistry/clarity because previous studies have found significant relationships between landscape position and lake water chemistry/clarity when measuring landscape position based on a single aspect of surface hydrologic connections (Soranno et al. 1999; Riera et al. 2000; Quinlan et al. 2003). Second, for each lake, we quantify lake morphometry and the proportional area of surface and bedrock geology, land use/cover, and wetlands around each lake. We hypothesize that landscape position will be related to lake morphometry and some characteristics of a lake's catchment because of geomorphological constraints associated with landscape position (Riera et al. 2000) that will help explain landscape position's strong relationship with lake response variables (Fig. 1).

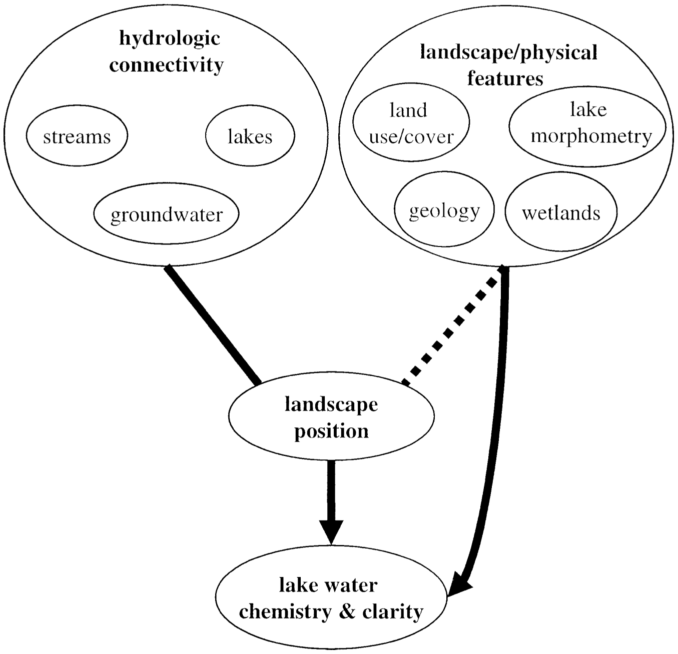

Fig. 1. Conceptual framework for the linkages among hydrologic connections, landscape/physical features, landscape position, and lake water chemistry/clarity. Solid lines and arrows indicate linkages found in published studies. Dotted line indicates additional linkages examined in this study.

Methods

Study area—This study was conducted within three major river watersheds (USGS 8-digit hydrologic units) of Michigan's lower peninsula: Muskegon, Au Sable, and Thunder Bay (Fig. 2). These three watersheds cover an area of 15,292 km^2. Lakes located within the boundaries of the same major river watershed were considered to be a part of the same lake network. The hydrology of lakes in the study area includes both groundwater and surface water (Seelbach et al. 1997). These three lake networks were chosen to minimize large regional differences in climate, land use/cover, and geology. Forested land use/cover makes up 65% of the study area (Muskegon 53%, Au Sable 79%, Thunder Bay 67%). The bedrock geology of the study area is 94% clastic sedimentary rock (Muskegon 96%, Au Sable 100%, Thunder Bay 78%). Surficial geology is 51% outwash (Muskegon 46%, Au Sable 72%, Thunder Bay 27%), 21% glacial till (Muskegon 18%, Au Sable 5%, Thunder Bay 50%), and 18% moraine (Muskegon 26%, Au Sable 8%, Thunder Bay 13%). Although the study area varies in surficial geology, the sampled lakes within the study area do not vary widely, with sampled lakes largely dominated by outwash surficial geology (Muskegon 63%, Au Sable 63%, Thunder Bay 47%).

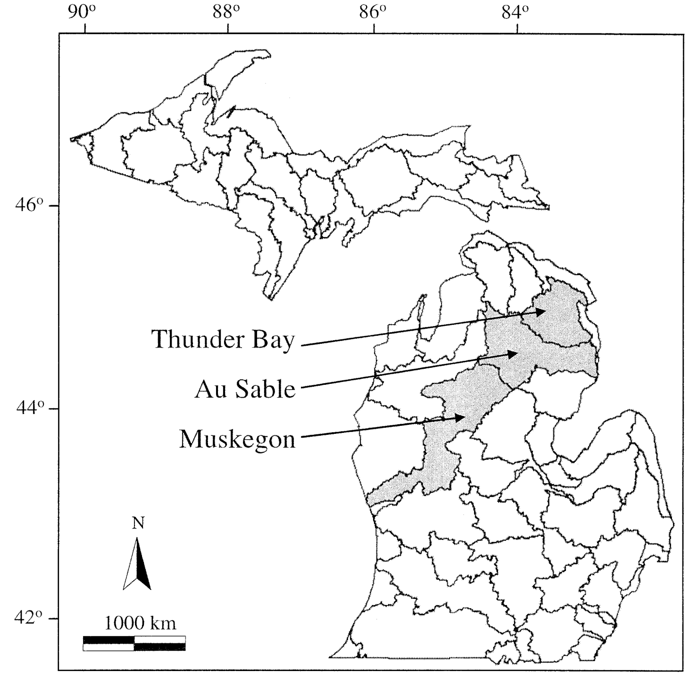

Fig. 2. Major river watersheds (USGS 8-digit hydrologic units) of Michigan with the three major river watersheds that represent different lake networks used in this study highlighted: Thunder Bay, Au Sable, and Muskegon.

Landscape position metrics—We define "metric" simply as any system differentiating between two or more objects, based on unique characteristics of those objects. We measured landscape position using four different metrics: (1) lake hydrology (LH), (2) LO, (3) lake network number (LNN), and (4) LNC (Fig. 3). Each lake in the study area was assigned a category for each landscape position metric using the surface water data and navigational tools of the National Hydrography Dataset (NHD; http://nhd.usgs.gov/). We describe each landscape position metric below.

LH measures landscape position by incorporating both connections to lakes and streams, providing the overall surface hydrologic position of a lake (Fig. 3). Lakes are assigned to one of seven categories based on the presence or absence of inflow and outflow stream connections and connections to other lakes located in the lake network. Seepage lakes (S) are isolated lakes unconnected to any permanent stream, and therefore to no other lakes. Inflow lakes (I) are connected to one permanent stream but not any other lakes. Inflow/outflow lakes (IO) are connected to two or more permanent streams but not to any other lakes. Headwater lakes (H) have no inflow stream but are connected to other lakes through an outflow stream. Inflow headwater lakes (IH) are connected to both inflow and outflow streams as well as to other downstream lakes. Flow-through lakes (F) are connected to both upstream and downstream lakes through inflow and outflow streams. Lastly, terminal lakes (T) are connected to upstream lakes through inflow streams but are not connected to any downstream lakes.

Lake order (LO) measures landscape position as connections to streams (Fig. 3). Lakes are assigned LO based pri-

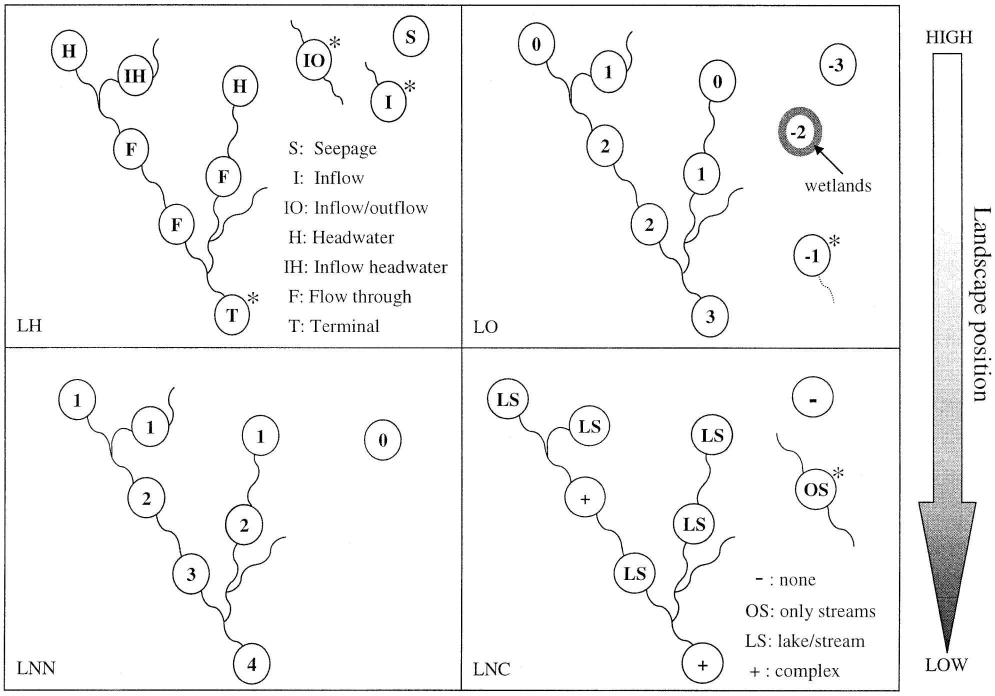

Fig. 3. Description of landscape position metrics: lake hydrology (LH), lake order (LO), lake network number (LNN), and lake network complexity (LNC). See text for further descriptions. Categories not included in this study are indicated with an asterisk.

marily on the Strahler stream order of the outflow stream (for complete details see Riera et al. 2000). Lakes not connected to a permanent inflow stream are separated into the following four categories: (1) lakes completely unconnected to any stream (permanent or temporary) or wetlands are assigned LO −3, (2) lakes connected to wetlands are assigned LO −2, (3) lakes connected to a temporary stream (defined as a stream represented on 1 : 24,000 map but not on a 1 : 100,000 map) are assigned LO −1, and (4) lakes connected to a permanent outflow stream but with no inflow stream are assigned LO 0.

LNN measures landscape position as connections to other lakes (Fig. 3) based on lake chain number (Soranno et al. 1999). However, LNN includes a category (0) for lakes located in the same lake network (i.e., major river watershed) that are not connected to any other lakes through stream connections. Lakes are assigned a network number based on the number of upstream lakes connected through the same stream, as defined by NHD navigational tools. Lakes located on tributary streams are assigned a network number according to the number of other lakes also located along the same tributary. However, these tributary lakes do not influence the network number of downstream lakes on any other streams.

Finally, LNC measures landscape position as the complexity of connections to other lakes by distinguishing simple linear lake chains from lakes with more than one upstream lake on different stream branches, reflecting a more complex branching structure (Fig. 3). LNC is assigned by using connections to any permanent stream that has an upstream lake. Lakes not connected to any other lakes are assigned a network complexity based on the presence (only streams, OS) or absence (−) of a stream connection. Lakes connected in a simple linear chain are assigned LS, and lakes connected to more than one lake immediately upstream through different streams are assigned a +. LNC was designed specifically to study the dendritic nature of many lake surface connections.

Sampling design—We examined only lakes that stratify completely and that contain true pelagic zones, which we define as lakes with a maximum depth of at least 3 m and larger than 0.2 km^2. For each of the three lake networks, we randomly selected three to five lakes from each of the following LH categories: (1) S, (2) H, (3) IH, (4) F with three or fewer upstream lakes, and (5) F with more than three upstream lakes. Lakes designated I, IO, and T were not included in the selection process because of low sample size in the study area ($n = 6$, $n = 1$, $n = 3$, respectively). Some landscape position categories were combined because of low sample size (i.e., LO $\geq$ 3, LNN $\geq$ 3). Although we aimed to create a balanced study, because of natural variation in the number of lake types as well as logistical issues, our sampling produced an unbalanced design. The numbers of lakes sampled within each lake network ranged between 3 and 9 (LH), 1 and 9 (LO), 1 and 13 (LNN), and 3 and 15 (LNC). The numbers of lakes sampled across all lake networks ranged between 12 and 22 (LH), 7 and 17 (LO), 9 and 30 (LNN), and 13 and 36 (LNC). Overall, our dataset includes a total of 71 lakes (Muskegon $n = 30$, Au Sable $n = 23$, Thunder Bay $n = 18$), although only 68 lakes were analyzed using LO because the −1 category was dropped because of low sample size.

Lake sampling and chemical analysis—We sampled each lake one time in 2003 during the summer stratification period (mid-July through August, although four lakes were sampled in mid-September while still strongly stratified) for a variety of physical, chemical, and biological variables. We conducted depth profiles using a YSI 6920 multi-probe (Yellow Springs Inc, Yellow Springs, Ohio) for dissolved oxygen, temperature, conductivity and pH. All water chemistry and clarity samples were taken using an integrated tube sampler from the epilimnion at the deepest point in the lake. Alkalinity samples were processed within 8–12 hours of sample collection using Gran titration (Wetzel and Likens 2000). Calcium and magnesium concentrations were determined by flame atomic absorption spectrophotometry (Wetzel and Likens 2000). Chloride, nitrate, and sulfate concentrations were determined using membrane-suppression ion chromatography (Wetzel and Likens 2000). Silica concentrations were determined using the molybdate colorimetric method (Wetzel and Likens 2000). Dissolved organic carbon (DOC) concentrations were determined using high-temperature platinum-catalyzed combustion followed by infrared gas analysis of CO_2 (Wetzel and Likens 2000). We consider DOC a measure of water clarity because DOC is often related to water color (Rasmussen et al. 1989; Jones 1992) and other optical properties (Morris et al. 1995).

We also measured water color using a Hach model CO-1 color test kit. Chl *a* samples were filtered within 8–12 hours of sample collection through glass fiber filters and immediately frozen in a dark container. Filters were soaked in 95% ethanol overnight and Chl *a* concentrations determined fluorometrically using phaeopigment correction (Nusch 1980; Sartory and Grobbelaar 1984). Total nitrogen concentrations were determined using the 2nd derivative of the absorbance curve at 224 nm following persulfate digestion (Crumpton et al. 1992; Bachmann and Canfield 1996). Total phosphorus concentrations were determined spectrophotometrically following persulfate digestion (Murphy and Riley 1962; Menzel and Corwin 1965).

Landscape and physical features—Most lake morphometry data were quantified from bathymetric maps, except maximum depth, which was obtained in the field using a handheld depth finder. Mean depth was calculated by taking the average depth of approximately 100 points evenly spaced across each bathymetric map (Omernik and Kinney 1983). Lake basin slope was calculated as: (surface area)$^{1/2}$/mean depth (Nurnberg 1995). Shoreline development factor (SDF) was calculated as the ratio of shoreline perimeter divided by the circumference of a circle of the same area (Wetzel and Likens 2000).

A GIS-based landscape feature database was created for all lakes in the study area, based on two buffer widths around each lake, representing a lake's riparian zone (100 m) or local catchment (500 m) (except for geology, in which we only calculated a catchment buffer). We separated wetland land use/cover from other land use/covers because we obtained more detailed and finer resolution wetland data than the other land use/cover data, and we hypothesized different relationships for wetlands than other land use/covers. Wetland data were obtained from the National Wetlands Inventory (NWI, http://wetlands.fws.gov/) where wetland location, type, and extent were determined using aerial photography in conjunction with USGS 1 : 24,000 topographic maps following Cowardin et al. (1979). For this study, wetland types were grouped by dominant vegetation (forest or scrub-shrub). All wetland types were also combined to produce a category for overall wetland coverage. Land use/cover data were obtained from the Michigan Resource Information Service (MIRIS 2000), where the location and extent of urban, agriculture, upland field, and forest land use/cover type was determined using the Anderson classification scheme (Anderson et al. 1976) from aerial photographs taken between 1978 and 1985 at a resolution of 0.025 km^2. Urban and agricultural land use/cover types were combined to form a human land use/cover category. Bedrock geology data were obtained from the Geologic Survey Division of the Michigan Department of Environmental Quality. Bedrock geology types were grouped into the following five categories: carbonate, clastic, hard rock, salt, and iron. Surficial geology data were provided by the Michigan Natural Features Inventory and Michigan Department of Natural Resources. We grouped surficial geology into the following five types: dune sand, glacial till (fine, medium and coarse-textured glacial till), lacustrine, moraine (fine, medium, and coarse-textured end moraine till), and outwash (glacial outwash sand and gravel and postglacial alluvium, ice-contact outwash sand and gravel).

Statistical analyses—The relationships between landscape position and lake response variables were tested for each landscape position metric using two-way analysis of variance (ANOVA) including an interaction term, with landscape position and lake network as categorical predictor variables. Lake water chemistry/clarity variables were modeled as the response for question 1 and landscape/physical features were modeled as the response for question 2. If the interaction term was not significant, a one-way ANOVA with landscape position as the predictor variable was used to analyze the relationship. If the interaction term was significant, then data from each lake network were analyzed separately using one-way ANOVA.

Principal components analysis (PCA) was computed using Systat version 9 (SPSS Inc.), to examine whether groups of landscape/physical features were organized around landscape position categories. We used the broken stick method to determine the number of meaningful components (Jackson 1993). Lakes were grouped by landscape position for each metric and plotted on the first two PCA axes, showing the 95% confidence ellipse on the centroid.

A conservative significance level ($p = 0.01$) was chosen and all response variables were transformed to meet normality assumptions. Tukey multiple means comparisons were used on combined data across the three lake networks to determine which landscape position categories differed ($p = 0.05$). Because each of the metrics had different numbers of categories, Akaike Information Criterion (AIC) values were calculated to determine which of the four metrics provided the best fit to the data. Metrics with AIC values more than 7 units lower compared to other metrics were considered to fit the data substantially better (Burnham and Anderson 2002). All univariate statistics were computed in SAS (version 8.02) software with PROC GLM using type III sums of squares, which accounts for unbalanced designs in the computation of the error term (SAS Institute Inc.).

Results

The study lakes varied widely in water chemistry/clarity and morphometry characteristics (Table 1). Lake area ranged from fairly small lakes (0.2 km^2, the lower limit included in the dataset) to the largest inland lake in Michigan (Houghton Lake, 81.24 km^2). On average, the study lakes were slightly basic, moderately to highly buffered, and moderately clear. However, Chl *a* had a relatively narrow range and most lakes were oligotrophic to mesotrophic.

Comparing the landscape position metrics—All landscape position metrics were significantly related to some water chemistry variables (Table 2). In particular, each of the landscape position metrics was significantly related to a majority of the dissolved conservative and dissolved reactive ions. In contrast, the landscape position metrics were significantly related to only one productivity variable (total nitrogen [TN] : total phosphorus [TP] ratio), although TN was marginally significant with LH and LO metrics. Also, these two metrics were the only ones significantly related to any measure of water clarity (DOC). All significant models show an increasing pattern with landscape position metrics (except for TN : TP, which shows a decreasing pattern), suggesting that dissolved materials accumulate along the landscape position gradient from high to low in the landscape (Fig. 4).

Although the interaction terms from two-way ANOVA models were not significant for a majority of lake water chemistry/clarity variables, some variables had a significant interaction term (Table 2). Two such variables were measures of lake productivity (TN and Chl *a*), meaning the lake networks show different patterns for these lake response variables. In the Au Sable network, Chl *a* was negatively related to landscape position as measured by LH ($F_{3,19} = 11.05$, $p < 0.0001$) and LNN ($F_{3,19} = 10.44$, $p < 0.0001$), both explaining similar amounts of variation (64% and 62%, respectively). However, landscape position was not significantly related to Chl *a* in either the Muskegon or Thunder Bay lake networks. There was no significant relationship between TN and landscape position in any of the three lake networks when analyzed by individual lake network, although there was marginal significance in Au Sable with LH ($F_{3,19} = 4.79$, $p = 0.012$) and Thunder Bay with LO ($F_{5,11} = 3.26$, $p = 0.048$).

Comparing among the four landscape position metrics using AIC and R^2 values, we found that LO was consistently the landscape position metric with the best AIC value (lower by at least 7 units) and the highest R^2 value for all significant models. Lake order (LO) explained from 22% (DOC) to 53% (conductivity and calcium) of variation (Table 2). LH was the second best metric for all lake water chemistry/clarity variables, with the exception of TN : TP ratio, where the AIC

Table 1. List of lake morphometry and water chemistry/clarity variables including minimum, maximum, mean, and standard deviation across 71 lakes. SDF, shoreline development factor (unitless); PCU, platinum cobalt units; DOC, dissolved organic carbon; TN, total nitrogen; TP, total phosphorus. Lake basin slope is unitless.

	Min.	Max.	Mean	SD
Morphometry				
Maximum depth (m)	3	36	13.8	7.7
Mean depth (m)	1.5	15.2	5.2	3.1
Lake area (km^2)	0.20	81.24	3.09	10.52
Lake basin slope	143	5,654	609	786
SDF	1.0	4.9	2.1	0.8
Dissolved conservative ions				
Alkalinity (μeq L^{-1})	170	3,722	2,232	792
Conductivity (μS cm^{-1})	24.0	401.0	253.8	79.7
Calcium (mg L^{-1})	2.1	57.7	30.7	10.6
Magnesium (mg L^{-1})	0.9	18.0	10.6	4.2
Chloride (mg L^{-1})	0.4	26.5	8.2	5.9
pH	6.5	9.3	8.1	0.5
Dissolved reactive ions				
Silica (mg L^{-1})	0.04	5.53	2.20	1.63
Nitrate (μg L^{-1})	0	913	39	111
Sulfate (mg L^{-1})	2.5	27.0	8.2	4.5
Water clarity				
Secchi (m)	1.3	9.2	3.9	1.4
Water color (PCU)	0	30	10	9
DOC (mg L^{-1})	<1	27.6	10.5	6.5
Productivity				
Chl *a* (μg L^{-1})	0.3	15.4	3.0	2.5
Total nitrogen (μg L^{-1})	102	1,509	540	289
Total phosphorus (μg L^{-1})	2.6	34.0	11.5	6.3
TN : TP ratio	15	130	52	25

values of LO, LH, and LNN were statistically indistinguishable (differing by less than 7 AIC units).

Because LO was found to be the metric of landscape position most strongly related to lake water chemistry/clarity, we show box-plots with Tukey multiple means comparisons of LO versus response variables (Fig. 4). For significant relationships, the LO categories seemed to be divided into two groups: lakes not connected or minimally connected to streams (−3, −2, and 0), and, lakes more highly connected to streams (1, 2, and ≥3), although there is much variation depending on the response variable examined. For example, although according to ANOVA results LO explains significant variation in DOC concentrations (Table 2), Tukey comparisons do not show significant differences between any individual LO pairs with a significance level of 0.05 (Fig. 4). However, if we use a p value of 0.1 for the Tukey comparisons, LO categories −3 and −2 differed significantly with LO category 2 (results not shown).

Relationships between landscape position and landscape/physical features—Landscape position was significantly related to two landscape/physical features: lake morphometry and the proportion of wetland in buffer areas surrounding the study lakes (Table 3). We found no significant relationships between any landscape position metric and land use/cover. We were not able to analyze agricultural and upland field land use/cover, surficial geology, or bedrock geology because of zero values for many study lakes. All landscape position metrics were positively related to lake area, with the largest lakes located lower in the landscape (Fig. 5). Three landscape position metrics (LH, LO, LNN) were significantly related to SDF, although patterns differed slightly among the three metrics. Only two metrics (LNN and LNC) were significantly related to lake-basin slope, both showing a positive relationship (lakes lower in the landscape having a more gradual slope than lakes higher in the landscape). All four landscape position metrics were significantly related to the proportion of all wetlands in both buffer areas (Table 3), with the proportion of wetlands generally increasing along the landscape position gradient (Fig. 6). Various landscape position metrics were also significantly related to wetlands when grouped by dominant vegetation type. Tukey multiple means comparisons show similarities between many LO categories, with few categories significantly different from one another. The percent variance explained for significant relationships ranged from 16% to 54% (Table 3).

Multivariate PCA of landscape/physical features generated results similar to univariate ANOVAs. Using the broken stick method for 17 variables, landscape/physical features were reduced to four principal components and explained ~81% of the total variance (Table 4). Urban, forest, and

Table 2. ANOVA results for lake water chemistry/clarity variables versus each of the four landscape position metrics: (A) lake hydrology (LH) and lake order (LO), (B) lake network number (LNN) and lake network complexity (LNC). Smaller Akaike Information Criterion (AIC) values indicate the most parsimonious model fit and are in bold. One-way ANOVA results are presented except where the two-way interaction term was significant (*). In these cases, two-way ANOVA results are presented. Results for the landscape position term only are provided, and *p* values are in bold if significant (≤0.01). DOC, dissolved organic carbon.

	LH					LO				
A	df	F	AIC	R^2	p	df	F	AIC	R^2	p
Dissolved conservative ions										
Alkalinity	3,67	18.64	1,060	0.46	<**0.0001**	5,62	12.05	**985**	0.49	<**0.0001**
Conductivity	3,67	18.82	752	0.46	<**0.0001**	5,62	13.90	**696**	0.53	<**0.0001**
Calcium	3,67	14.59	490	0.40	<**0.0001**	5,62	13.75	**446**	0.53	<**0.0001**
Magnesium	3,67	13.44	366	0.38	<**0.0001**	5,62	8.06	**345**	0.39	<**0.0001**
Chloride	3,67	2.04	204	0.08	0.117	5,62	2.21	190	0.15	0.064
pH	3,67	0.48	122	0.02	0.697	5,62	1.12	117	0.08	0.358
Dissolved reactive ions										
Silica	3,66	7.84	118	0.26	<**0.0001**	5,62	6.59	**108**	0.35	<**0.0001**
Nitrate	3,61	1.07	107	0.05	0.370	5,57	2.15	100	0.16	0.072
Sulfate	3,67	9.92	98	0.31	<**0.0001**	5,62	9.05	**88**	0.42	<**0.0001**
Water clarity										
Secchi	3,66	0.43	75	0.02	0.730	5,61	0.17	72	0.01	0.973
Water color	3,66	1.61	483	0.07	0.194	5,61	1.31	452	0.10	0.270
DOC	3,67	5.77	440	0.21	**0.001**	5,62	3.50	**413**	0.22	**0.008**
Productivity										
Chl *a*	3,59	2.76	125	0.53	0.050*	5,62	1.39	159	0.10	0.242
Total nitrogen	3,59	4.07	99	0.40	0.011*	5,50	3.08	82	0.51	0.017*
Total phosphorus	3,67	0.84	119	0.09	0.085	5,62	0.65	119	0.05	0.664
TN : TP ratio	3,67	9.04	**80**	0.29	<**0.0001**	5,62	6.44	**74**	0.34	<**0.0001**

	LNN					LNC				
B	df	F	AIC	R^2	p	df	F	AIC	R^2	p
Dissolved conservative ions										
Alkalinity	3,67	12.55	1,071	0.36	<**0.0001**	2,68	15.77	1,088	0.32	<**0.0001**
Conductivity	3,67	12.65	763	0.36	<**0.0001**	2,68	14.62	777	0.30	<**0.0001**
Calcium	3,67	10.35	498	0.32	<**0.0001**	2,68	10.72	509	0.24	<**0.0001**
Magnesium	3,67	8.55	376	0.28	<**0.0001**	2,68	11.92	380	0.26	<**0.0001**
Chloride	3,67	2.54	202	0.10	0.063	2,68	2.14	205	0.06	0.125
pH	3,67	1.92	118	0.08	0.014	2,68	0.67	121	0.02	0.514
Dissolved reactive ions										
Silica	3,66	5.44	123	0.20	**0.002**	2,67	8.04	122	0.19	**0.001**
Nitrate	3,61	1.02	107	0.05	0.390	2,62	3.75	102	0.11	0.029
Sulfate	3,67	6.02	106	0.21	**0.001**	2,68	7.22	108	0.18	**0.001**
Water clarity										
Secchi	3,66	0.70	74	0.03	0.556	2,67	1.89	70	0.05	0.159
Water color	3,66	2.05	482	0.09	0.116	2,67	0.87	490	0.03	0.425
DOC	3,67	2.58	448	0.10	0.061	2,68	4.60	450	0.12	0.013
Productivity										
Chl *a*	3,59	2.82	126	0.51	0.047*	2,62	1.77	169	0.01	0.643
Total nitrogen	3,67	2.29	118	0.09	0.087	2,68	0.65	123	0.02	0.527
Total phosphorus	3,67	1.68	119	0.07	0.180	2,68	2.61	118	0.07	0.081
TN : TP ratio	3,67	10.23	**78**	0.31	<**0.0001**	2,68	5.87	91	0.15	**0.004**

One-way ANOVA results are presented except where the two-way interaction term was significant (*). In these cases, two-way ANOVA results are presented.

human land use/cover dominated PCA axis 1 and all categories of wetlands dominated PCA axis 2. Maximum depth, mean depth, and lake basin slope dominated PCA axis 3. Lake area and SDF dominated PCA axis 4. Plots of the first two PCA axes show little separation between landscape position categories (Fig. 7). Thus, although our dataset contains fine scale variation in land use/cover (PCA axis 1) and a gradient of wetland coverage (PCA axis 2), these landscape/physical features are not strongly related to landscape position in combination.

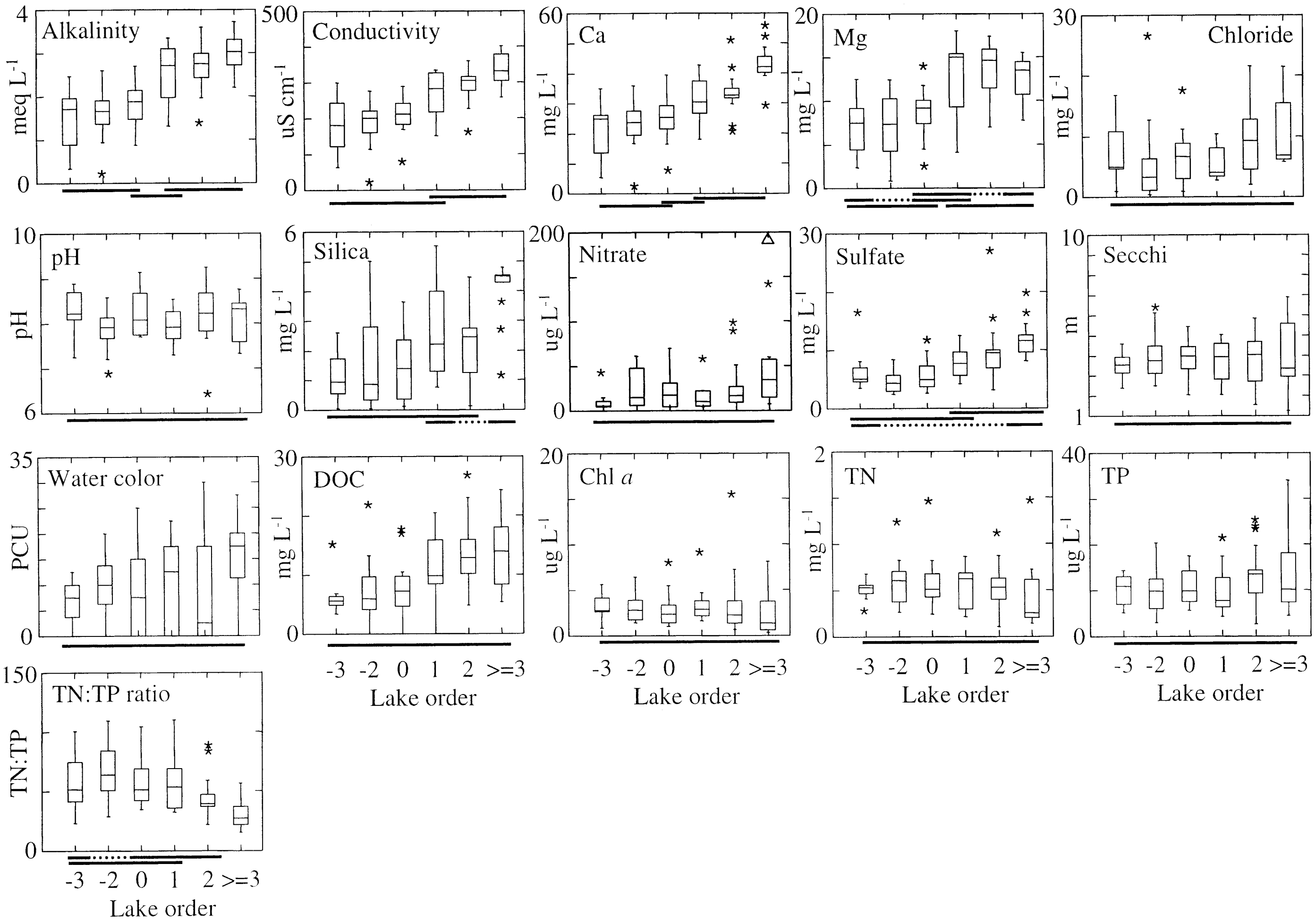

Fig. 4. Box-plots of lake order versus lake water chemistry/clarity variables. Water color is reported in platinum cobalt units (PCU). Note that alkalinity is plotted in meq L^{-1} and TN is plotted in mg L^{-1}. Solid lines show categories not significantly different using Tukey multiple means comparisons, and dotted lines indicate noncontiguous categories that are not significantly different. Some data points were omitted for graphical purposes (indicated by a triangle). Data points that fall outside the whiskers are indicated with an asterisk.

Discussion

By comparing the relationships among landscape position, hydrologic connections, and landscape/physical features, we can infer possible mechanisms driving relationships between lake landscape position and water chemistry/clarity (Fig. 1) and we make two main conclusions. First, the landscape position metric that measures the presence and magnitude of stream connections (rather than other surface hydrologic connections) is most strongly related to lake water chemistry/clarity. This result suggests that the magnitude of stream inputs is a major factor driving water chemistry/clarity patterns associated with lake landscape position. Second, landscape and physical features, such as lake morphometry and the presence and magnitude of wetland connections, are also significantly related to lake landscape position. This result suggests that patterns in these factors should help to explain the relationships between lake landscape position and water chemistry/clarity. Overall, for glaciated regions similar to ours, lakes lower in the landscape should be larger, be more connected to wetlands, and have more stream inputs.

Landscape position and hydrologic connections—Our results confirm many of the patterns that previous studies have shown to be associated with the landscape position of a lake. For example, many dissolved conservative ions and some dissolved reactive ions increase with increasing landscape position as measured by lake connections (Soranno et al. 1999; Kling et al. 2000) and stream connections (Lewis and Magnuson 2000; Riera et al. 2000; Quinlan et al. 2003). However, our study allows for comparison across metrics. Although we found that the presence and magnitude of stream connections (LO) was more strongly related to lake water chemistry/clarity than the presence and magnitude of lake connections, we also found strong relationships with landscape position metrics that measure hydrologic connections to other lakes (LH, LNN, LNC). In fact, LH explained only slightly less variation in lake water chemistry/clarity than LO, and all landscape position metrics (except LNC) explained TN : TP ratio equally well. Only one lake water chemistry/clarity variable (DOC) was explained solely by metrics of landscape position that included stream connections (LO and LH). This last pattern is not surprising, given

Table 3. ANOVA results for landscape/physical features versus each of the four landscape position metrics. SDF, shoreline development factor; other descriptors as in Table 2.

	LH					LO				
A	df	F	AIC	R^2	*p*	df	F	AIC	R^2	*p*
Lake morphometry										
Maximum depth	3,67	0.58	136	0.03	0.630	5,62	0.34	133	0.03	0.888
Mean depth	3,62	0.92	120	0.04	0.437	5,57	0.45	115	0.04	0.814
Lake area	3,67	4.96	−375	0.18	**0.004**	5,62	3.40	−344	0.22	**0.009**
Lake basin slope	3,62	1.72	−623	0.08	0.172	5,57	1.90	−568	0.14	0.108
SDF	3,67	8.72	−52	0.28	>**0.0001**	5,62	3.35	−38	0.21	**0.010**
Wetlands—100-m buffer										
Forested types	3,59	8.52	−41	0.46	<**0.0001***	5,50	4.92	−32	0.54	**0.001***
Scrub-shrub types	3,67	2.75	−40	0.11	0.050	5,62	3.24	−39	0.21	0.012
All wetland types	3,67	8.99	−16	0.29	<**0.0001**	5,62	4.64	−11	0.27	**0.001**
Wetlands—500-m buffer										
Forested types	3,67	4.19	−52	0.16	**0.009**	5,62	2.93	−46	0.19	0.020
Scrub-shrub types	3,67	3.34	−96	0.13	0.025	5,62	3.89	−94	0.24	**0.004**
All wetland types	3,67	7.44	−54	0.25	<**0.001**	5,62	3.40	−44	0.21	**0.009**
Land use/cover—100 m buffer										
Urban	3,67	1.63	54	0.07	0.190	5,62	0.57	56	0.04	0.723
Forest	3,67	1.04	42	0.04	0.379	5,62	0.63	44	0.05	0.677
All human uses	3,67	1.63	56	0.07	0.190	5,62	0.52	59	0.04	0.761
Land use/cover—500 m buffer										
Urban	3,67	0.50	−25	0.02	0.684	5,62	0.38	−17	0.03	0.864
Forest	3,67	0.85	−2	0.04	0.474	5,62	0.83	4	0.06	0.534
All human uses	3,67	0.29	−1	0.01	0.830	5,62	0.41	6	0.03	0.838
	LNN					LNC				
B	df	F	AIC	R^2	*p*	df	F	AIC	R^2	*p*
Lake morphometry										
Maximum depth	3,67	0.44	136	0.02	0.724	2,68	2.55	132	0.07	0.086
Mean depth	3,62	0.49	121	0.02	0.694	2,63	1.31	118	0.04	0.277
Lake area	3,67	7.82	−382	0.26	>**0.0001**	2,68	7.30	−383	0.18	**0.001**
Lake basin slope	3,62	5.85	−634	0.22	**0.001**	2,63	8.34	−646	0.21	**0.001**
SDF	3,67	10.01	−55	0.31	>**0.0001**	2,68	1.15	−36	0.03	0.323
Wetlands—100 m buffer										
Forested types	3,67	3.43	−36	0.13	0.022	2,68	4.41	−38	0.11	0.016
Scrub-shrub types	3,67	4.61	−45	0.17	**0.005**	2,68	4.51	−45	0.12	0.015
All wetland types	3,67	10.61	−20	0.32	<**0.0001**	2,68	11.15	−16	0.25	<**0.0001**
Wetlands—500 m buffer										
Forested types	3,67	1.65	−46	0.07	0.185	2,68	2.43	−49	0.07	0.096
Scrub-shrub types	3,67	4.56	−99	0.17	**0.006**	2,68	4.58	−100	0.12	0.014
All wetland types	3,67	4.91	−48	0.18	**0.004**	2,68	7.17	−51	0.17	**0.002**
Land use/cover—100 m buffer										
Urban	3,67	1.12	55	0.05	0.349	2,68	2.03	52	0.06	0.140
Forest	3,67	0.94	42	0.04	0.428	2,68	0.68	41	0.02	0.508
All human uses	3,67	1.12	57	0.05	0.347	2,68	1.85	55	0.05	0.165
Land use/cover—500 m buffer										
Urban	3,67	0.27	−25	0.01	0.848	2,68	1.44	−30	0.04	0.244
Forest	3,67	0.85	−2	0.04	0.472	2,68	1.40	−5	0.04	0.253
All human uses	3,67	0.16	−1	0.01	0.924	2,68	0.46	−4	0.01	0.632

One-way ANOVA results are presented except where the two-way interaction term is significant (*). In these cases, two-way ANOVA results are presented.

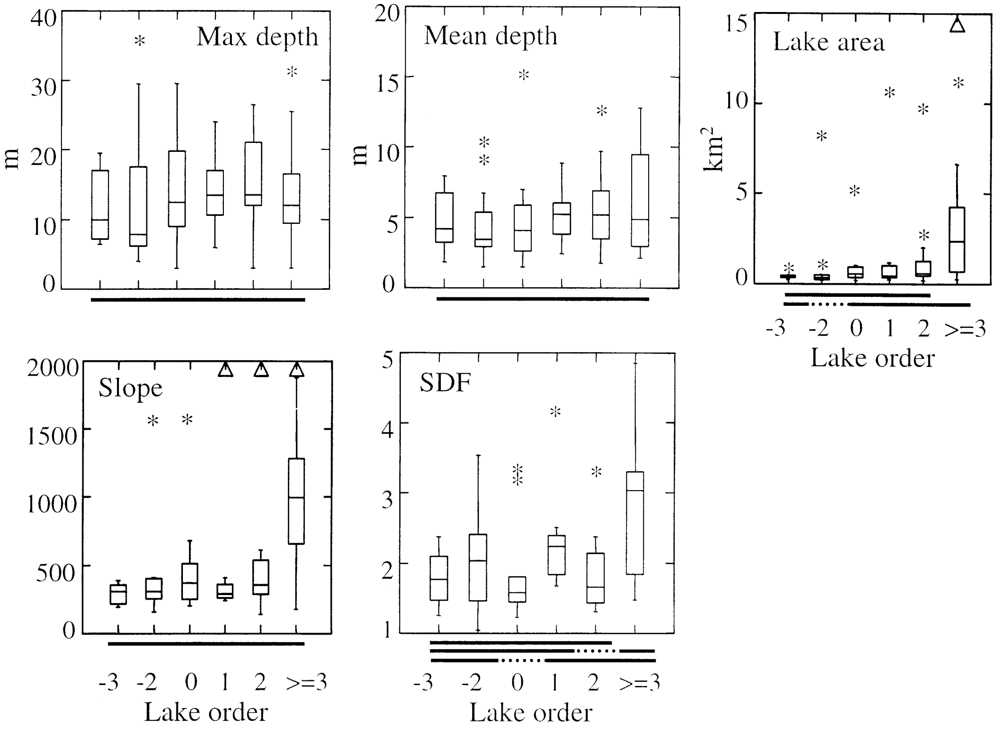

Fig. 5. Box-plots of lake order versus morphometry variables. Lake basin slope and SDF are unitless. Descriptors as in Figure 4.

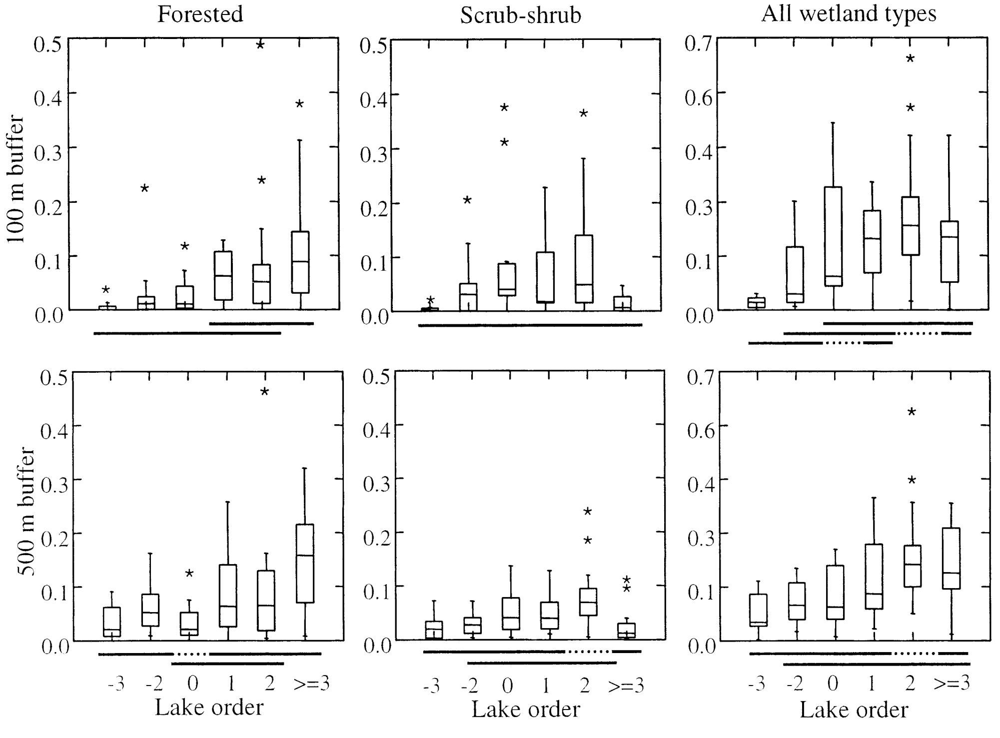

Fig. 6. Box-plots of lake order versus proportion of wetland types in the 100 m and 500 m area surrounding the study lakes (descriptors as in Figure 4).

Table 4. Component loadings from principal components analysis of landscape/physical features. Variables with component loadings greater than 0.6 are considered to dominate the axis and are in bold.

	PC1	PC2	PC3	PC4
Lake morphometry				
Maximum depth	0.179	−0.221	**0.799**	0.111
Mean depth	0.175	−0.215	**0.884**	0.150
Lake area	0.493	0.164	−0.141	**0.644**
Lake basin slope	0.245	0.250	−**0.688**	0.498
SDF	−0.171	0.100	−0.262	**0.626**
Wetlands—100-m buffer				
Forested types	0.066	**0.671**	0.512	0.289
Scrub-shrub types	0.158	**0.692**	−0.109	−0.509
All wetland types	0.099	**0.908**	0.242	−0.148
Wetlands—500-m buffer				
Forested types	0.106	**0.749**	0.240	0.409
Scrub-shrub types	0.248	**0.725**	−0.174	−0.378
All wetland types	0.210	**0.916**	0.077	0.107
Land use/cover—100-m buffer				
Urban	**0.895**	−0.317	0.024	0.052
Forest	−**0.925**	0.041	0.055	0.206
All human uses	**0.916**	−0.303	0.027	0.005
Land use/cover—500-m buffer				
Urban	**0.863**	−0.203	−0.036	0.199
Forest	−**0.841**	−0.135	0.129	0.240
All human uses	**0.920**	−0.089	0.000	−0.114
Total variance explained	31%	24%	14%	11%

SDF, shoreline development factor.

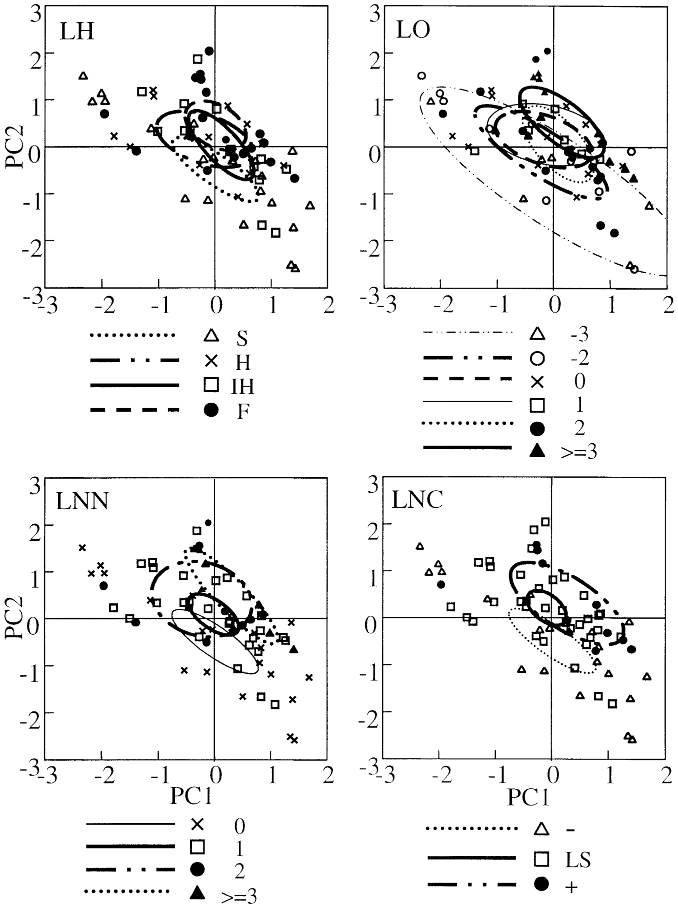

Fig. 7. PCA plots of landscape/physical features with lakes grouped by landscape position: lake hydrology (LH), lake order (LO), lake network number (LNN), and lake network complexity (LNC). 95% confidence ellipse around the centroid of each landscape position category is shown.

that a large portion of lake DOC originates from allochthonous material in the catchment and is transported via surface water flow (Schlesinger and Melack 1981; Molot and Dillon 1997; Schiff et al. 1997). In addition, previous studies have found that catchment characteristics explained more variation in DOC for drainage lakes (lakes connected to streams) than for seepage lakes, suggesting that streams are an important source of catchment-derived DOC to lakes (Kortelainen 1993; Gergel et al. 1999).

To examine the usefulness of LO across a range of different geomorphic settings, we compared our results with two previously published studies (Table 5): a groundwater-dominated lake district in northern Wisconsin (Riera et al. 2000), and a surface water–dominated lake district in Ontario (Quinlan et al. 2003). Although there are many common patterns across the three regions, there are also some interesting differences. LO explains a significant amount of variation in many dissolved conservative ions and dissolved reactive ions, all of which is related to weathering. However, Riera et al. (2000) did not find a relationship between LO and sulfate in Wisconsin lakes, which may be because of the small range and low mean concentration of sulfate found in their study lakes compared to the other study areas (Table 5). In contrast to weathering variables, productivity variables seem to be the most difficult to predict from LO. None of the three studies found a significant relationship between LO and TP, and there were mixed results for Chl *a* and TN. Riera et al. (2000) found that LO explained a significant amount of variation in Chl *a* concentrations in northern Wisconsin lakes, whereas our study of Michigan lakes did not. Lake order also explained a significant amount of variation in TN concentrations in northern Wisconsin and Michigan lakes, but not for lakes in Ontario. These results, again, may be because of regional differences in the ranges of values, because the range of Chl *a* concentrations in Wisconsin lakes was larger than in Michigan lakes, and the range of TN concentrations found in Ontario lakes was much more narrow than in the other two studies.

Another factor to consider when comparing results across studies is the number of lake networks included in the analysis. For example, we explicitly considered three different lake networks and included lake network as a parameter in our models, which allowed us to consider the issue of among lake network heterogeneity. Although it appears that Quinlan et al. (2003) include multiple lake networks in their analyses (based on visual interpretation of their map), they did not explicitly quantify a lake network effect. It is unclear how many lake networks Riera et al. (2000) include in their

Table 5. Comparison among three landscape position studies of lake water chemistry/clarity and lake morphometry variables using LO: Wisconsin lakes from Riera et al. (2000), Ontario lakes from Quinlan et al. (2003), and Michigan lakes from this study. Minimum, maximum, mean, and number of observations are listed. See Table 1 legend for units and abbreviations. Significant relationships are in bold ($P \leq 0.05$); note that this p value differs from the results of Michigan lakes presented in Table 2. na, not available.

	Wisconsin				Ontario				Michigan			
	Min.	Max.	Mean	*n*	Min.	Max.	Mean	*n*	Min.	Max.	Mean	*n*
Lake water chemistry/clarity												
Alkalinity	**10**	**2,420**	**345.9**	**386**	**8**	**806**	**165.6**	**84**	**170**	**3,722**	**2,232**	**68**
Conductivity	**6**	**250**	**42.1**	**365**	**18.4**	**119**	**46.4**	**84**	**24**	**401**	**254**	**68**
Calcium	**0.13**	**21.68**	**5.08**	**190**	**1.52**	**15.4**	**4.88**	**84**	**2.1**	**57.7**	**30.7**	**68**
Magnesium	**0.09**	**9.2**	**2.1**	**173**	**0.47**	**2.3**	**1.1**	**84**	**0.9**	**18**	**10.6**	**68**
Chloride	**0.15**	**5.19**	**0.86**	**97**	na	na	na	na	0.4	26.5	8.2	68
pH	**4.3**	**8.5**	**6.6**	**396**	**5.61**	**7.98**	**6.69**	**84**	6.5	9.3	8.1	68
Silica	**0**	**15.9**	**2.1**	**181**	**0.11**	**2.18**	**0.96**	**84**	**0.0**	**5.5**	**2.2**	**68**
Sulfate	0.61	6.56	3.08	102	**3.7**	**9.4**	**7.37**	**84**	**2.5**	**27.0**	**8.2**	**68**
Secchi	**0.6**	**10.1**	**3.4**	**268**	na	na	na	na	1.3	9.2	3.9	67
Water color	0	**192.5**	**27.7**	**213**	na	na	na	na	0	30	10	67
DOC	1.9	12.5	5.2	70	1.69	6.4	3.59	85	<**1**	**27.6**	**10.5**	**68**
Chl *a*	**0.7**	**33.3**	**5.04**	**78**	na	na	na	na	0.3	15.4	3.0	68
TN	**150**	**940**	**400**	**160**	130	541.3	242	84	**102**	**1,509**	**540**	**68**
TP	**2**	62	16	92	2.7	44.7	9.5	86	2.6	34	11.5	68
TN : TP	na	na	na	na	7.6	61.7	31.9	84	**15**	**130**	**52**	**68**
Lake morphometry												
Maximum depth	**0.3**	**35.1**	**8.8**	**314**	**4.5**	**93**	**30.4**	**86**	3	36	14	68
Mean depth	**1.8**	**15**	**5.6**	**59**	na	na	na	na	1.5	15.2	5.2	63
Lake area	**0.3**	**1,568**	**46.7**	**556**	**5.4**	**1,675**	**243**	**86**	**20.3**	**8,124**	**309**	**68**
SDF	**1.01**	**4.21**	**1.39**	**556**	na	na	na	na	**1.0**	**4.9**	**2.1**	**68**

study; however, the size of their study area (1,741 km^2) suggests that perhaps only one lake network (as defined by major river watersheds) was included in their study. We found that differences among lake networks may mask relationships between lake response variables and landscape position. For example, in our analysis, several ANOVA models relating the different landscape position metrics to Chl *a* and TN resulted in a significant interaction term between lake network and landscape position (Table 2). This result indicates that the lake networks had different relationships between productivity variables and landscape position and could not be modeled together. Therefore, another reason that findings from these three studies differ across all variables, but productivity variables in particular, may not only be because of narrow data ranges, but also differences among lake networks within each study.

It is clear that a variety of landscape position metrics can capture the importance of connections of both lakes and streams to lake water chemistry/clarity. However, choosing a metric of landscape position may depend not only on the response variable of interest, but also on data availability. The four metrics are based on relatively coarse map data (1 : 100,000); however, LO is more difficult to measure because three additional databases are needed: stream order (not currently available from NHD), finer scaled stream data (1 : 24,000), and wetland land cover. Therefore, a landscape position metric that is easier to measure but provides similar results may be more appealing for some applications (e.g., LH).

Landscape position relationships to landscape/physical features—In order to properly infer mechanisms driving the relationships between landscape position and lake water chemistry/clarity, it is necessary to also understand the relationship that landscape position has with other features that may influence lake water chemistry/clarity. In particular, we found that some measures of lake morphometry and wetlands around lakes were significantly related to landscape position. This result is relevant because these landscape/physical features have been shown to be directly related to lake water chemistry/clarity. For example, the presence and amount of wetlands surrounding lakes have been found to explain a significant amount of variation in concentrations of lake DOC (Gergel et al. 1999; Prepas et al. 2001; Xenopoulos et al. 2003), TP (Detenbeck et al. 1993; Devito et al. 2000; Prepas et al. 2001), and TN (Detenbeck et al. 1993; Prepas et al. 2001). In addition, lake area is an important factor driving fish and zooplankton community structure (Fryer 1985; Dodson 1992), and may be important in understanding subsequent relationships between biological communities and landscape position (Kratz et al. 1997).

We found support for the idea that the relationships between landscape position and lake water chemistry/clarity may be a result of some combination of changes in landscape/physical features and lake hydrologic connectivity (Fig 1). In particular, based on previous research, the relationships of DOC and TP should each be a product of changes in both landscape position and increasing amounts of wetland areas. We found support of this idea for DOC, but not for TP (Tables 2 and 3). Phosphorus concentrations in lakes have been found to be positively related to wetlands (D'Arcy and Carignan 1997; Halsey et al. 1997; Prepas et al. 2001), and landscape position was significantly related to increasing wetlands in our study (Table 3; Fig 6). However, TP was not related to any landscape position metric in our study (Table 2) or in studies conducted in northern Wisconsin and Ontario (Table 5). For Michigan lakes, this finding may be because of the low overall proportion of wetlands in the 500-m buffer around the lakes (mean 15%, range 0.3–59%). For example, Prepas et al. (2001) found a significant relationship between TP and wetlands only when wetland cover dominated the catchment area (>50%). Studies have also found an interaction between TP and wetland type (wet meadow, marsh, bog, poor fen, rich fen, etc.), with different types acting as a source or sink of TP (Detenbeck et al. 1993; Prepas et al. 2001). In addition, Devito et al. (2000) found that TP decreased in lakes as groundwater input (measured by calcium and magnesium concentrations) increased. Therefore, variation in phosphorus concentrations across lakes is a result of processes that have not been fully captured by the measures of landscape position compared in this study. The addition of groundwater information and the spatial arrangement of wetlands may improve the analysis of the relationship between landscape position and water clarity and productivity variables. Although LO includes information on the presence of wetlands, which may explain why this metric had the strongest relationship to water chemistry/clarity, it only does so for seepage lakes. It may be more beneficial to incorporate wetland information as a separate factor from lake hydrologic connectivity, allowing for the interpretation of each factor.

Although some of our findings support the concept of a geomorphic template, as proposed by Riera et al. (2000), we found that the nature of the geomorphic template may differ among regions (Table 5). For example, maximum depth increases with increasing landscape position, but only when a wide range of depth was included in the study. Although the Wisconsin and Michigan studies had similar maximum values for maximum depth, the Wisconsin study included very shallow lakes (maximum depth of 0.3 m). On the other hand, the Ontario and Michigan lakes shared similar minimum values for maximum depth, but the Ontario lakes were far deeper than the Michigan lakes. These differences in data range may explain the lack of pattern in maximum depth along a landscape position gradient and may indicate either a sampling artifact or true geomorphological differences between the three regions.

Our study should help to refine the concept of landscape position and suggest possible underlying mechanisms driving variability among lakes in seemingly similar settings. We have broadened the view of landscape position beyond solely considering lake hydrologic connectivity to specifically incorporate relationships to other landscape/physical features. This more comprehensive view of landscape position should help characterize lakes in regions where landscape features may play a larger role than hydrologic connectivity in explaining lake variability, such as in extremely wet or arid regions. The definition of landscape position will continue to expand as the concept is tested in diverse regions, allowing more accurate extrapolation to unsampled lakes and a clearer understanding of lake variability at the landscape scale.

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