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DEFINING LAKE LANDSCAPE POSITION: RELATIONSHIPS TO
HYDROLOGIC CONNECTIVITY AND LANDSCAPE FEATURES

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DEFINING LAKE LANDSCAPE POSITION: RELATIONSHIPS TO HYDROLOGIC CONNECTIVITY AND LANDSCAPE FEATURES

BY

Sherry L. Martin

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ABSTRACT

DEFINING LAKE LANDSCAPE POSITION: RELATIONSHIPS TO HYDROLOGIC CONNECTIVITY AND LANDSCAPE FEATURES.

By

Sherry Martin

The concept of landscape position provides a general framework for investigating spatial patterns among lakes in a region and can be defined as the position of a lake relative to features of the landscape. Although several studies have found that landscape position is related to many in-lake variables, it is unclear what underlying mechanisms are driving the relationships. To examine this issue, I measured landscape position emphasizing four different aspects of hydrologic connectivity, to ask two questions: (1) Which landscape position metric is most strongly related to lake water chemistry/clarity? And (2) what other features are related to landscape position? I found the metric that measured stream connections was most strongly related to in-lake variables and, therefore, the best way to measure landscape position. This result suggests that stream inputs, as opposed to upstream lake inputs, likely drive patterns associated with lake landscape position. I also found that landscape position was related to lake morphometry and the amount of surrounding wetlands, suggesting additional mechanisms for why landscape position explains variability in lake variables. These results suggest the need to develop measures of landscape position that incorporate multiple landscape features. Thus, landscape position is a composite variable, strongly correlated to a variety of in-lake variables due to its relationship to these major landscape features.

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Introduction

Recognition of spatial variability is an integral part of ecosystem research, and specifically, the quantification and study of the structure of spatial mosaics is one of the primary goals of landscape ecology (Palmer 2002, Liu and Taylor 2002, Wiens et al. 2002). Application of these principles to areas of ecological research that have not traditionally been viewed from a landscape perspective can enhance our understanding of ecosystem structure and function (Rabeni and Sowa 2002). For example, aquatic ecosystems have benefited tremendously from being viewed from this perspective in the past few decades (Hynes 1975, Kratz et al. 1997, Fisher et al. 2001).

Stream ecologists were among the first to develop spatially explicit models for aquatic ecosystems. For example, the River Continuum Concept (RCC) is one of the early spatial frameworks developed to describe variability among biological communities in rivers (Vannote et al. 1980). The RCC states that stream communities change as stream order increases in response to changes in physical habitat and are further structured by upstream inefficiencies in energy use. More recently, the RCC has been modified to account for other influences in rivers, such as nutrient inputs, climate change, and channel alterations (Brezonik 1996). Another example of a spatially explicit aquatic model is the serial discontinuity concept (SDC), which incorporates disruptions in the river continuum caused by reservoirs (Ward & Stanford 1983). The SDC proposes that changing the natural flow regime of a river will obscure RCC predictions for that stream. Since developing spatial frameworks for the study of rivers, it has become common practice to view flowing waters along a longitudinal gradient (Frissell et al. 1986, Hawkins et al. 1993).

In contrast, lakes have historically been viewed as independent microcosms and have been studied largely as individual ecosystems (National Research Council 1996). Only recently have lakes been viewed along a continuous spatial gradient, interconnected through groundwater and/or surface water pathways (Kratz et al. 1997, Soranno et al. 1999, Riera et al 2000, Webster et al. 2000, Lewis and Magnuson 2000, Quinlan et al 2003). By integrating concepts from landscape ecology, such as identifying and evaluating the importance of spatial structure in an ecosystem, studies have found that variability of some lake features follows a pattern consistent with the position of the lake within the landscape (Kratz et al. 1997, Soranno et al. 1999, Kling et al. 2000, Lewis and Magnuson 2000, Reed-Andersen et al. 2000, Riera et al. 2000, Webster et al. 2000, Quinlan et al. 2003).

The concept of lake landscape position provides a general framework to explicitly investigate spatial patterning of lake characteristics, analogous to the RCC for streams. 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*". For example, in northern Wisconsin, precipitation is the dominant source of water for lakes positioned high in the landscape, whereas surface and groundwater input are the dominant source of water of lakes lower in the landscape (Kratz et al. 1997). Therefore, lakes higher in the landscape respond more strongly and recover more slowly to drought than lakes lower in the landscape (Webster et al. 2000). Recognizing this difference in landscape position is important when determining mechanisms driving a variety of ecological processes in lakes.

Lake landscape position has been measured in three ways to date, each addressing a distinct aspect of a lake's hydrologic connectivity. The first measure is based on the relative position of a lake within a groundwater flow system (Kratz et al. 1997). This measure 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 lakes directly connected along a linear chain by surface or groundwater flow systems (Soranno et al. 1999). This measure was tested in seven different lake districts representing a wide range of geologic and hydrologic settings. In general, as lake chain number increased, loading of non-reactive weathering products (such as alkalinity, calcium, and magnesium) increased. Lake chain number was also correlated to increased concentrations of total nutrients and chlorophyll *a* along surface water dominated lake chains but not along groundwater dominated lake chains. Although lake chain number accounts for both groundwater and surface water connections, it only considers lakes directly connected to one another in a linear fashion. Finally, lake order has been defined by Riera et al. (2000) as measuring "*the type and strength of connections between a lake and the surface drainage network.*" Lake order is very similar to stream order and accounts only for the presence and strength of the outlet stream connection. This measure has been tested in the Northern Highlands Lake District of northern Wisconsin (Riera et al. 2000) as well as in Ontario, Canada (Quinlan et al. 2003). As with lake chain number, lake order also explains significant variability in alkalinity, conductivity, calcium, and chlorophyll *a* (Riera et al 2000, Quinlan et al 2003). However, unlike lake chain number, lake order was only weakly related to concentrations of total nutrients.

Although these studies have found that each of these individual measures has appeared to successfully quantify some aspect of lake landscape position, each one did so without incorporating the hydrologic connections the other measures emphasized. For example, lake chain number accounts for the influence of upstream lakes but ignores the influence of stream order, whereas lake order accounts for stream order but ignores connections to other lakes. In addition, some measures of landscape position explained significant variation in lake productivity variables whereas others did not. Thus, it is unclear which measure of landscape position explains the most variation in lake water chemistry/clarity variables. Furthermore, few studies have analyzed other features of the landscape that 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 surficial and bedrock geology regulates patterns of 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 my study is to improve our understanding of lake variability and spatial patterns in lake districts by identifying the best way to measure lake landscape position and to examine what other features of the landscape are related to it (Figure 1). I argue that lake landscape position is characterized both by the hydrology of a lake (defined by the presence of lake, stream or groundwater connections), and by other landscape and physical features that may also vary along a landscape position gradient. I hypothesize that landscape position is strongly related to lake response variables because of its relationship to both hydrology and to these major landscape features.

To examine these issues, I ask two questions: (1) which landscape position metric is most strongly related to lake water chemistry/clarity variables? I define 'metric' simply as a measurement system differentiating between two or more objects, based on unique characteristics of those objects. And (2) what landscape and physical features are related to landscape position? To answer the first question, I compare four different landscape position metrics based on the different surface hydrologic connections of a lake (stream only, lake only, stream and lake combined, and lake complexity). Due to the difficulty of obtaining groundwater data, I was not able to compare landscape position based on groundwater connections. Because previous studies have found significant relationships between landscape position and lake water chemistry/clarity variables when measuring landscape position based on surface connections to lakes (Soranno et al. 1999) or streams (Riera et al. 2000), I hypothesize that a metric of landscape position that combines both types of hydrologic connections will explain the most variability in lake water chemistry/clarity. To answer the second question, I examine possible reasons why landscape position is such a good predictor of many lake variables by examining whether other important landscape features, besides hydrology, are related to landscape position. Because of geomorphological constraints associated with landscape position, I expect landscape position to also be correlated to lake morphometry, geology, land use/cover, and wetlands (Figure 1).

Methods

Landscape position metrics

I measured landscape position using four different metrics, each emphasizing different surface hydrologic connections. These metrics are: (1) lake hydrology, (2) lake order, (3) lake network number, and (4) lake network complexity (Figure 2). Each lake was assigned a category for each landscape position metric using surface water data and navigational tools provided in the National Hydrography Dataset (NHD, http://nhd.usgs.gov/). Lakes located within the same major river watershed (USGS 8-digit hydrologic unit, HUC-8) were considered to be a part of the same lake network. Descriptions of each metric of landscape position follow.

Lake hydrology (LH) measures landscape position by incorporating both connections to lakes and streams, providing the overall surface hydrologic position of a lake (Figure 2A). 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 in the watershed. Seepage lakes (S) are isolated lakes unconnected to any permanent stream, and therefore no other lakes. Inflow lakes (I) are connected to one permanent stream (regardless of the actual direction of water flow) 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 other downstream lakes. Flow through lakes (F) are connected to both inflow and outflow streams as well as upstream and downstream lakes. Lastly, terminal lakes (T) are connected to upstream lakes through inflow streams but no downstream lakes.

Lake order (LO) measures landscape position by emphasizing connections to streams (Figure 2B). Lakes are assigned a lake order based on the Strahler stream order of the outflow stream (see Riera et al. 2000 for complete details). Lakes not connected to permanent inflow streams are separated into the following four categories: (1) lakes completely unconnected to any stream (permanent or temporary) or wetlands are assigned lake order '-3', (2) lakes unconnected to a permanent stream but do have a connection to wetlands are assigned lake order '-2', (3) lakes unconnected to a permanent stream but do have a connection to a temporary stream (defined as a stream represented on 1:24 000 map but not on a 1:100 000 map) are assigned lake order '-1', and (4) lakes connected to a permanent outlet stream but with no inlet stream are assigned lake order '0'. Lake order -1 was not included in this study due to low sample size (n=3).

Lake network number (LNN) measures landscape position by emphasizing connections to other lakes (Figure 2C). 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. Lake network number is based on lake chain number as described in Soranno et al. (1999), however I have modified it by adding a category for lakes in the same HUC-8 major river watershed that are not directly connected to any other lakes through stream connections (0).

Finally, lake network complexity (LNC) measures landscape position by emphasizing connections to other lakes and accounting for the complex branching nature of most stream networks (Figure 2D). Lakes are assigned a network complexity based on the number and location of other lakes connected immediately upstream through any stream, mainstem or tributary. Lakes not connected to any other lakes are assigned a network complexity based on the presence (only streams, OS) or absence (-) of a permanent stream connection. Lakes connected to other lakes are differentiated between: 1) those lakes connected to another lake immediately upstream through the same stream (lake/stream, LS), and 2) those lakes connected to at least two lakes immediately upstream through different streams (+). Lake network complexity was designed specifically to capture the intricacy of this last category (+).

Description of study area

My study was conducted in three different lake networks that were defined as major river watersheds (HUC-8) of Michigan's lower peninsula: Muskegon, Au Sable, and Thunder Bay (Figure 3). These watersheds are all hydrologically variable (Sellbach et al. 1997) and were chosen to minimize differences in climate, land use/cover, and geology and to maximize the number of lakes per landscape position category. 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%).

Sampling design

Lakes larger than 20 hectares were included in the study. For each of the three watersheds, I randomly selected 3-5 lakes from each the following lake hydrology (LH) categories: (1) seepage, (2) headwater, (3) inflow headwater, (4) flow through lakes with three or fewer upstream lakes, and (5) flow through lakes with more than three upstream lakes. Inflow, inflow/outflow, and terminal lakes were not included due to low sample size. I sampled a total of 71 lakes, although, only 68 lakes were analyzed for lake order because the three -1 lakes were dropped from the analysis (Table 1).

Lake sampling and chemical analysis

I sampled each lake one time in 2003 during the summer stratification period (mid-July through August, although four lakes were visited in mid-September while the lakes were still strongly stratified) for a variety of physical, chemical, and biological variables. I 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 infra-red gas analysis of CO_2 (Wetzel and Likens 2000). Water color was determined using a Hach model CO-1 color test kit (Loveland, Colorado). Chlorophyll *a* samples were filtered within 8-12 hours of sample collection through glass fiber filters, stored in a dark container, and immediately frozen. Filters were soaked in 95% ethanol overnight and chlorophyll *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

Lake morphometry data were quantified from bathymetric maps. Maximum depth was obtained using a handheld depth finder. Mean depth was calculated by taking the average depth of approximately 100 points evenly spaced across each lake bathymetry 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 perfect circle of the same area (Wetzel and Likens 2000).

A GIS-based landscape feature database was created for all lakes in the study area. 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 my 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. The proportion of each wetland type present in the 100 m and 500 m buffer areas around each lake was calculated. 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 2.5 ha. Urban and agricultural land use/cover types were combined to form a new land use/cover category for analysis of all land dominated by human uses. The proportion of each land use/cover type present in the 100 m and 500 m buffer areas around each lake was calculated. 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 categories: (1) carbonate, (2) clastic, (3) hard rock, (4) salt, and, (5) iron. Surficial geology data were provided by the Michigan Natural Features Inventory and Michigan Department of Natural Resources. For my study, surficial geology types were grouped into the following types: (1) dune sand, (2) glacial till = fine, medium and coarse-textured glacial till, (3) lacustrine, (4) moraine = fine, medium, and coarse-textured end moraine till, and, (5) outwash = glacial outwash sand and gravel and postglacial alluvium, ice-contact outwash sand and gravel. The proportion of each bedrock and surficial geology type present was determined for the 500 m buffer areas around each lake.

Statistical analyses

The relationship between landscape position and lake response variables was tested for each landscape position metric using two-way analysis of variance (2-way ANOVA). These models include landscape position and watershed as categorical predictor variables, as well as an interaction term. This design evaluates the role of each watershed and landscape position metric and determines whether patterns with landscape position vary among watersheds. An example of a 2-way ANOVA model is as follows:

(1) $$Y_{ijk} = \mu + x_j + y_k + (x_j * y_k) + e_{ijk}$$

Where:

Y_{ijk}= response variable for lake *i* in watershed *j* with landscape position *k*

μ = overall mean of response variable

x_j = watershed *j*

y_k = landscape position *k*

$(x_j * y_k)$ = watershed *j* by landscape position *k* interaction

e_{ijk} = error term for lake *i* in watershed *j* with landscape position *k*

All response variables were first analyzed using a 2-way ANOVA. If the interaction term from the 2-way ANOVA was not significant (p-value less than or equal to 0.01), a one way analysis of variance (1-way ANOVA) with landscape position as the only predictor variable was used to analyze the relationship. An example of a 1-way ANOVA follows:

(2) $$Yijk = \mu + y_k + e_{ijk}$$

Where:

Y_{ijk}= response variable for lake *i* in watershed *j* with landscape position *k*

μ = overall mean of response variable

y_k = landscape position *k*

e_{ijk} = error term for lake i in watershed j with landscape position k

If the interaction term was significant, then 1-way ANOVA was used to analyze the relationship for each watershed separately.

A conservative significance level was chosen (p-value less than or equal to 0.01) to minimize the probability of finding spurious significance due to the large number of comparisons (minimizing type II error). All response variables were transformed to meet normality assumptions. Tukey multiple means comparisons were used to determine which landscape position categories differed significantly (p-value 0.05). Because each of the metrics of landscape position 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. AIC allows for the unbiased comparison between models of different size whereas comparing R^2 does not. Metrics with AIC values more than 7 units lower compared to other metrics were considered to be substantially better (Burnham and Anderson 2002). SAS version 8 software was used to compute all statistics (SAS Institute Inc.).

Results

The study lakes varied widely in water chemistry/clarity and morphometry characteristics (Table 2). Lake area ranged from fairly small lakes (20 ha, the lower limit included in the dataset) to the largest inland lake in Michigan (Houghton Lake, 8124 ha). On average, the study lakes were slightly basic, moderately to highly buffered, and moderately clear. However, chlorophyll *a* had a narrow range and most lakes were oligotrophic to mesotrophic.

Measuring landscape position using different hydrologic connections

To determine how best to measure landscape position, I evaluated the ability of the four different metrics of landscape position to explain variation in lake water chemistry/clarity variables. All landscape position metrics explained significant variation in some water chemistry variables (Table 3). In particular, a majority of dissolved conservative ions and dissolved reactive ions were significantly related to each of the landscape position metrics (Table 3). In contrast, only one productivity variable (TN:TP ratio) was significantly related to the landscape position metrics, although, TN is moderately significant for LH and LO (Table 3). Also, only two of the landscape position metrics (LH and LO) explained significant variation in any measures of water clarity (DOC). Therefore, variation in many dissolved ions, as well as TN:TP ratio, is explained by landscape position metrics that measure either type of surface hydrologic connection (lake, stream, or a combination of the two), whereas DOC is explained only by landscape position metrics that incorporate connections to streams (LH and LO). All significant models show a positive relationship with landscape position metrics, suggesting that dissolved materials accumulate along the landscape position gradient, from high to low in the landscape. The ratio TN:TP, on the other hand, shows a negative relationship with landscape position.

Although a majority of lake response variables were analyzed using a 1-way ANOVA model, that included landscape position only, some variables required a 2-way ANOVA model, that included landscape position and terms for watershed and the interaction between landscape position and watershed (Table 3). Two measures of lake productivity (TN and chlorophyll *a*) resulted in significant interaction terms, meaning that the watersheds show different patterns between landscape position and the lake response variable, so each watershed required its own model. In the Au Sable watershed, chlorophyll *a* was negatively related to landscape position as measured by LH and LNN, both explaining similar amounts of variation (64% and 62%, respectively) (Table 4, Figure 4). Landscape position was not significantly related to chlorophyll *a* in either the Muskegon or Thunder Bay watersheds, although a negative pattern in the Thunder Bay watershed is apparent, similar to that found in the Au Sable watershed (Table 4, Figure 4). There was no significant relationship between TN and landscape position in any of the three watersheds (Table 4, Figure 5).

To compare the different landscape position metrics, I used AIC and R^2 values. I found that LO was consistently the landscape position metric with the best AIC value (lower by 7 units) and the highest R^2 value for all significant models, ranging from 22% (DOC) to 53% (conductivity and calcium) of variation explained (Table 3). Lake hydrology was the second best metric for all lake water chemistry/clarity variables, with the exception of TN:TP ratio, where the AIC values for LO, LH, and LNN were very close, with an overall difference of only 6 units among the three metrics, thus being statistically indistinguishable. Because LO was found to be the best overall metric of landscape position, only box-plots of LO versus response variables are shown (Figure 6).

I used Tukey multiple means comparisons to examine differences among LO categories (Figure 6). Generally, I found the formation of 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) (Figure 6), although there is much variation in this general pattern depending on the lake variable examined. For example, although LO categories have significantly different DOC concentrations, Tukey comparisons do not show significant differences between any individual pairs.

Relationships between landscape position and landscape features

I examined whether several landscape features were related to landscape position by analyzing landscape position as a predictor variable and various landscape features as the response variable. Landscape position was significantly related to two general features of the landscape - lake morphometry and the proportion of wetland types in buffer areas surrounding the study lakes (Table 5). All landscape position metrics were positively related to lake area, with LO category >=3 having the largest lakes (Table 5 and Figure 7). Three landscape position metrics (LH, LO, LNN) were significantly related to SDF, although patterns differed slightly among the three metrics (Table 5). Only two metrics (LNN and LNC) were significantly related to lake basin slope, both showing a positive relationship (Table 5). All four landscape position metrics were significantly related to the proportion of all wetlands in both the 100 m and 500 m buffer areas, with the proportion of wetlands generally increasing or showing a unimodal relationship along the landscape position gradient (Table 5). Various landscape position metrics were also significantly related to wetlands when grouped by dominant vegetation type (Table 5). Tukey multiple means comparisons show similarities between many LO categories, with few categories significantly different from one another (Figure 8). The percent variance explained for significant relationships was generally low, ranging from 16% to 33% (Table 5).

I found no significant relationship between any landscape position metrics and land use/cover (Table 5). I was not able to statistically analyze total agricultural land use/cover due to zero values for many study lakes (58 zeros in the 100m area, 40 zeros in the 500m area). I was also not able to statistically analyze bedrock or surficial geology due to zero values for most geology types. Thus, geology and land use/cover change little in these watersheds along the landscape position gradient.

Discussion

There are two important conclusions about lake landscape position stemming from this research. The first is that the landscape position metric that measures the presence and magnitude of stream connections (rather than other surface hydrologic connections) was most strongly related to lake water chemistry/clarity variables. This result suggests that the magnitude of stream inputs is a major factor driving patterns associated with lake landscape position. The second conclusion is that landscape and physical features, such as lake morphometry and the presence and magnitude of wetland connections, are significantly related to lake landscape position. These relationships should help to uncover additional possible mechanisms driving the relationships between landscape position and lake response variables. In addition, these patterns may allow us to define landscape position better in regions where surface hydrologic connections are difficult to measure or absent.

Landscape position and hydrologic connections

Previous studies have shown many common patterns associated with the landscape position of a lake. My results confirm many of these patterns. For example, many dissolved conservative ions and some dissolved reactive ions increase with increasing landscape position as measured by groundwater connections (Kratz et al.

1997, Webster et al. 2000), 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). Even though these previous studies have shown the utility of using landscape position in modeling the spatial variation of lake water chemistry/clarity variables, none has compared the different measures of landscape position.

Because LO was most strongly correlated to lake response variables, it appears that the presence and magnitude of stream connections is a stronger driver of the relationship between landscape position and lake water chemistry/clarity variables than the presence and magnitude of lake connections. However, I also found strong relationships with landscape position metrics that measure hydrologic connections to other lakes (LH, LNN, LNC). Lake hydrology (LH) explained only slightly less variation in lake response variables than LO, and all landscape position metrics (except LNC) explained TN:TP ratio equally well. Only one lake response variable (DOC) was explained solely by metrics of landscape position that included stream connections (LO and LH). This last pattern is not surprising given that a large portion of DOC originates from allochthonous material in the watershed and is transported via surface water flow (Likens and Bormann 1979,Kaplan et al. 1980, Molot and Dillon 1997, Schiff et al. 1997). In addition, previous studies have found that watershed characteristics explained more variation in DOC for drainage lakes (lakes connected to streams) than for seepage lakes, suggesting that streams provide a constant source of DOC to lakes (Kortelainen 1993, Gergel et al.1999). Based on the above evidence, it is clear that both connections to lakes and to streams influence lake water chemistry/clarity variables through landscape position. In some instances choosing the best metric of landscape position may depend not only on what one is trying to predict, but also on data availability. All of these metrics are based on relatively coarse map data (1:100 000); however, for LO, some categories are more difficult to measure because they also require wetland and finer scale stream maps (1:24 000), making LO the most difficult to quantify.

To examine the usefulness of LO across a wide range of different geomorphic settings, I examined whether there were common patterns in studies from three different lake districts by comparing my results with two previously published studies (Table 6): a groundwater dominated lake district in Wisconsin (Riera et al. 2000), and a surface water dominated lake district in Ontario (Quinlan et al. 2003). Although there are many common patterns, there are also some interesting differences across regions. Lake order explains a significant amount of variation in many dissolved conservative ions and dissolved reactive ions, all of which are related to weathering. However, Riera et al. (2000) did not find a relationship between LO and sulfate, which may be due to the small range and low mean concentration of sulfate found in their study lakes compared to the other lake districts (Table 6A). In contrast to weathering variables, productivity variables seem to be the most difficult to predict from LO. For example, none of the three studies found a significant relationship between LO and TP and there are mixed results for TN and chlorophyll *a*. Riera et al. (2000) found that LO explained a significant amount of variation in chlorophyll *a* concentrations whereas I did not. This result, again, may be due to regional differences in the ranges of values. The range of chlorophyll *a* values in Wisconsin lakes was larger than in Michigan lakes. Differences among Michigan watersheds may also explain why there was no relationship with chlorophyll *a*. Lake order was significant with chlorophyll *a* in only one of the three watersheds, and surprisingly exhibited a decreasing pattern with LO (Table 4, Figure 4). This result may be due to the contrasting patterns of nutrients and DOC, which may increase the importance of DOC induced shading in controlling chlorophyll *a* (Carpenter et al. 1998, Beisner et al. 2003). Analyzing data at different levels of aggregation (ie. watersheds combined vs. watersheds separated) as well as regional differences in the data ranges can help clarify many of the discrepancies in findings across these three studies.

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 important to also understand the relationship that landscape position has with other features that may influence lake water chemistry/clarity. Many features of the landscape have been shown to be directly related to lake water chemistry/clarity and may explain as much variation as landscape position. 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). My results show that landscape position was significantly related to some measures of lake morphometry and the amount of wetlands surrounding lakes. Lake area and SDF were related to increasing landscape position (Table 5A), and specifically to increasing LO across three regions (Table 6B). Therefore, analyzing relationships between landscape position and measures of morphometry may be important in understanding shifts in the food web from lake to lake. For example, lake area is an important factor driving fish and zooplankton community structure (Fryer 1985, Dodson 1992), and may be important in understanding subsequent relationships with landscape position (Kratz, 1997).

Other measures of lake morphometry show slightly different relationships with landscape position when compared among the three studies measuring LO. Maximum depth appears to increase with increasing landscape position, but only when a wide range of lake depth was included in the study. Although Wisconsin and Michigan lakes had similar maximum values for lake depth, the Wisconsin study also included very shallow lakes. On the other hand, the Ontario and Michigan lakes shared similar minimum values for lake depth, but the Ontario lakes were far deeper than the Michigan lakes. Although Riera et al. (2000) reports a significant relationship between LO and mean depth, they temper their results in light of statistical artifacts stemming from their highly unbalanced sample design. This comparative analysis suggests that regional differences in data ranges may influence the relationships between landscape position and landscape/physical features.

For my study site, I also analyzed relationships to other landscape features such as land use/cover, geology and presence and magnitude of wetlands surrounding lakes. Given that the design of this study was to minimize variation in land use/cover and geology, it is not surprising that none of these features were related to landscape position. However, the presence and magnitude of wetland areas increased significantly along the landscape position gradient. Therefore, the relationship between landscape position and lake water chemistry/clarity variables may be responding to some combination of increasing wetland areas and increasing hydrologic connectivity. Specifically, the relationship I found with DOC may be a product of changes in landscape position or increasing amounts of wetland areas. In contrast, although total phosphorus has been found to be significantly related to increasing wetlands; and landscape position was significantly related to increasing wetlands in this study; nevertheless, total phosphorus was not related to any landscape position metrics in any of the three regions (Wisconsin, Ontario, Michigan). For Michigan lakes, this finding may be due the low overall proportion of wetlands (>40%) included in the study. Prepas et al. (2001) found a significant relationship between total phosphorus and wetlands only when wetland cover exceeded 40%, approximately. Studies have also found an interaction between total phosphorus and wetland type (wet meadow, marsh, bog, poor fen, rich fen, etc.), with different types acting as a source or sink of total phosphorus (Detenbeck et al. 1993, Prepas et al. 2001). In addition, Devito et al. (2000) found that total phosphorus decreased in lakes as groundwater input (measured by calcium and magnesium concentrations) increased. The contradictory nature of these findings helps to explain the lack of pattern in total phosphorus in my study. The addition of groundwater information and more detailed wetland information 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 variables, it may be more beneficial to incorporate wetland information as a separate factor from hydrologic connectivity, allowing for the interpretation of each factor. In conclusion, incorporating other landscape features, such as the presence and magnitude of wetlands around lakes, into future definitions of landscape position may explain additional variation in lake water chemistry/clarity and help to identify underlying mechanisms.

Implications

This study should help to refine the concept of landscape position and suggest possible underlying mechanisms driving variability among lakes in seemingly similar settings. By taking a comparative approach, I have identified the type of hydrologic connection most related to lake landscape position in a region of variable hydrology. I have also broadened the view of landscape position beyond solely considering hydrologic connections to specifically incorporate relationships to other landscape/physical features. This more comprehensive definition 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.

Table 1. Total number of lakes sampled and number of lakes sampled per watershed for each category of each landscape position metric. LP= landscape position, LH= lake hydrology, LO= lake order, LNN= lake network number, LNC= lake network complexity.

		Watershed			
LP Metric	LP category	Muskegon	Au Sable	Thunder Bay	TOTAL
LH	S	8	8	6	22
	H	5	4	3	12
	IH	8	5	5	18
	F	9	6	4	19
	subtotal	30	23	18	71
LO	-3	3	3	1	7
	-2	5	3	4	12
	0	5	4	3	12
	1	3	1	3	7
	2	9	6	2	17
	>=3	5	4	4	13
	subtotal	30	21	17	68
LNN	0	8	8	6	22
	1	13	9	8	30
	2	4	3	3	10
	>=3	5	3	1	9
	subtotal	30	23	18	71
LNC	-	8	8	6	22
	LS	15	12	9	36
	+	7	3	3	13
	subtotal	30	23	18	71

Table 2. List of lake morphometry and water chemistry/clarity response variables including minimum, maximum, mean and standard deviation across 71 lakes. SDF = shoreline development factor (unitless), DOC = dissolved organic carbon, TN = total nitrogen, TP = total phosphorus.

Morphometry	**Min**	**Max**	**Mean**	**SD**
Maximum depth (m)	3	36	13.8	7.7
Mean depth (m)	1.5	15.2	5.2	3.1
Lake area (ha)	20	8124	309	1052
Lake basin slope	143	5654	609	786
SDF	1.0	4.9	2.1	0.8

Dissolved Conservative Ions	**Min**	**Max**	**Mean**	**SD**
Alkalinity (ueq/L)	170	3722	2232	792
Conductivity (uS/cm)	24.0	401.0	253.8	79.7
Calcium (mg/L)	2.1	57.7	30.7	10.6
Magnesium (mg/L)	0.9	18.0	10.6	4.2
Chloride (mg/L)	0.4	26.5	8.2	5.9
pH	6.5	9.3	8.1	0.5

Dissolved Reactive Ions	**Min**	**Max**	**Mean**	**SD**
Silica (mg/L)	0.04	5.53	2.20	1.63
Nitrate (ug/L)	0	913	39	111
Sulfate (mg/L)	2.5	27.0	8.2	4.5

Water Clarity	**Min**	**Max**	**Mean**	**SD**
Secchi (m)	1.3	9.2	3.9	1.4
Water color (PCU)	0	30	10	9
DOC (mg/L)	0.0	27.6	10.5	6.5

Productivity	**Min**	**Max**	**Mean**	**SD**
Chlorophyll *a* (ug/L)	0.3	15.4	3.0	2.5
Total nitrogen (ug/L)	102	1509	540	289
Total phosphorus (ug/L)	2.6	34.0	11.5	6.3
TN:TP ratio	15	130	52	25

Table 3. ANOVA results for landscape position metrics versus all lake response variables. Smallest AIC values indicate the most parsimonious model fit and are bolded. Some variables required a 2-way ANOVA model (^) due to significant interaction term (see methods for further explanation). Only p-values for landscape position term are provided and are bolded if significant (less than or equal to 0.01). Positive/negative relationship with increasing landscape position (from high to low in landscape for each metric) indicated by +/- signs. "ns" indicates not significant.

Table 3.

Dissolved Conservative Ions	Lake Hydrology (LH)				Lake Order (LO)			
	p-value	AIC	R^2	Pattern	p-value	AIC	R^2	Pattern
Alkalinity	**<0.0001**	1060	0.46	+	**<0.0001**	**985**	0.49	+
Conductivity	**<0.0001**	752	0.46	+	**<0.0001**	**696**	0.53	+
Calcium	**<0.0001**	490	0.40	+	**<0.0001**	**446**	0.53	+
Magnesium	**<0.0001**	366	0.38	+	**<0.0001**	**345**	0.39	+
Chloride	0.117	204	0.08	ns	0.064	190	0.15	ns
pH	0.697	122	0.02	ns	0.358	117	0.08	ns
Dissolved Reactive Ions								
Silica	**<0.0001**	118	0.26	+	**<0.0001**	**108**	0.35	+
Nitrate	0.370	107	0.05	ns	0.072	100	0.16	ns
Sulfate	**<0.0001**	98	0.31	+	**<0.0001**	**88**	0.42	+
Water Clarity								
Secchi	0.730	75	0.02	ns	0.973	72	0.01	ns
Water color	0.194	483	0.07	ns	0.270	452	0.10	ns
DOC	**0.001**	440	0.21	+	**0.008**	**413**	0.22	+
Productivity								
Chlorophyll *a*	0.050 ^	125	0.53	ns	0.242	159	0.10	ns
Total nitrogen	0.011 ^	99	0.40	ns	0.017 ^	82	0.51	ns
Total phosphorus	0.085	119	0.09	ns	0.664	119	0.05	ns
TN:TP ratio	**<0.0001**	**80**	0.29	-	**<0.0001**	**74**	0.34	-

Table 3 cont.

Dissolved Conservative Ions	Lake Network Number (LNN)				Lake Network Complexity (LNC)			
	p-value	AIC	R^2	Pattern	p-value	AIC	R^2	Pattern
Alkalinity	**<0.0001**	1071	0.36	+	**<0.0001**	1088	0.32	+
Conductivity	**<0.0001**	763	0.36	+	**<0.0001**	777	0.30	+
Calcium	**<0.0001**	498	0.32	+	**<0.0001**	509	0.24	+
Magnesium	**<0.0001**	376	0.28	+	**<0.0001**	380	0.26	+
Chloride	0.063	202	0.10	ns	0.125	205	0.06	ns
pH	0.014	118	0.08	ns	0.514	121	0.02	ns
Dissolved Reactive Ions								
Silica	**0.002**	123	0.20	+	**0.001**	122	0.19	+
Nitrate	0.390	107	0.05	ns	0.029	102	0.11	ns
Sulfate	**0.001**	106	0.21	+	**0.001**	108	0.18	+
Water Clarity								
Secchi	0.556	74	0.03	ns	0.159	70	0.05	ns
Water color	0.116	482	0.09	ns	0.425	490	0.03	ns
DOC	0.061	448	0.10	ns	0.013	450	0.12	ns
Productivity								
Chlorophyll *a*	0.047 ^	126	0.51	ns	0.643	169	0.01	ns
Total nitrogen	0.087	118	0.09	ns	0.527	123	0.02	ns
Total phosphorus	0.180	119	0.07	ns	0.081	118	0.07	ns
TN:TP ratio	**<0.0001**	**78**	0.31	-	**0.004**	91	0.15	-

Table 4. ANOVA results from individual watershed analyses. P-values less than or equal to 0.01 in bold.

Lake response variable	LP metric	Watershed: Muskegon p-value	Muskegon R^2	Au Sable p-value	Au Sable R^2	Thunder Bay p-value	Thunder Bay R^2
Chlorophyll *a*	LH	0.801	0.04	**0.000**	0.64	0.239	0.25
	LNN	0.734	0.05	**0.000**	0.62	0.632	0.11
TN	LH	0.233	0.15	0.012	0.43	0.101	0.35
	LO	0.458	0.17	0.072	0.46	0.048	0.60

Table 5. ANOVA results for landscape position metrics versus landscape/physical features: (A) lake morphometry, (B) proportion of wetland type within the surrounding 100 and 500 meter area, and (C) proportion of land use/cover types within the surrounding 100 and 500 meter area . "All Human Uses" category combines urban and agriculture land use/cover types. Agriculture land use/cover type was not analyzed separately, see methods for further explanation. Some variables required a 2-way ANOVA (^) due to significant interaction term (see methods for further explanation). Only p-values for landscape position term are provided and are bolded if significant (less than or equal to 0.01). Positive/negative relationship with increasing landscape position (from high to low in landscape) indicated by +/- signs. "u" indicates an unimodal relationship. "ns" indicates not significant. "np" indicates no discernable pattern.

Table 5.

A.

Lake Morphometry	Lake Hydrology (LH) p-value	AIC	R^2	Pattern	Lake Order (LO) p-value	AIC	R^2	Pattern
Maximum depth	0.630	136	0.03	ns	0.888	133	0.03	ns
Mean depth	0.437	120	0.04	ns	0.814	115	0.04	ns
Lake area	**0.004**	-375	0.18	+	**0.009**	-344	0.22	+
Lake basin slope	0.172	-623	0.08	ns	0.108	-568	0.14	ns
SDF	**>0.0001**	-52	0.28	+	**0.010**	-38	0.21	np

B.

Wetland Type	Lake Hydrology (LH)				Lake Order (LO)			
100m buffer	p-value	AIC	R^2	Pattern	p-value	AIC	R^2	Pattern
Forested types	**0.001**	74	0.29	+/u	**0.008**	73	0.30	+
Scrub-shrub types	0.025	113	0.17	ns	**0.008**	107	0.27	+/u
All Wetland types	**>0.0001**	-30	0.29	+/u	**0.001**	-24	0.28	+
500m buffer								
Forested types	0.020	126	0.14	ns	0.063	122	0.16	ns
Scrub-shrub types	0.195	131	0.07	ns	**0.005**	118	0.24	+/u
All Wetland types	**>0.0001**	-102	0.24	+/u	**0.009**	-87	0.21	+

C.

Land use/cover	Lake Hydrology (LH)				Lake Order (LO)			
100m buffer	p-value	AIC	R^2	Pattern	p-value	AIC	R^2	Pattern
Urban	0.098	18	0.09	ns	0.573	-75	0.06	ns
Upland Field	0.152	96	0.12	ns	0.078	78	0.22	ns
Forest	0.362	24	0.05	ns	0.633	-12	0.05	ns
All Human Uses	0.101	21	0.09		0.640	-7	0.05	ns
500m buffer								
Urban	0.724	-88	0.02	ns	0.925	22	0.02	ns
Upland Field	0.818	^ 65	0.39	ns	0.563	87	0.07	ns
Forest	0.547	-19	0.03	ns	0.635	27	0.05	ns
All Human Uses	0.811	-15	0.01	ns	0.819	26	0.03	ns

Table 5 cont.

A.

Lake Morphometry	Lake Network Number (LNN) p-value	AIC	R^2	Pattern	Lake Network Complexity (LNC) p-value	AIC	R^2	Pattern
Maximum depth	0.724	136	0.02	ns	0.086	132	0.07	ns
Mean depth	0.694	121	0.02	ns	0.277	118	0.04	ns
Lake area	**>0.0001**	-382	0.26	+	**0.001**	-383	0.18	+
Lake basin slope	**0.001**	-634	0.22	+	**0.001**	-646	0.21	+
SDF	**>0.0001**	-55	0.31	+	0.323	-36	0.03	ns

B.

Wetland Type	Lake Network Number (LNN) p-value	AIC	R^2	Pattern	Lake Network Complexity (LNC) p-value	AIC	R^2	Pattern
100m buffer								
Forested types	0.059	81	0.15	ns	0.028	81	0.14	ns
Scrub-shrub types	**0.002**	106	0.26	ns	**0.007**	111	0.17	u
All Wetland types	**>0.0001**	-33	0.33	u	**>0.0001**	-30	0.25	u
500m buffer								
Forested types	0.744	134	0.02	ns	0.533	133	0.02	ns
Scrub-shrub types	**0.008**	123	0.17	u	0.286	132	0.04	ns
All Wetland types	**0.006**	-96	0.17	+/u	**0.002**	-101	0.16	+/u

C.

Land use/cover	Lake Network Number (LNN) p-value	AIC	R^2	Pattern	Lake Network Complexity (LNC) p-value	AIC	R^2	Pattern
100m buffer								
Urban	0.159	-89	0.07	ns	0.044	15	0.09	ns
Upland Field	0.111	66	0.14	ns	0.074	95	0.12	ns
Forest	0.376	-20	0.05	ns	0.489	23	0.02	ns
All Human Uses	0.170		0.07	ns	0.058	19	0.08	ns
500m buffer								
Urban	0.612	19	0.03	ns	0.147	-95	0.06	ns
Upland Field	0.734	^ 95	0.36	ns	0.708	^ 67	0.33	ns
Forest	0.521	23	0.03	ns	0.288	-23	0.04	ns
All Human Uses	0.923	22	0.01	ns	0.607	-19	0.02	ns

Table 6. Comparison of data ranges between Riera et al. 2000, Quinlan et al. 2003, and this study for: (A) lake water chemistry/clarity, and (B) lake morphometry variables. Minimum, maximum, and mean values listed. n = number of observations. Significant relationships found with LO are in bold (p-value less than or equal to 0.05).

Table 6.

A.

Lake water chemistry/clarity	Riera et al. 2000				Quilan et al. 2003				This Study			
	min	max	mean	n	min	max	mean	n	min	max	mean	n
Alkalinity	**10**	**2420**	**345.9**	**386**	**8**	**806**	**165.6**	**84**	**170**	**3722**	**2232**	**71**
Conductivity	**6**	**250**	**42.1**	**365**	**18.4**	**119**	**46.4**	**84**	**24**	**401**	**254**	**71**
Calcium	**0.13**	**21.68**	**5.08**	**190**	**1.52**	**15.4**	**4.88**	**84**	**2.1**	**57.7**	**30.7**	**71**
Magnesium	**0.09**	**9.22**	**2.11**	**173**	**0.47**	**2.3**	**1.06**	**84**	**0.9**	**18**	**10.6**	**71**
Chloride	**0.15**	**5.19**	**0.86**	**97**	n/a				0.4	26.5	8.2	71
pH	**4.3**	**8.5**	**6.6**	**396**	**5.61**	**7.98**	**6.69**	**84**	6.5	9.3	8.1	71
Silica	**0**	**15.9**	**2.1**	**181**	**0.11**	**2.18**	**0.96**	**84**	**0.0**	**5.5**	**2.2**	**70**
Sulfate	0.61	6.56	3.08	102	**3.7**	**9.4**	**7.37**	**84**	**2.5**	**27.0**	**8.2**	**71**
Secchi	**0.6**	**10.1**	**3.4**	**268**	n/a				1.3	9.2	3.9	70
Water Color	**0**	**192.5**	**27.7**	**213**	n/a				0	30	10	70
DOC	1.9	12.5	5.2	70	1.69	6.4	3.59	85	**0**	**27.6**	**10.5**	**71**
Chlorophyll *a*	**0.7**	**33.3**	**5.04**	**78**	n/a				0.3	15.4	3.0	71
TN	**150**	**940**	**400**	**160**	130	541.3	242	84	**102**	**1509**	**540**	**71**
TP	2	62	16	92	2.7	44.7	9.5	86	2.6	34	11.5	71
TN:TP	n/a				7.6	61.7	31.9	84	**15**	**130**	**52**	**71**

B.

Lake Morphometry	Riera et al. 2000				Quilan et al. 2003				This Study			
	min	max	mean	n	min	max	mean	n	min	max	mean	n
Max Depth	**0.3**	**35.1**	**8.8**	**314**	**4.5**	**93**	**30.4**	**86**	3	36	14	71
Mean Depth	**1.8**	**15**	**5.6**	**59**	n/a				1.5	15.2	5.2	66
Lake area	**0.3**	**1568**	**46.7**	**556**	**5.4**	**1675**	**243.1**	**86**	**20.3**	**8124**	**309.2**	**71**
SDF	**1.01**	**4.21**	**1.39**	**556**	n/a				**1.0**	**4.9**	**2.1**	**71**

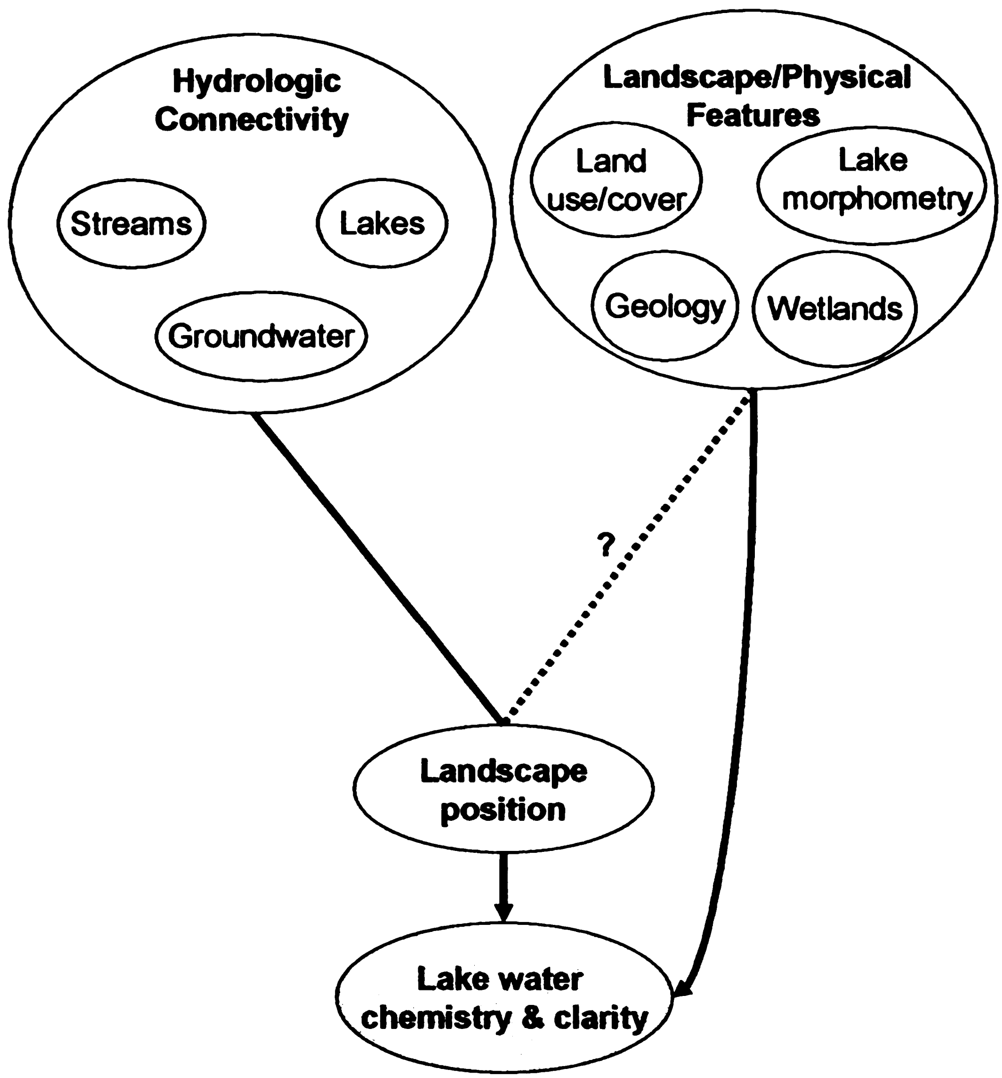
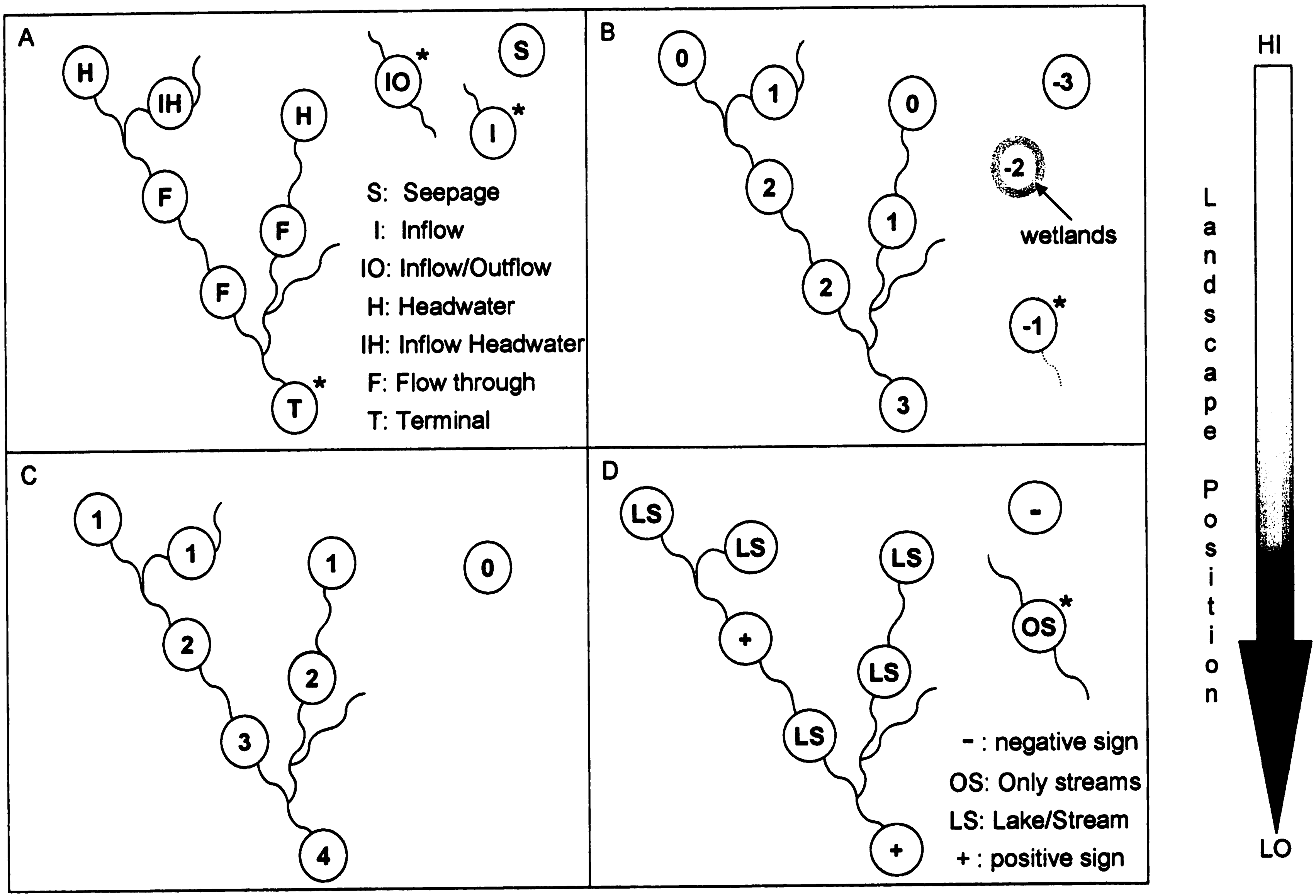


Figure 1. Conceptual framework for the linkages among hydrologic connections, landscape/physical features, landscape position and in-lake variables. Solid line and arrow indicates linkages found in published studies. Dotted line indicates additional linkages examined in this study.

Figure 2. Description of landscape position metrics. A) Lake Hydrology (LH). B) Lake Order (LO). C) Lake Network Number (LNN). D) Lake Network Complexity (LNC). See text for further descriptions. Categories not included in this study are indicated with * .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S: Seepage
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IO: Inflow/Outflow
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IH: Inflow Headwater
F: Flow through
T: Terminal
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-
OS
- : negative sign
OS: Only streams
LS: Lake/Stream
+ : positive sign
HI
Landscape Position
LO

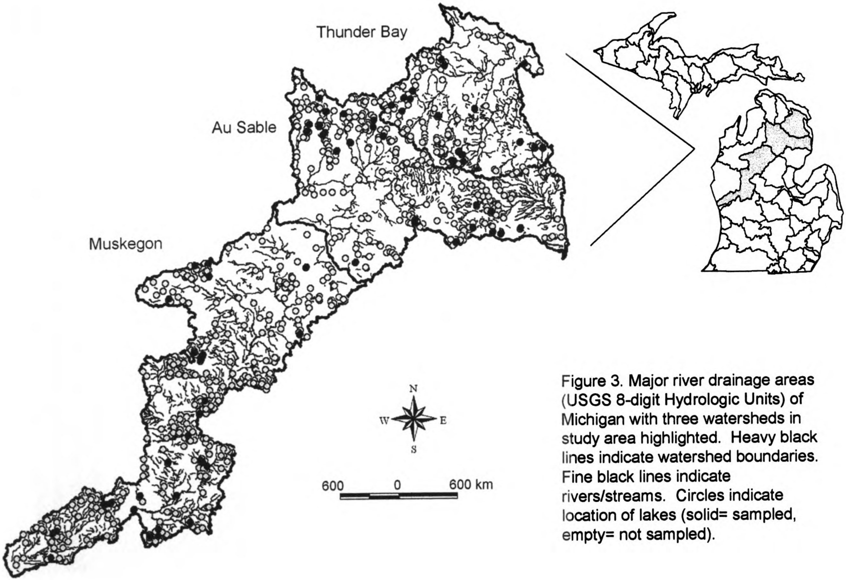


Figure 3. Major river drainage areas (USGS 8-digit Hydrologic Units) of Michigan with three watersheds in study area highlighted. Heavy black lines indicate watershed boundaries. Fine black lines indicate rivers/streams. Circles indicate location of lakes (solid= sampled, empty= not sampled).

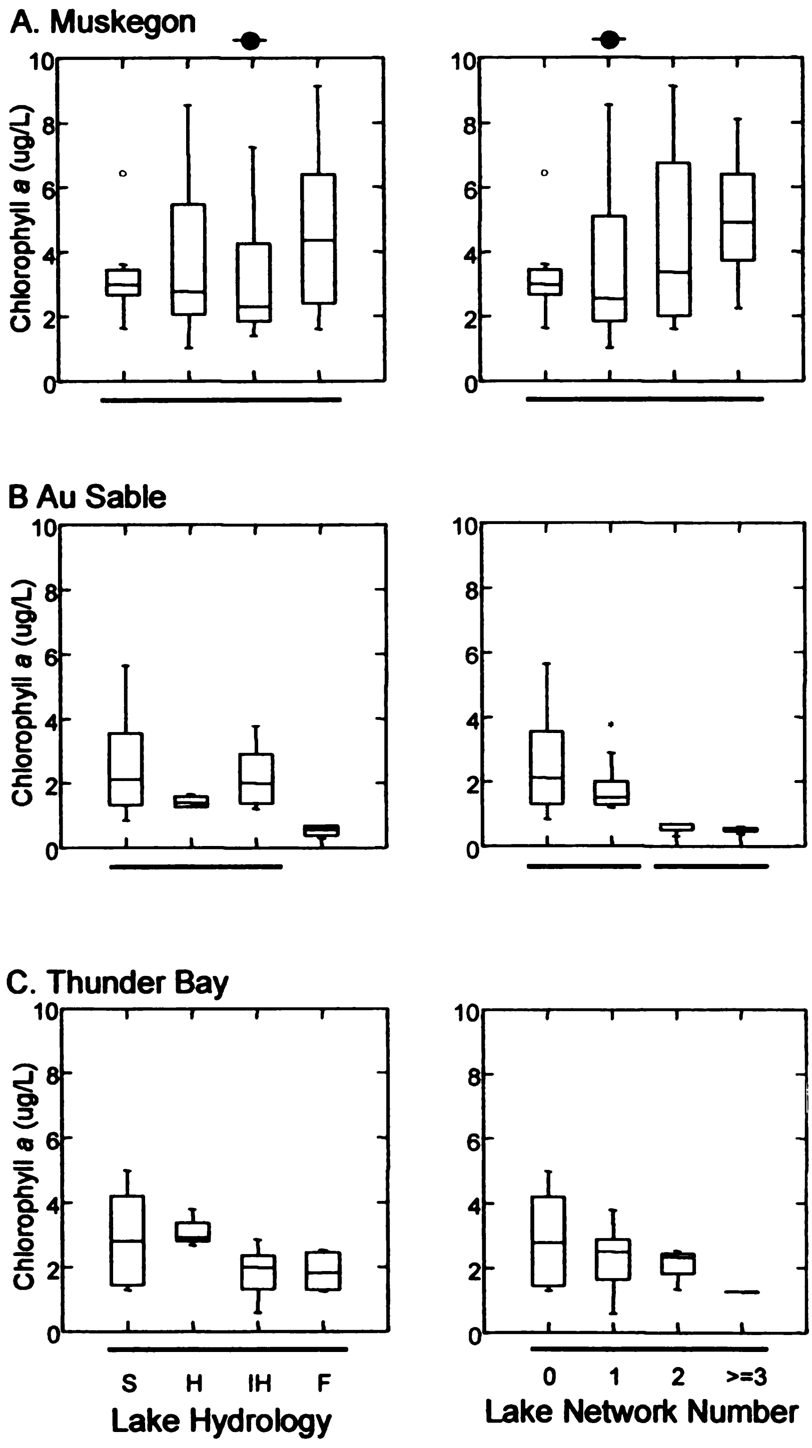


Figure 4. Box-plots of lake hydrology and lake network number versus chlorophyll *a* for each individual watershed: (A) Muskegon, (B) Au Sable, and (C) Thunder Bay. Solid lines show categories not significantly different using Tukey multiple means comparisons. Some data points were omitted for graphical purposes indicated by -●-.

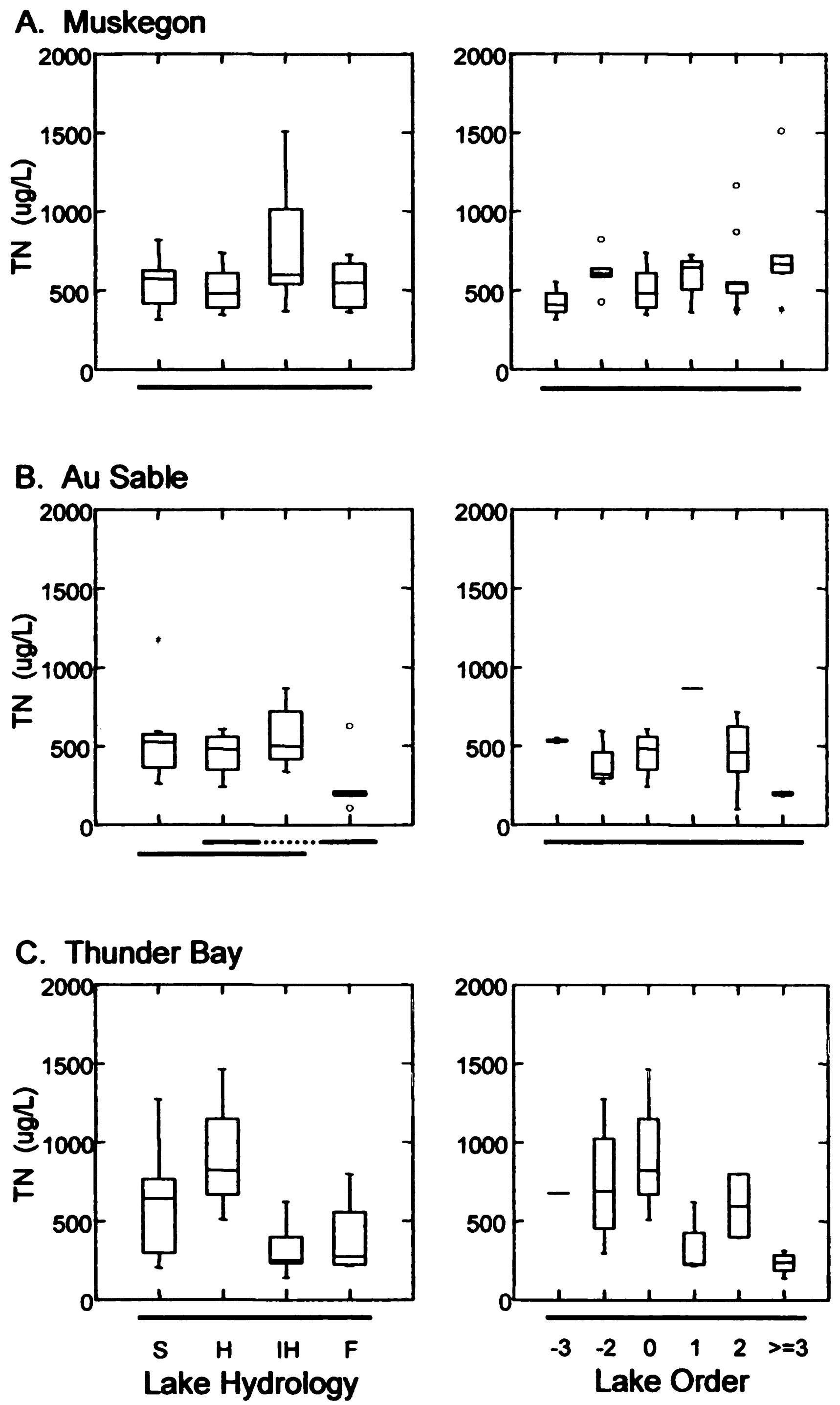
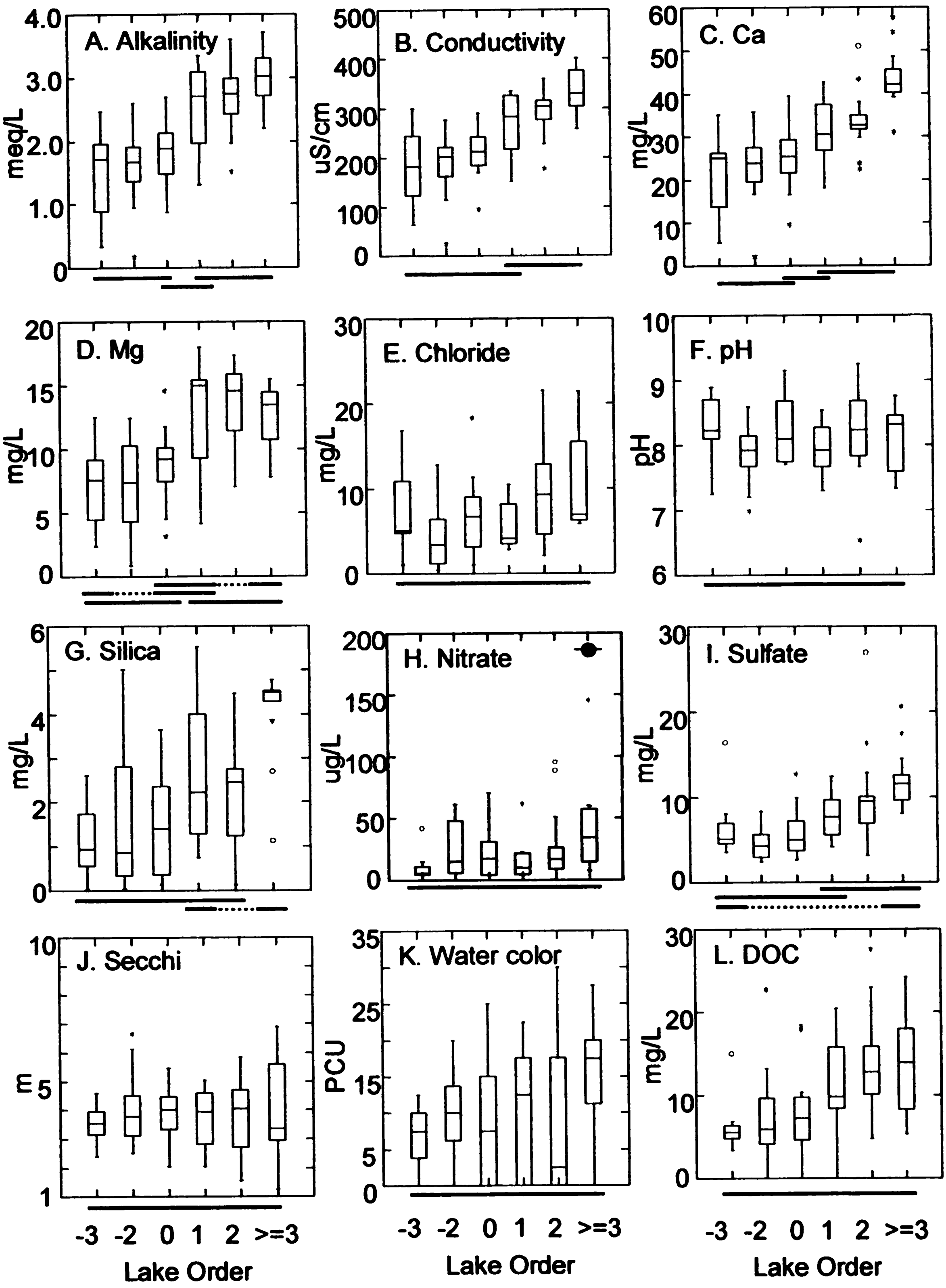


Figure 5. Box-plots of lake hydrology, and lake order versus total nitrogen for each individual watershed: (A) Muskegon, (B) Au Sable, and (C) Thunder Bay. Solid lines show categories not significantly different using Tukey multiple means comparisons, and dotted lines indicate non-contiguous categories that are not significantly different.

Figure 6. Box-plots of LO versus all lake response variables: (A) alkalinity, (B) calcium, (C) magnesium, (D) chloride, (E) pH, (F) conductivity, (G) silica, (H) nitrate, (I) sulfate, (J) Secchi, (K) water color, (L) DOC, (M) chlorophyll *a*, (N) TN, (O) TP, and (P) TN:TP ratio. Solid lines show categories not significantly different using Tukey multiple means comparisons, and dotted lines indicate non-contiguous categories that are not significantly different. Some data points were omitted for graphical purposes indicated by -●- .



A. Alkalinity
meq/L
B. Conductivity
uS/cm
C. Ca
mg/L
D. Mg
mg/L
E. Chloride
mg/L
F. pH
pH
G. Silica
mg/L
H. Nitrate
ug/L
I. Sulfate
mg/L
J. Secchi
m
K. Water color
PCU
L. DOC
mg/L
-3 -2 0 1 2 >=3
Lake Order

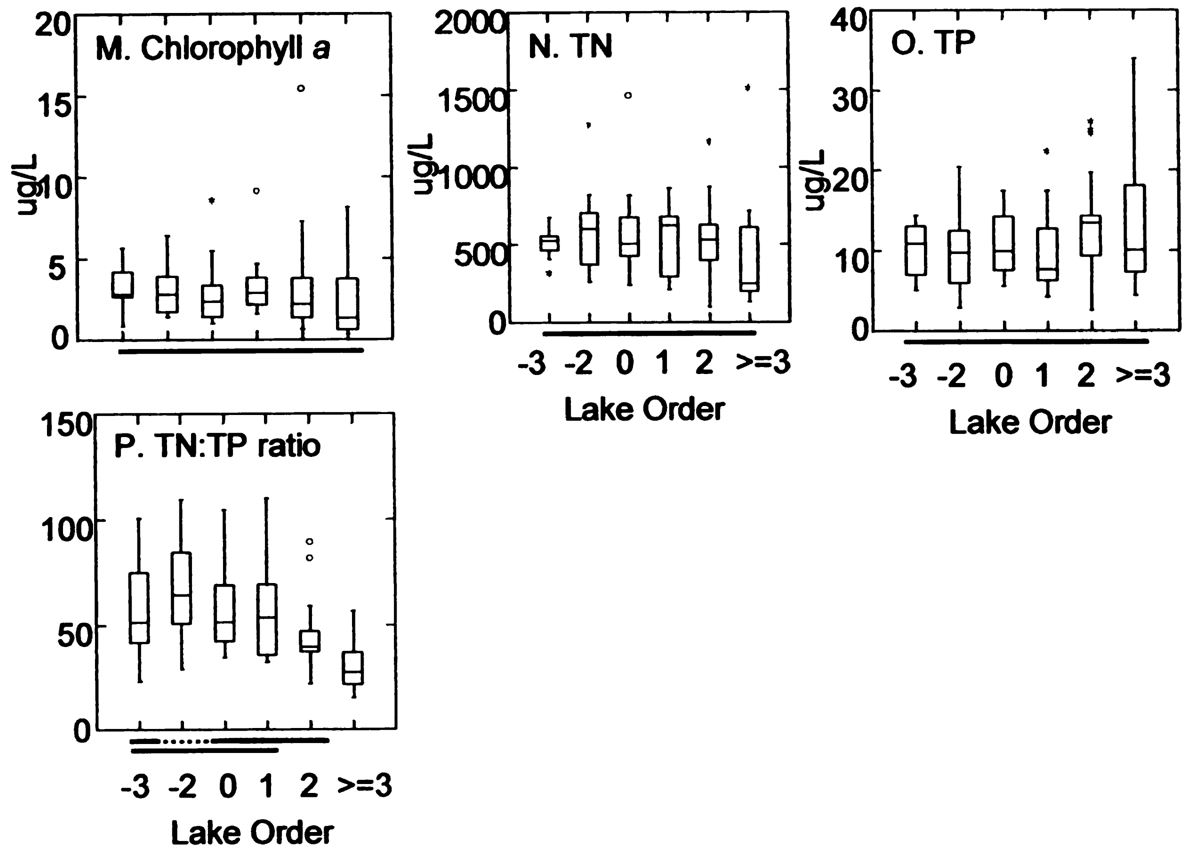


Figure 6 cont.

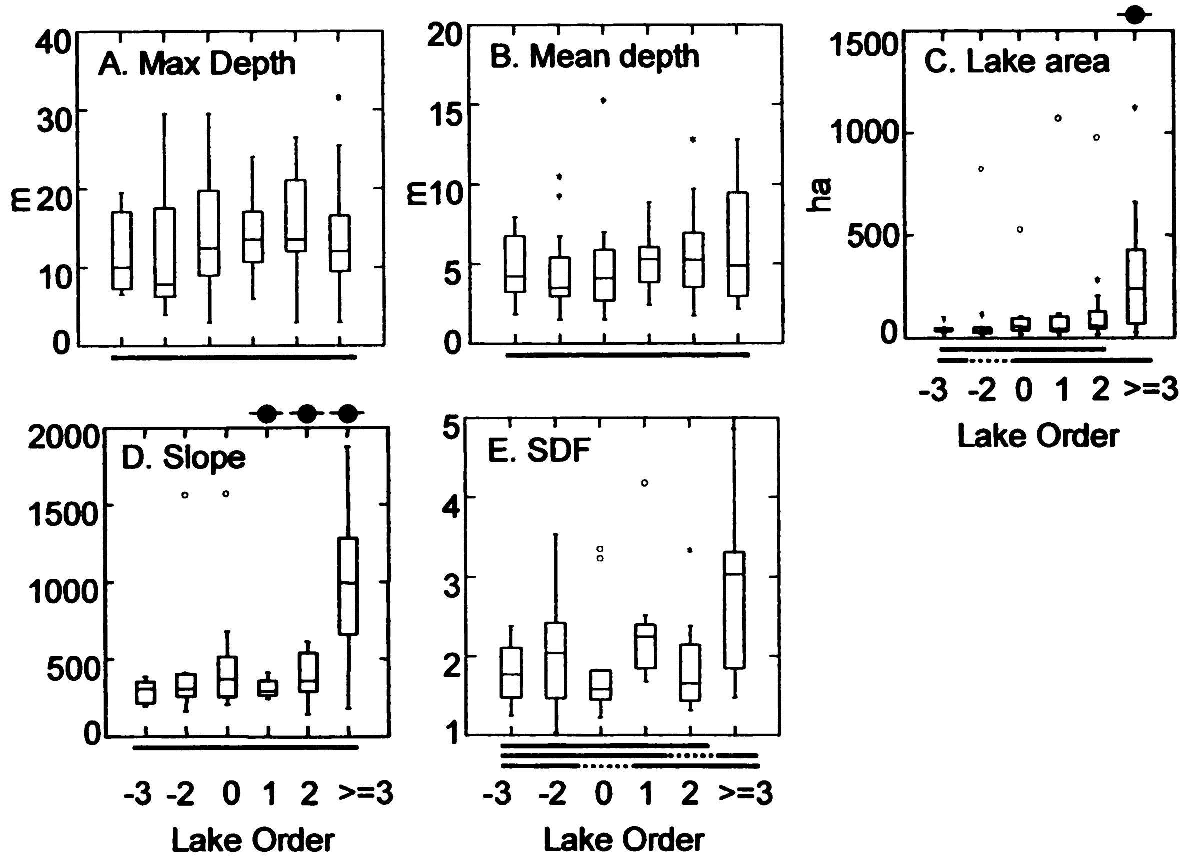


Figure 7. Box-plots of LO versus morphometry variables: (A) maximum depth, (B) mean depth, (C) lake area, (D) lake basin slope, and (E) shoreline development factor (SDF). Solid lines show categories not significantly different using Tukey multiple means comparisons, and dotted lines indicate non-contiguous categories that are not significantly different. Some data points were omitted for graphical purposes indicated by -●-.

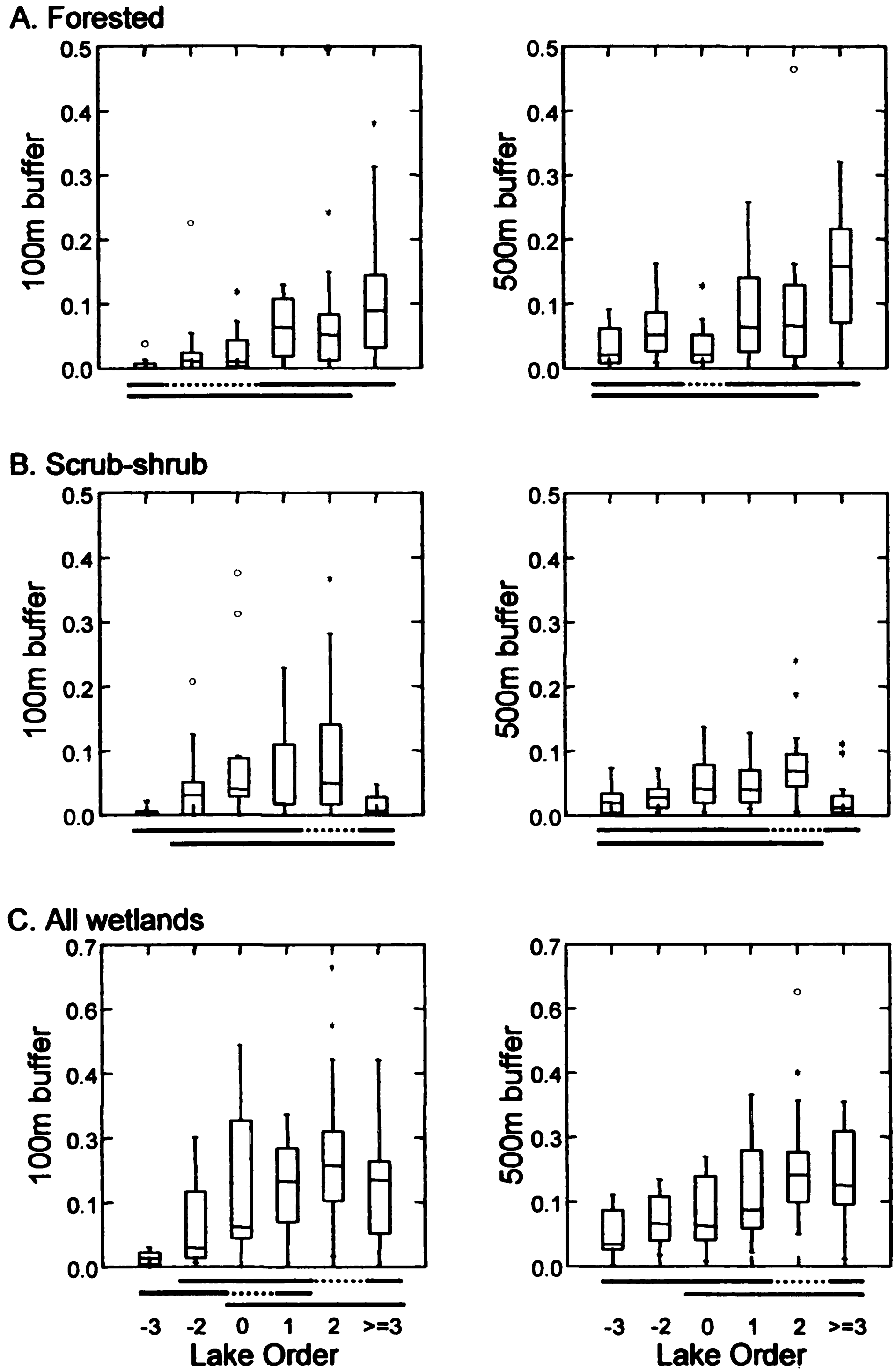


Figure 8. Box-plots of lake order versus proportion of wetland types in the 100m and 500m area surrounding the study lakes: (A) forested wetlands, (B) scrub-shrub wetlands, and (C) all wetland types. Solid lines show categories not significantly different using Tukey multiple means comparisons, and dotted lines indicate non-contiguous categories that are not significantly different. Note differences in scale.

APPENDIX

Table 7. ANOVA results for selected landscape/physical features versus all lake response variables. SDF and 100m scrub-shrub did not have any significant results. Some variables required a 2-way ANOVA model (^) due to significant interaction term (see methods for further explanation) . P-values and R2 are provided and are bolded if significant (less than or equal to 0.01). Positive/negative relationship with increasing landscape position (from high to low in landscape) indicated by +/- signs. "ns" indicates not significant.

Table 7.

Dissolved Conservative Ions	Morphometry Lake area			Wetland type 100m Forested			100m All types			500m Scrub-shrub			500m All types		
	p	R^2		p	R^2		p	R^2		p	R^2		p	R^2	
Alkalinity	**0.007**	0.10	+	**0.001**	0.21	+	0.015	0.08	ns	0.195	0.03	ns	0.025	0.07	ns
Conductivity	**0.002**	0.13	+	**0.000**	0.25	+	0.045	0.06	ns	0.150	0.03	ns	0.070	0.05	ns
Calcium	0.015	0.08	ns	**0.000**	0.33	+	0.012	0.09	ns	0.045	0.06	ns	0.016	0.08	ns
Magnesium	0.027	0.07	ns	0.011	0.13	ns	0.045	0.06	ns	0.661	0.00	ns	0.133	0.03	ns
Chloride	**0.001**	0.15	+	0.509	0.01	ns	0.373	0.01	ns	0.707	0.00	ns	0.516	0.01	ns
pH	0.110	0.04	ns	0.039	0.09	ns	0.640	0.00	ns	0.737	0.00	ns	0.952	0.00	ns
Dissolved Reactive Ions															
Silica	0.031	0.07	ns	**0.001**	0.22	+	**0.003**	0.35	^ +	0.066	0.05	ns	**0.001**	0.16	+
Nitrate	0.851	0.00	ns	0.692	0.00	ns	0.489	0.01	ns	0.333	0.02	ns	0.903	0.00	ns
Sulfate	**0.004**	0.11	+	**0.008**	0.14	+	0.926	0.00	ns	0.040	0.06	ns	0.847	0.00	ns
Water Clarity															
Secchi	0.984	0.00	ns	0.442	0.01	ns	0.672	0.00	ns	0.087	0.32	^ ns	0.835	0.00	ns
Water color	0.296	0.02	ns	0.021	0.11	ns	**0.007**	0.10	+	0.786	0.00	ns	**0.004**	0.12	+
DOC	0.163	0.03	ns	**0.000**	0.24	+	**0.000**	0.18	+	0.540	0.01	ns	**0.004**	0.12	+
Productivity															
Chlorophyll *a*	0.031	0.43	^ ns	0.030	0.09	ns	0.461	0.01	ns	**0.004**	0.12	+	0.194	0.02	ns
Total nitrogen	0.024	0.07	ns	**0.007**	0.14	-	0.484	0.01	ns	0.068	0.05	ns	0.311	0.02	ns
Total phosphorus	0.854	0.00	ns	0.257	0.03	ns	0.363	0.01	ns	0.332	0.01	ns	0.466	0.01	ns
TN:TP ratio	**0.003**	0.12	-	0.037	0.09	ns	0.056	0.05	ns	0.321	0.02	ns	0.038	0.06	ns

Because some measures of lake morphometry and the presence and magnitude of wetlands were significantly related to lake order, I examined whether these landscape features alone could explain variation in lake response variables. I ran regressions (ignoring watershed) and ANCOVA's (with watershed as a covariate), using landscape/physical features as the predictors in these new analyses, and lake water chemistry/clarity variables were used as the response variables. I found that lake area and the presence and magnitude of wetlands explained a significant amount of variation in some dissolved conservative ions and dissolved reactive ions, but the explanatory power of these direct relationships was far lower than of landscape position (Tables 3 and 7). For example, the presence and magnitude of forested wetlands in the 100m buffer area explained 33% of variation in calcium concentrations, whereas lake order explained 53%. These results suggest the use of landscape position instead of directly modeling the relationship between landscape features and these lake response variables. However, for some productivity and water clarity variables, which were not related to landscape position, I did find direct relationships to landscape features. In particular, DOC, chlorophyll *a* and TN were all related to some measure of wetland connection (Table 7).

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