Available online at www.sciencedirect.com

SCIENCE DIRECT®

Ecological Modelling 192 (2006) 385–409

ECOLOGICAL MODELLING

www.elsevier.com/locate/ecolmodel

Exploring ecological patterns with structural equation modeling and Bayesian analysis

G.B. Arhonditsis[a,*], C.A. Stow[b], L.J. Steinberg[c], M.A. Kenney[a], R.C. Lathrop[d], S.J. McBride[a], K.H. Reckhow[a]

[a] *Nicholas School of the Environment and Earth Sciences, Duke University, Durham, NC 27708, USA*
[b] *Department of Environmental Health Sciences, Arnold School of Public Health, University of South Carolina, Columbia, SC 29208, USA*
[c] *Department of Civil and Environmental Engineering, Tulane University, New Orleans, LA 70118, USA*
[d] *Wisconsin Department of Natural Resources and Center for Limnology, University of Wisconsin, Madison, WI 53706, USA*

Received 7 December 2004; received in revised form 26 May 2005; accepted 18 July 2005

Abstract

Structural equation modeling is a multivariate statistical method that allows evaluation of a network of relationships between manifest and latent variables. In this statistical technique, preconceptualizations that reflect research questions or existing knowledge of system structure create the initial framework for model development, while both direct and indirect effects and measurement errors are considered. Given the interesting features of this method, it is quite surprising that the number of applications in ecology is limited, and even less common in aquatic ecosystems. This study presents two examples where structural equation modeling is used for exploring ecological structures; i.e., summer epilimnetic phytoplankton dynamics. Both eutrophic (Lake Mendota) and mesotrophic (Lake Washington) conditions were used to test an initial hypothesized model that considered the regulatory role of abiotic factors and biological interactions on lake phytoplankton dynamics and water clarity during the summer stratification period. Generally, the model gave plausible results, while a higher proportion of the observed variability was accounted for in the eutrophic environment. Most importantly, we show that structural equation modeling provided a convenient means for assessing the relative role of several ecological processes (e.g., vertical mixing, intrusions of the hypolimnetic nutrient stock, herbivory) known to determine the levels of water quality variables of management interest (e.g., water clarity, cyanobacteria). A Bayesian hierarchical methodology is also introduced to relax the classical identifiability restrictions and treat them as stochastic. Additional advantages of the Bayesian approach are the flexible incorporation of prior knowledge on parameters, the ability to get information on multimodality in marginal densities (undetectable by standard procedures), and the fact that the structural equation modeling process does not rely on asymptotic theory which is particularly important when the sample size is small (commonly experienced in environmental studies). Special emphasis is given on how this Bayesian methodological framework can be used for assessing eutrophic conditions and assisting water quality management. Structural

---

[*] Corresponding author at: Department of Physical and Environmental Sciences, University of Toronto, Toronto, Ont., Canada M1C 1A4. Tel.: +1 416 208 4858; fax: +1 416 287 7279.

E-mail addresses: georgear@duke.edu, georgea@utsc.utoronto.ca (G.B. Arhonditsis).

doi:10.1016/j.ecolmodel.2005.07.028

equation modeling has several attractive features that can be particularly useful to researchers when exploring ecological patterns or disentangling complex environmental management issues.

Keywords: Structural equation modeling; Ecological patterns; Bayesian analysis; Phytoplankton dynamics; Water quality management

1. Introduction

"...Thinking only in terms of directly observable variables confines our horizons and limits our assessment of complex systems..." (Malaeb et al., 2000, Environmental and Ecological Statistics, pg 95)

Mechanistic understanding and prediction of patterns is a key feature in ecological research (Peters, 1991; Jorgensen, 1997; Pace, 2001; Carpenter, 2002; Arhonditsis and Brett, 2005). Given the hierarchical structure of biological information, observations in a particular study scale are usually associated with upper-level joint behaviors and lower-level processes, thus it is essential for ecologists, when exploring patterns, to be able to shift between different scales of description in space, time, and organizational complexity (Sugihara and May, 1990; Levin, 1992). For example, Vepsalainen and Spence (2000) advocated the development of "general explanatory frameworks" that comprise (i) the focal level, defined by the pattern/process of interest, and (ii) the contiguous lower and upper levels, associated with the initiating conditions and boundary constraints, respectively. Recognizing the intertwined nature of ecological hierarchies, this framework was proposed as a convenient means to select the appropriate level of information for understanding specific observations/events. Similarly, earlier studies by Salthe (1985) and O'Neill et al. (1986) acknowledged the importance of a basic triadic approach, which explicitly considers the effects of slow, larger-scale and fast, smaller-scale processes on the focal level observed ecological patterns. The problem of scale can also be raised from our inability to measure with absolute accuracy characteristics and properties of conceptual interest (McCune and Grace, 2002). Ecologists are frequently interested in processes that cannot be measured effectively by one single variable, and a common way to address this problem is to perceive the ecological concept as a nested hierarchy that can be decomposed into an infinite number of subprocesses and causal interactions. The premise behind this partitioning is that the selective measurement of some of these elements can improve our understanding about the collective behavior/mechanism. The attempt to abstract essential features and reduce the complexity of the real world is ubiquitous in ecological practice. Levin (1992) characterized the study of the transferability of ecological phenomena across scales and the development of laws of simplification and aggregation as a central problem in ecology and evolutionary biology.

Modeling as a tool for elucidating ecological patterns is subject to the same problem of complexity, and the optimal model dimension has been extensively debated in the ecological literature (Levins, 1966; Costanza and Sklar, 1985; Rastetter et al., 1992; Jorgensen, 1999; Reckhow, 1999; Arhonditsis and Brett, 2004). Applied ecologists are inclined to select realism and precision in favor of generality; driven by technical or conceptual limitations, they adopt "intuitively manageable scales" and develop models that aim to provide "faithful descriptions" of the data (Vepsalainen and Spence, 2000). A characteristic example is the application of regression analysis for analyzing data from experimental/observational studies and the use of the best-fit model for inference and hypothesis testing. While useful for investigating causality in nature, regression models have several limitations: (i) the predictor variables are assumed to be free of measurement error or uncontrolled variation, (ii) the assumption of normality is frequently violated by the errors in the resultant models, and (iii) hypotheses are formulated in a way that solely allow for the inclusion of directly observed variables (Malaeb et al., 2000). Therefore, it is increasingly recognized that what is missing from the common ecological practice is a statistical technique with the ability to unravel complex interrelationships and aid generalization and theory testing by relaxing some of these restrictions.

Structural equation modeling (SEM) is a method that can address several of the above restrictions, providing a robust technique for studying interdependencies among a set of correlated variables. We believe that it is well suited to provide insight into the relationships of the often correlated and error-contaminated physical, chemical, and biological variables in ecological research. To that end, we developed and tested a conceptual model concerning the regulatory role of abiotic conditions and biological interactions on lake phytoplankton dynamics and water clarity during the summer-stratified period in Lake Washington and in Lake Mendota. Our objectives are: (1) to assess the adequacy of this conceptual model, (2) to examine the value of structural equation modeling in empirical confirmation of scientific hypotheses, and (3) to discuss how this multivariate statistical method can be combined with Bayesian analysis and assist natural resource management.

2. Methods

2.1. Structural equation modeling

SEM is a multivariate statistical methodology that encompasses factor and path analysis (McCune and Grace, 2002; Pugesek et al., 2003). Even though the major advancements towards generalization of the method occurred after the 1970s (Keesling, 1972; Jöreskog, 1973), attempts to analyze multiple causal pathways and partition direct and indirect relationships among variables date back approximately 80 years (Wright, 1918; Wright, 1921). In contrast with multivariate regression, SEM allows the user to explicitly test indirect effects between two explanatory variables, where effects between two variables can be mediated by another intermediary variable (e.g., Bollen, 1989a; Kline, 1998). Additionally, SEM can explicitly incorporate uncertainty due to measurement error or lack of validity of the observed variables. The latter aspect refers to the essential feature of allowing theoretical uni- or multidimensional concepts to be amalgamated into single entities of variant “degrees of abstraction” (e.g., phytoplankton or zooplankton community versus environmental degradation or ecosystem health). More specifically, SEM can represent variables of conceptual interest that are not directly measurable, by using multiple indicator (observed) variables. An aquatic ecosystem example is the combination of several indicators such as photosynthetic pigments (chlorophylls, carotenoids), primary productivity, algal biovolume or carbon biomass, to model the latent (unobservable) variable “phytoplankton”. However, Bollen (1989a) emphasized the need for caution when developing latent variable models and discussed several validity tests for examining the correspondence between concepts and observed variables. It should be noted that principal component analysis has also the ability to reduce a set of correlated variables to higher-order components but has a limited flexibility to specify the model structure prior to the analysis and does not account for measurement error (McCune and Grace, 2002).

SEM is an “a priori” statistical technique, where the modeler proposes and tests a hypothesized structure/mechanism that usually reflects existing knowledge. The formulation of this initial model creates an expected covariance structure, which is tested against the covariance matrix from observed data. The null hypothesis H_0 that formalizes the idea of structural equation modeling is:

$$H_0 : \Sigma = \Sigma(\theta) \tag{1}$$

where Σ is the population (or sample) covariance matrix of observed variables, θ is a vector that contains the model parameters, and $\Sigma(\theta)$ is the model-implied covariance matrix (Bollen, 1989a). In contrast with conventional statistical models where rejection of the null hypothesis is sought, the objective of structural equation modeling is *acceptance* of the null hypothesis. Not rejecting H_0, means that existing data support the proposed model (hypothesized covariance structure). The model is fit by minimizing the differences between observed and model-predicted covariances. Commonly used fitting functions include maximum likelihood (ML), unweighted least squares (ULS) and generalized least squares (GLS). Finally, Jöreskog and Sörbom (1993) articulated the important issue of extracting the appropriate inferences from model results, by distinguishing among three situations: (i) *strictly confirmatory*: a single model is formulated and tested against datasets, ideally after model specification. In this case, the model can be accepted or rejected, (ii) *alternative models*: several prespecified models are tested against a single set of data. In this case, one of the models should be selected, and (iii) *model generating*: the analysis starts with a tentative model, which is subject to evaluation and modification. These respecifications should provide meaningful interpretations and the final model needs further confirmation (Raykov, 1992; McCune and Grace, 2002).

2.1.1. SEM applications in ecology

SEM has been extensively applied in research areas including social science, psychology, chemistry, and biology (e.g., Bollen, 1989a; Hair et al., 1995; Hayduk, 1996; Kline, 1998). Applications in ecology and environmental sciences, however, are still limited (e.g., Mitchell, 1992; Smith, 1995; Shipley, 1997; Grace and Pugesek, 1998; Shipley, 2000). For example, Grace and Pugesek (1997) provided an example of exploratory analysis in ecology by developing a general SEM that examined the relative effects of abiotic conditions (e.g., soil salinity, elevation, nutrient content), disturbances (e.g., herbivory) and biomass density on plant species richness. La Peyre et al. (2001) used SEM for evaluating a hypothesized model for national wetland management effort, which explained 60% of the observed variability in 90 nations and highlighted the role of social development for more effective wetland protection.

Even less common is SEM application in aquatic ecosystems and limited number of relevant studies can be found in the literature. In an illustrative application, Malaeb et al. (2000) tested a conceptual model to identify the relationships between four latent (unobserved) variables: sediment contamination (e.g., total PCBs, total pesticides, silt/clay percent), natural variability (e.g., salinity, water clarity), biodiversity, and growth potential (benthic abundance). Besides the good fit of the model, another interesting finding of this study was the positive total effect of natural variability on growth potential, as a result of a negative direct effect and a higher positive indirect mediated through biodiversity. The importance of path analysis when trying to elucidate patterns of causal association was also indicated by Stow and Borsuk (2003); the use of graphical models provided evidence that toxicity of *Pfiesteria*-like organisms was the effect rather than the cause of fishkills. Structural equation modeling was also the major component of a recently introduced methodological framework by Reckhow et al. (2005), which aimed to provide a predictive approach to water quality criteria.

2.1.2. Benefits of Bayesian approach

The importance of considering auxiliary prior information on individual parameters was recognized early in the SEM literature (Martin and McDonald, 1975; Bartholomew, 1981; Lee, 1981). Lee (1981) used a hierarchical Bayesian approach for analyzing the confirmatory factor analytic model, which led to an improvement of the factor loading, factor covariance, and unique variance estimates in comparison with the maximum likelihood method. Subsequent studies considered prior information in the form of stochastic functional relationships among the parameters, i.e., the classical identifiability constraints were restated as stochastic (Lee, 1992; Lee and Ho, 1993). They found that the Bayesian approach with stochastic constraints performed equally well with the classical approach when prior information was available, and provided more robust results when population parameters were misspecified. Scheines et al. (1999) demonstrated how the Bayesian estimation along with informative priors can assist for obtaining posterior distributions for parameters of underidentified models; he replaced a regression model with a SEM where the predictors were measured with substantial error and the available prior information was not sufficient to associate the respective parameters with unique values. An interesting finding of the same study was the ability of the Bayesian approach to identify the existence of more than one local maximum value (multimodality) in the likelihood surface, which were not detectable by the standard procedures (see their example with Wheaton's model). Recent developments in Markov Chain Monte Carlo (MCMC) methods (e.g., see Paap (2002) for an extensive discussion about the computational advantages of MCMC application on latent variable models) have increased the application of Bayesian inference in non-linear factor analysis models (Arminger and Muthen, 1998; Zhu and Lee, 1999) that also account for polytomous (Lee and Zhu, 2000) and dichotomous data (Lee and Song, 2003), or assess the contribution of incomplete datasets to model selection (Lee and Song, 2004). Generally, the advantages of the Bayesian approach over the classical methods are the ability to incorporate prior knowledge about the parameters and the fact that the modeling process does not rely on asymptotic theory (Congdon, 2003). The latter issue is particularly important when the sample size is small (commonly experienced in environmental studies), and thus the classical estimation methods (maximum likelihood, generalized and weighted least squares) are not robust. MCMC samples are taken from the posterior distribution, and as a result the procedure works for all sample sizes and various sources of non-normality.

We formulated a structural model that describes epilimnetic phytoplankton dynamics as the interplay between physical, chemical, and biological factors. The latent and observed variable selection and the model temporal resolution were based on data available from routine monitoring programs (bimonthly samplings, standard limnological variables). This model specification allowed us to assess the adequacy of the underlying information to give plausible results with SEM and identify the relative role of several ecological processes known to regulate water quality variables of management interest. The model is tested in two lakes with different trophic status (i.e., the mesotrophic Lake Washington and the eutrophic Lake Mendota). We also introduced a Bayesian hierarchical framework and tested its results against the classical likelihood approach. Using the same identification conditions and uninformative priors, we firstly compared the consistency between Bayesian, maximum likelihood, and bootstrap estimates. The sensitivity of the structural model results was then evaluated by treating these identification restrictions as stochastic. A brief description of the SEM terminology and typical notation along with the matrix representation of the Lake Washington model is provided in Appendix 1, while the Bayesian SEM configuration is presented in Appendix 2.

We recognize that a single example can only partially cover the general principles of this statistical technique. Thus, our intention is at least to show that SEM's ability to estimate both direct and indirect effects between variables, to account for measurement error, and to simultaneously evaluate several cause-effect relationships warrant its consideration for ecological pattern description. The addition of latent variables enables the linkage between theoretical concepts and observed variables, which provides a defensible method to quantify natural properties of interest measured with uncertainty (Bollen, 1989a). Most importantly, SEM can serve as a useful tool for delineating general abstract theories/hypotheses and transform them into controllable-scale entities that can be incorporated in experimental/observational frameworks. This is particularly important in the field of ecology where the directions of the dependence relationships are largely known and prior knowledge can be easily translated in models testable against present and future datasets (McCune and Grace, 2002).

2.2. *Case study sites*

2.2.1. *Lake Washington*

Lake Washington is the second largest natural lake in the State of Washington, with a surface area of 87.6 km^2 and a total volume of 2.9 km^3. The mean depth of the lake is 32.9 m (maximum depth 65.2 m), the summer epilimnion depth is typically 10 m with a epilimnion: hypolimnion volume ratio of 0.39. The retention time of the lake is 2.4 years on average. Lake Washington is a mesotrophic ecosystem after a successful lake restoration by sewage diversion (Edmondson, 1994). The limnological processes are strongly dominated by a recurrent spring diatom bloom with epilimnetic chlorophyll concentration peaks of 10 μg/L on average, which is 3.2 times higher than the summer-stratified period concentrations (Arhonditsis et al., 2003). Generally, the strongly phosphorus limiting conditions along with the zooplankton grazing pressure sustain summer phytoplankton at an approximate level of 3 μg chl a/L. In its current restored state, Lake Washington has not experienced major cyanobacteria blooms and the summer phytoplankton assemblage on average comprises 26% diatoms (*Aulacoseira*, *Stephanodiscus*, *Asterionella*, *Fragilaria*), 37% chlorophytes (*Oocystis*, *Sphaerocystis*), and 25% cyanobacteria (*Anabaena*, *Anacystis*, *Microcystis*) (Arhonditsis et al., 2003). Thus, Lake Washington provided an environmental set up where we tested the ability of our conceptual model to describe phytoplankton patterns under mesotrophic conditions.

The dataset for SEM development was based on a recent (1994–2001), spatially intensive (12 stations) limnological sampling program carried out by King County/ Metro (http://dnr.metrokc.gov/wlr/waterres/lakes/Wash.HTM). Detailed description of this sampling network along with the analytical methods used is provided elsewhere (Arhonditsis et al., 2003, 2004a).

For this project, we selected data from the deeper parts of the lake and sampling dates that spanned from the onset of thermal stratification until the fall overturn ($n = 57$).

2.2.2. Lake Mendota

Lake Mendota (12.7 m mean depth, surface area of 38.95 km^2 and flushing rate of 0.15 per year) is a culturally eutrophic lake located in south-central Wisconsin, USA. The lake is relatively deep (maximum depth of 25.3 m) and is characterized by a dimictic circulation pattern. Agricultural areas cover a large portion (≈85%) of the lake's watershed (604 km^2 total surface area), while urban and forested areas and wetlands account for the remaining 15%. Agricultural and urban non-point loadings are the dominant external nutrient (mostly P) inputs and have maintained the lake's eutrophic character, despite the diversion of sewage effluents in 1971 (Lathrop et al., 1998). In addition, nutrient intrusions from the hypolimnion (internal loading) play a significant role in the epilimnetic P budget, albeit the high interannual variability in the relative contribution of the various (exogenous versus endogenous) sources (Soranno et al., 1997). The lake has been characterized by the occurrence of cyanobacteria blooms during the summer, while the unsuccessful implementation of several management programs necessitated the adoption of more aggressive non-point pollution reduction strategies (Betz et al., 1997). The summer cyanobacteria assemblage is dominated by colonial and filamentous species, *Aphanizomenon flos-aquae*, *Oscillatoria agardhii,* and *Microcystis aeruginosa*, capable of surface scum formation under appropriate weather and water quality conditions (Lathrop and Carpenter, 1992a; Soranno, 1997). Hence, in contrast with Lake Washington, the eutrophic Lake Mendota provides an alternative environment to detect differences in the relative importance of the various pathways of the hypothesized model of Fig. 1 and its ability to illuminate epilimnetic phytoplankton dynamics.

The dataset used for this analysis was assembled from the Northern Temperate Lakes Long Term Ecological Research (LTER) program (Center for Limnology, University of Wisconsin, Madison). The data were collected approximately twice a month from one station at the deepest part of the lake (for further sampling and methodological details, see http://lterquery.limnology.wisc.edu/index.jsp?project_id=LTER1. SEM development was based on a 5-year period (1997–2001), when consistent measurements for all the observed variables of the conceptual model existed in the dataset.

2.2.3. Statistical assumptions and data transformations

The datasets used for SEM development were collected from conventional monitoring programs with moderate sampling intensity during the summer period (i.e., once or twice a month), which was also the temporal resolution of our study (no time-averaging was considered). For maximum likelihood estimation, the χ^2-test is the commonly used goodness-of-fit measure where the observed variables are assumed to follow a multivariate normal distribution. We tested for both univariate and multivariate normality (skewness and kurtosis) and applied transformations when necessary. Multivariate kurtosis was examined with Mardia's coefficient (Mardia, 1974). We also examined for influential observations and outliers before and after transformations were applied. The squared Mahalanobis distance was used as a screening test for detecting multidimensional outliers (Legendre and Legendre, 1983). According to this distance measure, the deviation d_i^2 of the i-th observation from the centroid of all observations, is given by the formulation:

$$d_i^2 = (x_i - \bar{x})' \hat{S}^{-1} (x_i - \bar{x}) \qquad (2)$$

where x_i is the i-th observation on the p observed variables, $\bar{x}$ is the vector of their means, and $\hat{S}^{-1}$ is the unbiased estimate of their population covariance matrix. The overall mean of each observed variable was also used to fill gaps in the dataset due to missing values. The number of missing values was less than 2% of the existing data, and thus the use of the respective means did not cause distortions (shrinking) of the variances (Malaeb et al., 2000). Finally, no significant problems of temporal autocorrelation were found in the datasets, and thus the independent observations assumption was not violated.

2.2.4. The conceptual model

Our conceptual model considers the regulatory role of abiotic conditions and biological interactions on lake phytoplankton dynamics and water clarity during the summer-stratified period (Fig. 1). Abiotic condi-

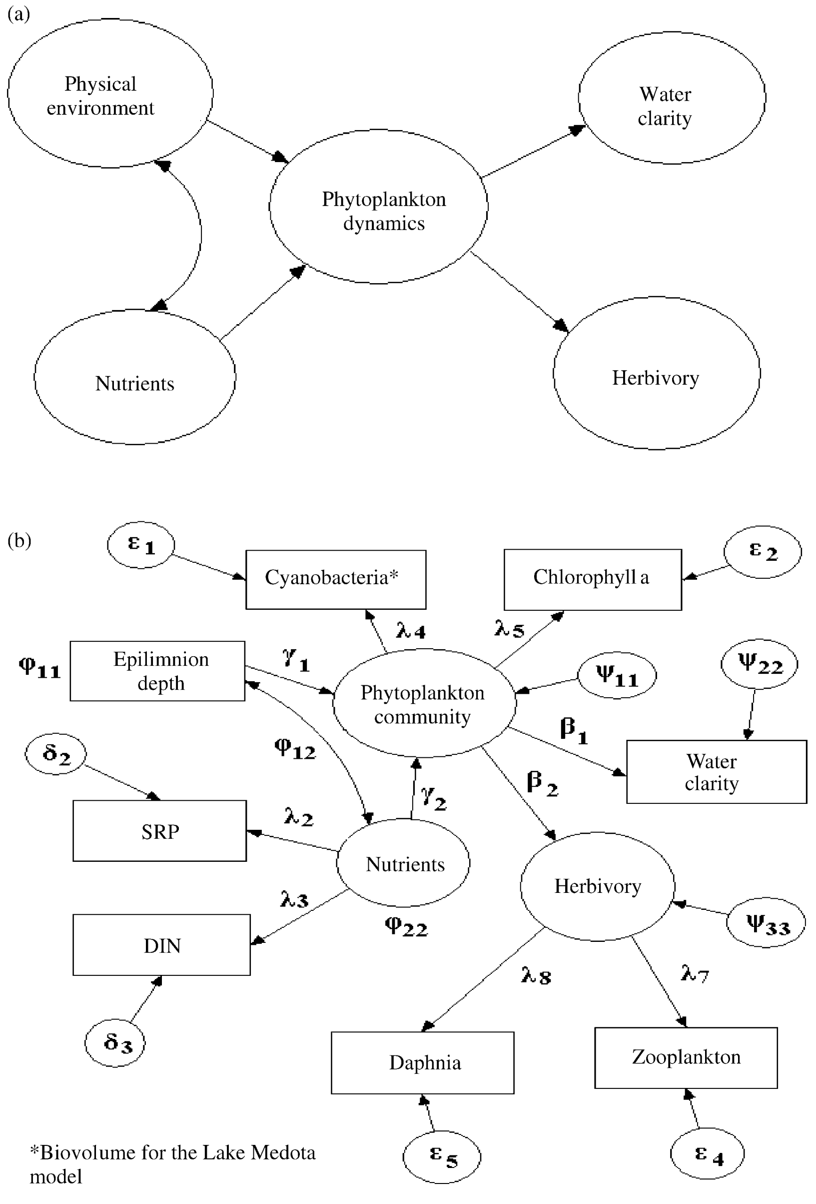

Fig. 1. (a) The hypothesized conceptualization and (b) the actual structural equation model used for predicting epilimnetic phytoplankton dynamics. The use of a rectangular box for the epilimnion depth and the water clarity implies that the variable was considered as directly observable with no measurement error ($\lambda_1 = \lambda_6 = 1.0$, and $\delta_1 = \varepsilon_3 = 0$). The metrics of the latent variables were set by fixing $\lambda_2 = \lambda_5 = \lambda_8 = 1.0$. The notation is similar to that in Appendix 1.

tions refer to the physical and chemical properties of the epilimnetic environment, and our intention is to examine the relative importance of their effects on the phytoplankton community. We hypothesized that the physical environment will be represented by the changes of the epilimnion depth (defined as the depth where the temperature change was $\geq 1\,^{\circ}\mathrm{C\,m^{-1}}$). For simplicity, we did not include other surrogate variables of the physical environment (e.g., the Schmidt stability index), although we recognize that the present indicator does not reflect the entire range of macro- and microscale advection and diffusion processes that can occur in a lake's epilimnion. The latent variable nutrients along with the two indicator variables soluble reactive phosphorus (SRP) and dissolved inorganic nitrogen (DIN) concentrations comprised the measurement model for the chemical environment. Zooplankton grazing pressure on phytoplankton represented the food–web interactions. We used the latent variable herbivory and two surrogate variables: the first, referred to as total zooplankton included all the herbivorous zooplankton species, while the second included only *Daphnia* species. Both herbivory indicator variables were formed as the sum of the species abundances (expressed as organisms per litre) weighted by the respective mean lengths (Carpenter et al., 1996). Secchi transparency was considered as a perfect measure (no measurement error) of water clarity, and thus we only considered the latent (structural) error in the equation that relates phytoplankton to water clarity. Due to differences in data availability, the physical interpretation of the latent variable phytoplankton were different between the two case studies because different indicators were used (Lake Washington and Lake Mendota). For the Lake Mendota SEM, we included two measures of phytoplankton (i.e., chlorophyll a and total algal biovolume), which resulted in a quantitative configuration of the phytoplankton latent variable. In contrast, the Lake Washington SEM development was based on the combination of two variables, chlorophyll a and a polytomous characterization of cyanobacteria abundance. Therefore, the respective latent variable was labeled as phytoplankton community to stress the dual nature (phytoplankton abundance and composition) of this measurement model. Aside from this difference, the application and evaluation of the model was strictly confirmatory; the model was constructed in advance to accommodate current knowledge of the epilimnetic phytoplankton dynamics, no changes (i.e., number of latent variables, direct or indirect effects between latent and observed variables) were made during the application, and the prespecified model's fit was assessed against the two datasets (Bollen, 1989a). Thus, our strategy differs from the usual two-step approach, where SEM development starts with testing the fit of the measurement models to the data and then proceeds to the structural equation model (Anderson and Gerbing, 1992; Malaeb et al., 2000). Finally, for the sake of simplicity, we adopted a recursive approach (i.e., all causal effects were unidirectional and the disturbances were uncorrelated), but we recognize that some of the considered ecological paths would be more realistically represented by a non-recursive model.

3. Results and discussion

3.1. Lake Washington

Variance resolution for phytoplankton (24%), herbivory (31%) and water clarity (32%) (Fig. 2) was relatively low. The χ^2-test statistic value was 27.795 with 17 d.f. with a p-value of 0.047. [Note that a significant χ^2 value calls for rejection of the proposed model.] The root mean square error of approximation (RMSEA) was 0.106, which under the null hypothesis of "close fit" (i.e., RMSEA is no greater than 0.05 in the population) corresponds to a p-value of 0.108. Based on their experience, Browne and Cudeck (1993) argued that a value of about 0.08 or less for the RMSEA would indicate a close fit, while a model with a RMSEA greater than 0.1 would not be satisfactory. The values of the incremental fit index (IFI; Bollen, 1989b) and comparative fit index (CFI; Bentler, 1990) were 0.858 and 0.834, respectively. These indices provide information for the comparison between the hypothesized and the baseline model and a value close to 1 indicates a good fit. The baseline model is defined as the simplest model that is a reasonable standard for comparison with the tested one. For example, a baseline model can suggest that no common factors underlie the indicators and that the correlations between the observed variables are zero. Generally, the baseline model has a very constrained structure (i.e., many restrictions on the population moments), and thus it is expected to provide a poor fit to the dataset (Bollen, 1989a; Arbuckle, 1995). Finally, Hoelter's critical N test (i.e., the largest sample size for accepting the model) indicated a marginal model rejection (CN = 56) and model acceptance (CN = 68) at the 0.05 and 0.01 significance levels (Hoelter, 1983). The observed variables dissolved inorganic nitrogen and soluble reactive phosphorus were moderately correlated with the latent variable nutrients ($r \approx 0.46$). Chlorophyll a was strongly correlated with phytoplankton ($r \approx 0.75$), while cyanobacteria abundance showed a relatively weak negative corre-

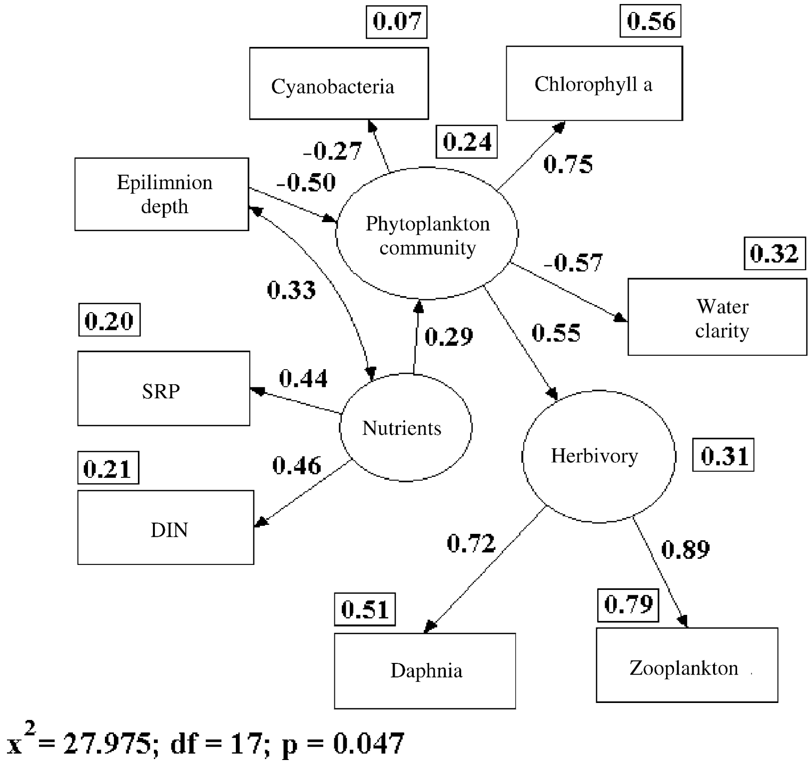

Fig. 2. Structural equation model for Lake Washington ($N = 57$). The numbers correspond to the standardized path coefficients and the R-squared values (numbers in rectangles); χ^2, d.f. and p correspond to the chi-square test values, the degrees of freedom and the probability level for rejecting the null hypothesis, respectively.

lation ($r \approx -0.27$). Both *Daphnia* ($r \approx 0.72$) and total zooplankton ($r \approx 0.89$) length weighted biomass were strongly correlated with the latent variable herbivory.

Generally, there was a good agreement between observed and model-implied values in 30 out of 36 moments of the covariance matrix (Table 1). Six residual covariances were large and the respective standardized estimates (i.e., the residual covariances divided by their standard error) were above one. All the paths between the latent variables of the initial hypothesized structural model were significant with the only exception being the direct path from nutrients to phytoplankton ($p = 0.427$; see Table 2). In addition, the covariance between epilimnion depth and nutrients was positive but non-significant ($p = 0.251$). The standardized direct effect (i.e., the unstandardized partial regression coefficients multiplied by the ratio of the standard deviation of the explanatory variable to the standard deviation of the variable it affects) of the epilimnion depth on phytoplankton was −0.498. The standardized direct paths from phytoplankton to herbivory (0.554) and water clarity (−0.567) were nearly equal in magnitude, but opposite in sign.

Interpreting these results, we highlight the absence of significant linkage between the inorganic nutrient stock and phytoplankton variability in the Lake Washington summer epilimnion. The epilimnion also lacks significant replenishments from the hypolimnion (non-significant covariance between nutrients and epilimnion depth) probably due to the low nutrient levels below the thermocline (DIN $\leq$ 300 μg/L and SRP $\leq$ 15 μg/L; see Lehman, 1988). The two regulatory factors for the phytoplankton community structure are the mixing processes and grazing pressure imposed by the zooplankton community. While the negative path from epilimnion depth to phytoplankton is plausible (i.e., dilution effects of epilimnetic erosion/deepening) the positive relationship with herbivory invites further explanation. During the summer-stratified period, a co-dependence between

Table 1
The analyzed covariance matrix for the Lake Washington model with predicted values and residuals (study periods 1994–2001)

	Epilimnion depth	Secchi depth	log(SRP)	$\sqrt{\text{DIN}}$	Total zooplankton	*Daphnia*	log(chlorophyll a)	Cyanobacteria
Epilimnion depth								
Observed	12.646							
Predicted	12.646							
Residual	0							
Secchi depth								
Observed	1.029	1.380						
Predicted	0.951	1.380						
Residual	0.078	0						
log(SRP)								
Observed	0.262	−0.061	0.243					
Predicted	0.257	−0.018	0.243					
Residual	0.005	−0.043	0					
$\sqrt{\text{DIN}}$								
Observed	2.593	0.569	0.489	23.900				
Predicted	2.643	−0.189	0.489	23.900				
Residual	−0.049	0.758	0	0				
Total zooplankton								
Observed	−2.976	−1.767	0.430	5.309	23.878			
Predicted	−3.438	−1.603	0.067	0.685	23.878			
Residual	0.462	−0.164	0.363	4.624	0			
Daphnia								
Observed	−0.585	−0.244	0.035	0.106	3.636	1.362		
Predicted	−0.663	−0.309	0.013	0.132	3.636	1.362		
Residual	0.078	0.065	0.022	−0.026	0	0		
log(chlorophyll a)								
Observed	−0.206	−0.123	−0.002	0.088	0.375	0.086	0.052	
Predicted	−0.244	−0.114	0.005	0.049	0.412	0.079	0.052	
Residual	0.038	−0.009	−0.007	0.040	−0.037	0.006	0	
Cyanobacteria								
Observed	13.498	−0.876	0.949	5.936	−7.055	−1.425	−0.539	92.039
Predicted	3.722	1.735	−0.072	−0.742	−6.272	−1.209	−0.446	92.039
Residual	9.775	−2.612	1.021	6.677	−0.783	−0.215	−0.093	0

the phytoplankton and zooplankton community exists in the Lake Washington epilimnion, when a significant portion of the phosphorus supply (60–90%) in the mixed layer is provided by zooplankton excretion (Richey, 1979; Arhonditsis et al., 2004b). Thus, zooplankton nutrient recycling fuels phytoplankton growth, which in turn has a positive feedback and sustains herbivore biomass. Interestingly, the standardized total effects of nutrients differed in sign between cyanobacteria (−0.079 = −0.272 × 0.292) and chlorophyll a (0.219 = 0.751 × 0.292). A possible explanation for this difference is a pattern where small-pulsed nutrient inputs from thermocline migrations/external sources selectively subsidize the taxonomic groups of the Lake Washington phytoplankton community with affinity and velocity competitive advantages (e.g., diatoms, chlorophytes) over cyanobacteria (Sommer, 1989). The use of fully quantitative information will further assist the elucidation of the interspecific phytoplankton response to discrete nutrient fluxes in mesotrophic environments during the stratified period.

We used the modified bootstrap procedure proposed by Bollen and Stine (1992) for testing the Lake Washington SEM. The Bollen and Stine method introduces

Table 2
Comparison of the maximum likelihood, bootstrap ($N = 2000$) and Markov Chain Monte Carlo sampling estimates and standard errors of the Lake Washington model path coefficients and error variances. The second pairs of the Bayesian estimates (medians and respective standard errors) correspond to a limited movement around the three fixed loading coefficients by sampling the normal distribution (1, 1). The notation is similar to that in Appendix 1

Parameters	Symbol	Maximum likelihood		Bootstrap		Markov Chain Monte Carlo sampling			
		Estimate	S.E.	Estimate	S.E.	Median	S.E.	Median	S.E.
Phytoplankton ← Nutrients	γ_2	0.229	0.289	0.345	0.570	0.155	0.299	0.122	0.306
Phytoplankton ← Epilimnion	γ_1	−0.024	0.009	−0.025	0.016	−0.020	0.010	−0.035	0.020
Herbivory ← Phytoplankton	β_2	2.711	1.217	3.190	1.931	2.337	0.995	1.710	1.282
Cyanobacteria ← Phytoplankton	λ_4	−15.225	9.510	−17.776	24.838	−13.761	9.511	−13.710	3.046
Chlorophyll a ← Phytoplankton	λ_5	1.000		1.000		1.000		0.527	0.215
Daphnia ← Herbivory	λ_8	1.000		1.000		1.000		0.929	0.441
Zooplankton ← Herbivory	λ_7	5.186	1.747	6.211	3.730	5.781	1.511	5.146	2.197
DIN ← Nutrients	λ_3	10.294	9.739	14.586	17.329	15.361	12.631	10.640	3.072
SRP ← Nutrients	λ_2	1.000		1.000		1.000		0.476	0.499
Water Clarity ← Phytoplankton	β_1	−3.890	1.371	−4.179	2.228	−3.841	1.281	−2.251	1.095
Var(Nutrients)	φ_{22}	0.047	0.055	0.088	0.172	0.029	0.026	0.037	0.071
Var(Epilimnion)	φ_{11}	12.646	2.390	12.476	2.345	12.572	2.485	12.445	2.474
Covar(Nutrients, Epilimnion)	φ_{12}	0.257	0.224	0.283	0.214	0.154	0.186	0.213	0.233
Var(Phytoplankton)	ψ_{11}	0.022	0.013	0.019	0.024	0.029	0.010	0.060	0.051
Var(Cyanobacteria)	$\mathrm{var}(\varepsilon_1)$	85.248	16.854	79.194	18.640	87.260	18.642	83.403	19.026
Var(Chlorophyll a)	$\mathrm{var}(\varepsilon_2)$	0.023	0.011	0.021	0.022	0.031	0.009	0.035	0.010
Var(Herbivory)	ψ_{33}	0.486	0.225	0.487	0.438	0.466	0.233	0.523	6.978
Var(*Daphnia*)	$\mathrm{var}(\varepsilon_5)$	0.661	0.251	0.601	0.432	0.736	0.226	0.727	0.228
Var(Total Zooplankton)	$\mathrm{var}(\varepsilon_4)$	5.018	5.930	1.990	11.256	2.238	4.087	2.453	4.235
Var(DIN)	$\mathrm{var}(\delta_3)$	18.869	6.230	16.008	9.798	16.624	9.206	12.986	8.886
Var(SRP)	$\mathrm{var}(\delta_2)$	0.196	0.061	0.152	0.078	0.222	0.052	0.221	0.059
Var(Water Clarity)	ψ_{22}	0.937	0.230	0.901	0.278	0.936	0.280	1.016	0.275

a transformation of the data matrix to ensure that the bootstrap samples will not be drawn from a set of observations for which the null hypothesis does not hold (Bollen and Stine, 1992). As a result, this scheme is more objective than the naïve bootstrapping, and thus H_0 will not be rejected regardless of whether it holds or not for the entire population. We formed 2000 bootstrap samples by taking independent draws with replacement from the transformed dataset. Testing the null hypothesis that the model is correct, we found a $p = 0.048$; comparing the model performance when using the full dataset, the fit was worse 98 out of 2000 bootstrap samples. Interestingly, during the bootstrap procedure several samples resulted in singular covariance matrices, while the standard error for at least three bootstrap estimates ($\mathrm{var}(\varepsilon_4)$, λ_3, λ_4) was notably higher than those from the classical method (Table 2). However, these discrepancies did not alter the inference regarding their significance. The first pairs of Bayesian estimates (medians and respective standard errors) show that the Bayesian SEM provided consistent results with the maximum likelihood method. Fig. 3 presents the comparison between the observed chlorophyll a and total zooplankton abundance and the posterior predictive median, quartiles, and 95% credible sets. In addition, when the assumptions regarding the metrics of the latent variables ($\lambda_2 = \lambda_5 = \lambda_8 = 1$) were relaxed by sampling from the normal distribution (1,1), the interpretation of the structural model remained unaltered. Using the posterior medians, the predicted structural equation models were: $n_1 = -0.035\xi_1 + 0.122\xi_2$, $n_2 = -2.251n_1$, and $n_3 = 1.710n_1$. By comparing the standard error relative to the medians, we infer that the weak relationship between nutrients and phytoplankton was also evident with the Bayesian approach, while the path between phytoplankton and herbivory was still positive but weaker (Table 2). Interestingly, the DIN loading (λ_3) over the latent variable nutrients was stronger after the stochastic treatment of the assumption, whereas the SRP loading (λ_2) was not significant. This finding probably reflects the phosphorus-limiting conditions in Lake Washington

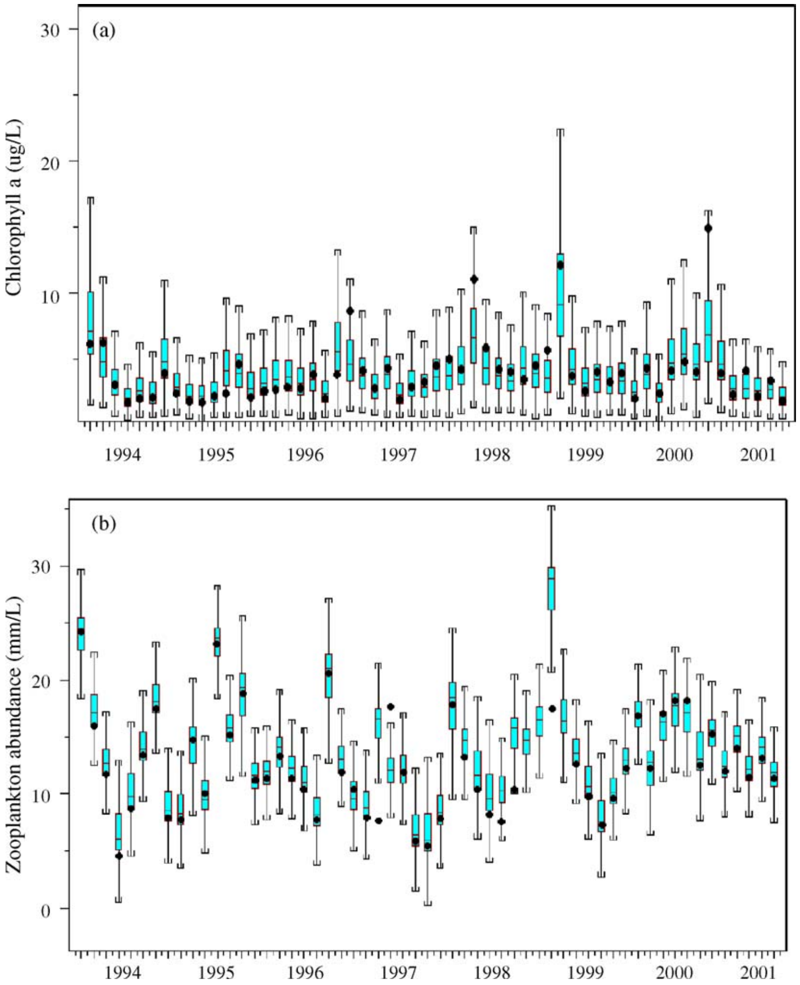

Fig. 3. Comparison between the observed data and the posterior predictive distributions for (a) chlorophyll a and (b) total zooplankton abundance of the Lake Washington SEM.

where SRP is usually below the detection limit and the largest fraction of the phosphorus stock of the system is sequestered in the phytoplankton cells. In contrast, the non-limiting DIN (mostly NO_3) ranges in detectable levels (DIN $\geq 80\ \mu g/L$), and thus seems to more closely portray the phytoplankton fluctuations. Moreover, both herbivory and phytoplankton were strongly associated with their pair of indicator variables.

Generally, even though there were some discrepancies, both the bootstrap testing and the Bayesian approach provided similar results to the maximum likelihood method. The hypothesized conceptualization of the epilimnetic phytoplankton dynamics provided satisfactory results, which were also consistent with the existing Lake Washington literature. However, it should not be neglected that the model explained a relatively low proportion of the observed variability, while several tests of fit were in the marginal area between model acceptance/rejection. We highlight two possible aspects of the model that warrant reconsideration/enhancement:

(i) The inclusion of the soluble form of phoshorus as a sole limiting nutrient indicator in the nutrients measurement model is not sufficient to completely capture the phytoplankton dynamics. In a strongly phosphorus limiting epilimnetic environment, the usually small-sized subsidies from the hypolimnion and/or the zooplankton recycling are rapidly uptaken by the primary producers. As a result, the use of SRP data from a moderate sampling intensity monitoring program provides limited sensitivity in describing the phosphorus-phytoplankton relationship. The incorporation of an additional indicator variable that also accounts for the particulate or organic phosphorus fraction (e.g., TP) is likely to improve the model.

(ii) The dual nature of the latent variable phytoplankton community might be another cause of the moderate model performance. It is possible that the combination of chlorophyll a and cyanobacteria into one common factor is not the most effective way to model phytoplankton response because the relationship of these two variables is not always clear in a mesotrophic environment. Even though it is reasonable to expect an improvement after the inclusion of a fully quantitative cyanobacteria characterization, the description of a stochastic and non-linear phenomenon (i.e., species competition) with a linear and fairly simple model is probably overoptimistic. There are several physical, chemical, biological factors that can affect the phytoplankton composition in the summer epilimnion, which dynamically interact and regulate the growth-minus-loss balance for each phytoplankton group and determine the "superior" competitor under any specific set of conditions (Dokulil and Teubner, 2000; Downing et al., 2001). The recognition of this model limitation raises the classical "simplicity versus complexity" dilemma; the realistic selection of a model that simply focuses on a quantitative description of the phytoplankton community (e.g., the Lake Mendota SEM) or a more complicated non-linear SEM approach that requires several additional latent and

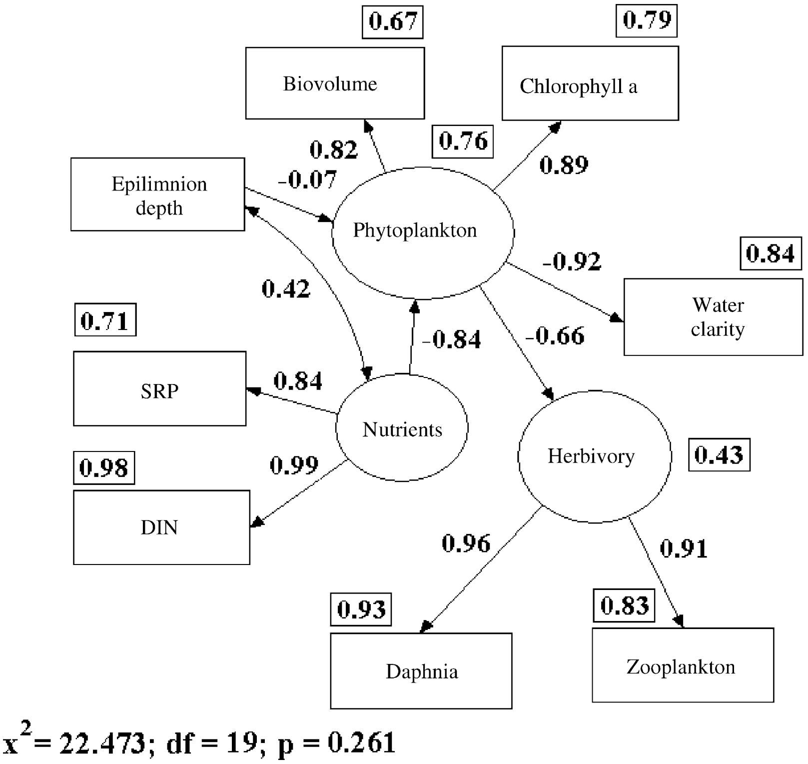

Fig. 4. Structural equation model for Lake Mendota ($N = 48$). The numbers correspond to the standardized path coefficients and the R-squared values (numbers in rectangles); χ^2, d.f. and p correspond to the chi-square test values, the degrees of freedom and the probability level for rejecting the null hypothesis, respectively.

observed variables (e.g., turbulence, pH, TN/TP, CO_2, trace elements, toxins) that can potentially cause cyanobacteria dominance.

3.2. Lake Mendota

In constrast to Lake Washington, the Lake Mendota model accounts for a large amount of the observed variability in phytoplankton (76%), herbivory (43%), and water clarity (84%). The χ^2-test statistic value was 22.473 with 19 d.f. and non-significant p-value (= 0.261) (Fig. 4). In initial maximum likelihood calculation runs, we found that the model yielded several negative error variances. These improper solutions – also referred as “Heywood cases” – can be caused by several factors, e.g., not “typical” samples, outliers or influential observations, and fundamental faults on model specification (Bollen, 1989a). For example, Boomsma (1982) found that implausible values were possible when small sample sizes and two indicators per factor were used, and Anderson and Gerbing (1984) suggested the use of large sample sizes (≥150) and more than three indicators per factor to avoid negative error variances.

Table 3
The analyzed covariance matrix for the Lake Mendota model with predicted values and residuals (study periods 1997–2001)

	Epilimnion depth	Secchi depth	SRP	$\sqrt{\text{DIN}}$	$\sqrt{\text{Total zooplankton}}$	$\sqrt{\textit{Daphnia}}$	log(chlorophyll a)	log(total biovolume)
Epilimnion depth								
Observed	16.496							
Predicted	16.496							
Residual	0							
Secchi depth								
Observed	2.666	2.923						
Predicted	2.744	2.923						
Residual	−0.077	0						
SRP								
Observed	49.018	36.558	1097.123					
Predicted	48.168	38.192	1097.124					
Residual	0.850	−1.634	−0.001					
$\sqrt{\text{DIN}}$								
Observed	16.821	13.437	272.742	96.427				
Predicted	16.832	13.346	272.146	96.442				
Residual	−0.010	0.092	0.596	−0.014				
$\sqrt{\text{Total zooplankton}}$								
Observed	0.673	0.921	17.824	5.810	1.571			
Predicted	1.313	1.179	18.275	6.386	1.571			
Residual	−0.639	−0.259	−0.450	−0.576	0			
$\sqrt{\textit{Daphnia}}$								
Observed	0.691	1.143	22.965	7.368	1.303	1.381		
Predicted	1.307	1.175	18.200	6.360	1.293	1.388		
Residual	−0.617	−0.032	4.765	1.008	0.010	−0.007		
log(chlorophyll a)								
Observed	−0.730	−0.566	−7.655	−3.088	−0.234	−0.283	0.165	
Predicted	−0.630	−0.566	−8.777	−3.067	−0.271	−0.270	0.165	
Residual	−0.099	0	1.122	−0.021	0.037	−0.013	0	
log(total biovolume)								
Observed	−0.821	−0.796	−10.639	−4.005	−0.366	−0.431	0.177	0.369
Predicted	−0.866	−0.778	−12.057	−4.213	−0.372	−0.371	0.179	0.369
Residual	0.045	−0.018	1.418	0.208	0.006	−0.060	−0.002	0

To prevent the Lake Mendota model from yielding negative values, we added specification of two error variances (DIN, *Daphnia*), thus increasing the d.f. from 17 to 19. To compute the prespecified error variances, we ran the Bayesian SEM configuration and used the median error variances, which resulted from this model as the prescribed values for the maximum likelihood model. We ran the Bayesian SEM model keeping the three loading coefficients fixed (equal to one; see below and Appendices 1 and 2) and using "flat" (uninformative) priors for the rest of the model parameters. Note that in a Bayesian framework, the use of a conjugate prior distribution specifies the variances in a region of positive values, and thus the inadmissible values are avoided (Lee and Shi, 2000; see also Martin and McDonald, 1975 for another Bayesian approach to avoid inadmissible estimates in unrestricted factor analysis). Researchers using SEM for environmental data sets are likely to find that such methods may be needed in their analyses, since datasets of similar size are frequent in environmental science.

The RMSEA was 0.062, which under the null hypothesis of "close fit" corresponds to a *p*-value of 0.388. The IFI and CFI values were 0.989 and 0.987, respectively. Hoelter's critical *N* test indicated a model acceptance (CN = 64) at the 0.05 significance level. The latent variable nutrients was well correlated with dissolved inorganic nitrogen ($r \approx 0.99$) and soluble reactive phosphorus ($r \approx 0.84$). Chlorophyll a and total algal biovolume were also highly correlated with phytoplankton and the respective coefficients were 0.89 and 0.81. Finally, both *Daphnia* ($r \approx 0.96$) and total zooplankton ($r \approx 0.91$) length weighted biomass were strongly correlated with the latent variable herbivory.

Generally, there was a good agreement between the observed and model-implied moments and all the standardized estimates of the residuals were below one (Table 3). The largest residual covariances were found between the epilimnion depth and the two herbivory indicators and between SRP and *Daphnia* (standardized estimates of the residuals ≥ 0.7). The initial

Table 4
Comparison of the maximum likelihood, bootstrap ($N = 2000$) and Markov Chain Monte Carlo sampling estimates and standard errors of the Lake Mendota model path coefficients and error variances. The second pairs of the Bayesian estimates (medians and respective standard errors) correspond to a limited movement around the three fixed loading coefficients by sampling the normal distribution (1, 1). The notation is similar to that in Appendix 1

Parameters	Symbol	Maximum likelihood		Bootstrap		Markov Chain Monte Carlo sampling			
		Estimate	S.E.	Estimate	S.E.	Median	S.E.	Median	S.E.
Phytoplankton ← Nutrients	γ_2	−0.011	0.002	−0.011	0.002	−0.011	0.002	−0.037	0.024
Phytoplankton ← Epilimnion	γ_1	−0.006	0.008	−0.007	0.009	−0.007	0.007	−0.008	0.014
Herbivory ← Phytoplankton	β_2	−2.074	0.416	−2.078	0.444	−2.035	0.436	−1.452	0.854
Total biovolume ← Phytoplankton	λ_4	1.374	0.186	1.380	0.196	1.361	0.193	1.053	0.336
Chlorophyll a ← Phytoplankton	λ_5	1.000		1.000		1.000		0.756	0.237
Daphnia ← Herbivory	λ_8	1.000		1.000		1.000		1.102	0.530
Zooplankton ← Herbivory	λ_7	1.004	0.082	1.009	0.081	1.006	0.091	1.095	0.536
DIN ← Nutrients	λ_3	0.349	0.033	0.353	0.036	0.367	0.042	0.935	0.295
SRP ← Nutrients	λ_2	1.000		1.000		1.000		2.553	0.748
Water Clarity ← Cyanobacteria	β_1	−4.352	0.464	−4.391	0.510	−4.335	0.486	−3.381	1.013
Var(Nutrients)	φ_{22}	778.817	217.263	759.919	209.328	699.311	217.721	109.322	165.721
Var(Epilimnion)	φ_{11}	16.496	3.403	16.121	3.240	16.312	3.533	16.280	3.513
Covar(Nutrients, Epilimnion)	φ_{12}	48.168	18.608	46.929	17.905	44.215	18.481	17.432	11.081
Var(Phytoplankton)	ψ_{11}	0.035	0.010	0.029	0.010	0.040	0.012	0.062	0.146
Var(Total Biovolume)	var(ε_1)	0.123	0.030	0.118	0.029	0.131	0.034	0.131	0.034
Var(Chlorophyll a)	var(ε_2)	0.031	0.010	0.033	0.010	0.043	0.012	0.044	0.012
Var(Herbivory)	ψ_{33}	0.728	0.177	0.694	0.166	0.759	0.200	0.651	1.809
Var(*Daphnia*)	var(ε_5)	0.100		0.100		0.100	0.059	0.083	0.059
Var(Total Zooplankton)	var(ε_4)	0.273	0.076	0.259	0.075	0.291	0.092	0.292	0.094
Var(DIN)	var(δ_3)	1.344		1.344		1.344	1.920	0.627	3.563
Var(SRP)	var(δ_2)	318.306	67.864	304.697	63.891	332.557	76.999	330.907	77.673
Var(Water Clarity)	ψ_{22}	0.458	0.153	0.435	0.151	0.449	0.174	0.448	0.172

hypothesized structural model was confirmed and all the paths between the latent variables were significant. The only exception was the direct path from epilimnion depth to phytoplankton ($p = 0.436$; see Table 4). The standardized direct effect of nutrients on phytoplankton was −0.841. The standardized direct paths from phytoplankton to herbivory (−0.659) and water clarity (−0.918) were negative and highly significant. Finally, the correlation ($r = 0.425$) between epilimnion depth and nutrients ($p = 0.01$) was also significant. The latter result is consistent with previous studies that emphasized the internal loading contribution to the epilimnetic nutrient stock in Lake Mendota. Soranno et al. (1997) found that major entrainment events can occur and result in nutrient fluxes that are significantly higher than those from external nutrient sources. These nutrient pulses stimulate phytoplankton (cyanobacteria) blooms (≥30 μg chl a/L), surface scum formation with adverse effects on the water clarity and the aesthetic value of the lake (Lathrop et al., 1996; Soranno, 1997). Our SEM approach also highlighted the control that herbivory exerts on summer epilimnetic phytoplankton dynamics. Several past Lake Mendota studies based on both short and long-term datasets, variant temporal resolution (from days to seasonal averages), and contemporaneous or lagged measurements provided similar evidence and underscored the role of zooplankton grazing pressure (especially from the large bodied *Daphnia* spp.) on phytoplankton dynamics (e.g., composition, abundance) and the water clarity (Lathrop and Carpenter, 1992b; Lathrop et al., 1996; Soranno, 1997; Lathrop et al., 1999). Overall, the conceptual model resulted in a good fit with the data and it provided a plausible interpretation of the ecological processes in a eutrophic environment that is consistent with the existing literature.

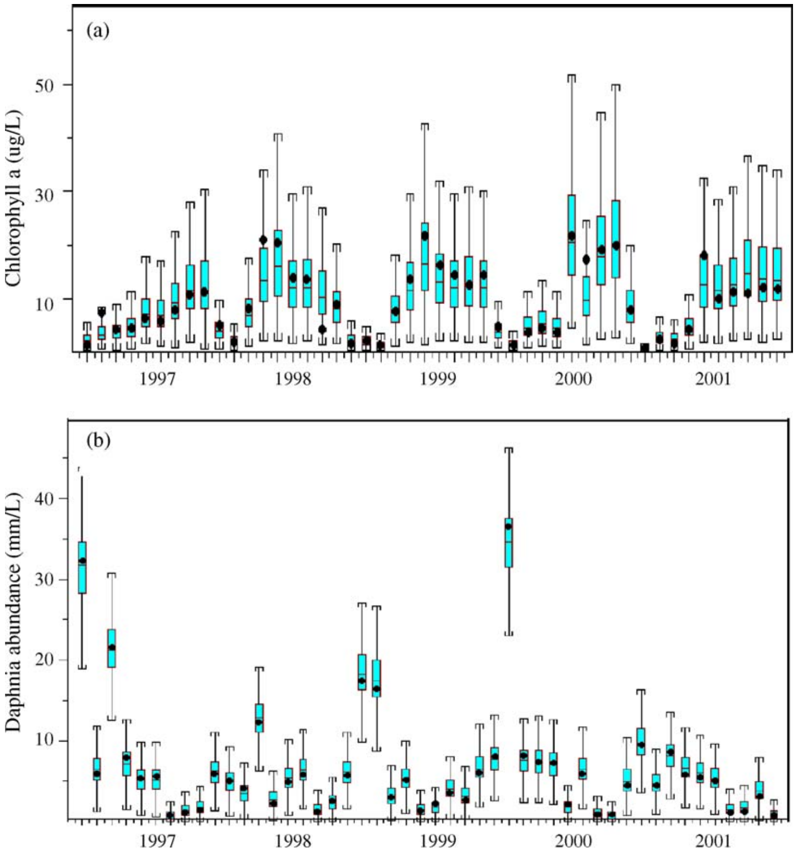

Fig. 5. Comparison between the observed data and the posterior predictive distributions for (a) chlorophyll a and (b) *Daphnia* abundance of the Lake Mendota SEM.

Both bootstrap estimates (Table 4) and model fit ($p = 0.367$) were consistent with the maximum likelihood results. Fig. 5 presents the comparison between the observed chlorophyll a and *Daphnia* abundance and the posterior predictive median, quartiles, and 95% credible sets of the Bayesian model with the three identification restrictions ($\lambda_2 = \lambda_5 = \lambda_8 = 1$). Moreover, interesting findings were raised when these three constraints were relaxed. Using the posterior medians, we have the structural equation model $n_1 = -0.008\xi_1 - 0.037\xi_2$, $n_2 = -3.381n_1$, and $n_3 = -1.452n_1$. Comparing these estimates with the respective standard errors, we infer that the Bayesian approach also underlined the importance of the paths from nutrients to phytoplankton, and from phytoplankton to herbivory and water transparency. In contrast, the variance of the nutrients (φ_{22}) and the covariance between nutrients and epilimnion depth (φ_{12}) were notably lower. The lower φ_{12} and φ_{22} variance estimates were related to the assumption that determines the metric of the latent variable nutrients ($\lambda_2 = 1$) in combination with the high variance of the used SRP values (Table 3), which in turn is indicative of the role of the hypolimnetic fluxes. [Also note that the best fit to the normal distribution was provided by the raw (untransformed) SRP data for the Lake Mendota SEM.] The discrepancies were minimized when we sampled values for the λ_2 loading from a normal distribution with mean 1 and precision 5 or when keeping this loading factor fixed. Finally, significant loadings were

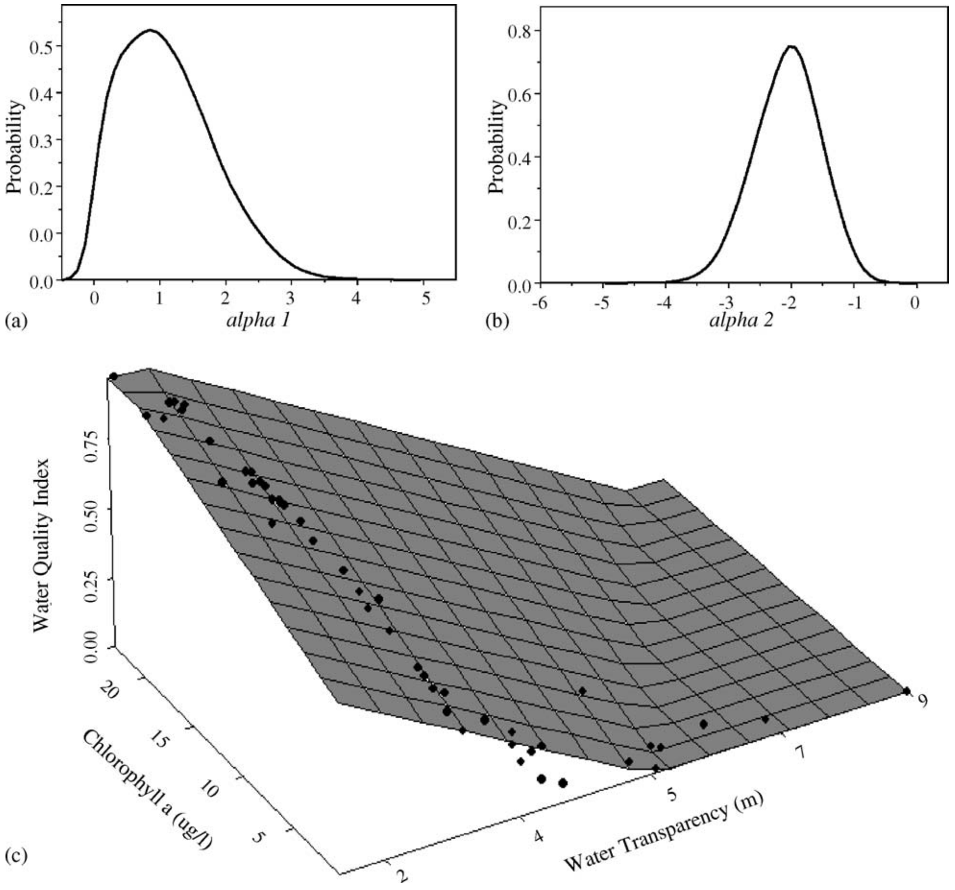

Fig. 6. Posterior distributions for the two parameters associated with (a) chlorophyll a, (b) water transparency, and (c) water quality predictions of the Lake Mendota structural equation model: each point corresponds to the mean value of the posterior predictive distribution of the water quality index for each sampling date (study period 1997–2001, $N = 48$). The water quality index is based on a binary characterization (0, 1) of satisfactory/non-satisfactory water quality conditions.

found between the three latent variables and the respective pairs of indicators.

3.3. Application in natural resource management

To illustrate one way of how this methodological framework can be used for assessing trophic conditions and assist water quality management, we linked the Bayesian configuration of the Lake Mendota SEM with the following model:

$$\text{logit}(p[i]) = \alpha_0 + \alpha_1\,\text{chlorophyll a}[i] + \alpha_2\,\text{water transparency}[i],$$

$$\text{where } Y = 1 \text{ if chlorophyll a}[i] \geq 10\,\mu\text{g/L or Secchi depth}[i] \leq 2\,\text{m else } Y = 0,$$

$$Y[i]|p[i] \sim \text{Bernoulli}\,(p[i]), \qquad \text{logit}\ \ p[i] = \log_e(p[i]/(1 - p[i])) \tag{3}$$

The indicator variable for identifying trophic state (referred to as “Water Quality Index” in Fig. 6) was based on a binary characterization (0, 1) of satisfactory/non-satisfactory water quality conditions. More specifically, the observed $Y[i]$ was modeled as a realization from a random Bernoulli process where $p[i]$, the probability of non-satisfactory conditions, is a function of chlorophyll a and water transparency (coincides with Secchi depth in this model) for this categorization. The respective cutoff points were 10 μg/L and 2 m. Fig. 6(a) and (b) show the posterior distribution for the parameters associated with the two water quality variables. Fig. 6(c) illustrates how the proposed conceptualization of the Lake Mendota epilimnetic phytoplankton dynamics can be used for water quality predictions. The mean values of the posterior predictive distribution of the water quality index (study period 1997–2001, $N = 48$) were used for the delineation of this surface, where the joint chlorophyll a and water transparency SEM estimations provide predictions – through the model (3) – on the water quality of the lake. In addition, the inclusion of surrogate variables for watershed dynamics (e.g., nutrient loadings) will further elaborate the ability of the present modeling framework to be used as management tool.

It should be noted that the combination of SEM with Bayesian analysis offers two additional strategies for the development of a framework that will integrate into the model information over time and space: (i) the sequential updating, which in this particular case is relatively easy since the basis for the present modeling construction was data from conventional sampling programs (moderate sampling intensity, standard limnological variables used), and (ii) the ability to test a single model simultaneously for multiple waterbodies (multi-group analyses or stacked models), where the use of constraints across groups enables the identification of the longitudinal differences (Pugesek and Tomer, 1996). Bayesian analysis can also be advantageous along this line, since the stochastic treatment of the cross-sectional constraints improves the accuracy of the estimation and results in a more meaningful interpretation of the model (Lee, 1992; Lee and Ho, 1993).

4. Conclusions

We presented an illustrative example that examined the efficiency of a multivariate statistical method to explore ecological patterns. Structural equation modeling was used to formulate a simple conceptual model regarding epilimnetic phytoplankton dynamics, which was then tested in two lakes with different trophic status (i.e., eutrophic Lake Mendota and mesotrophic Lake Washington). The basic feature of the confirmation theory is the recognition that science is a hypothetico-deductive process and observations/experimental data should be considered a consequence of a theory or a general law (Oreskes et al., 1994). While the formulation of our hypothetical model was based on existing knowledge from the limnological literature, the use of existing data undermines somewhat the “confirmatory” character of our study. Ideally, ecologists when conducting confirmatory analysis must design their mental models in advance and then proceed to data collection (McCune and Grace, 2002). Nevertheless, our intention with this simple (and very familiar to aquatic ecologists) example was to show the flexibility of the method to: (i) translate a fairly complicated ecological phenomenon and express it as a function of several conceptual environmental factors, (ii) link the conceptual factors of interest with routinely measured variables by explicitly acknowledging that none of those reflects perfectly the underlying property, and (iii) test both direct and indirect paths of this ecological structure and identify the importance of their role.

Model acceptance in two or more case studies is not evidence for a general statement, but merely the start of a "perpetual race" for confirmation (Oreskes et al., 1994). This realization might be misinterpreted as a necessity for good starting models, where the ecologist has to embody conceptualizations with a high likelihood of confirmation in a variety of conditions. In typical SEM practice, what is needed is a tentative initial model and probably prior knowledge of the variety of observed variables that can reflect the studied ecological conditions. The initial model can be respecified and effectively optimized, as long as the modifications are done through a combination of data and theory-driven exploratory analysis (McCune and Grace, 2002). By integrating intuition, theory, and evidence from the data, we insure that the final model has not only the best fit but also meaningful paths. Thus, the resulting modeling development provides a plausible framework that seeks for further confirmation. For several reasons, SEM has received criticism with regards to its ability to serve as a methodological tool in ecology and evolutionary biology (e.g., Petraitis et al., 1996), which however have been addressed on a vis-à-vis basis in the SEM literature (e.g., Pugesek and Tomer, 1995; Grace and Pugesek, 1998). For example, SEM does not require larger sample sizes than other multivariate methods (e.g., multiple regression, MANOVA); can account for non-linear relationships; can include categorical data and can overcome deviations from multinormality.

Several benefits can also be gained by a Bayesian approach to structural equation modeling. We argue that a Bayesian SEM that subjects a realistic ecological structure to sequential updating with routinely monitored environmental variables is likely to lead to an effective, easily implementable framework and assist natural resource management (Dorazio and Johnson, 2003). In the present study, we used uninformative prior parameter distributions where the posterior is proportional to the likelihood, and thus the Bayesian and maximum likelihood estimates did not differ. However, even though it was not encountered here, local maxima or non-Gaussian likelihood surfaces from small sample sizes can cause major discrepancies (Scheines et al., 1999). The adoption of a Bayesian approach, where MCMC samples are taken from the true posterior distribution over parameters, can assist to tackle such problems (Congdon, 2003). Moreover, as our study showed, additional insight can be gained by the stochastic treatment of the assumptions used to determine the latent variable metrics. Another aspect where the Bayesian strategy can be particularly useful, though it was not explored in this study, is the treatment of unidentified initial models; the problem of exact identification restrictions can be overcome by exploiting existing information and defining plausible informative prior distributions (Scheines et al., 1999).

It should also be stressed that SEM can be more complicated than the presented model and more information can be easily included. McCune and Grace (2002) discussed that SEMs can become problematic after the inclusion of more than 10 latent variables. For example, the ecological structure of our model can be augmented by the inclusion of more indicators for each of the already existing latent variables (e.g., total nutrient forms, silica, trace elements, primary productivity, Schmidt stability index), higher predators of the food web, external nutrient loadings or concepts that reflect recent advancements in aquatic ecology such as algal food quality for zooplankton (e.g., highly unsaturated fatty acid, amino acid, protein content, and/or digestibility, see Sterner and Hessen, 1994; Kilham et al., 1997; Brett and Müller-Navarra, 1997; Kleppel et al., 1998). Finally, another methodological advancement for the analysis of complex ecological systems is likely to result from the delineation of the correspondence between SEM and system dynamic modeling and the integration of these two techniques into one comprehensive tool (Grace, 2001; Hovmand, 2003).

Holling (1978) emphasized the popular notion that everything in ecological systems is tightly connected to everything else is, in fact, false. Rather, there are key linkages that dominate ecosystem dynamics. SEM models are useful to help identify these important connections. Striving to elucidate ecological patterns, researchers can use SEM as a tool that lends flexibility to compromise between generality, realism and precision and obtain the optimal scale of description; the integration of this technique in the ecological practice is warranted.

Acknowledgments

This study was funded by a grant from the Water Environment Research Foundation through the University of North Carolina Water Resources Research Institute. We thank Curtis L. DeCasperi (King County, Washington State, Department of Natural Resources and Parks), Michael T. Brett (Department of Civil and Environmental Engineering, University of Washington), and Olli Malve (Finnish Environment Institute) for helpful comments to an earlier draft of the manuscript. We also wish to thank Daniel E. Schindler (School of Aquatic and Fisheries Sciences, University of Washington) for supplying zooplankton data for Lake Washington.

Appendix 1

A.1. General description

By expressing the observations as deviations from their means, the following set of three equations provides the general matrix representation of a structural equation model:

$$X = \Lambda_x \xi + \delta,$$

$$Y = \Lambda_y \eta + \varepsilon \text{ (Measurement model)},$$

$$\eta = B\eta + \Gamma\xi + \zeta \text{ (Latent variable model)} \qquad \text{(A.1)}$$

where X is a $q \times 1$ vector of observable indicators of the independent latent variables ξ; Y is a $p \times 1$ vector of observable indicators of the dependent latent variables η; η is a $m \times 1$ vector of dependent (endogenous) latent variables; ξ is a $n \times 1$ vector of independent (exogenous) latent variables; ζ is a $m \times 1$ vector of latent (structural) errors; ε is a $p \times 1$ vector of measurement errors for Y; δ is a $q \times 1$ vector of measurement errors for X; Λ_y is a $p \times m$ matrix of coefficients relating Y to η; Λ_x is a $q \times n$ matrix of coefficients relating X to ξ; Γ is a $m \times n$ matrix of coefficients for the latent exogenous variables; B is a $m \times m$ matrix of coefficients for the latent endogenous variables.

The statistical assumptions are: (1) $E(\eta) = E(\xi) = E(\varepsilon) = E(\delta) = E(\zeta) = 0$, (2) ε is uncorrelated with η, (3) δ is uncorrelated with ξ, (4) ζ is uncorrelated with ξ, (5) ζ, ε and δ are mutually uncorrelated, and (6) $(I-B)^{-1}$ is non-singular. In addition, the associated covariance matrices are: $\mathrm{Cov}(\xi) = \Phi(n \times n)$: covariances between the independent variables ξ; $\mathrm{Cov}(\varepsilon) = \Theta_\varepsilon(p \times p)$: covariances between the measurement errors in Y; $\mathrm{Cov}(\delta) = \Theta_\delta(q \times q)$: covariances between the measurement errors in X; $\mathrm{Cov}(\zeta) = \Psi(m \times m)$: covariances between the structural errors ζ.

The $(p+q)$ model-implied covariance matrix $\Sigma(\theta)$ of the observed variables can be partitioned into four matrices $\Sigma_{yy}(\theta)$, $\Sigma_{yx}(\theta)$, $\Sigma_{xy}(\theta)$ and $\Sigma_{xx}(\theta)$ that denote the model-implied covariances between the Y observed variables, the X observed variables, and the X and Y observed variables, respectively.

$$\Sigma(\theta) = \begin{bmatrix} \Sigma_{yy}(\theta) & \Sigma_{yx}(\theta) \\ \Sigma_{xy}(\theta) & \Sigma_{xx}(\theta) \end{bmatrix} \qquad \text{(A.2)}$$

Based on the previous assumptions, the matrix (A.2) takes the following form (Bollen, 1989a):

$$\Sigma(\theta) = \begin{bmatrix} \Lambda_y(I-B)^{-1}(\Gamma\Phi\Gamma' + \Psi)[(I-B)^{-1}]'\Lambda_y' + \Theta_\varepsilon & \Lambda_y(I-B)^{-1}\Gamma\Phi\Lambda_x' \\ \Lambda_x\Phi\Gamma'[(I-B)^{-1}]'\Lambda_y' & \Lambda_x\Phi\Lambda_x' + \Theta_\delta \end{bmatrix} \qquad \text{(A.3)}$$

A.2. Lake Washington structural equation model

As an illustrative example, we present the matrices' forms and the specific assumptions made for the Lake Washington structural equation model. The extraction of the Lake Mendota SEM can be obtained in a similar way. The Lake Washington SEM included two ($n = 2$) exogenous latent variables ξ, which were described from three ($q = 3$) indicators; i.e., SRP and DIN were used for the latent variable "Nutrients" and the epilimnion depth for the respective latent variable. Thus, the exogenous latent variable measurement model consists of the following four matrices:

$$X = \begin{bmatrix} X_1 = \text{Epilimniondepth} \\ X_2 = \text{SRP} \\ X_3 = \text{DIN} \end{bmatrix}, \quad \Lambda_X = \begin{bmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \\ 0 & \lambda_3 \end{bmatrix},$$

$$\xi = \begin{bmatrix} \xi_1 = \text{Epilimniondepth} \\ \xi_2 = \text{Nutrients} \end{bmatrix}, \quad \delta = \begin{bmatrix} \delta_1 \\ \delta_2 \\ \delta_3 \end{bmatrix} \qquad \text{(A.4)}$$

Five indicators ($p = 5$) were used for the representation of the three ($m = 3$) endogenous latent variables; i.e., cyanobacteria counts and chlorophyll a were used as indicators for the latent variable phytoplankton community, the Secchi depth for the Water clarity, *Daphnia* and total zooplankton were used to characterize the latent variable Herbivory. Thus, the exogenous latent variable measurement model can be described from the four matrices:

$$Y = \begin{bmatrix} Y_1 = \text{Cyanobacteria} \\ Y_2 = \text{Chlorophyll a} \\ Y_3 = \text{Secchi depth} \\ Y_4 = \text{Total Zooplankton} \\ Y_5 = \text{Daphnia} \end{bmatrix},$$

$$\Lambda_Y = \begin{bmatrix} \lambda_4 & 0 & 0 \\ \lambda_5 & 0 & 0 \\ 0 & \lambda_6 & 0 \\ 0 & 0 & \lambda_7 \\ 0 & 0 & \lambda_8 \end{bmatrix},$$

$$\eta = \begin{bmatrix} \eta_1 = \text{Phytoplankton community} \\ \eta_2 = \text{Water clarity} \\ \eta_3 = \text{Herbivory} \end{bmatrix},$$

$$\varepsilon = \begin{bmatrix} \varepsilon_1 \\ \varepsilon_2 \\ \varepsilon_3 \\ \varepsilon_4 \\ \varepsilon_5 \end{bmatrix} \qquad \text{(A.5)}$$

The additional three matrices of the structural equation for the latent variable model are:

$$\Gamma = \begin{bmatrix} \gamma_1 & \gamma_2 \\ 0 & 0 \\ 0 & 0 \end{bmatrix}, \quad B = \begin{bmatrix} 0 & 0 & 0 \\ \beta_1 & 0 & 0 \\ \beta_2 & 0 & 0 \end{bmatrix}, \quad \zeta = \begin{bmatrix} \zeta_1 \\ \zeta_2 \\ \zeta_3 \end{bmatrix} \qquad \text{(A.6)}$$

As it can be inferred from the path diagram (Fig. 1) and the form of the matrix *B*, the Lake Washington structural equation model is recursive (no feedback causal relations and uncorrelated measurement or structural errors). Thus, the associated covariance matrices are:

$$\Theta_\varepsilon = \begin{bmatrix} \text{var}(\varepsilon_1) & & & & \\ 0 & \text{var}(\varepsilon_2) & & & \\ 0 & 0 & \text{var}(\varepsilon_3) & & \\ 0 & 0 & 0 & \text{var}(\varepsilon_4) & \\ 0 & 0 & 0 & 0 & \text{var}(\varepsilon_5) \end{bmatrix},$$

$$\Theta_\delta = \begin{bmatrix} \text{var}(\delta_1) & & \\ 0 & \text{var}(\delta_2) & \\ 0 & 0 & \text{var}(\delta_3) \end{bmatrix},$$

$$\Psi = \begin{bmatrix} \psi_{11} & & \\ 0 & \psi_{22} & \\ 0 & 0 & \psi_{33} \end{bmatrix}, \quad \Phi = \begin{bmatrix} \phi_{11} & \\ \phi_{12} & \phi_{22} \end{bmatrix} \qquad \text{(A.7)}$$

By substituting (A.4)–(A.7) into (A.3), we determine the four sub-matrices of (A.2):

$$\Sigma_{xx}(\theta) = \begin{bmatrix} \lambda_1^2\phi_{11} + \text{var}(\delta_1) & & \\ \lambda_1\lambda_2\phi_{12} & \lambda_2^2\phi_{22} + \text{var}(\delta_2) & \\ \lambda_1\lambda_3\phi_{12} & \lambda_2\lambda_3\phi_{22} & \lambda_3^2\phi_{22} + \text{var}(\delta_3) \end{bmatrix},$$

$$\Sigma_{yy}(\theta) = \begin{bmatrix} \lambda_4^2 A_{\text{aux}} + \text{var}(\varepsilon_1) & & & & \\ \lambda_4\lambda_5 A_{\text{aux}} & \lambda_5^2 A_{\text{aux}} + \text{var}(\varepsilon_2) & & & \\ \lambda_4\lambda_6\beta_1 A_{\text{aux}} & \lambda_5\lambda_6\beta_1 A_{\text{aux}} & \lambda_6^2\beta_1^2 A_{\text{aux}} + \lambda_6^2\psi_{22} + \text{var}(\varepsilon_3) & & \\ \lambda_4\lambda_7\beta_2 A_{\text{aux}} & \lambda_5\lambda_7\beta_2 A_{\text{aux}} & \lambda_6\lambda_7\beta_1\beta_2 A_{\text{aux}} & \lambda_7^2\beta_2^2 A_{\text{aux}} + \lambda_7^2\psi_{33} + \text{var}(\varepsilon_4) & \\ \lambda_4\lambda_8\beta_2 A_{\text{aux}} & \lambda_5\lambda_8\beta_2 A_{\text{aux}} & \lambda_6\lambda_8\beta_1\beta_2 A_{\text{aux}} & \lambda_7\lambda_8\beta_2^2 A_{\text{aux}} + \lambda_7\lambda_8\psi_{33} & \lambda_8^2\beta_2^2 A_{\text{aux}} + \lambda_8^2\psi_{33} + \text{var}(\varepsilon_5) \end{bmatrix}$$

where $A_{\text{aux}} = \gamma_1(\gamma_1\phi_{11} + \gamma_2\phi_{12}) + \gamma_2(\gamma_1\phi_{12} + \gamma_2\phi_{22}) + \psi_{11}$, and

$$\Sigma_{yx}(\theta) = [\Sigma_{xy}(\theta)]' = \begin{bmatrix} \lambda_1\lambda_4(\gamma_1\phi_{11} + \gamma_2\phi_{12}) & \lambda_2\lambda_4(\gamma_1\phi_{12} + \gamma_2\phi_{22}) & \lambda_3\lambda_4(\gamma_1\phi_{12} + \gamma_2\phi_{22}) \\ \lambda_1\lambda_5(\gamma_1\phi_{11} + \gamma_2\phi_{12}) & \lambda_2\lambda_5(\gamma_1\phi_{12} + \gamma_2\phi_{22}) & \lambda_3\lambda_5(\gamma_1\phi_{12} + \gamma_2\phi_{22}) \\ \lambda_1\lambda_6\beta_1(\gamma_1\phi_{11} + \gamma_2\phi_{12}) & \lambda_2\lambda_6\beta_1(\gamma_1\phi_{12} + \gamma_2\phi_{22}) & \lambda_3\lambda_6\beta_1(\gamma_1\phi_{12} + \gamma_2\phi_{22}) \\ \lambda_1\lambda_7\beta_2(\gamma_1\phi_{11} + \gamma_2\phi_{12}) & \lambda_2\lambda_7\beta_2(\gamma_1\phi_{12} + \gamma_2\phi_{22}) & \lambda_3\lambda_7\beta_2(\gamma_1\phi_{12} + \gamma_2\phi_{22}) \\ \lambda_1\lambda_8\beta_2(\gamma_1\phi_{11} + \gamma_2\phi_{12}) & \lambda_2\lambda_8\beta_2(\gamma_1\phi_{12} + \gamma_2\phi_{22}) & \lambda_3\lambda_8\beta_2(\gamma_1\phi_{12} + \gamma_2\phi_{22}) \end{bmatrix}$$

According to the null hypothesis, this model-implied 8×8 matrix $\Sigma(\theta)$ is equal to the known sample covariance matrix S. The 36 [= (1/2) (8) (9)] non-redundant elements of the two matrices provide 36 equations that can be solved with one of the common fitting methods (e.g., maximum likelihood, unweighted or generalized least squares). In this study, we used the maximum likelihood (ML) method, where the fitting function that is minimized is (Bollen, 1989a):

$$F_{\text{ML}} = \log|\Sigma(\theta)| + tr(S\Sigma^{-1}(\theta)) - \log|S| - (p + q) \tag{A.8}$$

Before evaluating the identification status of the model, it is essential to set the metric of the latent variables. One way that this can be accomplished is by fixing one loading in each column of Λ_X and Λ_Y to 1.0. In this particular case, we assumed that $\lambda_2 = \lambda_5 = \lambda_8 = 1.0$. Moreover, implicit in the assumption that the latent variables epilimnion depth and water clarity coincide with the observed variables epilimnion depth and Secchi depth is: $\lambda_1 = \lambda_6 = 1.0$, and $\delta_1 = \varepsilon_3 = 0$. Having determined the metric of the latent variables, there are several rules that can be used to check SEM identification. The easiest test to apply is the so-called *t*-rule. If *t* is the total number of model parameters that are to be estimated, then this number *t* must be less than or equal to the number of non-redundant elements in the covariance matrix of the observed (endogenous and exogenous) variables:

$$t \le (1/2)(p + q)(p + q + 1) \tag{A.9}$$

In the Lake Washington SEM, the unknown model parameters were 19, i.e., $\theta = (\lambda_3, \lambda_4, \lambda_7, \gamma_1, \gamma_2, \beta_1, \beta_2, \text{var}(\varepsilon_1), \text{var}(\varepsilon_2), \text{var}(\varepsilon_4), \text{var}(\varepsilon_5), \text{var}(\delta_2), \text{var}(\delta_3), \psi_{11}, \psi_{22}, \psi_{33}, \varphi_{11}, \varphi_{12}, \varphi_{22})$ which left 17 (36 − 19) d.f. in the model. Even though in practice, the *t*-rule works for the majority of models (except from very complex ones), it should be noted that it is a *necessary* but not *sufficient* condition and does not guarantee model identification (Kaplan, 2000). Additional rules exist and can be used to establish model identification (Bollen, 1989a). We used the software Amos 5 for SEM development (Arbuckle, 1995).

Appendix 2

Using the previous notation, the hierarchical Bayesian configuration of the Lake Washington SEM can be specified as

$$\begin{aligned} &X_{1i} = \lambda_1\xi_{1i} + \delta_1, \quad X_{2i} = \lambda_2\xi_{2i} + \delta_2, \\ &X_{3i} = \lambda_3\xi_{2i} + \delta_3, \quad \delta \sim N(0, \Theta_\delta), \quad \xi \sim N(0, \Phi); \\ &Y_{1i} = \lambda_4\eta_{1i} + \varepsilon_1, \quad Y_{2i} = \lambda_5\eta_{1i} + \varepsilon_2, \\ &Y_{3i} = \lambda_6\eta_{2i} + \varepsilon_3, \quad Y_{4i} = \lambda_7\eta_{3i} + \varepsilon_4, \\ &Y_{5i} = \lambda_8\eta_{3i} + \varepsilon_5, \quad \varepsilon \sim N(0, \Theta_\varepsilon), \\ &\eta_{1i} = \gamma_1\xi_{1i} + \gamma_2\xi_{2i} + \zeta_1, \quad \eta_{2i} = \beta_1\eta_{1i} + \zeta_2, \\ &\eta_{3i} = \beta_2\eta_{1i} + \zeta_3, \quad \zeta \sim N(0, \Psi) \end{aligned} \tag{B.1}$$

Let $w_i = \{y_i, x_i, \quad i = 1, \ldots, n\}$ be the joint vector of the observed variables for an arbitrary observation *i*. According to the model (B.1), each observation *i* comes from a multivariate normal distribution $f(\mu(\theta)_i, \Sigma(\theta))$ where $\mu(\theta)_i$ is the conditional mean (expected) vector, $\Sigma(\theta)$ is the conditional covariance matrix and θ is the vector of the unknown model parameters both given in Appendix 1. The likelihood of $w = (w_1, \ldots, w_n)$ is:

$$p(w|\theta) = \prod_{i=1}^{n} (2\pi)^{-(p+q)/2} |\Sigma(\theta)|^{-1/2} \exp\left[-\frac{1}{2}[w_i - \mu(\theta)_i]' \Sigma(\theta)^{-1} [w_i - \mu(\theta_i)]\right] \tag{B.2}$$

where $q = 3$ and $p = 5$ are the number of exogenous and endogenous manifest variables. In the context of the Bayesian statistical inference, the focus is on the posterior density of θ given the observed data w, which is defined as

$$p(\theta|w) = \frac{p(w|\theta)p(\theta)}{\int p(w|\theta)p(\theta)\mathrm{d}\theta} \propto p(w|\theta)p(\theta) \tag{B.3}$$

where $p(\theta)$ is the prior density of θ which is required to be specified for each of the unknown model parameters. We used a Wishart distribution (ρ, R) over the precision matrix Φ^{-1} that corresponds to vague prior knowledge; i.e., we chose the degrees of freedom ρ to be as small as possible (2, the rank of Φ), and a prior guess at the order of magnitude of the covariance matrix Φ to be $R = 0.1\mathrm{I}$ (Ansari et al., 2000). Aside from the cases where no measurement error was assumed between the latent and indicator variables (i.e., epilimnion depth, water clarity), we used independent non-informative conjugate gamma priors (0.01, 0.01) for the elements of the matrices Θ_δ^{-1}, Θ_ε^{-1}, and Ψ^{-1} (Spiegelhalter et al., 1996; pg 39). Effectively “flat” normal prior distributions with means equal to the maximum likelihood estimates and precisions equal to 0.0001 were used for the structural parameters and the factor loadings when we compared the Bayesian model configuration with the classical approach (λ_2, λ_5 and λ_8 were kept fixed and equal to 1). The sensitivity of the model results was then tested by sampling the loadings λ_2, λ_5 and λ_8 from the normal distribution (1,1), which allowed a limited movement (Congdon, 2003). In this case, the remaining parameters were sampled from a normal prior distribution with mean equal to the maximum likelihood estimates and precisions equal to 0.1. MCMC simulation was used as the computation tool implemented in the WinBUGS software (Spiegelhalter et al., 2003). We used three chain runs of 50000 iterations and samples were taken every 50th iteration to avoid serial correlation, and convergence was assessed using the modified Gelman–Rubin convergence statistic (Brooks and Gelman, 1998). Generally, we noticed that the sequences converged very rapidly (≈1000 iterations), while the summary statistics reported in this study were based on the last 20,000 draws by keeping every 5th iteration (thin = 5). In addition, the accuracy of the posterior estimates was inspected by assuring that the Monte Carlo error (an estimate of the difference between the mean of the sampled values and the true posterior mean; see Spiegelhalter et al., 2003) for all the parameters was less than 5% of the sample standard deviation.

References

Anderson, J.C., Gerbing, D.W., 1984. The effect of sampling error on convergence, improper solutions, and goodness-of-fit indexes for maximum-likelihood confirmatory factor-analysis. Psychometrika 49, 155–173.

Anderson, J.C., Gerbing, D.W., 1992. Assumptions and comparative strengths of the two-step approach. Socio. Meth. Res. 20, 321–333.

Ansari, A., Jedidi, K., Jagpal, S., 2000. A hierarchical Bayesian methodology for treating heterogeneity in structural equation models. Market. Sci. 19, 328–347.

Arbuckle, J.L., 1995. Amos Users’ Guide. Small Waters Corporation, Chicago, IL.

Arhonditsis, G.B., Brett, M.T., 2005. Eutrophication model for Lake Washington (USA): Part II. Model calibration and system dynamics analysis. Ecol. Model. 187, 179–200.

Arhonditsis, G.B., Brett, M.T., DeGasperi, C.L., Schindler, D.E., 2004a. Effects of climatic variability on the thermal properties of Lake Washington. Limnol. Oceanogr. 49, 256–270.

Arhonditsis, G.B., Winder, M., Brett, M.T., Schindler, D.E., 2004b. Patterns and mechanisms of phytoplankton variability in Lake Washington (USA). Water Res. 38, 4013–4027.

Arhonditsis, G.B., Brett, M.T., 2004. Evaluation of the current state of mechanistic aquatic biogeochemical modeling. Mar. Ecol. - Prog. Ser. 271, 13–26.

Arhonditsis, G., Brett, M.T., Frodge, J., 2003. Environmental control and limnological impacts of a large recurrent spring bloom in Lake Washington, USA. Environ. Manage. 31, 603–618.

Arminger, G., Muthen, B.O., 1998. A Bayesian approach to nonlinear latent variable models using the Gibbs sampler and the Metropolis-Hastings algorithm. Psychometrika 63, 271–300.

Bartholomew, D.J., 1981. Posterior analysis of the factor model. Brit. J. Math. Stat. Psychol. 34, 93–99.

Bentler, P.M., 1990. Comparative fit indexes in structural models. Psychol. Bull. 107, 238–246.

Betz, C.R., Lowndes, M.L., Porter, S., 1997. Non-point Source Control Plan for the Lake Mendota Priority Watershed Project. Wisconsin Department of Natural Resources Publication No WT-481-97.

Bollen, K.A., 1989a. Structural Equations with Latent Variables. Wiley and Sons, New York.

Bollen, K.A., 1989b. A new incremental fit index for general structural equation models. Sociol. Meth. Res. 17, 303–316.

Bollen, K.A., Stine, R.A., 1992. Bootstrapping goodness-of-fit measures in structural equation models. Sociol. Meth. Res. 21, 205–229.

Boomsma, A., 1982. The robustness of LISREL against small sample sizes in factor analysis models. In: Jöreskog, K.G., Wold, H. (Eds.), System under Indirect Observation, Part I. North-Holland, Amsterdam, pp. 149–173.

Brett, M.T., Müller-Navarra, D.C., 1997. The role of highly unsaturated fatty acids in aquatic food–web processes. Freshwater Biol. 38, 483–499.

Brooks, S.P., Gelman, A., 1998. Alternative methods for monitoring convergence of iterative simulations. J. Comput. Graph Stat. 7, 434–455.

Browne, M.W., Cudeck, R., 1993. Alternative ways of assessing model fit. In: Bollen, K.A., Long, J.S. (Eds.), Testing Structural Equation Models. Sage, Newbury Park, CA, pp. 136–162.

Carpenter, S.R., 2002. Ecological futures: building an ecology of the long now. Ecology 83, 2069–2083.

Carpenter, S.R., Kitchell, J.F., Cottingham, K.L., Schindler, D.E., Christensen, D.L., Post, D.M., Voichick, N., 1996. Chlorophyll variability, nutrient input, and grazing: evidence from whole-lake experiments. Ecology 77, 725–735.

Congdon, P., 2003. Applied Bayesian Modeling. Wiley Series in Probability and Statistics, West Sussex, England.

Costanza, R., Sklar, F.H., 1985. Articulation, accuracy and effectiveness of mathematical models—A review of fresh-water wetland applications. Ecol. Model. 27, 45–68.

Dorazio, R.M., Johnson, F.A., 2003. Bayesian inference and decision theory—A framework for decision making in natural resource management. Ecol. Appl. 13, 556–563.

Dokulil, M.T., Teubner, K., 2000. Cyanobacterial dominance in lakes. Hydrobiologia 438, 1–12.

Downing, J.A., Watson, S.B., McCauley, E., 2001. Predicting cyanobacteria dominance in lakes. Can. J. Fish Aquat. Sci. 58, 1905–1908.

Edmondson, W.T., 1994. Sixty years of Lake Washington: a curriculum vitae. Lake Reserv. Manage. 10, 75–84.

Grace, J.B., 2001. The roles of community biomass and species pools in the regulation of plant diversity. Oikos 92, 193–207.

Grace, J.B., Pugesek, B.H., 1998. On the use of path analysis and related procedures for the investigation of ecological problems. Am. Nat. 152, 151–159.

Grace, J.B., Pugesek, B.H., 1997. A structural equation model of plant species richness and its application to a coastal wetland. Am. Nat. 149, 436–460.

Hair Jr., J.F., Anderson, R.E., Tatham, R.L., Black, W.C., 1995. Multivariate Data Analysis, 4th ed. Prentice-Hall, New York.

Hayduk, L.A., 1996. LISREL: Issues, Debates and Strategies. John Hopkins University Press, Baltimore.

Hoelter, J.W., 1983. The analysis of covariance structures: goodness-of-fit indices. Sociol. Meth. Res. 11, 325–344.

Holling, C.S., 1978. Adaptive Environmental Assessment and Management. John Wiley and Sons, NY.

Hovmand, P.S., 2003. Analyzing dynamic systems: a comparison of structural equation modeling and systems dynamic modeling. In: Pugesek, B.H., Tomer, A., Von Eye, A. (Eds.), Structural Equation Modeling: Applications in Ecological and Evolutionary Biology. Cambridge University Press, Cambridge, UK, pp. 85–112.

Jöreskog, K.G., 1973. A general method for estimating a linear structural equation system. In: Goldberger, A.S., Duncan, O.D. (Eds.), Structural Equation Model in the Social Sciences. Academic Press, New York, pp. 85–112.

Jöreskog, K.G., Sörbom, D., 1993. LISREL 8: Structural Equation Modeling with the SIMPLIS Command Language. Erlbaum Associates, Hillsdale, NJ.

Jorgensen, S.E., 1999. State-of-the-art of ecological modeling with emphasis on development of structural dynamic models. Ecol. Model. 120, 75–96.

Jorgensen, S.E., 1997. Integration of Ecosystem Theories: A Pattern. Kluwer Academic Publishers, Dordrecht.

Kaplan, D., 2000. Structural Equation Modeling: Foundations and Extensions. Sage Publications, Newbury Park, Calif.

Keesling, J.W., 1972. Maximum likelihood approaches to causal analysis. PhD Dissertion. University of Chicago, Chicago.

Kilham, S.S., Kreeger, D.A., Goulden, C.E., Lynn, S.G., 1997. Effects of algal food quality on fecundity and population growth rates of *Daphnia*. Freshwater Biol. 38, 639–647.

Kleppel, G.S., Burkart, C.A., Houchin, L., 1998. Nutrition and the regulation of egg production in the calanoid copepod Acartia tonsa. Limnol. Oceanogr. 43, 1000–1007.

Kline, R.B., 1998. Principles and Practice of Structural Equation Modeling. The Guildford Press, New York.

La Peyre, M.K., Mendelssohn, I.A., Reams, M.A., Templet, P.H., Grace, J.B., 2001. Identifying determinants of nations' wetland management programs using structural equation modeling: an exploratory analysis. Environ. Manage. 27, 859–868.

Lathrop, R.C., Carpenter, S.R., Robertson, D.M., 1999. Summer water clarity responses to phosphorus, *Daphnia* grazing, and internal mixing in Lake Mendota. Limnol. Oceanogr. 44, 137–146.

Lathrop, R.C., Carpenter, S.R., Stow, C.A., Soranno, P.A., Panuska, J.C., 1998. Phosphorus loading reductions needed to control blue-green algal blooms in Lake Mendota. Can. J. Fish Aquat. Sci. 55, 1169–1178.

Lathrop, R.C., Carpenter, S.R., Rudstam, L.G., 1996. Water clarity in Lake Mendota since 1900: responses to differing levels of nutrients and herbivory. Can. J. Fish Aquat. Sci. 53, 2250–2261.

Lathrop, R.C., Carpenter, S.R., 1992a. Phytoplankton and their relationship to nutrients. In: Kitchell, J.F. (Ed.), Food web management: a case study of Lake Mendota, Wisconsin. Springer-Verlag, New York, pp. 99–128.

Lathrop, R.C., Carpenter, S.R., 1992b. Zooplankton and their relationship to phytoplankton. In: Kitchell, J.F. (Ed.), Food Web Management: A Case Study of Lake Mendota, Wisconsin. Springer-Verlag, New York, pp. 129–152.

Lee, S.Y., 1981. A Bayesian-approach to confirmatory factor analysis. Psychometrika 46, 153–160.

Lee, S.Y., 1992. Bayesian-analysis of stochastic constraints in structural equation equation models. Brit. J. Math. Stat. Psychol. 45, 93–107.

Lee, S.Y., Ho, W.T., 1993. Analysis of multisample identified and non-identified structural equation models with stochastic constraints. Comput. Stat. Data Anal. 16, 441–453.

Lee, S.Y., Shi, J.Q., 2000. Joint Bayesian analysis of factor scores and structural parameters in the factor analysis model. Ann. I Stat. Math. 52, 722–736.

Lee, S.Y., Song, X.Y., 2003. Bayesian analysis of structural equation models with dichotomous variables. Stat. Med. 22, 3073–3088.

Lee, S.Y., Song, X.Y., 2004. Bayesian model comparison of nonlinear structural equation models with missing continuous and ordinal categorical data. Brit. J. Math. Stat. Psychol. 57, 131–150.

Lee, S.Y., Zhu, H.T., 2000. Statistical analysis of non-linear structural equation models with continuous and polytomous data. Brit. J. Math. Stat. Psychol. 53, 209–232.

Legendre, L., Legendre, P., 1983. Numerical Ecology. Elsevier Science Publications, Amsterdam.

Lehman, J.T., 1988. Hypolimnetic metabolism in Lake Washington—Relative effects of nutrient load and food web structure on lake productivity. Limnol. Oceanogr. 33, 1334–1347.

Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73, 1943–1967.

Levins, R., 1966. The strategy of model building in population biology. Am. Sci. 54, 421–431.

Malaeb, Z.A., Summers, J.K., Pugesek, B.H., 2000. Using structural equation modeling to investigate relationships among ecological variables. Environ. Ecol. Stat. 7, 93–111.

Mardia, K.V., 1974. Applications of some measures of multivariate skewness and kurtosis in testing normality and robustness studies. Sankhya, Ser B 36, 115–128.

Martin, J.K., McDonald, R.P., 1975. Bayesian estimation in unrestricted factor analysis: a treatment for Heywood cases. Psychometrika 40, 505–517.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM Software Design, Oregon, USA.

Mitchell, R.J., 1992. Testing evolutionary and ecological hypotheses using path-analysis and structural equation modeling. Funct. Ecol. 6, 123–129.

O'Neill, R.V., DeAngelis, D.L., Waide, J.B., Allen, T.F.H., 1986. A Hierarchical Concept of Ecosystems. Princeton University Press, Princeton, New Jersey, USA.

Oreskes, N., Shrader-Frechette, K., Belitz, K., 1994. Verification, validation, and confirmation of numerical models in the earth-sciences. Science 263, 641–646.

Paap, R., 2002. What are the advantages of MCMC based inference in latent variable models? Stat. Neerl. 56, 2–22.

Pace, M.L., 2001. Prediction and the aquatic sciences. Can. J. Fish Aquat. Sci. 58, 63–72.

Peters, R.H., 1991. A Critique for Ecology. Cambridge University Press, Cambridge, UK.

Petraitis, P.S., Dunham, A.E., Niewiarowski, P.H., 1996. Inferring multiple causality: the limitations of path analysis. Funct. Ecol. 10, 421–431.

Pugesek, B.H., Tomer, A., Von Eye, A., 2003. Structural Equation Modeling: Applications in Ecological and Evolutionary Biology. Cambridge University Press, Cambridge, UK.

Pugesek, B.H., Tomer, A., 1996. The Bumpus house sparrow data: a reanalysis using structural equation models. Evol. Ecol. 10, 387–404.

Pugesek, B.H., Tomer, A., 1995. Determination of selection gradients using multiple-regression versus structural equation models (SEM). Biomet. J. 37, 449–462.

Rastetter, E.B., King, A.W., Cosby, B.J., Hornberger, G.M., O'Neill, R.V., Hobbie, J.E., 1992. Aggregating fine-scale ecological knowledge to model coarser-scale attributes of ecosystems. Ecol. Appl. 2, 55–70.

Raykov, T., 1992. On structural models for analyzing change. Scand. J. Psychol. 33, 247–265.

Reckhow, K.H., 1999. Water quality prediction and probability network models. Can. J. Fish Aquat. Sci. 56, 1150–1158.

Reckhow, K.H., Arhonditsis, G.B., Kenney, M.A., Hauser, L., Tribo, J., Wu, C., Elcock, K.J., Steinberg, L.J., Stow, C.A., McBride, S.J., 2005. A predictive approach to nutrient criteria. Environ. Sci. Technol. 39, 2913–2919.

Richey, J.E., 1979. Patterns of phosphorus supply and utilization in Lake Washington and Findley Lake. Limnol. Oceanogr. 24, 906–916.

Salthe, S.N., 1985. Evolving Hierarchical Systems. Columbia University Press, New York, USA.

Scheines, R., Hoijtink, H., Boomsma, A., 1999. Bayesian estimation and testing of structural equation models. Psychometrika 64, 37–52.

Shipley, B., 2000. Cause and Correlation in Biology: A User's Guide to Path Analysis, Structural Equations and Causal Inference. Cambridge University Press, Cambridge UK.

Shipley, B., 1997. Exploratory path analysis with applications in ecology and evolution. Am. Nat. 149, 1113–1138.

Smith, F.A., 1995. Scaling of digestive efficiency with body-mass in *Neotoma*. Funct. Ecol. 9, 299–305.

Sommer, U., 1989. The role of competition for resources in phytoplankton succession. In: Sommer, U. (Ed.), Phytoplankton ecology. Succession in plankton communities. Springer-Verlag, New York, pp. 57–106.

Soranno, P.A., 1997. Factors affecting the timing of surface scums and epilimnetic blooms of blue-green algae in a eutrophic lake. Can. J. Fish Aquat. Sci. 54, 1965–1975.

Soranno, P.A., Carpenter, S.R., Lathrop, R.C., 1997. Internal phosphorus loading in Lake Mendota: response to external loads and weather. Can. J. Fish Aquat. Sci. 54, 1883–1893.

Spiegelhalter, D., Thomas, A., Best, N., Gilks, W., 1996. Bayesian Version Using Gibbs Sampling Manual, Version ii. Available at http://www.mrc-bsu.cam.ac.uk/bugs.

Spiegelhalter, D., Thomas, A., Best, N., Lunn, D., 2003. WinBUGS User Manual, Version 1.4. Available at http://www.mrc-bsu.cam.ac.uk/bugs.

Sterner, R.W., Hessen, D.O., 1994. Algal nutrient limitation and the nutrition of aquatic herbivores. Annu. Rev. Ecol. Syst. 25, 1–29.

Stow, C.A., Borsuk, M.E., 2003. Enhancing causal assessment of estuarine fishkills using graphical models. Ecosystems 6, 11–19.

Sugihara, G., May, R.M., 1990. Applications of fractals in ecology. Trends Ecol. E 5, 79–86.

Vepsalainen, K., Spence, J.R., 2000. Generalization in ecology and evolutionary biology: from hypothesis to paradigm. Biol. Philos. 15, 211–238.

Wright, S., 1918. On the nature of size factors. Genetics 3, 367–374.

Wright, S., 1921. Correlation and causation. J. Agr. Res. 20, 557–585.

Zhu, H.T., Lee, S.Y., 1999. Statistical analysis of non-linear factor analysis models. Brit. J. Math. Stat. Psychol. 52, 225–242.