Aquat Sci (2014) 76:145–154
DOI 10.1007/s00027-013-0324-5

Aquatic Sciences

RESEARCH ARTICLE

Phosphorus loading, transport and concentrations in a lake chain: a probabilistic model to compare management options

Stephen R. Carpenter · Richard C. Lathrop

Received: 12 August 2013 / Accepted: 22 October 2013 / Published online: 30 October 2013

Abstract Phosphorus (P) loading, exports and concentrations of the four lakes of the Yahara chain (Wisconsin, USA) were compared under four load-reduction plans using a model calibrated with 29–33 years of annual data. P mitigation goals must balance reductions in P concentrations in the four lakes and the export from the lake chain to downstream waters. Lake Mendota, the uppermost lake, is most responsive to P load reductions, and benefits diminish downstream. Nonetheless, the greatest reductions in export from the lake chain to downstream waters derive from P load reductions to lakes lower in the chain. The effective grazer *Daphnia pulicaria* causes large improvements in water quality. Management to maintain populations of *D. pulicaria* has substantial benefits that augment those from reductions in P loading. Model projections show high variability in water quality and exports under all load-reduction plans. This variability is driven by inter-annual variation in runoff. Thus lake managers and the public should expect ongoing year-to-year variability in water quality, even though P load mitigation will improve water quality on average. Because of high variability from year to year, ongoing monitoring is essential to assess the effects of management of this chain of lakes.

Keywords Lakes · Landscape limnology · Phosphorus · Water quality

S. R. Carpenter (✉)
Center for Limnology, University of Wisconsin,
680 North Park Street, Madison, WI 53706, USA
e-mail: srcarpen@wisc.edu

R. C. Lathrop
Bureau of Science Services, Wisconsin Department of Natural Resources, 2801 Progress Road, Madison, WI 53716, USA
e-mail: rlathrop@wisc.edu

Introduction

Lakes have long been viewed as singular entities (Forbes 1887). Comparisons of lakes treating each one as an independent replicate, long-term studies of particular lakes and whole-lake experiments have made many fundamental contributions to ecosystem science (Pace and Groffman 1998). In applied limnology, steady-state mass balance models have been powerful tools for management of individual lakes (Reckhow and Chapra 1983). More recently, however, research has expanded on connected systems of streams and lakes, and the patterns that emerge among networks of lakes on complex landscapes (Magnuson et al. 2006; Soranno et al. 2010). In landscape limnology, lakes and streams are seen as interdependent components of a spatially distributed system, rather than isolated ecosystems (Soranno et al. 2010).

In chains of lakes, one might expect downstream trends to be predictable from hydrology and mass-balance principles. Unreactive solutes such as chloride should be distributed in proportion to flows of water along hydrologic paths, and biologically active substances such as phosphorus (P) should tend to diminish in concentration as they are trapped in upstream basins by uptake and sedimentation. However, the observed patterns of solutes in lake chains are more complicated due to lake-to-lake variation in water residence time as well as solute inputs, outputs and reactions such as biotic uptake or sedimentation (Soranno et al. 1999; Kling et al. 2000; Sadro et al. 2012). Organic carbon, for example, is both created and processed as it passes through networks of lakes in a landscape, leading to complex spatial patterns of variability among lakes (Cardille et al. 2007; Einola et al. 2011).

Water quality variables such as nutrient or algal concentrations often increase downstream in chains of lakes (Fisher et al. 2009; Hillbricht-Ilkowska 2002; Soranno et al. 1999). However, the reverse trend occurs if nutrients are sequestered in sediments of upstream lakes (Leavitt et al. 2006) or diluted by downstream sources of low-nutrient water (Alvarez-Cobelas et al. 2006). Moreover, management actions can generate unexpected responses in lake chains. When sewage treatment decreased P loads to the upper lake of one chain, water quality improvements were greatest in the upper lake and diminished downstream (Choulik and Moore 1992). In a different chain of eutrophic lakes, benefits of decreased P load to upstream lakes were countered by increased recycling from sediment which became a P source to downstream lakes (Belmont et al. 2009). In chains of shallow lakes that exhibit clear or turbid alternate stable states, management actions can trigger a domino effect of state reversals that propagates downstream (Hilt et al. 2011).

These examples show that intuition may not be a reliable guide for managing nutrients to mitigate eutrophication in a chain of lakes. It is not surprising, therefore, that limnologists have developed models to understand nutrient dynamics in lake chains (Epstein et al. 2013). Building on a well-established framework for mechanistic water quality modeling of a single lake (Chapra and Reckhow 1983), Epstein et al. (2013) constructed a linked model of four lakes. The first lake in the chain acted as a sink for P and organic carbon and a source for inorganic nitrogen, while downstream lakes were sources of all three solutes. This mechanistic model was calibrated successfully using only a year of data.

Empirical modeling is an alternative to mechanistic modeling that can be considered when extensive data are available (Reckhow and Chapra 1983; Chapra and Reckhow 1983). We studied P dynamics in a chain of four lakes using 29–33 years of data for P inputs, outputs and in-lake concentrations. We also considered the role of grazing by zooplankton in the two upper lakes. Management of the four lakes must balance water-quality improvements among the individual lakes as well as P export from the chain to downstream ecosystems. Moreover, projections must account for the known variability of water quality in order to be credible and useful. To understand these tradeoffs and uncertainties, we constructed an empirical model for P loads, downstream exports, and summer concentrations in surface waters of each lake. The model was used to project probability distributions of summer total P concentrations and P output from the chain under current conditions and four management plans. Results allow management alternatives to be compared with respect to water quality outcomes and their variability.

Methods

Study site

The Yahara chain of lakes—Mendota, Monona, Waubesa and Kegonsa—lies near Madison in south-central Wisconsin USA (43°4′N, 89°22′W). Lake Mendota is among the best-studied lakes in the world, owing to a long tradition of limnological research that began in the 1880s and continues today (Kitchell 1992; Magnuson 2002; Carpenter et al. 2006; Lathrop 2007). Fewer studies have been published on lakes Monona, Waubesa and Kegonsa even though these lakes have been monitored and managed to mitigate eutrophication for many years (Lathrop 2007). Flows of phosphorus studied in this paper are shown in Fig. 1.

The watershed of the four lakes occupies 1,026 km^2 of gently sloping glaciated terrain. The direct drainage area of Lake Mendota (553 km^2) is mostly agricultural with urban land uses around most of the shoreline. Urban land use is expanding (Carpenter et al. 2007). Lake Mendota is the largest (39.6 km^2) and deepest (mean depth 12.7 m) of the lakes, with a water residence time of 4.4 years. Lake Monona's direct drainage area (119 km^2) is mostly urban.

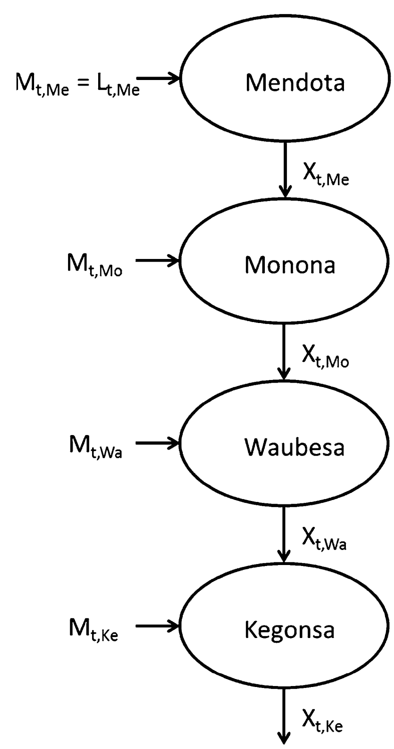

Fig. 1 Schematic diagram of the major phosphorus flows into the chain of four Yahara Lakes. *M* denotes direct drainage load, which is total load (L) in the case of the upper lake, Lake Mendota. *X* denotes export downstream. Subscript *t* denotes time and the lake subscripts are *Me* Mendota, *Mo* Monona, *Wa* Waubesa, *Ke* Kegonsa

Lake Monona is the second-largest (13.7 km^2) and second-deepest (mean depth 8.3 m) of the four lakes with a water residence time of 0.79 years. The direct drainage to Lake Waubesa (124 km^2) is mixed urban and agricultural with many buildings on the lake's shoreline. Lake Waubesa is the smallest (8.5 km^2) and shallowest (mean depth 4.7 m) lake with the shortest water residence time (0.23 years). Lake Kegonsa has a largely agricultural direct drainage area (155 km^2) with many buildings along the shoreline. Lake Kegonsa is nearly as large as Lake Monona (13.0 km^2) but shallow (mean depth 5.1 m) with a relatively short residence time (0.33 years).

Phosphorus data

For each of the four lakes, we developed time series of direct drainage loads, exports, and summer surface water TP using monitoring data gathered by the North Temperate Lakes Long-Term Ecological Research (NTL-LTER) program, US Geological Survey, and Wisconsin DNR (Lathrop et al. 1998; Lathrop 2007; Carpenter and Lathrop 2008; Lathrop and Carpenter 2013). Annual direct drainage loads and exports of phosphorus were computed from November 1 of the previous year through October 31 of the stated year. Thus the transition between annual steps occurred during fall turnover, which is a convenient time to measure total phosphorus mass in the lake water. This time frame proved to be suitable for relating summer water quality conditions to terms of the phosphorus budgets.

Annual P loads for 1976 through 2008 (33 years) were derived using approaches that were updated and expanded from previous studies of Lake Mendota (Lathrop et al. 1998; Carpenter and Lathrop 2008; Lathrop and Carpenter 2013). Briefly, rural P loads to Mendota were based on two subwatersheds with long-term monitoring data (streamflow and P concentrations) with computed loads that were extrapolated to unmonitored rural areas. Loads from urban basins draining directly to Lake Mendota were computed using a combination of SWAT(Gassman et al. 2007) and SLAMM (Pitt and Voorhees 2002) stormwater runoff modeling, an approach that was also used for computing Monona's direct drainage loads given its land use is almost entirely urban. Direct drainage loads to Waubesa and Kegonsa were computed via SWAT modeling. Outlet P loads for all four lakes were computed by multiplying discharge volumes for each lake's outlet times surface water P concentration data. Waubesa and Kegonsa outlet loads prior to 1980 were not computed due to the lack of reliable lake P data.

In addition to P loads entering the four lakes via streams and storm sewers, P can also enter via dry fallout and precipitation directly on the lake surfaces, and from groundwater inputs, with dry fallout being the most important of the three miscellaneous sources. Early estimates for these sources were developed for Lake Mendota (Lathrop et al. 1998) and treated as a constant annual input of P in our loading analyses. We applied estimates for these miscellaneous sources to the lower Yahara lakes based on a unit lake surface area conversion from Mendota's estimate (excluding groundwater, which has much less inflow to the lower Yahara lakes). For Mendota, the miscellaneous sources of loading represented 11 % of the long-term annual average P load; for the lower Yahara lakes the sources represented 5–6 % of the average load. For modeling purposes, we added these small inputs to the direct drainage load.

Summer TP concentrations in the surface waters of the lakes were measured biweekly during summer starting in 1980 (Lathrop 2007). Sample-to-sample variability in TP concentration can be high in eutrophic lakes. Therefore we analyzed the mean log TP concentration over the summer period (30 June to 7 September) as an annual index of water quality for each lake. The lakes are stratified during this time interval. Thus the variability of our model projections of summer TP represents variability among years, and not the variability among samples within years.

Zooplankton data

The grazer *Daphnia pulicaria* strongly affects water quality in lakes Mendota and Monona (Lathrop et al. 1998, 1999). Therefore, the presence of *D. pulicaria* was included as a predictor of summer TP in models for these lakes. Presence of *D. pulicaria* could not be considered in lakes Waubesa and Kegonsa because measurements of zooplankton were not available in those lakes. Presence of *D. pulicaria* was determined by counting vertical net hauls obtained biweekly during the ice free season from lakes Mendota and Monona (Lathrop et al. 1999).

Model

Phosphorus flows studied in this paper include the direct drainage loads to each of the four lakes and the outflows through the Yahara River to downstream water bodies (Fig. 1). We constructed a model for the direct drainage loads, transfers through the Yahara River, and summer surface water TP concentrations of the four lakes and fit the model to the observed time series (Table 1). We then used the model to project summer surface water TP concentrations for contrasting management situations of direct drainage loads. The projections are probability distributions that account for the uncertainty in the fit of the model to the available data.

Table 1 Sources of time series used to estimate the model parameters

Time series	Mendota-1	Monona-2	Waubesa-3	Kegonsa-4
Phosphorus mass in water column near 1 November	Measured 1975–2008	Measured 1975–2008	Measured 1980–2008	Measured 1980–2008
Direct drainage loads from land	Rural: monitored in the two largest sub-watersheds; calculated by regression or export coefficients based on measured loads for sub-watersheds that were not continually monitored 1975–2008. Urban: estimated with SWAT and SLAMM 1976–2008	Estimated with SWAT and SLAMM 1976–2008	Estimated with SWAT 1980–2008	Estimated with SWAT 1980–2008
Exports from the outlet to downstream ecosystems	Measured 1976–2008	Measured 1976–2008	Measured 1980–2008	Measured 1980–2008
Summer TP in surface waters	Measured 1976–2008	Measured 1976–2008	Measured 1980–2008	Measured 1980–2008
Presence/absence of *Daphnia pulicaria*	Measured 1976–1980	Measured 1976–1980	NA	NA

The number following each lake name indicates the lake's position in the chain

NA not available

Direct drainage loads to the four lakes were modeled using the following empirical equations for the logarithm of load from all sources other than upstream lakes:

$$\begin{aligned} M_{t,Me} &= a_{Me} + \mu_{Me} + \phi_1 M_{t-1,Me} + \phi_2 M_{t-2,Me} + \varepsilon_{t,Me} \\ M_{t,Mo} &= a_{Mo} + \mu_{Mo} + \varepsilon_{t,Mo} \\ M_{t,Wa} &= a_{Wa} + \mu_{Wa} + \varepsilon_{t,Wa} \\ M_{t,Ke} &= a_{Ke} + \mu_{Ke} + \varepsilon_{t,Ke} \end{aligned} \tag{1}$$

In these equations, M is the logarithm of annual load (kg/year) in year t from all sources other than upstream lakes. In practice, log M is the direct drainage from the land in the lake's subwatershed. On the right side of the equations, μ is the mean M across years, ϕ_1 and ϕ_2 are autoregression coefficients for lags 1 and 2 years, respectively, and ε are error terms that are uncorrelated in time. The a terms are the adjustment of mean log load by lake management. For example, if there is no change to load then $a = \log(1) = 0$, or if load is cut in half then $a = \log(0.5) = -0.693$. The lake subscripts are *Me* for Mendota, *Mo* for Monona, *Wa* for Waubesa and *Ke* for Kegonsa. Although the error terms are uncorrelated in time, they are correlated among lakes. The distribution of the ε is multivariate Normal with a mean vector of zeros, and covariance matrix representing the variances of the four individual lakes and the covariances of each lake with the other three lakes. Samples of M for the four lakes were simulated by drawing random vectors from the posterior distribution of Eq. (1) computed from the observed time series of loads using an uninformative prior distribution (Box and Tiao 1973; Gelman et al. 2004).

For Lake Mendota, which has phosphorus inputs from land but no inflow of phosphorus from other lakes, the annual load for year k, $L_{k,Me}$ in kg/year is simply

$$L_{k,Me} = e^{M_{k,Me}} \tag{2}$$

where e is the base of natural logarithms. For the other lakes, annual loads also include transfers from upstream lakes.

$$\begin{aligned} L_{k,Mo} &= e^{M_{k,Mo}} + e^{E_{k,Me}} \\ L_{k,Wa} &= e^{M_{k,Wa}} + e^{E_{k,Mo}} \\ L_{k,Ke} &= e^{M_{k,Ke}} + e^{E_{k,Wa}} \end{aligned} \tag{3}$$

In Eq. (3), E is the logarithm of annual export (kg/year). The logarithm of annual export was modeled as a linear function of the log of annual load. For lake j in year t,

$$E_{t,j} = b_{j,0} + b_{j,1} L_{t,j} + v_{t,j} \tag{4}$$

In Eq. (4), $b_{j,0}$ is the intercept, $b_{j,1}$ is the slope, and $v_{t,j}$ is a sequence of errors that are independently and identically distributed normal. To simulate random samples of export X (kg/year), simulated values of $L_{k,j}$ were used in random draws of $X_{k,j}$ from the predictive posterior distribution of Eq. (4) (Box and Tiao 1973; Gelman et al. 2004). Export $X_{k,j}$ for random sample k in lake j is

$$X_{k,j} = e^{E_{k,j}} \tag{5}$$

Total phosphorus in surface water, averaged over all samples from the summer stratified season was modeled as a linear function of load and export

$$\ln(P_{t,j}) = c_o + c_1 L_{t,j} + c_2 X_{t,j} + c_3 Z_{t,j} + \omega_{t,j} \tag{6}$$

$P_{t,j}$ is phosphorus concentration in year t and lake j, c_0 is the intercept, c_1 is the load effect, c_2 is the export effect, c_3 is the effect of zooplankton Z, and $\omega_{t,j}$ are errors that are independently and identically distributed normal. The binary zooplankton variable Z represents the absence

($Z = 0$) or presence ($Z = 1$) of the highly effective grazer *Daphnia pulicaria* which strongly affects water quality in lakes Mendota and Monona (Lathrop et al. 1999). Zooplankton data were not available for lakes Waubesa and Kegonsa. For these lakes, the zooplankton term was removed from Eq. (6). To simulate random samples of ln(P), simulated values of $L_{k,j}$ were used in generating random draws of $X_{k,j}$ from the predictive posterior distribution of Eq. (4) (Box and Tiao 1973; Gelman et al. 2004).

Simulation of load reduction plans

Responses of all four lakes were simulated for five different Load-Reduction Plans (LRP) that represent plausible approaches for managing P loads to the lakes. The simulations compute predicted posterior probability distributions for epilimnetic total P concentrations during summer stratification in all four lakes. In addition, predicted posterior probability distributions for P export from Lake Kegonsa were computed to assess the contribution of the Yahara lakes to water quality downstream. All results presented here are based on 10,000 random draws from the posterior predicted distributions.

The five LRPs are summarized below. The first situation, current conditions, maintains median loading rates that are the same as those observed for 1975–2008. The other four LRPs halve the total loading, in kg/year, to all four lakes combined but allocate the load reductions differently among lakes.

LRP-1: current conditions

Projections of current conditions were computed to provide a reference distribution for effects of management and also to compare model results with observations.

LRP-2: 50 % reduction of land loads to all lakes

At the time of writing, discussions of management targets for the Yahara lakes revolve around 50 % load reductions to all lakes. The final plans that are implemented may be somewhat different, but nonetheless 50 % reductions are a useful benchmark for load reductions that are viewed as aggressive but feasible.

LRP-3: all load reductions from Mendota

Lake Mendota has the largest subwatershed and contributes phosphorus to all downstream lakes through the Yahara River. If all mitigation efforts focused on Lake Mendota, it might be possible to cause great improvements in that lake and still obtain considerable benefits downstream. In this situation, the reduction in P load to Lake Mendota is the same, in kg/year, as the sum of the reductions to all four lakes in the plan with 50 % reduction of loads to all four lakes combined.

LRP-4: Kegonsa direct drainage load to zero, remaining load reductions from Mendota

The export of P from the Yahara Lakes to downstream waters is the export from Lake Kegonsa. Thus there may be additional benefits downstream if direct drainage loads to Lake Kegonsa are decreased to zero. To simulate this situation, 100 % of the watershed loads to Lake Kegonsa were eliminated by setting $a_{Ke} = -\mu_{Ke}$. All other reductions of load occurred in Lake Mendota. The total load reductions to all four lakes were the same as in the plan with 50 % reduction of loads to all four lakes combined.

LRP-5: Monona, Waubesa, Kegonsa load to zero, remaining load reduction from Mendota

Further reductions in P export from the Yahara Lakes to downstream lakes could plausibly occur if direct drainage loads to the three lower lakes, Monona, Waubesa and Kegonsa, were cut to zero. To simulate this situation, the reduction of direct drainage loads to these three lakes was 100 %. The total load reductions to all four lakes were the same as in the plan with 50 % reduction of loads to all four lakes combined. The remainder of the load reduction in kg/year was taken from Lake Mendota.

Results

For all four lakes, measured export of phosphorus was linearly related to measured load on log-log axes (Fig. 2). Note that export is smaller than load and the slopes are less than one, indicating that each lake retains some fraction of influent phosphorus in its sediments (Frisk et al. 1981).

Model predictions of summer TP are linearly related to observed summer TP on log-log axes (Fig. 3). Though they are statistically significant, the relationships show considerable scatter. This uncertainty is an important contributor to the uncertainties seen in the projections of water quality under different management situations.

Simulated distributions of load and export for the four lakes are similar to observations (Table 2). There is a tendency for the 25th and 75th percentiles of simulated data to be smaller and larger, respectively, than observed. This occurs because the simulations are predicted distributions that account for the uncertainty of projections using models fitted to the data. Nonetheless, the median of the simulations is close to the median of the observations.

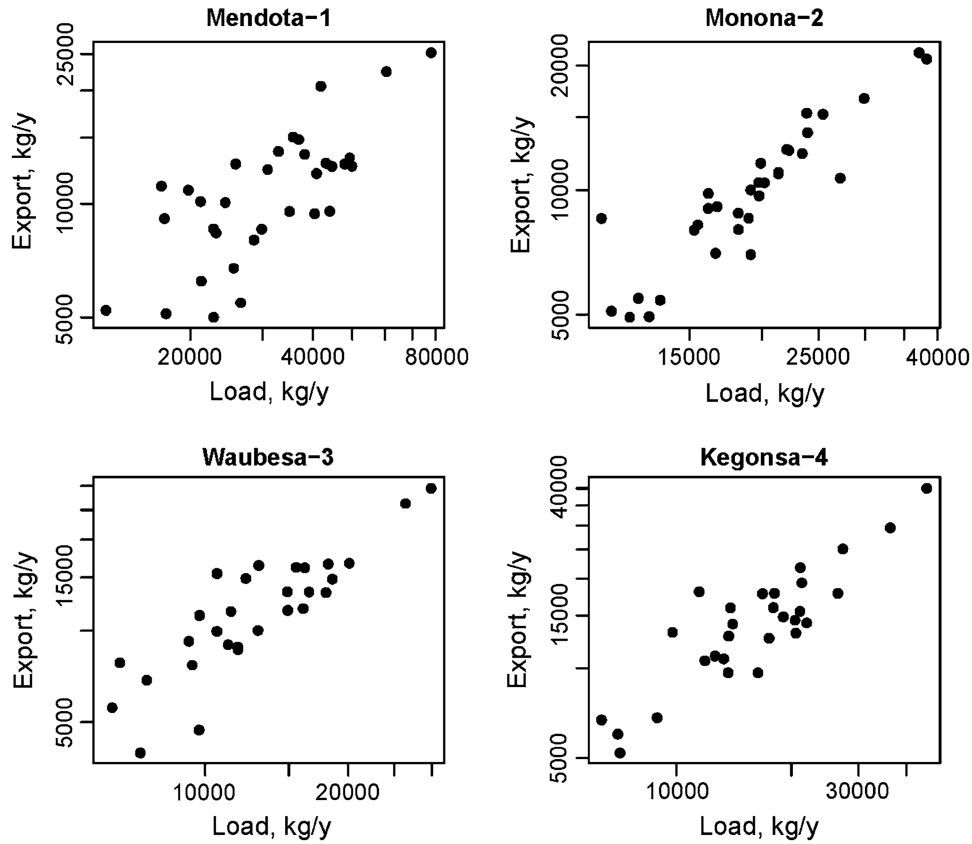

Fig. 2 Total P load (kg/year) from all sources versus export downstream (kg/year) for each of the four lakes. The number following each lake name indicates the lake's position in the chain. Note log-log axes. All linear regression slopes are less than one (slopes with s.e.: Mendota 0.26 ± 0.04; Monona 0.59 ± 0.04; Waubesa 0.93 ± 0.08; Kegonsa 0.77 ± 0.07). All regressions are significant at $p < 0.001$. Correlation coefficients: Mendota 0.79; Monona 0.94; Waubesa 0.91; Kegonsa 0.91

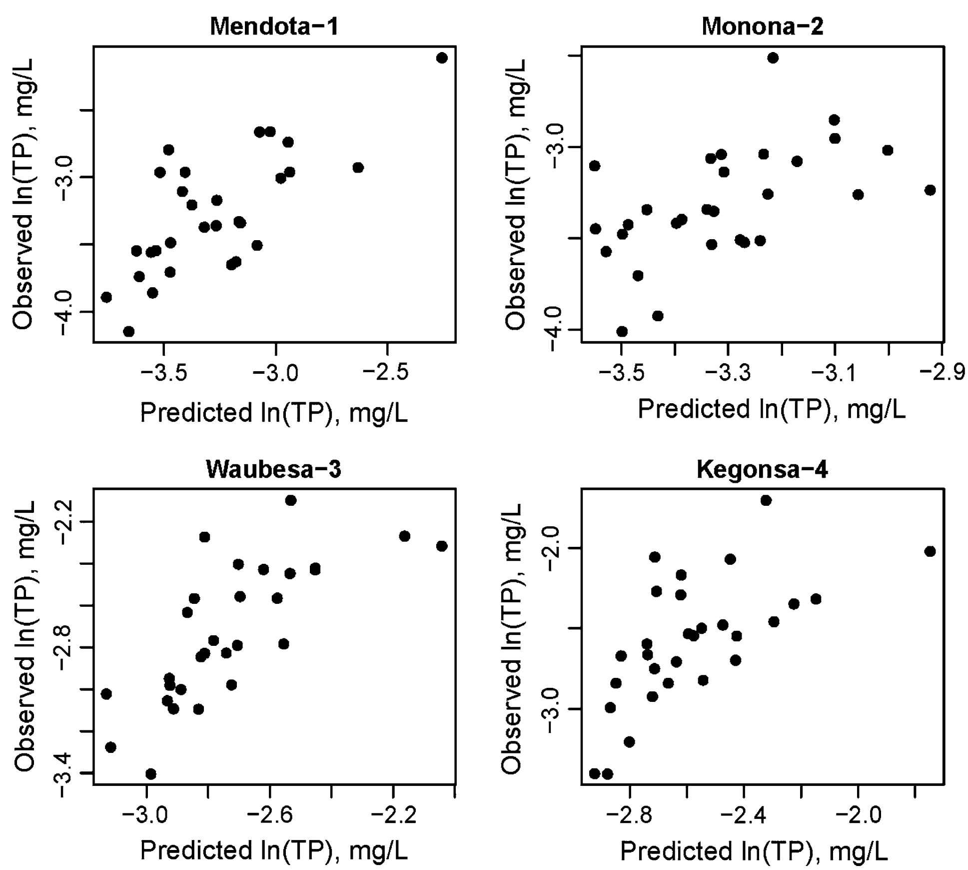

Fig. 3 Predicted log of summer TP versus observed log of summer TP (mg/L) for the four lakes. The number following each lake name indicates the lake's position in the chain. All regressions are significant with $p < 0.001$. Correlations of predictions and observations: Mendota 0.73, Monona 0.53, Waubesa 0.71, Kegonsa 0.64

Table 2 Observed and simulated quartiles of load (kg/year; from land and upstream lakes) and export (kg/year) for the four lakes

Lake	Sample	Annual P load (kg/year)			Annual P export (kg/year)		
		25th	50th	75th	25th	50th	75th
Mendota-1	Observed	22,820	30,980	41,880	8,587	10,890	12,850
	Simulated	23,090	31,080	41,560	7,964	10,510	13,950
Monona-2	Observed	16,170	19,140	22,250	8,054	9,835	12,280
	Simulated	15,800	19,120	23,450	7,334	9,758	13,200
Waubesa-3	Observed	9,749	11,750	16,080	8,870	11,720	15,500
	Simulated	9,537	12,490	16,660	7,583	11,140	16,750
Kegonsa-4	Observed	12,650	16,840	21,110	10,780	14,220	17,850
	Simulated	11,240	15,990	23,320	9,090	13,790	21,360

Observed loads are for 1976–2008 for Mendota and Monona, and 1980–2008 for Waubesa and Kegonsa. Simulated loads are 10,000 random draws from the posterior predicted distributions. The number following each lake name indicates the lake's position in the chain

Summer TP projections under current conditions and the hypothetical LRPs are presented for each lake in Fig. 4. Each panel presents summer TP in one of the four lakes. The x-axis represents the LRPs: 1 = current situation; 2 = 50 % decrease in loads to all lakes; 3 = all load reductions from Mendota; 4 = zero load to Kegonsa from direct drainage and remaining load reduction taken from Mendota; 5 = zero load from direct drainage to Monona, Waubesa and Kegonsa, and remaining load reduction taken from Mendota. The total load reduction (kg/year) from all four lakes combined is the same in LRPs 2–5. In Lakes Mendota and Monona, summer TP was projected with the presence or absence of the highly effective grazer *Daphnia pulicaria*. Zooplankton data were not available for model calibration in lakes Waubesa and Kegonsa.

In Lake Mendota, the presence of *Daphnia pulicaria* improves summer TP in all LRPs (Fig. 4a). The 50 % load reduction (LRP 2) substantially improves summer TP. However, LRP 3, in which all P load mitigation is focused on Mendota, yields the greatest improvement in summer TP in that lake. LRP 5, in which P load mitigation focuses on the other three lakes, yields the least improvement in Lake Mendota.

In Lake Monona, as in Lake Mendota, *Daphnia pulicaria* improves summer TP in all situations (Fig. 4b). The 50 % load reduction from all four lakes (LRP 2) and the case where P mitigation focuses on Monona, Waubesa and Kegonsa (LRP 5) yield similar improvements to summer TP for Lake Monona. LRP 4, in which P mitigation focuses on lakes Kegonsa and Mendota, is less favorable for summer TP in Lake Monona. Nonetheless, the differences among the four mitigation situations (LRPs 2–5) are minor for Lake Monona.

Summer TP in Lake Waubesa is most improved by LRP 5, in which P mitigation effort focuses on eliminating direct drainage loads to the three lower lakes (Fig. 4c). However, LRP 2, which reduces loads by 50 % in all subwatersheds, is almost as beneficial for decreasing summer TP in Lake Waubesa.

The outcome for summer TP concentrations in Lake Kegonsa is similar to that for Lake Waubesa (Fig. 4d). Summer TP is most improved by LRP 5, in which P mitigation effort focuses on eliminating direct drainage loads to the three lower lakes, but LRP 2, which reduces loads by 50 % in all subwatersheds, is almost as beneficial. All LRPs notably decrease the extreme high TP concentrations (95th percentiles) in Lake Kegonsa.

Phosphorus exports from the entire Yahara chain of lakes are equivalent to the exports from Lake Kegonsa. These outflows are important for management of downstream ecosystems. P exports from Lake Kegonsa are most improved by LRP 5, which focuses on elimination of direct drainage loads of phosphorus to the three lower lakes (Fig. 5). LRP 4, which eliminates direct drainage loads to Kegonsa and focuses the remaining P mitigation effort on Mendota, and LRP 2, which reduces loads by 50 % in all watersheds, are almost as beneficial. LRP 3, which focuses P mitigation effort on Lake Mendota, causes the smallest change in median P export from Lake Kegonsa, and projected variability of the exports is rather high.

Discussion

Implications for the Yahara chain

In this chain of lakes, phosphorus load mitigation goals must consider water quality improvements in the lakes themselves as well as exports from the lakes that affect downstream water bodies. If all mitigation effort focuses on Lake Mendota, the largest lake highest in the drainage, there are substantial improvements of summer TP in Lake Mendota. Improvements also occur downstream because P exports from Lake Mendota through the Yahara River are

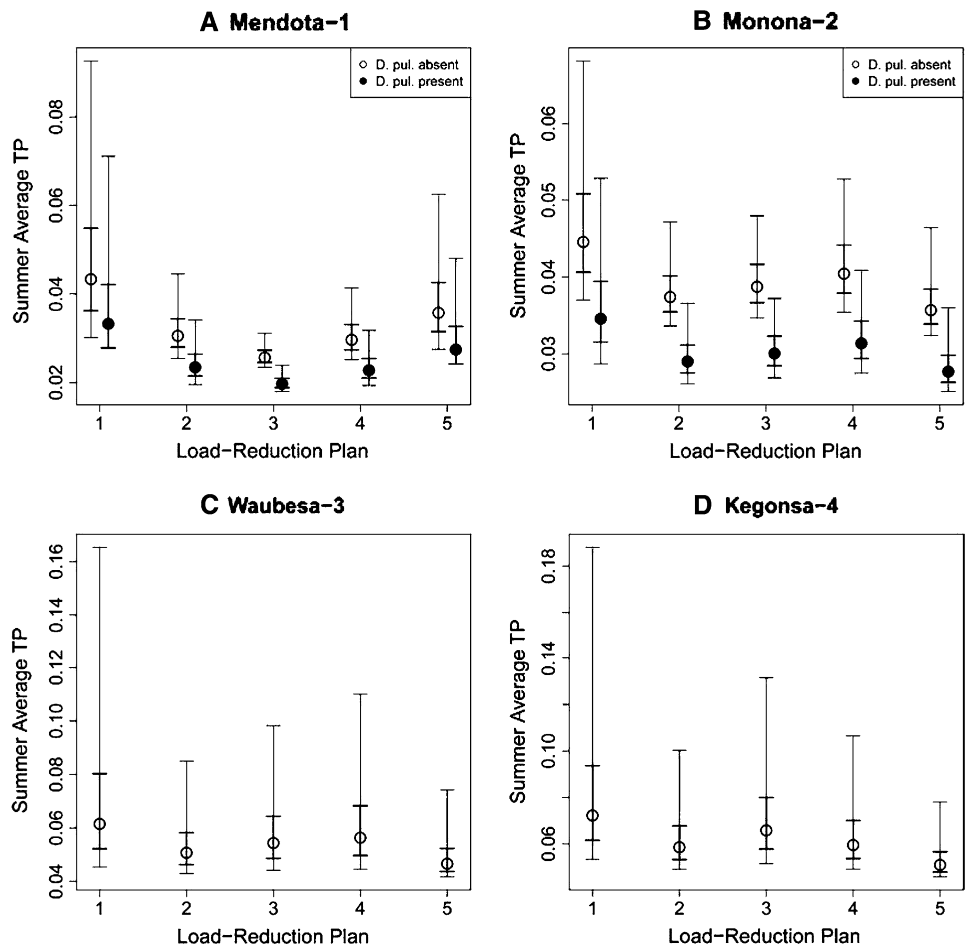

Fig. 4 Posterior density plots for summer average total P concentration (mg/L) in four lakes under five load-reduction plans. For each load-reduction plan, the median (*circle*), first and third quartiles (*thicker line with horizontal bars*) and 5th and 95th percentiles (*thinner line with horizontal bars*) are shown. Load-reduction plans: *1* current situation, *2 50 %* decrease in loads to all lakes, *3* all load reductions from Mendota, *4* zero load to Kegonsa from land and remaining load reduction taken from Mendota, *5* zero load from land to Monona, Waubesa and Kegonsa, and remaining load reduction taken from Mendota. The average total load reduction (kg/year) is the same in load-reduction plans 2–5. **a** Lake Mendota with (*closed circles*) and without (*closed circles*) *Daphnia pulicaria*. **b** Lake Monona with (*closed circles*) and without (*closed circles*) *D. pulicaria*. **c** Lake Waubesa. **d** Lake Kegonsa. The number following each lake name indicates the lake's position in the chain

an important nutrient source to the lower lakes. However, water quality improvements are muted in the lowest lake of the chain, Lake Kegonsa, and reductions in P export from Lake Kegonsa are modest and highly variable.

On the other hand, if phosphorus load mitigation emphasizes the lower lakes of the chain, median P exports from Lake Kegonsa are decreased by more than a factor of two, but improvements in Lake Mendota's summer TP are small.

A 50 % reduction in P load from direct drainage to all four lakes achieves an intermediate outcome. Summer TP concentration improves in all of the lakes, and P exports from Lake Kegonsa decrease by almost a factor of two.

While the P load reduction plans compared here do yield improvements in summer TP and P exports from the chain of lakes as a whole, the year-to-year variability is large compared the magnitude of the median changes. Moreover, variability may be underestimated by this model. Our information about variability of P loads and exports comes from 1976 to 2008. However, future climate and land use change is expected to bring more extreme precipitation events and these could increase variability in runoff and P loads. In addition, impervious surface is increasing in the watershed, and could also contribute to more variable P loads in the future.

Daphnia pulicaria causes substantial improvements in water quality of lakes Mendota and Monona, as noted in several earlier papers about these lakes (Lathrop et al. 1998, 1999, 2002). For Lake Monona, the beneficial effects of *D. pulicaria* are comparable to the benefits of any of the P load reduction plans. Therefore, maintenance of the *D. pulicaria* populations of these lakes should be a priority for water quality managers. *D. pulicaria* populations can be promoted by maintaining high densities of piscivorous fish and low densities of planktivorous fish (Kitchell 1992; Lathrop et al. 2002). It is also important to exclude invasive species that may consume *D. pulicaria*.

Our findings have specific implications for P load mitigation in this chain of lakes. (1) The 50 % load reduction from all subwatersheds appears to balance the goals of improving summer TP and decreasing exports of P from the chain of lakes as a whole. Because of the high variability among different load mitigation situations, it may be difficult to find an optimal combination of load reduction goals among the subwatersheds. (2) *Daphnia pulicaria* causes large improvements in water quality. Management

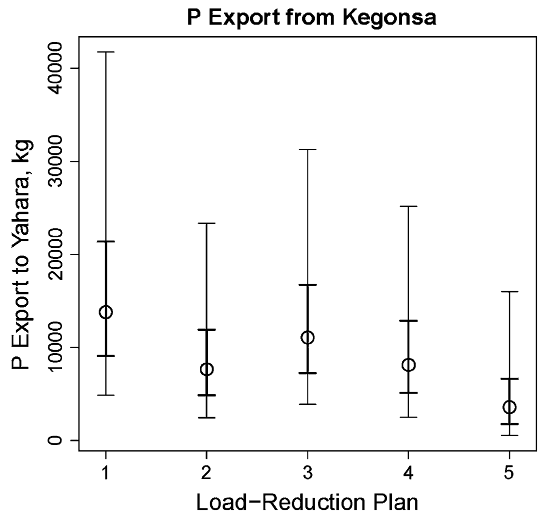

Fig. 5 Posterior density plots for export from Lake Kegonsa (kg/year) under five load-reduction plans. For each load-reduction plan, the median (*circle*), first and third quartiles (*thicker line with horizontal bars*) and 5th and 95th percentiles (*thinner line with horizontal bars*) are shown. Load-reduction plans: *1* current situation, *2* 50 % decrease in loads to all lakes, *3* all load reductions from Mendota, *4* zero load to Kegonsa from land and remaining load reduction taken from Mendota, *5* zero load from land to Monona, Waubesa and Kegonsa, and remaining load reduction taken from Mendota. The average total load reduction (kg/year) is the same in load-reduction plans 2–5

to prevent invasion by predators of *D. pulicaria* and maintain fish community structure compatible with *D. pulicaria* has benefits that substantially augment those from reductions in P loading. (3) While 50 % load reduction in all watersheds will produce benefits, these benefits could be offset by changes in climate and increased impervious area in the watershed. However, the most extreme P load reduction (load reduction plan 3 in Lake Mendota) suggests that substantial decreases in summer TP (to mesotrophic conditions in most years) are possible along with a considerable decrease in year to year variability. Therefore, managers should consider reductions in P loading even larger than 50 %. (4) Variability of loads, exports and water quality is expected to be large in every situation we considered. Therefore, any improvements in P flows or water quality will have to be discerned against a background of high variability. Without sustained, long-term high quality data, it will be impossible to tell if P load management is having any effects. Sustained long-term monitoring of P loads, exports and water quality should be a high priority to guide future expenditures of funds for management of the Yahara lakes.

P dynamics in lake chains

In the Yahara chain of lakes, the uppermost lake is most responsive to P load reductions, and benefits diminish downstream. For each lake in the chain, the lake immediately upstream is the largest source of P. The proportion of annual load from the upstream lake, averaged over all years, is 0.56 for Monona, 0.79 for Waubesa, and 0.72 for Kegonsa. Additional P from direct drainage augments the P received from the upstream lake. In addition, recycling of P from sediments may be important in the shallow lakes Waubesa and Kegonsa. Thus, P concentrations increase down the chain. Although direct drainage loads to the four lakes are positively correlated over time, Lake Kegonsa has been much less responsive than Lake Mendota to fluctuations in direct drainage load over time. Consequently, summer TP in Lake Kegonsa and its exports to downstream ecosystems can be expected to exhibit muted responses to management.

The downstream pattern of P dynamics in the Yahara lakes resembles those found in other lake chains where the lower lakes act as additional sources of P to the water as it passes through the chain (Fisher et al. 2009; Epstein et al. 2013). In a system with sewage pollution of the uppermost lake, lakes acted as sinks for P although benefits of sewage treatment diminished downstream in the chain (Choulik and Moore 1992). This outcome may be common in lake chains afflicted by point-source inputs of phosphorus. In contrast, lake chains in agricultural regions subject to nonpoint inputs of phosphorus may behave similarly to the Yahara lakes, with increasing P flow into successive lakes downstream.

Our modeling approach is simple to fit to data and projections rely on rigorous, well-known methods for calculating predicted distributions for linear models. Model projections present variability of expected outcomes as well as averages. Assessment of variability and its responses to management actions is a strength of our approach. Knowledge of this variability allows researchers to convey more realistic expectations to managers and the public, and design monitoring programs that have adequate statistical power to detect changes. The approach requires time series data on P inputs, outputs and summer concentrations. Such data are often, but not always, collected for management of eutrophic lakes. Where long time series are not available, mechanistic models such as that of Epstein et al. (2013) can be calibrated using limited data. Moreover, long term observations may provide unique opportunities for testing mechanistic models. Long ago, Reckhow and Chapra (1983), Chapra and Reckhow (1983) pointed out the value of multiple modeling approaches for management of individual lakes. Because chains of lakes can exhibit much more complicated biogeochemical dynamics than single lakes, diverse approaches to modeling are likely to prove valuable for advancing our understanding of networks of lakes on the landscape.

Acknowledgments Our work was supported by the US National Science Foundation through the North Temperate Lakes Long-Term

Ecological Research Program and the Water Science and Sustainability program, and by the Wisconsin Department of Natural Resources.

References

Alvarez-Cobelas M, Cirujano S, Rojo C, Rodrigo MA, Piña E, Rodríguez-Murillo JC, Montero E (2006) Effects of changing rainfall on the limnology of a Mediterranean, flowthrough-seepage chain of lakes. Int Rev Hydrobiol 91(5):466–482. doi:10.1002/iroh.200510836

Belmont MA, White JR, Reddy KR (2009) Phosphorus sorption and potential phosphorus storage in sediments of Lake Istokpoga and the Upper Chain of Lakes, Florida, USA. J Environ Qual 38(3):987–996. doi:10.2134/jeq2007.0532

Box GEP, Tiao GC (1973) Bayesian inference in statistical analysis. Wiley, New York

Cardille JA, Carpenter SR, Coe MT, Foley JA, Hanson PC, Turner MG, Vano JA (2007) Carbon and water cycling in lake-rich landscapes: landscape connections, lake hydrology, and biogeochemistry. J Geophys Res 112

Carpenter S, Lathrop R (2008) Probabilistic estimate of a threshold for eutrophication. Ecosystems 11(4):601–613. doi:10.1007/s10021-008-9145-0

Carpenter SR, Lathrop RC, Nowak P, Bennett EM, Reed T, Soranno PA (2006) The ongoing experiment: restoration of Lake Mendota and its watershed. In: Magnuson JJ, Kratz TK, Benson BJ (eds) Long-term dynamics of lakes in the landscape. Oxford University Press, London

Carpenter SR, Benson BJ, Biggs R, Chipman JW, Foley JA, Golding SA, Hammer RB, Hanson PC, Johnson PTJ, Kamarainen AM, Kratz TK, Lathrop RC, McMahon KD, Provencher B, Rusak JA, Solomon CT, Stanley EH, Turner MG, Vander Zanden MJ, Wu C-H, Yuan H (2007) Understanding regional change: a comparison of two lake districts. Bioscience 57(4):323–335. doi:10.1641/b570407

Chapra SC, Reckhow KH (1983) Engineering approaches for lake management. Mechanistic modeling, vol 2. Butterworth, Boston

Choulik O, Moore TR (1992) Response of a subarctic lake chain to reduced sewage loading. Can J Fish Aquat Sci 49(6):1236–1245. doi:10.1139/f92-139

Einola E, Rantakari M, Kankaala P, Kortelainen P, Ojala A, Pajunen H, Mäkelä S, Arvola L (2011) Carbon pools and fluxes in a chain of five boreal lakes: a dry and wet year comparison. J Geophys Res Biogeosci 116 (G3):G03009. doi:10.1029/2010jg001636

Epstein D, Neilson B, Goodman K, Stevens D, Wurtsbaugh W (2013) A modeling approach for assessing the effect of multiple alpine lakes in sequence on nutrient transport. Aquat Sci 75(2):199–212. doi:10.1007/s00027-012-0267-2

Fisher MM, Miller SJ, Chapman AD, Keenan LW (2009) Phytoplankton dynamics in a chain of subtropical blackwater lakes: the Upper St, Johns River, Florida, USA. Lake Reservoir Manage 25(1):73–86

Forbes SA (1887) The lake as a microcosm. Ill Natural Hist Survey Bull 15(9):537–550

Frisk T, Niemi JS, Kinnunen KAI (1981) Comparison of statistical phosphorus-retention models. Ecol Model 12(1–2):11–27. doi:http://dx.doi.org/10.1016/0304-3800(81)90022-3

Gassman PW, Reyes MR, Green CH, Arnold JG (2007) The soil and water assessment tool: historical development, applications, and future research directions. Trans Am Soc Agric Biol Eng 50:1211–1250

Gelman A, Carlin JB, Stern HS, Rubin DB (2004) Bayesian data analysis. Chapman and Hall, New York

Hillbricht-Ilkowska A (2002) Eutrophication rate of lakes in the Jorka river system (Masurian Lakeland, Poland): long-term changes and trophic correlations. Polish J Ecol 50(4):475–487

Hilt S, Köhler J, Kozerski H-P, van Nes EH, Scheffer M (2011) Abrupt regime shifts in space and time along rivers and connected lake systems. Oikos 120(5):766–775. doi:10.1111/j.1600-0706.2010.18553.x

Kitchell JF (ed) (1992) Food web management: a case study of Lake Mendota. Springer, New York

Kling GW, Kipphut GW, Miller MM, O'Brien WJ (2000) Integration of lakes and streams in a landscape perspective: the importance of material processing on spatial patterns and temporal coherence. Freshw Biol 43(3):477–497. doi:10.1046/j.1365-2427.2000.00515.x

Lathrop RC (2007) Perspectives on the eutrophication of the Yahara lakes. Lake Reservoir Manage 23:345–365

Lathrop RC, Carpenter SR (2013) Water quality implications from three decades of phosphorus loads and trophic dynamics in the Yahara chain of lakes. Inland Waters 3 (in press)

Lathrop RC, Carpenter SR, Stow CA, Soranno PA, Panuska JC (1998) Phosphorus loading reductions needed to control blue-green algal blooms in Lake Mendota. Can J Fish Aquat Sci 55(5):1169–1178. doi:10.1139/f97-317

Lathrop RC, Carpenter SR, Robertson DM (1999) Summer water clarity responses to phosphorus, *Daphnia* grazing and internal mixing in Lake Mendota. Limnol Oceanogr 44:137–146

Lathrop RC, Johnson BM, Johnson TB, Vogelsang MT, Carpenter SR, Hrabik TR, Kitchell JF, Magnuson JJ, Rudstam LG, Stewart RS (2002) Stocking piscivores to improve fishing and water clarity: a synthesis of the Lake Mendota biomanipulation project. Freshw Biol 47(12):2410–2424. doi:10.1046/j.1365-2427.2002.01011.x

Leavitt PR, Brock CS, Ebel C, Patoine A (2006) Landscape-scale effects of urban nitrogen on a chain of freshwater lakes in central North America. Limnol Oceanogr 51(5):2262–2277

Magnuson JJ (2002) Three generations of limnology at the University of Wisconsin-Madison. Verh Internat Verein Limnol 28:856–860

Magnuson JJ, Kratz TK, Benson BJ (eds) (2006) Long-term dynamics of lakes in the landscape. Oxford University Press, Oxford

Pace ML, Groffman PM (eds) (1998) Successes, frontiers and limitations in ecosystem science. Springer, New York

Pitt R, Voorhees J (2002) SLAMM, the source loading and management model. In: Field R, Sullivan D (eds) Wet-weather flow in the urban watershed: technology and management. CRC Press, Boca Raton, pp 103–139

Reckhow KH, Chapra SC (1983) Engineering approaches for lake management. Data analysis and empirical modeling, vol 1. Butterworth, Boston

Sadro S, Nelson C, Melack J (2012) The influence of landscape position and catchment characteristics on aquatic biogeochemistry in high-elevation lake-chains. Ecosystems 15(3):363–386. doi:10.1007/s10021-011-9515-x

Soranno PA, Webster KE, Riera JL, Kratz TK, Baron JS, Bukaveckas PA, Kling GW, White DS, Caine N, Lathrop RC (1999) Spatial variation among lakes within landscapes: ecological organization along lake chains. Ecosystems 2(5):395–410

Soranno PA, Spence Cheruvelil K, Webster KE, Bremigan MT, Wagner T, Stow CA (2010) Using landscape limnology to classify freshwater ecosystems for multi-ecosystem management and conservation. Bioscience 60(6):440–454. doi:10.1525/bio.2010.60.6.8