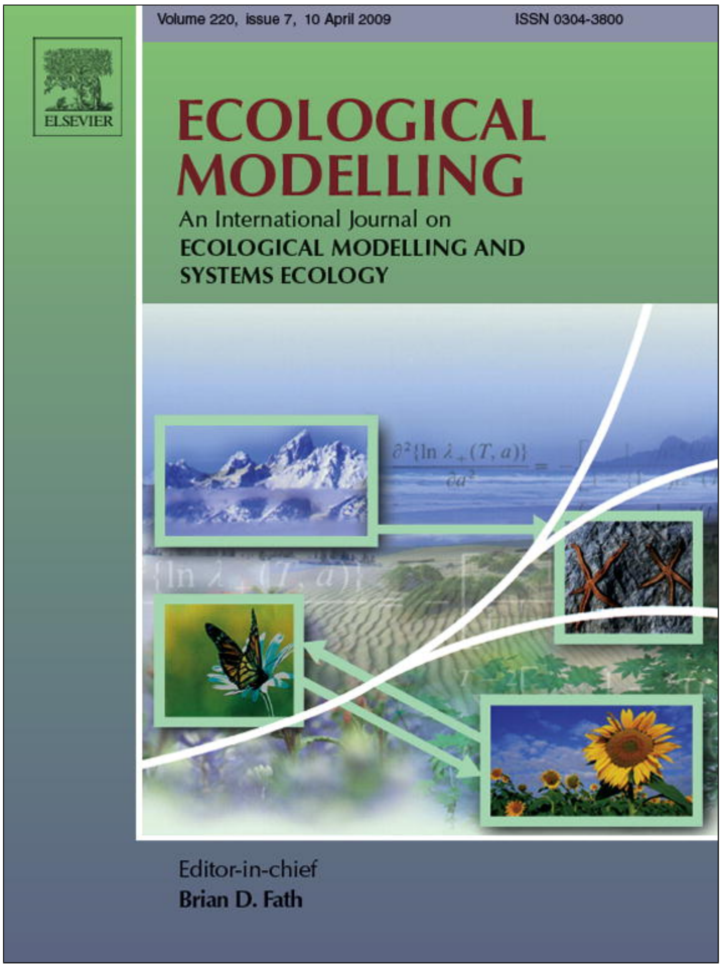
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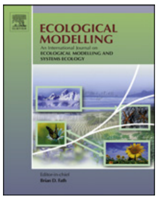

Structural changes in lake functioning induced from nutrient loading and climate variability

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ABSTRACT

Climate variability is increasingly recognized as an important regulatory factor, capable of influencing the structural properties of aquatic ecosystems. Lakes appear to be particularly sensitive to the ecological impacts of climate variability, and several long time series have shown a close coupling between climate, lake thermal properties and individual organism physiology, population abundance, community structure, and food web dynamics. Thus, understanding the complex interplay among meteorological forcing, hydrological variability, and ecosystem functioning is essential for improving the credibility of model-based water resources/fisheries management. Our objective herein is to examine the relative importance of the ecological mechanisms underlying plankton seasonal variability in Lake Washington, Washington State (USA), over a 35-year period (1964–1998). Our analysis is founded upon an intermediate complexity plankton model that is used to reproduce the limiting nutrient (phosphate)–phytoplankton–zooplankton–detritus (particulate phosphorus) dynamics in the lake. Model parameterization is based on a Bayesian calibration scheme that offers insights into the degree of information the data contain about model inputs and allows obtaining predictions along with uncertainty bounds for modeled output variables. The model accurately reproduces the key seasonal planktonic patterns in Lake Washington and provides realistic estimates of predictive uncertainty for water quality variables of environmental management interest. A principal component analysis of the annual estimates of the underlying ecological processes highlighted the significant role of the phosphorus recycling stemming from the zooplankton excretion on the planktonic food web variability. We also identified a moderately significant signature of the local climatic conditions (air temperature) on phytoplankton growth ($r = 0.41$), herbivorous grazing ($r = 0.38$), and detritus mineralization ($r = 0.39$). Our study seeks linkages with the conceptual food web model proposed by Hampton et al. [Hampton, S.E., Scheuerell, M.D., Schindler, D.E., 2006b. Coalescence in the Lake Washington story: interaction strengths in a planktonic food web. Limnol. Oceanogr. 51, 2042–2051.] to emphasize the “bottom-up” control of the Lake Washington plankton phenology. The posterior predictive distributions of the plankton model are also used to assess the exceedance frequency and confidence of compliance with total phosphorus ($15\ \mu g\ L^{-1}$) and chlorophyll *a* ($4\ \mu g\ L^{-1}$) threshold levels during the summer-stratified period in Lake Washington. Finally, we conclude by underscoring the importance of explicitly acknowledging the uncertainty in ecological forecasts to the management of freshwater ecosystems under a changing global environment.

1. Introduction

One of the central questions that often arise in limnological research is the future response of lacustrine ecosystems to climate variability so that sustainable management policies can be effectively implemented (Schindler, 2001, 2006). Lake physical properties appear to be particularly sensitive to climate forcing and existing empirical evidence underscores the strong association between local climatic conditions (e.g., air temperature, rainfall and wind patterns), large-scale oceanic fluctuations (e.g., North Atlantic Oscillation, El Niño-Southern Oscillation and Pacific Decadal Oscillation), and lake thermal structure (e.g., onset of stratification, thermocline depth, mean epilimnetic temperature, turnover date, and duration of ice cover) (Schindler, 1997; Magnuson et al., 1997; Peeters et al., 2007; Thackeray et al., 2008). Climate-induced chemical and biological responses in lakes are another important issue, and several ecological and biogeochemical studies have shown a coupling among lake temperatures and water chemistry, individ-

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ual organism physiology, population abundance, and community structure (Gerten and Adrian, 2001; Straile, 2002; Weyhenmeyer, 2004; Blenckner et al., 2007). Climate variability is also likely to be causing food web alterations. These structural shifts may be more severe in aquatic environments with strong seasonality, where growth and reproduction of many species is usually restricted to short time windows over the annual cycle and the spatiotemporal synchronies largely determine the magnitude of the prey–predator interactions, i.e., the so-called "match-mismatch" hypothesis (Cushing, 1974; Stenseth and Mysterud, 2002; Durant et al., 2007). Climate forcing can have different effects on various taxonomic groups/trophic levels, and decouple species from favorable food conditions with dire consequences for ecosystem functioning (Thomas et al., 2001; Winder and Schindler, 2004b). Therefore, the development of holistic understanding of the climate-driven lacustrine ecosystem responses requires consideration of the complex interplay among physical, chemical factors and multiple trophic levels at a variety of spatial and temporal scales (Schindler, 2001, 2006).

The role of mathematical and statistical modeling has been instrumental for assessing how climate signals cascade through freshwater ecosystems shaping abiotic variability and/or biotic responses. Empirical examination of statistical links between lake dynamics and meteorological conditions has usually provided evidence and/or generated hypotheses about "if" and "how" climate variability affects lake phenology, while mechanistic understanding and insights into the actual nature of the hypothesized cause–effect relationships have been gained by mathematical (process-based) models (DeStasio et al., 1996; Ferguson et al., 2008; Johnk et al., 2008). However, both mechanistic and statistical approaches are hampered by substantial uncertainty, and their results are often de-emphasized as indicators of the global warming effects on the phenology of freshwater ecosystems (Clark et al., 2001; Blenckner, 2008). Furthermore, human activities (e.g., nutrient enrichment) and restoration efforts (e.g., biomanipulations) along with the intricate nature of the ecological processes are confounded with the climate signals, and lead to misleading results in ill-defined modeling frameworks (Scheffer et al., 2001; Van Donk et al., 2003; Jeppesen et al., 2003). Given the growing evidence that the evaluation of the effects of climate change on natural ecosystems is still in an early stage, the demand for reliable modeling tools that can offer insights into the ecosystem dynamics and effectively support environmental management is more pressing than ever before. In particular, the limnological research needs novel modeling techniques that can accommodate the natural complexity underlying system dynamics, assess the relative importance of causal connections, conform to the scientific process of progressive learning, and provide realistic uncertainty estimates of the long-term ecological forecasts (Arhonditsis et al., 2007).

Our current knowledge about the climatic change effects on the phenology of lake processes has greatly advanced from the detailed, long-term records from Lake Washington, where a series of analyses have shown the effects of climate variability on the thermal structure, the timing of the spring bloom, the coupling of the trophic interactions between phytoplankton and zooplankton, the interspecific niche differentiation, and the sockeye salmon (*Oncorhynchus nerka*) behavioral patterns (Arhonditsis et al., 2004a,b; Winder and Schindler, 2004a,b; Hampton, 2005; Hampton et al., 2006a). For example, Arhonditsis et al. (2004a) showed that Lake Washington has experienced a warming trend, with overall increases of 1.5 (0.045 °C year^{-1}) and 0.9 °C (0.026 °C year^{-1}) for temperature data weighted over the surface (0–10 m) and entire lake volume, respectively. This warming trend was greatest for the period from April to September and was positively correlated with interannual variability in air temperature and the Pacific Decadal Oscillation. The phytoplankton spring bloom has advanced by approximately 15–20 days in response to earlier stratification onset, whereas the timing of the clear-water phase showed high variability driven by the concerted effects of a suite of abiotic and biotic factors (Winder and Schindler, 2004a). Importantly, the lake experiences a growing mismatch between the timing of the spring diatom bloom and the peak of the *Daphnia* populations which has led to a significant decrease of their abundance with potentially adverse repercussions on the energy flow along the food web (Winder and Schindler, 2004b). By refining the resolution at the species level, Hampton et al. (2006a) further discerned species-specific differences in *Daphnia* phenology (i.e., the large-bodied and nutritious *Daphnia pulicaria* vis-à-vis the relatively unpredictable *Daphnia thorata* dynamics) which may induce shifts on the sockeye fry feeding upon less profitable prey (e.g., copepods). Existing evidence also suggests that the increase of the length of the growing season in Lake Washington offers windows of opportunity for niche differentiation of the colonial rotifers *Conochilus hippocrepis* and *Conochilus unicornis*, which allows to overcome the competition of the dominant herbivores of the summer zooplankton community (i.e., *Daphnia*) and to obtain higher mean annual abundance in recent years (Hampton, 2005). Finally, a recent quantitative food web model re-emphasizes the role of lake warming on plankton phenology and also pinpoints the importance of the "bottom-up" control mediated by picoplankton and cryptomonads in Lake Washington food web dynamics (Hampton et al., 2006b).

In this paper, we conducted a modeling analysis of the plankton seasonal variability in Lake Washington over a 35-year period (1964–1998). Our analysis is founded upon an intermediate complexity plankton model that is used to reproduce the limiting nutrient (phosphate)–phytoplankton–zooplankton–detritus (particulate phosphorus) dynamics in the lake. The main objective is to unravel the temporal evolution of the ecological mechanisms (direct and indirect pathways) that drive the planktonic patterns and to elucidate the structural changes in lake functioning induced from nutrient loading and climate variability during the study period. Model parameterization is based on a Bayesian calibration scheme that offers insights into the degree of information the data contain about model inputs and allows obtaining predictions along with uncertainty bounds for modeled output variables. The predictive uncertainty estimates are also used to assess the exceedance frequency and confidence of compliance with total phosphorus (15 $\mu\text{g L}^{-1}$) and chlorophyll *a* (4 $\mu\text{g L}^{-1}$) threshold levels during the summer stratified period. We conclude by emphasizing the importance of explicitly acknowledging the uncertainty in ecological forecasts to the management of freshwater ecosystems under a changing global environment.

2. Methods

2.1. Study area—dataset description

With a surface area of 87.6 km^2 and a total water volume of 2.9 km^3, Lake Washington is the second largest natural lake in the State of Washington (USA). Its deep and narrow basin with steeply sloping sides has a mean depth of 32.9 m (maximum depth 65.2 m). Lake Washington is situated in an urbanized environment with 63% of its 1274 km^2 catchment area fully developed. The two major tributaries flowing into Lake Washington are the Sammamish River at the northern and the Cedar River at the southern part of the lake, and together the two rivers contribute approximately 84% and 66% of the annual hydraulic and phosphorus load in the system, respectively (Arhonditsis et al., 2003). The Lake Washington Ship Canal is the main outlet of the lake. Lake Washington is one of the most intensively studied lakes in North America and its recovery from eutrophication in the 1970s by sewage diversion is arguably the best documented example of successful lake restoration in the world (Edmondson, 1994). Lake Washington received increasing amounts of secondary sewage from 1941 to 1963. This point nutrient source was eventually eliminated in 1968, and since then the only wastewater entering the lake is a relatively negligible amount of overflow from Seattle's combined sewer system. Lake Washington rapidly responded to the decreasing nutrient loadings; cyanobacteria abundance dramatically declined and water quality was greatly improved. Since 1975, Lake Washington has been regarded to be successfully recovered from eutrophication (Edmondson and Lehman, 1981).

The data used in this study include the average monthly concentrations for the state variables (phosphate, phytoplankton, zooplankton, and detritus) at the three spatial compartments (epilimnion, thermocline/mesolimnion, and hypolimnion) from 1964 to 1998. Detailed description of the sampling/analytical protocol and the data processing prior to the analysis have been provided elsewhere (Scheuerell et al., 2002; Arhonditsis et al., 2003, 2004b). We also considered the average monthly values for lake temperature, exogenous nutrient loading, hydraulic inflows and outflows (Figs. A1–A3). Annual hydraulic loading data from 1964 to 1978 were taken from the classical Edmondson and Lehman (1981) study, and beyond that year were based on a linear regression between the hydraulic loading and the rainfall data measured at the Seattle-Tacoma International Airport ($r^2 = 0.62$, SE = 12.62%). Annual nutrient (TP and PO_4) loading values due to secondary sewage between 1964 and 1968 were taken from the same study, and monthly nutrient loadings due to other sources (fluvial and atmospheric) were calculated (along with their error estimates) using the regression equations presented in their Table 3 (Edmondson and Lehman, 1981).

2.2. Model description

The conceptual diagram of the model used in this study is depicted in Fig. 1, and the mathematical formulations and parameter definitions are given in Tables 1 and 2, respectively. We developed a simple model that considers the interplay among four state variables, i.e., the limiting nutrient (phosphate), phytoplankton, zooplankton, and detritus (particulate phosphorus). The spatial segmentation of the model consists of three compart-

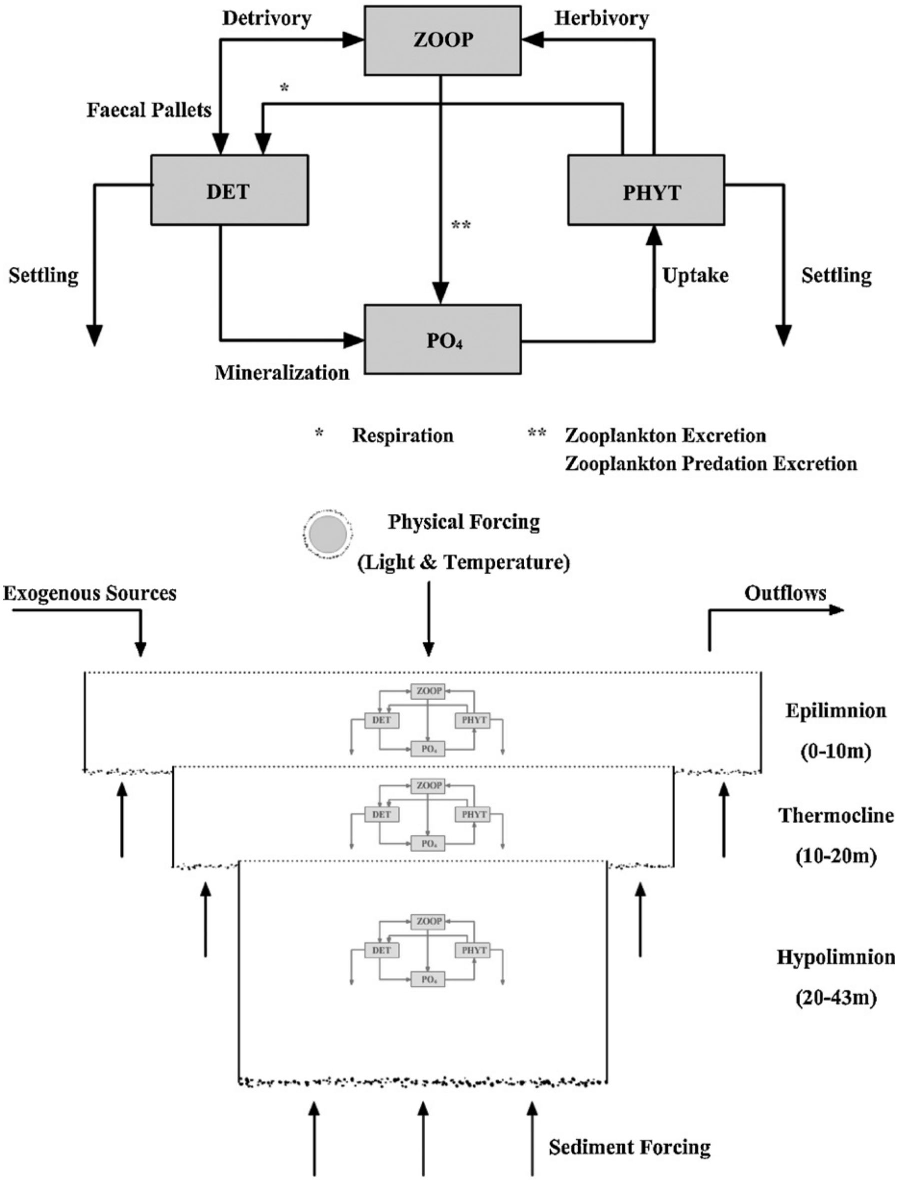

Fig. 1. The flow diagram and the spatial segmentation of the phosphate (PO_4)–phytoplankton (PHYT)–zooplankton (ZOOP)–detritus or particulate phosphorus (DET) model used for reproducing the plankton dynamics in Lake Washington.

Table 1
The plankton model equations and their constituent processes.

$\frac{dPO_{4i}}{dt} =$	$-aPO_{4i}/(ee+PO_{4i})fT_i\,fL_i PHYT_i\,P/C_{phyto}$	Phytoplankton growth
	$+\frac{\beta\lambda((PHYT_i\,P/C_{phyto})^2+\omega DET_i^2)}{\mu^2+(PHYT_i\,P/C_{phyto})^2+\omega DET_i^2}fTz_i ZOOP_i P/C_{zoop}$	Zooplankton excretion
	$+\gamma d\frac{ZOOP_i^3}{pred^2+ZOOP_i^2}fTz_i P/C_{zoop}$	Zooplankton predation
	$+\phi\, fT_i\, DET_i$	Mineralization
	$-kd(1-\sigma_t)(PO_{4i}-PO_{4(i+1)})\frac{A_{i+1}}{V_i(H_{i+1}-H_i)}$	Diffusion
	$+(PO_4 sed)_i\sigma_t\frac{A_i-A_{i+1}}{V_i}$	Sediment forcing
	$+(PO_4 exog^*)$	Exogenous loading
	$-\text{outflows } PO_{4i}{}^*$	Outflows
$\frac{dPHYT_i}{dt} =$	$a\frac{PO_{4i}}{ee+PO_{4i}}fT_i fL_i PHYT_i$	Phytoplankton growth
	$-r\, fT_i\, PHYT_i$	Phytoplankton respiration
	$-\frac{\lambda(PHYT_i\,P/C_{phyto})^2}{\mu^2+(PHYT_i\,P/C_{phyto})^2+\omega DET_i{}^2}fTz_i ZOOP_i$	Herbivory
	$-s(PHYT_i-PHYT_{i-1})\frac{A_i}{V_i}$	Settling
	$-\text{outflows } PHYT_i*$	Outflows
$\frac{dZOOP_i}{dt} =$	$\frac{\alpha\lambda((PHYT_i\,P/C_{phyto})^2+\omega DET_i^2)}{\mu^2+(PHYT_i\,P/C_{phyto})^2+\omega DET_i^2}fTz_i ZOOP_i$	Zooplankton grazing
	$-d\frac{ZOOP_i^3}{pred^2+ZOOP_i^2}fTz_i$	Predation
	$-\text{outflows } ZOOP_i{}^*$	Outflows
$\frac{dDET_i}{dt} =$	$r\, fT_i\, PHYT_i\, P/C\text{phyto}$	Phytoplankton respiration
	$+\frac{\lambda[(1-\alpha-\beta)(PHYT_i\,P/C_{phyto})^2-(\alpha+\beta)\omega DET_i^2]}{\mu^2+(PHYT_i\,P/C_{phyto})^2+\omega DET_i^2}fTz_i ZOOP_i P/C_{zoop}$	Detrivory minus zooplankton excretion
	$-\phi\, fT_i\, DET_i$	Mineralization
	$-\psi(DET_i-DET_{i-1})\frac{A_i}{V_i}$	Settling
	$+\text{DETexog}^*$	Exogenous loading
	$-\text{outflows } DET_i{}^*$	Outflows
$fT_i = e^{-kt(Temp_i-Temp_{ref})^2}$		
$fTz_i = e^{-ktz(Temp_i-Temp_{ref})^2}$		
$fL_i = 2.718FD\left(\frac{e^{-\alpha_1}-e^{-\alpha_0}}{ke_i H_i}\right)$	$FD = 0.15\sin\left[2\pi\left(\frac{t}{365}-0.22\right)\right]+0.51$	
$\alpha_0 = \frac{I_a}{I_s}e^{-ke_i H_1}$	$I_a = 220\sin\left[2\pi\left(\frac{t}{365}-0.23\right)\right]+290$	
$\alpha_1 = \frac{I_a}{I_s}e^{-ke_i H_2}$	$\sigma_t = \frac{1-\varepsilon\cos\left[2\pi\left(\frac{t}{365}\right)\right]}{1+\varepsilon}$	
$ke_i = kb + kcPHYT_i/50$		
$H_i = H_2 - H_1$		
$i = \begin{cases} 1(epi\lim nion) \\ 2(thermocline) \\ 3(hypo\lim nion) \end{cases}$		

* Exogenous loading and outflows are only considered in the epilimnion ($i = 1$)

ments representing the epilimnion, thermocline (mesolimnion), and hypolimnion of the lake. The simulation model was solved numerically using the fourth-order Runge-Kutta method with a time step of 1 day.

2.2.1. Phytoplankton

The equation for phytoplankton biomass accounts for phytoplankton production, losses due to basal metabolism, herbivorous zooplankton grazing, and settling. Phosphate limitation on phytoplankton growth is modeled using the Michaelis–Menten kinetics. The basal metabolic losses include all internal processes that decrease algal biomass as well as natural mortality. Phytoplankton settling considers the net change in biomass due to settling between adjacent compartments.

2.2.2. Zooplankton

The zooplankton biomass equation considers zooplankton growth and losses due to natural mortality and predation. Zooplankton feeds upon two food sources (phytoplankton and detritus) of equal palatability ($\omega = 1$); both herbivory and detrivory are formulated using the Holling Type III function. A fraction of the zooplankton grazing is assimilated and fuels growth, another fraction is excreted as phosphate, while the remaining fraction represents the faecal pellets contributing to the detritus pool. The zooplankton losses due to consumption by higher predators is modeled using a sigmoid closure term which represents a “switchable”-type of predator behaviour controlled by a prey threshold concentration (Edwards and Yool, 2000).

2.2.3. Phosphate

The phosphate equation considers the phytoplankton uptake, the gains due to zooplankton excretion/predation, the bacteria-mediated mineralization of detritus, and the net diffusive fluxes between adjacent compartments.

Table 2
The parameter definitions of the plankton model.

Parameter	Description	Unit
a^*	Maximum phytoplankton growth rate	day^{-1}
d^*	Zooplankton mortality rate	day^{-1}
$pred^*$	Half-saturation constant for predation	mg C m^{-3}
ee^*	Half-saturation constant for PO_4 uptake	mg P m^{-3}
kd^*	Molecular plus eddy diffusion coefficient	$\text{m}^2\ \text{day}^{-1}$
r^*	Phytoplankton respiration rate	day^{-1}
s^*	Phytoplankton sinking loss rate	m day^{-1}
α^*	Zooplankton assimilation efficiency	
β^*	Zooplankton excretion fraction to phosphate	
γ^*	Zooplankton predation excretion fraction to phosphate	
λ^*	Maximum zooplankton grazing rate	day^{-1}
μ^*	Zooplankton grazing half-saturation coefficient	mg P m^{-3}
φ^*	Detritus remineralization rate	day^{-1}
ψ^*	Detritus sinking rate	m day^{-1}
kt^*	Effect of temperature on phytoplankton processes	$^\circ\text{C}^{-2}$
ktz^*	Effect of temperature on zooplankton processes	$^\circ\text{C}^{-2}$
kb^*	Background light extinction coefficient	m^{-1}
kc^*	Light extinction coefficient due to chlorophyll *a*	$\text{m}^2\ \text{mg}^{-1}$
Is^*	Half saturation light intensity	$\text{MJ/m}^2\ \text{day}^{-1}$
ω	Relative zooplankton preference for detritus compared to phytoplankton	1
P/C_{phyto}	Phosphorus to carbon ratio for phytoplankton	$0.015\ \text{mg P (mg C)}^{-1}$
P/C_{zoop}	Phosphorus to carbon ratio for zooplankton	$0.029\ \text{mg P (mg C)}^{-1}$
$Temp_{ref}$	Reference temperature	$20\,^\circ\text{C}$
ε	Shape parameter for the trigonometric function σ_t	0.9

*Parameters used during the Bayesian calibration of the model.

2.2.4. Detritus

The detritus equation takes into account the contributions from phytoplankton respiration and zooplankton excretion, and the losses due to bacteria-mediated mineralization and settling.

2.2.5. Forcing functions

The effects of the seasonal cycle of temperature on the PO_4 diffusion and sediment forcing are described by a trigonometric function σ_t (Arhonditsis et al., 2007). The dependence of the planktonic processes on temperature is modeled by two functions *fT* and *fTz*; both resembling a Gaussian-like probability curve (Cerco and Cole, 1994). The light dependence of phytoplankton growth is modeled using Steele's equation with Beer's law to scale photosynthetically active radiation to depth. The extinction coefficient considers both background and chlorophyll *a* attenuation (Arhonditsis and Brett, 2005a). The sediment fluxes in the three compartments were represented by probability distributions, founded upon estimates from previous studies in the lake (Edmondson and Lehman, 1981; Kuivila and Murray, 1984; Quay et al., 1986; Kuivila et al., 1988), which then were updated on a year-to-year basis from the Bayesian calibration exercise. As previously described, our model also considers the exogenous loading of phosphate and detritus (mainly particulate phosphorus) entering the epilimnion as well as the outflows to the Lake Union Ship Canal.

2.3. Bayesian calibration framework

2.3.1. Statistical formulation

Environmental models developed to guide pressing management decisions can be confidently embraced by policy makers only if they properly acknowledge the uncertainty pertaining to parameter values, model structure, and measurement error. In this context, the Bayesian calibration provides an effective means to rigorously quantify the different sources of error and obtain uncertainty bounds that properly convey our confidence in the predictions made. In this study, we used a statistical formulation founded upon the basic assumption that the eutrophication model is an imperfect simulator of the environmental system and the model discrepancy is invariant with the input conditions, i.e., the difference between model and lake dynamics was assumed to be constant over the annual cycle for each state variable (Arhonditsis et al., 2007, 2008a,b). In our model, a monthly observation *i* for the state variable *j* in the year *k* and the compartment *l*, y_{ijkl}, can be described as follows:

$$y_{ijkl} = \underbrace{f(\theta_k,\ \zeta_{ijkl},\ x_{ijkl},\ y_{0kl}) + \delta_{jkl}}_{g(\theta_k,\ \zeta_{ijkl},\ x_{ijkl},\ y_{0kl},\ \delta_{jkl}) \sim N(f(\theta_k, \zeta_{ijkl},\ x_{ijkl},\ y_{0kl}), \sigma^2_{jkl})} + \varepsilon_{ijkl},\ i = 1, \ldots, 12;$$

$$j = 1, \ldots, 4; k = 1, \ldots, 35;\ \text{and } l = 1, \ldots, 3) \qquad (1)$$

where $f(\theta_k,\ \zeta_{ijkl},\ x_{ijkl},\ y_{0kl})$ denotes the eutrophication model, δ_{jkl} and ε_{ijkl} represent the modeling and measurement error, respectively; θ_k is a vector of year-specific calibration model parameters (i.e., the 19 parameters identified in Table 2), ζ_{ijkl} is a vector of time-dependent control variables treated stochastically during the model updating process (i.e., nutrient loading and sediment nutrient fluxes), x_{ijkl} is a vector of time-dependent control variables with no error pertaining to their values (i.e., light, temperature, and outflows), and y_{0kl} is a vector of the initial values for the state variables at time t_0. The modeling error δ_{jkl}, which accounts for the discrepancy between the model and the natural system, is assumed to be constant over the annual cycle. The time-dependent measurement error ε_{ijkl} accounts for both analytical error and monthly variability, and it is assumed to be multiplicative with standard deviations proportional (15%) to the monthly average values of the epilimnetic state variables (Van Oijen et al., 2005). A lower measurement error (10 and 5%) was assigned to the state variables in the thermocline and hypolimnion because of the lower variability observed towards the lake bottom. [Note that the measurement error here also encompasses the natural variability not explicitly accounted for by the model.] The $g(\theta_k,\ \zeta_{ijkl},\ x_{ijkl},\ y_{0kl},\ \delta_{jkl})$ term represents a normally distributed variable with first and second order moments based on the model predictions and the time-independent model structural error σ^2_{jkl}.

In the context of the Bayesian statistical inference, the posterior density of the parameters θ, the exogenous/sediment nutrient fluxes ζ, and the initial conditions of the four state variables y_0 given the observed data y is defined as

$$p(\theta, \zeta, y_0, \sigma^2 \,|\, y) = \frac{p(y|f(\theta, \zeta, x, y_0, \sigma^2))p(\theta)p(\zeta)p(y_0)p(\sigma^2)}{\int\int\int\int p(y|f(\theta, \zeta, x, y_0, \sigma^2))p(\theta)p(\zeta)p(y_0)p(\sigma^2)d\theta d\zeta dy_0 d\sigma^2}$$

$$\propto p(y|f(\theta, \zeta, x, y_0, \sigma^2))p(\theta)p(\zeta)p(y_0)p(\sigma^2) \qquad (2)$$

where $p(y|f(\theta,\zeta,x,y_0,\sigma^2))$ is the model likelihood while $p(\theta)$, $p(\zeta)$ and $p(y_0)$ are the prior densities of θ, ζ and y_0, respectively. Similar to the measurement error, the characterization of the prior density $p(y_0)$ is based on the assumption of a Gaussian distribution with a mean value derived from the January monthly averages and a standard deviation that is 15, 10, and 5% of the mean value for the epilimnion, thermocline, and hypolimnion, respectively; the prior density $p(\sigma^2)$ are based on the conjugate inverse-gamma distribution (Gelman, 2005). With our model assumptions, the model likelihood is given by the following formula:

$$p(y|f(\theta,\zeta,x,y_0,\sigma^2)) = \prod_{k=1}^{35}\prod_{l=1}^{3}\prod_{j=1}^{4}(2\pi)^{-12/2}\left|\Sigma_{Totjkl}\right|^{-1/2}\exp\left[-\frac{1}{2}[y_{jkl}-f_{jkl}(\theta,\zeta,x,y_0)]^T\,{\Sigma_{Totjkl}}^{-1}[y_{jkl}-f_{jkl}(\theta,\zeta,x,y_0)]\right] \tag{3}$$

$$\Sigma_{Totjkl} = \Sigma_{\delta jkl} + \Sigma_{\varepsilon jkl} \tag{4}$$

where $y_{jkl} = [y_{1jkl},\ldots,y_{12jkl}]^T$ and $f_{jkl}(\theta,\ \zeta,\ x,\ y_0) = [f_{1jkl}(\theta_k,\ \zeta_{1jkl},\ x_{1jkl},\ y_{0k}),\ldots,f_{12jkl}(\theta_k,\ \zeta_{12jkl},\ x_{12jkl},\ y_{0k})]^T$ correspond to the vectors of the field observations and the model predictions for the state variable j, respectively; $\Sigma_{\delta jkl} = I_{12}{\sigma_{jkl}}^2$ and $\Sigma_{\varepsilon jkl} = I_{12}(ME_l)^2 \cdot {y_{jkl}}^T \cdot y_{jkl}$, with ME_l equal to 15, 10 and 5% for the epilimnion ($l = 1$), thermocline ($l = 2$), and hypolimnion ($l = 3$), respectively. Substituting the model likelihood into the Eq. (2) results in the posterior distribution for θ, ζ, y_0, and σ^2:

$$\begin{aligned} p(\theta,\zeta,y_0,\sigma^2|y) \propto & \prod_{k=1}^{35}\prod_{l=1}^{3}\prod_{j=1}^{4}(2\pi)^{-12/2}\left|\Sigma_{Totjkl}\right|^{-1/2}\exp\left[-\frac{1}{2}[y_{jkl}-f_{jkl}(\theta,\zeta,x,y_0)]^T\,{\Sigma_{Totjkl}}^{-1}[y_{jkl}-f_{jkl}(\theta,\zeta,x,y_0)]\right] \\ & \times\prod_{k=1}^{35}(2\pi)^{-19/2}\left|\Sigma_{\theta k}\right|^{-1/2}\prod_{\theta=1}^{19}\frac{1}{\theta_{\theta k}}\exp\left[-\frac{1}{2}[\log\theta_k-\theta_{0k}]^T\,\Sigma_{\theta k}^{-1}[\log\theta_k-\theta_{0k}]\right] \\ & \times\prod_{k=1}^{35}\prod_{l=1}^{3}(2\pi)^{-4/2}\left|\Sigma_{y0kl}\right|^{-1/2}\exp\left[-\frac{1}{2}[y_{0kl}-y_{0mkl}]^T\,{\Sigma_{y0kl}}^{-1}[y_{0kl}-y_{0mkl}]\right] \\ & \times\prod_{k=1}^{35}\prod_{l=1}^{3}\prod_{q=1}^{3}(2\pi)^{-3/2}\left|\Sigma_{\zeta klq}\right|^{-1/2}\exp\left[-\frac{1}{2}[\zeta_{klq}-\zeta_{mklq}]^T\,\Sigma_{\zeta klq}^{-1}[\zeta_{klq}-\zeta_{mklq}]\right] \\ & \times\prod_{k=1}^{35}\prod_{l=1}^{3}\prod_{j=1}^{4}\frac{{\beta_j}^{\alpha jkl}}{\Gamma(\alpha_{jkl})}{\sigma_j}^{-2(\alpha_{jkl}+1)}\exp\left(-\frac{\beta_{jkl}}{\sigma_{jkl}^2}\right) \end{aligned} \tag{5}$$

where θ_{0k} indicates the vector of the mean values of θ in logarithmic scale; $\Sigma_{\theta k} = I_{19}\sigma_{\theta k}^T\sigma_{\theta k}$ and $\sigma_{\theta k} = [\sigma_{\theta k1},\ldots,\sigma_{\theta k19}]^T$ corresponds to the vector of the shape parameters of the 19 lognormal distributions (standard deviation of $log\,\theta$); the vector $y_{0mkl} = [y_{1,1,kl},\ldots,y_{1,4,kl}]^T$ corresponds to the average January values of the four state variables; $\Sigma_{y0kl} = I_4(ME_l)^2 y_{0mkl}^T y_{0mkl}$; α_{jkl} (=0.001) and β_{jkl} (=0.001) correspond to the shape and scale parameters of the non-informative inverse-gamma distributions used in this analysis; q(=3) corresponds to the three phosphorus loading forms (PO_{4exog}, DET_{exog}, PO_{4sed}) with year- and compartment-specific mean values ζ_{mklq} and covariance matrix $\Sigma_{\zeta klq}$ derived as previously described. [It should be noted that the thermocline and the hypolimnion only receive sediment nutrient fluxes, while the matrix $\Sigma_{\zeta klq}$ also considers the error of the relationships connecting rainfall to fluvial inflows, and then to the exogenous phosphorus loading.] The prior densities for the nineteen model calibration parameters were formulated based on field observations, laboratory studies, literature information, and expert judgement (Arhonditsis et al., 2007, 2008a). Specifically, the minimum and maximum values for each parameter are identified using the aforementioned sources, and then each parameter was assigned a lognormal distribution parameterized such that 95% of its values were lying within the identified range (Steinberg et al., 1997).

2.3.2. Numerical computation-model performance assessment

To efficiently sample the multidimensional parameter space of the model, sequence of realizations from the posterior distribution of the model were obtained using Markov Chain Monte Carlo (MCMC) simulations (Gilks et al., 1998). Specifically, we used the general normal-proposal Metropolis algorithm as implemented in the WinBUGS software (Lunn et al., 2000); this algorithm is based on a symmetric normal proposal distribution, whose standard deviation is adjusted over the first 4000 iterations such as the acceptance rate ranges between 20 and 40%. An ordered over-relaxation was used to reduce within-chain correlation (Neal, 1998). We used 20,000 iterations and convergence was assessed with the modified Gelman–Rubin convergence statistic (Brooks and Gelman, 1998). 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 approximately less than 5% of the sample standard deviation. Our framework was implemented in the WinBUGS differential Interface (WBDiff); an interface that allows numerical solution of systems of ordinary differential equations within the WinBUGS software. The goodness-of-fit of the model predictions over the observations was assessed by examining the model structural error σ_{jkl} as well as the average monthly root mean squared error (RMSE), relative error (RE), and average error (AE) for each of the four state variables in each spatial compartment.

3. Results

The MCMC sequence of the model converged rapidly (≈5000 iterations) and the statistics reported were based on the last 15,000 draws by keeping every 4th iteration (thin = 4). Despite its relatively simple structure, we found that the model realistically reproduces the TP, PO_4, Chl a, and zooplankton variability, both spatially (across the three compartments) and temporally (across the 35-year simulation period). The medians of the posterior predictions follow closely the field observations, although the spring algal bloom (March–April) and the subsequent peak zooplankton concentrations (May–June) were usually underestimated (Fig. 2). In addition, all the observed values (except one epilimnetic zooplankton value) were included within the 95% uncertainty bounds. The discrepancy terms (σ_{jkl}) together with the average values of the monthly root mean squared error (RMSE), relative error (RE), and average error (AE) are shown in Fig. 3. Because of their relatively "static" character, the thermocline and hypolimnion are easier to model and thus the corresponding predictions were character-

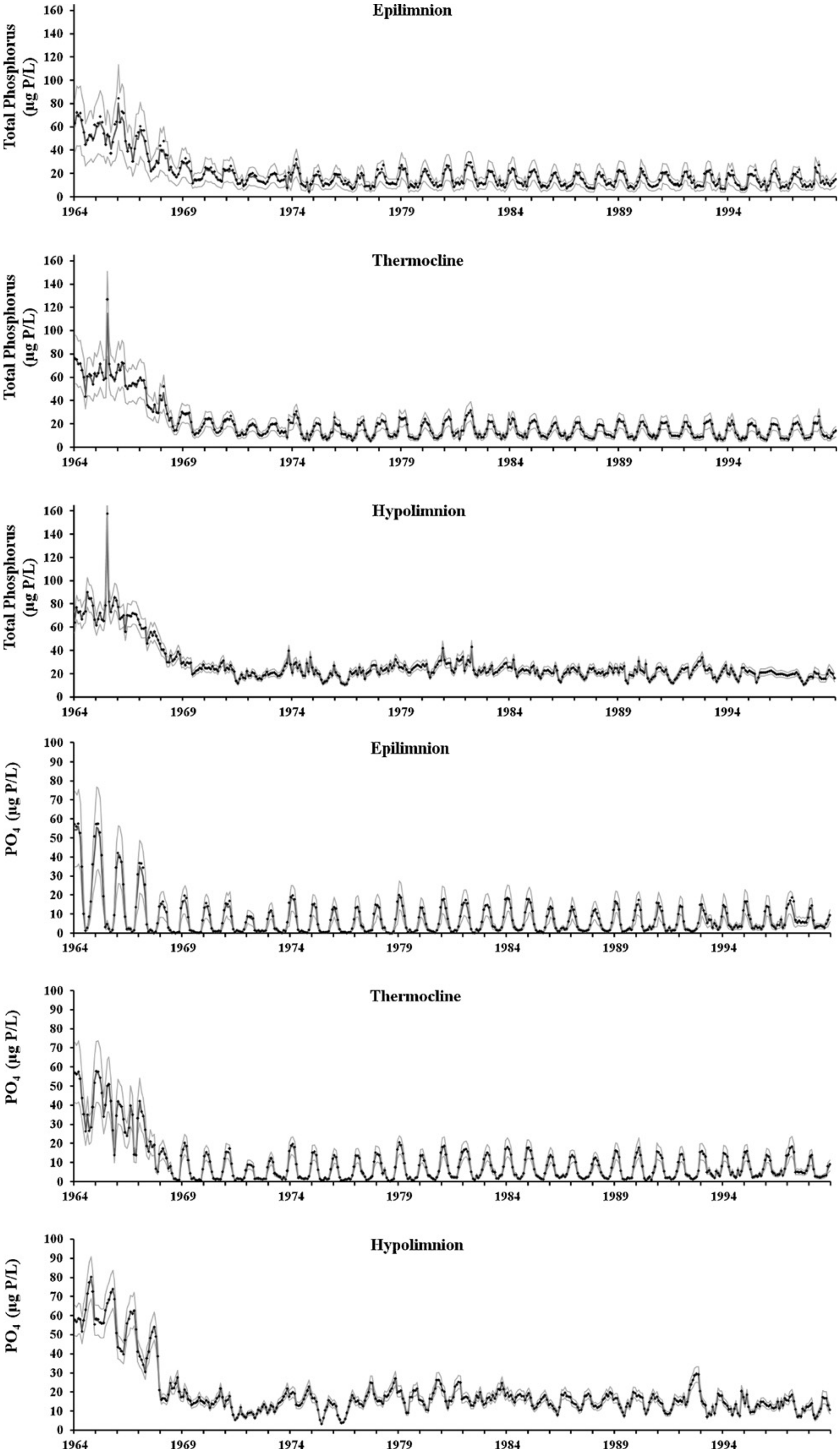

Fig. 2. Comparison between the observed data (solid dots) and the model predictive monthly distributions for total phosphorus, phosphate, chlorophyll *a*, and zooplankton in the epilimnion, thermocline, and hypolimnion. Dark grey line corresponds to the median value of model prediction and lighter grey lines correspond to the 2.5 and 97.5% uncertainty bounds.

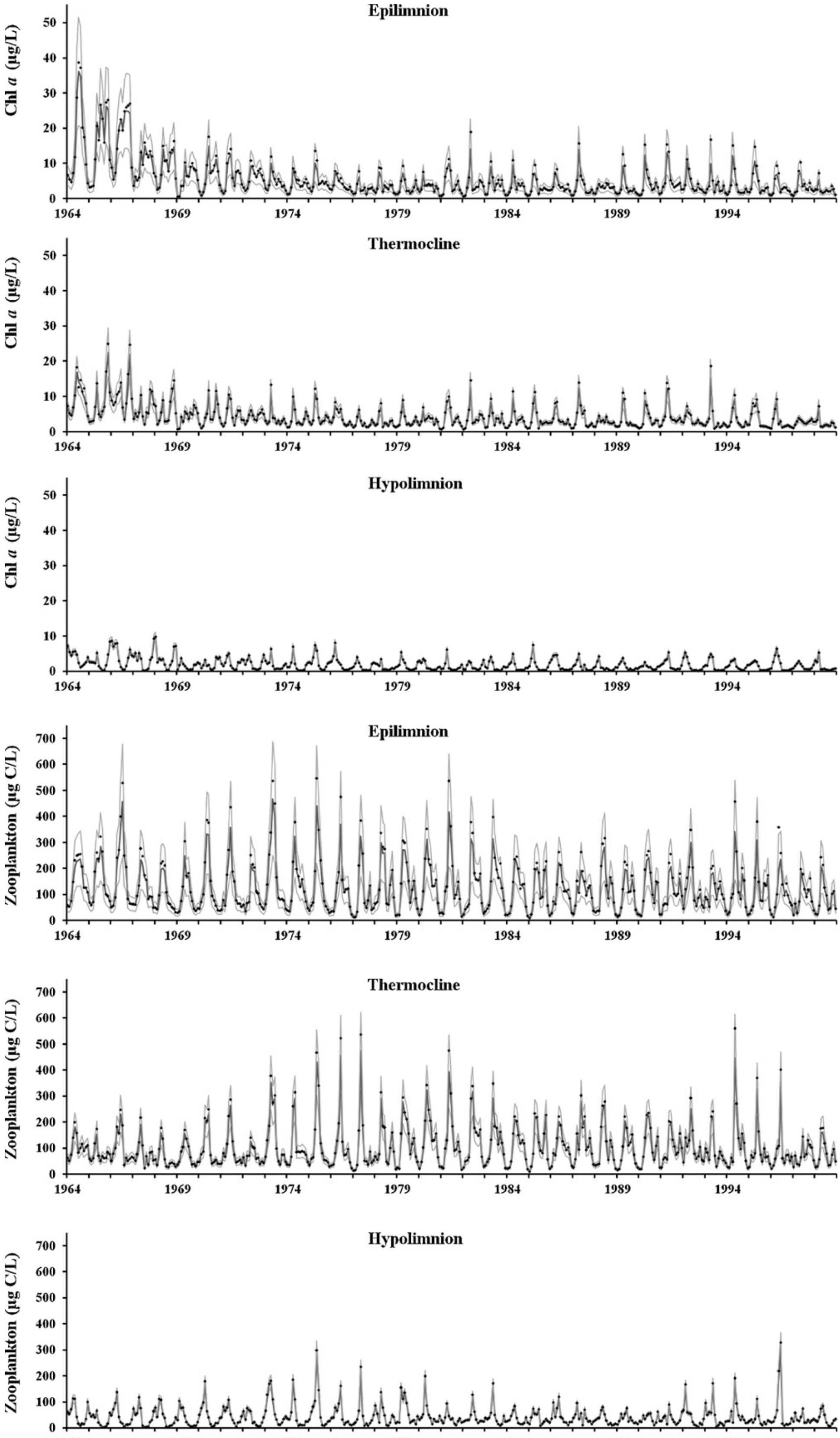

Fig. 2. (*Continued*).

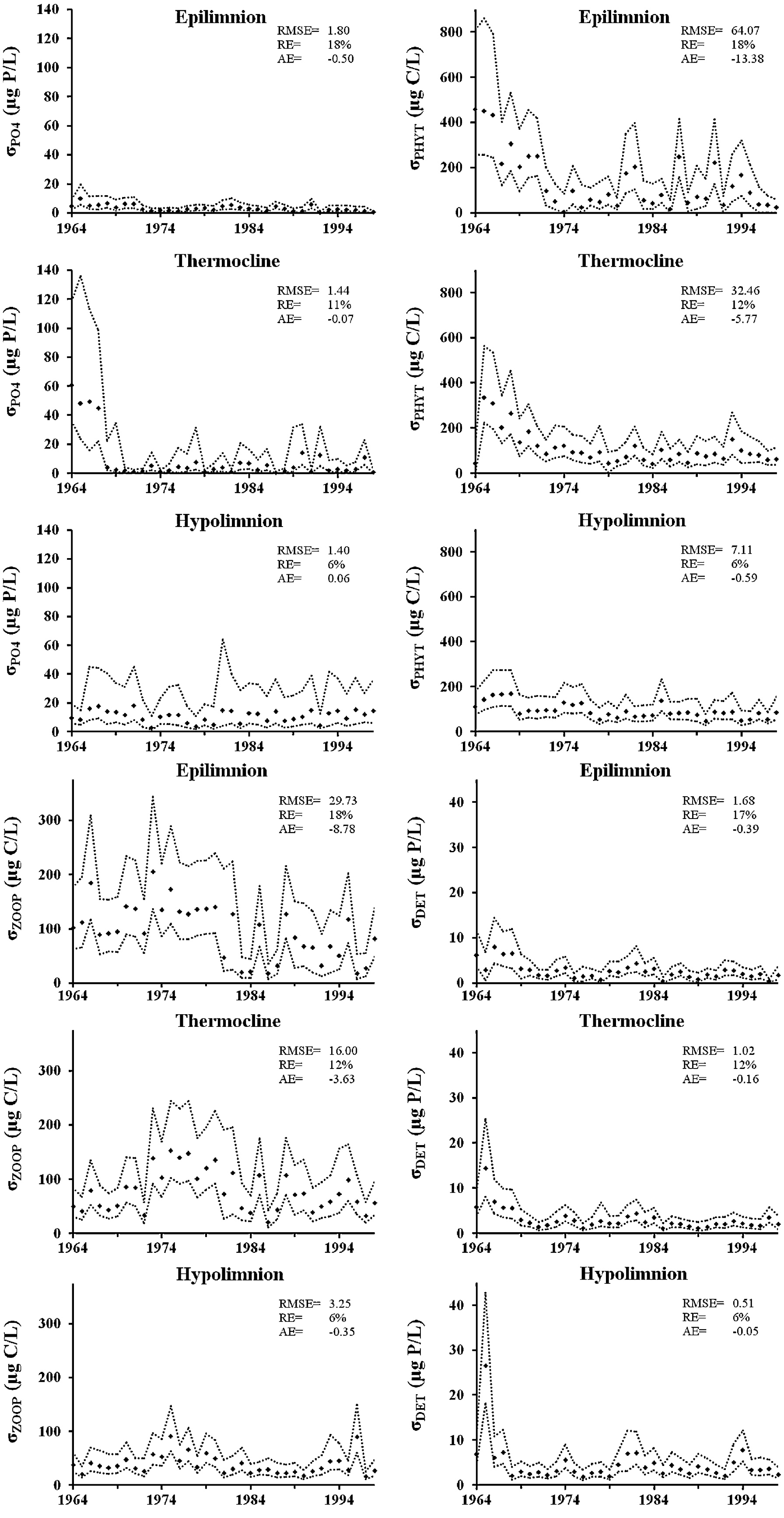

Fig. 3. Time series plots of the discrepancy between the model and the natural system for the phosphate, phytoplankton, zooplankton, and detritus biomass concentrations in the epilimnion, thermocline and hypolimnion. Solid dots correspond to the median values while the dashed lines correspond to the 2.5 and 97.5% percentile values of the error terms. The average values of the root mean square error (RMSE), relative error (RE), and average error (AE) are also indicated.

ized by lower error values. Based on the results of a performance assessment of 153 aquatic biogeochemical models (Arhonditsis and Brett, 2004, see their Fig. 3 and Table 1), we infer that the phosphate and phytoplankton biomass relative errors (both < 18% for all compartments) are lying within the 10th percentile of the best performing models, while the relative error of the zooplankton biomass concentrations (also < 18%) is slightly inferior than the top 10th percentile for this class of models. Aside from the model-fit and the model discrepancy plots, the temporal evolution of the error associated with the monthly values of the four state variables during the simulation period is provided in Fig. A3 (Appendix A).

Most of the median values of the marginal posterior parameter distributions are comparable to those reported in previous studies (Arhonditsis et al., 2007, 2008a), with exceptions being the phytoplankton respiration rate (*r*), the phytoplankton sinking rate (*s*), and the detritus sinking rate (ψ). In addition, the posterior median values of the parameters associated with the physical forcing effects on plankton growth (i.e., *kt*, *ktz*, *kb*, and *kc*) are very similar to the calibrated values reported by Arhonditsis and Brett (2005a). The time series plots of the posterior parameter medians (along with the 2.5 and 97.5% uncertainty bounds) show that there were year-specific parameter estimates with relatively constant median values, enclosed within their prior distribution ranges, and with-

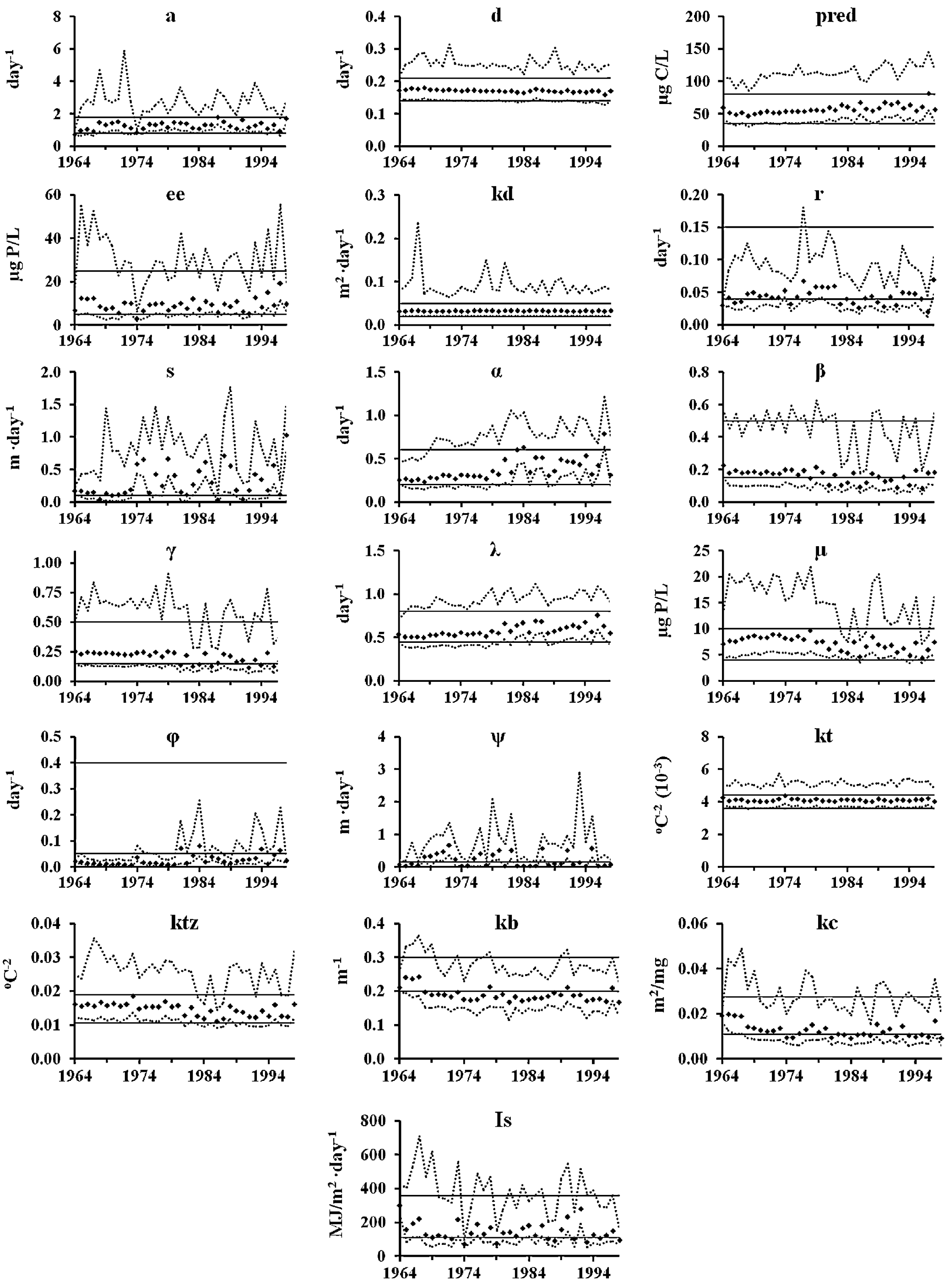

Fig. 4. Time series plots of the posterior parameter estimates. Solid dots correspond to the median values while the dashed lines correspond to the 2.5 and 97.5% percentile values of the marginal parameter posterior distributions. The two horizontal lines indicate the prior minimum and maximum parameter values.

out systematic trends throughout the study period; characteristic examples were the parameters a, d, kd, γ, μ, kt, and ktz (Fig. 4). Some posterior parameter estimates (φ and kb) are also relatively stable but are consistently falling outside their prior distribution ranges, and this result may reflect a misspecification of the respective prior distributions; at least, in the context of the Lake Washington dynamics. Notably, both phytoplankton (s) and detritus (ψ) sinking rates exhibited significant year-to-year variability, although the former parameter was characterized by lower posterior median values during the eutrophic period of the lake; a plausible result reflecting a phytoplankton community dominated by the buoyant cyanobacterium *Oscillatoria rubescens*. The most interesting results were observed by examining the plots for half-saturation constant for predation (*pred*), zooplankton growth efficiency (α), maximum zooplankton grazing rate (λ), and detritus remineralization rate (φ); all of these parameters demonstrated increasing trends in the period representing the new mesotrophic era of the lake. It is also interesting to note that the half-saturation constant for PO_4 uptake (*ee*) shows (plausibly) high values during the earlier years and noticeable increasing trend towards the end of the study period; the latter result seems counterintuitive as the more recent *ee* values refer to a diatom-dominated phytoplankton community with well-documented superior phosphorus kinetics.

To gain insights into the plankton dynamics of the system, we also examined the relative magnitudes and the temporal trends of all the ecological processes considered in our plankton model. A summary of the relative (percentage) contribution of the various planktonic processes to the annual phosphorus budget in Lake Washington epilimnion is shown in Fig. 5. All the phosphorus mass fluxes (10^3 kg P L^{-1}) associated with the simulated ecological mechanisms were reduced by an average of 30% between the pre- and the post-diversion periods; in particular, the phytoplankton respiration and the detritus settling rates showed a 58 and 48% decrease, respectively. Consequently, the percentage contribution of the two processes to the total annual phosphorus budget has significantly decreased. On the other hand, the detritus grazing and zooplankton excretion to detritus rates were two ecological paths with relatively minor decrease (<15%), and thus had the highest increase in fraction of the annual phosphorus budget in the post-diversion period. We also attempted to elucidate the interrelationships among the planktonic processes by conducting two principal component analyses (PCA) based on the corresponding annual phosphorus fluxes; one for the entire 35-year study period and another for the post-diversion period (1975–1998) (Table 3). The selection of significant principal components (PCs) was based on the Kaiser criterion which means that we retained only PCs with eigenvalues greater than 1, i.e., a factor is considered only if the variability explained is greater than the equivalent of one original variable (Jassby, 1999; Legendre and Legendre, 1998). The significant modes of variability were then rotated using the normalized varimax strategy to calculate the new component coefficients (Richman, 1986). The two PCA applications identified three significant (and relatively similar) PCs: (i) the most significant mode of variability was primarily associated with the herbivorous and detrivorous grazing, the zooplankton excretion to detritus, the detritus mineralization to PO_4, and the phytoplankton growth explaining 38 and 28% of the total interannual variability in the entire and post-diversion period of the lake, respectively; (ii) a second mode that was more strongly related

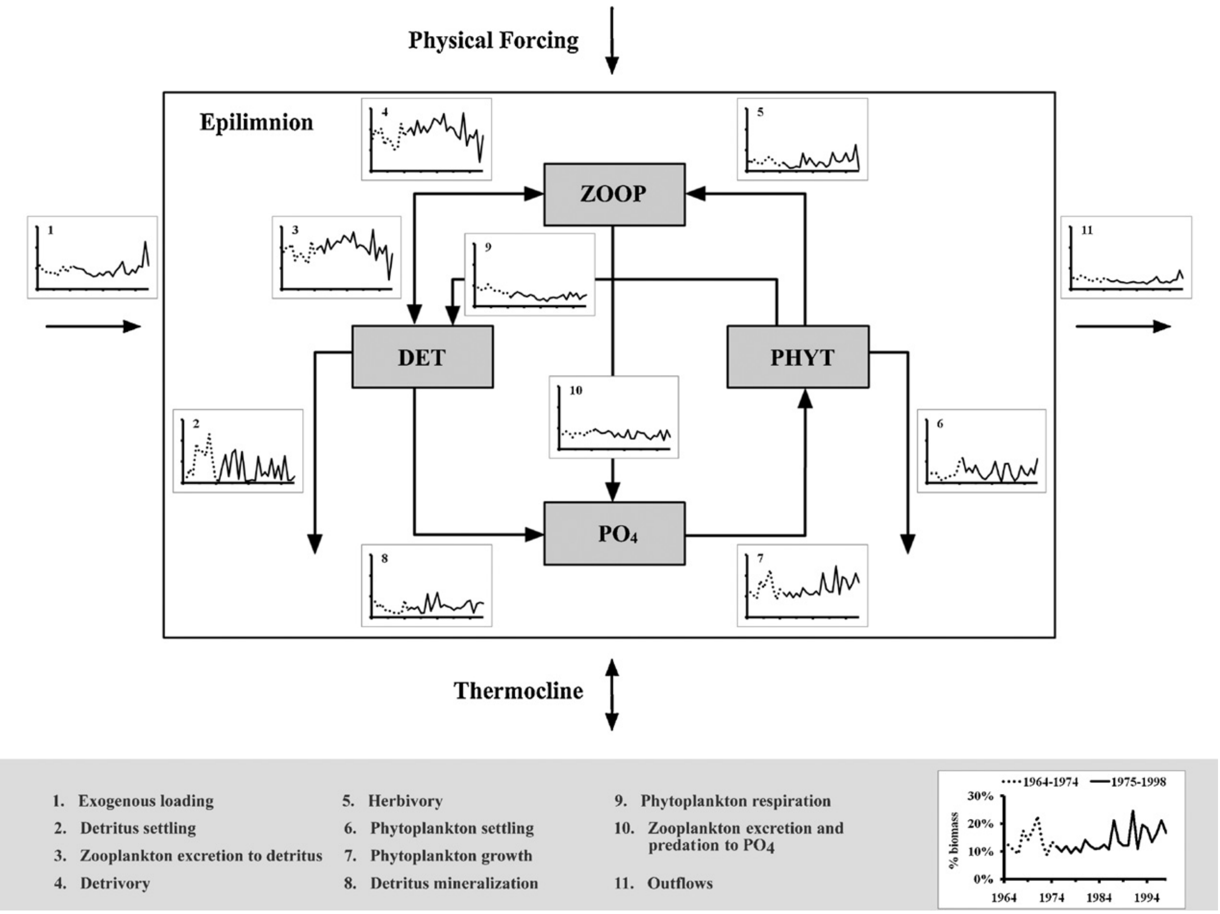

Fig. 5. Flow diagram that illustrates the relative contribution (percentage) of the various planktonic processes to the annual phosphorus budget in the Lake Washington epilimnion. Dashed and solid lines correspond to the 1964–1974 and the 1975–1998 periods, respectively.

Table 3

Component coefficients for the principal components extracted from the PCA of the mean values of the epilimnetic plankton processes (10^3 kg P year^{-1}). Processes with loading values greater than 0.700 are indicated with bold numbers.

Processes	1964–1998 (all years)			1976–1998		
	1st mode (38%)	2nd mode (30%)	3rd mode (14%)	1st mode (28%)	2nd mode (22%)	3rd mode (17%)
Phytoplankton growth	**0.706**	0.136	0.478	0.570	0.187	−0.119
Phytoplankton respiration	0.584	0.630	0.390	0.319	0.687	−0.163
Herbivory	**0.815**	0.165	0.182	**0.807**	−0.233	0.068
Detrivory	**0.722**	0.352	−0.199	**0.710**	0.362	0.089
Zooplankton excretion to phosphate	0.620	**0.746**	0.153	0.415	**0.795**	0.305
Zooplankton excretion to detritus	**0.789**	0.352	−0.131	**0.797**	0.358	0.078
Zooplankton predation to phosphate	0.125	**0.879**	0.176	−0.300	**0.831**	0.190
Detritus settling	−0.108	0.124	**0.918**	−0.078	**0.809**	−0.261
Detritus mineralization	**0.866**	0.139	−0.337	**0.821**	−0.183	0.056
Phytoplankton settling	0.051	**0.752**	−0.515	−0.386	0.071	0.592
Phosphate diffusion	0.657	0.640	−0.025	0.420	−0.121	−0.426
Outflows	0.594	0.671	0.167	0.323	0.031	**0.847**
Exogenous loading	0.592	0.689	0.048	0.117	−0.202	**0.864**

to the amount of phosphate directly supplied from the zooplankton excretion and mortality/higher predation as well as the phytoplankton (1964–1998) or the detritus settling rates (1975–1998); and (iii) the "post-diversion" PCA identified another mode driven by the exogenous loading and outflows which accounted for 17% of the total interannual variability.

The MCMC posterior samples were also used to examine the exceedance frequency and confidence of compliance with different water quality standards during the post-recovery period. For illustration purposes, we selected two water quality variables of management interest, i.e., the chlorophyll *a* and total phosphorus concentrations, and then specified their threshold values (numerical criteria) at 4 μg Chl *a* L^{-1}, and 15 μg *TP* L^{-1}, respectively. For each Monte Carlo run, we calculated the monthly predicted values and the corresponding probabilities of exceeding the two water quality criteria. These probabilities were calculated as follows:

$$p = P(c > c'|\theta, \zeta, x, y_0) = 1 - F\left(\frac{c' - g(\theta, \zeta, x, y_0, \delta)}{\sigma_\varepsilon}\right) \quad (6)$$

where p is the probability of the response variable exceeding a numerical criterion c', given values of θ, ζ, x, and y_0, σ_ε is the measurement error/within-month variability, and $F(\cdot)$ is the value of the cumulative standard normal distribution. The monthly predicted values along with the calculated exceedance frequencies were then averaged over the July–September period. The distribution of these statistics across the posterior space can be used to assess the expected exceedance frequency and the confidence of compliance with the two water quality standards, while accounting for the model input uncertainty. Fig. 6 illustrates these probabilistic risk assessment statements using the predictive distribution of chlorophyll *a* during the summer stratified period (July to September) in 1988. The two plots can be interpreted as follows: "*There is* 31% *probability that chlorophyll a will be higher than* 4 μg L^{-1} *during the summer period in Lake Washington, and our confidence that this value won't be exceeded more than* 10% *in time and space is less than* 3.5%." Based on the same Chl *a* and *TP* criteria, we created time series plots of the exceedance frequency and the confidence of compliance during the 35-year study period (Fig. 7). The plots showed relatively high levels of exceedance frequency (and correspondingly low confidence of compliance) for both criteria during the 1964–1974 period. In fact, Lake Washington was not attaining at all the two water quality goals until the early 1970s. On the other hand, the Chl *a* exceedance frequency and confidence of compliance plots are characterized by significant interannual variability, whereas the lake seems to be (almost consistently) in attainment with the *TP* water quality criterion of 15 μg L^{-1} during the post-recovery period.

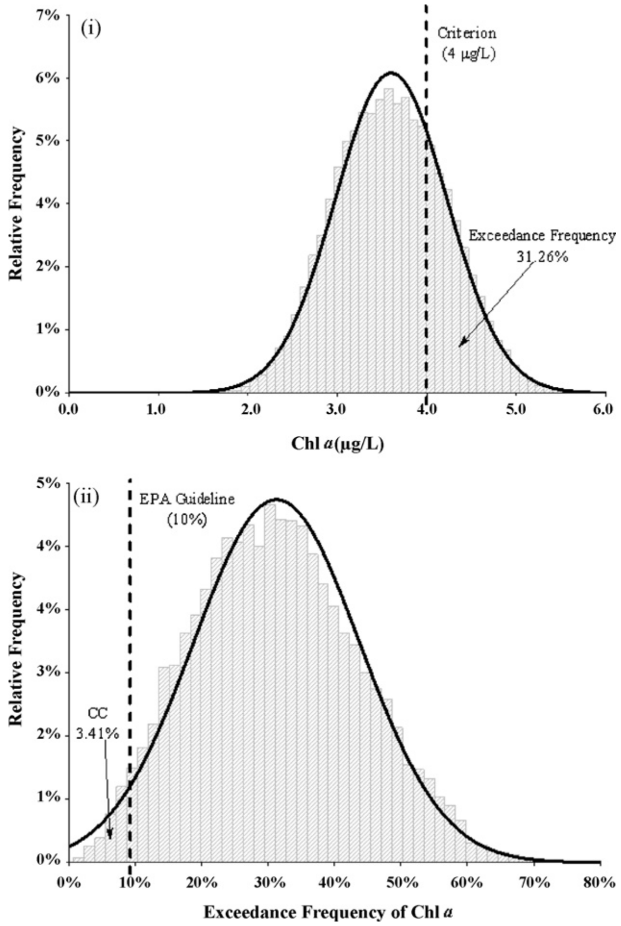

Fig. 6. (i) Predictive distribution for chlorophyll *a* during the summer stratified period (July to September) in 1988. The dashed line corresponds to the numerical criterion used to determine the frequency of violations. (ii) The exceedance frequency of chlorophyll *a* (>4 μg L^{-1}) during the summer stratified period (July to September) in 1988. The area below the 10% cutoff point is termed the confidence of compliance (CC), and represents the probability that the true exceedance frequency is below the 10% EPA guideline.

4. Discussion

The delineation of the climate change vis-à-vis nutrient loading effects on freshwater ecosystem phenology is a "thorny" issue that has not been unequivocally addressed in the literature (Anneville et al., 2004, 2005). While it is acknowledged that failure to explicitly

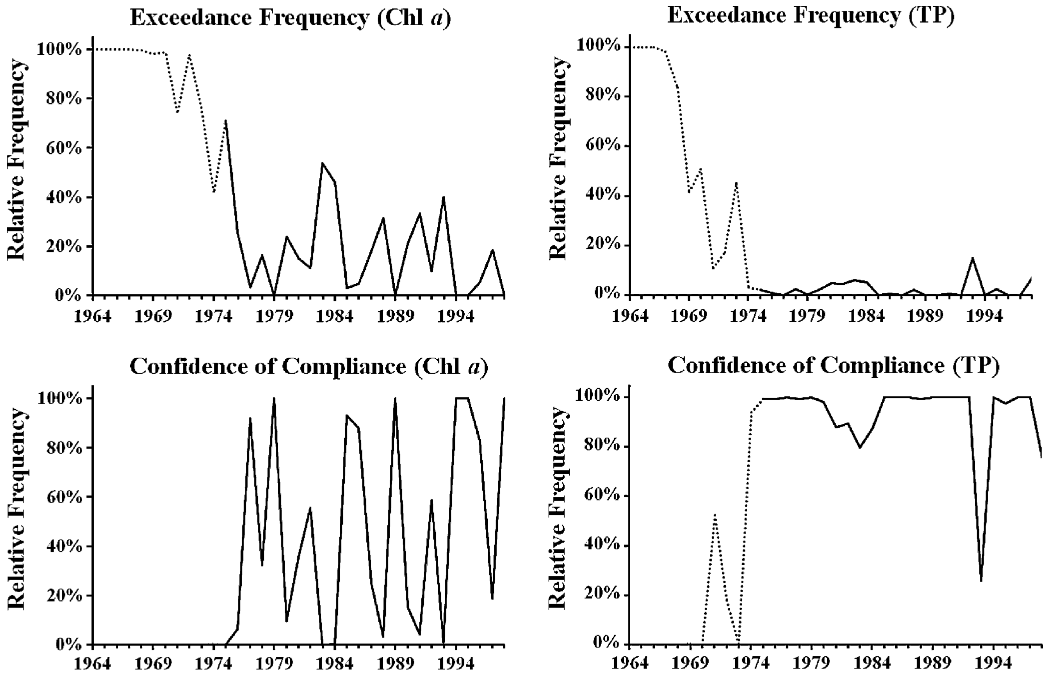

Fig. 7. Time series plots of the exceedance frequency and the confidence of compliance for the summer (July to September) epilimnetic chlorophyll *a* (Chl *a*) and total phosphorus (*TP*) concentrations. The dashed and solid lines represent the 1964–1974 and the 1975–1998 periods, while the criteria used for chlorophyll *a* and total phosphorus concentrations are 4 and 15 μg L^{-1}, respectively.

account for the multitude of stressors impacting system behaviour can provide controversial results (Scheffer et al., 2001; Scheffer and Carpenter, 2003; Van Donk et al., 2003; Jeppesen et al., 2003), most analyses of long-term data focused either on the role of climate variability or on the phenological implications of changes in trophic states due to alternative management schemes. Controlled experimentation with numerical models predicts that the interplay between climate forcing and nutrient supply may induce changes in the seasonal succession plankton patterns, alter the relative importance of the bottom-up and top-down control, favour prolonged cyanobacteria blooms, and ultimately lead to significant loss of the diversity of plankton communities (Horn, 2003; Elliott et al., 2006; Huber et al., 2008). Yet, empirical evidence suggests that the control exerted from nutrient loading management (e.g., re-oligotrophication signals) is much stronger, while many of the ominous ecological forecasts of climate warming arguably remain in the realm of speculation (McKee et al., 2003; Moss et al., 2003; Jeppesen et al., 2005; Thackeray et al., 2008). In this context, the present analysis offers another perspective in that our model is not used as a device to reproduce system response under extreme external forcing scenarios, but rather as an inverse analysis exercise that uses the year-specific parameterizations to detect regime shifts and structural changes induced in Lake Washington functioning from eutrophication restoration efforts as well as climate variability. For this purpose, we opted for a parsimonious model structure to keep the fitting process within the bounds of data-based parameter estimation and thus alleviate the (inevitable) overidentification problems (Arhonditsis et al., 2008a).

Our results primarily highlight the quantitative alterations of the mass fluxes associated with the major planktonic processes brought about by the sewage diversion from the lake. Namely, all the ecological rates considered in the model were reduced by an average of 30%, although their percentage contribution to the carbon and phosphorus budgets remained relatively similar between the pre- and the post-diversion periods of the lake. The most notable exceptions to the latter pattern were the detrivory and the detritus mineralization rates characterized by an approximate 2–5% increase of their relative contribution. Generally, the absence of significant long-term (linear) trends in the annual estimates of the majority of the ecological mechanisms suggests that the year-to-year variability dominates the Lake Washington dynamics in the post-diversion period. According to the model outputs, the net phytoplankton growth (uptake minus metabolic losses) utilizes 52×10^3 kg P year^{-1} of phosphorus; an estimate that is very close to the value reported by Arhonditsis and Brett (2005b). Similar agreement between the two modeling studies was also obtained with regards to the zooplankton consumption of particulate phosphorus in the lake ($\approx 140 \times 10^3$ kg P year^{-1}), although the partitioning between phytoplankton and detritus grazing was somewhat different from the Arhonditsis and Brett (2005b) study in that the present plankton model predicts a 15–20% higher detrivory rate. This discrepancy probably stems from the representation of the Lake Washington zooplankton community by one aggregated biotic entity along with the assumption of equal zooplankton preference for the two food types used herein compared to the more realistic distinction between a copepod-like group with selective feeding ability and a filter-feeding *Daphnia*-like functional group of the Arhonditsis and Brett (2005a) model. While we acknowledge that the representation of the plankton community by two aggregated biotic entities (i.e., phytoplankton, zooplankton) is not appropriate to accommodate the qualitative shifts in the underlying ecological processes that may follow the seasonal succession plankton patterns (Zhao et al., 2008a,b), the importance of feeding selectivity in shaping the total grazing patterns in Lake Washington remains to be resolved. Nonetheless, the good fit to the observed data and the considerable similarity of most of the estimated ecological rates to those obtained from a conceptually (model complexity) and methodologically (calibration scheme, dataset used) distinct modeling exercise increase our confidence in some of the conclusions drawn herein about the “average” planktonic food web processes in the lake.

The interplay among the phytoplankton growth, zooplankton grazing, zooplankton excretion to detritus, and detritus mineralization appears to be closely associated with the interannual variability in Lake Washington. This finding may render support to the hypothesis that the zooplankton excretion is an important mechanism for supplying bioavailable phosphorus to the phosphorus pool in the lake (Arhonditsis et al., 2004b). In particular, there are estimates of the zooplankton nutrient recycling to provide 60–90% of the phosphorus supply to the mixed layer during the summer stratified period in Lake Washington (Richey, 1979; Devol, 1979), although the long-term significance of this ecological path has not been evaluated yet. Generally, the total amount and the relative importance of the phosphorus recycled depends on the trophic status of the lake, the water temperature as well as on the abundance and composition of the zooplankton community, with the smallest organisms being associated with higher rates of phosphorus excretion per unit of biomass (Gulati et al., 1989; Teubner et al., 2003; Ejsmont-Karabin et al., 2004; Kowalezewska-Madura et al., 2007). Thus, it is conceivable that the change from the eutrophic to the mesotrophic state along with the well-documented structural shifts in the summer zooplankton community (see also following discussion) have modulated the phosphorus recycling rates. Yet, the question arising is to what extent our findings can also be driven by the climatic variability? Despite the tight coupling between meteorological forcing and lake temperature (Arhonditsis et al., 2004a), we only found a moderately significant signature of the local climatic conditions (i.e., air temperature) on the phytoplankton growth ($r = 0.41$), herbivorous grazing ($r = 0.38$), and detritus mineralization ($r = 0.39$) rates during the post-diversion period (1975–1998). Thus, contrary to Blenckner et al.'s (2002) predictions that one of the most pronounced effects of climate warming may be the increased lake productivity due to enhanced remineralization of nutrients at higher temperatures, our study provides evidence that the climatic forcing has not been the most significant regulatory factor of the corresponding processes in Lake Washington during the 35-year study period.

We also found that the sedimentation of particulate matter is characterized by significant interannual variability and is positively related to the amount of phosphate supplied from zooplankton excretion and mortality/higher predation; especially during the post-recovery period (see the corresponding principal component in Table 3). Viewing the positive relationship among these ecological processes from a model calibration standpoint, it seems counterintuitive that the year-specific model solutions usually combine higher values for the zooplankton phosphate release rates with high detritus sinking rates and vice versa. According to the detritus equation, a negative relationship under which the effects of these terms cancel each other out would have seemed more plausible. The positive correlation probably reflects the predominance of other ecological paths considered in our eutrophication model, e.g., higher fraction of the zooplankton excretion provides phosphate which fuels phytoplankton growth, and then the resulting increase in phytoplankton respiration and zooplankton grazing replenish the detritus pool. Thus, higher detritus sinking fluxes probably compensate for this increase and the model can still reproduce the observed patterns (Arhonditsis et al., 2007).

It is also interesting to note that the amount of phosphate directly supplied from zooplankton excretion ($-487\,\mathrm{kg\,P\,year^{-1}}$, $r^2 = 0.27$) and mortality/higher predation ($-431\,\mathrm{kg\,P\,year^{-1}}$, $r^2 = 0.37$) were the only processes characterized by a relatively significant linear trend during the sewage post-diversion period (Fig. 8). To interpret this systematic decrease of the zooplankton excretion fraction to phosphate, we can invoke the mineral phosphorus limitation hypothesis under which zooplankton regulates the elemental release rates to cope with nutritionally imbalanced food and maintain homeostasis (Elser et al., 2000; Anderson et al., 2005). Nonetheless, while the significant reduction of the external loading along with the prolongation of the stratification period are likely to have reduced the nutritional seston quality, the carbon to phosphorus molar ratio in the lake rarely exceeds the critical level (>300) proposed as limiting for zooplankton growth (Brett et al., 2000). In fact, several recent studies advocate the critical role of the food quantity rather than the food quality on zooplankton growth in Lake Washington (Winder and Schindler, 2004a,b; Ravet et al., in press). Another possible explanation may be the year-to-year variability of the zooplankton community composition and the succession patterns among groups with higher (rotifers) or lower (cladocerans, copepods) phosphorus excretion rates (Gulati et al., 1989; Kowalezewska-Madura et al., 2007). Even though the simple structure of our plankton model does not allow to delve into the plausibility of the latter hypothesis, the elucidation of whether the consistent decrease of the zooplankton phosphate release rates stems from the accentuation of the phosphorus-limiting lake conditions (typical summer epilimnetic phosphorus concentrations: $\leq 5\,\mu g\,PO_4\,L^{-1}$ and $\leq 12\,\mu g\,TP\,L^{-1}$) and the compositional shifts in zooplankton community or whether is simply an artefact of the model structure and/or the calibration exercise warrants further consideration; especially since the dependence on nutrient regeneration mechanisms in resource-limited environments can be associated with major reconfiguration of the food web dynamics (Capblancq, 1990; Teubner et al., 2003).

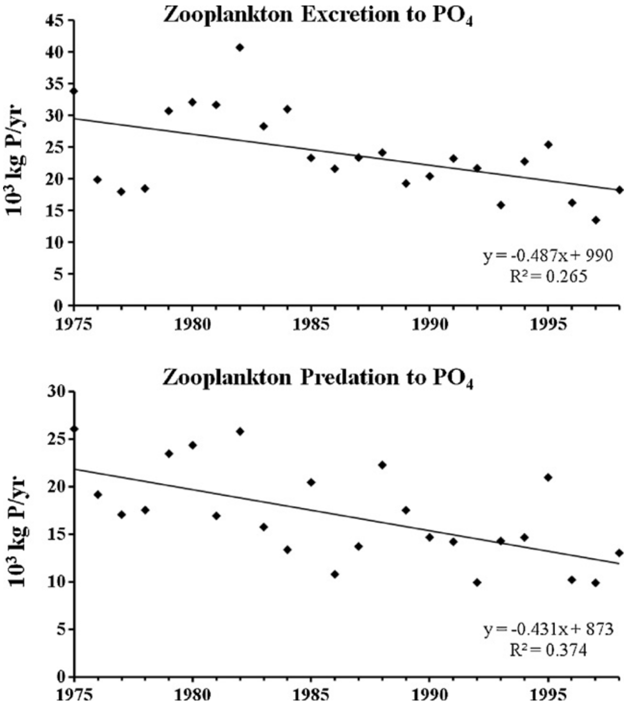

Fig. 8. Long-term trends in the amount of phosphate directly supplied in the system from zooplankton excretion and mortality/higher predation during the sewage post-diversion period (1975–1998).

Despite the simple model structure, the temporal evolution of some of the posterior parameter values captures the major historical structural changes in the Lake Washington plankton community (Edmondson, 1994); that is (i) the dominance of the filamentous cyanobacterium *Oscillatoria* during the eutrophic period is reflected on the higher half-saturation for PO_4 uptake values (inferior phosphorus kinetics), the lower sinking loss rates, the higher self-shading effects, and the lower assimilation efficiency (lower food quality for zooplankton growth); and (ii) the establishment of *Daphnia* in 1976, as a result of bottom-up (due to the disappearance of the filamentous *Oscillatoria*) and top down (due to reduced predation by the mysid shrimp, *Neomysis mercedis*) biotic control, which has superior grazing abilities. The current phytoplankton seasonal succession patterns are characterized by a diatom-dominated (e.g., *Aulacoseira*, *Stephanodiscus*, *Asterionella* and *Fragilaria*) spring bloom followed by a summer phytoplankton community that mainly consists of chlorophytes (e.g., *Oocystis*, *Sphaerocystis*), diatoms (e.g., *Aulacoseira*, *Fragilaria*) and cyanobacteria (e.g., *Anabaena*, *Anacystis*) (Arhonditsis et al., 2003). Moreover, Hampton et al. (2006b) recently proposed a conceptual food web model which offers new insights in that it also emphasizes the role of picoplankton and cryptomonads on the "bottom-up" control of the Lake Washington plankton phenology. Because of their well-documented high nutritional value (Brett and Muller-Navarra, 1997; Bec et al., 2003), the importance of cryptomonads as a food resource for zooplankton is not surprising and the successful *Daphnia* resurgence may be closely related to the contemporary *Cryptomonas* increase in the system (Hampton and Schindler, 2006). On the other hand, the tight linkage of picoplankton to secondary production in non-oligotrophic systems is a relatively new idea that invites further investigation. It has become broadly accepted that small-sized algal cells have a higher surface-area-to-volume ratio and more area of membrane per cell that allows rapid nutrient uptake and enhanced photosynthesis in resource-limited environments (Kononen, 2001; Reynolds, 2006). Consequently, these species can easily adapt and potentially thrive under the conditions of intensified stratification expected with climate warming (Winder and Hunter, 2008). If our assertions that the longer stratification will increase the reliance of the lake on nutrient regeneration, then the positive relationship between zooplankton abundance and the mixed category of widely edible but nutritionally variable picoplankton is likely to become stronger. Yet, the question that remains to be resolved is the ability of such a diet to maintain the integrity of zooplankton community and thus to allow the transfer of energy to the highly selective sockeye salmon populations (Hampton et al., 2006a).

According to the PCA results, a substantial amount of the year-to-year lake variability during the post-diversion period is still associated with the nutrient subsidies from non-point nutrient sources. Thus, the control exerted from the external nutrient loading has important implications for the phenological patterns of the lake (e.g., level and duration of the spring algal bloom) and, from an environmental management point of view, the exceedance frequency and confidence of compliance with water quality standards. For example, the interannual variation associated with the risk assessment of the $4\,\mu\mathrm{g\,Chl}\,a\,\mathrm{L}^{-1}$ threshold level is indicative of the challenges imposed by the weather variability and the intrinsic system stochasticity when setting numerical criteria and making policy decisions. We believe that the Bayesian nature of our modeling work can be particularly useful in this direction. For the purpose of probabilistic risk assessment, the Bayesian approach generates a posterior predictive distribution that represents the current estimates of water quality variables of management interest, while taking into account the uncertainty about input parameters, model structure, measurement error and interannual variability (Arhonditsis et al., 2007, 2008a,b; Tomassini et al., 2007). Therefore, the predictive uncertainty with the Bayesian approach is more realistic (usually larger) than the one based on the classical procedures and the management decisions can be made by explicitly acknowledging the risk of non-attainment. It should be noted, however, that our illustration treats each year independently and inevitably puts greater weight on unusual lake responses driven by extreme meteorological events, e.g., the *TP* risk assessment for the year 1993 in Fig. 7. In this regard, by relaxing the conditional independence assumption, the Bayesian inference offers the ability to sequentially update the model in time and thus support probabilistic risk assessment that effectively accommodates the history of the system (Dorazio and Johnson, 2003; Qian and Reckhow, 2007).

In conclusion, we examined the relative importance of the ecological mechanisms underlying plankton seasonal variability in Lake Washington over a 35-year period (1964–1998). Overall, our analysis showed that the observed changes in the lake primarily reflect the impact of lower nutrient loading rather than climate variability. This conclusion is in accordance with several recent studies which likewise suggest that the detection of the climatic change impact on biological processes is difficult and that even in the same ecosystem different structural properties may be altered by different mechanisms (Jeppesen et al., 2005; Thackeray et al., 2008). Nonetheless, our results provide evidence that apart from the prolongation of the stratification period, the earlier timing of the spring bloom, and the possible uncoupling of the phytoplankton–zooplankton interactions the lake may experience a greater dependence on the internal nutrient regeneration mechanisms (i.e., bacterial mineralization, zooplankton excretion). The interannual variability of the strength of the recycling feedback loop appears to be moderately related to climate forcing, while other biotic factors (e.g., zooplankton community composition) may also be equally important. The recently proposed food web conceptualization that highlights the role of the "bottom-up" control mediated by picoplankton and cryptomonads in Lake Washington phenology offers new insights into the anticipated system responses to a changing climate. In this context, a critical issue that remains to be resolved is the extent to which the increasing dependence of the zooplankton community on the mixture of widely edible but nutritionally variable picoplankton can maintain the integrity of the zooplankton community. The year-to-year variability in Lake Washington can also vary significantly depending on the non-point nutrient loading from the surrounding watershed which underscores the necessity of integrating the landscape with the in-lake processes to obtain holistic understanding of the climate-related effects on lake ecosystems (Blenckner, 2005). The latter assertion also emphasizes the importance of explicitly acknowledging the uncertainty in ecological forecasts to the management of freshwater ecosystems under a changing global environment. In this regard, the Bayesian inference offers a new perspective in that it allows distinguishing among scientific knowledge, lack of understanding, and natural variability, thereby offering a convenient means to effectively communicate long-term projections along with the underlying uncertainty to the policy making process.

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Appendix A

See Figs. A1–A3.

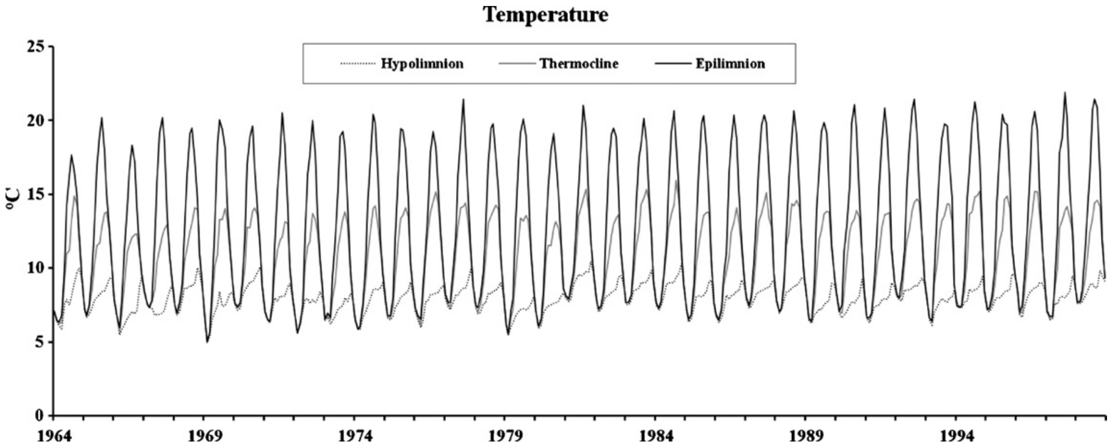

Fig. A1. Temperature variability in the Lake Washington epilimnion, thermocline, and hypolimnion during the study period 1964–1998.

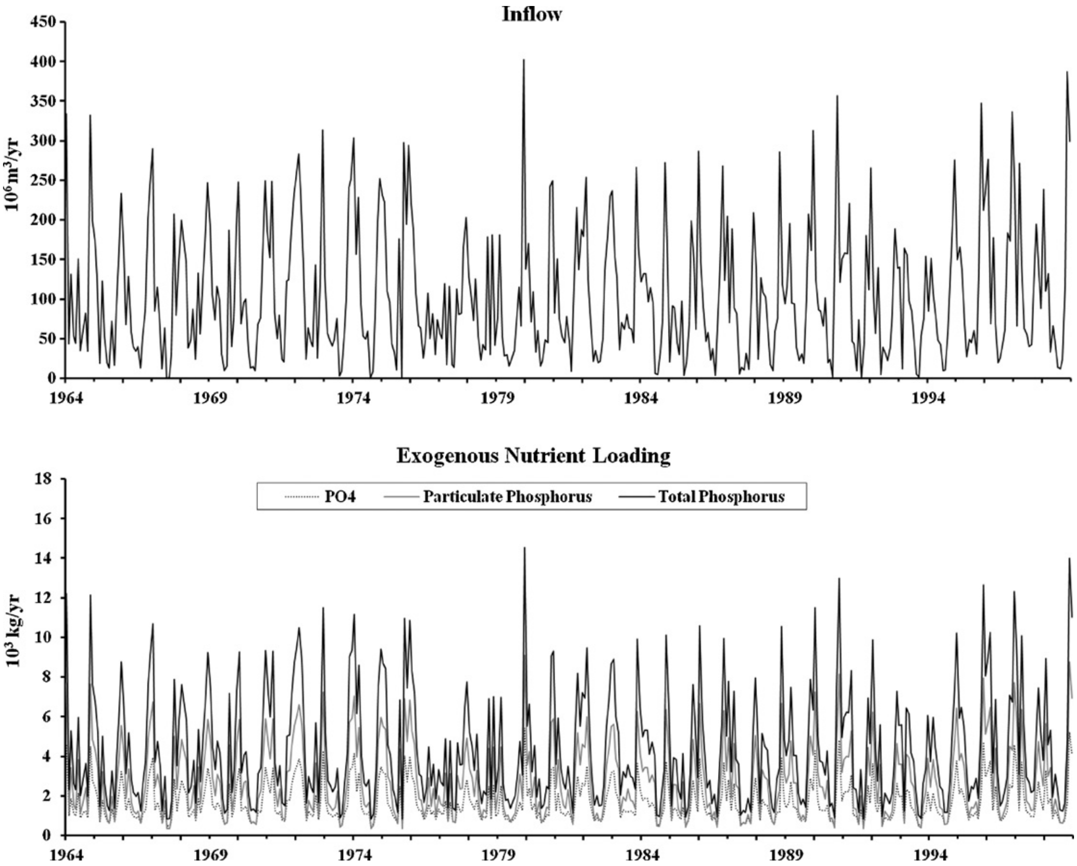

Fig. A2. Hydraulic and nutrient loadings in Lake Washington during the study period 1964–1998. The hydraulic loadings were corrected for evaporation at the lake surface, while the nutrient loadings represent the contribution of both terrestrial and atmospheric sources.

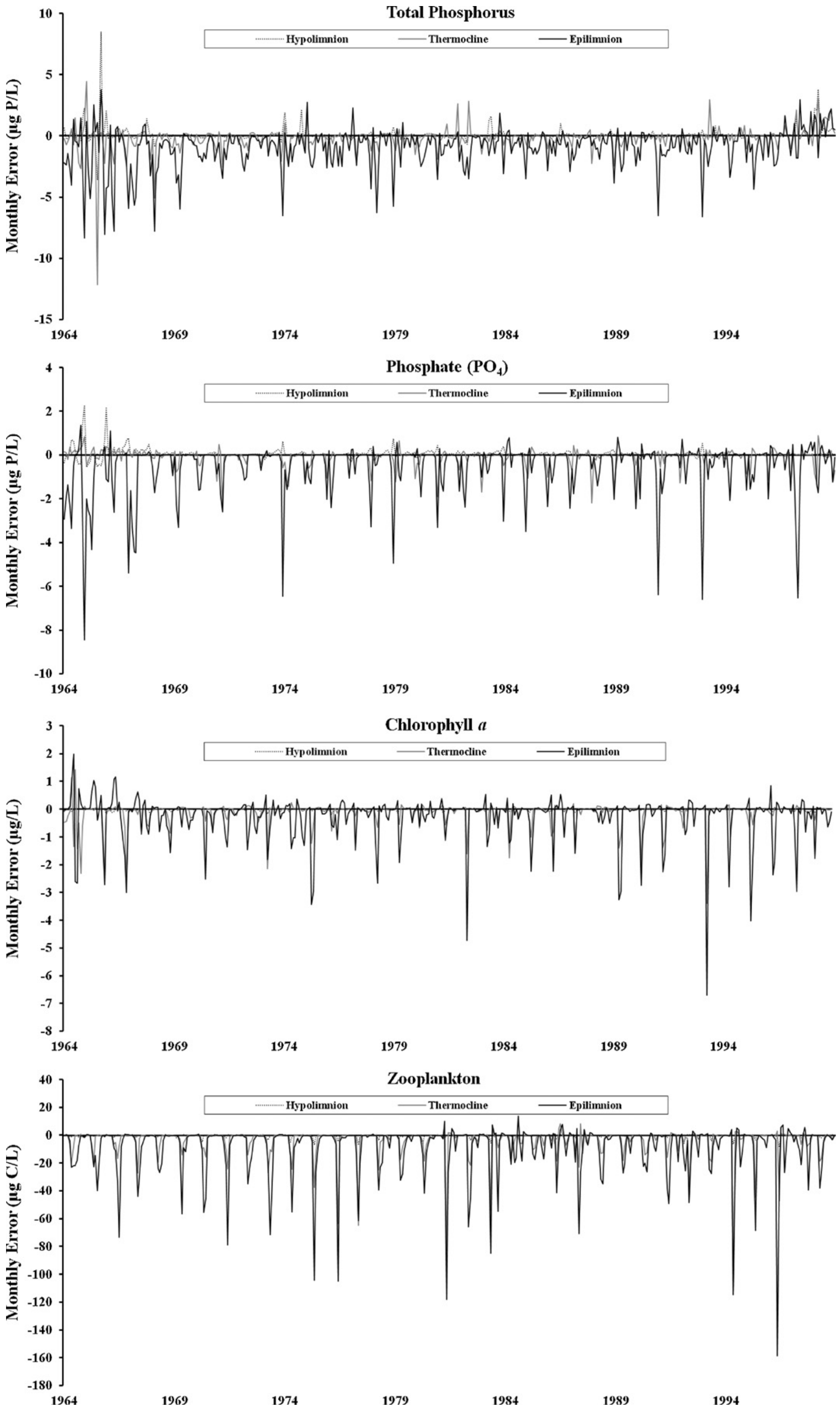

Fig. A3. The error associated with the mean monthly values of total phosphorus, phosphate, chlorophyll *a*, and zooplankton in the Lake Washington epilimnion, thermocline, and hypolimnion during the study period 1964–1998.

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