Effects of changes in the driving forces on water quality and plankton dynamics in three Swiss lakes - long-term simulations with BELAMO

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Summary

1. With a modified version of the lake model BELAMO we were able to describe the essential features of the dynamics of nutrients, dissolved oxygen, phyto- and zooplankton in three lakes of different trophic status over periods of 19 to 30 years, with essentially the same model parameters for all three lakes. This is remarkable, as the measured nutrient inputs decreased considerably during the simulated time period.

2. Despite having done this before for a period of 4 years with an earlier version of the model, a considerable effort was required that led to a series of model modifications without which the data could not be matched. This demonstrates that long-term calibration of a model that combines processes in the water column with mineralization in the sediment can be difficult.

3. Due to the necessarily simplified processes within the model, there is a bias in its output. We applied a recently developed technique for model calibration and uncertainty analysis to address bias and multiple calibration criteria. To account for the demanding long-term simulations, a simplified numerical implementation of this technique was used.

33 4. Our results demonstrate good knowledge of the chemical state of the lake during the
34 calibration period and less knowledge of the biological variables. The credibility intervals
35 used to visualize this knowledge widen substantially during the prediction period
36 consisting of the last 10 years of the simulation.

37 5. The joint calibration of the model to long-term data from lakes of different trophic
38 status is possible but only with considerable prediction uncertainty. Due to the explicit
39 consideration of bias in our calibration technique we are able to estimate quantitatively
40 the uncertainty of our knowledge about chemical and biological variables in the lake.

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42 **Keywords:** Lake modelling; Input loads; Long-term; Universality; Model bias.
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Introduction

Water quality and plankton dynamics are important indicators of the ecological status of a lake. In addition to a general responsibility to conserve ecosystems, deterioration in lake water quality affects human interests directly. However, water quality and plankton dynamics are affected by many factors. For example, wastewater is discharged into lakes, agriculture produces diffuse loads of herbicides and nutrients directly, and similarly polluted flow into lakes. Due to the installation and improvement of wastewater treatment plants and to changes in the use of chemicals in households and industry, in agricultural practice, in the human population and the climate, these external driving forces shift significantly over time.

To understand the behaviour of a lake under changing driving forces (such as nutrient loads or climate change), modelling is an important tool. A model used for this purpose should represent our quantitative understanding of the main biogeochemical and ecological processes within the lake and it should be as universal as possible. As stated by Mieleitner & Reichert (2006), a high degree of universality of ecological models is important for two main reasons. First, from a fundamental research perspective, indicates that the model captures the dominant underlying mechanisms. Second, from an applied perspective, universality gives a model predictive power even when driving forces are changing. To evaluate and check the universality of biogeochemical-ecological lake models, case studies should be performed for different lakes and over time periods during which the external driving forces may shift considerably.

Several lake models have been developed and applied over the past few decades (for reviews about lake modelling see Arhonditsis & Brett (2004), Jørgensen (2010) and Mooij *et al.* (2010)). These include SALMO (Benndorf & Recknagel, 1982), its further developments SALMO-2, SALMO-1D and SALMO-HR (Baumert & Benndorf, 2005, Petzoldt *et al.*, 2005), (DYRESM-)CAEDYM (Hamilton & Schladow, 1997; Schladow & Hamilton, 1997; Romero *et al.*, 2004; Bruce *et al.*, 2006; Tanentzap *et al.*, 2007; Trolle *et al.*, 2008; Rinke *et al.*, 2009), PROTECH (Elliott *et al.*, 1999a, b, 2000, 2005, 2006, 2007, 2010; Reynolds *et al.*, 2001; Elliott & Thackeray, 2004) and BELAMO (Omlin *et al.*, 2001a, b; Mieleitner & Reichert, 2006, 2008). We used the

Biogeochemical and Ecological **LA**ke **MO**del (BELAMO) and assessed its of the universality by applying it to lakes of different trophic status over a long period. The main reason for this choice (and for the development of BELAMO) was the emphasis of the model on closing the element cycles by coupling a lake water column model with a sediment model and explicitly modelling mineralization of organic particles in the sediment rather than parameterizing only the effect of the sediment on the water column by source or sink terms of nutrients and dissolved oxygen. This was identified as a major deficit of most lake models by Mooij *et al.* (2010) and it is of relevance for investigations of the effect of changes in nutrient inputs.

The model BELAMO aims at a joint calculation of mass balances of nutrients, oxygen, organic particles, phytoplankton and zooplankton in the lake water column and two sediment layers. The results of applying BELAMO, originally implemented for Lake Zurich only (Omlin *et al.* 2001a, b), to the lakes Greifensee and Walensee indicated that it is possible to devise a more universal model applicable to three lakes that are similar in many properties, but have different trophic status (Mieleitner & Reichert, 2006). Later, Mieleitner *et al.* (2008) and Mieleitner & Reichert (2008) analysed the influence of taxonomic plankton aggregation on the universality of the lake model by extending it to consider different functional groups of phytoplankton. To refrain the computational burden, the continuous vertical resolution of the original model was reduced to four mixed compartments representing the epilimnion and the hypolimnion of the lake and two sediment layers that were already considered in the one-dimensional model (Mieleitner & Reichert, 2008). The results indicated that the universality of the relatively simple plankton sub-model was not improved by introducing functional groups, as the predictive capability was reduced. The main reason for this was that the additional state variables of the functional groups model were less constrained by mass-balance equations than the state variables of the aggregated (i.e. total phytoplankton) model (the division of phosphate conversion by phytoplankton into contributions by different functional groups is not determined by mass-balance constraints). Additionally, total biomass was not assessed more accurately by the sum of the functional groups than by the aggregated model, and the representation of the separate concentrations of the different functional groups was poor (Mieleitner & Reichert, 2008).

The simulations reported by Mieleitner & Reichert (2006) and Mieleitner & Reichert (2008) were conducted for a period of four years only, during which the driving forces did not change significantly. Longer-term simulations covering a period of change would provide a further test of the universality of the model. In the present study, therefore, we performed simulations over the last 19 or 30 years (depending on the data available for particular lakes) of Greifensee (19 years), Lake Zurich (30 years) and Walensee (30 years), to test the model for time-independency of parameters and process formulations and for predictive power under changing environmental conditions (in particular decreasing phosphate inputs).

Our focus was to find model formulations and parameter values that led to model outputs consistent with empirical data over a long period, to reduce the systematic model errors and to estimate all the remaining uncertainties in the model, including model bias. This required the development of new, computationally efficient techniques based on work on statistical bias description (Craig *et al.*, 1996; Craig *et al.*, 2001; Kennedy & O'Hagan, 2001; Higdon *et al.*, 2004; Bayarri *et al.*, 2007). Using the calibration technique explained in detail in Dietzel & Reichert (2012), long-term simulations were performed with the existing data. While data for the first 9 or 20 years of the simulation period were used for calibration purposes, the last 10 years of lake data served for model validation. The uncertainty estimates for the validation period assesses the predictive power of the model.

Methods

Study Area

Greifensee and Lake Zurich are both located in the north-eastern part of the Swiss plateau (Fig. 1). The area around Greifensee is mainly agricultural, while the catchment of Lake Zurich is more urban. Walensee is south-east of the other two lakes, in the foothills of the Swiss Alps. Linthkanal, the outflow of Walensee, flows into Lake Zurich. Lake Zurich is separated into two parts by a natural dam, Seedamm. As vertical profiles were taken in the lower basin, for

modelling we therefore concentrated on lower Lake Zurich. As measured by prevailing phosphate concentrations, Greifensee is still eutrophic, Lake Zurich mesotrophic and Walensee oligotrophic.

BELAMO: Model Description

Basic model version

The first version of BELAMO was a one-dimensional (vertical) mechanistic model of the nutrient and plankton dynamics in Lake Zurich. It calculates horizontally averaged concentrations changing with the depth of the lake. The concentrations of biochemical variables and particles in the sediment, divided into two layers, are also considered. For an introduction to the model see Omlin *et al.* (2001b). Mieleitner & Reichert (2006) modified the one-dimensional model and analysed its transferability to the lakes Greifensee and Walensee.

To reduce simulation time, and to be able to conduct many simulations over several years to analyse functional phytoplankton groups, the continuous vertical resolution of the model was simplified to a box approach (Mieleitner & Reichert, 2008). To ensure the persistence of all functional groups and to represent all groups reasonably well were difficult with this model version. At the level of total biomass, the results did not appear to be significantly better than when modelling only the total phytoplankton (Mieleitner & Reichert, 2008). As it showed a higher predictive capability in the preceding project, we elected to use the aggregated version of the model, describing the total biomass of phyto- and zooplankton. We used the box version of the model to save computational time.

The box model describes the lake as four 'boxes', each with constant volume: epilimnion, hypolimnion and two sediment boxes. In these boxes, concentrations of ammonium, nitrate, phosphate, oxygen, degradable and inert dead organic particles and (in the aggregated version) the total biomass of phytoplankton and zooplankton are calculated.

The following biogeochemical and ecological processes are considered: growth, respiration and death of phyto- and zooplankton, aerobic, anoxic and anaerobic mineralization, nitrification and phosphate uptake by sinking particles. Physical processes that are included are:

inflows into epi- and hypolimnion and outflow from the epilimnion, gas exchange with the atmosphere, mixing of all dissolved substances between epi- and hypolimnion (mixing coefficients were estimated from temperature data), vertical migration of zooplankton in the water column, sedimentation of particles, advection (if the inflow to the lake is into the hypolimnion), diffusion of dissolved substances between the two sediment layers and the water in the hypolimnion, as well as accumulation of sediment and permanent burial.

Here, we concentrated on an application of one model to several lakes that cover range of trophic conditions. However, the three study lakes are all pre-alpine European lakes subjected to similar climatic conditions.

For a detailed description of the original box version of BELAMO see Mieleitner & Reichert (2008). All structural model extensions discussed in the next section are included in Figs. 2 and 3.

Model extensions

Using the model for long-term simulations required considerable adaptations to the model used by Mieleitner & Reichert (2008). We assumed that not all phosphorus released by sloppy feeding and excretion during zooplankton growth is dissolved, but only a fraction f_{sol} . The fraction $1 - f_{sol}$ remains as organic particles.

To account for phytoplankton that grows when phosphate is limiting, we assumed the fraction of phosphorus in organic particles entering the lakes from another lake to be smaller than from rivers ($a_{P,inflow,lake} < a_{P,inflow}$). This was used where inflowing particles had to be assessed from measurements of particulate organic phosphorus or *vice versa*. The fraction $a_{P,inflow,lake}$ accounts for the inflow from the upper basin of Lake Zurich at Seedamm and from Aa Uster, a river flowing from Lake Pfäffikon into Greifensee ("Aa (U.)" in Fig. 1).

Initial conditions in the sediment

One main feature of our model is the joint mechanistic description of the processes in the sediment. As stated by Mooij *et al.* (2010), sediment nutrient cycling is rarely dynamically

accounted for in lake modelling but can have a strong influence on the ecosystem. To describe this feature, initial conditions for the different kinds of particles considered are needed that ensure both mass and volume balance. As we made some modifications to the version applied by Mieleitner & Reichert (2008), we give a short description here. The initial conditions of degradable organic (X_S), inert organic (X_I) and inorganic (X_{II}) particles in the sediment (sed), modelled as concentrations of particulate matter (symbolized by X) in $gDM\ m^{-3}$, were parameterized as follows. As the organic phosphorus content of degradable and inert organic particles were modelled as separate state variables in BELAMO, and the state variables of organic particles (X_S and X_I) describe the mass without the phosphorus content, we introduced the mass of organic fractions including phosphorus as X_S^P and X_I^P . In so doing, the first important constraint for the calculation of initial conditions of particles in the sediment was derived from the volume balance of overall particles in the sediment:

$$1 - \theta = \frac{X_{S, sed}^P}{\rho_{X_S}} + \frac{X_{I, sed}^P}{\rho_{X_I}} + \frac{X_{II, sed}}{\rho_{X_{II}}} \quad (1)$$

where θ is the volumetric water content of the sediment and ρ the density of the respective particles. Second, the mass fraction (symbolized by a) of organic material in total sediment material, $a_{org, sed}$, and the mass fraction of degradable material in organic sediment material, $a_{deg, sed}$ provided two more equations:

$$X_{S, sed}^P + X_{I, sed}^P = a_{org, sed} \cdot (X_{S, sed}^P + X_{I, sed}^P + X_{II, sed}) \quad (2)$$

and:

$$X_{S, sed}^P = a_{deg, sed} \cdot (X_{S, sed}^P + X_{I, sed}^P) \quad (3)$$

By assuming $a_{org, sed_{ini}}$ and $a_{deg, sed_{ini}}$ as initial conditions of organic and degradable material mass fractions, conversion of these three equations led to the first initial condition for inorganic particles, X_{II} :

$$X_{II, sed_{ini}} = \frac{1 - \theta}{\frac{1}{\rho_{X_{II}}} + \frac{a_{deg, sed_{ini}} \cdot a_{org, sed_{ini}}}{\rho_{X_S} \cdot (1 - a_{org, sed_{ini}})} + \frac{(1 - a_{deg, sed_{ini}}) \cdot a_{org, sed_{ini}}}{\rho_{X_I} \cdot (1 - a_{org, sed_{ini}})}} \quad (4)$$

The parameters $a_{org, sed_{ini}}$ and $a_{deg, sed_{ini}}$ are input parameters of the model and were set to 0.1

and 0.3, respectively. By introducing the organic fractions without phosphorus content, X_S and X_I , it follows:

$$X_S^P = \frac{X_S}{(1-a_{P,S})}, \quad X_I^P = \frac{X_I}{(1-a_{P,I})} \quad (5)$$

with the phosphorus contents, $a_{P,S}$ and $a_{P,I}$, which were assumed to conform to the Redfield ratio ($a_{P,red}$) initially (Redfield 1958). Hence, the other two initial conditions resulted in:

$$X_{S, sed_{ini}} = \frac{a_{deg, sed_{ini}} \cdot a_{org, sed_{ini}} \cdot (1-a_{P,red})}{1-a_{org, sed_{ini}}} \cdot X_{II, sed_{ini}} \quad (6)$$

and:

$$X_{I, sed_{ini}} = \frac{(1-a_{deg, sed_{ini}}) \cdot a_{org, sed_{ini}} \cdot (1-a_{P,red})}{1-a_{org, sed_{ini}}} \cdot X_{II, sed_{ini}} \quad (7)$$

Equations (4), (6) and (7) served as initial conditions of inorganic (X_{II}), degradable organic (X_S) and inert organic (X_I) particles in the sediment. Note that the notation for the phosphorus mass fractions $a_{P,S}$ and $a_{P,I}$ follows the equations:

$$a_{P,S} = \frac{X_S^P - X_S}{X_S^P}, \quad a_{P,I} = \frac{X_I^P - X_I}{X_I^P} \quad (8)$$

This notation differs from the one described in Omlin *et al.* (2001b) and Mieleitner & Reichert (2006), where the mass fractions of phosphorus in organic particles were related to the organic fractions without phosphorus content. As the phosphorus content is small, this change did not have a significant effect on the model results, but is in better agreement with common notation. The calculation of phytoplankton phosphorus content was changed accordingly.

Active movement of zooplankton

In order to make the zooplankton sub-model of BELAMO more realistic, we decided not to compare with model results the volume-weighted averages of zooplankton concentration over the whole lake depth, but to use the two depth-integrated samples for an estimate of epilimnial and hypolimnial concentrations. This is described in more detail in the Supporting Information (Appendix S1) and was possible only for Lake Zurich and Walensee. With the

originally zooplankton mobility component of the model, implemented in addition to normal turbulent diffusion, the model tended to overestimate the zooplankton concentrations in the hypolimnion and to underestimate the concentrations in the epilimnion. This was avoided by switching off this active mobility component, which was originally implemented as a diffusive exchange process between the two compartments, hence balancing the concentration of zooplankton in the epi- and hypolimnion. The data gave hints that zooplankton moves more actively towards food. Therefore, we introduced an advection process that represents the movement of zooplankton to the epilimnion, where phytoplankton is present. The mass flux of zooplankton from hypo- to epilimnion was formulated as follows:

$$F_{up,ZOO} = -v_{up,ZOO} \cdot A_{surf} \cdot X_{ZOO,hypo} \quad (9)$$

where A_{surf} is the surface area of the specific lake and $X_{ZOO,hypo}$ is the zooplankton concentration in the hypolimnion. The upwards velocity of zooplankton, $v_{up,ZOO}$, was set to 5 m d^{-1} .

Zooplankton grazing

Compared to Omlin *et al.* (2001b) and Mieleitner & Reichert (2008), the implementation of zooplankton growth by feeding on phytoplankton was modified. Zooplankton growth rate was formulated as:

$$r_{gro,ZOO} = k_{gro,ZOO,T_0} \cdot e^{\beta_{ZOO} \cdot (T - T_0)} \cdot \frac{S_{O_2}}{K_{O_2,ZOO} + S_{O_2}} \cdot f_{ALG} \cdot X_{ZOO} \quad (10)$$

where k_{gro,ZOO,T_0} is the specific maximum zooplankton growth rate at the reference temperature T_0 (in our case 20°C), β_{ZOO} is the temperature dependence coefficient of zooplankton and T the actual temperature. Furthermore, the growth rate includes a Monod-type limitation term for O_2 (S refers to a concentration of a dissolved substance, in this case measured in gO m^{-3}) with the half-saturation concentration for zooplankton growth with respect to oxygen, $K_{O_2,ZOO}$, and depends on the actual zooplankton concentration, X_{ZOO} . The term f_{ALG} describes the dependence of the zooplankton growth on the phytoplankton

concentration. Rather than using a simple linear approach $f_{ALG} = X_{ALG}$, as did Omlin *et al.* (2001b) and Mieleitner & Reichert (2008), we chose the following non-linear approach:

$$f_{ALG} = \begin{cases} \frac{X_{ALG} - \lim_a}{K_{ALG,ZOO} + X_{ALG} - \lim_a} & \text{if } X_{ALG} > K_{Feed} \\ \lim_b \cdot X_{ALG}^2 & \text{else} \end{cases} \quad (11)$$

with:

$$\lim_a = \frac{K_{ALG,ZOO} + 2 \cdot K_{Feed} - \sqrt{K_{ALG,ZOO} \cdot (K_{ALG,ZOO} + 2 \cdot K_{Feed})}}{2} \quad (12)$$

and:

$$\lim_b = \frac{K_{Feed} - \lim_a}{K_{Feed}^2 \cdot (K_{ALG,ZOO} + K_{Feed} - \lim_a)} \quad (13)$$

For small phytoplankton concentrations below the threshold for feeding (K_{Feed}), calibrated to 0.95 gDM m^{-3} for all three lakes, the dependence on phytoplankton is quadratic; above that threshold it has a Monod-type limitation. This accounts for the assumption that zooplankton consume disproportionately less phytoplankton when food concentration is low. Test simulations showed that this modified growth rate solved the problem of very low modelled phytoplankton concentrations (in data not shown) as described by Mieleitner & Reichert (2006) and Mieleitner & Reichert (2008). The Monod-type limitation guarantees that zooplankton do not grow too much at high phytoplankton concentrations. For the Monod limitation, $K_{ALG,ZOO}$ is the half-saturation concentration for the growth of zooplankton on phytoplankton and was set to 0.8 gDM m^{-3} . The two factors, $\lim_a$ and $\lim_b$, were chosen such that f_{ALG} and its derivative are continuous for every value of X_{ALG} . For a visualization of the function f_{ALG} , see Fig. S1 in the Appendix. It is apparent that the visualized response is similar to the more common ecological modelling approach of a Holling-type III functional response (Holling, 1959a; Holling, 1959b). One reason for the choice of such a functional response is the spatially heterogeneous distribution of prey, which is also the reason for the choice of the approach here. The main difference between the two approaches is that the point for switching from a quadratic to a Monod-type limitation is not fixed to half of the maximal rate, as in the Holling-type III definition. The threshold K_{Feed} was calibrated to a value

corresponding to 30% (and not 50%) of the maximal rate in our application.

Feeding by Diptera

Mieleitner & Reichert (2008) mentioned that modelled zooplankton concentrations are also often too low, especially in the Greifensee. After discussions with a plankton specialist (H.-R.Bürigi, Eawag), it was decided to change the formulation of the zooplankton death rate by introducing the predation by Diptera larvae (genus *Chaoborus*), most abundant in the shallow Greifensee (Mieleitner & Reichert, 2006). To account explicitly for that, we introduced a Diptera model part by splitting the death rate of zooplankton into two processes. "Normal" mortality has the rate $r_{death,ZOO} = k_{death,ZOO,T_0} \cdot e^{\beta_{ZOO} \cdot (T - T_0)} \cdot X_{ZOO}$, which is linearly dependent on the zooplankton concentration and includes predation by fish. k_{death,ZOO,T_0} is the specific death rate and β_{ZOO} describes the temperature dependence. The specific zooplankton death rate was set to the same value for all three lakes before calibration. An additional source of mortality due to predation by *Chaoborus*, only active in Greifensee, was specified and implemented in a similar way as zooplankton grazing on phytoplankton described above to account for lower grazing efficiency at low concentrations. Equation (14) shows the formulation of the process rate

$$r_{death,ZOO,Dipt} = k_{death,ZOO,Dipt,T_0} \cdot e^{\beta_{ZOO} \cdot (T - T_0)} \cdot f_{ZOO} \quad (14)$$

The dependence on zooplankton, f_{ZOO} , is described as

$$f_{ZOO} = \begin{cases} \frac{X_{ZOO}^2}{2 \cdot K_{Feed,ZOO,Dipt}} & \text{if } X_{ZOO} < K_{Feed,ZOO,Dipt} \\ X_{ZOO} - \frac{K_{Feed,ZOO,Dipt}}{2} & \text{else} \end{cases} \quad (15)$$

At the threshold zooplankton concentration, $K_{Feed,ZOO,Dipt}$, predation by *Chaoborus* switches from a quadratic to a linear dependency on zooplankton concentration, rather than switching to a Monod-type limitation as for zooplankton grazing. Test simulations showed that this new implementation no longer allows the concentration of zooplankton to decrease dramatically, in better agreement with the data. The specific death rate due to Diptera feeding was set to 0.085 d⁻¹, and was not included in the calibration, but the parameter calibration resulted in different

values of the specific zooplankton death rate, k_{death,ZOO,T_0} , for the three lakes. This could be due to differences in the fish population in the three lakes and could be represented by a separated fish model component.

Nutrient preference of phytoplankton

Another model change resulted in a more realistic description of the nutrient preference of phytoplankton. To ensure that phytoplankton favours ammonium over nitrate in a way that is still valid at low concentrations of both ammonium and nitrate, we used the following rate descriptions for phytoplankton growth implemented as two processes (one for growth on ammonium and one for growth on nitrate):

$$r_{gro,ALG,NH_4} = k_{gro,ALG,T_0,I_0} \cdot f_{lim,T} \cdot f_{lim,I} \cdot \text{pref}_{NH_4,NO_3} \cdot \min \left(\frac{S_{NO_3} + S_{NH_4}}{K_{N,ALG} + S_{NO_3} + S_{NH_4}}, \frac{S_{HPO_4}}{K_{HPO_4,ZOO} + S_{HPO_4}} \right) \cdot X_{ALG} \quad (16)$$

and:

$$r_{gro,ALG,NO_3} = k_{gro,ALG,T_0,I_0} \cdot f_{lim,T} \cdot f_{lim,I} \cdot (1 - \text{pref}_{NH_4,NO_3}) \cdot \min \left(\frac{S_{NO_3} + S_{NH_4}}{K_{N,ALG} + S_{NO_3} + S_{NH_4}}, \frac{S_{HPO_4}}{K_{HPO_4,ZOO} + S_{HPO_4}} \right) \cdot X_{ALG} \quad (17)$$

The terms $f_{lim,T}$ and $f_{lim,I}$ account for the limitations of phytoplankton growth due to temperature, T and light intensity, I . The temperature dependence is formulated as an exponential limitation, and the dependence on light intensity as a Monod-type limitation. Hence, the specific growth rate, k_{gro,ALG,T_0,I_0} , refers to reference temperature and saturating light intensity. Furthermore, both growth processes are limited by phosphate (S_{HPO_4}) and total nitrogen concentration ($S_{NO_3} + S_{NH_4}$). For nutrient concentrations below their specific half-saturation constant, $K_{N/P,ALG}$, the nutrient concentration at which the difference to the half-saturation constant is larger, controls the limitation, following Liebig's law of the minimum. The “preference factor”, pref_{NH_4,NO_3} , was newly introduced into the equations as:

$$\text{pref}_{NH_4,NO_3} = \frac{p_{NH_4,ALG} \cdot S_{NH_4}}{p_{NH_4,ALG} \cdot S_{NH_4} + S_{NO_3}} \quad (18)$$

where the preference coefficient, $p_{NH_4,ALG}$, which determines the magnitude of preference for ammonium over nitrate, was set to 10. As the concentration of ammonium is much lower than that of nitrate, and also because phytoplankton is more limited by phosphate than by nitrogen in these lakes, this change in the growth formulation changes the model results only slightly. Hence, neither is the absolute value of the parameter crucial. However, this description is also valid for low nitrate concentrations.

Anaerobic mineralization and methane

In the first version of BELAMO, anaerobic mineralization of organic matter was not considered (Omlin *et al.*, 2001b). As it seemed to be relevant, especially for the sediments of the eutrophic Greifensee, it was introduced in the subsequent study (Mieleitner & Reichert, 2006) and also transferred to the box version of the model (Mieleitner & Reichert, 2008). The process of anaerobic mineralization was implemented with a specific anaerobic mineralization rate, $k_{miner,anae,sed,T_0}$, a bacterial temperature dependency, β_{BAC} , inhibition terms for nitrate and oxygen, and a dependence on the concentration of organic particles, X_s :

$$r_{miner,anae,sed} = k_{miner,anae,sed,T_0} \cdot e^{\beta_{BAC} \cdot (T - T_0)} \cdot \left(1 - \frac{S_{NO_3}}{K_{NO_3,miner} + S_{NO_3}}\right) \cdot \left(1 - \frac{S_{O_2}}{K_{O_2,miner} + S_{O_2}}\right) \cdot X_s \quad (19)$$

This process combines anaerobic mineralization by reduction of manganese oxide (MnO_2 to Mn^{2+}), iron hydroxide ($FeOOH$ to Fe^{2+}), sulphate (SO_4^{2-} to HS^-) and methanogenesis (C_{org} to CH_4). It was assumed that at least one of these processes occurs in the absence of oxygen and nitrate and that there is no limitation due to a lack of reducible substances.

The re-oxidation of the reduced substances Mn^{2+} , Fe^{2+} , HS^- and CH_4 that are released into the hypolimnion after anaerobic mineralization in the sediment and the subsequent depletion of oxygen needed for this oxidation, was not considered. This oxidation

can have a significant effect on the oxygen balance in lakes. As there are no data available for any of the four reduced substances, however we cannot compare any modelled concentrations with data. Furthermore, the stoichiometry of all four oxidation processes is the same with respect to the amount of oxygen needed for oxidation per mole of mineralized organic carbon in the corresponding reduction process. For this reason, we can describe anaerobic mineralization and subsequent oxidation of the reduced compound as methanogenesis. Therefore we explicitly considered the production of methane (CH_4) during anaerobic mineralization and introduced oxidation of methane as a new process.

The process rate of re-oxidation of methane in the hypolimnion (after anaerobic reduction of particulate organic carbon and diffusion of methane into the hypolimnion) is described as

$$r_{oxid,CH_4} = k_{oxid,CH_4} \cdot S_{CH_4} \cdot S_{O_2} \quad (20)$$

with an oxidation rate constant, k_{oxid,CH_4} . For the oxidation of 1 gC m^{-3} methane 5.33 gO m^{-3} oxygen is needed. The concentration of methane increases with a total net transformation rate dependent on the actual anaerobic mineralization rate referred to equation (19). According to the stoichiometry of the process of methanogenesis (Reichert & Schuwirth, 2010), resulting from Redfield composition, per 1 gDM m^{-3} organic matter, $1/2 \cdot a_c \text{ gC m}^{-3}$ methane is produced, where a_c is the fraction of carbon (a_c equals $0.358 \text{ gC gDM}^{-1}$ as for Redfield composition) in degradable particulate organic matter (X_s). Diffusion of methane between all boxes and gas exchange with the atmosphere are considered as well. According to Cussler (2009), molecular diffusivity of methane was set to $0.000129 \text{ m}^2 \text{ d}^{-1}$. By a comparison with the similar diffusivity of oxygen, the methane exchange velocity was set to the same as the oxygen exchange velocity, according to Schwarzenbach *et al.* (2003).

Inert fraction of organic particles

Sobek *et al.* (2009) found that the negative correlation of organic carbon burial efficiency with oxygen exposure time is stronger for lakes with significant allochthonous input, for example from land erosion. It follows that the rate of permanent sedimentation of organic

carbon is larger for allochthonous input than for autochthonous material. This leads to the implication that allochthonous organic particles are less degradable than autochthonous ones. As possible reasons, Sobek *et al.* (2009) implicated the greater age of allochthonous material, its higher degree of degradation and transformation and its richness in molecules resistant to anaerobic mineralization. These findings are supported by the fact that the phosphate concentration of Walensee is decreasing in the long term, which is not true of the inflow of organic particles, which are the main source of the annual phosphorus load. We concluded that a large fraction of these particles are only slowly degradable, because they mainly originate from allochthonous input discharged by the river Linth. Hence, the fraction of slowly degradable organic particles within allochthonous input, $f_{X_I, rivers}$, was assumed to be large (calibration resulted in a value of 0.93), whereas that of inputs from lakes (Lake Zurich, upper basin and Lake Pfäffikon), $f_{X_I, lake}$, was set to 0.2, close to the fraction of the cadavers of organisms that turns into slowly degradable material in the death process, f_p , which has the value 0.1. In the model, the slowly degradable particles are assumed not to be degraded within the observed time span and hence were considered as inert.

Sorption of inorganic phosphorus to inert particles

The higher inert fraction of organic particles that reaches Greifensee and Walensee could not solely explain the marked decrease in phosphate concentration in Walensee over the past few decades. We assumed that inorganic phosphorus, in addition to the sorption to degradable organic particles introduced by Omlin *et al.* (2001b) as the state variable $X_{PI,S}$, also adsorbs to slowly degradable organic particles while those are settling down to the sediment. Another state variable, $X_{PI,I}$, was included into the model which represents the concentration of inorganic phosphorus adsorbed to organic particles that are considered as inert and represented by the state variable X_I . The phosphorus uptake rate of inert organic particles follows the subsequent equation:

$$r_{uptake, X_I} = k_{upt, X_I} \cdot (a_{P, max, X_I} - a_{PI, I}) \cdot \frac{S_{O_2}}{K_{O_2, ads} + S_{O_2}} \cdot S_{HPO_4} \cdot X_I. \quad (21)$$

In this equation, k_{upt,X_I} represents the phosphorus uptake rate constant of X_I . The uptake rate includes a Monod-type limitation to the concentration of oxygen, S_{O_2} . It depends on the concentration of inert organic particles, X_I , the concentration of dissolved phosphate, S_{HPO_4} , and the difference between the actual fraction of inorganic phosphorus on inert organic particles, $a_{PI,I}$, and the maximal fraction, a_{P,max,X_I} . This maximal fraction was set to 0.001 gP / gDM, three times smaller than the maximal phosphorus fraction of degradable organic particles, a_{P,max,X_S} .

Additionally to these model extensions, we also considered the possibility of internal nutrient storage capacity of plankton as potential reason for observed lake nutrient concentrations lower than predicted by the model. We studied the Droop model (Droop, 1973) accounting for internal storages as a possible alternative to the Monod model. It was concluded that the two model equations are equivalent (Burmaster, 1979) for time steps larger than several days. Hence, in the considered time steps given by the monthly averaged driving forces, these processes do not play a role and the Monod model seems to be appropriate.

Table 1 summarizes all new parameters and those that have a new meaning compared to the most recent published version of the lake model (Omlin *et al.*, 2001b; Mieleitner & Reichert, 2008) and their actual values. For the description of parameters that changed their values due to automatic calibration, see Table 4. For their assumed prior distributions, see Table 2. There, also the parameters of the new error model are listed.

Data

Monthly measured profiles of physical, chemical and biological variables for Lake Zurich and Walensee were obtained from the Water Supply Authority of Zurich (Wasserversorgung Zürich (WVZ)) from 1976 to the spring of 2006. For Greifensee, monthly to daily measurements of physical, chemical and biological variables were obtained from the Aquatic Ecology Department of Eawag (Swiss Federal Institute of Aquatic Science and Technology) and the environmental agency of the canton of Zurich (Amt für Abfall, Wasser, Energie und Luft der Baudirektion des Kantons Zürich (AWEL Zürich)). For chemical and physical variables for

Greifensee, data were collected from 1985-2006. Phytoplankton data of Greifensee were available from 1987-2004, while zooplankton data were available for the years 1987 to 2006.

Information on inflows to the lakes (physical and chemical variables) and meteorological data were received directly from federal (Bundesamt für Umwelt (BAFU)) and cantonal agencies (Amt für Umweltschutz des Kantons St. Gallen (AFU St. Gallen) and AWEL Zürich) and from WVZ. Technical reports from these institutions provided insights into sampling techniques and methodological details (Gammeter *et al.*, 1996; Gammeter *et al.*, 1997; Gammeter & Forster, 2002). A detailed description of the data availability, compilation and processing can be found in Appendix S1.

A comparison of the nutrient input loads (bioavailable nitrogen and phosphorus) per lake surface area from inflowing rivers, waste water treatment plants (WWTPs) and wet deposition is shown in Fig. 4. In our model formulation, bioavailable nitrogen and phosphorus represent the sum of the dissolved compounds (nitrate, ammonium and phosphate, respectively) and the N- and P-fraction of the non-inert part ($1 - f_{X_I, rivers}$ or $1 - f_{X_I, lake}$) of the inputs of organic material. It became obvious that for all three lakes the input load of bioavailable phosphorus decreased considerably during the measurement period. This is particularly true of Lake Zurich and Walensee, and for the period 1976 to 1987. This is due to the introduction of phosphate-free detergents, restrictions in the use of phosphate fertilizers and the connection of more households to WWTPs. The introduction of phosphate precipitation in WWTPs and the ultimate prohibition of detergents containing phosphate in 1986 also resulted in a decline. Exceptions were the years around 2001, when some WWTPs exported higher phosphate loads to the lakes. Over the same time period the mean nitrogen load did not change significantly. A comparison of the inputs to the three is broadly consistent with their trophic status. For most years, the bioavailable phosphorus and nitrogen loads per surface area of Greifensee were higher than for Lake Zurich and Walensee, for which the loads were similar. After the significant decrease in phosphorus input into Walensee, the phosphorus load to Lake Zurich exceeded that for the Walensee in most years.

Sensitivity Analysis

As stated by Mieleitner & Reichert (2006), the calibration of complex models with a large number of parameters is done best by an iterative procedure of sensitivity analysis, parameter estimation and identifiability analysis. A sensitivity analysis measures how strongly parameter changes influence the model output. A preliminary sensitivity analysis can help to identify potential parameters that must be estimated. After estimation, identifiability analysis can be used to check for problems in producing a unique estimate. The set of parameters to be estimated can then be updated according to a new sensitivity analysis. Finally, a posterior sensitivity analysis can serve as a reassessment of the subset of fitted parameters and model properties.

We conducted sensitivity analyses for the model results of the three lakes separately, as well as jointly for all lakes. The analyses were done according to Brun *et al.* (2001) and Omlin *et al.* (2001a) as local sensitivity analyses using linear error propagation as a measure of the contribution of each parameter to the model output error. The overall sensitivity measure $\delta_{\theta_j}^{msqr}$ is calculated as

$$\delta_{\theta_j}^{msqr}(\boldsymbol{\theta}) = \sqrt{\frac{1}{n_L} \sum_L \left(\frac{\Delta\theta_j}{sc_{y_M^L}} \cdot \frac{\partial y_M^L(\mathbf{x}, \boldsymbol{\theta})}{\partial \theta_j} \right)^2} \quad (22)$$

using the square root of the average of the squared derivatives of all model outputs, y_M^L , of the layout L (of length n_L) with respect to the parameter θ_j times the ratio of the uncertainty range, $\Delta\theta_j$, of the parameter θ_j and the scaling factor, $sc_{y_M^L}$. The layout L characterizes the model output, i.e. which output variables are considered at which point of the output dimension (e.g. time/space). In our case the layout consists of combinations of the five output variables phytoplankton, zooplankton, oxygen, nitrate and phosphate, a (monthly) date and a specification of the compartment (epilimnion or hypolimnion). The chosen layout mostly equals the description of available measurements.

For local sensitivity analyses, the results differ for each combination of parameter values, $\boldsymbol{\theta}$. We will show the results of the posterior sensitivity analysis conducted for the best parameter estimate found during model calibration in the next section. The model results for

this point in the parameter space served as scaling factor, $sc_{y_M^L}$, to get non-dimensional sensitivity measures and to make the influences of parameters on different output variables with different units comparable to each other. The uncertainty of the parameters was chosen according to Omlin *et al.* (2001a) by classifying all parameters into three groups of relative uncertainty (accurately known parameters = class 1 = 5%; stoichiometric parameters/specific growth rates = class 2 = 20%; most kinetic/poorly known parameters = class 3 = 50%). We did not group the parameters into those able to be fitted or not in order to compare the sensitivity of all parameters. Nevertheless, this distinction influenced our choice of calibration parameters. We also analysed the sensitivity of the model to the parameters $a_{P, inflow, lake}$, $f_{X_I, rivers}$ and $f_{X_I, lake}$ which are related to input fluxes, but are new or have a new meaning due to model extensions. Beside those, we did not include input fluxes in the sensitivity analysis, as inflow parameters did not seem to be meaningful to calibrate.

Model Calibration

Manual calibration of simulation models by experts in the presence of bias in model outputs has often been judged superior to automatic calibration, as experts take a more “holistic” view of the quality of the fit and emphasize certain characteristic patterns rather than merely minimizing the average deviation of model results from observations (Boyle *et al.*, 2000). However, for computationally demanding models with high-dimensional parameter and output spaces, manual calibration is almost impossible and a more systematic procedure is required. As it is difficult to formalize and automate the weighting process of multiple criteria carried out by experts during manual calibration, the use of multi-objective optimization techniques has been suggested to determine a Pareto-set of good solutions rather than trying to find the optimal one (Gupta *et al.*, 1998; Yapo *et al.*, 1998; Madsen, 2000; Madsen *et al.*, 2002; Gupta *et al.*, 2003; Boyle *et al.*, 2003). Reichert & Schuwirth (2012) recently adapted a statistical bias description technique (Craig *et al.*, 1996; Craig *et al.*, 2001; Kennedy & O’Hagan, 2001; Higdon *et al.*, 2004; Bayarri *et al.*, 2007) to provide a statistical basis for an estimation procedure that attempts to imitate and systematize expert calibration while considering systematic model errors, a

particularly typical phenomenon in environmental modelling. This technique is based on prior specification of the magnitude of “acceptable bias” in different model variables to take into account the expert's choice of relative importance of fit objectives. An approximation to the technique of Reichert & Schuwirth (2012) for computationally demanding models has been developed by Dietzel & Reichert (2012) and was applied in this paper.

This technique is based on describing system observations as the sum of the output of the deterministic model, bias (systematic errors) and observation error to account explicitly for the contribution of bias in model results:

$$\mathbf{Y}_M^L(\mathbf{x}, \boldsymbol{\theta}, \boldsymbol{\psi}, \boldsymbol{\xi}) = \mathbf{y}_M^L(\mathbf{x}, \boldsymbol{\theta}) + \mathbf{B}_M^L(\mathbf{x}, \boldsymbol{\xi}) + \mathbf{E}^L(\boldsymbol{\psi}) \quad (23)$$

where $\mathbf{Y}_M^L$ is the vector of random variables representing the observations as described by the model, M , at the layout, L , that defines the output variables and the time points and locations at which they are observed or evaluated. $\mathbf{Y}_M^L$ depends on the external influence factors, $\mathbf{x}$, unknown model parameters, $\boldsymbol{\theta}$, and additional parameters, $\boldsymbol{\psi}$ and $\boldsymbol{\xi}$, of the error terms. It is composed of the deterministic function $\mathbf{y}_M^L(\mathbf{x}, \boldsymbol{\theta})$, representing our knowledge of the system response (i.e. the output of our model), of the random process $\mathbf{B}_M^L(\mathbf{x}, \boldsymbol{\xi})$, expressing our knowledge of model bias depending on external inputs and additional parameters and of $\mathbf{E}^L(\boldsymbol{\psi})$, a vector of random variables that represents the observation error, which may also depend on additional parameters. Note that when propagating the appropriate parameter distribution (either prior or posterior, depending on which output distribution we are interested in) the representation (23) allows us to distinguish the random variables representing our knowledge of the true state of the system, $\mathbf{y}_M^L + \mathbf{B}_M^L$, from the random variable representing observations, $\mathbf{Y}_M^L$, including observation errors.

Under normality assumptions for both the bias and the observation error, and after integrating out the bias, we obtain the likelihood function:

$$f_{\mathbf{Y}_M^L | \boldsymbol{\theta}, \boldsymbol{\psi}, \boldsymbol{\xi}}(\mathbf{y}^L | \boldsymbol{\theta}, \boldsymbol{\psi}, \boldsymbol{\xi}, \mathbf{x}) = \frac{1}{\sqrt{2\pi}^{n_L}} \frac{1}{\sqrt{\det(\boldsymbol{\Sigma}_{\mathbf{E}^L} + \boldsymbol{\Sigma}_{\mathbf{B}_M^L})}} \cdot \exp\left(-\frac{1}{2}[\mathbf{y}^L - \mathbf{y}_M^L(\mathbf{x}, \boldsymbol{\theta})]^T (\boldsymbol{\Sigma}_{\mathbf{E}^L} + \boldsymbol{\Sigma}_{\mathbf{B}_M^L})^{-1} [\mathbf{y}^L - \mathbf{y}_M^L(\mathbf{x}, \boldsymbol{\theta})]\right), \quad (24)$$

where $\Sigma_{\mathbf{E}^L}$ and $\Sigma_{\mathbf{B}_M^L}$ are the variance-covariance matrices of observation error and bias, respectively. The posterior of the parameters is then given by:

$$f_{\boldsymbol{\theta}, \boldsymbol{\psi}, \boldsymbol{\xi}}(\boldsymbol{\theta}, \boldsymbol{\psi}, \boldsymbol{\xi} | \mathbf{y}^L, \mathbf{x}) \propto \frac{f_{\boldsymbol{\theta}, \boldsymbol{\psi}, \boldsymbol{\xi}}(\boldsymbol{\theta}, \boldsymbol{\psi}, \boldsymbol{\xi})}{\sqrt{\det(\Sigma_{\mathbf{E}^L} + \Sigma_{\mathbf{B}_M^L})}} \cdot \exp\left(-\frac{1}{2}[\mathbf{y}^L - \mathbf{y}_M^L(\mathbf{x}, \boldsymbol{\theta})]^T (\Sigma_{\mathbf{E}^L} + \Sigma_{\mathbf{B}_M^L})^{-1} [\mathbf{y}^L - \mathbf{y}_M^L(\mathbf{x}, \boldsymbol{\theta})]\right), \quad (25)$$

where $f_{\boldsymbol{\theta}, \boldsymbol{\psi}, \boldsymbol{\xi}}(\boldsymbol{\theta}, \boldsymbol{\psi}, \boldsymbol{\xi})$ represents the prior distribution of the parameters $\boldsymbol{\theta}$, $\boldsymbol{\psi}$ and $\boldsymbol{\xi}$ (see Reichert & Schuwirth (2012) for more details). This posterior is not much more difficult to maximize than another objective function used in other calibration techniques (there are a few additional parameters in $\Sigma_{\mathbf{B}_M^L}$). As described in Dietzel & Reichert (2012), we use a Box-Cox transformation (Box & Cox, 1964) of model results and data (with $\lambda_1 = 0.5$ and $\lambda_2 = 0$) to account for heteroscedasticity, we derive a normal approximation to the posterior and we use linearized error propagation for deriving the posteriors of parameters and model results.

After identifying major calibration problems by manual calibration and improving the model as described above (Model extensions) to reduce these problems, this technique was applied to solve the calibration problem and to estimate uncertainties in model output due to parameter uncertainty, structural uncertainty and observation error. The identifiability problem between deterministic model output and bias was addressed by specifying a prior with a mean of zero for the bias and a prior for its standard deviation which favours a small value. This prior was parameterized by an exponential distribution with different means for different observed substances or organisms. This formalizes the preference for a small bias, but allows different magnitudes of bias for different state variables. For the measurement error, a lognormal prior distribution for its standard deviation was chosen, representing our uncertainty about the amount of observation error in each output variable. The prior distributions of all calibrated model parameters, as well as the parameters of the error model, are summarized in Table 2. The modes of the distributions were fixed approximately at the previously assumed model parameter value. The correlation length of the bias was fixed to a little under two months. Due to the use of Box-Cox transformation, the parameters of the error model are expressed in transformed units (as shown in Table 2). The parameter $f_{X_1, rivers}$, referring to a fraction, was

transformed by an arctan function to keep it within the interval [0,1]. In general, most influential and least known parameters were chosen to be calibrated, while trying to keep the calibration and identifiability problem as small as possible. The mixing parameters were not included in the automatic calibration, because they were already manually calibrated to the aggregated values of the temperatures in epi- and hypolimnion. The respiration rate constants were not included, as it had been found previously that growth and respiration rate constants show a large collinearity and are hence non-identifiable when calibrated jointly (Omlin *et al.*, 2001a). The very influential parameter K_{Feed} was used for calibration, whereas the parameter $K_{I,ALG}$ was excluded, because it was found to be non-identifiable in earlier studies (Mieleitner & Reichert, 2006). Stoichiometric parameters were not included either, as it was assumed that prior knowledge was the more reliable source of information than the fit of a lake model that could lead to unrealistic values. A normal approximation to the posterior was calculated by first estimating the mean and covariance matrix by importance sampling from a uniform ball around the maximum, followed by importance sampling using the normal distribution with this mean and covariance matrix as a new sampling distribution. The mean and covariance matrix of this second importance sampling are unbiased estimates of mean and covariance matrix of the posterior and were used to characterize the approximating normal distribution. This technique has proved to be the most robust for addressing the challenging problem of approximating a potentially complex shape of the posterior by a normal distribution in Dietzel & Reichert (2012).

Parameter estimation was done for 9 years for Greifensee (1987-1995) and 20 years for Lake Zurich and Walensee (1976-1995). To assess the predictive capability of the model, simulations were done also for the following 10 years without re-calibration.

Model Implementation

As previously, the model was implemented using the computer program AQUASIM for simulation and identification of aquatic systems (Reichert, 1994; <http://www.aquasim.eawag.ch>). Initial model calibration was done manually; sensitivity analyses and calibrations in later stages were performed by coupling AQUASIM to UNCSIM, a tool for statistical inference and sensitivity, identifiability and uncertainty analysis with arbitrary

simulation programs (Reichert, 2005). The uncertainty analysis was done by coupling AQUASIM to the statistics software R (<http://www.r-project.org/>).

Results

Sensitivity Analysis

Table 3 shows the sensitivity ranking of all model parameters including the input parameters $a_{P,inflow,lake}$, $f_{X_I,rivers}$ and $f_{X_I,lake}$. It reflects, in linear approximation, the amount of influence of each parameter, θ_j , within its uncertainty range, $\Delta\theta_j$, (see above Sensitivity Analysis for the choice of the uncertainty ranges of the parameters) on all the model results of the five output variables phytoplankton, zooplankton, oxygen, nitrate and phosphate in the two water compartments of the three lakes. Larger values of $\delta_{\theta_j}^{msqr}$ [equation (22)] indicate a larger change in the model results due to a change in the respective parameter. An explanation of the parameter names can be found in Tables 1 and 2, as well as in Omlin *et al.* (2001b) and Mieleitner & Reichert (2006).

It becomes obvious that the parameters describing the mixing of the three lakes in summer and winter (for example $K_{z,summer,gre}$ and $K_{z,winter,zh}$, as well as the temperature difference at which the mixing switches from winter to summer conditions, $tempdif_{gre}$, $tempdif_{zh}$ and $tempdif_{wal}$) are very influential. This is a meaningful result as those parameters influence the distribution of the concentrations of all output variables between the two lake model compartments and the onset of stratification in spring is a very crucial determinant of the initiation of phytoplankton growth. As mentioned above, these parameters were calibrated manually to the measured temperatures. Also influential were kinetic parameters describing the growth, death and respiration of the phyto- and zooplankton. The respiration rate coefficients contributed less to model output changes than did the growth and death rates of the same plankton community. The parameters K_{Feed} and $K_{I,ALG}$ were strongly influential, as well as

some of the stoichiometric parameters, such as the factor converting zooplankton dry mass to wet mass, w_{ZOO} , and the maximum phosphorus content of newly produced phytoplankton, $b_{P,max}$. The results of the joint sensitivity analysis (Table 3) were mostly in agreement with the results of the lake-specific analyses. More information about the lake-specific sensitivity analyses can be found in Appendix S2 and Table S1.

Model Calibration

In the following, the model outputs for phyto-, zooplankton, nitrate, phosphate and oxygen are compared to data from the three lakes over the whole simulation period (19/30 years). For each output variable we chose to depict the results of the compartment that showed the strongest dynamics (hypolimnion for oxygen, epilimnion for the others). The model results are the medians of the posterior (see below a discussion of uncertainty) calculated by linearized propagation of a normal approximation to the posterior of the parameters, as summarized above in Methods and described in detail by Dietzel & Reichert, 2012). The posterior of the parameters was calculated based on a calibration period of 9 and 20 years. In general, we tried to calibrate as few parameters as possible, to not increase the identifiability problem, but as many parameters as needed to get reasonable results. Table 4 summarizes all parameter values changed due to automatic calibration, with the best estimates of their values representing the maximum of the (non-approximated) posterior distribution. For the remaining parameter values, we refer to Omlin *et al.* (2001b), Mieleitner & Reichert (2006), Mieleitner & Reichert (2008) and Table 1. Except for the mixing coefficients, the thicknesses of the sediment boxes and sediment mineralization rate constants, as well as lake-specific zooplankton death rates and gas exchange velocities differing by wind speeds, these parameter values were kept the same for all three lakes.

Compared to Mieleitner & Reichert (2008) some parameter values changed during calibration. The growth rate coefficient of zooplankton took a new meaning (and unit) due to the changes in model formulation (see Model extensions). For this reason, the change from $0.4 \text{ DM}^{-1}\text{m}^3\text{d}^{-1}$ to 1.27d^{-1} only reflects the change in model structure. The specific growth rate of phytoplankton decreased slightly from 1.6 d^{-1} to 1.51 d^{-1} . Except for Greifensee, the death rate

coefficients of zooplankton decreased somewhat, while the order of magnitude stayed the same. The lowest death rate coefficient was still found for Walensee and the highest for Greifensee. This agrees with expected fish densities across the eutrophication gradient of these lakes. Mineralization rate coefficients in the sediment are parameters that can be expected to vary because they aggregate effects of bacterial density, growth rate and geometric resolution of the sediment. Except for the aerobic mineralization rate coefficient of Greifensee, all mineralization rate constants increased by 1-2 orders of magnitude. Largest increases were found for the anaerobic mineralization and for Walensee. As before, Greifensee showed the greatest mineralization rate coefficients and Walensee the smallest. This is in agreement with our perception of the bacterial abundance at the different trophic levels. Compared to the model calibration for Lake Zurich only (see Dietzel & Reichert, 2012), the results of the calibrated parameter values showed some similarities. The parameters of the error model in particular were in good agreement with the joint calibration results. For the mineralization rates of Lake Zurich, the lake-specific calibration led to smaller values, but to the same order of magnitude and the same succession of the three mineralization processes. As those parameters are lake-specific parameters, they should result in very similar values during the different calibrations. The divergences demonstrate the difficulty and complexity of the calibration problem. During calibration of Lake Zurich only, the growth rate of phytoplankton was found to be smaller than during joint calibration of all lakes, while the zooplankton growth rate was larger. This can result from differences in the composition of plankton communities between lakes that effect growth rates. Also, the divergences can again be an indication for the complexity of the calibration problem or for an identifiability problem.

Greifensee

For a comparison of data and model results, data points (markers) only have to be compared with the dashed line during the calibration period, which becomes a bold line during validation and represents the output of the deterministic model at the maximum of the approximate posterior distribution (Fig. 5). The other lines and areas are discussed below. For a more direct comparison of data and best simulation results gained by calibration, as well as

results for compartments not shown herein, see Fig. S2 in Appendix S3.

For most state variables the modelled concentrations were in good agreement with the measured concentrations. The long-term trends in plankton and phosphate concentrations were well represented by the model, whereas the modelled annual patterns of plankton showed a less dynamic behaviour than the measurements. Year-to-year variability of plankton was less pronounced in the calculations. Additionally, calculated zooplankton concentrations were still too low, as well as phosphate concentrations in some years. Nitrate and oxygen concentrations in the compartment shown tended to be too high; the model was not always able to show the anoxic conditions in summer.

Lake Zurich

Even better results are found for the mesotrophic Lake Zurich (Fig. 6). The long-term trends of plankton, nutrients and oxygen were well represented by the model. Best results were achieved for oxygen and phosphate. For the latter, the model results captured the decreasing long-term trend very well. Nitrate matched the data less well, as the model indicated higher concentrations and less annual dynamics in the epilimnion than the measurements. More results for Lake Zurich can be found in Fig. S3 in Appendix S3.

Walensee

In the progress of calibration, the results for Walensee showed the greatest discrepancies with the data. This was especially true for phosphate concentration that did not represent the significant decline apparent in the data. Introducing the additional sorption process, which decreased the actual phosphate load, reduced the problem. After intensive calibration studies, the calculations agreed with the data about as well as for the other lakes (Fig. 7). In general, the model captured the measured long-term trends. However, in Walensee the oxygen concentration in the hypolimnion also tended to be too high. Modelled nitrate concentrations showed similar problems as for Lake Zurich, concentrations were too high and not so dynamic as the data. Phosphate concentration showed the decreasing trend over time,

but the decline was rather too rapid in the first years. See Fig. S4 in Appendix S3 for a comparison of epilimnion and hypolimnion results of Walensee.

All Lakes

In general, most output variables showed a good agreement with the measured concentrations. The long-term trends, where present, of all output variables were reproduced well by the model. This was especially obvious in the temporal changes in phosphate and plankton, in particular for Lake Zurich and Walensee. Recurring problems for all three lakes included annual dynamics of some of the output variables that were too smooth or even out-of-phase, as for the zooplankton in the hypolimnion of Lake Zurich (Appendix S3). Furthermore, concentrations of nitrogen and oxygen were too high and plankton too low (especially zooplankton). These are persistent problems while applying BELAMO. Overall, the results indicate only a coarse representation of the plankton dynamics in these lakes but a more detailed representation of the biogeochemistry.

Uncertainty Analysis

The dark shaded areas in the plots shown in Figs. 5-7 represent the 95% credibility intervals of our posterior knowledge of the true states (marginal posterior distributions of the components of $\mathbf{y}_M^L + \mathbf{B}_M^L$ in equation (23)) of the variables shown in the different plots. The light shaded extensions of these areas represent our uncertainty about new observations (including observation error).

The results demonstrate that our knowledge of the true state was much more accurate during the calibration period (up to 1995) than during the prediction period (after 1995) (Figs. 5-7). This follows from the information about the bias gained during the calibration period due to comparison with data. For the prediction period, we lost information about the direction and the absolute amount of bias at each time point, but we kept knowledge about the uncertainty due to bias. This led to larger credibility intervals and to merged results of the deterministic model and the median of the posterior of model results plus bias during the prediction period.

The model was significantly more accurate for the chemical variables than for phyto- and zooplankton. A comparison of the light shaded extensions with the dark shaded areas indicates that the observation error can be neglected compared to the bias for all chemical variables, whereas it led to increased uncertainty for observations of phyto- and zooplankton.

As the objective of this study was a joint calibration of the same model to all investigated lakes, the same parameters for the bias were applied to all lakes. This implies that the bias considers not only bias within the time series of a single lake, but also across lakes.

Nutrient Mass Fluxes

Nutrient fluxes for the three lakes were calculated with the calibrated version of BELAMO and encompass the dissolved nutrients as well as their fractions in degradable organic material (Figs. 8 & 9). Within the model, the bioavailable parts of the nutrients were represented by the state variables of their dissolved compounds (S_{HPO_4} ; $S_{NO_3} + S_{NH_4}$) and their fractions in degradable organic material ($X_{P,S}$ (the variable fraction of phosphorus within degradable organic particles X_S), $X_{PI,S}$ (see Model extensions), $X_{P,ALG}$ (the variable fraction of phosphorus in phytoplankton X_{ALG}), the constant fraction of phosphorus in X_{ZOO} and the constant fractions of nitrogen in X_{ALG} , X_{ZOO} and X_S). Figs. 8 & 9 depict the main transfer processes as input, output, sedimentation, mineralization and subsequent release of the dissolved compounds to the water phase, diffusion between water and sediment and denitrification in case of nitrogen. The accumulation in the water phase shows the calculated accumulation in the model. It did not completely match the difference between input and output fluxes in all cases. Those errors are below 5% and within the range of numerical inaccuracies due to non-continuous model outputs used for the calculation of fluxes. Fig. 8 visualizes the importance of denitrification that increases with increasing nutrient richness. For oligotrophic Walensee only slightly more than 10% of the nitrogen input was denitrified, for mesotrophic Lake Zurich this fraction amounted to around 35% and for eutrophic Greifensee to even more than 55%.

Discussion

We discuss two major aspects of this study. In the first section, we discuss what we have learned about causes, reduction and dealing with remaining systematic errors. In the second, we elaborate on relevant ecological processes in the studied lakes.

Bias

As systematic errors are the main concern in any predictive modelling, we discuss the following three aspects of systematic errors in the following section: causes of bias, reduction of bias, and consideration of bias for model calibration and prediction. We then discuss biogeochemical implications and findings resulting from the model presented.

Causes of Bias

Systematic deviations of model outputs from observations are primarily caused by the simplified description of reality by the model. Main problems are neglected or unknown external influence factors and the use of a simplified model structure, including potential simplifications by aggregation (in time, space or state variables; by the model or by sampling procedures) and by the choice and parameterization of processes considered in the model.

A first major problem in our current simulations was spatial aggregation. For computational reasons, the model divides the lake water column into two mixed boxes (with constant volumes) only, the epilimnion and the hypolimnion. This leads to a poorer representation of vertical mixing processes than in the 1d model used earlier for shorter simulation periods (Omlin *et al.*, 2001b; Mieleitner & Reichert, 2006) and it neglects variations in mixing depth. In addition, both model versions neglect horizontal inhomogeneity. This problem becomes even worse, as the depth-integrated samples of zooplankton (and phytoplankton, in case of Greifensee) do not fit directly to the resolution of compartments in the lake model. Hence, the aggregated and processed data might not represent the average

concentrations in epi- and hypolimnion as described by the model compartments. The amount of bias in these cases supports the finding. The problems caused by the high spatial aggregation, might be solved by simulations with the one-dimensional model version and comparison with concentration profiles where possible.

A second problem was the aggregation of more than 100 species to only single groups of phytoplankton and zooplankton. On the one hand, this may simplify the description of nutrient fluxes (see Mieleitner & Reichert (2008) for a discussion of potential problems), but on the other hand it makes it necessary to use average kinetic characteristics and behaviours for the whole group. This does not account for the variability in species attributes and composition of the ecological community, and in particular not for the succession of dominant species within each year. Least of all, genetic adaptation or acclimatization processes of the plankton community are considered, except for changes in phosphorus content.

A further important potential source of bias was our attempt to fit jointly three lakes of different trophic status with a single model and with a minimum of lake-specific parameters over a long simulation period during which the phosphorus input changed considerably. This requires a model structure and parameterization that is considerably more universal than for describing a single lake over a shorter period. In particular, the addition of potential bias across lakes to the bias within time series of each lake obviously increases the bias. Our task of jointly modelling all lakes over such a long period of time obviously challenges the model and it is a significant result of our study to demonstrate that this is possible.

Another challenge was the use of a model with closed mass balances that describes mineralization of sedimented organic particles rather than using sediment oxygen demand and ammonia and phosphate release as external parameters, as is still done in the majority of models (Mooij *et al.*, 2010). In addition to limiting the degrees of freedom of exchange processes, this required a mineralization model for the sediment. As the different mineralization processes were described by just a single overall lake-specific mineralization rate, the microbial community was (implicitly) assumed to be constant. For example, the problems in representing the anoxia in Greifensee in some years could result from difficulties in finding adequate mineralization rates for the whole simulation time due to changes in the bacterial community which the model does not describe. The dynamics of microbial communities, changes in

bacterial abundance and adaptation processes to nutrient loads and availability of organic material, were not explicitly taken into account. The introduction of biomass of mineralizing bacteria as an additional state variable would be a meaningful extension to tackle this problem. But one has to be aware that this would also cause additional difficulties, as it increases the complexity of the model. The increased number of parameters would also increase the calibration problem, especially because the number of model output variables that can be fitted to data cannot be increased, as there are no bacteria data available.

Reduction of Bias

Although the model used in previous studies led to good simulations of all three lakes over a period of four years without significant changes in input, the model required important changes in order to be able to describe correctly the observed trends in phosphate and plankton concentrations, while still being able to represent correctly nitrate and dissolved oxygen concentration. The most important changes were (see Model extensions for more details):

- introduction of active movement of zooplankton to the epilimnion;
- improvement of the formulation of zooplankton growth to decrease the growth rate for small phytoplankton concentrations more strongly than linearly;
- improvement of the formulation of predation on zooplankton by Chaoborus similarly to zooplankton growth on phytoplankton;
- improvement of the dissolved oxygen mass balance of anaerobic mineralization by introducing methane production and subsequent re-oxidation in the water column (this process also represents the effect of mineralization by sulphate, iron oxide and manganese oxide reduction and subsequent re-oxidation);
- reduction of the biodegradability of organic particles in the inflow to decrease their release of phosphate into the lake;
- addition of sorption of phosphate to sedimenting "inert" organic particles additionally to uptake by biologically degradable organic particles.

These modifications led to a considerable reduction in bias and a reasonable representation of key features of the data. Nevertheless, significant discrepancies between model results and

data remained. These discrepancies were larger and more systematic than expected for observational errors and must be considered during the model calibration process to make it possible to get adequate uncertainty estimates of model parameters and predictions.

Consideration/Description of Bias

The chosen calibration method used a bias description approach that was originally published in the statistical literature (Craig *et al*, 1996; Craig *et al.*, 2001; Kennedy & O'Hagan, 2001; Higdon *et al.*, 2004; Bayarri *et al.*, 2007), subsequently transferred to environmental applications and linked to multi-objective model calibration (Reichert & Schuwirth, 2012), and finally approximated to make it applicable for computationally demanding models (Dietzel & Reichert, 2012). Application of this technique to our long-term lake simulations led to the consideration of important aspects that are not yet commonly addressed in environmental modelling:

- *Separation of bias and observation error*: While the bias component shows autocorrelated behaviour characteristic of structural errors, the observation error is approximately independently and normally distributed (in our application on a Box-Cox transformed scale, see Model Calibration in Methods).
- *Consideration of bias in uncertainty estimates of model parameters*: The description of the bias as an autocorrelated process (partially) solves the problem that the uncertainty of model parameters is underestimated with an independent error model that does not account for bias.
- *Consideration of bias for model predictions*: The chosen technique allowed us to predict the current state of knowledge of the true model variables as well as about (future) observations. It naturally leads to narrow prediction credibility intervals during the calibration period, where the observations constrain the model output, and to (much) wider intervals during the prediction period. This is an important aspect that is not included in most calibration techniques currently applied in environmental modelling. However, consideration of bias for predictions is based on the assumption that model and bias structure do not change. This is obviously a strong assumption that can hardly be avoided for the bias component, as it describes the deviations that cannot easily be

described by a mechanistic model.

- *Bias of a joint simulation:* In our application, systematic errors were even increased by the objective of jointly describing three lakes of different trophic status and varying input loads over a long time period. This requires a very high degree of universality of the model. Such a high degree of universality is a desired property of a model as it increases our confidence of model predictions under changes in driving forces; but it makes calibration even more challenging.

Biogeochemical and Ecological Processes

This project with the lake model BELAMO provided some insights into the biogeochemistry and ecology of the Swiss lakes Greifensee, Lake Zurich and Walensee. The comparison of model results with measurements indicated a more complex than linear dependence of zooplankton grazing on phytoplankton concentration when phytoplankton concentrations are low. This functional description has similarities to a Holling-type III response (Holling, 1959a; Holling, 1959b). The heterogeneity of plankton abundance is a possible explanation for that. Furthermore, the upwards movement of zooplankton seems to be an important process impacting the grazing of zooplankton on phytoplankton and the distribution of zooplankton between epi- and hypolimnion. A comparison of the three lakes indicates the influence of insect larvae on zooplankton concentration in Greifensee, not present in Lake Zurich and Walensee. Additionally, the different calibration results (see Table 4 for calibrated parameter values) for the death rates of zooplankton in the three lakes give evidence for an increasing predation pressure by fish on zooplankton with increasing nutrient richness across the trophic gradient. The trophic status of the lakes is also the reason for the different importance of the three mineralization processes. When comparing the lake-specific sensitivity analyses (see results of lake-specific sensitivity analyses, Appendix S2), it becomes obvious that, for Walensee, aerobic mineralization is the dominant mineralization process. For Lake Zurich, the importance of anoxic mineralization is greater than in Walensee, whereas for Greifensee anaerobic mineralization also has an increased influence. These findings are supported by the calculated nitrogen mass balances, which indicated that the fraction of denitrification was

largest for eutrophic Greifensee and smallest for oligotrophic Walensee.

Moreover, the model study supports the assumptions that allochthonous organic particles are less degradable than autochthonous and that the sorption of inorganic phosphorus to slowly degrading organic particles can be an important loss process for nutrients.

In conclusion, despite the large simplifications in system description, BELAMO represented the main aspects of the biogeochemistry and, rather more coarsely, the ecological dynamics of plankton in the study lakes. With that we are able to apply the model also to other lakes with similar characteristics as the application cases shown herein. Further work could concentrate on comparing different models applied to the same lakes as well as the same model applied to an extended range of lakes, including lakes from other climate zones. This would be possible by changing the mixing parameters in the model, according to climate. In case that the climate is not expected to change significantly in the future, predictions about the future state of a lake can also be performed. To model the effects of climate change, BELAMO would have to be coupled to a hydrodynamic model.

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1132 **The Supporting Information to this manuscript contain:**

1133 Fig. S1. The dependency of zooplankton grazing on phytoplankton concentration according to
1134 equation (11).

1135 Appendix S1. Data compilation and processing.

1136 Appendix S2. Lake-specific sensitivity analysis.

1137 Table S1. Results of the lake-specific sensitivity analyses.

1138 Appendix S3: Results – Model calibration.

1139 Fig. S2. Simulation results for Greifensee for the years 1987-2005.

1140 Fig. S3. Simulation results for Lake Zurich for the years 1976-2005.

1141 Fig. S4. Simulation results for Walensee for the years 1976-2005.

Tables

Table 1: Parameters that were newly introduced into the model or have different values compared to the most recently published version of BELAMO (in alphabetical order). Lake-specific parameters adjusted to temperature measurements (WVZ, AWEL Zürich) are indicated by "*".

Name (Unit)	Value	Description
$a_{P, inflow, lake}$	0.0056	Mass fraction of phosphorus in organic material from lakes; < Redfield, accounting for phosphate limitation of phytopl. in lakes
a_{P, max, X_I}	0.001	Maximum mass fraction of phosphate adsorbed to inert organic material
a_{P, max, X_S}	0.004	Maximum mass fraction of phosphate adsorbed to degradable organic material
$b_{P, min}$	0.0025	Minimum phosphorus content of newly produced phytoplankton
$D_{CH_4} (m^2 d^{-1})$	0.000129	Molecular diffusivity of methane
f_{sol}	0.5	Dissolved fraction of phosphorus from excretion and sloppy feeding
$f_{X_I, lake}$	0.2	Inert fraction of autochthonous organic particles
$h_{epi} (m) (gre/wal/zh)$	5/10/10	Thickness of epilimnion (hypolimnion changed accordingly)
$K_{ALG, ZOO} (gDM m^{-3})$	0.8	Half-saturation phytoplankton concentration for zooplankton growth
$K_{Feed} (gDM m^{-3})$	0.97	Threshold phytoplankton concentration when zooplankton feeding switches to Monod limitation
$K_{Feed, ZOO, Dipt} (gDM m^{-3})$	0.15	Threshold zooplankton concentration when diptera feeding switches to linear dependence
$K_{NO_3, miner} (gN m^{-3})$	0.02	Half-saturation nitrate concentration for anoxic mineralization; Leads to a sharper transition between anoxic and anaerobic miner.
$K_{O_2, miner} (gO m^{-3})$	0.1	Half-saturation oxygen concentration for aerobic mineralization; Leads to a sharper transition between aerobic and anoxic miner.
$k_{oxid, CH_4} (m^3 gO^{-1} d^{-1})$	0.04	Reaction velocity of methane oxidation
$k_{resp, ZOO, T_0} (d^{-1})$	0.01	Respiration rate coefficient of zooplankton; more realistic including <i>Planktothrix rubescens</i>
$k_{upt, X_I} (m^3 gDM^{-1} d^{-1})$	30	Maximum uptake rate of phosphate uptake on inert particles
$K_{z, summer} / K_{z, winter} (m^2 d^{-1})$	*	Coefficient of vertical turbulent diffusion in the metalimnion
$P_{NH_4, ALG}$	10	Preference factor of phytoplankton growth on ammonium
tempdif (°C)	*	Temperature difference between epi- and hypolimnion; Switching between summer and winter mixing
$V_{CH_4, atm} (m d^{-1}) (gre/wal/zh)$	0.5/3/1	Methane exchange velocity with atmosphere, according to oxygen
$V_{O_2, atm} (m d^{-1}) (gre/wal/zh)$	0.5/3/1	Oxygen exchange velocity with atmosphere, differing by specific wind speed
$V_{sed, ALG} (m d^{-1})$	0.1	Sedimentation velocity of phytoplankton; better approximation for aggregated plankton model
$V_{up, ZOO} (m d^{-1})$	5	Upwards velocity of zooplankton

Table 2: Description and prior marginals of the calibrated parameters of the deterministic model and the error model.

Name	Unit	Distribution	Mean	StDev	Description
$f_{X_I, rivers}$ (transformed)	-	Normal	2	1	Inert fraction of allochthonous organic particles
k_{death, ALG, T_0}	d^{-1}	Lognormal	0.0721	0.05	Death rate of phytoplankton at reference temperature
$k_{death, ZOO, T_0, gre}$	d^{-1}	Lognormal	0.0675	0.05	Death rate of zooplankton at reference temperature (Greifensee)
$k_{death, ZOO, T_0, wal}$	d^{-1}	Lognormal	0.0432	0.05	Death rate of zooplankton at reference temperature (Walensee)
$k_{death, ZOO, T_0, zh}$	d^{-1}	Lognormal	0.0675	0.05	Death rate of zooplankton at reference temperature (Lake Zurich)
K_{Feed}	$gDM\ m^{-3}$	Lognormal	0.295	0.3	Threshold phytoplankton concentration when zooplankton feeding switches to Monod limit.
k_{gro, ALG, T_0, I_0}	d^{-1}	Lognormal	1.79	0.5	Growth rate of phytoplankton at reference temp./sat. light intensity
k_{gro, ZOO, T_0}	d^{-1}	Lognormal	0.397	0.25	Growth rate of zooplankton at reference temperature
$k_{miner, aero, sed, T_0, gre}$	d^{-1}	Lognormal	0.365	0.25	Aerobic mineralization rate at reference temperature (Greifensee)
$k_{miner, aero, sed, T_0, wal}$	d^{-1}	Lognormal	0.063	0.05	Aerobic mineralization rate at reference temperature (Walensee)
$k_{miner, aero, sed, T_0, zh}$	d^{-1}	Lognormal	0.295	0.3	Aerobic mineralization rate at reference temperature (Lake Zurich)
$k_{miner, anae, sed, T_0, gre}$	d^{-1}	Lognormal	0.365	0.25	Anaerobic mineralization rate at reference temperature (Greifensee)
$k_{miner, anae, sed, T_0, wal}$	d^{-1}	Lognormal	0.063	0.05	Anaerobic mineralization rate at reference temperature (Walensee)
$k_{miner, anae, sed, T_0, zh}$	d^{-1}	Lognormal	0.295	0.3	Anaerobic mineralization rate at reference temperature (Lake Zurich)
$k_{miner, anox, sed, T_0, gre}$	d^{-1}	Lognormal	0.365	0.25	Anoxic mineralization rate at reference temperature (Greifensee)
$k_{miner, anox, sed, T_0, wal}$	d^{-1}	Lognormal	0.063	0.05	Anoxic mineralization rate at reference temperature (Walensee)
$k_{miner, anox, sed, T_0, zh}$	d^{-1}	Lognormal	0.295	0.3	Anoxic mineralization rate at reference temperature (Lake Zurich)
$\sigma_{B, ALG}$	$gWM^{1/2}\ m^{-3/2}$	Exponential	0.3		Standard deviation of bias in phytoplankton
σ_{B, HPO_4}	$gP^{1/2}\ m^{-3/2}$	Exponential	0.035		Standard deviation of bias in phosphate
σ_{B, NO_3}	$gN^{1/2}\ m^{-3/2}$	Exponential	0.05		Standard deviation of bias in nitrate
σ_{B, O_2}	$gO^{1/2}\ m^{-3/2}$	Exponential	0.5		Standard deviation of bias in oxygen
$\sigma_{B, ZOO}$	$gWM^{1/2}\ m^{-3/2}$	Exponential	0.4		Standard deviation of bias in zooplankton

$\sigma_{E,ALG}$	$gWM^{1/2} m^{-3/2}$	Lognormal	0.07	0.02	Standard deviation of measurement error in phytoplankton
σ_{E,HPO_4}	$gP^{1/2} m^{-3/2}$	Lognormal	0.007	0.0002	Standard deviation of measurement error in phosphate
σ_{E,NO_3}	$gN^{1/2} m^{-3/2}$	Lognormal	0.022	0.002	Standard deviation of measurement error in nitrate
σ_{E,O_2}	$gO^{1/2} m^{-3/2}$	Lognormal	0.11	0.01	Standard deviation of measurement error in oxygen
$\sigma_{E,ZOO}$	$gWM^{1/2} m^{-3/2}$	Lognormal	0.08	0.02	Standard deviation of measurement error in zooplankton

Table 3: Results of the joint sensitivity analysis for all three lakes

Parameter	$\delta_{\theta_j}^{msqr}$	Parameter (continued)	$\delta_{\theta_j}^{msqr}$	Parameter (continued)	$\delta_{\theta_j}^{msqr}$
$K_{z,summer,gre}$	10.520	$h_{sed_1,zh}$	0.888	$\nu_{O_2,atm,gre}$	0.116
K_{Feed}	9.562	$h_{sed_1,gre}$	0.774	$K_{z,summer,wal}$	0.105
k_{gro,ALG,T_0,I_0}	7.967	$h_{sed_2,gre}$	0.756	$K_{z,winter,gre}$	0.104
$K_{z,winter,zh}$	7.024	$b_{P,min}$	0.707	D_{O_2}	0.101
w_{ZOO}	5.701	a_{P,max,X_I}	0.625	$k_{miner,anae,sed,T_0,wal}$	0.093
$K_{I,ALG}$	4.450	$\nu_{sed,ORG}$	0.571	$k_{upt,X_S,wal}$	0.066
$K_{z,summer,zh}$	4.236	c_e	0.548	$\nu_{O_2,atm,zh}$	0.062
$k_{death,ZOO,T_0,zh}$	4.159	$f_{X_I,rivers}$	0.544	$k_{miner,anae,sed,T_0,zh}$	0.057
$tempdif_{zh}$	4.059	$a_{P,inflow}$	0.463	$K_{NO_3,miner}$	0.048
k_{death,ALG,T_0}	3.891	w_{ORG}	0.427	k_{nitri,wat,T_0}	0.044
$\nu_{up,ZOO}$	3.747	$k_{miner,aero,sed,T_0,wal}$	0.360	$k_{upt,X_I,wal}$	0.043
$K_{ALG,ZOO}$	3.725	$k_{upt,X_S,gre}$	0.350	$k_{death,ZOO,T_0,wal}$	0.040
$b_{P,max}$	3.541	$h_{sed_1,wal}$	0.287	$k_{miner,aero,wat,T_0}$	0.035
k_{resp,ALG,T_0}	3.210	β_{BAC}	0.287	a_C	0.033
f_{sol}	3.143	$h_{sed_2,wal}$	0.265	p_{ALG,NH_4}	0.032
k_{gro,ZOO,T_0}	2.895	$K_{N,ALG}$	0.260	$k_{upt,X_I,gre}$	0.031
$k_{death,ZOO,T_0,gre}$	2.816	$K_{O_2,resp}$	0.247	$K_{O_2,ads}$	0.024
f_p	2.648	$k_{miner,anae,sed,T_0,gre}$	0.241	$k_{upt,X_I,zh}$	0.022
β_{ZOO}	2.534	$k_{upt,X_S,zh}$	0.235	k_{oxid,CH_4}	0.022
$tempdif_{gre}$	2.404	$K_{O_2,miner}$	0.230	k_{nitri,sed,T_0}	0.017
β_{ALG}	2.151	$K_{z,winter,wal}$	0.217	$k_{miner,anox,wat,T_0}$	0.012
k_{resp,ZOO,T_0}	2.100	$k_{miner,aero,sed,T_0,zh}$	0.207	$K_{O_2,nitri}$	0.012
$K_{HPO_4,ALG}$	1.695	a_{P,max,X_S}	0.206	$\nu_{O_2,atm,wal}$	0.012

$\nu_{sed,ALG}$	1.614	$k_{miner,anox,sed,T_0,gre}$	0.197	$k_{miner,anae,wat,T_0}$	0.011
$f_{porgpart}$	1.597	$k_{miner,aero,sed,T_0,gre}$	0.179	$\nu_{sed,INORG}$	0.009
θ	1.518	$h_{sed_2,zh}$	0.178	D_{CH_4}	0.009
$f_{X_I,lake}$	1.472	a_N	0.157	$\nu_{CH_4,atm,zh}$	0.007
$S_{HPO_4,crit}$	1.100	D_{NO_3}	0.154	$\nu_{CH_4,atm,wal}$	0.004
$tempdif_{wal}$	1.078	$k_{miner,anox,sed,T_0,zh}$	0.152	$\nu_{CH_4,atm,gre}$	0.003
$a_{P,inflow,lake}$	0.902	$k_{miner,anox,sed,T_0,wal}$	0.144		
w_{ALG}	0.894	$K_{O_2,ZOO}$	0.137		

Table 4: Estimated values of parameters used for automatic calibration.

Name (Unit)	Value	Name (Unit)	Value	Name (Unit)	Value
$f_{X_I,rivers}$ (-)	0.932	$k_{miner,aero,sed,T_0,gre}$ (d ⁻¹)	0.161	$\sigma_{B,ALG}$ (gWM ^{1/2} m ^{-3/2})	0.622
k_{death,ALG,T_0} (d ⁻¹)	0.046	$k_{miner,aero,sed,T_0,wal}$ (d ⁻¹)	0.018	σ_{B,HPO_4} (gP ^{1/2} m ^{-3/2})	0.126
$k_{death,ZOO,T_0,gre}$ (d ⁻¹)	0.119	$k_{miner,aero,sed,T_0,zh}$ (d ⁻¹)	0.116	σ_{B,NO_3} (gN ^{1/2} m ^{-3/2})	0.121
$k_{death,ZOO,T_0,wal}$ (d ⁻¹)	0.001	$k_{miner,anae,sed,T_0,gre}$ (d ⁻¹)	0.668	σ_{B,O_2} (gO ^{1/2} m ^{-3/2})	0.499
$k_{death,ZOO,T_0,zh}$ (d ⁻¹)	0.014	$k_{miner,anae,sed,T_0,wal}$ (d ⁻¹)	0.011	$\sigma_{B,ZOO}$ (gWM ^{1/2} m ^{-3/2})	1.093
K_{Feed} (gDM m ⁻³)	0.945	$k_{miner,anae,sed,T_0,zh}$ (d ⁻¹)	0.866	$\sigma_{E,ALG}$ (gWM ^{1/2} m ^{-3/2})	0.637
k_{gro,ALG,T_0,I_0} (d ⁻¹)	1.509	$k_{miner,anox,sed,T_0,gre}$ (d ⁻¹)	2.146	σ_{E,HPO_4} (gP ^{1/2} m ^{-3/2})	0.013
k_{gro,ZOO,T_0} (d ⁻¹)	1.265	$k_{miner,anox,sed,T_0,wal}$ (d ⁻¹)	0.869	σ_{E,NO_3} (gN ^{1/2} m ^{-3/2})	0.043
		$k_{miner,anox,sed,T_0,zh}$ (d ⁻¹)	1.880	σ_{E,O_2} (gO ^{1/2} m ^{-3/2})	0.210
				$\sigma_{E,ZOO}$ (gWM ^{1/2} m ^{-3/2})	0.660

Figures

Figure 1: The three lakes, their catchments including the river network, the measurement stations, cities with relevant meteorological stations and the waste water treatment plants in the study area (actual situation 2011).

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Figure 2: Structure and physical processes of the four-box version of BELAMO.

Figure 3: Biological and chemical processes taken into account in each of the model compartments of BELAMO. Some of them do not play a role in the sediment boxes and hence are not activated there.

Figure 4: Input loads of bioavailable nitrogen and phosphorus per lake surface area. Dashed, dotted and dash-dotted lines indicate measured input data, bold lines their moving averages over 12 months.

Figure 5: Phytoplankton (entire lake), zooplankton (entire lake), nitrate (epilimnion), phosphate (epilimnion) and oxygen (epilimnion) concentrations in Greifensee. Data points (markers), output of the deterministic model (long-dashed), median (solid) and 95% credibility bounds (dark grey area with dashed boundaries) of bias-corrected output and median (solid; same as for bias-corrected output) and 95% credibility bounds (dark and light grey areas with dotted boundaries) of predictions of new observations (including observation error).

Figure 6: Phytoplankton, zooplankton, nitrate and phosphate concentrations in the epilimnion and oxygen concentrations in the hypolimnion of Lake Zurich. Data points (markers), output of the deterministic model (long-dashed), median (solid) and 95%credibility bounds (dark grey area with dashed boundaries) of bias-corrected output and median (solid; same as for bias-corrected output) and 95% credibility bounds (dark and light grey areas with dotted boundaries) of predictions of new observations (including observation error).

Figure 7: Phytoplankton, zooplankton, nitrate and phosphate concentrations in the epilimnion and oxygen concentrations in the hypolimnion of Walensee. Data points (markers), output of the deterministic model (long-dashed), median (solid) and 95% credibility bounds (dark grey area with dashed boundaries) of bias-corrected output and median (solid; same as for bias-corrected output) and 95% credibility bounds (dark and light grey areas with dotted boundaries) of predictions of new observations (including observation error).

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Figure 8: Mass fluxes of bioavailable nitrogen in the water column and the sediment of Greifensee (left numbers), Lake Zurich (middle numbers) and Walensee (right numbers) in t/a (averaged over the 5 years 2001-2005) calculated with BELAMO. The errors for the overall mass balances are mostly around 1%, at most 5%.

Figure 9: Mass fluxes of bioavailable phosphorus in the water column and the sediment of Greifensee (left numbers), Lake Zurich (middle numbers) and Walensee (right numbers) in t/a (averaged over the 5 years 2001-2005) calculated with BELAMO. The errors for the overall mass balances are mostly around 1%, at most 5%.