Estimating the critical phosphorus loading of shallow lakes with the ecosystem model PCLake: Sensitivity, calibration and uncertainty

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ABSTRACT

There is a vast body of knowledge that eutrophication of lakes may cause algal blooms. Among lakes, shallow lakes are peculiar systems in that they typically can be in one of two contrasting (equilibrium) states that are self-stabilizing: a 'clear' state with submerged macrophytes or a 'turbid' state dominated by phytoplankton. Eutrophication may cause a switch from the clear to the turbid state, if the P loading exceeds a critical value. The ecological processes governing this switch are covered by the ecosystem model *PCLake*, a dynamic model of nutrient cycling and the biota in shallow lakes. Here we present an extensive analysis of the model, using a three-step procedure. (1) A sensitivity analysis revealed the key parameters for the model output. (2) These parameters were calibrated on the combined data on total phosphorus, chlorophyll-*a*, macrophytes cover and Secchi depth in over 40 lakes. This was done by a Bayesian procedure, giving a weight to each parameter setting based on its likelihood. (3) These weights were used for an uncertainty analysis, applied to the switchpoints (critical phosphorus loading levels) calculated by the model. The model was most sensitive to changes in water depth, P and N loading, retention time and lake size as external input factors, and to zooplankton growth rate, settling rates and maximum growth rates of phytoplankton and macrophytes as process parameters. The results for the 'best run' showed an acceptable agreement between model and data and classified nearly all lakes to which the model was applied correctly as either 'clear' (macrophyte-dominated) or 'turbid' (phytoplankton-dominated). The critical loading levels for a standard lake showed about a factor two uncertainty due to the variation in the posterior parameter distribution. This study calculates in one coherent analysis uncertainties in critical phosphorus loading, a parameter that is of great importance to water quality managers.

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1. Introduction

1.1. Eutrophication of lakes

Eutrophication of lakes and other surface waters is a worldwide problem (e.g. Smith et al., 1999). Some 40 years of study have led to increasing insight in the response of lake ecosystems to nutrient loading, starting with the pioneering work of Schindler (1974, 1977) on phosphorus as limiting nutrient for algal crop, and Sakamoto (1966) and Vollenweider (1968, 1975, 1982) on TP and chlorophyll models. These steady-state models were the first to use the mass balance approach to lakes. Several modifications were made to the Vollenweider model (e.g. Dillon and Rigler, 1974; Kirchner and Dillon, 1975; Jones and Bachmann, 1976; Larsen and Mercier, 1976; Reckhow, 1979; Canfield and Bachmann, 1981; and

others; see e.g. Reckhow and Chapra (1983) and Harper (1992) for overviews). All these models allowed to derive average nutrient and chlorophyll concentrations (and sometimes transparency) to P and N loading and some basic lake features of which mean depth and retention time proved to be the most important. Loading criteria, together with uncertainty bounds (Reckhow and Chapra, 1983), were derived for the classification of lakes in different trophic states (ultra-oligotrophic, oligotrophic, mesotrophic, eutrophic or hypertrophic). These states could be defined both in terms of TP, TN and chlorophyll concentrations, in terms of transparency and also in terms of characteristic species composition. Because of the limitations of static models, a.o. to predict response times to management measures and to account for the role of sediments and, later, also food web effects (e.g. Carpenter et al., 1985), dynamic models for TP and chlorophyll were developed (see overviews by Chapra and Reckhow (1983), Jørgensen (1995), Jørgensen et al. (1995), Jørgensen and Bendoricchio (2001), among others). All these models were made for more or less deep, phytoplankton-dominated lakes. Data on shallow lakes (up to several metres)

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revealed that nutrient dynamics is strongly influenced by the presence of macrophytes in these lakes (e.g. Scheffer, 1998; Jeppesen et al., 1998), as they constitute an additional pool (permanent or seasonal) for retention of nutrients and an additional link between water column and sediment. Hence, macrophyte-dominated lakes can have a high transparency and a low chlorophyll level despite a rather high nutrient loading (whereas in the traditional models, shallow lakes would end up almost inevitably as (hyper)eutrophic regardless of their loading). A high transparency is also is a key factor for the survival of submerged macrophytes (e.g. Spence, 1982; Chambers and Kalff, 1985; Jeppesen et al., 1998); hence it can be both cause and result of macrophyte dominance. These mutual relationships, besides other mechanisms, lead to the often observed non-linear behaviour of shallow lakes (Scheffer, 1998). Shallow lakes typically can be in one of two contrasting (equilibrium) states: a clear state with submerged macrophytes or a turbid state dominated by phytoplankton. Eutrophication by excess input of nutrients (phosphorus and nitrogen) may cause a switch from the clear to the turbid state, if the nutrient loading exceeds a critical value (e.g. Carpenter et al., 1992; Scheffer et al., 1993; Gunderson and Pritchard, 2002). This is generally considered as undesirable, because natural communities characterized by macrophytes and a rich fish fauna disappear and biodiversity decreases. Recovery of the clear state is difficult, as the critical loading for the switch back is often lower (hysteresis). A system of interacting ecological processes makes both states stabilize themselves (Scheffer, 1998).

These phenomena were studied extensively by means of 'minimal models' (Scheffer, 1998), but few models combine both nutrient cycles, phytoplankton and macrophytes in a dynamic way. This is the aim of the model *PCLake* (Janse, 1997, 2005), a dynamic model of nutrient cycling and biota (including phytoplankton, macrophytes and a simplified food web) in shallow lakes. The objectives of this model are to estimate the critical nutrient loading levels for this switch, both 'forward' and 'backward', to determine how these levels depend on lake features and management factors, and to identify the key processes determining the switch.

Janse et al. (2008) showed that the model can indeed be used to estimate these threshold values, and concluded that the critical loading levels depend, among others, on the water depth, lake area, retention time, type of sediment and relative area of marsh zone. The present paper concentrates on the model calibration and on the estimation of the uncertainty in the predictions due to parameter variations.

1.2. Uncertainty

Although ecosystem models are often useful tools for the study of environmental problems, they contain a great deal of uncertainty, coming from different sources (e.g. Chapra and Reckhow, 1983; Van Straten, 1986; Somlyódi and Van Straten, 1986; Beck, 1987; Hilborn and Mangel, 1997; De Blois, 2000; Jørgensen and Bendoricchio, 2001). (a) Some of the uncertainty lies in the model structure itself, as we do not know whether the model is a correct representation (in view of the objectives of the model) of the system studied. Several possible model structures might be an equally good representation of the system. (b) Another source of uncertainty are the parameter values, which often can only be estimated and/or exhibit an inherent variability because of spatial, temporal and/or species variations. (c) This problem is even enhanced if the model is to be suitable for different situations. (d) Among these parameters are also the initial conditions of the system, which might influence the results in non-linear models. (e) Finally, when model results are compared with measured data, also these data exhibit a certain level of uncertainty. So, we have to do with 'intentional' uncertainty (because of natural variability) and unintentional uncertainty (because our knowledge of the system is incomplete).

Ecological models thus typically are poorly identifiable systems, and PCLake is no exception. A compromise usually has to be found between 'physicality' (the model structure should be related to the causal mechanisms acting in the system under study) and 'identifiability' (it should be possible to estimate the unknown model parameters from available data) (Reichert and Omlin, 1997; Omlin et al., 2001). PCLake was set up in a way to remain close to the causal relationships in the lake, to meet the objective of applicability in a broad range of external factors (extrapolation). The disadvantage of this is the occurrence of many parameters which are poorly identifiable from an existing, typically limited, data set. Hence, an 'overparameterized' model was preferred over an 'overly simple' model. For this kind of models, the Bayesian approach for parameter estimation and prediction uncertainty is regarded as the most adequate (e.g. Reckhow and Chapra, 1983, p. 51; Klepper, 1997; Reichert and Omlin, 1997; Omlin and Reichert, 1999; Hilborn and Mangel, 1997), for several reasons:

- The Bayesian method can deal with *probability distributions* of parameters (and model structures), in contrast to traditional calibration where one seeks for single-point estimates.
- The method combines in the analysis prior knowledge of parameters and processes with information contained in the data. This prior knowledge replaces to some extent the (non-existing) data outside the domain of the data set.
- The approach directly yields an uncertainty analysis when used as a prediction tool.

Drawbacks of the method are a loss of accuracy, with wider (but probably more realistic) uncertainty bounds, and an increase in computational demands because many model runs are required.

Hence, we adopt the Bayesian way of model evaluation, realizing that model parameters are ill-defined, intrinsically variable entities, rather than well-defined, fixed numbers. The focus in this project is on the model predictions; the parameter values are only of intermediate interest. The main topic is how the parameter uncertainties propagate in the uncertainties of the model results and predictions, which then can be given in a probabilistic way. We follow the method previously outlined by Aldenberg et al. (1995). In brief, the so-called posterior parameter distribution is based on a combination of prior knowledge and the likelihood, a measure for the degree of fit between model and data. The likelihood is used as a weighing factor for each run (parameter combination). The resulting set of predictions is the posterior predictive distribution (which is usually narrower than the prior predictive distribution, i.e. before the calibration). In practice, the weight is based on the sum of squared residuals (differences between simulations and data) as commonly used in regression analysis (Box and Tiao, 1973/1992). The posterior parameter distribution is thus inversely proportional to the sum of squares raised to the power $n/2$, with n the number of observations. For two or more variables, the probability function can be approximated as the product of the sums-of-squares.

Prior to the likelihood calculations, however, a sensitivity analysis is needed as a first step in the model analysis, to determine which parameters have the most influence on the model results. This step is important in order to make a preselection of parameters for calibration. The parameters to focus on are the ones that are both sensitive and uncertain (Van Straten, 1986). The sensitivity analysis can be applied to both the model outputs themselves, and to the likelihood measure (or fit function). The latter set may be smaller than the first one, e.g. a parameter may have great influence in a region with low likelihood (Ratto et al., 2000).

In this paper, the PCLake model is evaluated by a method combining these three steps, viz. sensitivity analysis, calibration and
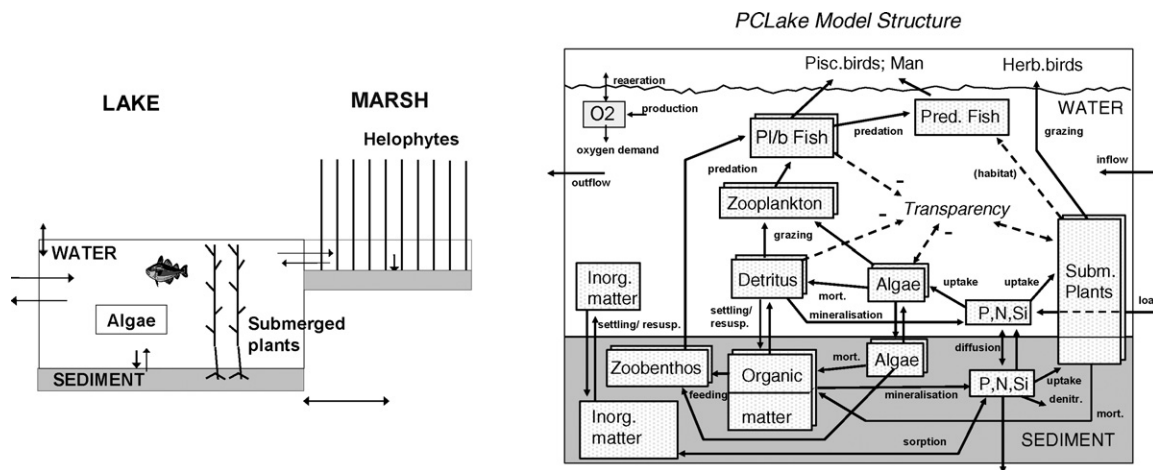
PCLake Model Structure

Fig. 1. PCLake model structure. a, overview; b, lake part.

uncertainty analysis, using a Bayesian likelihood measure based on a multi-lake data set. After this analysis, the model can be used to calculate threshold loading levels for the transition between the phytoplankton- and the vegetation-dominated state, which is an important (derived) output variable (Janse et al., 2008). The results of the analysis are applied to estimate the uncertainty in the critical loading levels due to the variation of model parameters.

2. Methods

2.1. Model description

The *PCLake* model includes what are considered as the most important ecological interactions that determine what state will prevail in a shallow lake: the turbid, algae-dominated state or the clear state dominated by macrophytes. Both bottom-up, top-down and indirect effects are included, within the general framework of closed nutrient cycles. A complete description of the model is given in Janse (2005); the main features are also described in Janse (1997). The main biotic variables are phytoplankton (cyanobacteria, diatoms and small edible algae) and submerged vegetation, the main abiotic factors are transparency and the nutrients phosphorus, nitrogen and silica (Fig. 1). The sediment top layer is included because of its intensive interaction with the lake water, and to cope with the lake's 'history'. A simplified food web is included made up of zooplankton, zoobenthos, zooplanktivorous and benthivorous fish and piscivorous fish. The lake is assumed to be homogeneous and well-mixed, but optionally, a wetland zone with marsh vegetation can be included in the model. The model calculates nutrient concentrations and fluxes, chlorophyll-*a*, transparency, phytoplankton types, vegetation coverage and fish biomass. Inputs to the model are: lake hydrology, nutrient loading, temperature and light, dimensions (lake depth and size), size of the marsh zone, sediment properties and initial conditions (Fig. 2). All model calculations were performed using the software package ACSL (Aegis, 2001).

2.2. Analysis set-up

The analysis was composed of three steps (Fig. 3):

a. sensitivity analysis (S.A.), in order to select the most sensitive parameters;
b. identification: calibration of the selected parameters on data from a multi-lake dataset;
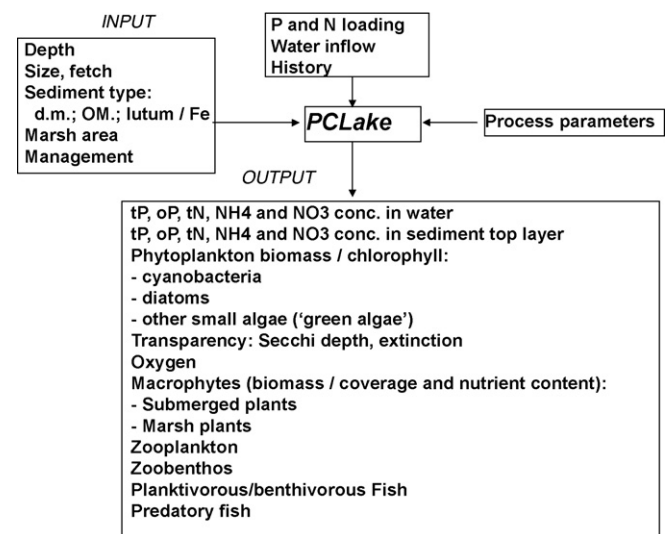

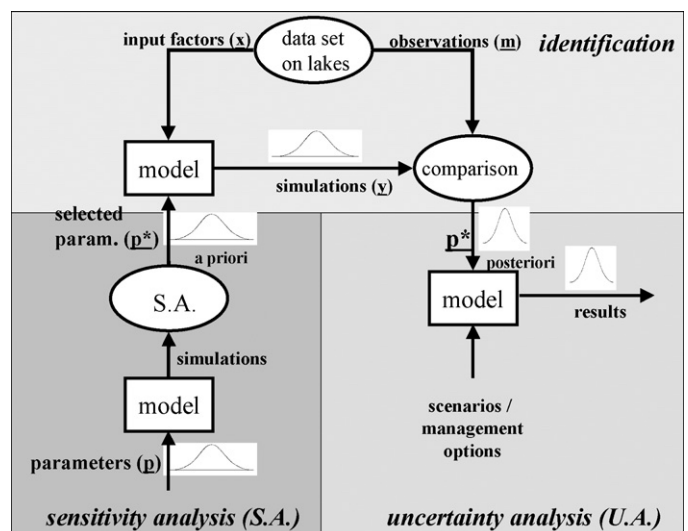Fig. 2. Overview of input and output of PCLake.

Fig. 3. Schematic view of the procedure of model analysis applied. p = distribution of all parameters, p^* = distribution of selected parameters.

c. uncertainty assessment (U.A.), determining (a posteriori) uncertainty in the predictions.

A distinction is made between input factors and model parameters (Fig. 2). Although mathematically comparable, these categories have a different meaning when using the model. *Input factors* are the 'steering buttons' of the model, they are different per case (lake, region, situation) and (in principle) manageable. The *parameters*, in contrast, describing biological or chemical processes, are assumed to be independent of the location and therefore set identical for all cases (although they may show a natural variability that is reflected in the uncertainty of the model output). A complete list of the parameters can be found in Janse (2005), p. 344 sqq.

2.3. Sensitivity analysis

This step aims at selecting the most influential parameters. Following the guidelines in Saltelli et al. (2000), a two-step approach was followed for PCLake: (a) a screening method to select the most important parameters from the over 200 parameters in the model; (b) a more quantitative global method applied to a subset of parameters. The focus is on the *global sensitivity* of the output for the different parameters p and input factors x, rather than on the local sensitivity at the default setting only.

The screening phase was performed using the Morris method (Morris, 1991; De Wit, 1997), to make a rough selection of those parameters and input factors that control most of the output variability, with a relatively low computational effort (Saltelli et al., 2000). This method gives only qualitative (ranking) rather than quantitative information on the parameters, but has the advantage that it does not rely on specific assumptions on model behaviour. The Morris method computes a number of 'samples' (r) of local sensitivity coefficients ('elementary effects'), repeated at different points in the input space and then calculates their average and standard deviation, thereby constituting a global sensitivity analysis. Based on a specification file with the minimum and maximum values for the parameters and input factors, a sample was created of size $(k+1) \cdot r$, with k the number of parameters. Every parameter can take p different values, equally divided within its range; the sample is thus drawn from a k by p grid. In this study we used $p = 8$ and $r = 15$, values that are usually sufficient for the purpose (P. Heuberger, pers. comm.). The number of runs was thus 16 times the number of parameters. The method has been applied to the main output variables of the model. The Morris analysis was repeated several times, with different seeds of the random number generator, giving rise to another sample based on the same specification file.

Besides the Morris method, the results were also analyzed by a stepwise linear regression.

A subset of parameters (and no input factors) was analyzed more quantitatively by a variance-based method, the FAST ('Fourier amplitude sensitivity test') method (Saltelli et al., 2000). This method is most suited for non-linear or non-monotonic models (or models for which this is not known beforehand). It is also called non-linear sensitivity analysis. The FAST approach is based on numerical calculations to obtain the variance of a model prediction, and the contribution of individual input factors to this variance. The basis of this calculation is a transformation that converts a multidimensional integral over the complete parameter domain to a one-dimensional integral. We used the 'extended' form of FAST, that calculates both the 'first order' (direct effects) and the 'total-order effects' (=including interactions) of the parameters, scaled to dimensionless units. The minimum number of runs needed is 65 times the number of parameters. We made use of the software package SIMLAB (EC-JRC-ISIS, 2002). The 16 selected parameters are listed in Table 1. The initial parameter ranges were

estimated from literature (among others Straškraba and Gnauck, 1985; Jørgensen et al., 1991) as well as literature on specific processes—listed in Janse (2005), and from experimental data and previous model applications on specific lakes (e.g. Janse et al., 1992). Ten other parameters were coupled to the sampled parameters in order to achieve the most reasonable parameter sets while reducing the computational demand. In particular, parameters were coupled that influence the same process (such as maximum growth rate and half-saturation value for zooplankton) or are counteracting each other (for instance maximum growth rate and respiration rate of phytoplankton) The method was applied not only to the main output variables themselves (e.g. chlorophyll-*a*), but also to the *likelihood* (goodness of fit) of these values: the degree of conformance between simulations and measurements (see next section), a combination called GSA-GLUE: Global Sensitivity Analysis and Generalized Likelihood Uncertainty Estimate (Ratto et al., 2000, 2001).

2.4. Bayesian calibration

Following a model verification and calibration by hand, a more formal calibration was performed of a selected subset of parameters that were both sensitive and uncertain This was a combined calibration on data from a multi-lake dataset (see Fig. 3). The model is run for all cases (with known input, $\boldsymbol{x}$) for a sample of the selected parameters ($\boldsymbol{p}^*$). The likelihood ('fit') of each run is assessed by comparison of the output ($\boldsymbol{y}$) with the observations ($\boldsymbol{m}$). Hence, the parameter space can be narrowed *by selecting the well-fitting runs*. We aimed at maximum likelihood for all lakes and output variables together (a 'compromise fit') rather than calibration on a specific lake.

The analysis was based on data on 43 actual or historic cases (lakes), for which both input factors ($\boldsymbol{x}$) and observations ($\boldsymbol{m}$) were known. The data were combined from different sources and are of variable quality. Most lakes are in The Netherlands, but some lakes in other European countries (Belgium, Poland, Ireland) were included. Table 2 gives a summary of the data set. The lakes differed in factors such as mean water depth, lake area or fetch, water inflow or retention time, type of sediment, nutrient loading, and some other ones.

The calibration data set encompasses a great variety of lakes, both 'clear' and 'turbid', several sediment types, with P inflow concentration ranging from 0.03 to 2 mgP l^{-1}, depth from 0.8 to 6.8 m, area from 1 to 4500 ha and retention time from 7 to over 500 days. Total P concentrations measure between 0.001 and 1.5 mgP l^{-1}, total N between 0.2 and 6.6 mgN l^{-1}, chlorophyll-*a* between 2 and >200 mg m^{-3}, vegetation cover between 0 and 90% and Secchi depth between 0.2 and 2.0 m.

Simulations with PCLake were carried out for these lakes for 20 years, for a grid sample of 7 varying parameters for which the model had shown to be sensitive, while 4 other parameters were coupled to these parameters with a correlation of 1 (Table 3). Also other kinds of sampling were tried, as well as an optimisation procedure using PEST (Watermark, 2000), but these are not further described here.

The likelihood functions of these runs were based on the (quasi-)steady-state summer-averages of the output variables chlorophyll-*a*, vegetation coverage, Secchi depth and total P, for all 43 lakes. Total N was left out for this purpose, because of the lesser accuracy of the data and because P is generally the limiting nutrient in aquatic systems. Other variables like zooplankton and fish densities or sediment variables were not used either, because these data were available for a subset of the lakes only.

The squared residuals were based on the natural logarithms of the measured and simulated values after adding a small value, the 'minimum significant difference' (ε); the residuals were squared to

Table 1
Parameters and ranges for the FAST sensitivity analysis.

	Min	Max	Unit	Description
Sampled parameters:				
fWinVeg	0.1	0.5	–	Overwintering fraction of subm. vegetation
cVSetIM	0.02	1.0	$m\,d^{-1}$	Settling rate of inorganic matter
coPO$_4$Max	0.5	5.0	$mgP\,l^{-1}$	Max. PO$_4$ conc. in pore water
cAffPUptVeg	0.001	0.1	$m^2\,g^{-1}\,D\,d^{-1}$	P uptake affinity of subm. vegetation
cKPAdsOx	0.5	3.0	$m^3\,g^{-1}P$	Max. P adsorption affinity
cVSetDiat	0.175	0.525	$m\,d^{-1}$	Settling rate of diatoms
cTurbDifNut	1	50	–	Bioturbation factor for diffusion
kDRespVeg	0.012	0.036	d^{-1}	Subm. vegetation respiration rate
cMuMaxDiat	1.0	2.5	d^{-1}	Max. growth rate of diatoms
kDMinDetS	0.001	0.1	d^{-1}	Mineralisation rate in sediment
kDAssFiJv	0.1	0.3	d^{-1}	Max. growth rate of zooplanktivorous fish
cMuMaxBlue	0.5	0.75	d^{-1}	Max. growth rate of cyanobacteria
kDRespZoo	0.075	0.225	d^{-1}	Zooplankton respiration rate
hFilt	0.5	1.5	$g\,m^{-3}$	Half-sat. food conc. for zooplankton
cVSetDet	0.05	0.25	$m\,d^{-1}$	Detrital settling rate
cMuMaxGren	1.0	2.25	d^{-1}	Max. growth rate of green algae
Coupled parameters:				
cFiltMax	=4 × hFilt		$l\,mg^{-1}\,D\,d^{-1}$	Max. zooplankton filtering rate
hDZooFiJv	=5 × kDAssFiJv		$mgD\,l^{-1}$	Half-sat. food conc. for zooplanktiv. fish
kDRespGren	=0.033 × cMuMaxGren		d^{-1}	Green algal respiration rate
kDRespDiat	=0.05 × cMuMaxDiat		d^{-1}	Diatoms respiration rate
kDRespBlue	=0.04 × cMuMaxBlue		d^{-1}	Cyanobacterial respiration rate
cMuMaxVeg	=13.33 × kDRespVeg		d^{-1}	Max. growth rate of subm. vegetation
kDMinDetW	=1 × kDMinDetS		d^{-1}	Mineralisation rate in water
cAffNUptVeg	=1 × cAffPUptVeg		$m^2\,g^{-1}\,D\,d^{-1}$	N uptake affinity of subm. vegetation
cVPUptMaxVeg	=2.5 × cAffPUptVeg		$gP\,g^{-1}\,D\,d^{-1}$	Max. P uptake rate of subm. vegetation
cVNUptMaxVeg	=25 × cAffPUptVeg		$gN\,g^{-1}\,D\,d^{-1}$	Max. N uptake rate of subm. Vegetation

obtain the fit function Phi$_{i,j}$ for every parameter combination i and every variable j.

$$\Phi_{i,j} = [\log(y_{j,\,meas} + \varepsilon_j) - \log(y_{j,\,sim} + \varepsilon_j)]^2$$
$$= [\log\{(y_{j,\,meas} + \varepsilon_j)/(y_{j,\,sim} + \varepsilon_j)\}]^2$$

This implies that the focus is on the *relative* differences, while downweighting the effect of small absolute values. In this way, the large differences in ranges (e.g. total-P in $mgP\,l^{-1}$, chlorophyll-*a* in $mg\,m^{-3}$, vegetation coverage in %) are corrected for, as to give each variable a comparable weight. The values for ε have been chosen as powers of *e*: $0.0074\,mg\,l^{-1}$ for total P, $0.074\,mg\,l^{-1}$ for total N, $0.074\,m$ for the Secchi depth, $7.4\,mg\,m^{-3}$ for chlorophyll-*a*, $0.074\,mg\,d.w.\,l^{-1}$ for cyanobacterial biomass and 2.7% for submerged vegetation coverage. The squared residual for each variable may range from 0 (perfect fit) to about 20 (very bad fit) over the observed range. A residual of 1.0 means a difference of a factor *e* (=2.72) (or, for low absolute values a difference equal to ε).

The average squared residuals for all lakes and variables were combined (summed and averaged), as to give a measure of the 'overall' *combined fit* for all of the available data:

$$\Phi\text{ave} = \frac{Sum[\Phi_{i,j}]}{n_j}.$$

A compromise, i.e. a reasonable fit for most cases, is preferred over a good fit of some cases at the expense of others. This implies that the procedure will not always be conclusive about the parameters, as several sets may give the same fit ('pareto-optimal' sets (Klepper, 1997)).

The *best run* (with the maximum likelihood) from these simulations was selected, and the corresponding parameter set used as a default.

2.5. Uncertainty analysis

The *distribution* of the calculated likelihood values was used for uncertainty assessment. Every run (parameter combination) was weighted based on its likelihood, giving rise to posterior distributions of parameters and model output. We focussed on the uncertainty in a *derived* model output, viz. the threshold loading rate for the switch between the clear, macrophyte-dominated state and the turbid, phytoplankton-dominated state (Janse, 1997, 2005; Janse et al., 2008) (Fig. 4). The threshold was defined as the loading at which the summer-averaged vegetation coverage crosses the value of 20%.

The analysis was performed for a 'default Dutch shallow lake', with a mean depth of 2 m, a fetch of 1000 m, a water inflow of $20\,mm\,d^{-1}$, a lightly clayish soil, and no wetland zone. Simulations were performed for the same grid sample as used in the calibration (Table 3). For each parameter combination, runs were performed
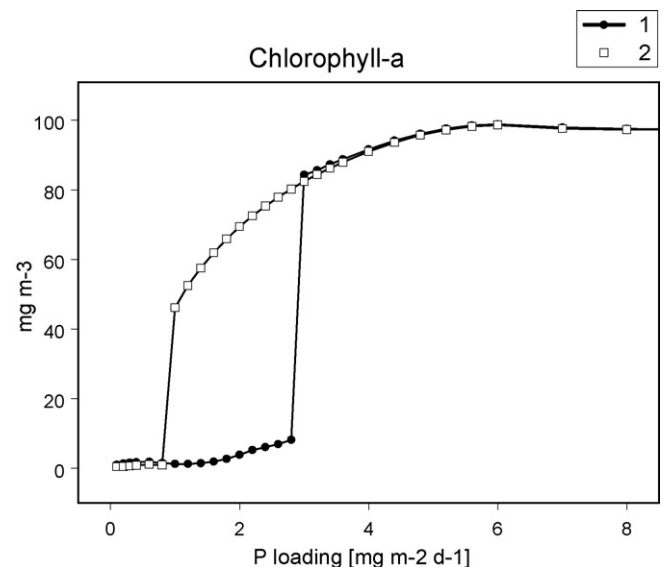

Fig. 4. Chlorophyll-*a* as a function of P loading, for two different initial states: 1 = clear state; 2 = turbid state.

Table 2
Overview of the data set. Quality data are summer-averaged values.

#	Name	Mean depth [m]	Area [ha]	Ret. Time [d]	Sed. type[a]	P Load [mg m^{-2} d^{-1}]	Chl-a [mg m^{-3}]	Cyanobacteria [% of phyt. d.m.]	Subm. veg. [% cover]	Secchi [m]	NH$_4$ [mgN l^{-1}]	NO$_3$ [mgN l^{-1}]	N-tot [mgN l^{-1}]	PO$_4$ [mgP l^{-1}]	P-tot [mgP l^{-1}]
1	Hollands-Ankeveen	1.3	85	357	p	0.14	16	–	25	0.59	0.06	0.09	1.79	0.02	0.09
2	Bergse Achterplas	2	41	103	c	8.1	218	–	0	0.24	0.05	0.03	3.68	0.06	0.43
3	Bergse Voorplas	2	60	95	c	8.16	213	–	0	0.25	0.05	0.04	3.51	0.04	0.33
4	Beulakerwijde	1.8	1300	175	p	5.12	99	52	0	0.38	0.46	0.45	2.23	0.02	0.14
5	Botshol, Grote Wije	2	53	157	p	0.88	6	57	32	1.46	0.04	0.13	1.04	0.01	0.04
6	Kaag, Norremeer	2.4	320	22	c	96.71	35	–	–	1.18	0.25	2.35	2.86	0.43	0.52
7	Langeraar, Geerplas	1.9	28	431	p	1.46	131	53	0	0.43	0.08	0.04	3.14	0.12	0.33
8	Loosdrecht	2.2	940	256	p	0.89	44	86	0	0.34	0.75	0.07	1.85	0.01	0.07
9	Naarden, Grote Meer	1.3	170	125	s	0.68	15	21	90	1.00	0.09	0.08	1.33	0.02	0.09
10	Naarden, Wijde Blik	1	38	193	s	0.68	16	18	30	0.58	0.09	0.07	2.45	0.02	0.15
11	Reeuwijk, Nieuwenbroek	1.8	104	327	p	1.1	136	55	0	0.35	0.11	0.04	3.49	0.01	0.12
12	Nieuwkoop, Noordeinder	3	150	475	p	0.85	74	61	1	0.54	0.07	0.03	2.06	0.00	0.06
13	Nieuwkoop, Zuideinder	3	100	110	p	1.75	165	60	0	0.43	0.07	0.05	2.68	0.01	0.12
14	Reeuwijk, Elfhoeven	2	109	122	p	5.48	109	41	0	0.40	0.09	0.04	2.34	0.01	0.16
15	Westeinderplassen	2.8	852	135	s	12.88	52	10	–	0.68	0.11	0.23	2.25	0.17	0.29
16	Zuidlaardermeer	1	600	23	s	11.95	89	–	0	0.41	0.19	1.00	3.98	0.01	0.30
17	Nannewijd	1	100	148	p	0.96	83	25	0	0.36	0.15	0.03	3.46	0.02	0.25
18	Blankaart (B)	1	30	14	c	18.7	28	8	0	0.33	0.14	3.65	4.36	–	0.35
19	Maten 13 (B)	0.8	3	8	s	9.32	10	2	84	0.75	0.05	0.03	–	–	0.02
20	Visvijver (B)	0.8	1	267	c	0.16	3	7	59	0.78	0.10	0.09	0.20	–	0.55
21	Gara, South (IR)	1	203	7	p	10.18	5	6	–	0.96	–	0.10	1.08	–	0.02
22	Maumwee (IR)	2	27	37	p	1.84	2	–	–	2.00	–	0.05	0.30	–	0.00
23	Mullagh (IR)	2.3	35	489	p	0.83	29	61	–	1.55	–	0.15	1.07	–	0.05
24	Pollaphuca (IR)	6.8	1974	204	p	1.83	6	10	–	1.44	–	0.49	0.84	–	0.01
25	Ramor (IR)	3	741	62	p	6.36	71	44	–	0.87	–	0.55	1.70	–	0.09
26	Łuknajno (PL)	1.8	630	567	s	0.11	18	–	42	1.32	–	–	1.91	–	0.07
27	Waalboezem	3.8	78	190	c	11.23	25	4	–	0.61	0.18	0.43	1.74	0.06	0.13
28	Binnenbedijkte Maas	4	158	274	c	5.48	97	38	–	0.31	0.15	0.34	2.51	0.08	0.22
29	Brielse Meer	5.5	491	135	c	17.26	34	10	–	1.14	0.13	1.57	2.79	0.08	0.16
30	Volkerak	5	4570	109	s	12.99	23	9	12	1.82	0.14	3.23	4.53	0.08	0.15
31	Zoommeer	6	1580	57	s	14.13	28	19	12	1.87	0.09	0.06	1.54	0.06	0.13
32	Oude Venen 2	1.3	10	73	p	6.84	34	2	0	0.51	0.32	0.03	3.00	0.26	0.41
33	Veluwemeer	1.6	3240	58	m	3.73	59	20	17	0.39	0.05	0.43	2.25	0.01	0.11
34	Wolderwijd	1.9	1800	117	s	1.37	84	40	13	0.38	0.04	0.11	2.19	0.06	0.14
35	Nuldernauw	2.1	870	44	s	7.53	90	–	8	0.36	0.05	0.11	2.29	0.04	0.20
36	Drontermeer	1.3	540	18	s	9.84	113	–	2	0.34	0.06	0.26	2.76	0.02	0.21
37	Braassemermeer	3.9	452	62	c	37.26	44	30	–	1.26	0.16	1.62	3.43	0.27	0.35
38	Langeraar, Noordeinde	1.9	75	558	p	2.6	185	53	0	0.29	0.13	0.03	3.95	0.14	0.45
39	Mooie Nel	4.5	116	51	s	179.45	101	14	–	0.61	1.01	3.04	6.62	1.35	1.55
40	Het Hol	1	30	157	p	0.87	14	12	90	0.98	0.13	0.10	1.10	0.02	0.06
41	Kortenhoef	1.2	193	204	p	4.58	153	–	0	0.31	0.11	0.12	2.92	0.02	0.23
42	Stichts-Ankeveen	1	100	303	p	0.09	15	26	60	0.91	0.13	0.18	1.36	0.02	0.06
43	Frisian Lakes (average)	1.4	518	147	p	3.9	88	55	1	0.32	0.20	0.57	3.82	0.05	0.24

– = no data.

References to the data are given in the 'Acknowledgements'.

[a] c = clay, p = peat, s = sand, m = mixed.

Table 3
Calibration parameters.

Parameter	Description	Unit	Range	Best run	Optimum
FWINVEG	Overwintering fraction of vegetation	–	0.3–0.7	0.3	0.345
CVSETDET	Detrital settling rate	$m\,d^{-1}$	0.2–0.3	0.25	0.251
CFILTMAX	Maximum zooplankton filtering rate	$l\,mg^{-1}\,d^{-1}$	3.5–4.5	4.5	4.442
CPREFGREN	Zoopl. pref. factor for green algae	–	0.25–0.75	0.75	0.743
CMUMAXVEG	Max. growth rate of vegetation	d^{-1}	0.2–0.3	0.2	0.204
CMUMAXGREN	Max. growth rate of green algae	d^{-1}	1.5–2.5	1.5	1.936
CMUMAXDIAT	Max. growth rate of diatoms	d^{-1}	1.5–2.5	2.0	1.960
Coupled parameters:					
CPREFDIAT	Zoopl. pref. factor for diatoms	d^{-1}		=CPREFGREN	
KDRESPGREN	Respiration rate of green algae	d^{-1}		=0.05 * CMUMAXGREN	
KDRESPDIAT	Respiration rate of diatoms	d^{-1}		=0.05 * CMUMAXDIAT	
KDRESPVEG	Respiration rate of vegetation	d^{-1}		=0.1 * CMUMAXVEG	

for two initial states (clear and turbid) and for a range of loading rates, and the critical loading rates were calculated for each combination.

3. Results

3.1. Sensitivity analysis

A ranking of the parameters was derived from their distance to the origin (0,0) in the μ–σ-plane of their 'elementary effects'. Fig. 5 shows the result for chlorophyll-*a*. The two lines in the plot forming a wedge correspond to $\mu \pm$ twice the standard error of the mean (SEM), with SEM $= \sigma/\sqrt{r}$. Parameters outside this wedge have an undoubtedly positive or negative impact of the parameter, parameters inside it have non-linear and/or interaction effects. An important conclusion is that for most parameters in PCLake, the effect is non-linear and/or interactive. With some obvious exceptions (e.g. a definite negative effect of water depth on vegetation biomass), most output variables are influenced by a large number of parameters, not only the ones that directly affect their own growth, but also parameters from other parts of the model (Janse,

Fig. 5. Results of Morris sensitivity analysis for chlorophyll-*a*. The place of every parameter is depicted in the plain of the mean and standard deviation of their elementary effect.

2005, Section 4.2). This points to the many indirect effects that can (potentially) occur in the model.

When repeating the Morris analysis starting with another sample (based on the same specification file), the more obvious effects still hold, but some parameters in the list are now replaced by related parameters; e.g. maximum growth rate of a biotic group is sometimes interchangeable with the half-saturating food value, respiration or mortality rate of the same group. These related parameters end up in the same cluster when performing a cluster analysis of the sensitivity coefficients, in accordance with the conclusions by Klepper et al. (1994) and Klepper (1997) by a somewhat different clustering method.

Combining the results for the main output variables, the sensitivity analysis points to the following ranking of parameters and factors for which the model is the most sensitive. Process parameters are in normal typeset, external input factors in italics.

water depth,
P loading,
N loading,
water inflow,
fetch, sediment properties and resuspension parameters,
zooplankton filtering rate and/or assimilation and/or respiration,
zooplankton food preference factors,
settling rates,
max. growth rates and/or respiration rate of algae,
max. growth rate and/or respiration rate of macrophytes,
fish assimilation rate and/or half-saturation food concentration,
infiltration rate,
overwintering fraction of macrophytes,
minimum nutrient content of algae,
mineralisation rate.

The results of the FAST method is shown in Fig. 6, which depicts the influence of the selected parameters on the combined likelihood measure (Φave) for six output variables, viz. chlorophyll-*a*, Secchi depth, vegetation cover, blue-greens, total N and total P, as well as on the combined likelihood measure (Φ_{tot}) for the 43 calibration lakes. (The 'coupled' parameters do not appear in this figure, as they are dependent on the other ones in this analysis following the formulas given in Table 1.) The total-order effects are shown (scaled to 100%), so including the direct and indirect effects of the parameters. The fit for chlorophyll, vegetation, Secchi depth and also blue-greens were mainly affected by the zooplankton filtering rate. Vegetation and algae were also strongly affected by their own maximum growth rates (or respiration rates) and those of their competitors. The macrophytes' P uptake rate is important not only for the macrophytes, but also for blue-greens and Secchi depth. Total N and total P are mainly dependent on the bioturbation coefficient, total P also on the adsorption constant, the maximum PO$_4$
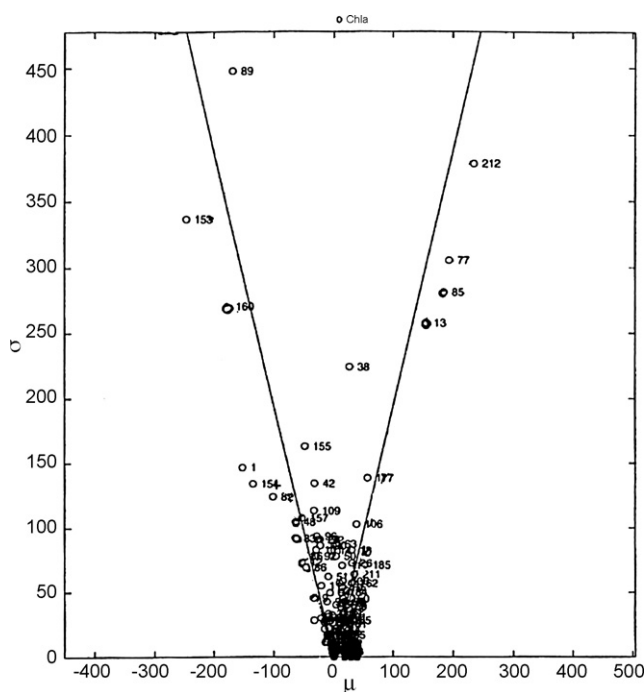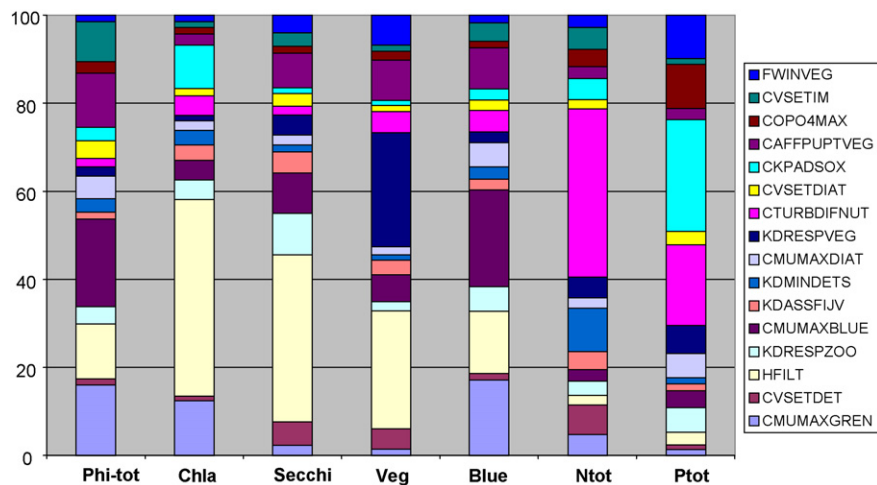
Fig. 6. FAST total-order effects of the subset of parameters on the likelihood of 6 output variables as well as on the total likelihood Phi-tot, scaled to 100%. Parameters are explained in Table 1.

concentration in the pore water, and the overwintering fraction of the vegetation. For total N also the mineralisation constant and settling rates are rather important. Not surprisingly, the total Φ is dependent on a mix of all parameters mentioned.

The remaining parameters thus have less impact on the model fit, or, to put it the other way round, these parameters cannot be estimated very well from this data set.

We also analyzed the results for specific lakes. In lakes that are (in reality) vegetated, the macrophyte parameters are in general more important for the fit results than in turbid lakes; the opposite is true for the zooplankton parameters.

Only a few distinct relations could be observed between a certain likelihood and specific parameters. This may, on the one hand, be a reflection of the compromise character of the fit (viz. summed over all lakes), on the other hand it may be caused by the rather high number of direct and indirect interactions in the model, leading to mostly multi-factorial relations. The correlation between parameters in the well-behaving runs was generally low. There thus exist multiple parameter combinations leading to the same result.

Hence, the sensitivity analysis revealed that the model is very sensitive to the most important lake features and input factors, among which the policy-relevant ones. Secondly, there are a number of sensitive process parameters which are to be further assessed by calibration. Most of these parameters are *a priori* judged as difficult to determine and quite variable in nature.

3.2. Bayesian calibration

The parameter values for the best run (with maximum likelihood) are given in Table 3. Besides the optimal parameter combination for the best run, also the 'optimal' values for the individual parameters were calculated as the likelihood-weighted average of the parameter values (more properly: using the weights for the runs with a given parameter value). These may differ, as they are not restricted to the exact values in the sample. The combination of 'optimal' values had, however, a lower likelihood than the best run, which may be due to correlation effects. In general, there was no simple relation between the value of every single parameter and the likelihood. The values from the best run were used as default values.

For this run, the summer-averages of the last simulated year for a number of output variables were compared to measured values (Fig. 7). The 'summer' is defined as the period April 1–Sep 30, in accordance with the period used in Dutch water quality regula-

tions. The results are shown for total P, total N, chlorophyll-*a* (as a measure for algal biomass), vegetation coverage, Secchi depth (transparency) and *relative* euphotic depth. The latter is calculated as:

$$\frac{z_{eu}}{z_m} = \frac{1.7 \times \text{Secchi}}{\text{Depth}}.$$

(Please note that in some of the graphs, especially the one for vegetation, several dots overlap near the zero value.) Several statistical methods were used to quantify the agreement between model and data (Janssen and Heuberger, 1995):

- the linear correlation coefficients;
- a test whether the calculated = observed line lies within the 95-confidence interval obtained from a linear regression between the observed and calculated values. As all five variables are zero-bounded and span a wide range, the natural log-transformed values after adding a small value (ε) were used to approximate normally distributed residuals.
- the Mean Relative Error (MRE), calculated as:

$$\text{MRE} = \text{Sum}\{(|\log(y_m + \varepsilon) - \log(y_o + \varepsilon)|)/\log(y_o + \varepsilon)\}/n$$

in which y_m and y_o are the modelled and observed values, respectively, and n is the number of cases. The MRE thus denotes the mean relative difference (in natural log units) between simulations and observations.

In general, the model behaves reasonably well for total phosphorus, chlorophyll-*a* (although in general somewhat overpredicted) and macrophytes; the predictions do not significantly differ from the observations (Table 4). The variability for total nitrogen is larger. The Secchi depth itself shows quite some deviations, but matches very well if expressed as relative to the water depth.

Furthermore, the results were compared in terms of 'clear' or 'turbid' state, which is the model's main objective. The values of 25 µg l^{-1} chlorophyll-*a*, 20% vegetation cover and a relative euphotic depth of 0.90 were chosen as reasonable criteria for this distinction. With an exception of one lake (with a high vegetation coverage despite a euphotic depth of only 0.80), these criteria coincide for the measured data. As for the simulations, 100% of the lakes are classified well according to the vegetation criterion, 95% following the chlorophyll criterion (two lakes were overpredicted) and also 95% based on the relative euphotic depth criterion (one
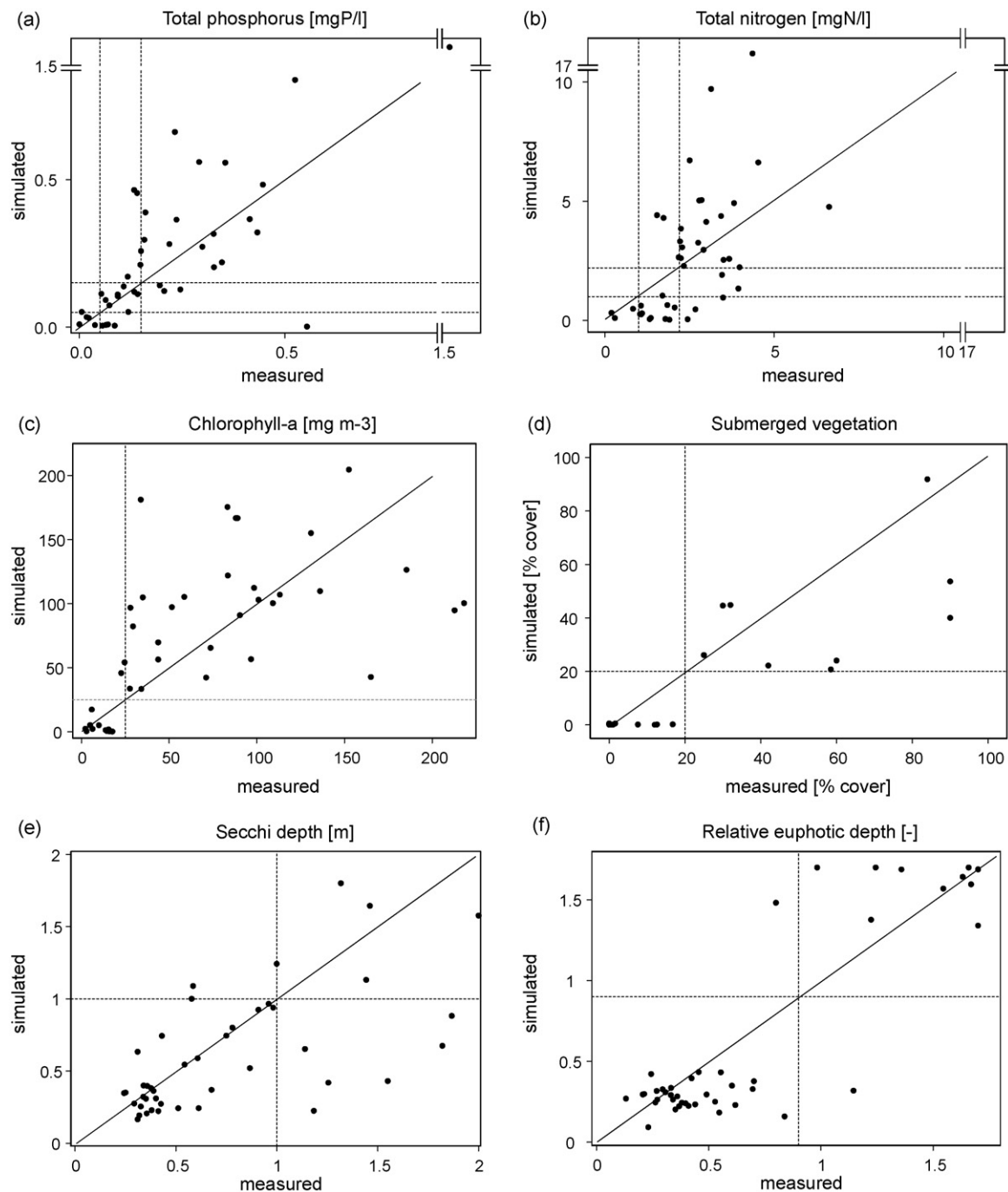
Fig. 7. PCLake simulations compared to measurements (summer-averages) for a multi-lake data set. a, total P; b, total N; c, chlorophyll-*a*; d, submerged vegetation; e, Secchi depth; f, relative euphotic depth. The 1:1 lines and the (proposed) quality standards have been added in the graphs.

lake was over-, one was underpredicted) (Fig. 7); 91% met all three criteria together.

For nutrients, it was tested whether an exceedance or not of the Dutch water quality standards was simulated correctly. The general standards are $0.15\,\text{mgP}\,\text{l}^{-1}$ and $2.2\,\text{mgN}\,\text{l}^{-1}$, those for water bodies designated as 'ecologically valuable' are $0.05\,\text{mgP}\,\text{l}^{-1}$ and $1.0\,\text{mgN}\,\text{l}^{-1}$. With the low phosphorus standard of $0.05\,\text{mgP}\,\text{l}^{-1}$ as criterion, 81% of the predictions classified the lakes in the right group; most of the others were underpredicted. When put against the high standard of $0.15\,\text{mgP}\,\text{l}^{-1}$, 86% of the predictions were correct; four lakes were under-, two were overpredicted. For nitrogen, the results were somewhat less convincing. For the low nitrogen standard of $1.0\,\text{mgN}\,\text{l}^{-1}$, only 71% was classified cor-

rectly (all others were underpredicted). For the high standard of $2.2\,\text{mgN}\,\text{l}^{-1}$, 81% of the prediction were right; five lakes were under- and three overpredicted in this case. A comment may be that the nutrient criteria do not always match with the biotic and transparency criteria as defined above. Especially, some lakes are clear even with a total P concentration >0.05 (but in general <0.15) $\text{mgP}\,\text{l}^{-1}$. Other factors than nutrients co-influence the biotic response.

3.3. Comparison for some other lakes

A model application on an independent data set of nine other lakes gave reasonable results, at least in terms of clear/turbid

Table 4
Comparison between simulated and observed values, based on natural logarithms + ε. Shown are the correlation coefficient, the mean relative error and the results of linear regression of the simulated values on the observed ones.

	Ptot	Ntot	Chla	Veg	Secchi	Rel. euphotic depth
Correlation coefficient	0.63	0.61	0.71	0.74	0.70	0.86
MRE	0.71	0.83	0.52	0.44	0.37	0.29
Regression:						
intercept	−0.64	−0.64	0 (forced)	0 (forced)	0 (forced)	−0.08
std. error	0.33	0.26	–	–	–	0.08
Pr(>|t|)	0.06	0.02	–	–	–	0.27
coefficient	0.81	1.34	1.02	0.99	0.62	1.03
std. error	0.16	0.26	0.02	0.06	0.07	0.09
Pr(>|t|)	<10^{-4}	<10^{-4}	<10^{-4}	<10^{-4}	<10^{-4}	<10^{-4}
R^2	0.40	0.40	0.98	0.86	0.58	0.76
meets 1:1?	Yes	No	Yes	Yes	No	Yes

(De Meester et al., 2006). The model was also applied to another set of lakes in The Netherlands, partly overlapping with the set described, partly differing. The hydraulic and nutrient loadings of the 'new' lakes were estimated by applying a combination of a leaching model with emission data at the catchment scale (Van Puijenbroek et al., 2004). The PCLake simulations based on these loadings gave reasonable results, at least in classifying the lakes in terms of mesotrophic or eutrophic state.

3.4. Uncertainty analysis

The *prior predictive distribution* of the critical loading rate for the default lake is shown in Fig. 8a, c. The threshold for the switch to the turbid state ranges from 0.5 to 7.9 mgP m^{-2} d^{-1}, with a median value of 2.4. The opposite switch takes place at a loading rate between 0.34 and 4.0, median 0.74 mgP m^{-2} d^{-1}. The switch point for 'clarification' (restoration) is always lower than the one for 'turbidification' (graph not shown).

Next, the runs were weighted according to their likelihood (the degree of fit with the data), giving rise to the *posterior predictive distribution*. This could, of course, only be done in an indirect way, firstly because only the actual state of the lakes could be measured and not their critical loading, secondly because the data set contained lakes of different types (differing from the 'default lake'). It was thus assumed that the likelihood of the different parameter combinations, as derived from the degree of fit between measurements and simulations for the lakes in the data set, can also be applied to the critical loading for the 'default lake'. The weighted switchpoints are shown in Fig. 8b, d. Compared to the
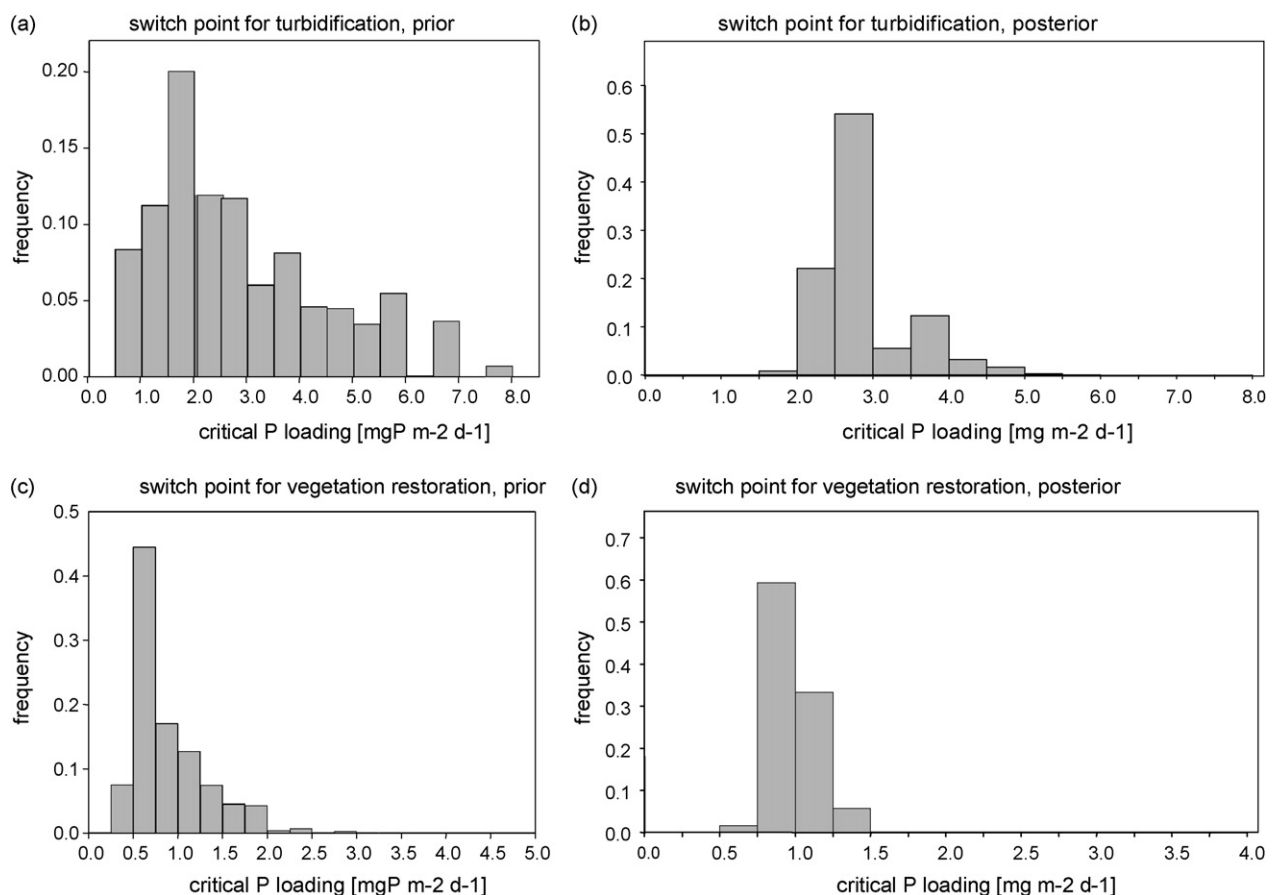

Fig. 8. Predictive distributions of the threshold loading rates. a, b, distributions of the 'turbidification' switchpoint: a, prior; b, posterior. c, d, distributions of the 'clarification' switchpoint: c, prior; d, posterior.

priors, the bandwidth of both switchpoints is markedly reduced. The threshold for restoration of the vegetation most likely lies between 0.75 and 1.25 mgP m^{-2} d^{-1}, the value for the best run is 0.94 mgP m^{-2} d^{-1}. The bandwidth of the threshold for 'turbidification' is somewhat wider and lies between 2 and 4 mgP m^{-2} d^{-1}, with 2.56 mgP m^{-2} d^{-1} for the best run. 95% of the density was made up by 50 runs, while 20% was comprised by the best run. Again, the switch point for 'clarification' (restoration) is always lower than the one for 'turbidification'.

4. Discussion

In general, it may be concluded that the model simulations correspond reasonably well to the observations in a wide variety of lakes. The results cannot easily be 'biased' by calibration of certain parameters on data from a specific lake, as this would be counteracted by the results for other lakes. Also a number of lakes that had *not* been used in the multi-lake calibration fitted in quite well (with some exceptions), which may be regarded as a partly validation. Apparently, the influence of the main input factors (water depth, nutrient loading, retention time, lake size) is reflected in the model results in the right way, so the quality of the model can be regarded as sufficient for practical purposes. In an earlier paper (Janse et al., 2008) we applied these results to calculate critical loading values for eutrophication and oligotrophication for different lake types. The results are no absolute 'proof', however, that all relations in the model are 'true'; it is still possible that other assumptions could explain the same results (e.g. Scheffer and Beets, 1994).

The mentioned dominant input factors are compatible with those found in empirical studies and with other models (see discussion in Janse et al., 2008), for some factors even with the first generation of input–output models reviewed by Reckhow and Chapra (1983). Also these models pointed to nutrient loading, retention time and water depth as important factors affecting the chlorophyll-*a* concentration in a lake. *PCLake*, however, adds a number of additional ecological mechanisms, besides the traditional mass balance, dilution and euphotic zone for phytoplankton, that contribute to the effect. These are the relation between water depth, water transparency and macrophytes, and the mutual competition for nutrients between macrophytes and phytoplankton. Hence, the interpretation and also the values of the limits between the lake categories (such as 'turbid' and 'clear') differ from the traditional limit between, for instance, 'eutrohic' and 'mesotrophic'. The factor 'lake area' is extra to *PCLake*. Another important difference is the non-linearity of the relations, in contrast to the (log) linear relations in the early models. Non-linear results are also produced by more simple dynamic models like minimodels, though (Scheffer, 1998).

The multi-lake calibration has proven to be a useful tool. The uncertainty in the output could be markedly reduced. The remaining uncertainty is still quite high, however. This is partly due to the fact that the data set did not contain enough information to estimate all the uncertain and sensitive parameters. Additional data might reduce the parameter variability still further, although a complete calibration of the model will be practically impossible in view of its complexity. A principal point is that the one and only 'true' model setting does not exist and that natural variability should be accepted. This principle is reflected in the Bayesian way of looking at calibration and validation of models.

Application on 'new' cases should best be done in a probabilistic way, viz. taking the inevitable variation into account, for instance by performing multiple runs.

The uncertainty derived from the calibration should be regarded as a conservative estimate, as only a subset of the parameters has been varied and the effect of variations in model structure was not assessed. The uncertainty in the restoration switchpoint appeared to be less than the one in the turbidification switchpoint, and the latter seems to be influenced by more factors than the former.

4.1. Model structure and model analysis

In the choice of a model structure there is usually a trade-off between model complexity and the ability to fit specific data. However, the urge for 'parsimony', i.e. a complexity not greater than can be validated by these data, may interfere with the urge for 'universality', e.g. applicability of the model in other systems and under different circumstances (e.g. Reichert and Omlin, 1997; Omlin and Reichert, 1999). On the other hand, an increasing complexity also increases the uncertainty if many parameters have to be estimated; true 'validation' of complex models is therefore not possible, it can only be tested whether a model meets the required criteria for its purpose (Rykiel, 1996). Useful directions are: (a) multi-case comparisons, giving parameter estimations based on combined data from different situations, (b) making use of previous knowledge in a more systematic way, (c) the use of models for the design of experiments, and (d) uncertainty analysis, allowing the evaluation of variation in model parameters or structure (see also Hilborn and Mangel, 1997). Modern sensitivity analysis tools are indispensable for parameter selection. The Bayesian approach as applied in this study makes use of those principles and thus can be regarded as a promising approach. Disadvantages are (a) that the method is computationally very demanding, and (b) that it often, also in our case, does not lead to a unique selection of model structure and parameters. The computational problems may be partly solved by the ever increasing computer speed, but the analysis of a many-parameter model will never be exhaustive. The second problem might be inevitably related to the complexity of natural systems and the limitations of observations.

Overall, the modelling approach presented here, taking into account both the biological structure and the nutrient cycle, seems a useful tool for the underpinning of nutrient regulations and lake management strategies.

Acknowledgements

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