Model studies on the eutrophication of shallow lakes and ditches

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Aan mijn ouders

We are thankful to the earth, which gives us our home.
We are thankful to the rivers and lakes, which give away their fruits and nuts to us.
We are thankful to the wind, which refreshes our life and brings rain and snow to water the plants.
We are thankful to the sun, which brings warmth and light for all beings on the Earth.
The trees, the animals, the sun, the wind, the rivers and the lakes share with
one another their unique qualities and so maintain universal balance.

.…

We all live on one Earth.
We all live under one sun, one moon, one sky.
We all breathe the same air.
We all drink the same water.
We all have the same desires.

.….

We all living beings have equal right to live on the Earth
The air, the water, the earth and the sun
are not the monopolies of human beings, only but equally belong to all living beings.
We should respect and protect all life on the Earth.
We should respect and protect all trees and plants.
We will not consume or use more than our actual needs.

..…

We will live in love and harmony with nature and animals.
We promise to live in balance with all on the earth.

…..

Ven. Bhikkhu Sanghasena
Mahabodhi Centre, Leh, Ladakh, India
December 2004

Contents

1. Introduction and thesis outline

1.1. Introduction; objectives

Eutrophication is an excess input of nutrients, especially phosphorus and nitrogen, to naturally oligotrophic or mesotrophic ecosystems. This causes the degradation or disappearance of natural plant and animal communities. Shallow, more or less stagnant waters like lakes, ponds and ditches are the most vulnerable for eutrophication. The naturally occurring communities of these waters prevailing under mesotrophic conditions, mostly dominated by aquatic plants (macrophytes) as primary producers, tend to change dramatically. Besides a collapse of the macrophytes, the related communities of algae, invertebrates, fishes and so on also change completely, and biodiversity as a whole generally decreases. This study concentrates on the effects in *shallow lakes and ponds* on the one hand and in *ditches* on the other. In shallow lakes, the clear-water community characterized by macrophytes is generally replaced by a dominance of phytoplankton and turbid water, while a diverse fish community including piscivores is transferred into a species-poor community dominated by bream. In ditches, small water discharge channels in agricultural areas, eutrophication causes the typical, richly structured community of submerged macrophytes to be replaced by a monotonous layer of small floating plants, duckweeds. This leads, among others, to an anaerobic environment and loss of aquatic life.

As these biotic effects are considered as undesirable, it is important to be able to *predict*, as far as possible in a quantitative way, at what degree of eutrophication these changes will occur, and whether they are reversible or not. Mathematical models are a useful tool to address prediction questions.

This thesis describes two mathematical models made for this purpose, a model for lakes and a model for ditches. The aim of both models is to answer the following questions:

a. At what nutrient loading the system changes from the natural state to the degraded state
b. How long does this take
c. Is this change reversible, i.e. how far should the nutrient loading be decreased to restore the natural state once the system is degraded
d. Why are some types of lakes more susceptible to eutrophication than others
e. What are the key processes determining this
f. What is the effect of different management options for restoration of degraded ecosystems, or increasing the resilience of natural ecosystems.
g. What is the uncertainty of these predictions

1.2 Thesis outline

The section MODEL SETUP (Chapter **2**) shortly describes the eutrophication process in both lakes and ditches and, based on this, gives an outline of the model features (type of model as compared to other types), and a short description of the models PCLake (for lakes) and PCDitch (for ditches). For a comprehensive description of the models the reader is referred to the Appendix.

The section SYSTEMATIC ANALYSIS comprises five chapters describing the general behaviour of the models. Chapters **3 and 4** deal with sensitivity and uncertainty analysis and calibration. The need was felt for a combined model calibration on a set of lakes with different features, loading and ecological state, rather than on separate cases. The methodological basis for a calibration on a multi-lake dataset based on Bayesian principles is described in chapter **3**. The calibration itself, preceded by a sensitivity analysis and combined with an uncertainty analysis, is the subject of chapter **4**. The uncertainty analysis is applied to the ‘critical loading’ as a derived model output. The topic of critical loading is further explored in the chapters **5-6** for lakes and **7** for ditches. In chapter **5** the critical loading is simulated for an ‘average Dutch lake’, and chapter **6** treats systematically the dynamic and long-term behaviour of the model at different initial conditions, and how this is affected by different lake features (bifurcation analysis). Chapter **7** deals with the critical loading for duckweed dominance in ditches.

In the section APPLICATIONS, a number of case studies have been brought together in which the models have been applied to specific lakes or regarding specific aspects. Chapters 8-13 deal with PCLake. Chapters **8-10** are devoted to Lake Loosdrecht (The Netherlands), a eutrophicated lake where phosphorus loading has been reduced (this version of the model was then called PCLoos). Chapters **11-12** describe simulations of a biomanipulation measure in Lake Zwemlust (also in The Netherlands). Other applications (not included in this thesis) were: Lakes Reeuwijk (Janse et al (1993), Janse (1995)), Kortenhoef (Aysever (1994), Kortenhoef and Ankeveen (Zamurovic-Nenad, 1993; Dekker et al., 1996)), a number of lakes in The Netherlands (Van Puijenbroek et al., 2003) and in some other European countries (Dagevos et al (2003). All these cases were modelled with the lake model proper. The effect of a wetland zone connected to a lake is illustrated in chapter **13**, making use of the combined lake and wetland modules.
Examples of PCDitch applications are described in chapters **14-15**. Chapter 14 deals with a set of 8 experimental ditches varying in sediment type and nutrient loading, chapter 15 discusses the effects of nitrogen loading and depth to an average clay ditch and makes a comparison with field situations. The model has also been applied to ditches in the Dutch regions of Hollands Noorderkwartier (Janse & Van Puijenbroek, 1997) and Bergambacht (Van Liere et al., 2002) (not included in this thesis).

Overall conclusions and summary can be found in the SYNTHESIS section, chapter **16.**

2. Model setup

2.1. Eutrophication of shallow lakes

As a result of high nutrient loadings during the past decades, many shallow lakes have become highly eutrophic. They are now characterized by dense algal blooms of cyanobacteria, high turbidity, absence of vegetation and a fish community dominated by bream. This in contrast to the original, mesotrophic, state, characterized by a high coverage of submerged macrophytes, low turbidity, low algal levels and a higher proportion of piscivores in the fish community (Fig. 2.1). (Note: in river delta areas like The Netherlands, the original state of lakes was mesotrophic rather than oligotrophic.) Although these effects were caused by increased nutrient loadings, restoration of the underwater vegetation often could not be achieved by external load reduction alone: eutrophic lakes often show resistance to recovery. Apparently, once the system has switched from a clear to a turbid state, this switch cannot simply be reversed.

There is now ample evidence that, grossly speaking, shallow lakes may be in either of these two alternative states, viz. a clear-water state dominated by macrophytes and a turbid-water state dominated by phytoplankton (*e.g.* Timms & Moss, 1984; Hosper, 1989; Van Liere et al., 1989; Jeppesen *et al.*, 1991; Gulati *et al.*, 1990b, Scheffer, 1998; and many others). Several factors determine which state prevails in a certain case, but a key factor is the external nutrient loading. At high loading, only the turbid state is stable, whereas the opposite is true for a low nutrient

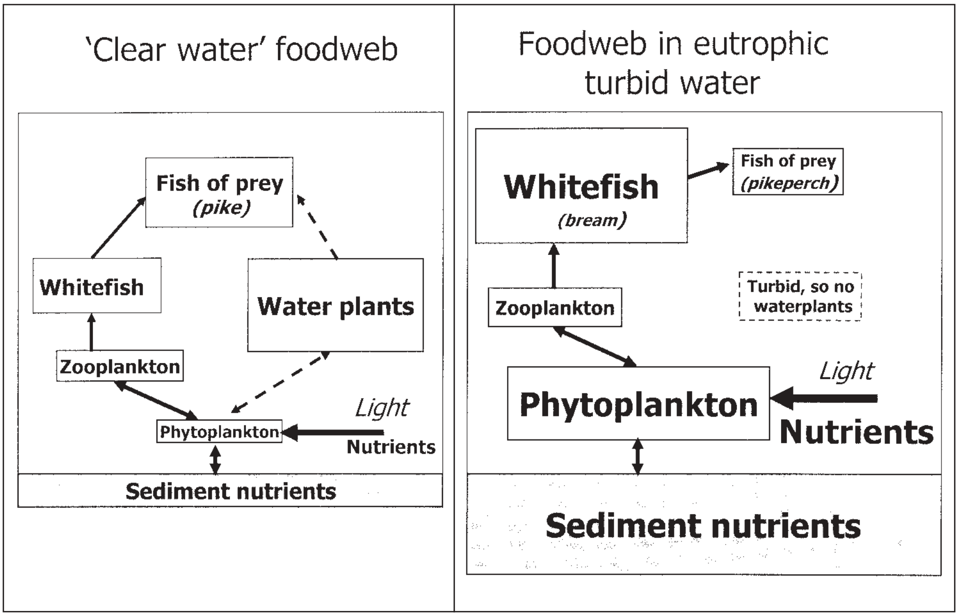

Fig. 2.1. *Dominant components in a clear lake (left) and a turbid lake (right).*

loading. In the intermediate range, both states may exist and switches between the two states are possible. Because both states possess a number of self-stabilizing buffering mechanisms, the critical loading level at which a shift occurs is dependent on the initial state of the system: the shift from turbid to clear occurs at a much lower loading level than the opposite one (hysteresis). In the intermediate range, a shift may be invoked by a natural or anthropogenic disturbance of the system. For example, a shift from turbid water to clear water might be induced by a natural fish kill or by a biomanipulation measure: removal of benthivorous and zooplanktivorous fish (Gulati *et al.*, 1990).

During the course of eutrophication of an originally mesotrophic, vegetated lake, changes occur in all abiotic and biotic parts of the ecosystem. In a vegetated system, the different components keep each other in equililibrium, and phytoplankton biomass is kept low due to nutrient limitation and grazing. If the nutrient loading (especially with phosphorus, usually the limiting nutrient for freshwater phytoplankton) increases above the uptake capacity of the system, the phytoplankton biomass increases, usually first with green algae. Macrophytes disappear due to shortage of light. At increasing turbidity the algae are often replaced by better shade-adapted cyanobacteria (Van Liere, 1979), provided that the retention time is not too short. The disappearance of the macrophytes results in a disturbance of the food web, leading to a bream-dominated fish community, which itself contributes to the water turbidity and to recycling of nutrients. Zooplankton cannot handle the high concentration of phytoplankton. The cyanobacteria, which are very phosphorus efficient, are able to maintain a high biomass even if the phosphorus loading would decrease again.

Both states possess a number of self-stabilizing mechanisms (Fig. 2.2). Several, often interacting, mechanisms for the resistance of the turbid state have been proposed (see e.g. Scheffer, 1998). Firstly, a prolonged internal loading from nutrient-rich sediments may delay the response (Ryding & Forsberg, 1977). Secondly, an increase of the nutrient utilization efficiency of the phytoplankton makes them produce the same biomass with less nutrient (Van Liere & Janse, 1992). Thirdly, the zooplankton grazing pressure on the phytoplankton is low, both because of the poor edibility of cyanobacteria by zooplankton and the strong predation on it by bream (Gulati *et al.*, 1990a). Finally, the high density of adult bream, by its feeding behaviour in the sediment top layer, keeps the water turbid and impedes return of the vegetation. Clearly, both direct effects of nutrients and indirect effects through the food web may contribute to the often observed resistance to recovery. Therefore, besides nutrient load reduction, additional measures such as direct food web manipulation are sometimes considered (Gulati et al., 1990a).

On the other hand, also the clear-water state of shallow lakes, dominated by submerged macrophytes, shows a certain resistance to external forcings, like a moderate increase in nutrient loading (Moss, 1990). Several stabilising mechanisms may play a role (Scheffer, 1998; Jeppesen et al., 1998). Nutrient uptake by macrophytes may suppress algal growth due to nutrient limitation, they may indirectly reduce the predation pressure on zooplankton by providing favourable conditions for predatory fish and a hiding place for zooplankton, and they may reduce wind-induced resuspension by stabilising the sediment. Allelopathic effects may play a role as well. Fig. 2.2 (from Scheffer, 1993) gives a (non-exhaustive) schematic overview of these relationships.

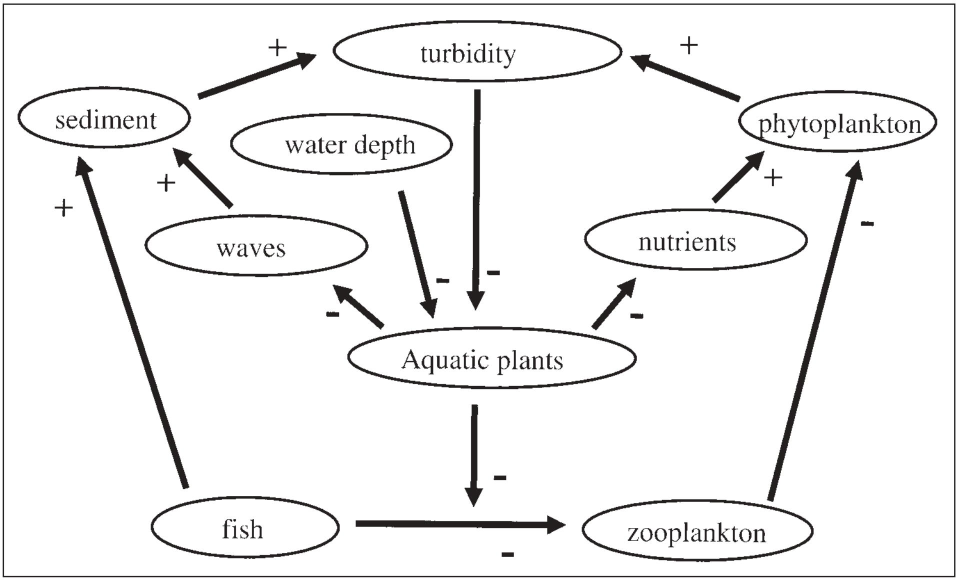

Fig. 2.2. *Main interactions in a lake ecosystem concerning water turbidity. Slightly modified after Scheffer (1993).*

A central factor for the prevailing state is thus the transparency of the water. The probability of a switch at a certain nutrient loading depends on both physico-chemical and biological factors. The former include lake depth, size, sediment type, water retention time, nutrient chemistry, etc. Biological factors involve the properties of the organisms in the system, like their life cycle, growth and loss rates and feeding behaviour. Growth parameters determine the competition between the different primary producers for environmental factors like nutrients and light. Loss factors include natural mortality, zooplankton grazing and fish predation.

The central question addressed in this study is the probability of either state, or a switch between them, as a function of the main lake characteristics and input factors, with a focus on the factors manageable by man.

2.2. Modelling approach

This topic is approached by means of the simulation model *PCLake*, an integrated ecological model of shallow lakes, describing phytoplankton, macrophytes and a simplified food web, within the framework of closed nutrient cycles. Its aim is to analyze the probability of a transition from the vegetation-dominated clear-water state to the phytoplankton-dominated turbid state, or vice versa, as a function of the external nutrient loading and other factors (fig. 2.3). Apart from loading scenarios, the effects of hydrological and morphological changes, climate change, regional management options like dredging and biomanipulation, or combinations of those, may be evaluated in at least a semi-quantitative way (fig. 2.3, b).

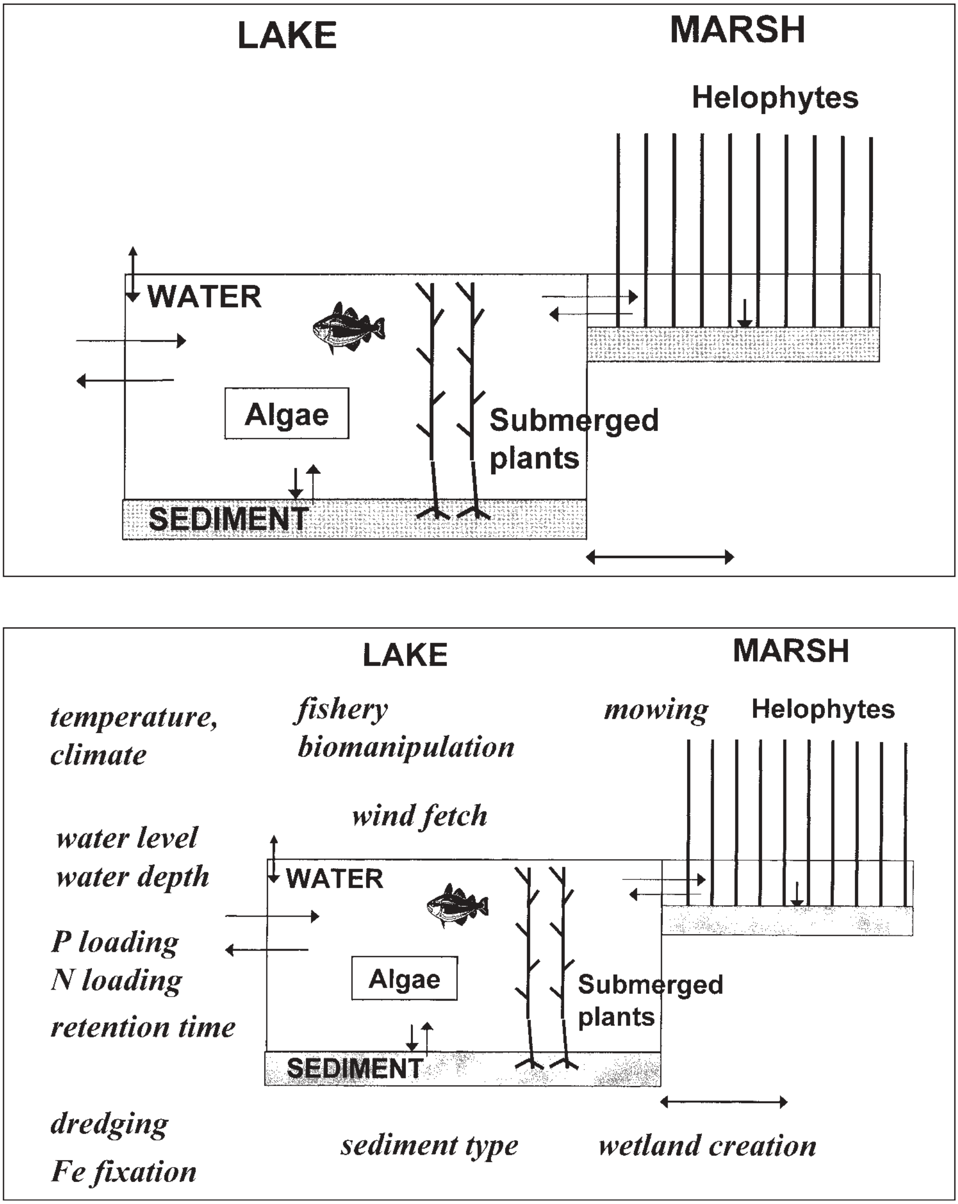

Fig. 2.3. *Schematic view of the scope of PCLake. a. schematic model structure; b. idem, with indications of the 'management buttons'.*

Secondly, the model gives the opportunity to evaluate the impact of different assumptions on ecological interactions (as derived, for instance, from ecophysiological knowledge).

The model describes the most important ecological interactions in a shallow lake ecosystem that determine what state will prevail. Both bottom-up, top-down and indirect effects are accounted for, within the general framework of the nutrient cycles. The model holds an intermediate position between eutrophication models focusing mainly on the nutrients and phytoplankton (e.g. Ambrose et al, 1988; Van der Molen et al, 1993; STOWA, 1999), more detailed biological species models (e.g. Van Nes et al, 2002) and so-called minimodels (Scheffer, 1989, 1998).

Key biotic variables are phytoplankton and submerged vegetation, key abiotic factors are transparency and nutrients. The model is based on closed nitrogen and phosphorus cycles; therefore, nutrient-to-biomass ratios are modelled dynamically. This is done to account for adaptation of nutrient ratios of phytoplankton and macrophytes to the nutrient availability, and because the nutrient ratios of organisms increase with their trophic level. For transport and retention, it is essential to discern dissolved and particulate nutrient forms. In order to properly include the available nutrients, it is essential to include the sediment top layer and its exchange with the water column. This is also crucial for the water transparency as central factor, as is the inclusion of organic and inorganic matter. The sediment is also necessary to model the lake's 'history', the effects of measures like dredging, and, generally, the time needed for a reaction (if any) to restoration measures. This is also an important reason to choose a dynamical calculation method. A second one is to account for the fact that between every two growing seasons (summers), there is a dormant season in which the importance of key ecological factors may be quite different.

As of the higher trophic levels, only the essential influences are included, viz. the grazing pressure on algae and the importance of whitefish for transparency and as a 'nutrient storage'. All organisms are considered as dependent, directly or indirectly, on the nutrients that are available in the system as a whole, so trophic structure and nutrient cycles are coupled. The inclusion of a trophic web makes it also possible to model the effects of biomanipulation.

The effect of variations in water level can be modelled, as the water depth is a state variable in the model. The wetland module can be used to model the effects of marsh zone restoration on lake quality. In the stand-alone version of the model, any further spatial variation in a lake can not be taken into account, but this is indeed possible in the DUFLOW implementation (e.g. depth, flow or sediment variations within a lake).

The model structure thus provides various 'slots' to account for differences in system properties or to impose (combinations of) changes in input factors, with special emphasis on the factors manageable by man. The model is meant to be an integrated evaluation tool.

2.3. Short description of PCLake

Structure

The model describes a completely mixed water body and comprises both the water column and the sediment top layer, with the most important biotic and abiotic components. The model is thus meant for shallow, non-stratifying lakes. No further horizontal or vertical distinction within the lake is taken into account, but optionally, a wetland zone with marsh vegetation may be included. The model can also be used in a spatial setting, in conjunction with the water transport model DUFLOW (STOWA, 1999, 2000). The results described in this thesis are all obtained with the zero-dimensional model, i.e. only one water body, with or without wetland zone.

Mathematically, the model is composed of a number of coupled differential equations, one for each state variable, as listed in table 2.1. The structure of the lake model is shown in Fig. 2.4, that of the marsh module in Fig. 2.5. All biota are modelled as functional groups. Besides mass fluxes (food relations etc.), the model also contains some ‘empirical’ or indirect relations between components, such as the impact of fish and macrophytes on resuspension (see below). The overall nutrient cycles for N, P and Si are described as completely closed (except for external fluxes such as in- and outflow and denitrification). This was done by modelling most components in three elements (as indicated by the ‘shadowed’ blocks in the pictures), viz. dry-weight (abbreviated as D), nitrogen (N) and phosphorus (P), detritus also in silica (Si). Inorganic carbon (CO_2) is not explicitly modelled. The nutrient-to-dry-weight ratios are thus variable. As the nutrient ratios of organisms increase with their trophic level (i.e. phytoplankton < fish), mechanisms are included to allow for those differences, such as a higher assimilation efficiency for nutrients than for carbon. The total mass balances per element are dynamically checked during the calculations. ‘Day’ was chosen as a uniform time unit for all processes (but the simulation time can be chosen as variable); however, the relevant time scale for the output is about weeks to 1 month.

The main inputs to the model are: water inflow, infiltration or seepage rate (if any), nutrient (N, P) loading, particulate loading, temperature and light, dimensions (lake depth and size), size of the marsh zone, sediment features and loading history (initial conditions). As output, the biomass and concentrations of all state variables, as well as a number of derived variables and fluxes, are calculated.

The model structure is made flexible so that the user may lump, split or leave out certain groups, but the default configuration (that was used in the ‘systematic analysis’ chapters of this thesis) is described here. In the applications in other chapters other configurations and previous model versions were used. The differences are described there. In particular, chapters 8-10 (Lake Loosdrecht), the macrophytes as well as the nitrogen cycle were left out, whereas in chapters 11-12 (biomanipulation in Lake Zwemlust) in contrast, the macrophytes were split in three functional groups.

Processes

The processes in the model will be briefly described here; a complete description of the model can be found in the Appendix.

a. Abiotic and microbial processes

At the base of the model are the transport processes: in- and outflow and external loading by nutrients and by organic and inorganic matter. The water depth (water level) can be made variable, by defining (seasonal) differences between inflow and outflow rate. Infiltration to, or seepage from, the groundwater can also be defined.

Table 2.1. State variables in PCLake. Abbreviations: D = dry-weight, P = phosphorus, N = nitrogen, Si = silica, O_2 = oxygen.

Component (state variable)	In water column		In sediment top layer	
	as element(s)	[unit]	as element(s)	[unit]
Water				
water depth	water	[m]	-- (fixed)	
Abiotic components				
inorganic matter (IM)	D	[g m^{-3}]	D	[g m^{-2}]
humus	--		D	[g m^{-2}]
detritus	D, P, N, Si	[g m^{-3}]	D, P, N, Si	[g m^{-2}]
inorganic nutrients	PO_4, P_{ads}; NH_4, NO_3; SiO_2	[g m^{-3}]	PO_4, P_{ads}; NH_4, NO_3	[g m^{-2}]
oxygen	O_2	[g m^{-3}]	-- (aerobic fraction)	
Phytoplankton[1]				
diatoms	D, P, N, (Si)	[g m^{-3}]	D, P, N, (Si)	[g m^{-2}]
small edible algae	D, P, N	[g m^{-3}]	D, P, N	[g m^{-2}]
cyanobacteria	D, P, N	[g m^{-3}]	D, P, N	[g m^{-2}]
Vegetation:				
submerged vegetation[2]	D, P, N	[g m^{-2}]		
Animal groups[3]:				
zooplankton	D, P, N	[g m^{-3}]		
zoobenthos	D, P, N	[g m^{-2}]		
juvenile whitefish	D, P, N	[g m^{-2}]		
adult whitefish	D, P, N	[g m^{-2}]		
piscivorous fish	D, (P, N)	[g m^{-2}]		
Marsh vegetation[4]:				
reed shoots	D, P, N	[g m^{-2}]		
reed rhizomes	D, P, N	[g m^{-2}]		

[1] Optionally, the phytoplankton may be lumped into one group.

[2] Optionally, several groups of macrophytes may be defined rather than one. The submerged vegetation may be split into several groups: rooted, non-rooted and charophytes, and/or floating-leaved plants may be added. (The vegetation can also be left out.)

[3] The food-web module optionally can be left out.

[4] The wetland module is optional.

The sediment top layer has a fixed thickness (default 0.1 m) and consists of inorganic matter (IM) (with a fixed lutum fraction), humus, detritus and pore water. Exchange of IM and detritus between water and sediment may take place via settling (described as a first-order process) and resuspension (zero-order process). The settling rate decreases, and the resuspension increases, with the size of the lake. The resuspension also increases with the sediment porosity and with the amount of benthivorous fish (see below), while it decreases with the vegetation cover. A net increase of sediment material is met by an equal amount considered as buried to deeper layers; also the siltation effect of this (a slight decrease of the water depth) can be accounted for.

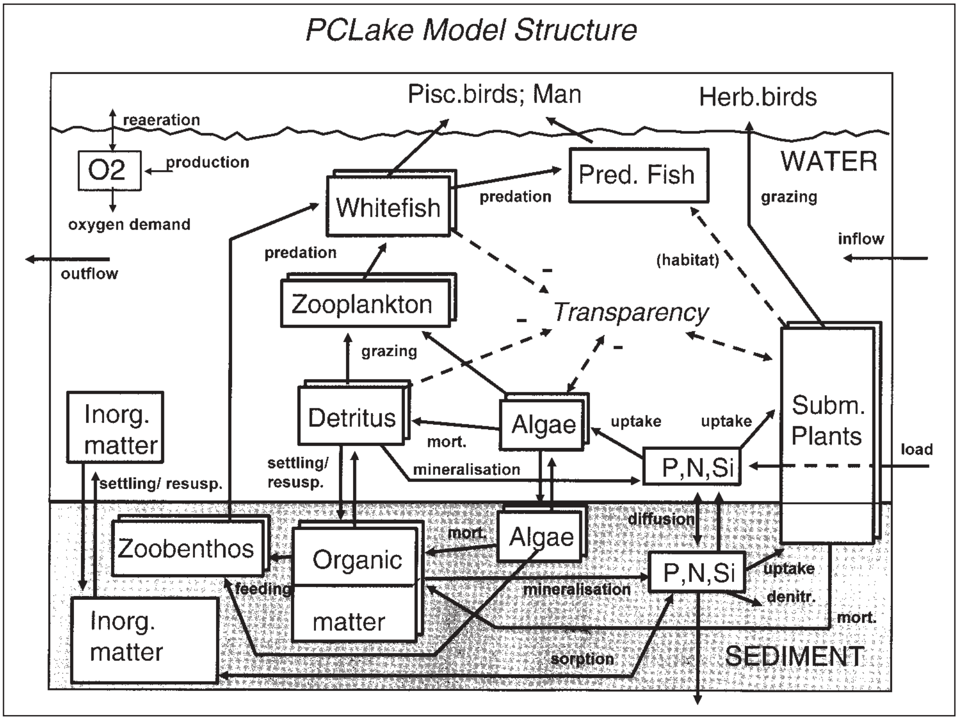

Fig. 2.4. *PCLake model structure (lake part). 'Shadowed' blocks denote compartments modelled in both dry weight and nutrient units. Three functional groups of phytoplankton are distinguished: cyanobacteria, diatoms and other small edible algae. Whitefish is split into a juvenile (zooplanktivorous) and an adult (benthivorous) subgroup. Arrows with solid lines denote mass fluxes (e.g. food relations), arrows with dotted lines denote 'empirical' relations (minus sign denotes negative influence, otherwise positive influence). Egestion and mortality fluxes of animal groups and respiration fluxes are not shown.*

Mineralisation of detritus (degradable organic matter) is described as a first-order process, dependent on temperature. Humus (refractory organic matter) is assumed to be mineralised only very slowly. The released nutrients are dissolved in the pore water. Inorganic P is subject to reversible adsorption to IM according to a Langmuir isotherm. It might also precipitate in case of a very high concentration. The relative adsorption increases with the sediment lutum content and with the aerobic proportion of the sediment. The latter is modelled in a highly simplified way by defining a quasi-steady state oxygen penetration depth (or aerobic sediment fraction), which is a function of the oxygen concentration in the water, the potential sediment oxygen demand and the diffusion rate. Nitrification of NH_4 increases, denitrification of NO_3 decreases with the aerobic proportion of the sediment. Exchange of dissolved P and N between pore water and water column is modelled according to the concentration differences. The combined result of the described processes is that the PO_4 release rate follows a seasonal cycle, dependent on the temperature and the amount of detritus in the system.

Mineralisation and nitrification are described in the water column as well. Oxygen in the water column is modelled dynamically, dependent on the BOD and SOD, the reaeration from the atmosphere, and the oxygen production by phytoplankton and/or submerged plants.

b. Phytoplankton

The phytoplankton module describes the growth and loss of the three functional groups of phytoplankton, *viz.* cyanobacteria, diatoms and other small edible algae. This distinction was made because of their different characteristics and because of management interests. The biomass of each group is described by the following differential equations:
dx/dt = production – respiration – mortality – settling + resuspension – grazing ± transport
and by parallel equations for phytoplankton expressed in N and P units:
dy/dt = uptake – excretion – mortality – settling + resuspension – grazing ± transport

The production (carbon fixation, for simplicity taken as equivalent to growth) depends on the maximum growth rate, temperature, day length, under-water light, P and N, for diatoms also on silica. The temperature dependence is described using an optimum function. The light dependent growth of cyanobacteria and diatoms is described according to Di Toro & Matystik (1980), using Steele's equation integrated with respect to the depth. This equation implies growth inhibition at high light intensities. For other algae, a similar equation is based on a Monod-type equation, assuming no light inhibition. The available light is determined by the light intensity at the water surface and its extinction in the water column (Lambert-Beer's law). The extinction coefficient is the sum of the background extinction of the water and the contributions of IM, detritus and phytoplankton (and submerged plants) to it, thus accounting for the self-shading effect, that sets a limit to the maximum biomass. P and N affect the growth rate via the internal nutrient contents of the phytoplankton rather than the external concentrations. Nutrient uptake is thus described separately from the production, to allow for this variable stoichiometry. The uptake rate increases with the external nutrient concentration up to a maximum that is determined by the actual ratio ('cell quota'), the minimum cell quota giving the highest maximum rate (Riegman & Mur, 1984). The biomass production is then dependent on the cell quota according to the Droop (1974) equation: the growth rate increases asymptotically with the cell quota provided is it above the minimum. For the silica-dependent growth of diatoms, the more simple Monod formulation was chosen based on the external SiO_2 concentration, with a fixed Si content of the diatoms. The actual growth rate is calculated by multiplying the maximum growth rate with the combined reduction functions for light and temperature and the one for nutrients. The latter is taken as the minimum of the functions for N and P (and Si for diatoms), following Liebig's law. The chlorophyll-a content of the phytoplankton, a derived variable in the model, is assumed to be variable, being higher in case of a more severe light limitation (Riegman, 1985).

The loss processes maintenance respiration and natural mortality are desribed as first-order processes, respiration as temperature-dependent. Excretion of nutrients parallel to respiration is assumed to decrease if the internal nutrient ratio is low. Settling is also described as first-order, the rate being the settling velocity [m/d] divided by the water depth. For reasons of ‘logic’, the settled algae are included as separate state variables, which may re-enter the water column by resuspension, coupled to the resuspension of other particles (see above). It is assumed that the settled algae do not grow, but are subject to respiration and mortality and may be eaten by zoobenthos.

The parameter values of the three algal groups in the model differ. The cyanobacteria have a higher light affinity (they are shade-adapted) as well as a higher phosphorus uptake rate than the other groups. On the other hand, they have a much lower maximum growth rate and a stronger sensitivity to temperature. The diatoms have a lower temperature optimum, while the other small algae are not inhibited by high light intensities. Both these groups have higher growth rates, but also higher loss rates through settling and zooplankton grazing (see below). The diatoms are the only group that might be limited by silica.

c. *Aquatic vegetation*

The submerged vegetation is described as one lumped group by the following differential equation for the biomass:

dx/dt = production - respiration - mortality (- bird grazing) (- management)

and for nutrients (N and P) stored in the plants:

dy/dt = uptake - excretion - mortality (- bird grazing) (- management)

It is assumed that the biomass is divided in an under-ground part (roots) and an above-ground part (shoots), and that the latter is homogeneously divided over the water column. Seasonality is modelled in a simplified way by assuming a high root fraction in the winter period and a low one during the growing season (default 0.6 and 0.1, resp.). The switch between both values in spring (triggered by water temperature) and autumn (triggered by season) mimicks allocation and reallocation processes. The modelled vegetation thus stands for plants with overwintering parts. Biomass production by the shoot is modelled largely analogous to the phytoplankton production, viz. dependent on maximum growth rate, temperature, day length, under-water light, N and P. It is assumed that the macrophytes may extract nutrients from both the water and the sediment pore water, largely according to availability. In practice, sediment uptake is mostly higher. Respiration and nutrient excretion are modelled as for phytoplankton. Natural mortality is assumed to be low in the growing season and high at the end of it; a fixed fraction (default 0.3) is assumed to survive the winter. The description of the growth and mortality is combined with a density-dependent correction derived from the logistic growth equation, to account for other factors than the ones explicitly modelled, for instance space, that might be limiting for the plant density that could maximally be achieved, the ‘carrying capacity’. Optionally, grazing by herbivorous birds and/or vegetation removal by man may be defined. The vegetation is assumed to have some indirect impacts on other components of the system, *i.e.* a hampering of resuspension, a slight negative impact on the feeding efficiency of whitefish and a positive influence on the growth of predatory fish.

d. Food web

The food web module is kept as simple as possible and comprises zooplankton, macrozoobenthos, whitefish (juvenile and adult) and predatory fish. The general equation for the animal groups is:

dx/dt = (feeding – egestion) – respiration – mortality - predation

combined with a density-dependent correction derived from the logistic growth equation (Hallam et al., 1983; Traas, 2004). The carrying capacities have been set to high values.

Zooplankton feeds on both phytoplankton and detritus. Grazing is described as a Monod-like function of the seston concentration, the specific filtering rate decreasing hyperbolically with increasing seston concentration (Gulati et al., 1982; Gulati et al., 1985). A selectivity constant is used for each food species to account for preference of the zooplankton: ‘other’ algae > diatoms > detritus > cyanobacteria (e.g. Gliwicz, 1980). The assimilation efficiency for the consumed food is constant and quite low (0.3) for carbon (Gulati et al., 1985), but variable (depending on the internal P ratio of the food) and, therefore, mostly higher for phosphorus. This is one of the mechanisms by means of which the differences in P content between the trophic levels are maintained.

Zoobenthos is assumed to feed on sediment detritus and a bit on settled algae, also by a Monod-type (or ‘type II’) functional response. It is also assumed to be able to ‘accumulate’ P from its food comparable to zooplankton.

All fish predation processes are modelled as a so-called ‘type III’ response (Holling, 1965): the predation rate depends on prey density according to a sigmoid curve. Juvenile whitefish feeds on zooplankton, adult whitefish on zoobenthos, and predatory fish on both classes of whitefish. Spawning is simulated as the transfer, every May, of a small proportion of the adult biomass to the juvenile biomass. At the end of each year, half the juvenile biomass becomes ‘adult’. Also the whitefish is assumed to have a relatively higher phosphorus assimilation efficiency, as the internal P content of fish is again much higher than that of its food organisms (Kitchell et al., 1975). For predatory fish, this mechanism doe not play a role any more. An indirect effect of adult whitefish that is included in the model is its stirring up of the sediment during feeding, causing a flux of particles and nutrients to the water column (Breukelaar et al., 1994). Predatory fish is assumed to be dependent on the presence of vegetation. Its carrying capacity can be made dependent on the size of the marsh zone connected to the lake.

e. Wetland module

The wetland part of the coupled simulation model is composed of a simplified growth model for reed (Haslam, 1973; Dykyjová & Květ, 1978; Björndahl, 1983), coupled to a description of the nutrient processes in the water column and the sediment top layer of the marsh zone equal to the ones in the lake (fig. 2.5). The biomass of the marsh vegetation is divided in a root and a shoot fraction, as separate state variables. The seasonal development is modelled as allocation of a part of the root biomass to the shoots in spring, photosynthetic growth during summer and partly reallocation back to the roots in autumn. Summer growth is assumed dependent on the marsh water depth, N and P in the sediment top layer, daylight and temperature. Nutrients are taken up from the sediment top layer only. Optionally, regular

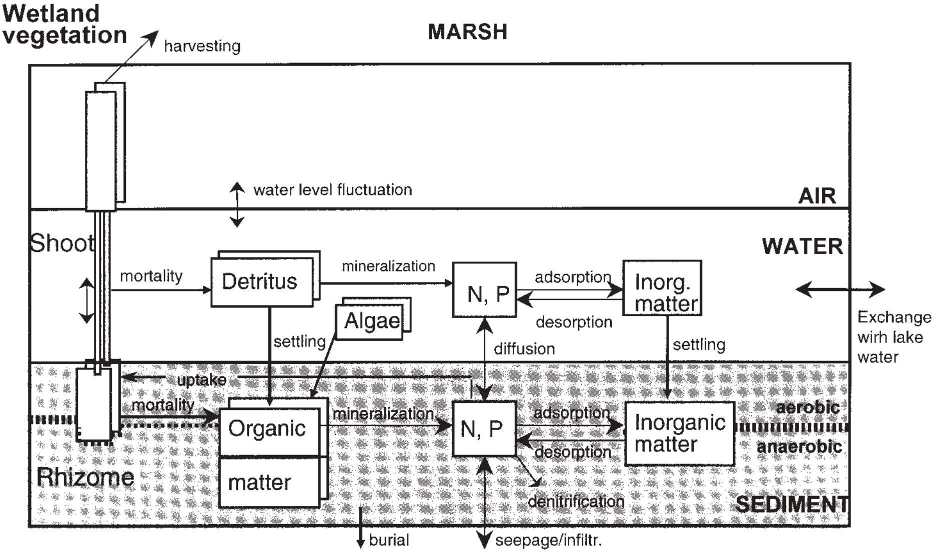

***Figure 2.5**. Model structure of the wetland module*

mowing of the vegetation can be taken into account.

The substances and process descriptions (mineralisation, settling, P adsorption, nitrification and denitrification) are analogous to those in the lake model, except that the water depth is much lower (default 0.5 m), settling velocities are higher due to the absence of wind action and resuspension is assumed to be zero. Phytoplankton is assumed not to grow in the shadow of the reed vegetation.

Mixing between the water columns of the lake and the wetland is described by an exchange coefficient (representing both dispersive transport and transport due to water level changes) multiplied by the concentration difference. The relation between the wetland zone and the fish population in the lake is simplified as its role as spawning and nursery area for predatory fish. It is assumed that the maximum possible biomass of these fish increases, within certain limits, with the relative area of wetland vegetation (Ligtvoet & Grimm, 1992).

Input and output

As input factors the user should supply:

(a) *Lake characteristics*

- Mean water depth [m]
- Lake size, expressed as fetch [m]
- Sediment:
  dry-weight content (d.m.) [%]
  organic content (or loss on ignition) (OM) [% of d.m.]

lutum [%] and/or Fe and Al [mg/g]

or (if not available) : estimate of sediment type, e.g. clay, sand, peat, mud

- Marsh area [-] (if any)

(b) *Water and nutrient input*

- Water inflow [mm/d] or retention time [d]
- Infiltration / seepage (if any)
- External P, N and Si loading [g m^{-2} d^{-1}] or concentrations in inflowing water [mg/l]: sum of point sources, diffuse and sources, surface inflow. Estimate of % dissolved / particulate loading
- Input or inflow concentrations of (inorganic) suspended matter

(c) Other input

- water temperature
- day light

(c) *Lake history and management*

- P and N concentrations in the sediment top layer (give depth), or estimate of historical nutrient loading
- Intensity of fishery [d^{-1}]
- Any management measures (being) conducted, like biomanipulation, dredging, mowing.

As *output*, the concentrations or biomass of all the state variables can be saved at any desired time scale. Some important derived output variables are:

- Total phosphorus (TP) [mgP/l] = PO_4 + P_{ads} + detrital P + algal P
- Total nitrogen (TN) [mgN/l] = NH_4 + NO_3 + detrital N + algal N
- Chlorophyll-*a* (Chla) [mg m^{-3}] = algal biomass * Chla/D-ratio, summed for all groups
- Water transparency:

+ Extinction coefficient [m^{-1}] = background extinction + contributions of IM, detritus, phytoplankton and submerged vegetation
+ Secchi depth [m] = penetration depth of light, measured by a black-and-white disk. It is calculated as a constant divided by the extinction coefficient (excluding the vegetation contribution).

Besides, the values of all fluxes can be saved as output as well.

Fig. 2.6 gives an overview of the main input and output of the model.

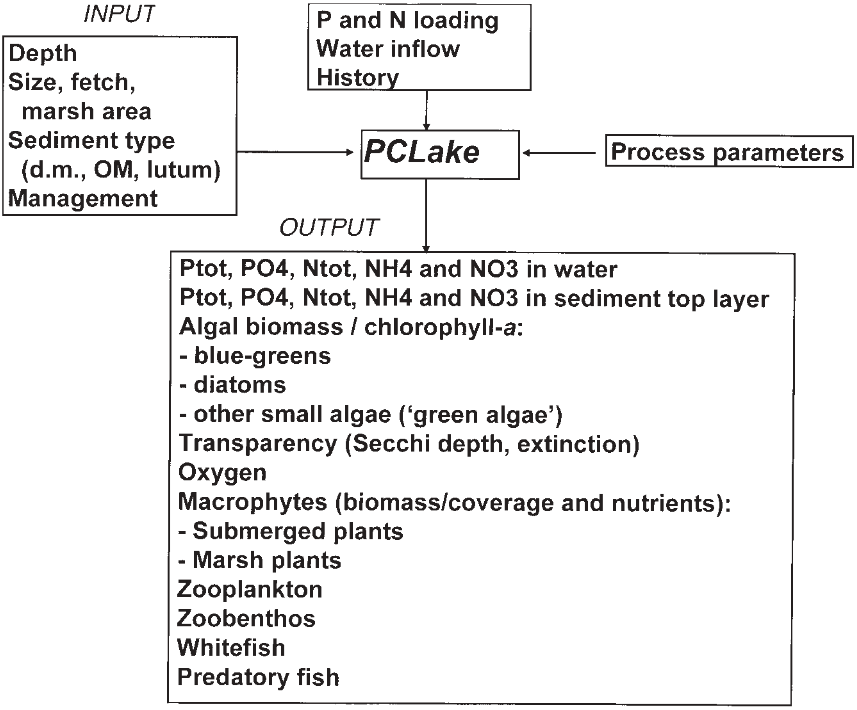

Fig. 2.6. *Overview of input and output of PCLake*

2.4. Eutrophication of ditches

Drainage ditches are small, linear water bodies, usually less than 1.5 m deep and several meters wide. With a total length of about 300,000 km, they are a common water type in the lowland parts of The Netherlands, where their main task is the discharge of excess rainwater from agricultural areas. They form the link between the farmland and larger water bodies such as lakes and canals (Fig. 2.7). The water transport from the lowland polder areas often is mediated by pumping stations (formerly by windmills). Many ditches also serve to transport water *to* the fields during dry periods. Besides their hydrological functions, ditches have an important ecological function, providing a habitat for many plant and animal species. They are also important as a source of drinking water for cattle. Because of their shallowness, ditches are often dominated by macrophytes. Most ditches require yearly maintenance (removal of the vegetation and/or the detrital layer) to ensure water flow.

Many ditches are strongly affected by eutrophication due to agricultural nutrient losses. This has a number of adverse effects on the quality and functioning of the ditches, i.e. related to duckweed coverage and oxygen household.

The vegetation structure in mesotrophic to moderately eutrophic ditches is often characterised by a dominance of submerged vegetation, besides emergent species (helophytes) and often a phytoplankton bloom in spring (De Groot et al., 1987; Veeningen, 1982). Yearly mowing usually hampers a further natural succession to helophyte dominance. Several tens of plant species may occur, together with a rich fauna of, among others, insect larvae and amphibians. Moderate enrichment with nutrients causes an increase of submerged vegetation biomass. Further eutrophication often stimulates the blooming of filamentous and/or epiphytic algae. Decreased light conditions cause a shift from species with a vertical growth strategy to those with a horizontal growth strategy (Sand-Jensen & Søndergaard, 1981; Bloemendaal & Roelofs, 1988) and the species diversity diminishes. At (very) high nutrient loading, the vegetation gets dominated by a surface layer of pleustophytic plants only, such as duckweed (*Lemnaceae*) or floating fern (*Azolla*), while submerged plants have disappeared (Portielje & Roijackers, 1995; Eugelink et al., 1998). Several adverse effects are related to this shift to duckweed. Because the oxygen produced is released into the atmosphere in stead of the water and reaeration is hampered, while decomposition continues to extract oxygen from the water, the water becomes often anoxic and mineralization occurs mainly anaerobically (Veeningen, 1982; Marshall, 1981; Portielje, 1994). This leads to loss of aerobic life in the ditch. Because of health effects and/or a bad taste, the water becomes unsuitable as drinking water for cattle (Hovenkamp-Obbema, 1998). Water passages and pumping stations are obstructed by duckweed. In some regions, duckweed is removed by man, thus increasing management costs (STOWA, 1997). There are indications that a shift from a predominantly submerged vegetation to a dominance of floating duckweeed vegetation often occurs quite suddenly when a certain nutrient level is exceeded. On theoretical grounds, it has been argued that both situations represent two different stable states, and that both states can potentially be stable in a certain range of nutrient loadings, analogous to the clear and turbid states in shallow lakes (Scheffer et al., 2003).

Duckweed dominance is now a fairly common phenomenon in The Netherlands (e.g. Van der Does & Klink, 1991; STOWA, 1992; BKH, 1995). There are large differences between regions, however. The main factor related to duckweed dominance is the degree of eutrophication. This was also shown in mesocosm experiments (Portielje, 1994; Eugelink et al., 1998). Several authors showed a positive correlation between duckweed cover on one hand, and nitrogen and phosphorus concentrations in the water or the nitrogen fertilizing level on the adjacent fields on the other (De Groot et al., 1987; Van der Does & Klink, 1991; STOWA, 1993; BKH, 1995), but the correlations were often obscured by other factors, such as BOD, conductivity, pH and water depth (Van der Does & Klink, 1991). Also transport processes and differences in soil type are important, while Boeyen et al. (1992) and Twisk (2002) found duckweed cover to decrease as a result of dredging. So, several factors co-influence the ecosystem’s response to nutrient loading, and the probability of a shift from a predominantly submerged to a floating vegetation depends on the ditch type.

For policy purposes, such as derivation of nutrient loading standards and the evaluation of agricultural scenarios, it is desirable to know how the probability of these adverse effects depends on the N and P losses from the fields and how this is depends on regional factors. The analysis and prediction of these effects is the purpose of the *PCDitch* model. The model focusses on the functional groups of water plants in relation to nutrients.

2.5. Short description of PCDitch

The *PCDitch* model includes the water column and the upper sediment layer of a ditch, both assumed to be well mixed, analogously to *PCLake*. The model is thus ‘zero-dimensional’, but, like *PCLake*, is also available as a module in the water transport model DUFLOW (STOWA, 1998) if one wants to model *networks* of ditches (Fig. 2.7). The model is confined to the ditch ecosystem itself (Fig. 2.8); the relation between land use and nutrient leaching is covered by other models (e.g. Meinardi & Van den Eertwegh, 1995; Groenendijk & Kroes, 1997), the results of which are used as input.

The model may be regarded as a competition model between several functional groups of water plants (submerged, floating and emergent), coupled to a description of the nutrient cycles. The model describes the cycling of four ‘substances’: dry weight (D), phosphorus (P), nitrogen (N) and oxygen (O_2). All plant groups as well as detritus are modelled in both D, N and P units. This is done to achieve closed nutrient cycles within the model system, and to account for variability of the nutrient ratios of water plants, e.g. depending on the loading level (e.g. Wetzel, 1983; Gerloff & Krombholz, 1966). The main ‘goal variables’ of the model are the biomasses of the different plant groups, as well as the phosphorus, nitrogen and oxygen concentrations. Plant biomasses are also converted to coverage percentages.

The components of the model are listed in table 2.2 and shown in Fig. 2.9. They comprise organic and inorganic matter, inorganic nutrients (P and N), oxygen, phytoplankton (lumped) and six functional groups of water plants, described below. Animal groups such as

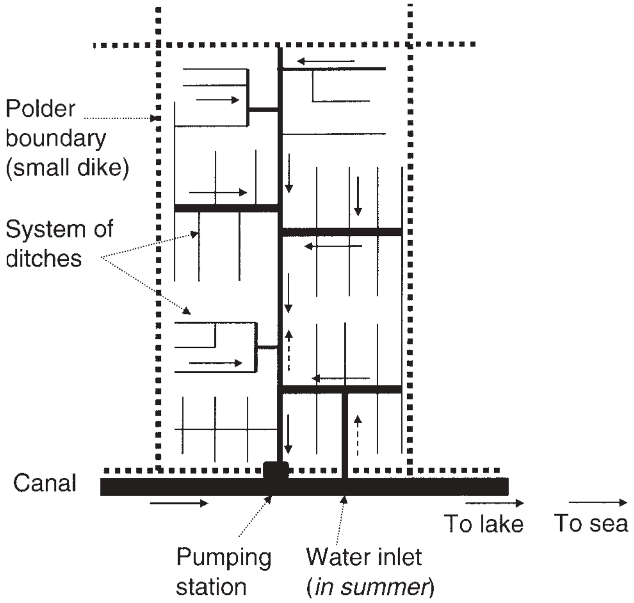

Fig. 2.7 *Schematic picture of the position of ditches in the polder catchment area*

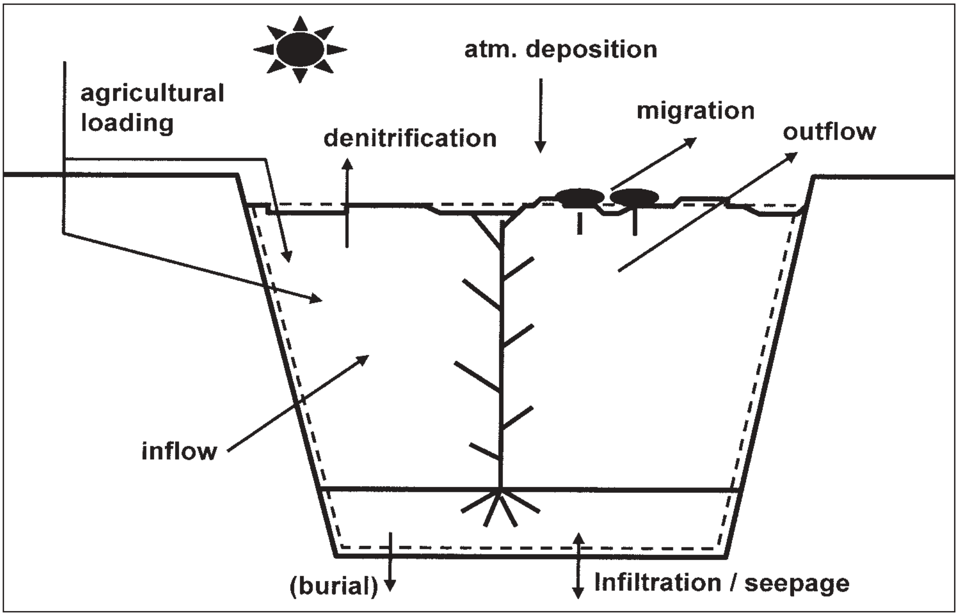

Fig. 2.8. *Schematic picture of PCDitch*

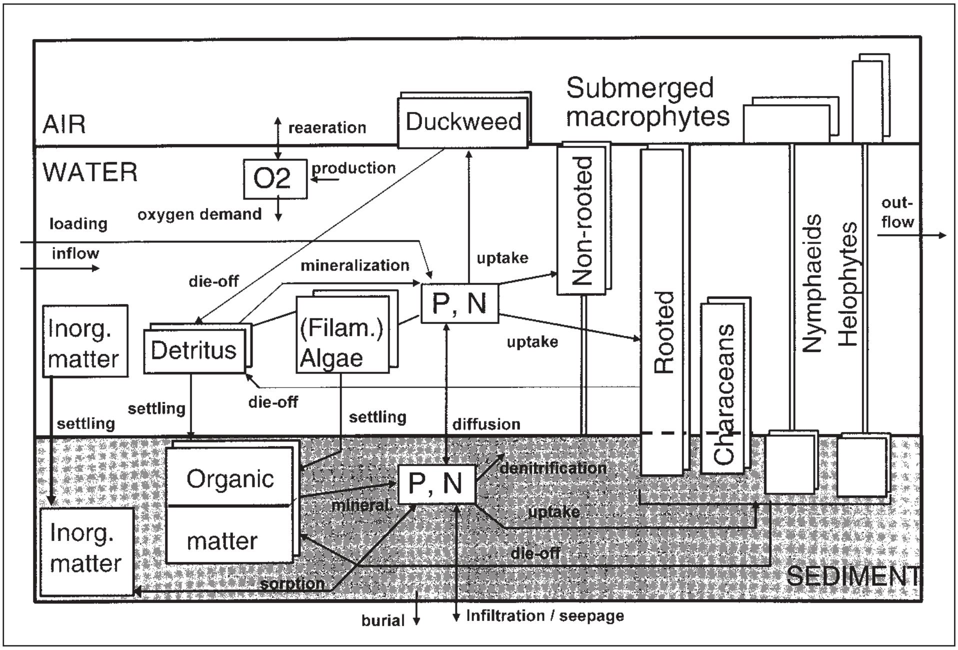

Fig. 2.9. *PCDitch model structure. Abbreviations of macrophyte groups are explained in the text. Shaded blocks denote components modelled in both dry-weight and nutrient units. Respiration fluxes are not shown.*

Table 2.2. State variables in PCDitch. Abbreviations: D = dry-weight, P = phosphorus, N = nitrogen, O_2 = oxygen.

Component (state variable)	In water column		In sediment top layer	
	as element(s)	[unit]	as element(s)	[unit]
Water				
water depth	water	[m]	--(fixed)	
Abiotic components				
inorganic matter (IM)	D	[g m^{-3}]	D	[g m^{-2}]
humus	--		D	[g m^{-2}]
detritus	D, P, N	[g m^{-3}]	D, P, N	[g m^{-2}]
inorganic nutrients	PO_4, P_{ads}; NH_4, NO_3	[g m^{-3}]	PO_4, P_{ads}; NH_4, NO_3	[g m^{-2}]
oxygen	O_2	[g m^{-3}]	-- (aerobic fraction)	
Phytoplankton[1]				
phytoplankton	D, P, N	[g m^{-3}]	D, P, N	[g m^{-2}]
Vegetation[2]				
submerged, rooted	D, P, N	[g m^{-2}]		
submerged, non-rooted	D, P, N	[g m^{-2}]		
charophytes	D, P, N	[g m^{-2}]		
floating (duckweed)	D, P, N	[g m^{-2}]		
nymphaeids	D, P, N	[g m^{-2}]		
helophytes	D, P, N	[g m^{-2}]		

[1] Optionally, the phytoplankton may be split into several groups.

[2] Optionally, one or several groups of macrophytes might be lumped, split or left out.

zooplankton, macrofauna and fish have been left out, as they are considered as generally not very important for the prediction of the primary producers in ditches. The components in the water column are modelled in [g m^{-3}], those in the sediment as well as the macrophytes in [g m^{-2}]. As in *PCLake*, seasonal dynamics is included because temporal processes can be very important for the outcome of the competition, and because the hydrology and loading of ditches are often different beween summer and winter.

The water plants were divided into six functional groups, besides one functional group of algae. The definition of the plant groups is primarily based on the layer(s) in which they grow and the layer(s) from which they take up nutrients. The classification into 16 growth forms given by Den Hartog & Segal (1964) and Den Hartog & Van der Velde (1988) has been used as a template. Several groups were lumped, while others were left out because they are not common in ditches. Duckweed and submerged plants were of course included; the latter were split into rooted and a non-rooted group, with charophytes (also rooted) as macro-algae as a special group. Helophytes (emergent plants) and floating-leaved plants are included because of their role in the nutrient household and light interception. (In practice, the natural succession to helophytes is impeded by regular ditch management.) The groups are defined by the relative size of emergent, floating, submerged and root fractions, and their vertical distribution. The number and the definition of the plant groups has been made flexible. The default configuration and their characteristics are:

1. Submerged plants, divided into:
    a. Rooted submerged angiosperms (abbreviated as '*Elod*'). This group comprises the elodeid and potamid growth forms. Assumed to fill the entire water column, nutrient uptake from both water and sediment. Root fraction set to 0.1 in summer, 0.6 in winter.
    b. Charophytes ('*Char*'). Confined to the lower half of the water column. Root fraction set to 0.05 in summer, 0.1 in winter. They were distinguished because of their special character as macro-algae.
    c. Non-rooted submerged angiosperms ('*Cera*'). Canopy-formers, confined to the upper half of the water column. Nutrient uptake from the water only.
2. Non-rooted, floating plants: duckweed ('*Lemn*'). This group includes floating fern (*Azolla*) as well. Nutrient uptake from the water only.
3. Rooted plants with floating or emergent leaves
    a. Floating-leaved plants: Nymphaeids ('*Nymp*'). Nutrient uptake from the sediment, root fraction set to 0.75 in summer, 0.95 in winter.
    b. Emergent plants: helophytes ('*Helo*'). Nutrient uptake from the sediment, root fraction set to 0.5 in summer, 0.8 in winter.

The phytoplankton comprises in reality both planktonic, epiphytic and filamentous species; for simplicity, they have been lumped into one group (which may be split if desired, however). The competition between the plant groups is mainly determined, in the model, by the factors light, temperature, N and P and - for algae and possibly duckweed – in- and outflow. For all groups, a logistic correction term based on a maximum carrying capacity has been included, which represents all non-modelled factors, for instance space. Duckweed, algae and non-rooted submerged plants are confined to the water column for their nutrient uptake, while helophytes take nutrients from the sediment only and rooted submerged plants are able to use both pools. Duckweed hampers the growth of submerged plants by light interception at the water surface. Most processes are described analogously to the *PCLake* model. The water depth (usually much lower than in lakes) can be made variable. Resuspension can ususally be neglected. Reaeration (exchange of oxygen with the atmosphere) is assumed to be hampered by duckweed (Marshall, 1981; Portielje & Lijklema, 1995). Default, yearly vegetation management in autumn is defined, as occurs in practice. For long-term management, a sediment dredging frequency can be set.

Input and output of the model

As input factors the user should supply:

(a) Ditch characteristics
Mean (initial) water depth [m]

Sediment:
- dry-weight content (d.m.) [%]
- organic content (or loss on ignition) (OM) [% of d.m.]
- lutum [%] and/or Fe and Al [mg/g]
- or (if not available) : estimate of sediment type, e.g. clay, sand, peat, mud

(b) Water and nutrient input
- Water inflow [mm/d] or retention time [d]
- Infiltration / seepage (if any)
- External P and N loading [g m^{-2} d^{-1}] or concentrations in inflowing water [mg/l]: sum of point sources, diffuse sources. Estimate of % dissolved / particulate loading
- Input or inflow concentrations of (inorganic) suspended matter

(c) Other input
- water temperature
- day light

(d) Ditch history and management
- P and N concentrations in the sediment top layer (give depth), or estimate of historical nutrient loading
- Nature and frequency of management measures (being) conducted: dredging, mowing.

As *output*, the concentrations or biomass of all the state variables can be saved at any desired time scale. The most important output variables are:
- Total phosphorus (TP) in water and sediment
- Total nitrogen (TN) in water and sediment
- Oxygen concentration in the water
- Algal biomass or chlorophyll-*a* (Chla)
- Submerged macrophytes (per group and total): biomass or coverage
- Duckweed: biomass or coverage
- Emergent vegetation: biomass or coverage

Besides, the values of all fluxes can be saved as output as well.

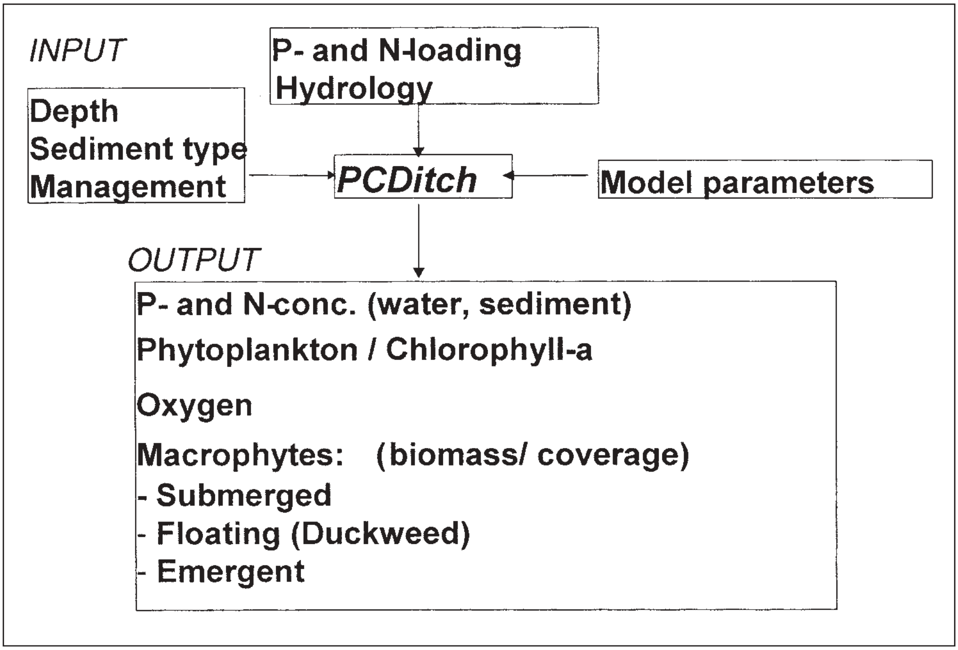

Fig. 2.10 *Overview of the main input and output of PCDitch*

Chapter 3

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Fitting the dynamic model *PCLake* to a multi-lake survey through Bayesian Statistics

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Abstract

A method is presented for the regression of dynamic lake ecosystem models on multi-lake data. The method draws upon Bayesian Statistics as the main inference engine, as outlined by Box and Draper (1965), M.J. Box (1971) and Box and Tiao (1973/1992). The Bayesian approach allows the calculation of the uncertainty of parameters and predictions both before and after the model is confronted with data.

There are several modelling objectives that can be dealt with through this technique in a unifying way: calibration of parameters, on the basis of prior knowledge and the available data; estimation of parameter uncertainty and correlation structure; estimation of predictive uncertainty for the assessment of trends and scenario analyses; validation of model structure in relation to residual errors. Moreover the method allows an iterative approach between hypothesis generation and data analysis.

The method is applied to perform a regression and uncertainty analysis of the model *PCLake* on data from an 18-lake Dutch survey. *PCLake* is a dynamic nutrient–ecosystem model with a closed nutrient budget, comprising one water and one sediment layer. The model was run until steady state was reached and results were compared to summer-averaged field data from the survey. The output variables selected are chlorophyll-*a* and total phosphorus concentrations.

The analysis was done for three selected parameters, considered uniformly distributed within predefined ranges. Posterior distributions were calculated for each lake on the basis of 125 three-parameter combinations. The residual error of the prediction of chlorophyll-*a* was reduced from a factor of 3.8 on the basis of the prior uncertainty analysis down to a factor of 2.3 after regression on both variables. For total P concentrations these factors were 1.4 before regression and 1.5 afterwards, hence a small trade-off to match chlorophyll levels. The prior uncertainty factor of mean chlorophyll predictions was reduced from 1.9 before regression to 1.1 after regression on both outputs, while for mean total P predictions these factors were 1.1 and 1.05, respectively. The conclusion can be drawn that chlorophyll-*a* is particularly sensitive to the three parameters, while total P is determined to a large extent by the lake-specific input parameters. The posterior parameter distributions reflected these differences in sensitivity. Pairwise correlations between parameters were low.

Analysis of systematic and case-specific deviations between model regression and data helps to identify other critical parameters and possible structural modifications.

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It is concluded that through Bayesian Statistics empirical and dynamical water quality modelling can be integrated.

Keywords: Bayesian statistics; Lake ecosystems; Regression models; Uncertainty analysis

1. Introduction

In ecological modelling – and water quality modelling in particular – two quite distinct ways of modelling have been used to tackle problems of assessment and prediction: the systems dynamics approach and the statistical approach. Confining the discussion to water quality modelling and lake management, this dichotomy is clearly exemplified in the two-volume monograph on Lake Management by Reckhow and Chapra (1983) and Chapra and Reckhow (1983).

In the dynamical view, systems are comprised of quantities that can be classified as state variables, input or control variables, parameters, and so on, and the focus is on predicting change or evolution of the system in response to stimuli. Often, these studies are directed towards a specific type of lake, or even one particular lake, and the general thought is that the more quantities are measured, and the larger the timespan of study, the better the understanding of that lake will be.

In the statistical view, one tries to deal with a more heterogeneous set of lake data at once, often comprised of several different lakes of different type and under different conditions, such as depth, residence time, nutrient loading, and so on. Here also, it is thought that the more lakes are entered in the study, the better the understanding of that lake data set will be.

There have been studies of direct comparison between dynamical model predictions and empirical relationships (e.g. Scavia and Chapra, 1977; Thomann, 1977; Chapra and Reckhow, 1983; Reckhow and Chapra, 1983; Aldenberg and Peters, 1990), but most are limited to individual lakes, or just treat the two approaches as possible alternatives with pros and cons.

One would be inclined to think that, if the aim of study is dynamical understanding of one particular lake, e.g. for future predictions or evaluating management alternatives, the dynamical approach is implied, while, if the aim is to detect patterns in a survey of different lakes, e.g. to assess their trophic state or other conditions, the statistical approach is indicated. Furthermore, one would conclude that there is not much in between these two approaches, and therefore, that there can not be much cross-fertilization between both methodologies.

The aim of this article is to show that these implications need not be automatic. We are going to fit a complex dynamic lake model, *PCLake*, to an 18-lake data set at once, to assess the predictive strength of the model for different lakes and to illustrate the statistical approach. In the present study, only three parameters of this model will be varied, namely those that were found to be most influential in earlier simulations, in order to see how the method works out. Unexpectedly, this yields already quite promising results, though the question remains, what will happen when one further climbs the parametric ladder, and where the phenomenon of overfitting will make results decline. It seems too early to speculate on that.

From the present findings, it appears that the apparent gap between empirical and dynamic modelling in water quality seems largely to be dictated by methodological difficulties of statistical nature, and is likely to disappear. It is easy to indicate that, in principle at least, there should not be any gap at all.

First, one can say that fitting a dynamical model to a particular lake essentially is a statistical problem, but only one of formidable difficulty for all but the simplest models.

Secondly, the distinction between empirical models and mechanistic models seems to be largely an artificial one, and one can say in Orwellian terms that all models are mechanistic, but some are more mechanistic than others.

Thirdly, there does not seem to be any basic difference in aims: both analyses collide in their wish to assess the strength of the model employed, i.e. the ability to reproduce and explain the data, and to assess its generality, e.g. in predicting outcomes under changed conditions. For example, a model that does well under different conditions is likely to be more reliable than one that has to be recalibrated each time conditions change. Clearly, being a reliable predictor is what we wish a model to be in the first place.

So, if there are no principal differences between the statistical and the dynamical approaches in lake modelling, what makes these approaches differ in current practice? The answer seems to be related to the nature of different statistical philosophies that may apply, and to the availability of algorithms to evaluate complex models in multi-case situations.

In this paper, we will show how one particular type of statistical thinking, called Bayesian Statistics or Bayesian Inference, suits the purposes of the ecosystems modeller very well. The method comprises several aspects of model analysis in a unifying way: uncertainty analysis, parameter calibration, regression on data, assessment of the regression variability, calculation of the predictive variability, and validation, i.e. the assessment of extreme departures between model and data, or of apparent trends in model deviations for some cases.

We will first treat the main principles and terminology of Bayesian Inference, which may be skipped if the theoretical side of the problem is not of interest to the reader, and then employ this statistical approach in calculating the regression of the dynamic model *PCLake* to a multi-lake survey.

2. Statistical methodology

2.1. Bayesian Statistics versus Sampling Statistics

Most of the statistics we learn in present-day courses belongs to a statistical philosophy that may be called Confidence or Sampling Statistics. The major alternative, and more suitable to our modelling purposes as we will see shortly, is Bayesian Statistics (Box and Tiao, 1973/1992; Box, 1980; Lee, 1989; Press, 1989). Different statistical philosophies have different inferential possibilities, and we must choose the one with most predictive power. However, Bayesian Statistics is hampered by the fact that most of the current statistical packages employ algorithms developed for Sampling Statistics.

In Sampling Statistics, parameters are thought to have true fixed values by hypothesis. Samples differ by mechanisms of chance, although one may have only one sample at hand. To estimate the parameters, estimators are considered, which are functions of the data, such as sample mean and sample standard deviation. To quantify one's uncertainty about the fixed parameters, still other functions of the data come into play, yielding estimated upper and lower bounds that, when calculated for an infinity of repeated but otherwise *hypothetical* data sets, would enclose the true value of the parameters with a certain amount of *confidence*.

This statistical philosophy is all right as long as the model parameters can reasonably be thought to be fixed and to have a true value, unknown to the modeller.

The ecosystems modeller can not maintain these presuppositions, however. The models are gross simplifications of nature and it is more realistic to assume from the outset that the parameters are ill-defined, exhibit spatial variability or other, e.g. genetic, heterogeneities, so that they can better be considered as probability distribution themselves. This is the realm of Bayesian Statistics.

Fighting structural uncertainty with parameter probability distributions is by no means the only way of adding flexibility to fixed structure models. One could make submodels for some parameters, add spatial or time-variable coefficients, separate lumped state variables into two or more groups, employ fuzzy sets instead of probability distributions (e.g. Keesman and Van Straten, 1990), apply the techniques of recursive parameter estimation in the time-domain (e.g. Whitehead and Hornberger, 1984; Young, 1993), and so on.

In Bayesian Statistics, the parameters of an otherwise deterministically conceived model, however complex, are thought to explicitly obey a *prior* probability distribution of some type. This distribution is supposed to express a state of knowledge or ignorance about them. Given this prior distribution, and a probability model for the discrepancy between model outcomes and data, it is possible by means of Bayes' Theorem to calculate the change in our ignorance about the parameters, after the model is confronted with the available data. This is the *posterior* parameter distribution. Moreover, both prior and posterior parameter uncertainty distributions can be used to calculate predictive distributions of any quantity that the model addresses. So, one can also calculate how well we are doing and what the resulting variation of our predictions will be, both before and after data become available.

The monographs on Bayesian Statistics cited above illustrate how problems of linear regression and analysis of variance are treated the Bayesian way. Thus, this methodology is applicable to the empirical style of water quality modelling. In mechanistic models, its basic statistical philosophy fits the case of nonlinear ill-defined parameters even more so. Hence, Bayesian Statistics is a good candidate for bridging the gap between empirical and mechanistic lake modelling. For lake management and extrapolating lake responses, the Bayesian spirit must be attributed to Reckhow (1983) and Reckhow and Chapra (1983). On p. 51 Reckhow and Chapra (1983) write: "It is our belief that Bayesian statistical inference will become increasingly valuable in water quality applications as its merits are recognized."

However, in the Bayesian realm, we have to face the problem of the availability of algorithms to do the analysis. We will show how a simple algorithmic approach allows for exploratory experimentation that can lead to quite useful insights. We think that this approach can guide more sophisticated numerical machinery.

We are not saying that classical Sampling Statistics can not provide a similar unifying framework, and, through confidence arguments, can do tricks analogous to calculating predictive uncertainties. The point is that neither in empirical lake modelling, nor in mechanistic lake modelling, the assumption of well-defined fixed parameters seems appropriate. Moreover, the philosophy of repeated sampling seems at variance with the unique character of natural data. And finally, since variability of parameters does not come in a priori, but by confidence limit arguments afterwards, the distinction between prior and posterior predictive variation is not easily made.

2.2. *Uncertainty analysis in probabilistic terms*

A distinction will be made between fixed parameters and uncertain parameters. Let

$$\eta = M(x,\theta)$$

denote an explicitly formulated model, where η is the predictive variable, e.g. chlorophyll, M (the model) is a more or less mechanistic function, formula or algorithm. M is both a function of x, constituting the fixed parameters that are given per case, but which may vary from case to case, e.g. depth of the lake, as well as a function of the variable parameters θ, e.g. settling velocity, that we are uncertain about.

The model may be a constant, or straight line, or numerical solution to a system of differential equations, etc., i.e. anything parameterized, that would yield deterministic results if the uncertain parameters were fixed as well.

If θ varies according to some prior probability distribution, the predictions will vary according to a predictive distribution that readily follows from the transformation M. Namely, in probabilistic terms one would write:

$$p(\eta) = \int p(\eta \mid \theta) \cdot p(\theta)\, \mathrm{d}\theta.$$

Here $p(\eta \mid \theta)$ is the conditional probability of η for fixed θ. This probability is multiplied by the prior chance on the value θ and summed over all such values.

Since η is a deterministic function M for given θ, we have the situation that all probability mass is located just in the η value the model calculates for that θ, i.e.:

$$p(\eta \mid \theta) = 1 \quad \text{if } \eta = M(x,\theta),$$
$$p(\eta \mid \theta) = 0 \quad \text{if } \eta \neq M(x,\theta).$$

For discrete θ, this means that all probability of those θ values that map to the same η value is added, and constitutes the prior predictive probability of η, i.e.

$$p(\eta) = \sum_{\theta = M^{-1}(\eta)} p(\theta)$$

For continuous θ, the Jacobian of transformation has to be taken into account

$$p(\eta) = \sum_{\theta = M^{-1}(\eta)} p(\theta) \cdot \left| \frac{\mathrm{d}\theta}{\mathrm{d}\eta} \right| .$$

This is uncertainty analysis in the purest sense, only couched into standard probabilistic form. The procedure is often applied intuitively, outside the probabilistic framework, and reasoning goes like this: the model is fixed, some of the parameters are uncertain, and so are the outcomes.

Although this procedure yields information on how uncertainties in parameter values are carried through in the predictions, this has little to do with how reliable the model is as a predictor. Quite precise predictions may be way off what they should be, i.e. have a high systematic bias, while imprecise ones may on average be near the truth. In other words, we have to confront the model with data.

2.3. Fitting equations using Bayes' Theorem

To allow for discrepancies between model and data to occur, and study them, the model is extended to include this discrepancy part. If y denotes a random variable describing the potential observations that may occur, one may write:

$$y = \eta + \varepsilon$$

where η is the mechanistic part as before, albeit uncertain due to uncertain parameters, and ε is an unstructured random part, e.g. a zero-based normal distribution. It is important to be aware of the word model being used in either of two ways: in the smaller sense referring to the mechanistic, or "explaining" part, η, and in the wider sense *including* the "unexplained" part, ε. This distinction will be relevant if we get to the point of prediction later on.

Now, if ε is supposed to be normally distributed

$$\varepsilon \sim N(0, \sigma^2),$$

it is in the Bayesian spirit to say that we do not know the performance of the model (M) beforehand, which amounts to a prior uncertainty about σ, next to the prior uncertainty about θ in M. The prior in σ should reflect our state of ignorance about σ, i.e. how wide model data discrepancies may be. Hence, one could employ Bayesian Statistics to let the data teach us how large σ should be taken, in order to make sense of the data.

Given the prior joint parameter distribution $p(\theta,\sigma)$, one can calculate the prior predictive probability distribution of potential observations, before any data are available, by

$$p(y) = \int p(y \mid \theta, \sigma) \cdot p(\theta, \sigma)\, \mathrm{d}\theta\, \mathrm{d}\sigma .$$

Now, given n actual, i.e. realized, observations y_i ($i = 1, \ldots, n$), one may calculate the posterior parameter distribution given these fixed data from Bayes' Theorem

$$p(\theta,\sigma \mid y_i) \propto p(y_i \mid \theta,\sigma) \cdot p(\theta,\sigma) .$$

Here, $p(y_i \mid \theta,\sigma)$ is the so-called likelihood function of (θ,σ), i.e. a measure of the degree of fitness of different parameter combinations given the actual observations, if there were no preferences for any parameter values whatsoever. Hence, the posterior parameter distribution is proportional to the product of what we first thought the parameters could be, times what the data say they could be.

From this posterior parameter distribution one can calculate the marginal parameter distribution of the mechanistic model part:

$$p(\theta \mid y_i) = \int p(\theta, \sigma \mid y_i)\, \mathrm{d}\sigma$$

and a similar equation for the marginal parameter distribution of the discrepancy part:

$$p(\sigma \mid y_i) = \int p(\theta, \sigma \mid y_i)\, \mathrm{d}\theta .$$

One also can calculate marginal parameter distributions for each individual parameter, as well as for all pairs of individual parameters, and so on, by suitably integrating or summing over non-wanted parameters.

2.4. Posterior predictive distributions

Now that one has obtained posterior parameter distributions, one can do predictions based on these posterior insights, analogous to the predictions based on prior distributions. Predictions can focus on the mechanistic part (η), on the discrepancy part (ε), or on the observational sum (y).

For the mechanistic part, we write for the posterior prediction

$$p(\eta \mid y_i) = \int p(\eta \mid \theta) \cdot p(\theta \mid y_i)\, \mathrm{d}\theta$$

which, since η is a function of θ, boils down to, for discrete θ:

$$p(\eta \mid y_i) = \sum_{\theta = M^{-1}(\eta)} p(\theta \mid y_i)$$

analogous to the prior mechanistic prediction. For continuous θ the Jacobian gets in, as was the case for the prior.

The prediction of potential observational values involves the joint posterior of both θ and σ. One could calculate, thus

$$p(y \mid y_i) = \int p(y \mid \theta, \sigma) \cdot p(\theta, \sigma \mid y_i)\, \mathrm{d}\theta\, \mathrm{d}\sigma$$

As indicated above, it is important to distinguish between predictions on the basis of the mechanistic part of the model (that is the model in the smaller sense) and predictions of observational values. The latter predictions would include our posterior understanding of the discrepancy part of the model output (the model taken in the wider sense).

2.5. Regression, the Bayesian way

Although we will confine the calculations in this paper to the predictional variation of the mechanistic part (η), just as a start, the authors would like to stress that, when prediction of the state of lakes under perhaps modified conditions, e.g. management alternatives, is wanted, one should employ posterior predictions that include the discrepancy between the mechanistic part and the observations.

Reckhow and Chapra (1983, p. 153) emphasize exactly this same point in the realm of ordinary regression in Sampling Statistics, based on the confidence approach. But, one seldomly sees analysts following this advice in regression analysis.

This relates to the difference between the statistical philosophies alluded to above. If the model is trusted, if the parameters are well-defined and have a true fixed value by hypothesis, as is the basic philosophy of Sampling Statistics, the discrepancy part becomes "noise" or "error", as stated literally, and one wants to get rid of it in hunting for the truth. In the Bayesian philosophy, truth is rather in the observations, while the model is uncertain through its probabilistic nature. Therefore, predictions of real cases, or future cases, should include the not mechanistically understood part of the model. This should be the more attractive standpoint to the ecologist.

Since in ordinary regression, the variability of the regression line, e.g. straight line, is assessed through the confidence interval around the line, and the line itself stands for the *mean* of potential observational values y, given a value of the fixed parameter x (see any textbook on regression), we can define regression values in the Bayesian way as the mean of the posterior predictive distribution of the mechanistic part of the model. That is, the regression value or *fit* is

$$\mathrm{Mean}(\eta) = \int \eta \cdot p(\eta \mid y_i)\, \mathrm{d}\eta .$$

These means may depend on the fixed parameters, x, on many occasions in a nonlinear way. Because of this nonlinearity, and because there may often be several fixed parameters that label a case (lake), we cannot expect the means to lie on a straight line if data and fit are plotted against case number. To stress the analogy with (linear) regression, the authors have joined the means in successive lakes with straight line segments (cf. Fig. 2). However, because the lakes may be in any order, intermediate values have no significance, other than to improve readability of the graphs.

Similarly, we recognize the variability of the regression values or fit as the predictive posteriors $p(\eta \mid y_i)$ themselves. The posterior standard deviation, or posterior percentiles, e.g other exploratory data summaries, may serve as measures of the variability, or skewness, etc., of the regression. In Fig. 2 (broken lines), Bayesian "confidence bands" are depicted as the successive means plus or minus two times the respective prior and posterior standard deviations. These bands are symmetric about the mean. The predictive distributions themselves, both prior and posterior, may not need to be symmetric at all.

Now that we have defined regression, we can define the standard error of estimate of the regression as

$$\sqrt{\sum_i (y_i - \mathrm{Mean}(\eta_i))^2/n}$$

where Mean (η_i) is the regression estimate in case i. This standard error of estimate constitutes some point estimate of the posterior σ, or, in classical terms, the residual error.

2.6. Priors and posteriors according to Box and Draper

In fact, the formulae presented so far are just shells for probability functions to be filled in, and integrals to be worked out, either explicitly or numerically. The reader is referred to the literature cited to see what can be done with different types of models and priors. There is one set of combinations of models and priors due to Box and Draper (1965), Box and Tiao (1973/1992), which is very powerful for ecological models.

The basic assumptions are that ε is normally distributed, and that the prior probabilities of θ and $\log(\sigma)$ are approximately independent and each distributed uniformly.

Then, if

$$S = \sum_i (y_i - M(x_i, \theta))^2$$

is the sum of squared deviations between observations and model outcomes (i.e. the mechanistic part), the posterior marginal parameter distribution is proportional to:

$$p(\theta \mid y_i) \propto S^{-n/2}.$$

This is a remarkable result: it does not matter whether the model is nonlinear in the parameters; the familiar sum of squares pops up and is the main element in the power function that yields the posterior, apart from a scaling factor. Here information about the posterior σ is not present anymore, but can be derived from other formulae.

Note that the fixed parameters x used in the model may depend on the case i. This makes the method especially useful in a multi-lake survey, since conditions specific to a lake, e.g. depth, nutrient loading, and so on, can be taken into account. The uncertain parameters are common to all cases. Hence, part of the predictive success of a parameter combination may be due to the fixed parameters.

In the multi-variate case of two or more predictive variables, for example the prediction of chlorophyll-*a* (1) and total P (2), the two sums of squares are calculated, and the sum of products of deviations:

$$S_{ii} = \sum_u (y_{ui} - M_i(x_{ui}, \theta))^2 \quad (i = 1, 2),$$

$$S_{12} = \sum_u (y_{u1} - M_1(x_{u1}, \theta)) \cdot (y_{u2} - M_2(x_{u2}, \theta)).$$

Then, the posterior parameter distribution given actual data sets on both quantities is also remarkably simple (Box and Tiao, 1973/1992, p. 428):

$$p(\theta \mid y_{u1}, y_{u2}) \propto (S_{11} \cdot S_{22} - S_{12}^2)^{-n/2}.$$

This proportionality factor can be readily calculated for different parameter combinations θ.

If the number of data per predictive variable differs, then one may follow Box (1971) and calculate

$$p(\theta \mid y_{u1}, y_{u2}) \propto S_{11}^{-n_1/2} \cdot S_{22}^{-n_2/2}.$$

The price to pay is that the residual discrepancies are supposed to be uncorrelated.

2.7. Numerical approach: grids

To numerically exercise with the Bayesian method, we evaluated the posterior parameter distribution at a rectangular equally-spaced grid of discrete parameter values. This is not useful for high-dimensional parameter spaces, but it makes further statistical evaluations very easy to program.

The discrete parameter values are calculated from

$$\theta_j = \theta_{\min} + \frac{(j-0.5)}{nBin} \cdot (\theta_{\max} - \theta_{\min})$$
$$j = 1, \ldots, nBin$$

where *nBin* is the number of discrete values, or "bins", wanted, say 5 for exploratory evaluations, or anything higher one can afford in simulation time.

For example, for FiltMax with prior minimum 2.0 and prior maximum 6.0, five bins lead to the sequence: 2.4, 3.2, 4.0, 4.8, 5.6.

Then, the different parameters, which may differ in the number of discrete values (some coarsely, others finely gridded), are systematically combined to form a grid of parameter combinations. The model is applied for each parameter combination, as many times as there are cases (lakes) to be fitted. Thus, we varied 3 parameters with 5 bins each for 18 lakes, which means 2250 runs. Missing values are substituted for crashing runs, or runs out of bounds.

In the univariate predictive case (e.g. chlorophyll), each parameter combination yields 18 predictions, one per lake, and these are combined with the 18 observations to build a posterior value, proportional to its probability (scaling afterwards), by calculating the sum of 18 squared deviations, and raising this sum to the power $-18/2 = -9$. This yields a table of 125 posterior entries, also called "weights". If there were missing predictions for one or more lakes, that parameter combination gets zero probability, or zero weight.

One easily obtains one-dimensional marginal posterior parameter distributions, by summing for each bin value of a particular parameter all weights that relate to that bin value. Similarly, two-dimensional marginals can be formed for all pairs of parameters.

Treating the posterior parameter distribution as a joint discrete distribution, standard statistics can be calculated like weighted means, weighted standard deviations, weighted covariances and weighted correlation coefficients. Univariate means and standard deviations employ the univariate weights, bivariate covariances are based on the bivariate weights. Correlation coefficients are calculated from the weighted covariances and weighted standard deviations.

Since the parameter values form a regular grid, the joint posterior parameter distribution can either be perceived as a discrete distribution with probabilities attached to the bin mids, or as a histogram, i.e. a coarse approximation to a theoretically continuous probability density. The predictive values, however, result from a nonlinear model, and may have values irregularly clustered. For each lake, 125 predictive values (one per parameter combination) become available. To each of these 125 values a prior and a posterior weight is attached, coming from the parameter combination that gave rise to it, or the sum of the parameter combinations that gave rise to it. We have treated these in two ways: either as discrete distributions as such with the probabilities associated to the individual values, or as regular equal-bin histograms by adding the weights of all values falling in a bin. The raw discrete distributions have been used for the weighted means, weighted standard deviations, and other statistics.

There is obviously no difference between the statistical treatment of prior and posterior parameter and predictive distributions. The interesting consequence is that the simulations are done only once for all parameter combinations and are written to disk files. The prior and posterior statistical analysis can then be done afterwards on the basis of these files alone. This phase can be extended to an extensive multivariate analysis, regarding questions of model sensitivity and multiple correlation and regression between parameters and predictions. No re-running is necessary, until other parameters have to be varied, parameter ranges narrowed, or grids refined. This is perhaps a more convenient and clean procedure than mixing simulation with other iterative or optimizing searches.

3. Application to a multi-lake survey

3.1. Model and methods

3.1.1. The dynamic model PCLake

PCLake is a combined nutrients–food web model of shallow lake ecosystems. Its aim is to simulate the effects of an increase or decrease of the nutrients input (N, P, Si) in shallow water bodies on a number of biotic and abiotic variables, in relation to lake characteristics and additional restoration measures. It is also meant to be used as a tool for Dutch water quality policy to assess the critical nutrient load for restoration of eutrophic water bodies. *PCLake* is an extension of *PCLoos*, developed originally for the Loosdrecht Lakes (Janse and Aldenberg, 1990a,b; Janse et al., 1992), and has been applied to several other Dutch lakes (e.g. Janse et al., 1993). Mathematically, the model consists of a set of differential equations. The model has been implemented in the simulation programming package ACSL (Mitchell and Gauthier, 1991). A copy of the ACSL source code is available from the authors.

The model comprises both the water compartment and the upper sediment layer (Fig. 1). Internal nutrient cycles in the model system are completely closed. The trophic structure of the ecosystem has been modelled on the basis of functional groups as depicted in Fig. 1: phytoplankton, detritus (both in water and upper sediment), zoobenthos, zooplankton, benthivorous/planktivorous fish, piscivorous fish and submerged vegetation. In the current application, the last two groups, as well as the consumption by birds, have been left out to save computing time, as attention is focussed on phytoplankton-dominated cases. The phytoplankton is divided into three groups: diatoms, green and blue-green algae. Apart from feeding relations, also some "informational relations" are included, e.g. benthivorous fish may affect the resuspension. Also the physical and chemical processes of phosphorus (e.g. adsorption), nitrogen (nitrification, denitrification) and silica are described, as well as the exchange between sediment and water (sedimentation, resuspension, diffusion of nutrients). Parameter values have mainly been derived from research in the Loosdrecht Lakes (Van Liere and Gulati, 1992) and sometimes have been adjusted during calibration on data for the Loosdrecht and the Reeuwijk Lakes.

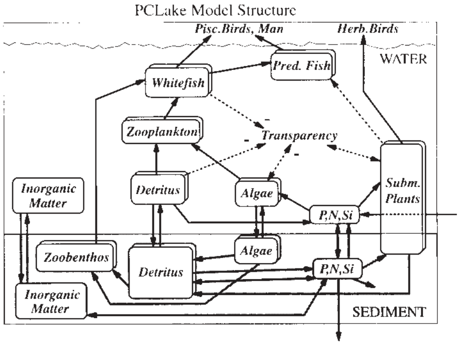


Fig. 1. Structure of the dynamic water quality model *PCLake*. Predatory fish, vegetation and consumption by birds are left out in the current application. State variables depicted with drop shadows are modelled in both dry-weight and nutrients. Algae are divided into three functional groups. Nutrients included are P, N and Si. Solid arrows: food web relations. Broken arrows: other ecological interactions. Mortality and respiration fluxes are not drawn.

In the current study, the model was run under steady state, average Dutch summer conditions (water temperature 20°C, day length 16 h, daily irradiation $1.5 \cdot 10^7 \ \mathrm{J \cdot m^{-2} \cdot d^{-1}}$). The main case-specific input data are: water depth, water retention time, nutrient inputs, average settling and resuspension rates (dependent on average wind speed distribution, fetch and lake morphometry) and the sediment dry-weight and iron content, as well as initial values of all state variables. Outputs are the average concentrations of all model components and the matter fluxes between them, in terms of dry weight and nutrients, as well as derived water quality variables like

Table 1
Lake-specific data and parameters

no.	Name	Chl-*a* (mg m^{-3})	Tot. P (mg P l^{-1})	Depth (m)	Water inflow (mm d^{-1})	Infiltr. (mm d^{-1})	PLoad (mg P m^{-2} d^{-1})	NLoad (mg N m^{-2} d^{-1})	Sedim. DW (–)	Sedim. Fe (g Fe g^{-1} DW)	Est. rel. resusp (–)	Est. rel. settl. (–)
1	Naarden	27	0.060	0.90	10.0	1.2	0.68	6.8	0.17	0.021	3.0	0.90
2	Brielle	34	0.240	5.50	48.7	1.0	16.33	236.7	0.24	0.026	3.0	0.90
3	Braassem	43	0.460	3.50	42.7	1.0	28.30	218.7	0.20	0.025	22.5	0.70
4	Kaag	47	0.690	2.80	88.6	1.0	58.87	307.2	0.20	0.014	22.5	0.70
5	Waalboezem	50	0.220	3.75	33.1	1.0	17.00	183.7	0.20	0.011	7.5	0.70
6	Vuntus	83	0.091	1.36	5.0	0.1	0.70	7.0	0.09	0.014	6.0	0.70
7	Elfhoeven	88	0.180	2.40	30.7	0.3	11.60	116.0	0.15	0.016	3.0	1.00
8	Breukeleveen	94	0.097	1.45	10.4	2.0	1.70	17.0	0.09	0.015	15.0	0.50
9	Wolderwijd	97	0.260	1.62	2.1	2.0	1.10	16.9	0.71	0.005	45.0	0.50
10	Nieuwenbroek	101	0.110	1.60	5.0	0.3	1.00	10.0	0.12	0.011	6.0	0.60
11	Loosdrecht	115	0.085	1.91	6.8	1.5	0.95	9.5	0.09	0.020	30.0	0.50
12	Veluwe	120	0.180	1.30	9.2	2.0	3.08	49.2	0.71	0.016	45.0	0.50
13	Brandemeer	124	0.190	1.25	44.5	0.3	18.99	305.4	0.12	0.031	7.5	0.70
14	Geerplas	125	0.290	2.50	4.9	0.3	1.00	10.0	0.06	0.005	15.0	0.70
15	Sloten	135	0.180	1.60	9.3	0.3	3.67	72.4	0.60	0.004	30.0	0.50
16	Tjeukemeer	161	0.220	1.70	9.2	0.3	4.12	70.2	0.65	0.007	30.0	0.50
17	Amstelveen	173	0.260	1.80	5.5	0.3	2.30	23.0	0.05	0.012	15.0	0.70
18	Bergseplassen	288	1.464	2.00	18.2	1.0	55.59	307.7	0.20	0.027	6.0	0.70

chlorophyll-*a*, total phosphorus and Secchi depth. For the current analysis, we used the chlorophyll-*a* [$\mathrm{mg \cdot m^{-3}}$] and total phosphorus [$\mathrm{mg \cdot l^{-1}}$] concentrations.

3.1.2. Selection of parameters and data

The model was run until steady state was reached for 18 cases (lakes) for which both the above-listed input parameters and data of the selected output variables were available (Table 1). Data were derived from CUWVO (1987), Hooykaas et al. (1989), Van der Vlugt and Klapwijk (1990), Van der Does et al. (1992), Van Liere and Gulati (1992), from staff of the Water Boards of Rijnland and Amstel- en Gooiland and, occasionally, from own estimates.

A grid was set up for three parameters with for each parameter five uniformly distributed values (within a predefined range) representing, in Bayesian terminology, a uniform prior parameter distribution $p(\theta)$. The parameters chosen are the detrital settling velocity (*VeloSedDet*, $\mathrm{m \cdot d^{-1}}$), the maximum filtering rate of the zooplankton (*FiltMax*, $\mathrm{m^3 \cdot g^{-1} \cdot d^{-1}}$) and the specific extinction of blue-green algae (*ExtSpecBlue*, $\mathrm{m^2 \cdot g^{-1}}$). The parameter values are summarized in Table 2. All other, ca. 130, parameters were kept at their nominal value. Thus, 125 runs were performed for each case. The integration was performed by means of a second-order Runge–Kutta–Fehlberg algorithm with a variable step size. A Range Check procedure ensured runs that produced very unrealistic values to be interrupted in order to prevent numerical errors and a collapse of the programme. (This turned out to be necessary in very few runs, though).

The results of the simulations, called η, were collected in files and fed to a Pascal computer programme to compute the Bayesian statistics. For both variables, we used the log10-transformed values of predictions and data in the respective sums of squares, and sum of products. This was done because the *percentual* deviation is the most meaningful for the output variables chosen. Statistics calculated are: prior and posterior predictive distributions, their summary statistics, the standard error of estimate, the average standard error of the predictions and the prior and posterior parameter distributions and pair-wise correlations of the three parameters. All of those were calculated according to the equations in Section 2, for four situations:

- based on the prior parameter distribution (viz. without making use of the data);
- based on the posterior distribution, making use of the chlorophyll-*a* data only;
- idem, based on the total P data only;
- idem, based on the data for both variables.

3.2. Results and discussion

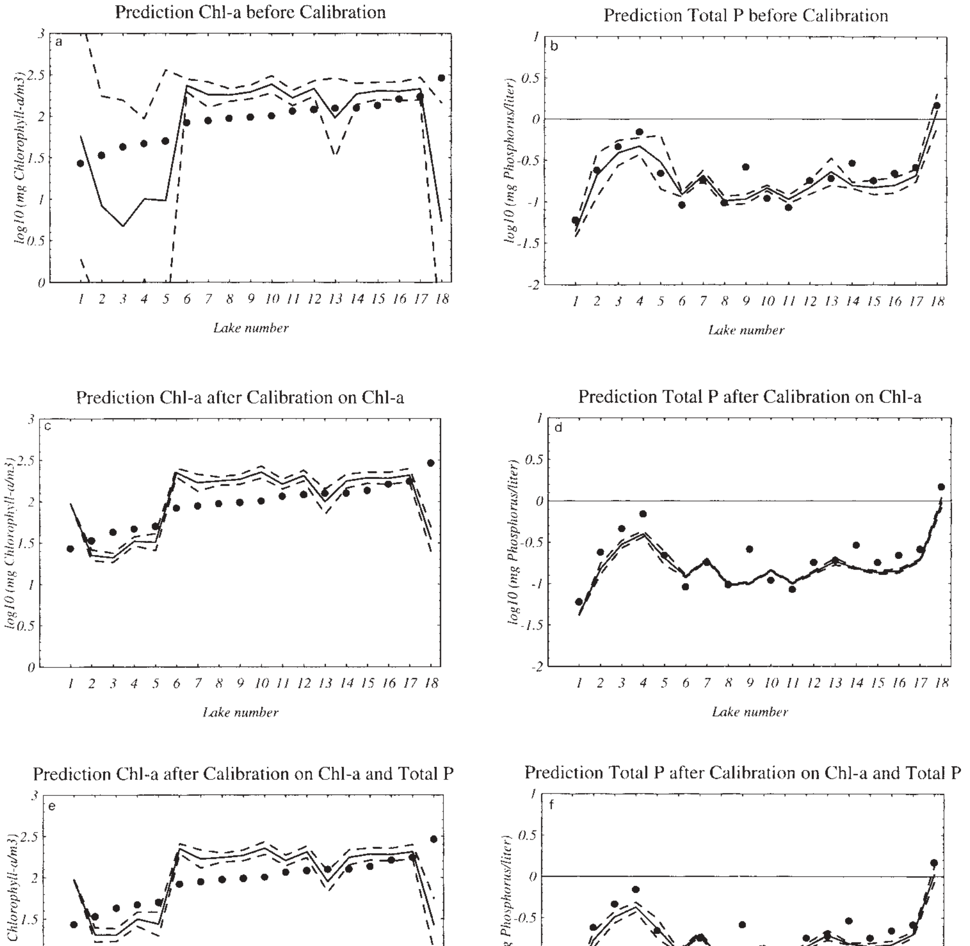
3.2.1. Regressions and standard errors of estimate

Fig. 2 shows the prior and posterior predictive means ("regressions"), and plus/minus two-sigma confidence bands, of simulated steady state chlorophyll-*a* and total P concentrations compared to observed summer averages for 18 different lakes. The lakes have been arranged in order of ascending chlorophyll-*a* concentration.

Figs. 2a and b depict the prior fit without using any observational information, in fact representing the means of pure uncertainty analysis. We observe that mean chlorophyll-*a* predictions show large deviations, while mean total P predictions are quite good from the outset. The substantial

Table 2
Uncertain parameters

Parameter	Explanation	Unit	Value 1	Value 2	Value 3	Value 4	Value 5
VeloSedDet	detrital settling velocity	$\mathrm{m\ d^{-1}}$	0.075	0.125	0.175	0.225	0.275
FiltMax	maximum filtering rate of zooplankton	$\mathrm{m^3\ g^{-1}\ d^{-1}}$	2.4	3.2	4.0	4.8	5.6
ExtSpecBlue	specific extinction of blue-greens	$\mathrm{m^2\ g^{-1}}$	0.17	0.21	0.25	0.29	0.33



Prediction Chl-a before Calibration

Prediction Total P before Calibration

Prediction Chl-a after Calibration on Chl-a

Prediction Total P after Calibration on Chl-a

Prediction Chl-a after Calibration on Chl-a and Total P

Prediction Total P after Calibration on Chl-a and Total P

Fig. 2. Prior and posterior means of predictive distributions (solid lines) of steady state chlorophyll-*a* and total P concentrations compared to observed summer averages for 18 lakes. Broken lines indicate plus and minus two standard deviations from the mean respectively. a, b: Prior predictions, before calibration to data. c, d: Posterior predictions, after calibration on chlorophyll-*a* data. e, f: Posterior predictions, after calibration on both chlorophyll-*a* and total P data.

underpredictions in lakes #1 to 5 are accompanied by large confidence bands. The symmetry of these bands is misguiding here, since the prior predictive distributions are heavily skewed to the left for these cases.

If chlorophyll-*a* data are used for the posterior predictive distributions, the mean regression fit on chlorophyll is much improved (Fig. 2c), that on total P (Fig. 2d) looks similar to the prior mean predictions (Fig. 2b). The confidence bands, however, shrink dramatically in both Figs. 2c and d. Although the predictions seem to capture trends very well, almost all data points are outside the confidence bands after calibration. This means that there is substantial variation left, that is not predicted by the mechanistic part of the model per se. As explained above, this does not mean that the model cannot be used for predictive purposes. The mechanistically unexplained part is estimated through the standard error of estimate of the regression. This "error" should be added to any managerial or lake-specific prediction.

The mean regression predictions, when using information on both chlorophyll and total P (Figs. 2e and f), do not differ very much from the ones using chlorophyll-*a* data alone. To match both observational quantities, the confidence bands have increased somewhat with respect to calibration on chlorophyll-*a* alone.

In all chlorophyll-*a* graphs (a, c, and e), there is a group of lakes which are underpredicted (nos. 2, 3, 4, 5, 13 and 18), the others are overpredicted. For all lakes, except no. 1, the regression estimates of chlorophyll-*a* are closer to the data than the prior ones (compare Figs. 2c and e to 2a).

Table 3
Standard errors of the estimate

	Prior	Posterior calibr. on chl.	Posterior calibr. on PTot	Posterior calibr. on both
log(Chla)	0.583	0.333	0.598	0.357
factor	3.83	2.15	3.96	2.28
log(PTot)	0.147	0.175	0.142	0.162
factor	1.40	1.50	1.39	1.45

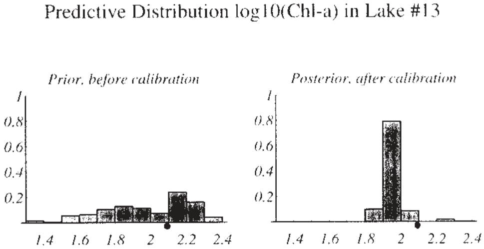


Fig. 3. Prior (left) and posterior (right) predictive distribution for chlorophyll-*a* in lake #13. Histograms correspond to Figs. 2a and 2e, entry #13, respectively. The posterior distribution is based on calibration on both chlorophyll-*a* and total P data in all lakes simultaneously. Dots indicate summer-averaged measurement (from Table 1) of $\log_{10}(124$ mg chlorophyll-$a/\mathrm{m}^3) = 2.09$ in this lake.

It is difficult to see some of the improvements between different fits. Therefore, estimates of the residual error, i.e. the standard errors of estimate are calculated. The standard error of estimate decreases for log10(chlorophyll-*a*) from 0.583 log-units for the prior to 0.333 log10-units for the regression on chlorophyll-*a* alone(Table 3). This means a decrease of the *relative* error from nearly a factor 4 to just over a factor 2.

By calibration on total P alone (not shown in Fig. 2), however, the fit of chlorophyll-*a* was not improved. Calibration on both variables gives a standard error of 0.357 log10-units (or a factor 2.28), which is slightly worse than the fit on chlorophyll-*a* alone.

For log(total P), the prior fit is much better than for chlorophyll: 0.147 log10-units, which is equivalent to a factor 1.40. The fit improves very little by calibration on total P and worsens somewhat by calibration on chlorophyll-*a* alone or calibration on both quantities.

The conclusion can be drawn that chlorophyll-*a* is particularly sensitive to the three parameters: the fit can be considerably improved by calculating posterior weights for the simulations based on chlorophyll-*a* data, while total P is determined to a large extent by the lake-specific input parameters already (the *x* matrix, Table 1). Chlorophyll-*a* and total P tend to have conflicting interest in optimum parameter combinations. However, the simultaneous fit on both variables is quite near the respective univariate optimum fits.

Table 4
Standard errors of predictions

	Prior	Posterior calibr. on chl.	Posterior calibr. on PTot	Posterior calibr. on both
log(Chla)	0.276	0.037	0.185	0.046
factor	1.89	1.09	1.53	1.11
log(PTot)	0.053	0.014	0.037	0.022
factor	1.13	1.03	1.09	1.05

3.2.2. Standard errors of prediction

Confidence bands are just summarizing statistics for the predictive distributions themselves. Fig. 3 gives an example of a prior and posterior predictive distribution, in this case chlorophyll-*a* in lake #13. The prior predictive distribution (Fig. 3 left) expresses the uncertainty without using the data. The variation results from the variation in the three parameters only. Fig. 3 (right) shows the posterior predictive distribution after calibration on chlorophyll-*a* and total P data in all lakes simultaneously. In fact, this distribution can be considered as the variation of the regression in the Bayesian sense (Section 2.5), and can be compared to classical confidence intervals for the mean. The uncertainty of mean predictions is obviously smaller than the overall deviation between data and means as indicated by the standard error of estimate, but in this case, chlorophyll-*a* in lake #13 (124 mg $\cdot$ m^{-3}) is within the reach of the predictive distribution.

Roughly the same trends as in the standard errors of estimate were found in the average standard errors of the predictions, i.e. the uncertainties of the regression estimates (Table 4). Also, one observes that predictive uncertainties of one output variable are not worsened by fitting on the other output alone, as occurred with the residual errors. There is at least a slight improvement each time. Of course, at this stage, conclusions apply only to the three-parameter analysis described here; the results might be different when more parameters are considered.

3.2.3. Some systematic and individual deviations

The group of underpredicted lakes coincides largely with the group where green algae are predicted in most runs (only no. 7, which also belongs to this group, is overpredicted). In the other lakes, blue-green algae are predicted. This

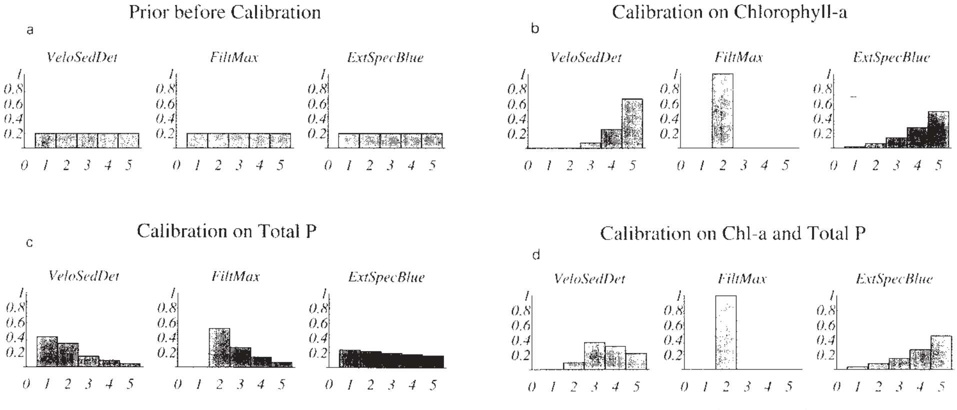


Fig. 4. Marginal univariate prior and posterior parameter distributions for detrital settling velocity (*VeloSedDet*), maximum filtering rate (*FiltMax*), and specific extinction of blue-green algae (*ExtSpecBlue*). a: Prior marginals before calibration. b: Posterior marginals after calibration on chlorophyll-*a*. c: Posterior marginals after calibration on total P. d: Posterior marginals after calibration on both chlorophyll-*a* and total P. Parameter indices 1,...,5 correspond to values in Table 2.

sen as uniform, viz. all five values have equal probabilities (Fig. 4a).

Calibration on chlorophyll-*a* alone (Fig. 4b) results in a strong preference for the higher values of the detrital settling velocity (*VeloSedDet*), value #2 (3.2) for the maximum filtering rate (*FiltMax*) and also preference for the higher specific extinction of blue-greens (*ExtSpecBlue*).

Calibration on total P alone (Fig. 4c) yields different results: a preference for the lower settling rates, also preference for one value of the filtering rate, but less explicit (also higher values are possible) and as good as no opinion about the specific extinction of blue-greens.

Calibration on both data sets (Fig. 4d) results in a compromising optimum curve for the settling rate; the other two distributions resemble those of the chlorophyll-*a* calibration. This indicates that both variables have something to tell about the settling rate, but each in a different way, while for the other two parameters the influence of chlorophyll-*a* seems predominant.

The same trends can be detected, when the parameter distributions are expressed in terms of mean and standard deviation (Table 5). In all cases, except the specific extinction calibrated on total P, the posterior standard deviation of the univariate marginal parameter distributions is considerably lower than the prior one. In this one exceptional case, total P seems insensitive to the parameter, as one would expect indeed, resulting into indifference of total P about the value of the specific extinction coefficient of the blue-greens.

3.2.5. Two-parameter distributions

Fig. 5 shows the marginal bivariate prior and posterior parameter distributions between detrital settling rate (*VeloSedDet*) and maximum filtering rate (*FiltMax*) for the three different regressions.

Table 5
Mean and standard errors of parameters

	Prior	Posterior calibr. on chl.	Posterior calibr. on PTot	Posterior calibr. on both
VeloSedDet	0.175	0.254	0.128	0.207
σ	0.071	0.033	0.057	0.047
FiltMax	4.000	3.201	3.807	3.202
σ	1.131	0.034	0.752	0.043
ExtSpecBlue	0.250	0.296	0.243	0.291
σ	0.057	0.041	0.056	0.045

Table 6
Parameter correlations

	VeloSedDet	*FiltMax*	*ExtSpecBlue*
(a) calibration on chlorophyll-*a*			
VeloSedDet	1.0	0.026	0.066
FiltMax		1.0	−0.037
ExtSpecBlue			1.0
(b) calibration on total P			
VeloSedDet	1.0	0.50	0.019
FiltMax		1.0	−0.012
ExtSpecBlue			1.0
(c) calibration on both			
VeloSedDet	1.0	0.070	0.161
FiltMax		1.0	−0.026
ExtSpecBlue			1.0

The correlation coefficients between the parameters are very low in most cases (Table 6). Only in case of calibration on total P, there appears to be some correlation ($r = 0.50$) between detrital settling rate and filtering rate (Fig. 5c). This may be attributed to some indirect effect.

4. Conclusions

It can be concluded from this study that Bayesian Statistics provides a promising framework for the integration of statistical and dynamical models in water quality assessment. The approach unites uncertainty analysis, calibration of parameters, regression analysis, and model validation in one methodology.

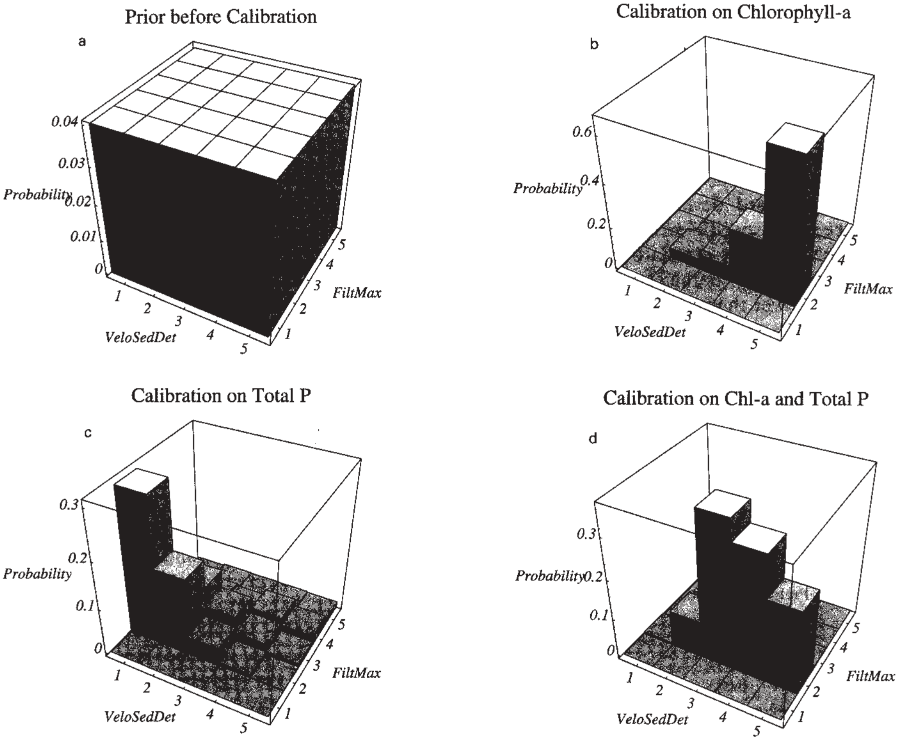
In this way, it is possible to fit a complex dynamic model on data of a multi-lake survey, and to calculate parameter and predictive uncertainties, both a priori and after confrontation with available data.

Although only three parameters were varied, residual errors of the fit on chlorophyll and total P were significantly reduced. Also, the predictive uncertainty of the regressions were smaller than the prior predictive uncertainties without using observational information. Whether the fits can be further improved by taking the uncertainty of other parameters into account, and what the in-division also coincides with a division based on water inflow: the underpredicted cases all have a water inflow exceeding 10 mm · d^{-1} due to inflow of water containing some algae already from the main water system in the Netherlands. The lakes with a predicted blue-green dominance also show this in reality (except for no. 1). The lakes where green algae are predicted in most runs in reality show either a green algal dominance or a dominance of *Microcystis*, a floating cyanobacterium which is not modelled separately. The result for the outlier no. 18, a lake with a very high external P loading, might be attributable to a wrong estimate of the ratio dissolved/particulate P in the input; an extra run using a higher ratio gave better results. We left this lake unchanged in the analysis to illustrate how this technique can point to possible explanations of individual departures.

An interesting aspect is that within the "blue-green" group, the residual error of the chlorophyll-*a* prediction decreases with increasing chlorophyll-*a* and, mostly, total P. This points towards some other parameters in the model to be calibrated, such as the blue-greens' phosphorus affinity.

3.2.4. One-parameter distributions

The marginal univariate posterior parameter distributions of the three parameters were analysed. The prior parameter distribution was cho-


Prior before Calibration

Calibration on Chlorophyll-a

Calibration on Total P

Calibration on Chl-a and Total P

Fig. 5. Marginal bivariate prior and posterior parameter distributions for detrital settling velocity (*VeloSedDet*) and maximum filtering rate (*FiltMax*). a, b, c, and d as in Fig. 4. Parameter indices 1,...,5 correspond to values in Table 2.

fluence will be on predictive uncertainties, needs further analysis.

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4. Sensitivity and uncertainty analysis and calibration

4.1. Approach and methods

Ecosystem models are often useful tools for the study of environmental problems. They contain, however, a great deal of uncertainty, coming from different sources (e.g. Janssen et al., 1990). (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 nonlinear 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 & Omlin, 1997). 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 & Chapra, 1983, p. 51; Klepper, 1997; Reichert & Omlin, 1997; Omlin & Reichert, 1999; Hilborn & 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. It is important to bear in mind that the focus in this project is on the model predictions; the parameter values are only of intermediate interest. The effects of these uncertainties on the model results are to be assessed and accounted for when the model is used for predictions (uncertainty analysis). The outcome of the model can thus be expressed in probabilistic terms.

According to Bayes' theorem, the posterior parameter distribution, conditional on the measurements, called $p(\theta \mid y_i)$, is proportional to: $p(y_i \mid \theta) * f_{prior}(\theta)$,
in which $p(y_i \mid \theta)$ is the *likelihood function* of the model, the degree of fit of different parameter combinations given the actual observations, and $f_{prior}(\theta)$ is the prior parameter distribution, i.e. the assumptions on the parameters before looking at these observations. The set of predictions based on this prior parameter distribution is called the *prior predictive distribution*.
Hence, the final parameter combinations are derived from a combination of (a) prior knowledge, e.g. derived from systems' knowledge, literature, experimental data, field data or previous calibration, and (b) evaluation and re-adjustment of parameter values in view of measured data ('calibration'). This step also involves validation, if the model is applied to different cases. The parameter set after calibration is thus called the posterior parameter distribution, and the resulting simulations the *posterior predictive distribution*. In fact, every (combination of) parameter value(s) is given a weight (likelihood), which increases with the degree of fit between model and data.
In practice, the weight can be based on the sum of squared residuals (differences between simulations and data) as commonly used in regression analysis (Box & 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:

$$SOS = Sum_i(y_i - M(x_i, \theta))^2$$
$$p(\theta \mid y_i) \sim SOS^{-n/2}$$

If two or more predictive variables are used, the probability function can be approximated as the product of the sum-of-squares:

$$p(\theta \mid y_1, y_2) \sim SOS_1^{-n1/2} {}_* SOS_2^{-n2/2}$$

with n1 and n2 the number of observations for each variable.

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 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 is 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 chapter, the PCLake model is evaluated by a method combining these three steps, *viz.* sensititvity analysis, calibration and uncertainty analysis, using a Bayesian likelihood measure based on a multi-lake data set. Finally, the model is used to calculate threshold loading levels for the transition between the phytoplankton- and the vegetation-dominated state, which is an important (derived) output variable. The dependence of this level on input factors as well as the uncertainty due to the variation of model parameters, is determined.

Fig. 4.1 gives a schematic overview of the model analysis procedure. A distinction is made between input factors and model parameters. 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). The question whether a certain quantity is regarded as parameter or as input factor is of course dependent on the type and scope of the model, but a workable definition was made within the context of this study (a complete list can be found in the appendix and the user's manual, Janse (2003)).

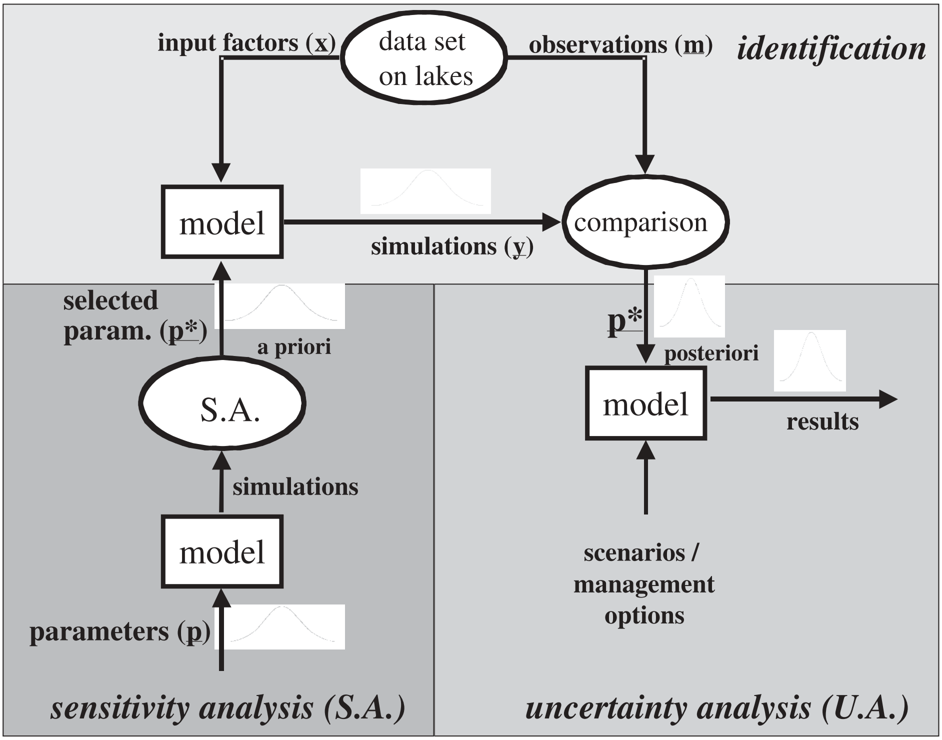


Fig. 4.1. *Schematic view of the procedure of model analysis applied. p = distribution of all parameters, p* = distribution of selected parameters.*

Step A: sensitivity analysis (S.A.).

The aim of this step is to select the most sensitive parameters. This was performed by applying several sensitivity analysis methods. The focus was 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 analysis was applied not only to the main output variables themselves (e.g. algal biomass), but also to the *likelihood* (goodness of fit) of these values (e.g. the degree of conformance between simulations and measurements of algal biomass). This is a combination of GSA-GLUE: Global Sensitivity Analysis and Generalized Likelihood Uncertainty Estimate (Ratto et al., 2000, 2001).

The sensitivity analysis itself made use of two methods (Saltelli et al., 2000):

a. a *screening method* in order to find the set of parameters and input factors that are globally spoken the most influential. This was performed by the Morris method (Saltelli et al., 2000; Morris, 1991; De Wit, 2000).
b. a *semi-quantitative method,* applied to the subset found by the previous method. For this, the FAST method (Saltelli et al., 2000) was chosen.

Some analyses were also compared with the more ‘classical’ methods of linear regression analysis and regression tree analysis.

Step B: identification.

After a pre-calibration by hand, a more formal calibration of a selected subset of parameters was performed. This was a combined calibration on data from a multi-lake dataset. The model is run for all cases (with known input, **x**) for a sample of the selected parameters (**p**). The likelihood (‘fit’) of each run is assessed by comparison of the output (**y**) with the observations (**m**). We aimed at maximum likelihood for all lakes and output variables together (a ‘compromise fit’) rather than calibration on a specific lake. The procedure is further explained in § 4.3.

Step C: uncertainty assessment (U.A.).

As there are, for a number of reasons, no unique answers, there will remain an (a posteriori) *uncertainty* in the predictions (i.e., after the confrontation of the model with the data). We focussed on the uncertainty in the critical loading levels as an important derived model result.

4.2. Sensitivity analysis

Many methods for sensitivity analysis are available. They can be roughly divided in three groups (Saltelli et al., 2000): screening methods, local methods and global methods. Following the guidelines in this textbook, a two-step aproach 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.

4.2.1. Screening phase

Method

The screening phase was performed using the Morris method, having in view a rough selection of those parameters that control most of the output variability, with a relatively low computational effort (Saltelli et al, 2000). The Morris design can be considered as an OAT ('one-at-a-time') design repeated at different points in the input space, thereby constituting a global sensitivity experiment. This is in contrast to a local experiment, in which the factors vary only around their nominal value and the results depend on the choice of these values. The Morris method estimates the effect of each factor on a chosen output variable by computing a number of 'samples', *r*, of local sensitivity measures (coefficients) at different points $\mathbf{x}_1,\ldots,\mathbf{x}_r$ in the input space, and then calculating their average and spread (standard deviation) (Morris, 1991; De Wit, 2000). The local sensitivity measures are called 'elementary effects'. Based on a specification file with the minimum and maximum values for every parameter and input factor, 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 our case, we used $p=8$ and $r=15$, values that are usually sufficient for the purpose (P. Heuberger, pers. comm.). The method does not rely on specific assumptions on input/output behaviour. The information one gets on the parameters is qualitative (ranking) rather than quantitative. The method allows to determine which factors have either negligible effects, linear and additive effects, or non-linear or interaction effects. (The method does not distinguish between those two possibilities.) It can provide an 'overall' measure of the interactions of a parameter with the rest of the model, but individual interactions among factors can not be estimated.

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

Results

The 'elementary effects' were calculated with respect to all important output variables. *Fig. 4.2* shows the results for chlorophyll-a and vegetation biomass. The place of every parameter is depicted as a circle (with the parameter number given to the right of it) in the plane of μ and σ, the means and standard deviations of the 'elementary effects', which have the same units as the output variable (viz. mg m^{-3} for chlorophyll-a and g m^{-2} for vegetation). (The parameters were scaled already according to their range.) A parameter with a μ close to zero has little effect on the output, a positive μ means that the parameter has an 'overall' positive effect on the output, and a negative μ the opposite. A low value of σ means that the effect of the parameter is mainly linear and is not much affected by the values of others, a high σ means that the effect is non-linear and/or shows interaction with others. The two lines in the plot forming a wedge correspond to $\mu \pm$ twice the standard error of the mean (SEM), with $\mathrm{SEM} = \sigma/\sqrt{r}$. If a point is situated outside the wedge, this can be interpreted as an undoubtedly positive or negative impact of the parameter. The method is qualitative, it gives a ranking of parameters but does not provide a significance level or the like.

An important conclusion that can be drawn from these plots is that for most parameters in PCLake, the effect is non-linear and/or interactive.

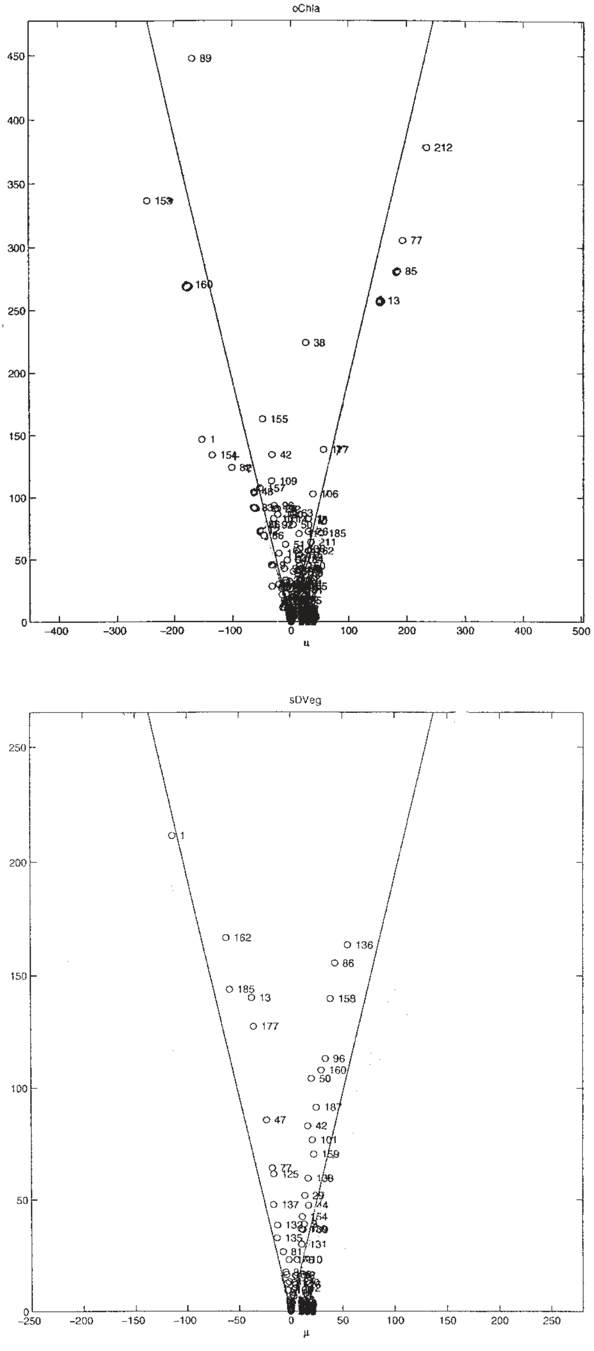


Fig. 4.2. *Results of Morris sensitivity analysis. The place of every parameter is depicted in the plain of the mean and standard deviation of their elementary effect. Parameter numbers are explained in table 4.1. a, chlorophyll-a; b, submerged vegetation biomass.*

For all output variables, a ranking of the parameters and input factors according to their impact has been made. The impact has been defined as the length of the vector of the parameter in the μ-σ plain. *Table 4.1* shows the top-25 for 10 output variables. Some effects are evident. Vegetation biomass, for instance, is affected most, and undoubtedly negative, by the water depth (#1), while the external P load and also the water depth primarily affect the TP concentration. However, most output variables are influenced by a large number of parameters, not only the ones that directly affect their own growth, but also parameters that play a role in other parts of the model. This points to the many indirect effects that can (potentially) occur in the model.

We repeated the Morris analysis starting with a different seed of the random number generator, giving rise to another sample based on the same specification file. While the more obvious effects still hold, it turns out that some parameters in the list are now replaced by related parameters; e.g. maximum growth rate is interchangeable with respiration or mortality rate of the same group, or with the half-saturating food value.

Likewise, a cluster analysis of the mean elementary effects of the parameters on all the output variables revealed that related parameters end up in the same cluster. This conclusion is comparable to the one drawn by Klepper (1989, 1997) and Klepper et al. (1994) on a model of an estuarine lake by a somewhat different clustering method.

The linear regression method that was applied to the same sample as a comparison, came up with a partly different list of significant parameters. This can be understood from the fact that the model shows many non-linear or interactive effects, that are not, or in a misleading way, grasped by a linear approach.

Table 4.1. Ranking of parameters and input factors according to sensitivity (Morris method). Only the 25 most sensitive ones are shown.
Note: The abbreviations are explained in the Appendix. 'coPIn' and 'coNIn' denote the P and N input concentrations, resp.; 'cFunTauResus' and 'cFunTauSet...' are lumped parameters of resuspension and settling rates. The numbers in the chlorophyll and vegetation columns correspond to those in Fig. 4.2.

Rank	Chlorophyll-a	#	Vegetation	#	Secchi	Pred.fish	Whitefish	Cyanob.	Diatoms	Greens	Ptot	Ntot
1	cVSetGren	89	sDepthW0	1	kDRespZoo	cFiltMax	fDAssZoo	cQIn	kDRespDiat	cFiltMax	coPIn	coNIn
2	coNIn	212	kDRespZoo	162	fDAssFiJv	hFilt	cFiltMax	cVSetGren	cSiDDiat	cVSetGren	sDepthW0	cFiltMax
3	cFiltMax	153	cQ10RespVeg	136	cFunTauSetDiat	cFunTauResus	kDRespZoo	sDepthW0	cMuMaxDiat	cMuMaxGren	cQIn	cQIn
4	cMuMaxGren	77	kDRespGren	86	cPrefDet	fDAssZoo	cTmOptFish	cMuMaxGren	kResusPhytRef	cQIn	cMuMaxGren	fNDissIn
5	cChDGrenMax	85	kDAssFiJv	185	kDAssFiJv	hDFishPisc	kDAssFiJv	cTmOptBlue	cFunTauSetDiat	cVSetIM	cQInf	sDepthW0
6	fDAssZoo	160	cFiltMax	153	fDAssZoo	cLDayAve	kDRespDiat	cLDayAve	cTurbDifNut	coNIn	kResusPhytRef	cTurbDifNut
7	cVSetIM	13	cVSetIM	13	hFilt	cExtSpIM	fDAssFiJv	kDRespBlue	cVSetDiat	cDCarrZoo	kDMinDetS	cVSetIM
8	cQIn	38	cDCarrZoo	155	coNIn	kHarvPiscSum	cVSetIM	coPIn	cQIn	fDAssZoo	cVSetGren	cQInf
9	sDepthW0	1	cDCarrFish	177	cFiltMax	cVSetIM	hFilt	kDRespZoo	sDepthW0	cExtSpGren	fDAssZoo	cDCarrZoo
10	hFilt	154	cNDGrenMin	96	cVSetIM	kDAssBent	sDepthW0	cQInf	cMuMaxGren	fNDissIn	kDRespZoo	cFunTauResus
11	cDCarrZoo	155	fDAssZoo	160	cQIn	cSigTmZoo	kDAssBent	coNIn	kDMinDetW	sDepthW0	cLDayAve	cLDayAve
12	cExtSpGren	82	kResusPhytRef	50	cMuMaxBlue	cPDBlueMin	coPIn	cMuMaxBlue	coNIn	cDCarrFish	cTurbDifNut	kDRespZoo
13	cDCarrFish	177	fDAssFiJv	187	kDMinDetS	cDCarrPiscMin	cFunTauSetDiat	cPDBlueMin	fDAssFiJv	hFilt	kDRespBlue	kDAssFiJv
14	fNDissIn	42	cFunTauSetDiat	47	sDepthW0	hDZooFiJv	cExtSpDet	kDAssFiJv	kDRespZoo	cKPAdsOx	cFiltMax	kDMinDetS
15	cFunTauSetGren	48	fNDissIn	42	cDCarrFish	fDAssFiJv	fAgeFish	cVSetIM	cPDDiatMin	cTmOptFish	cFunTauSetGren	cMuMaxGren
16	cPrefGren	157	cTmOptBlue	101	cMuMaxGren	coPIn	cFunTauSetOM	cExtSpBlue	hDZooFiJv	cFunTauSetGren	cVSetIM	cKPAdsOx
17	kDRespBlue	109	cPrefDet	159	cDCarrZoo	cQIn	cDCarrFish	cMuMaxVeg	cVNUptMaxGren	cPDGrenMin	cDCarrFish	kResusPhytRef
18	hLRefGren	83	cMuMaxGren	77	fNDissIn	cTmOptBlue	cPrefDet	cTurbDifNut	fNDissIn	kDRespDiat	cQ10RespVeg	fDAssZoo
19	cChDBlueMax	106	fRootVegWin	125	cFunTauResus	fPO4In	cFunTauSetIM	cFunTauSetIM	cPrefDiat	hLRefGren	cFunTauSetIM	hFilt
20	hDZooFiJv	186	fWinVeg	138	cPDBlueMin	cTmAve	fNDissIn	kMortBlueW	cAffNUptGren	cPrefGren	cMuMaxDiat	cVSetDet
21	cNDGrenMin	96	cKPAdsOx	29	cLDayAve	cPrefGren	hDZooFiJv	fPO4In	cFunTauSetGren	kDRespGren	cVSetDet	fMarsh
22	fDAssFiAd	192	cLDayAve	44	cExtSpBlue	cExtSpGren	cFunTauResus	cTmOptZoo	kDRespVeg	cFunTauResus	kMortVegMin	cDCarrFish
23	cKPAdsOx	29	kMortVegMin	137	coPIn	kDRespDiat	kHarvFishSum	kMortVegMin	cExtSpDet	cExtSpDet	cFunTauResus	
24	cFunTauResus	12	hFilt	154		kDRespZoo	cVSetDet	cFunTauResus		cFunTauSetOM	fRootVegWin	
25	cTmOptFish	180	cQInf	9		kDAssFiJv	kMortBent	cAffPUptBlue		hDZooFiJv	kDRespGren	

4.2.2. Second step: FAST method

Method

A subset of parameters (and no input factors), selected in the 'screening phase', was analysed 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).

We applied the method to the output variables directly and to their likelihood (as compared to the multi-lake data set, see next paragraph). The 16 selected parameters are listed in Table 4.2. Ten other parameters were coupled to the sampled parameters (for instance maximum growth rate and respiration rate were coupled), in order to achieve the most reasonable parameter sets while reducing the computational demand. The method was later also applied to the critical load, see § 4.5.

Results

Fig. 4.3 shows the results of the FAST method applied to the likelihood measure (for the 43 lakes combined) for six output variables, viz. chlorophyll-a, Secchi depth, vegetation cover, blue-greens, total N and total P, as well as for the combined likelihood measure, ϕ_{tot}. The total-order effects are shown (scaled to 100%), so including the direct and indirect effects of the parameters. 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 concentration in the sediment 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.

4.2.3. Conclusions

With some caution, the sensitivity analysis points to the following ranking of parameters and factors for which the model is the most sensitive. Parameters are in normal typeset, input factors in italics. Related parameters are mentioned in combination.

P loading
N loading
water depth
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

Hence, the first important conclusion is 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 candidates to be further assessed during calibration. Most of these parameters are *a priori* judged as difficult to determine and probably quite variable in nature.

Table 4.2. 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
coPO4Max	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 juvenile whitefish
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 x hFilt		l mg^{-1}D d^{-1}	max. zooplankton filtering rate
hDZooFiJv	= 5 x kDAssFiJv		mgD l^{-1}	half-sat. food conc. for juvenile whitefish
kDRespGren	= 0.033 x cMuMaxGren		d^{-1}	green algal respiration rate
kDRespDiat	= 0.05 x cMuMaxDiat		d^{-1}	diatoms respiration rate
kDRespBlue	= 0.04 x cMuMaxBlue		d^{-1}	cyanobacterial respiration rate
cMuMaxVeg	= 13.33 x kDRespVeg		d^{-1}	max. growth rate of subm. vegetation
kDMinDetW	= 1 x kDMinDetS		d^{-1}	mineralisation rate in water
cAffNUptVeg	= 1 x cAffPUptVeg		m^{2} g^{-1}D d^{-1}	N uptake affinity of subm. vegetation
cVPUptMaxVeg	= 2.5 x cAffPUptVeg		gP g^{-1}D d^{-1}	max. P uptake rate of subm. vegetation
cVNUptMaxVeg	= 25 x cAffPUptVeg		gN g^{-1}D d^{-1}	max. N uptake rate of subm. vegetation

4.3. Bayesian calibration of PClake

4.3.1. Method

This section describes step B of the method outlined in *Fig. 4.1*, the identification step. We made use of data on a number of actual or historic cases (lakes), for which both input factors (**x**) and observations (**m**) are known. (A case is defined as a certain combination of input factors.) Recalling chapter 2, the main *input factors* to the *PCLake* model are:

- Mean water depth [m]
- Fetch [m]
- Sediment type
- Marsh area [-] (if any)
- Water inflow [mm/d] or retention time [d]
- Infiltration / seepage [mm/d] (if any)
- External nutrient (P, N, Si) loading [g m^{-2} d^{-1}]
- Inflow concentrations of inorganic suspended matter [mg/l]
- Intensity of fishery [d^{-1}]

as well as the initial conditions.

The main *output variables* that are calculated by the model are: chlorophyll-*a*, transparency, phytoplankton types, vegetation coverage and fish biomass, as well as the concentrations and fluxes of the nutrients N, P and Si and oxygen. Input and output are again summarized in *Fig. 4.4* (equal to Fig. 2.6).

Data on both input factors and output variables were available for 43 lakes (see § 4.3.2). From

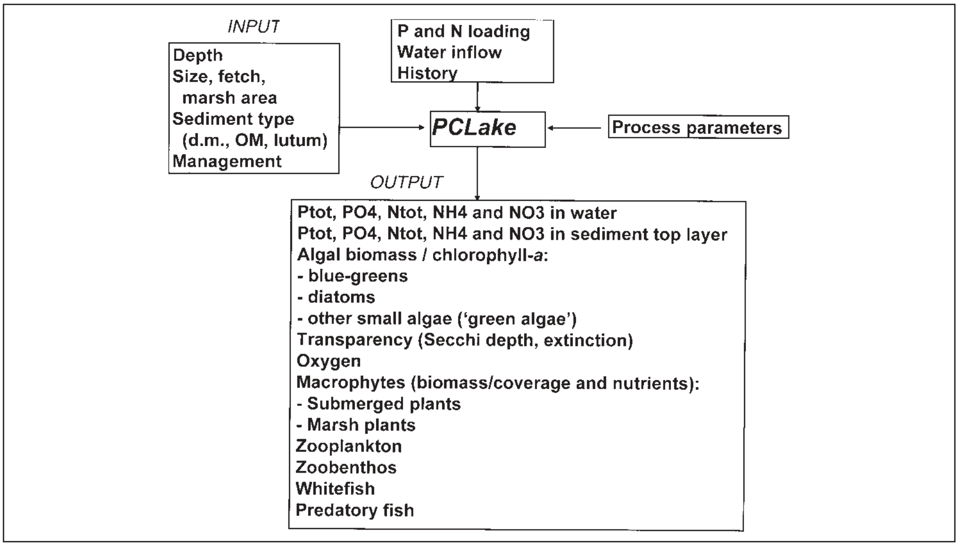


Fig. 4.4. *Overview of input and output of PCLake*

an evaluation of the model output **y** with respect to the observations **m** for these lakes (the 'fit'), some of the parameters **p** and/or some model equations, can be improved, by *selecting the well-fitting runs*. First, the model was calibrated by hand as far as possible, by visual comparison of simulations and measurements and by examining the overall performance of the model (sometimes called *verification*). Next, a more formal procedure was followed for a subset of the parameters that were both sensitive and uncertain. Different kinds of sampling were used, both FAST sampling (related to latin hypercube sampling, LHS) and grid sampling. In some cases, an *optimisation* technique was used to further reduce the parameter space, by mean of the programme PEST (Watermark Numerical Computing, 2000). These procedures were performed for a subset of the parameters only, as it was too time-consuming to perform an exhaustive analysis of all assumptions and parameters, and because the data set was considered too incomplete (for instance on animal groups) for that purpose.

The *likelihood function* is based on the (quasi-)steady-state summer-averages of the following variables, for the 43 lakes in the calibration data set:

- total-phosphorus
- total-nitrogen
- chlorophyll-a
- Secchi depth
- submerged vegetation coverage

The squared residuals were based on the natural logarithms of the measured and simulated values after adding a small value, the 'minimum significant difference' (δ); the residuals were squared to obtain the fit function $Phi_{i,j}$ for every parameter combination i and every variable j.

$Phi_{i,j} = [LOG(y_{j,\,meas} + \delta_j) - LOG(y_{j,\,sim} + \delta_j)]^2$
or: $Phi_{i,j} = [LOG\{(y_{j,\,meas} + \delta_j) / (y_{j,\,sim} + \delta_j)\}]^2$

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, chlorophyll-*a* in mg m^{-3}, vegetation coverage in %) are corrected for, as to give each variable a comparable weight. By choosing reasonable values for the δ's, 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 a difference equal to δ if this is higher (*i.e.* for low absolute values). The chosen values for δ are:

Blue	cyanobacterial biomass [mgD l^{-1}]	$\delta_{Phyt} = 0.074$
Chla	chlorophyll-*a* [mg m^{-3}]	$\delta_{Chla} = 7.4$
Cov	vegetation coverage [%]	$\delta_{Cov} = 2.7$
Sec	Secchi depth [m]	$\delta_{Sec} = 0.074$
Ntot	total N [mgN l^{-1}]	$\delta_{Ntot} = 0.074$
Ptot	total P [mgP l^{-1}]	$\delta_{Ptot} = 0.0074$

The average Phi per variable was calculated by dividing by the number of observations:

$\mathrm{avePhi}_{i,j} = \mathrm{Sum}[\mathrm{Phi}_{i,j}] / n_j$

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. 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)).

4.3.2. Data sets

Calibration data set

Data for 43 lakes were collected from different sources. Apart from lakes in The Netherlands, some lakes in other European countries (Belgium, Poland, Ireland) were included. An overview of the lake characteristics and input data is given in *table 4.3*, the water quality and biological data in *table 4.4*. Most data are from the nineteen-nineties, some from the nineteen-eighties. Most of them are averages over multiple years. The sources and quality of the data highly differ, most have been collected for other purposes than model validation and they might not always 'match' completely. Especially the loading data and the vegetation data are often based on estimates. Nevertheless, we decided to be not too strict on the data so as to get a database with enough variation.

The water inflow and loading data refer to year-averages (although for some lakes, half-year averages were actually used). 50% of the P loading was assumed to be in inorganic form. Of the remaining organic P load, most was defined as detritus, but a fraction of 2% (winter) to 10% (summer) of it was assumed to be in the form of phytoplankton. For lakes known to receive a substantial water inflow from other lakes, these fractions were taken as 5 and 25%, respectively. The N loading in detrital or algal form was calculated by means of a fixed ratio (7 gN/gP), wheras the remaining inorganic fraction was equally divided over NH_4 and NO_3. The input of inorganic matter (mostly no data) was set at a concentration of 5 mg/l, except when it was known to be higher. The silica inflow concentration was set at 3 $\mathrm{mgSi\ l^{-1}}$.

The reported sediment types were translated into the average dry-weight, organic matter and lutum fractions according to *table 4.5* (from Kroon et al., 2001); Fe and Al were both set at 10% of lutum. If available, lake-specific data were used, but these did not differ substantially from these average values. Fetch was set at the square-root of the water surface area. As the water exchange between lake and marsh zone was considered limited (the lakes have a fixed water level), its effects on the nutrient transport were neglected, but the positive effect on the habitat for predatory fish was included. The initial values of water and sediment quality and biota were taken from the average measured winter values. For water temperature and outdoor light, average sine curves were used. These were based on long-term averages for the Dutch situation.

The calibration data set encompasses a great variety of lakes, both 'clear' and 'turbid', all sediment types, with P inflow concentration ranging from 0.03 - 2 mgP l^{-1}, depth from 0.8 - 6.8 m, area from 1 – 4500 ha and retention time from 7 to over 500 days. Total P concentrations measure between 0.001 and 1.5 mgP/l, total N between 0.2 and 6.6 mgN/l, 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.

Data set used for comparison

Data on 9 Danish and Spanish lakes received later were not used in the calibration, but only for comparison. The data on these lakes have been added to the tables 4.3 and 4.4. The input data on temperature and day light were adapted to the different latitudes.

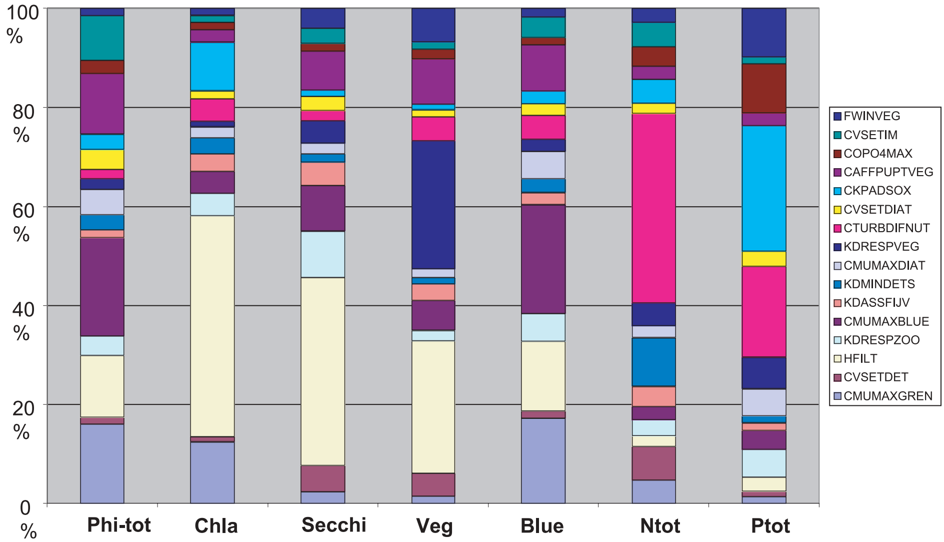


Fig. 4.3. *FAST total-order effects of the subset of parameters on the likelihood of 6 output variables as well as on the total likelihood Phi-tot, scaled to 100%. Parameters are explained in Table 4.2.*

Table 4.3. Lake data: input factors

Unit		m	ha	m	m2 m-2	–	–	mm/d	mgP/m2/d	mgN/m2/d	d	mgP/l	mgN/l
#	Name	Depth	Area	Fetch[a]	Marsh part[b]	Conn.[c]	Sed. type[**]	Inflow	P loading	N loading	Ret. time	P inflow	N inflow
	I. Calibration lakes												
1	Hollands-Ankeveen	1.3	85	922	0.1	n	5	3.5	0.1	4.4	357	0.04	1.2
2	Bergse Achterplas	2.0	41	640	0.001	n	1	19.3	8.1	81.0*	103	0.42	4.2
3	Bergse Voorplas	2.0	60	775	0.001	n	1	21.1	8.2	81.6*	95	0.39	3.9
4	Beulakerwijde	1.8	1300	3606	0.001	y	5	10.0	5.1	51.2*	175	0.51	5.1
5	Botshol, Grote Wije	2.0	53	731	0.1	n	5	12.9	0.9	20.5	157	0.07	1.6
6	Kaag, Norremeer	2.4	320	1789	0.001	y	1	109.6	96.7	602.2	22	0.88	5.5
7	Langeraar, Geerplas	1.9	28	529	0.001	y	5	4.4	1.5	96.4	431	0.33	21.9
8	Loosdrecht	2.2	940	3065	0.001	n	5	8.4	0.9	8.9	256	0.11	1.1
9	Naarden, Grote Meer	1.3	170	1304	0.1	n	6	10.0	0.7	6.8*	125	0.07	0.7
10	Naarden, Wijde Blik	1.0	38	612	0.1	n	6	5.2	0.7	6.8*	193	0.13	1.3
11	Reeuwijk, Nieuwenbroek	1.8	104	1020	0.001	n	5	5.5	1.1	11.0*	327	0.20	2.0
12	Nieuwkoop, Noordeinder	3.0	150	1225	0.001	n	5	6.3	0.8	8.5*	475	0.13	1.3
13	Nieuwkoop, Zuideinder	3.0	100	1000	0.001	n	5	27.4	1.7	17.5*	110	0.06	0.6
14	Reeuwijk, Elfhoeven	2.0	109	1044	0.001	n	5	16.4	5.5	54.8*	122	0.33	3.3
15	Westeinderplassen	2.8	852	2919	0.001	y	6	20.7	12.9	79.5	135	0.62	3.8
16	Zuidlaardermeer	1.0	600	2449	0.001	y	6	43.5	11.9	119.5*	23	0.27	2.7
17	Nannewijd	1.0	100	1000	0.001	n	5	6.8	1.0	21.5	148	0.14	3.2
18	Blankaart (B)	1.0	30	548	0.001	n	1	71.4	18.7	1390.0	14	0.26	19.5
19	Maten 13 (B)	0.8	3	171	0.001	n	6	92.0	9.3	764.4	8	0.10	8.3
20	Visvijver (B)	0.8	1	86	0.001	n	1	3.0	0.2	9.0	267	0.05	3.0
21	Gara, South (IR)	1.0	203	1425	0.001	n	5	137.0	10.2	101.8*	7	0.07	0.7
22	Maumwee (IR)	2.0	27	520	0.001	n	5	54.8	1.8	18.4*	37	0.03	0.3
23	Mullagh (IR)	2.3	35	592	0.001	n	5	4.7	0.8	8.3*	489	0.18	1.8

Table 4.3. Continued.

Unit # Name	m Depth	ha Area	m Fetch[a]	m2 m-2 Marsh part[b]	– Conn.[c]	– Sed. type**	mm/d Inflow	mgP/m2/d P loading	mgN/m2/d N loading	d Ret. time	mgP/l P inflow	mgN/l N inflow
24 Pollaphuca (IR)	6.8	1974	4443	0.001	n	5	33.3	1.8	18.3*	204	0.06	0.6
25 amor (IR)	3.0	741	2722	0.001	n	5	48.3	6.4	63.6*	62	0.13	1.3
26 Luknajno (PL)	1.8	630	2510	0.1	n	6	3.2	0.1	1.1*	567	0.04	0.4
27 Waalboezem	3.8	78	883	0.001	n	1	20.0	11.2	126.0	190	0.56	6.3
28 Binnenbedijkte Maas	4.0	158	1257	0.001	n	1	14.6	5.5	143.8	274	0.38	9.8
29 Brielse Meer	5.5	491	2216	0.001	y	1	40.7	17.3	247.7	135	0.42	6.1
30 Volkerak	5.0	4570	6760	0.001	y	6	45.9	13.0	387.8	109	0.28	8.5
31 Zoommeer	6.0	1580	3975	0.001	y	6	105.6	14.1	600.5	57	0.13	5.7
32 Oude Venen 2	1.3	10	316	0.001	y	5	17.1	6.8	100.6	73	0.40	5.9
33 Veluwemeer	1.6	3240	5692	0.05	y	2	26.7	3.7	124.7	58	0.14	4.7
34 Wolderwijd	1.9	1800	4243	0.001	y	6	16.5	1.4	57.5	117	0.08	3.5
35 Nuldernauw	2.1	870	2950	0.001	y	6	47.0	7.5	168.5	44	0.16	3.6
36 Drontermeer	1.3	540	2324	0.05	y	6	69.0	9.8	257.5	18	0.1	43.7
37 Braassemermeer	3.9	452	2126	0.001	y	1	62.9	37.3	324.1	62	0.59	5.2
38 Langeraar, Noordeinde	1.9	75	866	0.001	y	5	3.4	2.6	15.1	558	0.77	4.4
39 Mooie Nel	4.5	116	1077	0.001	y	6	88.1	179.5	486.3	51	2.04	5.5
40 Het Hol	1.0	30	548	0.1	n	5	6.4	0.9	20.7	157	0.14	3.2
41 Kortenhoef	1.2	193	1389	0.001	n	5	5.9	4.6	34.6	204	0.78	5.9
42 Stichts-Ankeveen	1.0	100	1000	0.1	n	5	3.3	0.1	4.8	303	0.03	1.4
43 Frisian Lakes (average)	1.4	518	2276	0.001	y	5	9.3	3.9	71.0	147	0.42	7.6
II. Lakes used for comparison												
44 Enso (DK)	1.9	11	326	0.001	n	3	27.1	0.1	3.3	70	0.002	0.12
45 Nederso (DK)	1.6	14	374	0.001	n	3	320.0	2.5	9.0	5	0.008	0.03

Table 4.3. Continued.

Unit # Name	m Depth	ha Area	m Fetch[a]	m2 m-2 Marsh part[b]	– Conn.[c]	– Sed.	mm/d Inflow type**	mgP/m2/d P loading	mgN/m2/d N loading	d Ret. time	mgP/l P inflow	mgN/l N inflow
46 Soby (DK)	3.0	72	849	0.001	n	6	10.1	0.2	13.2	300	0.02	1.3
47 Hinge (DK)	1.2	91	954	0.001	n	3	60.0	8.5	232.9	20	0.14	3.9
48 Kvind (DK)	1.9	15	387	0.001	n	6	126.7	11.0	575.3	15	0.09	4.5
49 Lading (DK)	1.0	45	671	0.001	n	3	14.7	1.4	76.7	68	0.09	5.2
50 Silkeborg-Langso (DK)	2.0	46	678	0.001	n	6	250.0	18.6	323.3	8	0.07	1.3
51 Honda (SP)	1.0	9	307	0.001	n	3?	7.8	4.2	33.8	128	0.53	4.3
52 Nueva (SP)	1.5	27	521	0.001	n	3?	1.8	0.1	2.0	820	0.07	1.1

* N loading unknown, estimated as 10 times the P loading.

** Explanation of sediment types in table 4.5. For some lakes, more specific data were available, otherwise the averages given in that table were used..

[a] Fetch is estimated as the square-root of the water surface area.

[b] If the existence of a marsh zone connected to the lake is known from the data, it is taken as 0.1 or 0.05, otherwise set to a low value of 0.001.

[c] ‘yes’ means that the lake is known to receive a substantial water inflow from other lakes, otherwise ‘no’.

Table 4.5. Definition of sediment types

Sed. type #	Dry matter [gDW/g sed.]	Organic fraction [g org./gDW]	Lutum [g lutum/g AFDW]	Fe [g Al/g AFDW]	Al [g lAl/g AFDW]
1 clay	0.3	0.08	0.4	0.04	0.04
2 clay/peat	0.2	0.165	0.4	0.04	0.04
3 clay/sand	0.4	0.08	0.215	0.0215	0.021
5 5peat	0.1	0.25	0.4	0.04	0.04
6 sand	0.5	0.08	0.03	0.003	0.003

Table 4.4. Lake data: water quality and biota

#	Name	mg m-3 Chloro-phyll-a	% Cyano-bact.	gD m-3 Zoopl.	gD m-2 Fish total	% Pred. fish	%cover Subm. veg.	mgN/l Secchi depth	mgN/l NH4	mgN/l NO3	mgN/l N-tot	mgP/l PO4	mgP/l P-total	mgD/l Seston	mgN/gD N-sedim.	mgP/gD P-sedim.
I. Calibration lakes																
1	Hollands-Ankeveen	16	–	–	–		25	0.59	0.06	0.09	1.79	0.02	0.09	12.9	–	–
2	Bergse Achterplas	218	–	–	–		0	0.24	0.05	0.03	3.68	0.06	0.43	43.8	–	–
3	Bergse Voorplas	213	–	–	–		0	0.25	0.05	0.04	3.51	0.04	0.33	42.4	–	–
4	Beulakerwijde	99	52	–	2.1	0.6	0	0.38	0.46	0.45	2.23	0.02	0.14	16.6	–	–
5	Botshol, Grote Wije	6	57	0.2	–		32	1.46	0.04	0.13	1.04	0.01	0.04	5.0	–	0.6
6	Kaag, Norremeer	35	–	–	–		–	1.18	0.25	2.35	2.86	0.43	0.52	–	–	–
7	Langeraar, Geerplas	131	53	0.4	–		0	0.43	0.08	0.04	3.14	0.12	0.33	23.5	–	–
8	Loosdrecht	44	86	0.8	4	10	0	0.34	0.75	0.07	1.85	0.01	0.07	21.7	–	–
9	Naarden, Grote Meer	15	21	–	0.7 - 1.2	14 - 30	90	1.00	0.09	0.08	1.33	0.02	0.09	6.0	–	0.7
10	Naarden, Wijde Blik	16	18	–	0.7 - 0.9	10 - 11	30	0.58	0.09	0.07	2.45	0.02	0.15	18.0	–	1.9
11	Reeuwijk, Nieuwenbroek	136	55	–	–		0	0.35	0.11	0.04	3.49	0.01	0.12	37.1	–	0.9
12	Nieuwkoop, Noordeinder	74	61	0.0	–		1	0.54	0.07	0.03	2.06	0.00	0.06	18.0	–	–
13	Nieuwkoop, Zuideinder	165	60	0.3	–		0	0.43	0.07	0.05	2.68	0.01	0.12	24.5	–	–
14	Reeuwijk, Elfhoeven	109	41	–	–		0	0.40	0.09	0.04	2.34	0.01	0.16	26.6	–	1.2
15	Westeinderplassen	52	10	–	–		–	0.68	0.11	0.23	2.25	0.17	0.29	–	–	–
16	Zuidlaardermeer	89	–	–	–		0	0.41	0.19	1.00	3.98	0.01	0.30	5.2	3.2	0.7
17	Nannewijd	83	25	0.2	–		0	0.36	0.15	0.03	3.46	0.02	0.25	32.4	–	–
18	Blankaart (B)	28	8	1.7	0.2	2	0	0.33	0.14	3.65	4.36	–	0.35	43.3	1.8	0.1

Table 4.4. Continued

#	Name	mg m-3 Chloro-phyll-a	% CÏyano-bact.	gD m-3 Zoopl.	gD m-2 Fish total	% Pred. fish	%cover Subm. veg.	mgN/l Secchi depth	mgN/l NH4	mgN/l NO3	mgN/l N-tot	mgP/l PO4	mgP/l P-total	mgD/l Seston	mgN/gD N-sedim.	mgP/gD P-sedim.
19	Maten 13 (B)	10	2	0.3	0.04	0	84	0.75	0.05	0.03	–	–	0.02	6.5	8.7	0.0
20	Visvijver (B)	3	7	0.7	0	–	59	0.78	0.10	0.09	0.20	–	0.55	5.8	10.2	0.0
21	Gara, South (IR)	5	6	0.0	–		–	0.96	–	0.10	1.08	–	0.02	–	–	–
22	Maumwee (IR)	2	–	0.2	–		–	2.00	–	0.05	0.30	–	0.00	–	–	–
23	Mullagh (IR)	29	61	3.0	–		–	1.55	–	0.15	1.07	–	0.05	–	–	–
24	Pollaphuca (IR)	6	10	0.3	–		–	1.44	–	0.49	0.84	–	0.01	–	–	–
25	Ramor (IR)	71	44	1.5	–		–	0.87	–	0.55	1.70	–	0.09	–	–	–
26	Luknajno (PL)	18	–	–	–		42	1.32	–	–	1.91	–	0.07	5.6	11.5	0.7
27	Waalboezem	25	4	–	–		–	0.61	0.18	0.43	1.74	0.06	0.13	–	–	–
28	Binnenbedijkte Maas	97	38	–	–		–	0.31	0.15	0.34	2.51	0.08	0.22	–	–	–
29	Brielse Meer	34	10	–	–		–	1.14	0.13	1.57	2.79	0.08	0.16	–	–	–
30	Volkerak	23	9	3.1	1.0 - 6.3	17	12	1.82	0.14	3.23	4.53	0.08	0.15	–	–	–
31	Zoommeer	28	19	1.1	0.4 - 3.5	16	12	1.87	0.09	0.06	1.54	0.06	0.13	–	–	–
32	Oude Venen 2	34	2	1.3	–		0	0.51	0.32	0.03	3.00	0.26	0.41	–	–	–
33	Veluwemeer	59	20	1.3	0.9	2.6	17	0.39	0.05	0.43	2.25	0.01	0.11	–	–	0.3
34	Wolderwijd	84	40	1.1	1.2 - 2.3	1.2	13	0.38	0.04	0.11	2.19	0.06	0.14	–	–	0.3
35	Nuldernauw	90	–	–	1.9	1	8	0.36	0.05	0.11	2.29	0.04	0.20	–	–	4.6
36	Drontermeer	113	–	–	2.3	5.6	2	0.34	0.06	0.26	2.76	0.02	0.21	–	–	–
37	Braassemermeer	44	30	–	–		–	1.26	0.16	1.62	3.43	0.27	0.35	–	–	5.7
38	Langeraar, Noordeinde	185	53	0.2	–		0	0.29	0.13	0.03	3.95	0.14	0.45	–	–	–

Table 4.4. Continued

#	Name	mg m-3 Chloro-phyll-a	% Cyano-bact.	gD m-3 Zoopl.	gD m-2 Fish total	% Pred. fish	%cover Subm. veg.	mgN/l Secchi depth	mgN/l NH4	mgN/l NO3	mgN/l N-tot	mgP/l PO4	mgP/l P-total	mgD/l Seston	mgN/gD N-sedim.	mgP/gD P-sedim.
39	Mooie Nel	101	14	–	–		–	0.61	1.01	3.04	6.62	1.35	1.55	–	–	–
40	Het Hol	14	12	–	–		90	0.98	0.13	0.10	1.10	0.02	0.06	–	–	–
41	Kortenhoef	153	–	–	–		0	0.31	0.11	0.12	2.92	0.02	0.23	–	–	1.5
42	Stichts-Ankeveen	15	26	1.2	–		60	0.91	0.13	0.18	1.36	0.02	0.06	–	–	1.0
43	Frisian Lakes (average)	88	55	2.2	4.9	7	1	0.32	0.20	0.57	3.82	0.05	0.24	30.7	–	0.2
II. Lakes used for comparison																
44	Enso (DK)	11	16	0.42	0.8	19	25	1.83	–	0.01	0.53	0.016	0.066	4.3	–	–
45	Nederso (DK)	36	12	0.33	0.8	23	1	1.26	–	0.13	1.13	0.023	0.116	8.5	–	–
46	Soby (DK)	6	0	0.09	0.3	100	34	3.04	–	0.05	0.35	0.002	0.016	1.9	–	–
47	Hinge (DK)	91	8	0.58	0.5	20	0.5	0.50	–	0.12	1.55	0.004	0.155	35.2	–	–
48	Kvind (DK)	28	66	0.49	0.8	16	0	0.90	–	0.81	2.58	0.011	0.117	9.7	–	–
49	Lading (DK)	62	13	1.23	0.7	53	7	0.69	–	0.02	1.50	0.015	0.155	20.9	–	–
50	Silkeborg-Langso (DK)	38	13	0.32	0.4	24	0	1.03	–	0.15	1.05	0.007	0.078	11.1	–	–
51	Honda (SP)	152	83	2.03	0.0	–	0	0.24	–	0.63	3.66	0.013	0.212	57.0	–	–
52	Nueva (SP)	35	3	0.84	0.0	–	5	0.77	–	0.47	1.15	0.003	0.046	18.6	–	–

As a check on the loading data, the in-lake nutrient concentrations were compared to the (theoretical) inflowing concentrations. In most cases, the in-lake phosphorus concentration is equal to, or lower than, the inflowing concentrations (*Fig. 4.5a*), as may be expected for lakes more or less in equilibrium. The one or two exceptions may indicate recent large changes in loading and/or questionable input data. For nitrogen (*Fig. 4.5b*) there are some more exceptions, which might be attributable to the crude estimates for the more than 1/3 of the lakes were input data were lacking.

4.3.3. Simulation setup

Simulations with PCLake were carried out for these lakes for 20 years, using the input values as listed in table 4.3. Recalling chapter 2, the main input factors to the model are:

- Mean water depth [m]
- Fetch [m]
- Sediment type
- Marsh area [-] (if any)
- Water inflow [mm/d] or retention time [d]
- Infiltration / seepage [mm/d] (if any)
- External nutrient (P, N, Si) loading [g m^{-2} d^{-1}]
- Inflow concentrations of inorganic suspended matter [mg/l]
- Intensity of fishery [d^{-1}]

as well as the initial conditions.

Output variables calculated by the model include:
tP, Po4, tN, NH4 and NO3 concentrations
Algal biomass / chlorophyll:

- blue-greens
- diatoms

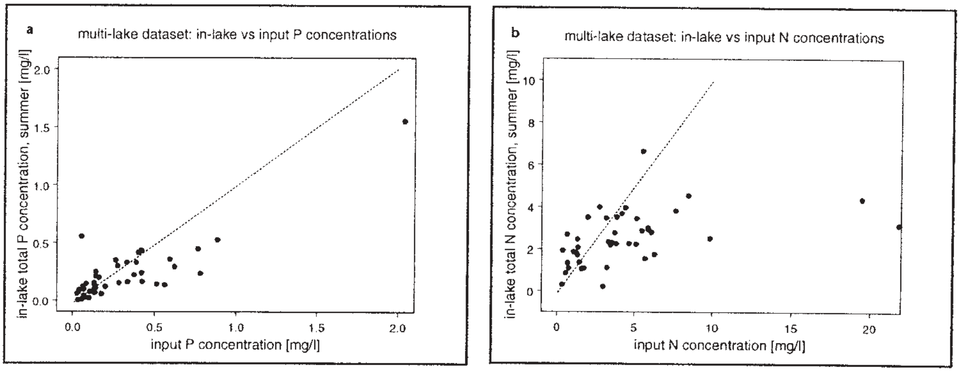


Fig. 4.5. *Summer-averaged nutrient concentrations versus input concentrations in the lakes in the dataset. a, total P; b, total N.*

– other small algae (‘green algae’)
Secchi depth (or extinction)
Oxygen
Macrophytes (in terms of biomass/coverage and nutrients):
– Submerged plants
– Marsh plants
Zooplankton
Zoobenthos
Whitefish
Predatory fish

The simulations were repeated, for all these lakes, 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 1.0 (*Table 4.6*).

The combined weights (likelihoods) of these runs were calculated according to the Bayesian method explained above, based on the output variables chlorophyll-a, vegetation coverage, Secchi depth and total P for all 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. This did not affect the results much, as there was in general a good correlation between the fit functions with or without total N). The likelihood distribution was used for uncertainty assessment, applied to the critical loading levels (see paragraph 4.4).
The *best run* (with the maximum likelihood) from these simulations was selected, and the corresponding parameter set used as a default. The results of this run are discussed first.

Table 4.6. 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	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		

4.3.4. Results

The summer-averages of the last simulated year for a number of output variables were recorded and compared to measured values. The ‘summer’ is defined as the period April 1 – Sep 30, in accordance with the period used in Dutch water quality regulations.

Fig. 4.6, a-f, shows the results for total P, total N, chlorophyll-*a* (as a measure for algal biomass), vegetation coverage and Secchi depth (transparency). The 1:1 lines are shown in each graph. (Please note that in some of the graphs, especially the one for vegetation, several dots overlap near the zero value.) In general, the model behaves reasonably well for total phosphorus, chlorophyll-a (although in general somewhat overpredicted) and macrophytes, while the variability for total nitrogen and Secchi depth is larger. The graph of the transparency looks much better if the transparency is expressed as *relative* euphotic depth (*Fig. 4.6, f*), calculated as:

$z_{eu}/z_m = 1.7 * \text{Secchi} / \text{Depth}$ [-]

Besides visual inspection of the graphs, several statistical methods were used to quantify the model performance (Janssen & Heuberger, 1995). The first, most simple, method are the linear correlation coefficients. A second method is to see 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 (the ‘MSD’ or δ, see paragraph 3.1) were used to approximate normally distributed residuals.

Other methods suggested by Janssen and Heuberger (1995) to quantify the agreement of a model are based on the residuals between the individual points and the calculated = observed (1:1) line. The calculation may be based on the Root Mean Square Error (RMSE), the Mean Absolute Error (MAE), which is less sensitive to outliers, or the Mean Relative Error (MRE), by dividing the residuals by the observed value. In this case, the MRE was calculated as the mean absolute residuals of the log-transformed data plus their δ:

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

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.

The results are in table 4.6.

Another approach is to evaluate the results in terms of ‘clear’ or ‘turbid’ state, which is the model’s main objective. The values of 25 $\mu g\ l^{-1}$ 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 1 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 (2 lakes were overpredicted) and also 95% based on the relative euphotic depth criterion (1 lake was over-, 1 was underpredicted) (Fig. 4.6); 91% met all three criteria together.

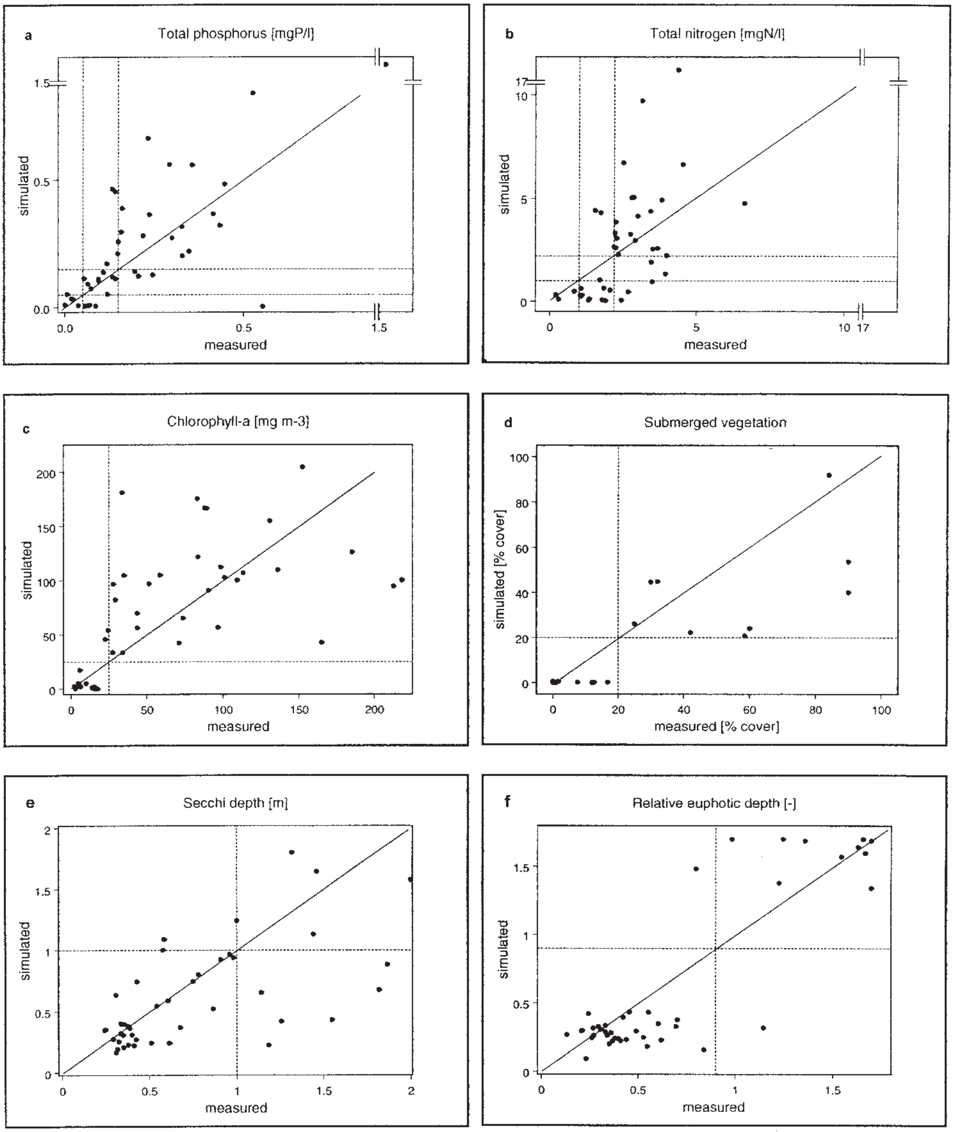


Fig. 4.6. *PCLake simulations compared to measurements (summer-averages) for a multi-lake data set. a, total P; b, total N; c, chlorophyll-a; d, submerged vegetation; e, Secchi depth; f, relative euphotic depth. The 1:1 lines and the (proposed) quality standards have been added in the graphs.*

Table 4.6. Comparison between simulated and observed values, based on natural logarithms + ?. Shown are the corelation coefficient, the mean relative error and the results of linear regression of the simulated values on the observed ones.

	Ptot	Ntot	Chla	Veg	Secchi
Correlation coeficient	0.63	0.61	0.71	0.74	0.70
MRE	0.71	0.83	0.52	0.44	0.37
Regression:					
- intercept	-0.64	-0.64	0 (forced)	0 (forced)	0 (forced)
- std. error	0.33	0.26	–	–	–
- Pr(>|t|)	0.06	0.02	–	–	–
- coefficient	0.81	1.34	1.02	0.99	0.62
- std. error	0.16	0.26	0.02	0.06	0.07
- Pr(>|t|)	$< 10^{-4}$	$< 10^{-4}$	$< 10^{-4}$	$< 10^{-4}$	$< 10^{-4}$
- R^2	0.40	0.40	0.98	0.86	0.58
- meets 1:1?	yes	no	yes	yes	no

For nutrients, it was tested whether an exceedance or not of the Dutch water quality standards was simulated correctly. There are as yet two kinds of standards in The Netherlands, one for all water bodies, viz. 0.15 mgP l^{-1} and 2.2 mgN l^{-1}, the other for water bodies designated as 'ecologically valuable' by the national or regional water authorities, for which the (proposed) standards are 0.05 mgP l^{-1} and 1.0 mgN l^{-1}.
With the low phosphorus standard of 0.05 mgP 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 mgP l^{-1}, 86% of the predictions were correct; 4 lakes were under-, 2 overpredicted. For nitrogen, the results were somewhat less convincing. For the low nitrogen standard of 1.0 mgN l^{-1}, only 71% was classified correctly (all others were underpredicted). For the high standard of 2.2 mgN l^{-1}, 81% of the prediction were right; 5 lakes were under- and 3 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) mgP l^{-1}. Other factors than nutrients co-influence the biotic response.

The results were further analysed by relating algal and macrophytes biomass to the nutrient concentrations and light climate. The relation between chlorophyll-a and total P (*Fig. 4.7, a-b*) shows a wide scatter for both the measurements and the simulations, but in general a positive relation, the maximum chlorophyll/total-P ratio [g/g] being about 1.2 (measurements) to 1.5 (simulations). The same applies to total N (*Fig. c-d*), with maximum ratios [g/g] of about 0.10 (measurements) to 0.12 (simulations), but the measurements show a 'lag' of about 1 mg/l that is not reproduced by the simulations. This has been attributed to some 'inert' N fraction made up of humic substances, which are not included in the model. The maximum ratios correspond reasonably well with earlier studies in Dutch lakes (Lijklema et al., 1988; Portielje & Van der

Molen, 1998). The total-N/total-P ratio ranges from about 5 to 25, with a few exceptions (*Fig. e-f*).

The vegetation coverage shows, as expected, a clear negative relation with total-P (*Fig. g-h*), which is, however, much steeper in the simulations as compared to the measurements. This is partly due to the fact that the model simplifies the lake as a mixed water body with a uniform depth, while in reality, shallower zones, with more favourable conditions for macrophytes, often coexist besides deeper zones. This may 'smoothen' the relation, while the model predicts more or less an 'all or none' response: macrophytes coverages of less than 20% do not exist in the simulations, as they fall back to zero. A second cause might be an overestimation of phosphorus uptake from the water column by the macrophytes.

The vegetation is clearly positively related to the relative euphotic depth (*Fig. i-j*), whereas the opposite is true for chlorophyll-a (*Fig. k-l*). A relative euphotic depth of about 0.8 – 1.0 marks the difference between dominance of algae versus submerged macrophytes. Again, the relations are somewhat steeper than in reality.

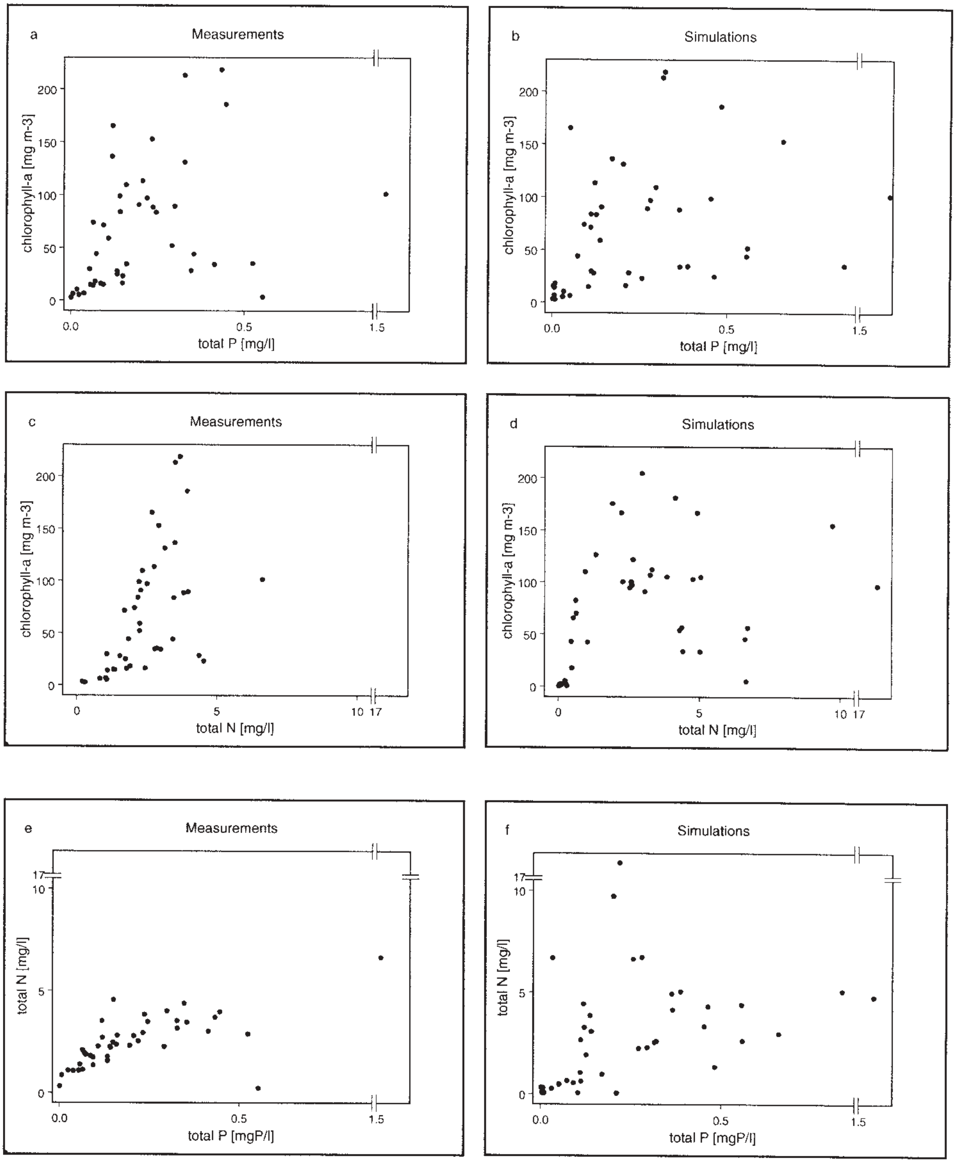
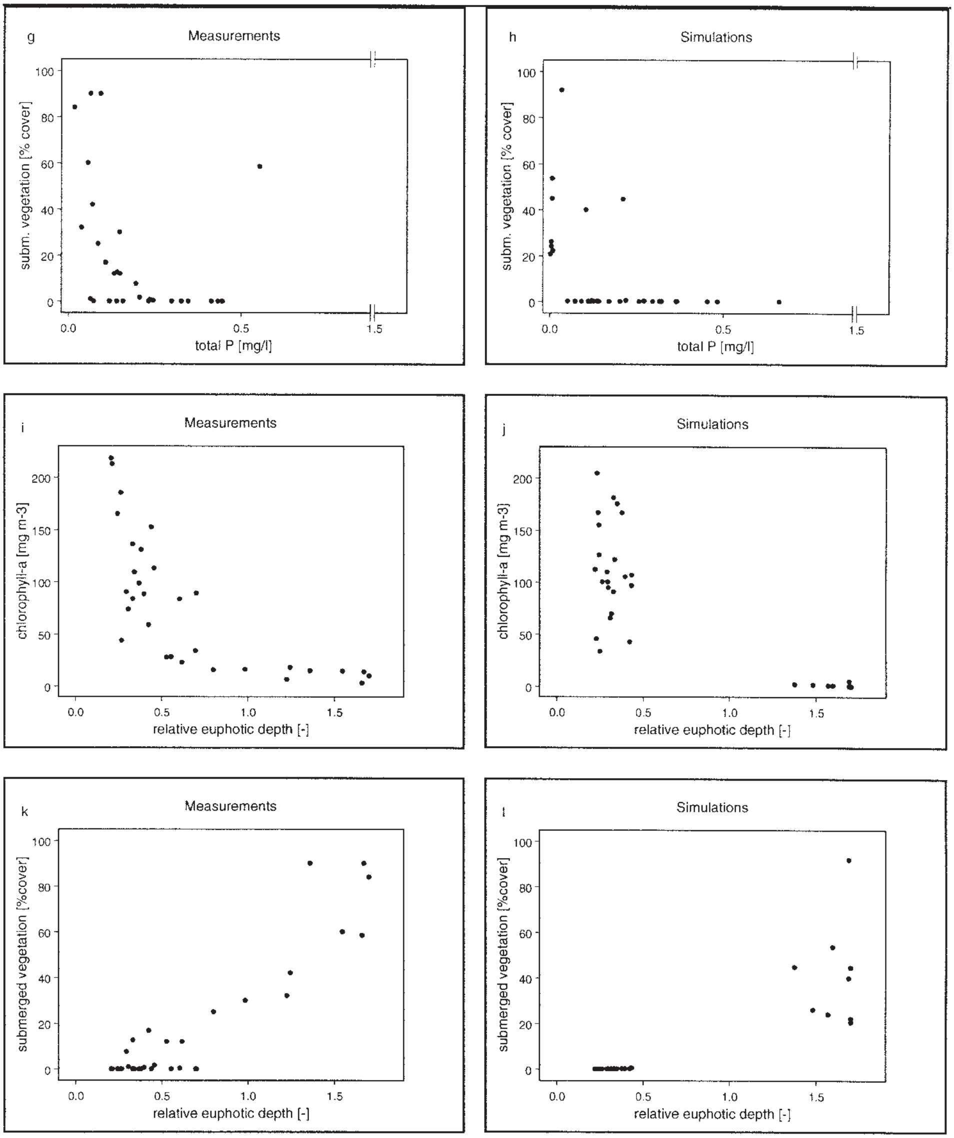


Fig. 4.7. Relation between main biotic and abiotic variables for the lakes in the dataset, measurements and simulations separately. a-b, chlorophyll-a vs. total P; c-d, chlorophyll-a vs. total N; e-f, total N vs. total P; g-h, vegetation vs. total P; i-j, chlorophyll-a vs relative euphotic depth; k-l, vegetation vs. relative euphotic depth.


g
Measurements
subm. vegetation [% cover]
0
20
40
60
80
100
0.0
0.5
1.5
total P [mg/l]
h
Simulations
subm. vegetation [% cover]
0
20
40
60
80
100
0.0
0.5
1.5
total P [mg/l]
i
Measurements
chlorophyll-a [mg m-3]
0
50
100
150
200
0.0
0.5
1.0
1.5
relative euphotic depth [-]
j
Simulations
chlorophyll-a [mg m-3]
0
50
100
150
200
0.0
0.5
1.0
1.5
relative euphotic depth [-]
k
Measurements
submerged vegetation [%cover]
0
20
40
60
80
100
0.0
0.5
1.0
1.5
relative euphotic depth [-]
l
Simulations
submerged vegetation [%cover]
0
20
40
60
80
100
0.0
0.5
1.0
1.5
relative euphotic depth [-]

4.4. Confirmation on other lakes

After performing the calibration as described, nine other lakes were simulated with the same parameter settings in order to perform a validation on independent data. These lakes are situated in Denmark and Spain; data have been collected in the framework of the BIOMAN project (De Meester et al., 2003). The main results are shown in Fig. 4.8, together with those for the calibration lakes (note: four of the calibration lakes also figured in this project). Although most of the BIOMAN lakes fitted reasonably well within the earlier results, at least in terms of clear/turbid, there are some lakes in which macrophyte coverage was overpredicted. Some of the assumptions on soil features and suspended matter, which had to be very rough due to lack of data, were possibly not correct. The outlier is a lake under recent restoration where macrophyte development has not (yet) started for unknown reasons (T. Lauridsen, pers. comm.). Nevertheless, the results were considered satisfactory to allow the model's applicability outside the calibration set.

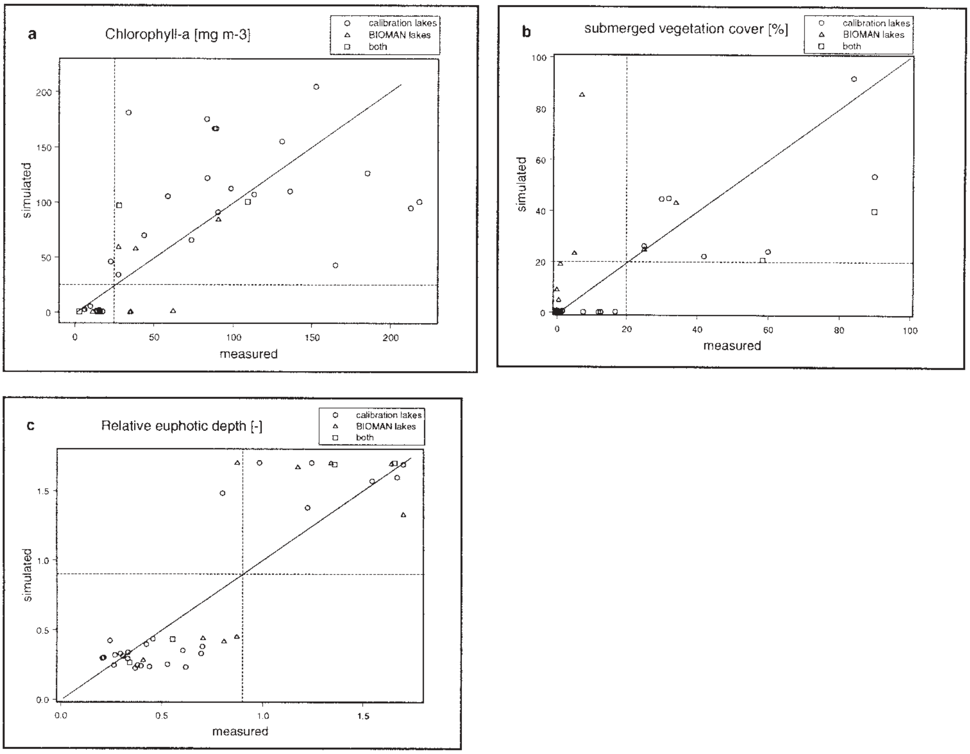


Fig. 4.8. PCLake simulations compared to measurements (summer-averages) for both the calibration and the 'BIOMAN' lakes used for comparison. a, chlorophyll-a; b, submerged vegetation; c, relative euphotic depth. The solid line is the 1:1 line; the dashed lines indicate the limits of 25 mg m^{-3} chlorophyll-a and 20 % coverage.

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.

4.5. Prediction uncertainty of the critical loading

Having discussed, in §§ 4.3 and 4.4, the results for the optimal parameter setting,we will now finish the Bayesian approach (outlined in § 4.1) by considering the *uncertainty* in the model predictions that is left after the model has been compared to the data. 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. (This topic is explained in chapters 5 and 6; here we only mention that the model indeed predicts such a threshold loading, the value of which often differs along with the initial state of the system.) The threshold was defined as the loading at which the summer-averaged vegetation coverage crosses the value of 20 %.

The analysis was performed for an ‘average Dutch lake’: mean depth = 2 m, fetch = 1000 m, water inflow = 20 mm d^{-1}, a lightly clayish soil, no wetland zone. As explained before, simulations were performed for a grid sample of 7 varying parameters, while 4 other parameters were coupled to these parameters with a correlation of 1.0 (Table 4.6 in the previous section). For each parameter combination, runs were performed for two initial states and for a range of loading rates. The critical loading rates (again for 20% vegetation coverage) were derived for each combination.

The *prior predictive distribution* of the critical loading rates, *i.e.* before confrontation with the data, is shown in Fig. 4.9, a, 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’ (Fig. 4.9, e).

Next, the runs were weighted according to their likelihood (the degree of fit with the data), giving rise to the *posterior predictive distribution* (see § 4.1). 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 ‘average lake’. The likelihoods were calculated as explained in the previous section, based on the total sum-of-squares for the variables chlorophyll-a, vegetation coverage, Secchi depth and total P for all simulated lakes.

The weighted switchpoints were again collected in bins with a fixed width and shown in a histogram (Fig. 4.9, b, d). Compared to the 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' (Fig. 4.9, f).

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.
Both sets are given in Table 4.6. The values from the best run were used as default values.
In general, there was no simple relation between the value of every single parameter and the likelihood.

Parameter sensitivity of the critical loading
To explore the parameters or processes that determine the critical loading, we performed a sensitivity analysis of the critical loading values for 18 process parameters, for the 'standard lake' defined earlier. The parameters were chosen from the different 'corners' of the model and were sampled according to the FAST method (Saltelli et al., 2000) uniformly within the ranges given in table 4.7. We ran the model again for 20 years with different loading values, starting from either the clear or the turbid initial state, and derived the loading that corresponded to a summer-averaged macrophyte coverage of 20% by interpolation. We applied an extended FAST sensitivity analysis (as explained in § 4.2.2) to find the spreading (uncertainty) and the parameter sensitivity factors.

The distributions of the critical P loadings are shown in Fig. 4.10; the sensitivity measures are depicted in Fig. 4.11, both for the critical P loading (with N in excess) and for the critical N loading (with P in excess). All results are *unweighted*, i.e. *prior* distributions: no comparison with observations was made. The 'turbidification' switchpoint varies from 0–10 mgP m^{-2} d^{-1}, the 'clarification' switchpoint only from 0–2(-3) mgP m^{-2} d^{-1}, a little bit wider than the prior distributions shown in Fig. 4.9, a,c. The differences between the first-order and total-order effects indicate that interaction effects between parameters are important (Fig. 4.11). The parameters explaining most of the variability in the 'restoration switchpoint' are the vegetation parameters: max. growth rate, overwintering fraction and light affinity, as well as the zooplankton half-saturating food concentration and the mineralisation rate. The 'turbidification switchpoint' is determined by the same vegetation parameters, but also by the growth rate of planktivorous fish, and a litte bit by the nitrification rate. With some precaution, this could be interpreted as an indication that top-down regulation is important for the stabilisation of the clear-water state, but not for that of the turbid state.

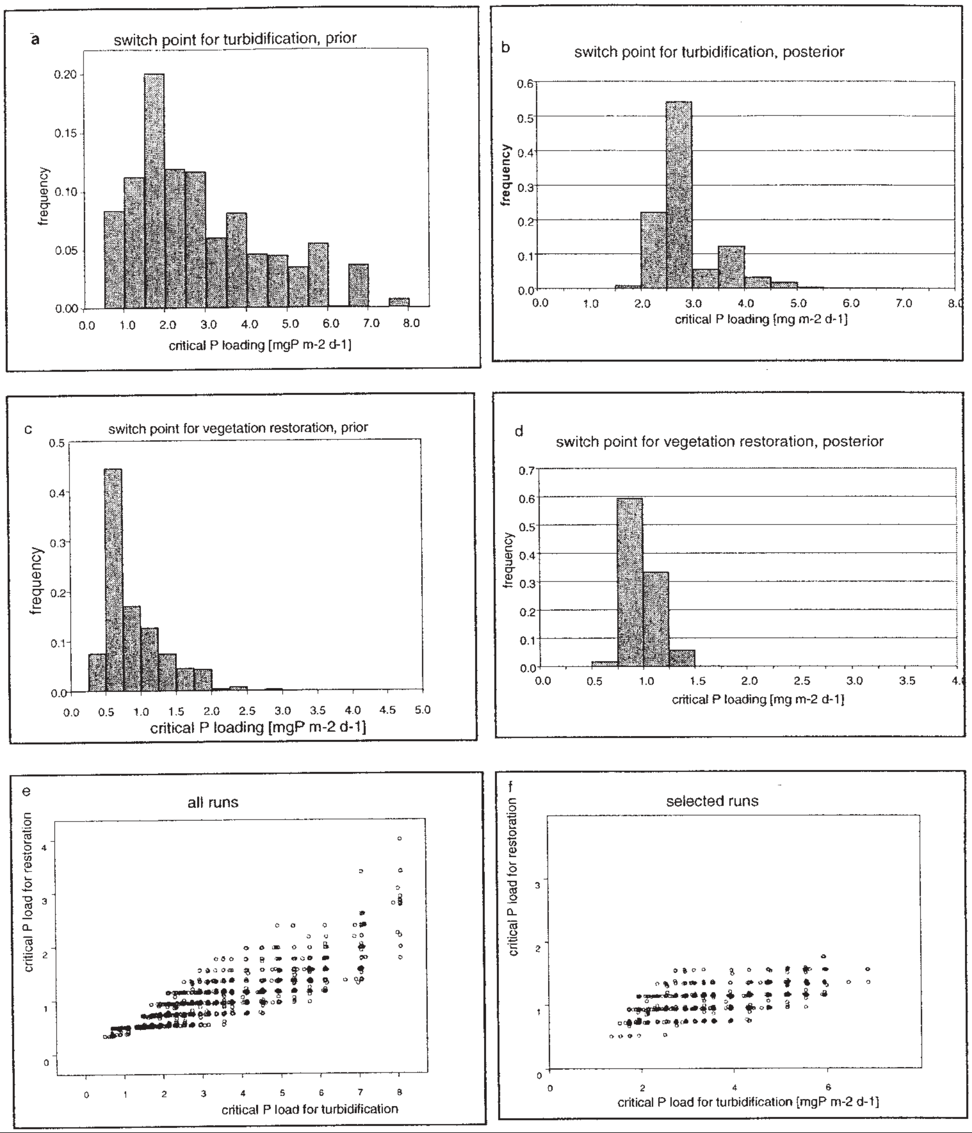


Fig. 4.9. *Predictive distributions of the threshold loading rates. a-b, distributions of the 'turbidification' switchpoint: a, prior; b, posterior. c-d, distributions of the 'clarification' switchpoint: c, prior; d, posterior. e-f, the thresholds plotted against each other: e, prior; f, posterior.*

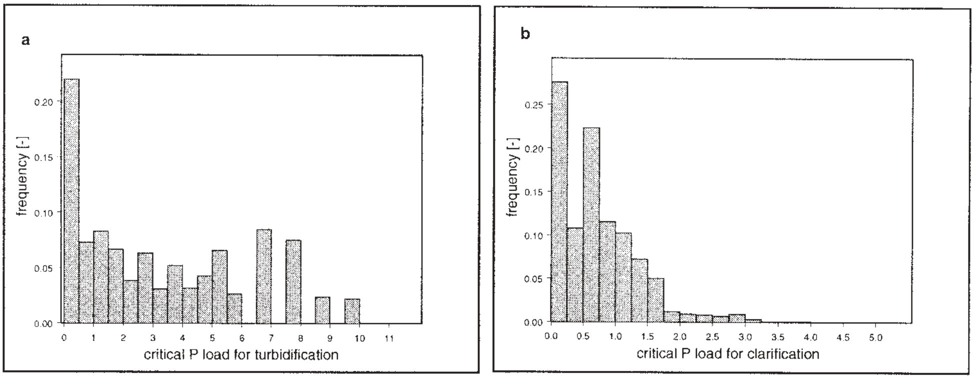


Fig. 4.10. *Distribution of the (prior) critical P loading values [mgP m^{-2} d^{-1}] for a, turbidification, and b, restoration.*

We also analysed the results by multiple linear regression (Table 4.8).
Comparable results are found for the critical N loading (if P is in excess).

Table 4.7. Parameters and ranges for the sensitivity analysis

	Min	Max	Unit	Description
CMUMAXBLUE	0.5	0.7	d^{-1}	max. growth rate of cyanobacteria
CMUMAXVEG	0.15	0.25	d^{-1}	max. growth rate of subm. vegetation
CLOPTREFBLUE	10	16	W m^{-2}	optium light for cyanobacteria
HLREFVEG	15	25	W m^{-2}	half-saturating light for subm. vegetation
FWINVEG	0.2	0.4	–	verwintering fraction of subm. vegetation
CPDBLUEMIN	0.002	0.003	gP g^{-1}D	min. P/D ratio of cyanobacteria
CPDVEGMIN	0.0006	0.0011	gP g^{-1}D	min. P/D ratio of subm. vegetation
CNDBLUEMIN	0.02	0.04	gN g^{-1}D	min. N/D ratio of cyanobacteria
CNDVEGMIN	0.008	0.012	gN g^{-1}D	min. N/D ratio of subm. vegetation
HFILT	0.8	1.2	g m^{-3}	half-sat. food conc. for zooplankton
KDASSFIJV	0.09	0.15	d^{-1}	max. growth rate of juvenile whitefish
KDASSFIAD	0.04	0.08	d^{-1}	max. growth rate of adult whitefish
KDASSPISC	0.02	0.06	d^{-1}	max. growth rate of piscivorous fish
KDMINDETS	0.001	0.004	d^{-1}	mineralisation rate in sediment
KNITRS	0.2	1.5	d^{-1}	nitrification rate in sediment
CSUSPMAX	20	30	g m^{-3}	max. value of suspended matter function
KTURBFISH	0.5	2	g g^{-1} d^{-1}	relative bioturbation by adult whitefish
CVSETDET	0.2	0.3	m d^{-1}	detrital settling rate

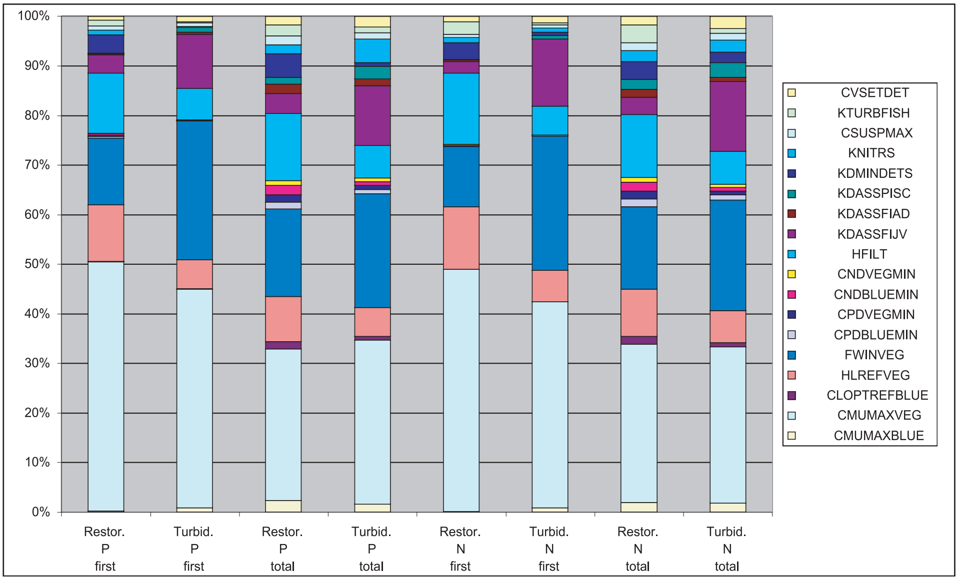


Fig. 4.11. *Sensitivity coefficients of the critical loading values for the parameters, FAST method. Restor. = critical loading for restoration; Turbid. = critical loading for turbidification; P = P-limited runs; N = N-limited runs; first = FAST first-order effects; total = FAST total-order effects. Parameters are explained in table 4.7.*

Table 4.8. Results of linear regression (without interactions)

	Turbidification switchpoint			Clarification switchpoint		
	Value	Std.error	Pr(>|t|)	Value	Std.error	Pr(>|t|)
(Intercept)	-11.7963	1.1778	$< 10^{-4}$	-2.9241	0.3147	$< 10^{-4}$
CMUMAXBLUE	-4.206	60.609	$< 10^{-4}$	-0.5063	0.1627	0.0019
CMUMAXVEG	89.2222	1.1393	$< 10^{-4}$	18.7295	0.3044	$< 10^{-4}$
CLOPTREFBLUE	-0.0086	0.021	0.6826	0.004	0.0056	0.4745
HLREFVEG	-0.4115	0.0126	$< 10^{-4}$	-0.0807	0.0034	$< 10^{-4}$
FWINVEG	13.678	0.652	$< 10^{-4}$	1.3208	0.1742	$< 10^{-4}$
CPDBLUEMIN	6.4242	136.5283	0.9625	27.1283	36.478	20.4572
CPDVEGMIN	-363.624	292.2091	0.2136	-59.4732	78.0736	0.4464
CNDBLUEMIN	12.3974	6.1969	0.0457	-4.5177	1.6557	0.0065
CNDVEGMIN	-116.574	34.5844	0.0008	-10.7432	9.2404	0.2452
HFILT	9.0531	0.3329	$< 10^{-4}$	2.256	0.0889	$< 10^{-4}$
KDASSFIJV	-45.9099	2.1089	$< 10^{-4}$	-7.9462	0.5635	$< 10^{-4}$
KDASSFIAD	-17.0245	3.3688	$< 10^{-4}$	1.7683	0.9001	0.0497
KDASSPISC	39.9123	3.1377	$< 10^{-4}$	0.7659	0.8383	0.3611
KDMINDETS	301.9624	45.8039	$< 10^{-4}$	168.227	12.2381	$< 10^{-4}$
KNITRS	0.1196	0.0995	0.2298	0.0895	0.0266	0.0008
CSUSPMAX	-0.1485	0.0151	$< 10^{-4}$	-0.0294	0.004	$< 10^{-4}$
KTURBFISH	-0.758	0.0829	$< 10^{-4}$	-0.1932	0.0221	$< 10^{-4}$
CVSETDET	18.9498	1.3649	$< 10^{-4}$	2.5624	0.3647	$< 10^{-4}$
Residual St.Error	*0.9738*			*0.2602*		
d.f.	*1151*			*1151*		
R^2	*0.8839*			*0.8273*		

Simulated critical loading of the calibration lakes

By the same method, the switch points corresponding to the lakes in the calibration data set were calculated, using the lake characteristics listed in table 4.3. The results are listed in table 4.9 and compared with the actual loading. Also shown are the in-lake TP concentrations and the Secchi depth ‘just before the switch’. All these figures are indicative only and should not be used too strictly on these specific lakes.

It appears that in 11 out of 43 lakes, the P loading is/was lower than the threshold for restoration, in 6 lakes the loading is between the two thresholds, and in the remaining 26 lakes the loading is higher than the turbidification switchpoint, in 12 of which a factor 5 or more. For most lakes, this corresponds to their actual state, clear or turbid. (Some lakes cannot unambiguously be classified, as they have distinct vegetated and unvegetated parts.)

The critical in-lake TP concentrations show much less variation than the critical loadings. This holds even more for the critical relative Secchi depth, as may be expected.

The critical TP concentration for restoration might be used as an in-lake indicator of how far one is still off from the switchpoint.

The critical TP concentration for turbidification might be used as an indication for the stability of the clear-water state in the lake, or as an ‘early warning signal’ in case the lake would be moving towards the switchpoint.

Table 4.9. Simulated critical loading levels for the lakes in the dataset, compared with the current or historic loading (from table 4.3).

#	Lake	Thresholds for restoration					Thresholds for turbidification							Current state (C/T)	
		P load [mg m^{-2} d^{-1}]	P-in-conc [mg/l]	P-lake [mg/l]	Secchi [m]	zeu/z [-]	P load [mg m^{-2} d^{-1}]	P-in-conc [mg/l]	P-lake [mg/l]	Secchi [m]	zeu/z [-]	Current P load [mg^{-2} d^{-1}]	Cat.*		Depth [m]
1	Hollands-Ankeveen	0.82	0.24	0.08	0.34	0.27	3.09	0.88	0.11	0.71	0.57	0.14	L	C	1.25
2	Bergse Achterplas	1.12	0.06	0.05	0.59	0.29	2.67	0.14	0.03	1.06	0.53	8.10	H	T	2.00
3	Bergse Voorplas	1.00	0.05	0.05	0.61	0.30	2.48	0.12	0.02	1.15	0.57	8.16	H	T	2.00
4	Beulakerwijde	0.22	0.02	0.03	0.51	0.29	0.32	0.03	0.01	0.82	0.46	5.12	HH	T	1.75
5	Botshol, Grote Wije	1.27	0.10	0.05	0.60	0.30	2.30	0.18	0.03	1.20	0.59	0.88	L	C	2.03
6	Kaag, Norremeer	3.07	0.03	0.03	0.68	0.28	5.29	0.05	0.02	1.53	0.64	96.71	HH	T	2.40
7	Langeraar, Geerplas	0.29	0.07	0.06	0.55	0.29	1.03	0.23	0.03	0.98	0.52	1.46	H	T	1.90
8	Loosdrecht	0.18	0.02	0.03	0.63	0.29	0.27	0.03	0.01	1.04	0.48	0.89	H	T	2.15
9	Naarden, Grote Meer	2.98	0.30	0.23	0.41	0.33	5.91	0.59	0.06	0.97	0.78	0.68	L	C	1.25
10	Naarden, Wijde Blik	4.31	0.83	0.51	0.32	0.32	5.69	1.10	0.07	1.08	1.08	0.68	L	C	1.00
11	Reeuwijk, Nieuwenbroek	0.25	0.05	0.05	0.53	0.29	0.75	0.14	0.02	0.94	0.52	1.10	H	T	1.80
12	Nieuwkoop, Noordeinder	0.15	0.02	0.04	0.97	0.32	0.54	0.09	0.01	1.55	0.52	0.85	H	T	3.00
13	Nieuwkoop, Zuideinder	0.72	0.03	0.03	0.94	0.31	1.28	0.05	0.01	1.75	0.58	1.75	H	T	3.00
14	Reeuwijk, Elfhoeven	0.60	0.04	0.04	0.61	0.31	1.09	0.07	0.01	1.10	0.55	5.48	HH	T	2.00
15	Westeinderplassen	0.78	0.04	0.03	0.89	0.32	0.98	0.05	0.01	1.92	0.681	2.88	HH	T	2.80
16	Zuidlaardermeer	6.06	0.14	0.12	0.29	0.29	9.48	0.22	0.07	0.65	0.65	11.95	H	T	1.00
17	Nannewijd	0.87	0.13	0.10	0.29	0.29	3.95	0.58	0.14	0.56	0.56	0.96	M	T	1.00
18	Blankaart (B)	12.33	0.17	0.15	0.28	0.28	16.95	0.24	0.15	0.39	0.39	18.70	H	T	1.00
19	Maten 13 (B)	68.71	0.75	0.67	0.19	0.257	3.05	0.79	0.51	0.31	0.41	9.32	L	C	0.75
20	Visvijver (B)	3.30	1.10	0.03	0.88	1.10	3.30	1.10	0.02	0.88	1.10	0.16	L	C	0.80
21	Gara, South (IR)	26.51	0.19	0.18	0.28	0.28	29.01	0.21	0.18	0.29	0.29	10.18	L	C	1.00
22	Maumwee (IR)	2.07	0.04	0.03	0.52	0.26	3.72	0.07	0.02	1.23	0.62	1.84	L	C	2.00

Table 4.9. Continued

#	Lake	Thresholds for restoration					Thresholds for turbidification							Current state	
		P load [mg m^{-2} d^{-1}]	P-in-conc [mg/l]	P-lake [mg/l]	Secchi [m]	zeu/z [-]	P load [mg m^{-2} d^{-1}]	P-in-conc [mg/l]	P-lake [mg/l]	Secchi [m]	zeu/z [-]	Current P load [mg^{-2} d^{-1}]	Cat.*	Cur-rent state (C/T)	Depth [m]
23	Mullagh (IR)	0.22	0.05	0.04	0.92	0.40	0.91	0.19	0.02	1.27	0.55	0.83	M	(C)	2.30
24	Pollaphuca (IR)	0.08	0.00	0.01	1.69	0.25	0.08	0.00	0.01	1.67	0.25	1.83	HH	C	6.80
25	Ramor (IR)	0.60	0.01	0.01	0.98	0.33	1.26	0.03	0.01	1.75	0.58	6.36	HH	T	3.00
26	Luknajno (PL)	0.54	0.17	0.10	0.63	0.35	0.57	0.18	0.01	1.58	0.88	0.11	L	C	1.80
27	Waalboezem	0.36	0.02	0.03	1.30	0.34	1.14	0.06	0.01	2.14	0.56	11.23	HH	T	3.80
28	Binnenbedijkte Maas	0.17	0.01	0.03	1.43	0.36	0.67	0.05	0.01	2.12	0.53	5.48	HH	T	4.00
29	Brielse Meer	0.10	0.00	0.01	1.86	0.34	0.10	0.00	0.00	1.88	0.34	17.26	HH	T	5.50
30	Volkerak	0.58	0.01	0.01	1.32	0.26	0.57	0.01	0.00	2.57	0.51	12.99	HH	(C)	5.00
31	Zoommeer	0.76	0.01	0.01	1.63	0.27	0.75	0.01	0.00	3.14	0.52	14.13	HH	(C)	6.00
32	Oude Venen 2	2.37	0.14	0.12	0.39	0.31	5.10	0.30	0.08	0.84	0.67	6.84	H	T	1.25
33	Veluwemeer	1.56	0.06	0.06	0.46	0.29	3.42	0.13	0.04	0.83	0.53	3.73	H	(C)	1.56
34	Wolderwijd	0.95	0.06	0.06	0.54	0.28	1.62	0.10	0.02	1.25	0.65	1.37	M	(C)	1.93
35	Nuldernauw	1.78	0.04	0.03	0.52	0.25	2.71	0.06	0.02	1.21	0.59	7.53	H	T	2.06
36	Drontermeer	6.48	0.09	0.08	0.35	0.28	10.28	0.15	0.07	0.73	0.58	9.84	M	T	1.26
37	Braassemermeer	0.81	0.01	0.02	1.20	0.31	1.64	0.03	0.01	1.99	0.51	37.26	HH	T	3.90
38	Langeraar, Noordeinde	0.19	0.05	0.06	0.57	0.30	0.66	0.19	0.02	1.02	0.54	2.60	H	T	1.90
39	Mooie Nel	1.19	0.01	0.01	1.38	0.31	1.64	0.02	0.01	2.72	0.60	179.45	HH	T	4.50
40	Het Hol	2.83	0.44	0.24	0.30	0.30	7.01	1.10	0.18	1.02	1.02	0.87	L	C	1.00
41	Kortenhoef	0.45	0.08	0.07	0.33	0.28	1.38	0.23	0.05	0.65	0.54	4.58	H	T	1.20
42	Stichts-Ankeveen	1.29	0.39	0.14	0.29	0.29	3.63	1.10	0.10	0.96	0.96	0.09	L	C	1.00
43	Frisian Lakes (average)	0.42	0.05	0.04	0.39	0.28	0.79	0.09	0.03	0.66	0.48	3.90	H	T	1.36

Table 4.9. Continued

#	Lake	Thresholds for restoration					Thresholds for turbidification							Current state (C/T)	
		P load [mg m^{-2} d^{-1}]	P-in-conc [mg/l]	P-lake [mg/l]	Secchi [m]	zeu/z [-]	P load [mg m^{-2} d^{-1}]	P-in-conc [mg/l]	P-lake [mg/l]	Secchi [m]	zeu/z [-]	Current P load [mg^{-2} d^{-1}]	Cat.		Depth [m]
44	Enso	2.40	0.09	0.07	0.51	0.27	5.91	0.22	0.05	1.02	0.54	0.05	L	C	1.90
45	Nederso	70.00	0.22	0.21	0.43	0.27	73.27	0.23	0.21	0.44	0.28	2.47	L	(C)	1.60
46	Soby	0.67	0.07	0.03	0.85	0.28	1.60	0.16	0.02	1.38	0.46	0.19	L	C	3.04
47	Hinge	8.13	0.14	0.11	0.32	0.26	13.03	0.22	0.12	0.41	0.34	8.49	M	T	1.20
48	Kvind	8.73	0.07	0.05	0.48	0.25	13.83	0.11	0.05	1.16	0.61	10.96	M	T	1.90
49	Lading	6.22	0.42	0.39	0.27	0.27	10.16	0.69	0.19	0.53	0.53	1.37	L	T	1.00
50	Silkeborg-Langso	21.28	0.09	0.08	0.51	0.25	24.68	0.10	0.07	0.71	0.36	18.63	L	T	2.00
51	Honda	1.08	0.14	0.15	0.32	0.32	4.62	0.59	0.03	0.96	0.96	4.16	M	T	1.00
52	Nueva	0.31	0.17	0.14	0.52	0.35	1.25	0.68	0.01	1.44	0.96	0.12	L	T	1.50

*Category: L= < lower threshold, M=between the two thresholds, H = > higher threshold, HH = > 5 * higher threshold

Discussion and conclusions

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 some form of validation. Apparently, the influence of the main input factors (listed in § 4.3.3) is reflected in the model results in the right way, so the quality of the model can be regarded as sufficient for practical purposes. This does not mean that all relations in the model are 'true'; it is still possible that other assumptions could explain the same results.

The multi-lake calibration has proven to be a useful tool. The uncertainty in the output could be reduced markedly Fig. 4.9). 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. But one should not thrive at a complete calibration of the model, as this is 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 acount, 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. The topic of the critical loading values is discussed further in chapter 6.

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Chapter 5

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A model of nutrient dynamics in shallow lakes in relation to multiple stable states

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Key words: model, phosphorus, eutrophication, hysteresis, lake, restoration

Abstract

There is increasing evidence that, within a range of nutrient loadings, shallow lakes may have two alternative stable states. One is dominated by phytoplankton and the other one by submerged macrophytes as the main primary producer. The question arises at what level of nutrient loading a transition may occur between the two states. This question was addressed by means of the integrated lake model *PCLake*. The model describes the competition between phytoplankton and macrophytes, within the framework of closed nutrient cycles in the lake system, including the upper sediment. Top-down effects via the food web were regarded as well. The model was run for a hypothetical shallow lake, representative for the situation in The Netherlands. Long-term simulations were carried out for a realistic range of nutrient loadings and starting from different initial conditions. The results showed a highly non-linear response, which also showed hysteresis: the loading level at which a transition occurs turned out to be dependent on the initial conditions. The results were compared with empirically derived chlorophyll *a* to phosphorus relations. Factors influencing the 'critical nutrient level' were the lake dimensions and the net sedimentation rate. The model was also used to evaluate the role of food web management in lake restoration. The results suggest that a long-term effect of additional management is possible only if combined with a decrease in nutrient loading.

Introduction

As a result of high nutrient loadings during the past decades, many shallow lakes have become highly eutrophic. They are now characterized by dense algal blooms of cyanobacteria, high turbidity, absence of vegetation and a fish community dominated by bream. Although these effects were caused by high nutrient loadings, restoration of the former macrophyte-dominated clear-water state often could not be achieved by external load reduction alone: eutrophic lakes often show resistance to recovery. Apparently, once the system has switched from a clear to a turbid state, this switch cannot simply be reversed (e.g. Jeppesen et al., 1991; Gulati et al., 1990b; De Haan et al., 1993; Boers et al., in press). Several, often interacting, mechanisms for this resistance have been proposed. Firstly, a prolonged internal loading from nutrient-rich sediments may delay the response (Ryding & Forsberg, 1977; Sas, 1989). Secondly, an increase of the nutrient utilization efficiency of the phytoplankton makes them produce the same biomass with less nutrient (Riegman, 1985; Van Liere & Janse, 1992). Thirdly, the grazing pressure on the phytoplankton is low, both because of the poor edibility of cyanobacteria and the strong predation by bream (Gulati et al., 1990a). Finally, the large amount of detritus accumulated in the system keeps the water turbid and impedes return of the vegetation (Van Dijk & Van Donk, 1991). Clearly, both direct effects of nutrients and indirect effects through the food web may contribute to the often observed resistance to recovery. Therefore, additional measures are sometimes considered apart from, or combined with, nutrient load reduction (Gulati et al., 1990a).

On the other hand, also the clear-water state of shallow lakes, dominated by submerged macrophytes, shows a certain resistance to external forcings, like a moderate increase in nutrient loading (Moss, 1990).

Several stabilising mechanisms may play a role. Nutrient uptake by macrophytes may suppress algal growth due to nutrient limitation (Van Donk et al., 1993), they may provide favourable conditions for predatory fish and they may reduce wind-induced resuspension by stabilising the sediment.

The question addressed in this paper is how the probability of a transition from the clear-water state to the turbid state, or vice versa, is related to the external nutrient loading. This topic is approached by means of a mathematical model, in order to facilitate a systematic analysis. The model used in this study, called *PCLake*, combines a description of the dominant biological components with a description of the nutrient cycle in shallow lake ecosystems. The model differs both from many eutrophication models, which confine themselves mainly to the nutrient cycling, as well as from more detailed biological models. It also differs from so-called minimodels (e.g. Scheffer, 1990) in that it is based on closed nutrient cycles, allowing a more quantified analysis. The aim of this study is to analyse the system's long-term response, in terms of phosphorus, algal and macrophytes biomass, as a function of the external nutrient loading and the initial conditions. Some implications for lake management are discussed.

Model structure

The *PCLake* model calculates the water quality parameters chlorophyll *a*, transparency, phytoplankton types and the density of submerged macrophytes. It also calculates the distribution and fluxes of the nutrients N and P. Inputs to the model are: lake hydrology, nutrient loading, dimensions (mean depth and size) and sediment characteristics. An extensive description of the model may be found in Janse & Aldenberg (1996).

The model describes a completely mixed water body and comprises both the water column and the upper sediment layer (Figure 1). A default sediment depth of 0.1 m has been used. Any further horizontal or vertical distinction is not taken into account. At the base of the model are the water and nutrient budgets (in- and outflow). The physico-chemical module describes the exchange of detritus, inorganic matter and nutrients between sediment and water. Processes involved are sedimentation, resuspension, diffusion, burial and chemical adsorption. Mineralization processes are described in both layers. Two modules, for phytoplankton and macrophytes, respectively, describe the primary production. The food web module is kept as simple as possible and comprises zooplankton, macrozoobenthos, whitefish and predatory fish. All biota are modelled on the basis of functional groups. In this way, effects of the food-web structure on the nutrient cycles are accounted for, and biomanipulation measures may be simulated. The user may choose between different model configurations according to his questions and the available data. In this study, only the phytoplankton has been split into three functional groups, *viz.* cyanobacteria, diatoms and other small edible algae, because of their different characteristics and because of management's interests. It is assumed that the zooplankton has a lower food preference for cyanobacteria and detritus than for the other groups. It is further assumed that the macrophytes may extract nutrients from both the water and the sediment pore water. Apart from mass fluxes (food relations etc.), some 'empirical relations' are included in the model: the resuspension rate is positively affected by the amount of whitefish and negatively by the vegetation density, while the vegetation is assumed to have a positive influence on the growth of predatory fish.

The overall nutrient cycles for N, P and Si are described as completely closed (except for in- and outflow and denitrification). This was done by modelling all nutrient- to-dry-weight ratios dynamically (as indicated by the doubled blocks in Figure 1). Mechanisms were included to cope with the often observed increase of the weight-specific nutrient contents of the organisms at higher trophic levels (e.g. Gulati et al., 1991) and with variations in algal nutrient contents. It should be stressed that all organisms are considered as dependent, directly or indirectly, on the nutrients that are available in the lake or the lake sediment.

The model has been implemented in the simulation package ACSL, version 10. Parameter values were derived from literature and from calibration on several case studies (Janse et al., 1992, 1993; Van Dijk & Janse, 1993). A partial calibration study on a multi-lake data set using Bayesian statistics has also been carried out (Aldenberg et al., 1995). The model has been used for several scenario analyses. These include studies on nutrient load reduction (Janse et al., 1992), biomanipulation (Janse et al., 1995; Janse et al., in press) and combinations of these with dredging (Janse et al., 1993; Zamurović-Nenad, 1993; Aysever, 1994).

In this study, simulations have been performed for a hypothetical lake system which may be considered as representative for many shallow lakes occurring in The Netherlands. Its main characteristics are: mean depth = 2 m, areal hydraulic loading = 20 mm

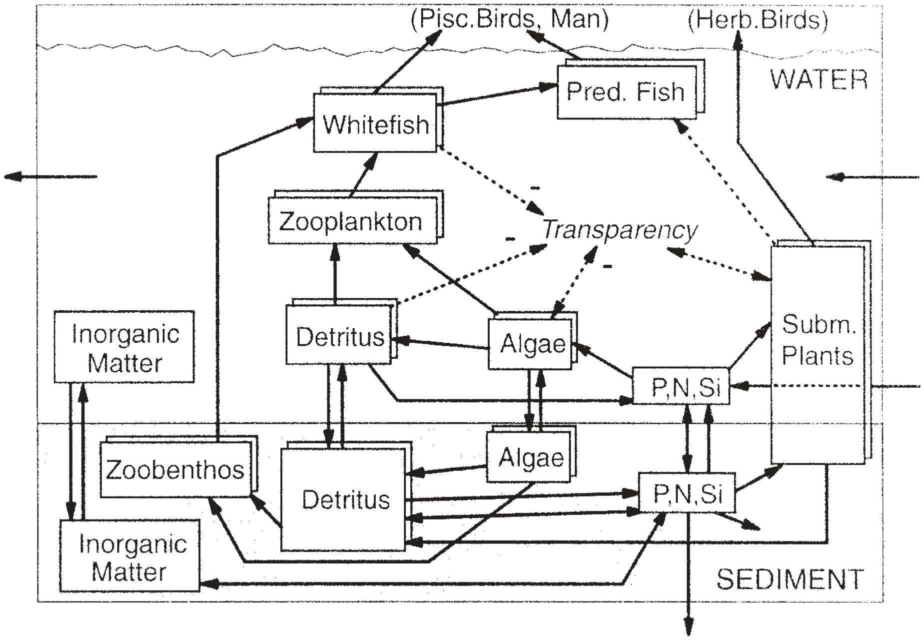


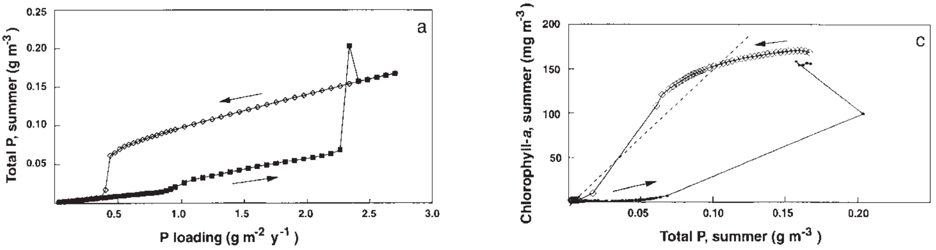
Figure 1. PCLake model structure. Doubled blocks denote compartments modelled in both dry weight and nutrient units. Three functional groups of phytoplankton are distinguished: cyanobacteria, diatoms and other small edible algae. Arrows with solid lines denote mass fluxes (e.g. food relations), arrows with dotted lines denote 'empirical' relations (minus sign denotes negative influence, otherwise positive influence). Egestion and mortality fluxes of animal groups and respiration fluxes are not shown.

d^{-1} (=7.2 m y^{-1}), no seepage, porosity of upper sediment = 0.9, sediment Fe content = 10 mg g^{-1}. Some of the simulations have also been carried out for a mean depth of 5 m and a mean depth of 10 m, with the same hydraulic loading. The (theoretical) total P concentration in the inflow to Dutch shallow lakes ranges from 0.1 to 1.0 mg P l^{-1}. Typical in-lake total phosphorus concentrations are between 0.05 and 0.5 mg P l^{-1}, while summer averaged chlorophyll-*a* concentrations are around 100–200 μg l^{-1} (Lijklema et al., 1989).

Results

Variation of nutrient loading and initial conditions

The long-term impact of different nutrient loadings on the above-mentioned 'average shallow lake', with a depth of 2 m, was simulated. Simulations have been performed for ten years, with the nutrient loading set to a fixed value, ranging from 0 to 2.5 g Pm $^{-2}$ d^{-1}. The nitrogen loading has been set to 10 times the phosphorus loading. For every loading value, the simulation has been done twice, starting either from a macrophyte-dominated state, or from a phytoplankton-dominated state with high chlorophyll *a*, respectively. The resulting summer-averaged total-P and chlorophyll *a* concentrations in the tenth year are shown (Figure 2a, b), as well as the relation between them (Figure 2c). The relations between nutrient input and both variables were highly non-linear, with a rather sudden switch between a macrophyte-dominated state with low chlorophyll *a* values and a phytoplankton-dominated state with high ones. Moreover, the response showed hysteresis, so that the 'critical' nutrient loading was considerably different whether one started from the 'clear' or from the 'turbid' side. The calculations were also repeated for some different parameter values. The values of



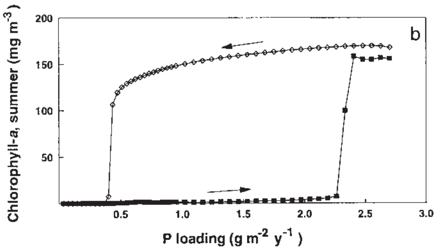


Figure 2. Simulations for an average shallow lake (see text) with a depth of 2 m, for a range of P loadings. The N loading is assumed to be always 10 times the P loading. All simulations have been done for two initial states, a clear-water state dominated by macrophytes (solid symbols) and a turbid state with a blue-green algal dominance (open symbols). Output values are summer-averages after 10 years with the same loading conditions. a. in-lake total P as a function of the P loading; b. chlorophyll *a* as a function of the P loading; c. relation between chlorophyll *a* and in-lake total P concentration. The broken line in Figure 2c is the empirically derived maximum for a data base of Dutch lakes (Lijklema et al., 1989).

the switch points were notably sensitive for the parameters determining resuspension and sedimentation, which are dependent on lake dimensions and sediment characteristics. The lower the net sedimentation rate, the lower were also the critical loading levels.

In comparable simulations of deeper lakes, where the mean depth had been set to 5 m and 10 m, respectively, this hysteresis phenomenon did not occur (Figure 3). These lakes were apparently too deep for macrophyte development so that a phytoplankton dominance appeared in all simulations, but with much lower chlorophyll *a* concentrations than in the simulations of the shallow lakes. The relation between phosphorus and chlorophyll *a* was more or less continuous in these cases. In the left part of the graphs, representing a nutrient-limited situation, all curves overlap. To the right, where light limitation occurs, the chlorophyll *a* concentrations decrease with lake depth, as expected.

The points in the left part of the graphs (Figures 2c and 3) coincide with the line of the maximum summer-averaged chlorophyll-*a* concentration at a given P concentration, empirically derived from a data set of 120 lakes in The Netherlands (Lijklema et al., 1989). All of these lakes were dominated by phytoplankton, the lakes with the higher chlorophyll *a* to total P ratios, up till 1.4 mg mg^{-1}, being dominated by cyanobacteria.

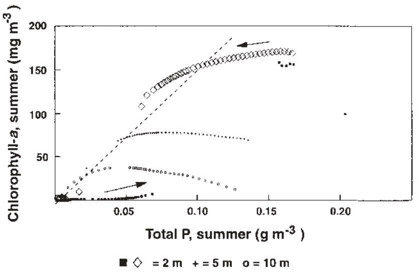


Figure 3. Chlorophyll *a* to in-lake total P relation for three lakes with a depth of 2 m, 5 m and 10 m, respectively, with equal water inflow, for a range of P loadings. Simulations as in Figure 2. Solid squares: depth 2 m, starting from clear state; diamonds: depth 2 m, starting from turbid state; plus signs: depth 5 m; circles: depth 10 m. The broken line is the empirically derived maximum for a data base of Dutch lakes (Lijklema et al., 1989).

These data are in agreement with the chlorophyll *a* and total-P model simulations.

Eutrophication, de-eutrophication and management

In order to study the dynamical behaviour of the model, the same hypothetical shallow lake with a depth of 2 m was simulated during the course of eutrophication and restoration (Figure 4). The simulation started under mesotrophic conditions with the inflowing water

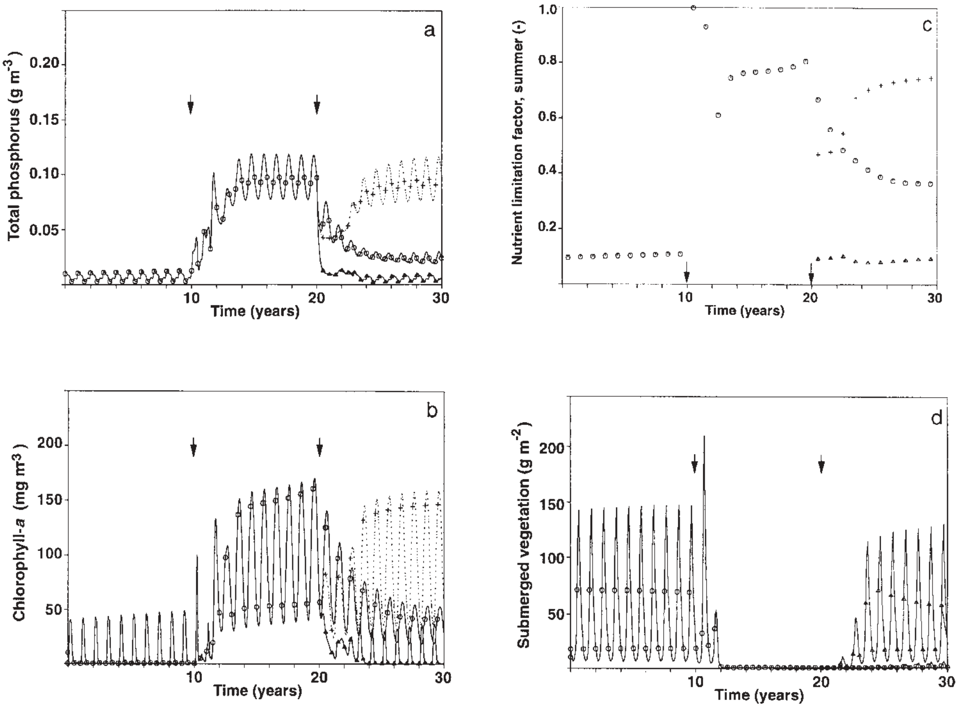


Figure 4. Simulations for an average shallow lake (see text) with a depth of 2 m. After 10 years, nutrient loadings have been increased sevenfold. After another 10 years, three options were simulated: (1) decrease in nutrient loading down to the starting value (circles); (2) idem combined with dredging and food web management (triangles); (3) dredging and fish management only (dashed line with 'plus' signs). a. total phosphorus; b. chlorophyll *a*; c. nutrient limitation function of phytoplankton; d. submerged vegetation.

containing 0.03 mg l^{-1} total phosphorus and 0.3 mg l^{-1} total nitrogen. After 10 years, these concentrations were increased sevenfold, thus bringing the lake into a hypertrophic state. After another 10 years, three options were simulated:

(a) cutting down the nutrient loadings to the former, low, values.

(b) idem, combined with dredging and fish management, each carried out once. This was done in the model by removing 80% of the sediment detritus, half of the zoobenthos and 80% of the whitefish, and introducing 0.1 g d.w. m^{-2} predatory fish.

(c) dredging and fish management without nutrient load reduction.

The effects of the increase and subsequent decrease in nutrient loading are discussed first. The simulated in-lake total phosphorus concentration (Figure 4a) generally followed the changes in inflow concentration with a lag time of about 4 years. This delay may be caused by a slower reaction of the sediment with respect to the water. After the load reduction at year 20, however, the concentration did not quite drop down to the starting value. The chlorophyll *a* concentration (Figure 4b) remained low during the 'mesotrophic period', with small edible algae dominating (data not shown). Their growth rate in mid-summer is severely limited by the availability of nutrients (Figure 4c). Within two years after the increase in loading, the algae were replaced by blue-greens, in high density. Their growth rate was hardly limited by nutrient supply. Algal biomass decreased again following the load reduction at year 20, but the phytoplankton remained to be dominated by blue-greens. As a consequence of the reduced loading, the algal growth rate became nutrient limited again to some extent. The zooplankton almost completely vanished when the blue-greens dominance established, while the whitefish density gradually increased and the predatory fish disappeared. The development of the submerged vegetation (Figure 4d) was more or less inverse to that of the blue-greens. The lake started in a stable, macrophyte-dominated situation. By uptake of the scarce nutrients, they clearly contributed to the nutrient limitation of the algae. The macrophyte density first increased after the load increase, followed by an almost complete disappearance. This was caused by a deteriorating light climate (decreasing Secchi disk depth) due to increasing seston concentrations. The load reduction 10 years later failed to restore the macrophyte dominance. Summarizing, eutrophication made the system change from a clear, macrophyte-dominated state to a turbid state, dominated by blue-greens. This process could not be reverted by nutrient load reduction alone, in agreement with field observations in comparable lakes.

Load reduction combined with dredging and fish stock management, however, proved to be able to make the system 'switch back': the blue-greens were replaced by small edible algae again, in low density, and the vegetation reestablished, as well as the piscivorous fish and the zooplankton. The phytoplankton growth rate became nutrient limited again. Apparently, the sudden improvement in light climate created favourable conditions for return of the vegetation, which was able to stabilize the new situation. To compare, the direct system manipulation as stand-alone measure, while the nutrient loading remained high, was only temporarily effective and failed to reestablish a stable clear state of the system.

Discussion

The model results confirm the existing evidence that shallow lakes may have two alternative states, a clear-water state dominated by macrophytes and a turbid state dominated by phytoplankton (Moss, 1990; Scheffer, 1990; Jeppesen et al., 1990). Several factors determine which state prevails in a certain case. A general constraint is set by the external nutrient loading. At a very high loading, only the turbid state is stable, whereas the opposite is true for very low loadings. In the intermediate range, both states may exist and switches between the two states are possible. Because both states possess a number of self-stabilizing buffering mechanisms, the critical loading level at which a shift occurs is dependent on the initial state of the system: the shift from turbid to clear occurs at a much lower loading level than the opposite one (hysteresis). Either state has a certain attraction field, which are separated by a so-called 'separation line'. A shift may be invoked by a (natural or anthropogenic) disturbance of the system, moving it across the separation line (cf. Scheffer, 1990). Such a shift seems to be always correlated with a dramatic change in water transparency, a key factor for survival of submerged macrophytes. An example of a disturbance might be food web management, possibly combined with physical measures as dredging. The model suggests that additional management is, on long term, more (or only) effective if combined with load reduction, as was also concluded from biomanipulation experiments (Gulati et al., 1990a). Analyses like this one may contribute to improved predictions of the chance of success of additional management at different nutrient levels.

The model analyses also stress the close interrelationship between the nutrient cycle on the one hand and the biological structure on the other. The competition between the different primary producers, phytoplankton and macrophytes, is related to both light climate, nutrient availability and food web interactions. Changes in trophic state may cause changes in food web structure, while the latter may influence the system's (resistance to) response to nutrient loading. Cascading effects in the food web may be analyzed also in terms of changes in nutrient cycles (cf. Carpenter et al., 1992), while the overall trophic state of the system sets a constraint to its total productivity and may be regarded as a general boundary condition. It may be concluded that it is a useful approach to integrate these aspects in one mathematical model in order to study the combined effects of bottom-up and top-down control. It also allows evaluation of different ecological hypotheses and mechanisms. This approach may be complementary to the existing modelling tools for the analysis of subsystems (e.g. Scheffer, 1990) and to the more detailed eutrophication models.

The results of the long-term simulations for total phosphorus and chlorophyll *a* are, in general, within realistic ranges, if compared with empirically derived relations. Also the general shape of the response is in agreement with observations from various shallow lake studies (*op. cit.*). The calculation of the 'critical loading value', the switch point between the turbid and the clear state, might be useful for the derivation of ecological standards for water quality. The calculated values should, however, only be regarded as indicative values at this stage, because they are dependent on model parameters which have only partly been calibrated. This is due to the rather limited range in the present water quality data in Dutch lakes, where, more specifically, clear lakes are lacking. More extensive calibration on a wider data set is needed. Secondly, many model parameters are more or less uncertain due to natural variability or other reasons. As (part of) this uncertainty is inavoidable, the results should be interpreted in a probabilistic rather than a deterministic way. The uncertainty in the results as a function of the combined uncertainty in the parameters should be established by means of appropriate statistical tools, such as Bayesian uncertainty analysis. The model outcome may then be expressed as, for instance, the chance for recovery of a lake or lake type under different circumstances or with different management options, or in terms of the minimum load reduction to be achieved. This approach resembles the ecological risk assessment adopted for toxic substances and other environmental issues.

Conclusions

The model results are in agreement with the concept of two possible stable states, dominated by macrophytes and phytoplankton, respectively. The simulated long-term response of a hypothetical 'average shallow lake system' as a function of the nutrient input was highly non-linear and showed hysteresis. The modelling approach presented here, taking into account both the biological structure and the nutrient cycle, may be a promising tool for the derivation of nutrient regulation and lake management strategies.

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6. Critical nutrient loading of shallow lakes

In this chapter, the long-term behaviour of the PCLake model is analysed in a systematic way. After illustrating the long-term dynamics, the focus will be on the (quasi) steady state behaviour of the various model components at different nutrient loadings, including the hysteresis effect. The topic of the critical loading levels will be further explored, and we will explain why these levels differ among lakes or lake types. These findings are discussed in view of empirical information, and management implications are discussed.

6.1. Long-term dynamics

It is generally known that aquatic ecosystems often adapt slowly to changing nutrient conditions. One of the causes of this is the slow reaction of the sediments and a high nutrient release from the sediment for many years after a load reduction.

To explore this topic with the PCLake model, long-term simulations have been carried out for a hypothetical lake which may be considered as representative for many Dutch shallow lakes. Its main characteristics are: mean depth = 2 m, fetch = 1000 m, areal hydraulic loading = 20 mm d^{-1} (= 7.2 m y^{-1}), no infiltration or seepage, no surrounding wetland zone, and a lightly clayish sediment (30% dry matter, of which 10% organic matter, and 10% lutum of inorganic matter).

This ‘average lake’ was first subjected to a high nutrient loading (20 mg P m^{-2} d^{-1} and 200 mg N m^{-2} d^{-1}) during 100 years so as to create a sediment rich in phosphorus and nitrogen: *ca* 13 g m^{-2} available P and 43 g m^{-2} available N in the 10 cm top layer. Available nutrient is defined as total nutrient except the refractory organic matter (‘humus’) fraction. The loading was then reduced to 10% of the original value (so, 2 mg P m^{-2} d^{-1} and 20 mg N m^{-2} d^{-1}) and the simulation was continued for another 100 years. As a result, available P in the sediment gradually decreased to its new equilibrium value of about 3.5 g m^{-2} and available N to about 9 g m^{-2} (*Fig. 6.1*). Also the concentration in the water column followed this pattern. Most of the reduction took place during the first 10-15 years. The loadings and concentrations are in the actual range that is, or was, applicable in many Dutch lakes (Lijklema *et al.*, 1989; Portielje & Van der Molen, 1997).

An even stronger load reduction, to 0.5 mg P m^{-2} d^{-1} and 5 mg N m^{-2} d^{-1}, starting from the same eutrophic conditions, resulted in a shift from algae to submerged macrophytes as the main primary producers (*Fig. 6.2*). Also in this case, it took about 15 years for sediment P to approach the new, lower, value. Refractory P did not even reach an equilibrium in this simulation, due to continued loss by the ‘burial’ process from the top layer (which had been defined by a fixed thickness and porosity). The algae gradually declined until very low levels in about 8 years, after which a shift to macrophytes occurred. Because it took the macrophyes a few years to attain a high biomass, the TP concentration in the water temporarily increased in

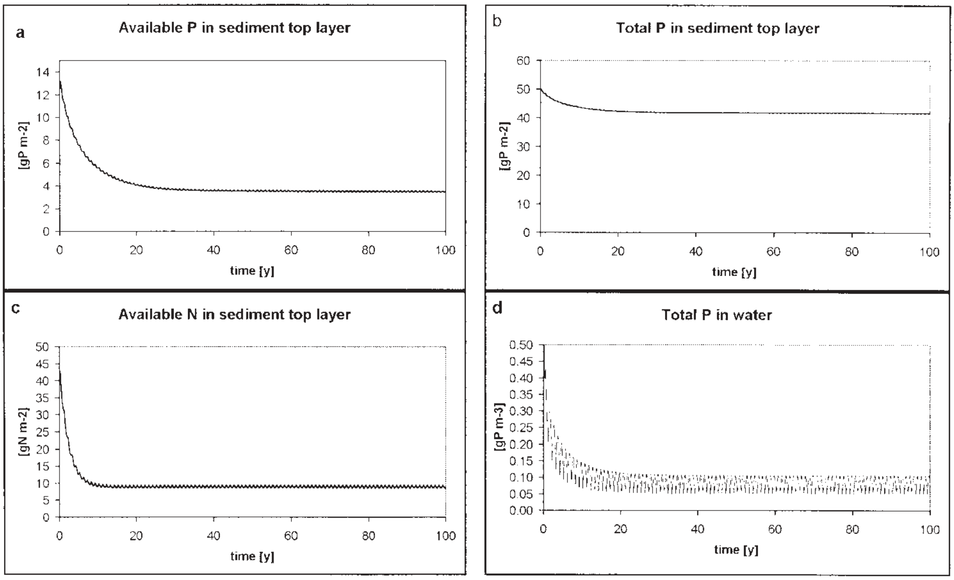


Fig. 6.1. *Long-term simulations with a low nutrient loading, starting from eutrophic conditions.*
a, Available P (= without humus) in sediment top layer [gP m^{-2}*]; b, Total P in sediment top layer [gP* m^{-2}*]; c, Available N (= without humus) in sediment top layer [gN* m^{-2}*]; d, Total P in water [gP* m^{-3}*].*

the switch period before further decreasing to the new, low equilibrium. The equilibrium value of available N in the sediment again increased a little after the macrophytes had settled, possibly due to a higher retention compared to the unvegetated situation.

As explained in chapter 5, reduction of the nutrient loading of a eutrophicated lake, to a value that previously supported the ‘clear’, macrophyte-dominated state, not always results in restoration of this clear state, even after many years. A shallow lake often shows hysteresis in its response to changes in nutrient loading. An example is shown in *Fig. 6.3*. The same ‘average Dutch lake’ is simulated starting from the ‘clear state’ (mesotrophic conditions) and a loading of 1.5 mg P m^{-2} d^{-1}, after 20 years followed by a five-fold increase (to 7.5 mg P m^{-2} d^{-1}), and after another 20 years a reduction back to the original value. The sediment P again follows, with some years of delay, the changes in loading, although it reacts more slowly after the load reduction and the equilibrium is not quite reached after 20 years. The macrophytes that disappear after the loading rise do not return after its decrease. The chlorophyll-*a* concentration decreases after the final load reduction, but does not return to its original low values. Hence, eutrophication made the system change from a clear, macrophyte-dominated state to a turbid state, dominated by cyanobacteria. This process could not be reverted by nutrient load reduction alone, in agreement with field observations in a number of lakes (see e.g. the review by Gulati & Van Donk, 2002).

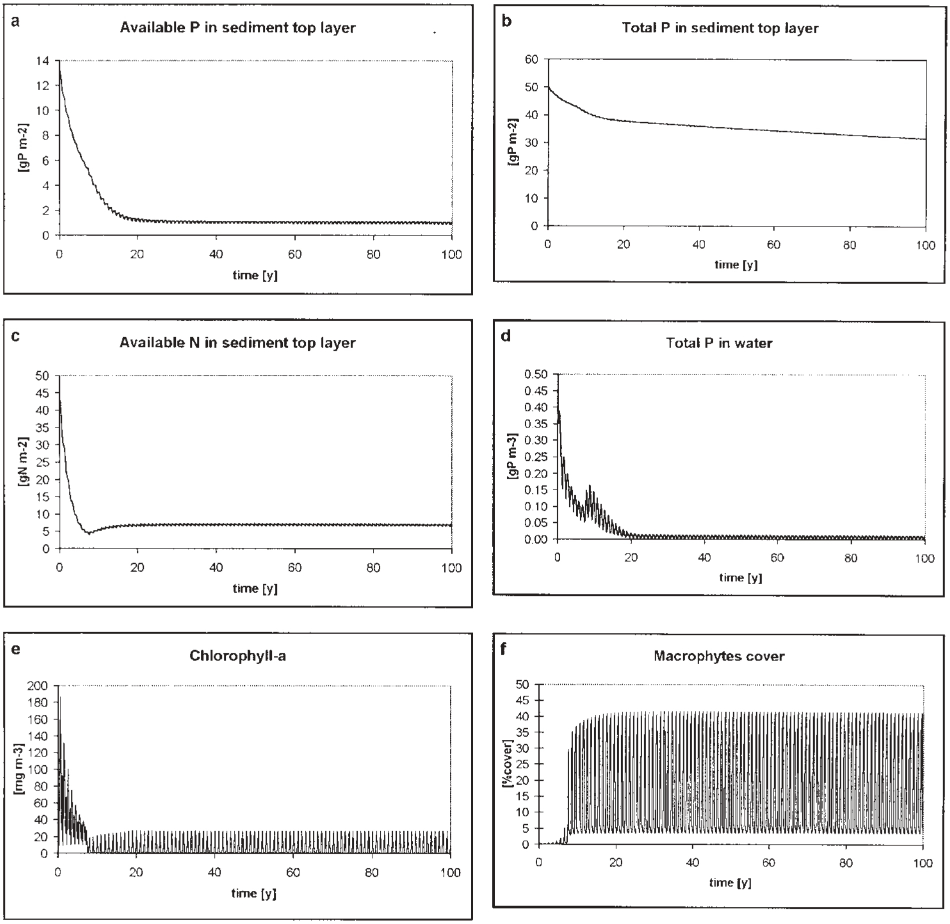


Fig. 6.2. *Long-term simulations with a very low nutrient loading, starting from eutrophic conditions. a, Available P (= without humus) in sediment top layer [gP m^{-2}]; b, Total P in sediment top layer [gP m^{-2}]; c, Available N (= without humus) in sediment top layer [gN m^{-2}]; d, Total P in water [gP m^{-3}]; e, Chlorophyll-a [mg m^{-3}]; f, Submerged macrophytes [% cover].*

Without causing a complete shift, a moderate decrease in nutrient loading may lead to more modest changes in a lake ecosystem, for instance a decrease of the chlorophyll/P ratio of the phytoplankton, changes in the relative abundance of phytoplankton groups, in zooplankton or fish densities, or in a small time shift of the biomass maxima. Examples, with time graphs of these variables and comparisons with measured data, can be found in the case studies described in Janse & Aldenberg (1990, 1991; chapters 8-9), Janse et al. (1992; chapter 10), Janse et al. (1993), Janse (1995), Zamurovic-Nenad (1993), Aysever (1994) and also in Dekker et al. (1996). A case study simulating a shift to macrophytes is described in Janse et al. (1995, 1998; chapters 11-12).

Concluding, the hysteresis in the reaction time of the system is caused by the delayed response

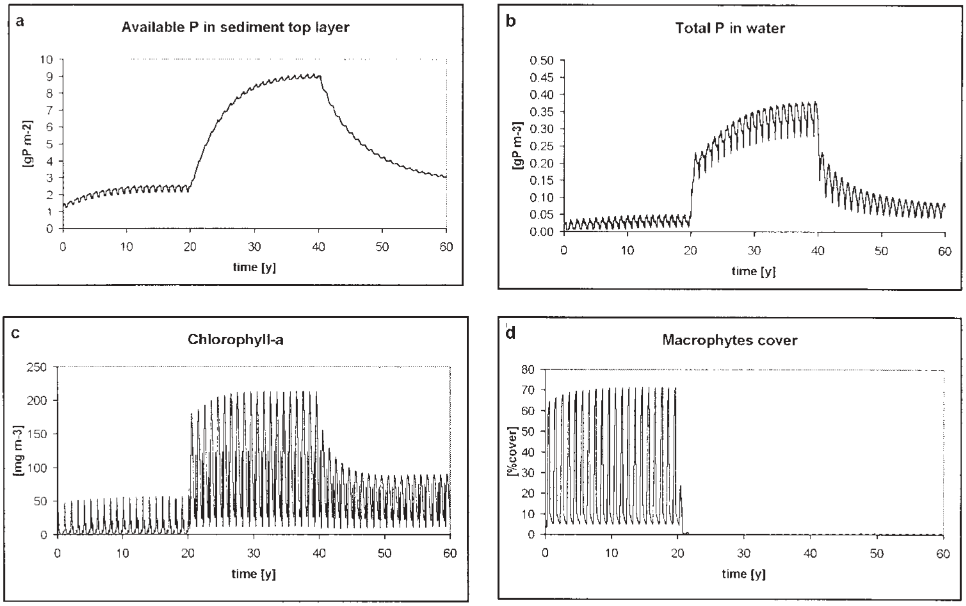


Fig. 6.3. *Simulation for an 'average Dutch lake', starting from a clear state; years 1-20 low loading, years 20-40 high loading, years 40-60 low loading, see text.*

of the sediment, but the hysteresis in the long-term reaction is caused by other factors as well. Several positive feedback mechanisms in the system are candidate for explaining (part of) this phenomenon, which are further discussed in the next paragraphs.

6.2. Effects of nutrient loading and initial conditions in an 'average lake'

The long-term impact of different nutrient loadings on the above-mentioned *'average shallow lake'* was simulated. Simulations have been performed for 50 years, with the nutrient loading set to a fixed value, ranging from 0 to 10 mg P m^{-2} d^{-1}. The nitrogen loading has been set to 10 times the phosphorus loading. For every loading value, the simulation has been done twice, starting either from a macrophyte-dominated state or from a phytoplankton-dominated state.

The simulated long-term summer-averaged concentrations and biomasses, as a function of the phosphorus loading, are shown in Fig. 6.4, a-k. The relations between nutrient input and chlorophyll, and between nutrient input and macrophytes biomass were highly non-linear, with a rather sudden switch between a macrophyte-dominated state with low chlorophyll-*a* values and a phytoplankton-dominated state with high ones. Moreover, the response showed hysteresis, so that the 'critical' nutrient loading was different whether one started from the ‘clear’ or from the ‘turbid’ side. The critical loading for the switch from ‘turbid’ to ‘clear’ was much lower than the one for the opposite switch, viz. *ca* 0.9 and 3 mgP m^{-2} d^{-1}, respectively, for this ‘default lake’. The multiple states only occurred in an intermediate range of nutrient loadings. At a low loading, the system was always macrophyte-dominated, whereas at high loading, it was always dominated by algae.

In accordance with this, also the Secchi depth (Fig. c) shows a rather sudden switch between high values in case of macrophytes dominance and low ones if phytoplankton is high. The in-lake total P and total N concentrations were proportional to the loading in the turbid situation, but were much lower than that when the lake was in the clear state. These switches and hysteresis were also found in the biomass of the different animal groups. When the lake was in the ‘turbid state’, zooplankton showed a more or less asymptotic relation with the loading. In the ‘clear state’ its biomass was lower, probably because of a lesser food availability, but the ratio of zooplankton to phytoplankton was much higher (higher relative grazing pressure). Zoobenthos was higher in the ‘clear state’, because of a higher food availability (organic matter in the sediment). Juvenile (planktivorous) whitefish had a higher biomass when the lake was in the ‘turbid state’ than in the ‘clear state’. The opposite was true for the adult (benthivorous) fish. Predatory fish biomass is high in the ‘clear state’ only (with a limit being set by the carrying capacity), reflected in a higher predatory fish / whitefish ratio.

From the relation between the simulated chlorophyll-a and in-lake total P concentrations (Fig. 6.4, l), a critical P *concentration* of about 0.05 mgP l^{-1} can be derived. The left part of the line starting from the turbid state (‘2’) is in the range of empirical relations between maximum summer-averaged chlorophyll-*a* and total P concentration, derived from data sets of phytoplankton-dominated lakes in The Netherlands (CUWVO, 1980, 1987; Lijklema *et al.*, 1989; Hosper, 1997; Portielje & Van der Molen, 1997).

Fig. 6.5 gives a summarizing pictural view of the hysteresis phenomenon.

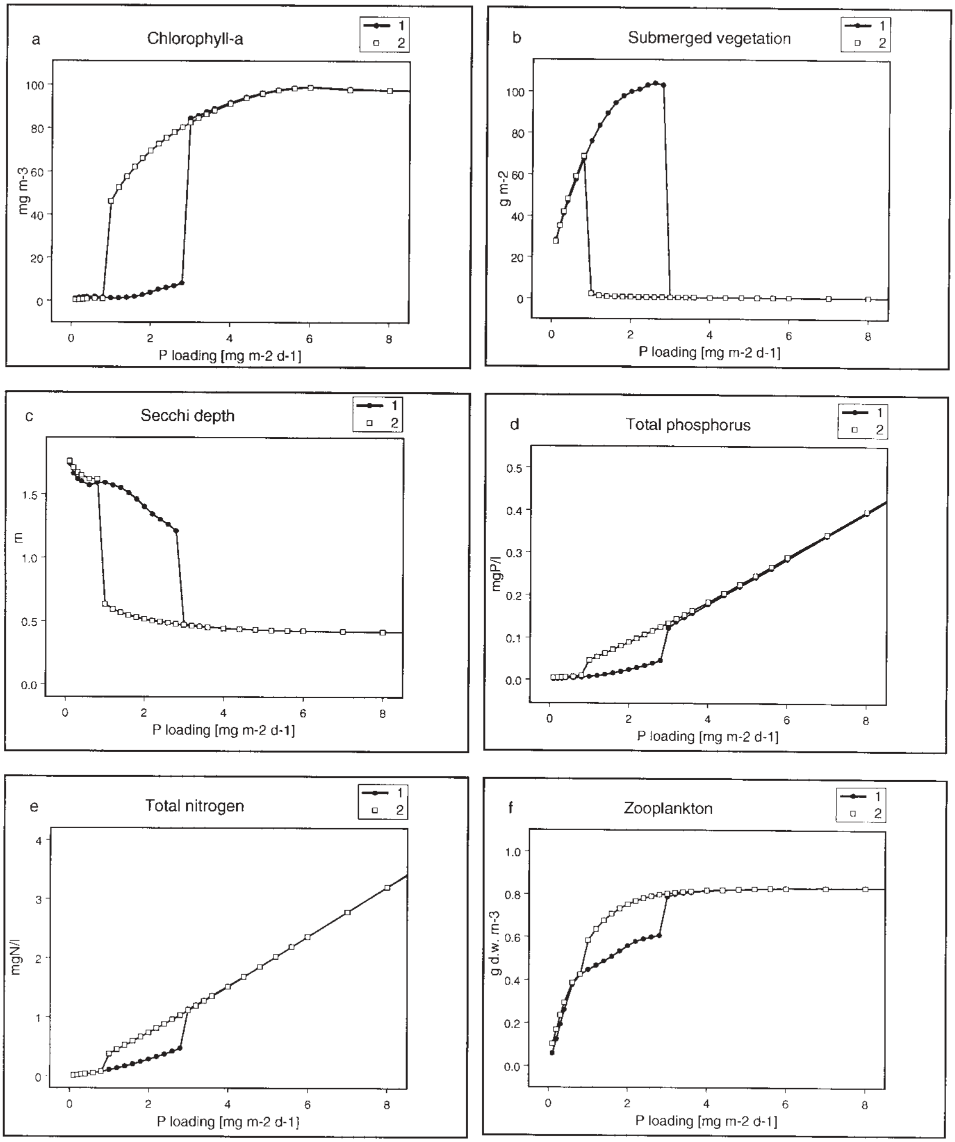
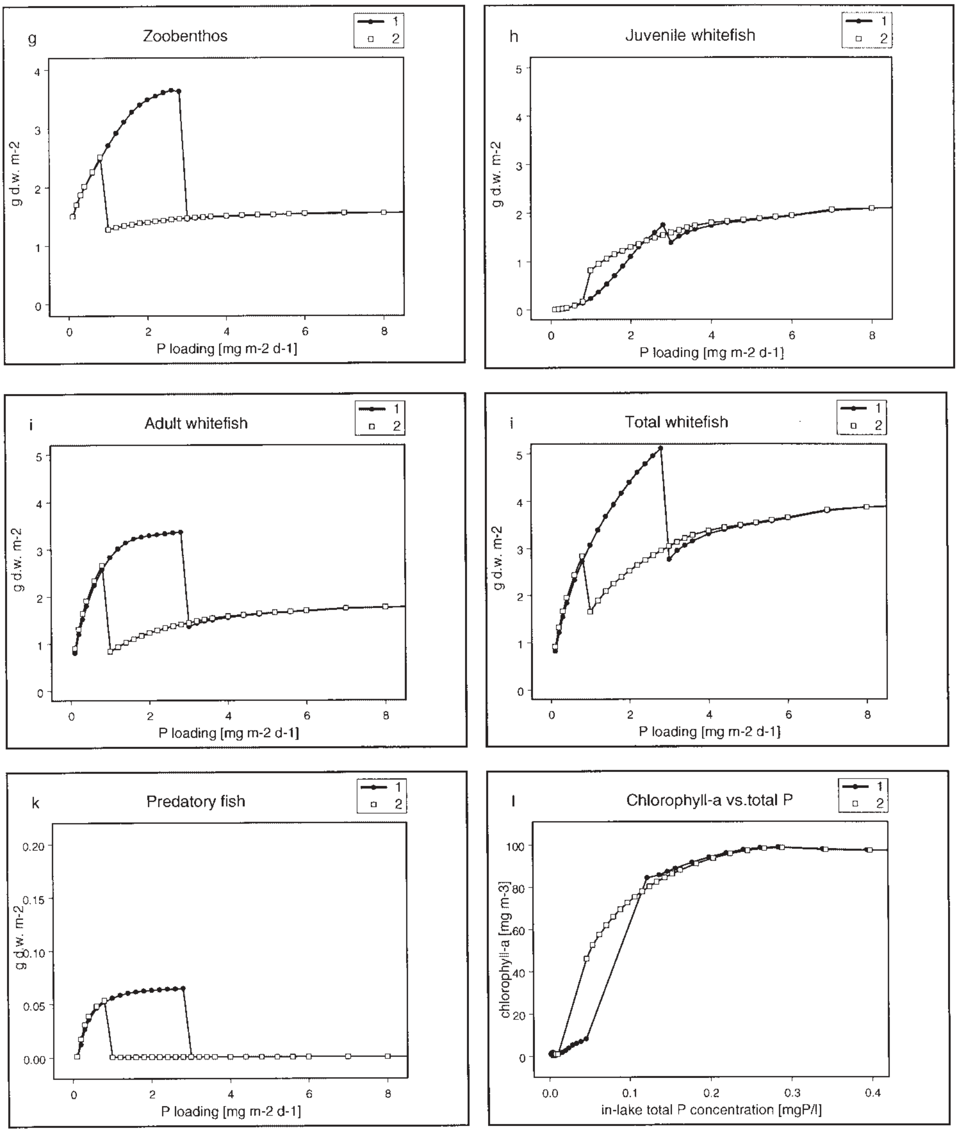
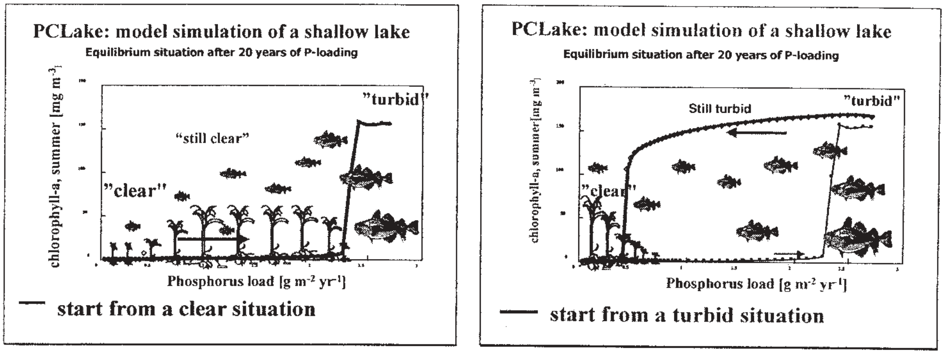


Fig. 6.4. *Simulations for an average shallow lake for a range of P loadings. All simulations have been done for two initial states, a clear-water state dominated by macrophytes ('1', circles) and a turbid state with a phytoplankton dominance ('2', triangles). Results are summer-averages after 50 years with the same loading conditions. a-k: output values as a function of the P loading: a, chlorophyll-a; b, submerged vegetation; c, Secchi depth; d, total P; e, total N; f, zooplankton; g, zoobenthos; h, juvenile whitefish; i, adult whitefish; j, total whitefish; k, predatory fish. l, chlorophyll-a vs. in-lake total P concentration.*


g
Zoobenthos
1
2
g d.w. m-2
0
1
2
3
4
P loading [mg m-2 d-1]
0
2
4
6
8
h
Juvenile whitefish
1
2
g d.w. m-2
0
1
2
3
4
5
P loading [mg m-2 d-1]
i
Adult whitefish
1
2
g d.w. m-2
P loading [mg m-2 d-1]
i
Total whitefish
1
2
g d.w. m-2
P loading [mg m-2 d-1]
k
Predatory fish
1
2
g d.w. m-2
0.00
0.05
0.10
0.15
0.20
P loading [mg m-2 d-1]
l
Chlorophyll-a vs.total P
1
2
chlorophyll-a [mg m-3]
0
20
40
60
80
100
in-lake total P concentration [mgP/l]
0.0
0.1
0.2
0.3
0.4



Fig, 6.5. *Pictural view of the hysteresis phenomenon as simulated by PCLake. Left: 'turbidification; right: 'clarification' (restoration). Adapted from Van Liere & Jonkers (2002).*

6.3. Critical loading for different lake types

The same kind of simulations were carried out for different combinations of other lake features. The following factors were varied, both one-at-a-time and combined:
(Note: an asterisk (*) denotes the value for the 'default lake'.)

- hydraulic loading rate: 10, 20*, 40 or 80 [mm d^{-1}]
- water depth: 1, 1.5, 2*, 3 or 4 [m]
- fetch: 100, 300, 1000* or 3000 [m]
- N/P ratio in loading: 10* or 3 [gN/gP]
- marsh area: 0.001*, 0.15, 0.3 or 1.0 [m^2 marsh . m^{-2} lake]
- sediment type: 1=clay*, 5=peat, 6=sand (see table 4.5 in chapter 4)
- fishery rate: 0, 0.00137* or 0.01 [d^{-1}]

and of course

- the initial state (1=clear, 2=turbid) and
- the P loading rate in terms of input concentration, ranging from 0.005 to 1.0 mgP l^{-1} in 35 steps: [0.005 0.01 0.015 0.02:0.01:0.18 0.20:0.02:0.30 0.35 0.40 0.45 0.5:0.1:1.0].

The simulated summer-averaged results after 20 years were used for the analyses. The dynamic results presented above and previous experience showed that in most instances, a period of 20 years is, for practical purposes, in general sufficient for the model to come quite close to the (new) equilibrium situation, although a complete equilibration of the phosphorus levels may take a longer period. The critical loading values were calculated by linear interpolation. A summer-averaged vegetation coverage of 20% has been chosen as a criterion for critical loading; as the relations are mostly quite steep, the exact value does not matter very much.

The long-term chlorophyll-a concentrations as a function of the P loading are plotted in Fig.

6.6, a-h. The impact of the different input factors is shown when they are varied one by one, keeping all others at their default value. Fig. 6.9 shows the critical loading values for the most important combinations of input factors.

In general, the results show the same qualitative pattern as shown in paragraph 6.2, but the values reached, as well as the two critical loading values, the switch points or trajectories between the two states, differ among lake types. For the most common lake types in The Netherlands, the critical loading for 'turbidification' is calculated as about 2–5 mgP m^{-2} d^{-1}, and the value for 'clarification' (or 'restoration') as 0.6 – 1.0 mgP m^{-2} d^{-1}.

The effect of increasing fetch (Fig. 6.6, a and 6.9) is a decrease of both critical loading values. Increase of the water depth (Fig. 6.6, b and 6.9) gives rise to lower chlorophyll-a concentrations and to a marked decrease of both critical loading values. The effect is most striking in the range between 1 and 2 m depth. The critical load increases with (but less than proportional to) the hydraulic loading rate (Fig. 6.6, c and 6.9). The critical loading is the lowest for peat lakes and the highest for sand lakes, with clay lakes in-between (Fig. 6.6, d and 6.9). Please note that, in this context, the impact of the factors is shown as independent of each other; in practice, nutrient loading and hydraulic loading rate are often positively correlated. A higher fishing rate tends to increases the critical loading, but the effect is modest (within the investigated range) and mainly confined to the 'turbidification' switchpoint (Fig. 6.6, e). The presence of a marsh zone increases the critical loadings markedly (Fig. 6.6, g and 6.9). These relations generally apply to the switch points for both initial states, be it that the variation in the 'turbidification' switch point is larger. Also the distance between the two switch points may differ in different settings; in extreme cases, they may even coincide. The relation with the N loading, when this nutrient is made limiting, with P in excess (N/P ratio in loading = 3 [g/g]), resembles the one for P limitation, but the hysteresis effect seems to be less marked (Fig. 6.6, f; left panel compared to right panel). For the 'default lake' the simulations indicate a critical N loading of *ca* 22 mgN m^{-2} d^{-1} for turbidification and *ca* 7 mgN m^{-2} d^{-1} for restoration if N is the limiting nutrient (and assumed that no N fixation takes place).

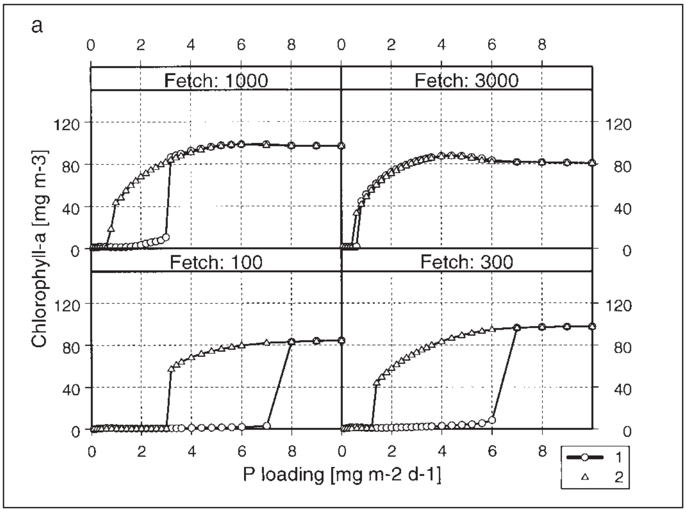
The hydraulic loading rate not only has an impact on the simulated algal biomass, but also on the ratio of the three algal groups. The proportion of cyanobacteria decreases with increasing hydraulic loading rate (or decreasing retention time) (Fig. 6.7).

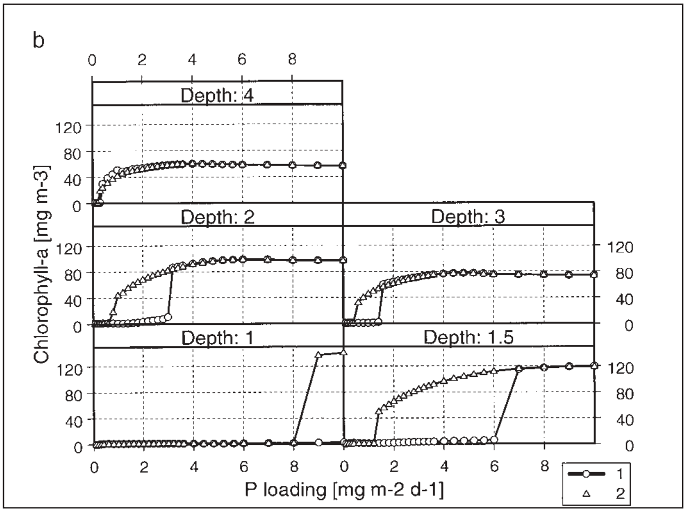
The chlorophyll concentrations were also plotted against in-lake total P, both again as summer-averages (Fig. 6.8), so that the critical loadings can be converted into critical P concentrations, a variable more easily obtained by lake managers. It can be seen that for the most frequently occurring lake types, the critical P concentration lies around 0.03 - 0.05 mgP m^{-3} when coming from the turbid state, and 0.05 – 0.1 mgP m^{-3} for the opposite direction.

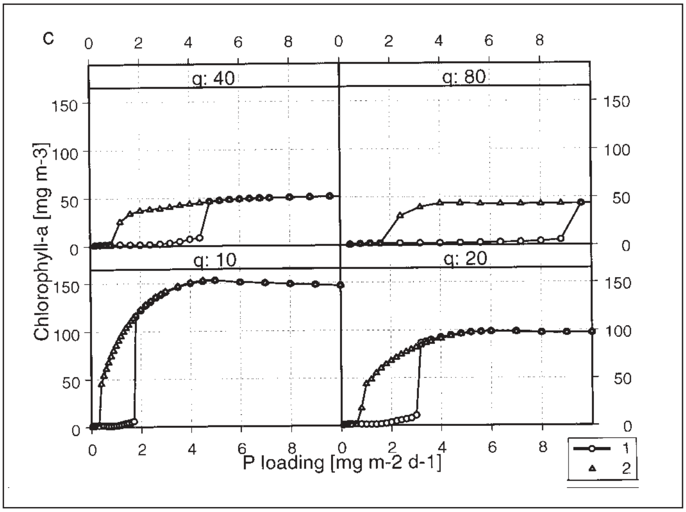
Following:

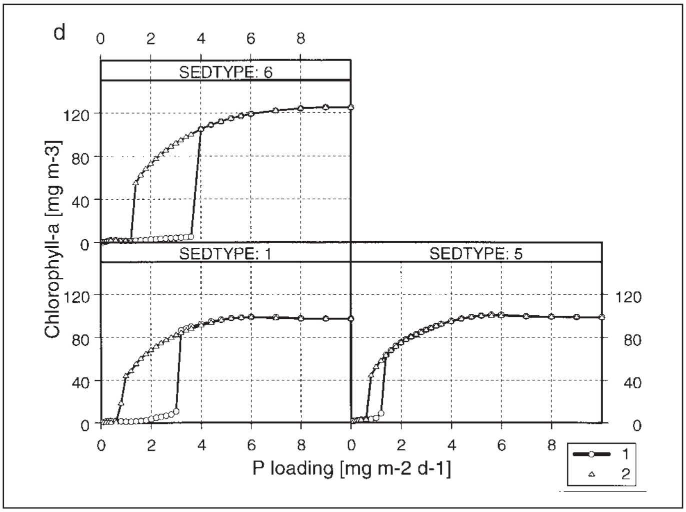
Fig. 6.6. *Simulations for different lake types for a range of P loadings. The different input factors were varied one by one, keeping the others at the value for the 'default lake'. All simulations have been done for two initial states, a clear-water state dominated by macrophytes ('1') and a turbid state with a phytoplankton dominance ('2'). Output values are summer-averaged chlorophyll-a levels after 20 years with the same loading conditions, as a function of the P loading.*

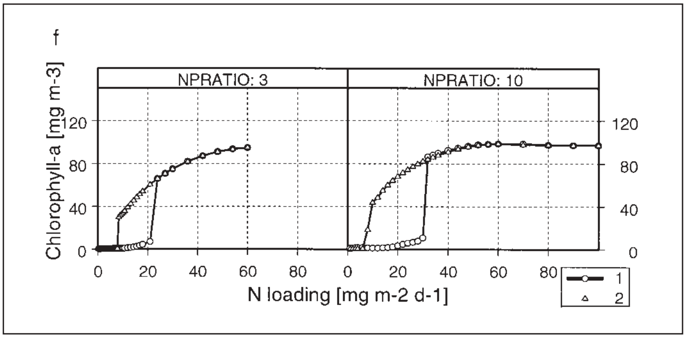
a, varying fetch [m]; b, varying water depth [m]; c, varying hydraulic loading rate [mm/d]; d, varying sediment type: 1=clay, 5=peat, 6=sand; e, varying fishery rate [d^{-1}*]; f, varying N/P ratio [gN g*$^{-1}$*P]; g, varying relative marsh area [-]; h, varying max. predatory fish density [gD m*$^{-2}$*] in case of no marsh (see text).*

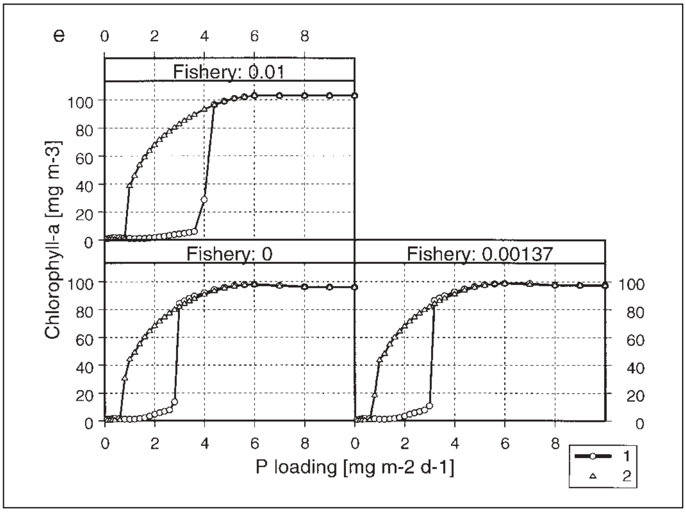


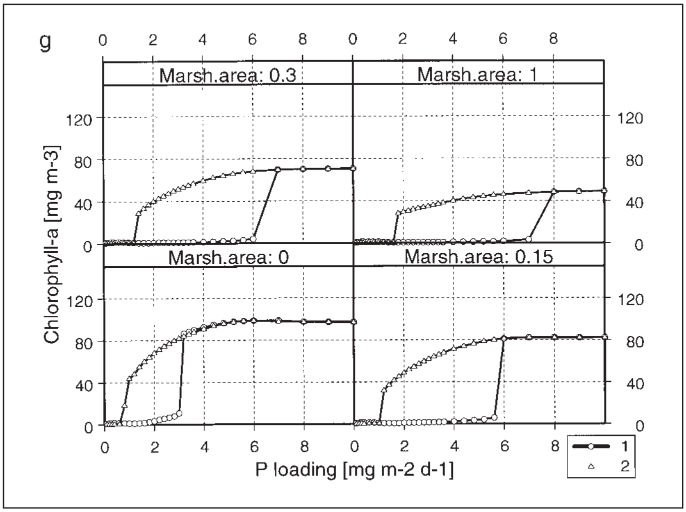


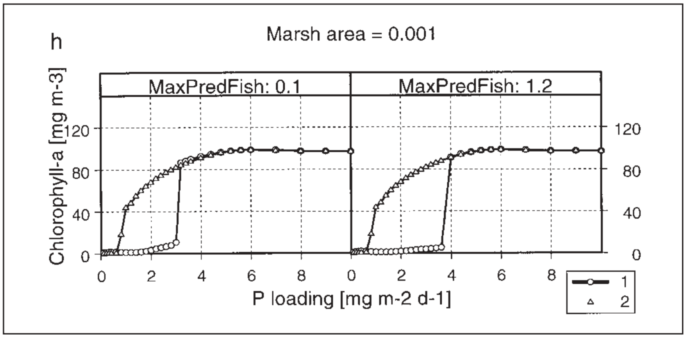

c
q: 40
q: 80
q: 10
q: 20
Chlorophyll-a [mg m-3]
0
50
100
150
0
2
4
6
8
P loading [mg m-2 d-1]
1
2


d
SEDTYPE: 6
SEDTYPE: 1
SEDTYPE: 5
Chlorophyll-a [mg m-3]
0
40
80
120
0
2
4
6
8
P loading [mg m-2 d-1]
1
2


f
NPRATIO: 3
NPRATIO: 10
Chlorophyll-a [mg m-3]
0
40
80
120
0
20
40
60
80
N loading [mg m-2 d-1]
1
2


e
Fishery: 0.01
Fishery: 0
Fishery: 0.00137
Chlorophyll-a [mg m-3]
0
20
40
60
80
100
0
2
4
6
8
P loading [mg m-2 d-1]
1
2


g
Marsh.area: 0.3
Marsh.area: 1
Marsh.area: 0
Marsh.area: 0.15
Chlorophyll-a [mg m-3]
0
40
80
120
0
2
4
6
8
P loading [mg m-2 d-1]
1
2


h
Marsh area = 0.001
MaxPredFish: 0.1
MaxPredFish: 1.2
Chlorophyll-a [mg m-3]
0
40
80
120
0
2
4
6
8
P loading [mg m-2 d-1]
1
2

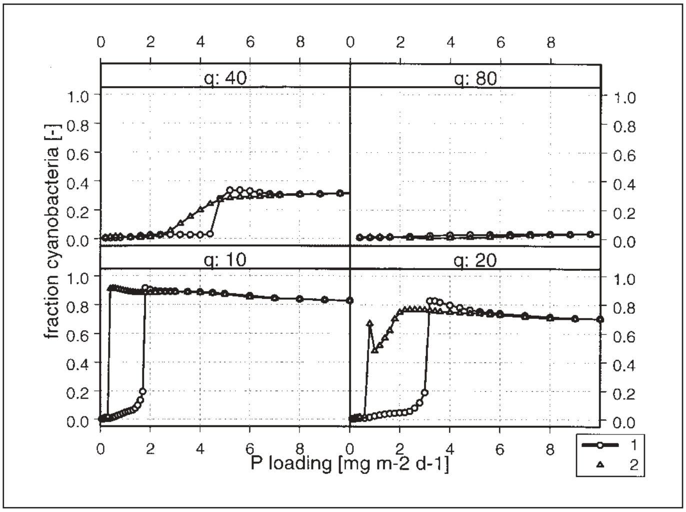
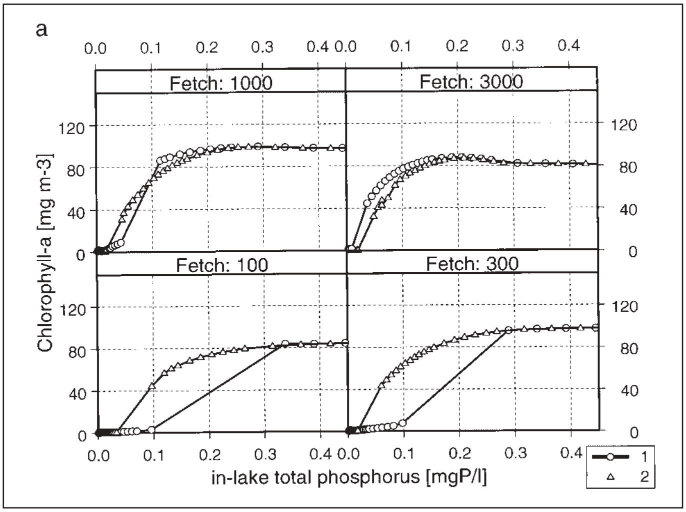
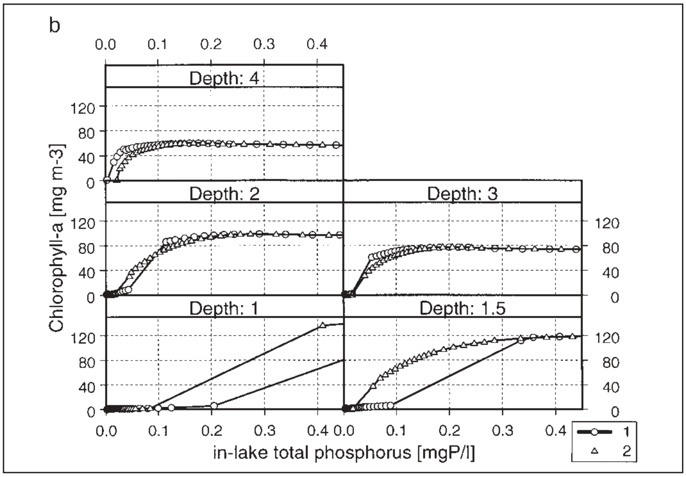
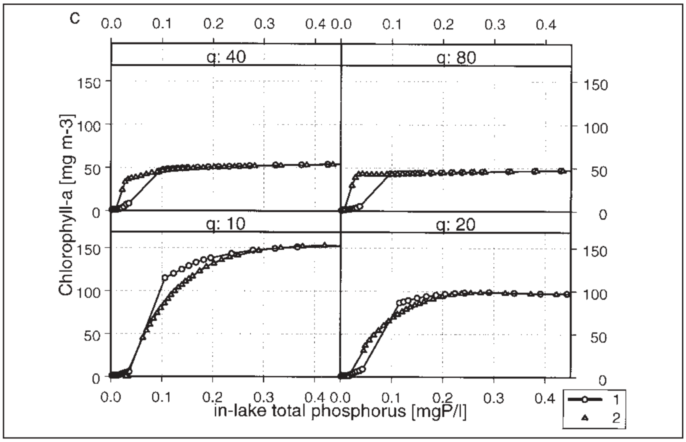


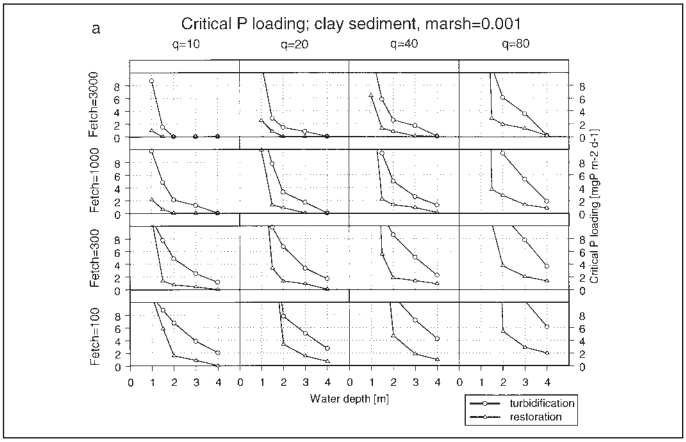
Fig. 6.7. *Fraction cyanobacteria in the phytoplankton as a function of P loading, for different hydraulic loading rate. Other settings as for the default lake. Simulations were performed as explained in Fig. 6.6.*

Fig. 6.8. *Simulations of chlorophyll-a against in-lake total P concentration for different lake types. Details as explained in Fig. 6.6.*
a, varying fetch [m]; b, varying water depth [m]; c, varying hydraulic loading rate [mm/d]. Following:




b
Depth: 4
Depth: 2
Depth: 3
Depth: 1
Depth: 1.5
Chlorophyll-a [mg m-3]
in-lake total phosphorus [mgP/l]
0.0
0.1
0.2
0.3
0.4
0
40
80
120
1
2

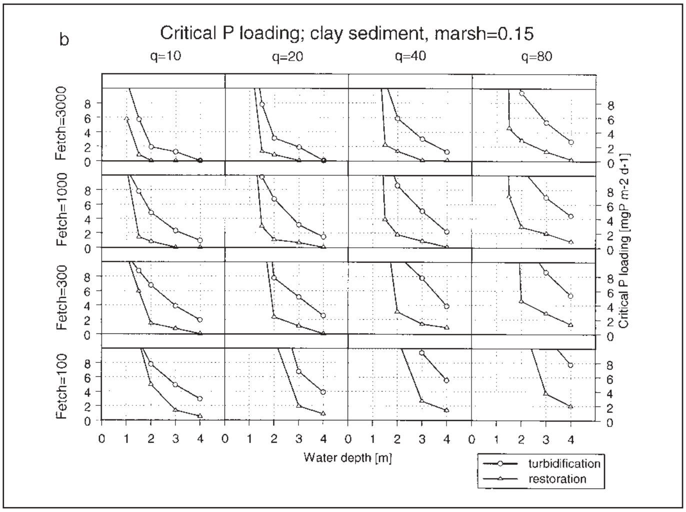

c
q: 40
q: 80
q: 10
q: 20
Chlorophyll-a [mg m-3]
in-lake total phosphorus [mgP/l]
0.0
0.1
0.2
0.3
0.4
0
50
100
150
1
2

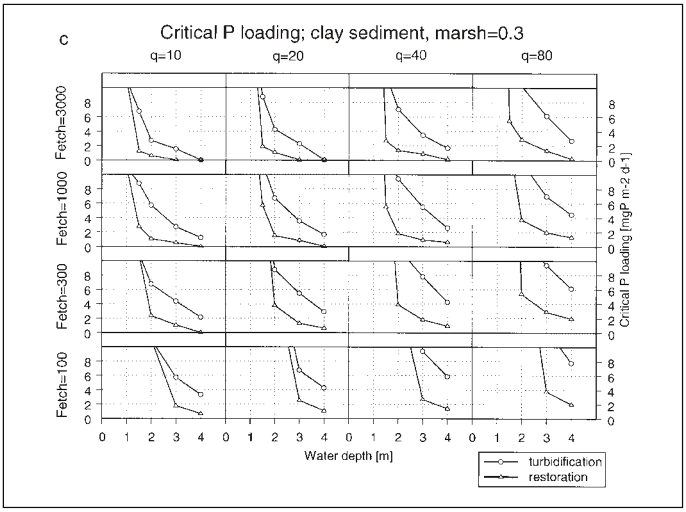

a
Critical P loading; clay sediment, marsh=0.001
q=10
q=20
q=40
q=80
Fetch=3000
Fetch=1000
Fetch=300
Fetch=100
Critical P loading [mgP m-2 d-1]
Water depth [m]
0
1
2
3
4
0
2
4
6
8
turbidification
restoration

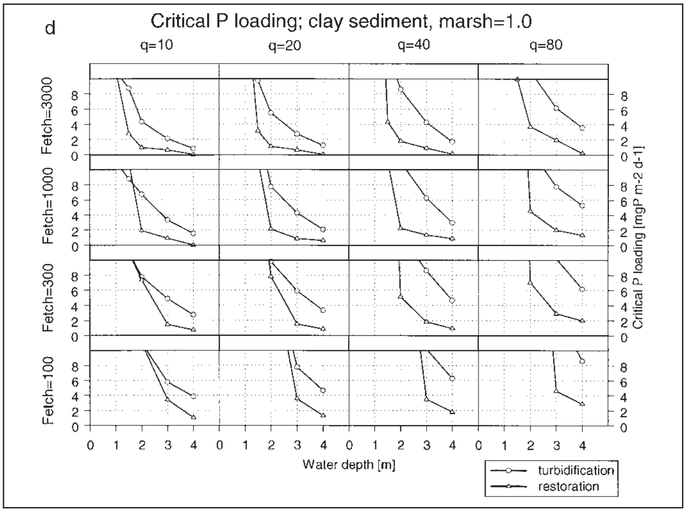
Following:

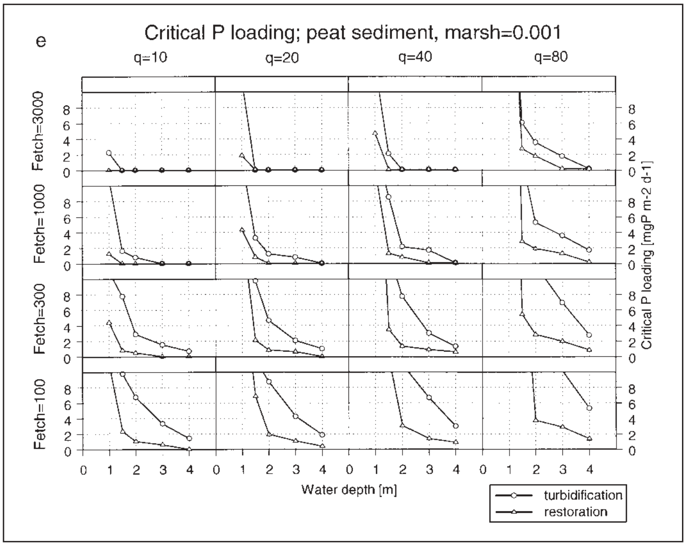
Fig. 6.9. *Threshold loading levels dependent on lake characteristics. Each composite graph shows the influence of the factors water depth, fetch and water inflow rate.*

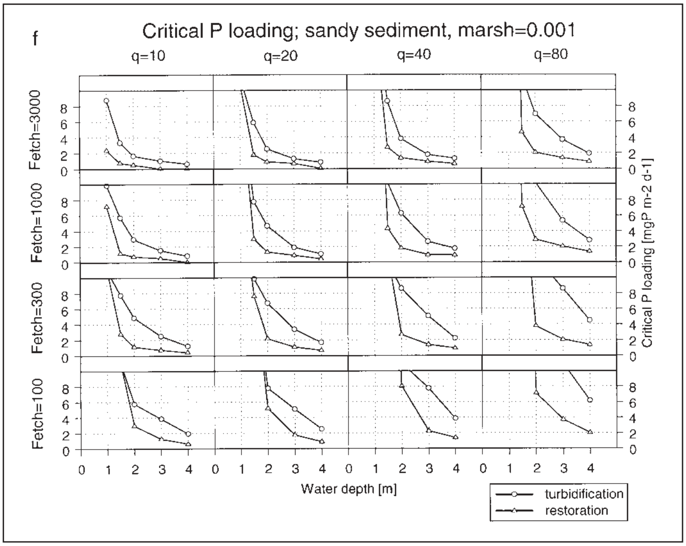
a, clay sediment, no marsh zone; b, clay sediment, relative marsh area = 0.15; c, clay sediment, relative marsh area = 0.3; d, clay sediment, relative marsh area = 1.0; e, peat sediment, no marsh zone; f, sandy sediment, no marsh zone.






d
Critical P loading; clay sediment, marsh=1.0
q=10
q=20
q=40
q=80
Fetch=3000
Fetch=1000
Fetch=300
Fetch=100
0 2 4 6 8
Critical P loading [mgP m-2 d-1]
0 1 2 3 4
Water depth [m]
turbidification
restoration


e
Critical P loading; peat sediment, marsh=0.001
q=10
q=20
q=40
q=80
Fetch=3000
Fetch=1000
Fetch=300
Fetch=100
0 2 4 6 8
Critical P loading [mgP m-2 d-1]
0 1 2 3 4
Water depth [m]
turbidification
restoration



A linear regression analysis was performed of the two critical loading values (as natural logarithm) on the variables reciprocal water depth, fetch, hydraulic loading, marsh area and sediment type, both with and without two-factor interaction terms (Table 6.1). Sediment type was included as two dummy variables (0/1), viz. ‘Clay’ and ‘Peat’; if both are 0 the sediment type is ‘Sand’. Excluding interactions (Table 6.1, a), all coefficients were significant for both critical loadings, except for the intercept for the lower switchpoint. The regression explained 61 resp. 72 % of the variation. Lake depth, water inflow rate and fetch are the most influential, followed by the marsh area and the sediment type.

Including interactions, the fraction explained variation (adjusted r-squared) increased to 0.71 resp. 0.78. Nearly all factors and interactions were significant (Table 6.1, b), which indicates that the impact of each factor is influenced by the other ones.

Analysis of residuals, as well as visual inspection of conditional plots, revealed that the linear model described the relations far from perfectly, despite the high regression coefficients. Other transformations of the variables that we tried did not improve this. It thus remains difficult to catch the relation between critical loadings and lake features in a simple formula. The critical loading of a particular lake type might better be estimated from the graphs presented or by an additional model run.

The relation between the two switchpoints themselves is also highly significant. A linear regression of the ‘forward’ switchpoint, $\mathrm{Pcrit}_{\mathrm{turbidif}}$ on the ‘backward’, $\mathrm{Pcrit}_{\mathrm{clarif}}$, both as natural logarithm, reveals (with the standard errors in italics between brackets):

$$\ln(\mathrm{Pcrit}_{\mathrm{turbidif}}) = 1.4476\ (\pm\ 0.0204) + 0.6410\ (\pm\ 0.0083) \cdot \ln(\mathrm{Pcrit}_{\mathrm{clarif}})$$

(residual SE = 0.7473, d.f. = 1918, $R^2 = 0.76$; both $P < 10^{-4}$)

Table 6.1. Regression analysis for the effect of lake characteristics on the log-transformed critical P loading values [mgP m^{-2} d^{-1}]. ‘Clay’ and ‘Peat’ are dummy variables for the sediment type with the value 0 or 1 (if both 0, the sediment type is ‘Sand’); CQIN = hydraulic loading rate [mm d^{-1}]; invDEPTH = inverse water depth [m^{-1}]; FETCHkm = fetch [10^3 m]; FMARSH = relative marsh area [-]. n.s. = not significant.

a. Regression without interactions

	turbidification switchpoint			clarification switchpoint		
factor	Value	Std. error	Pr(>|t|)	Value	Std. error	Pr(>|t|)
(Intercept)	-0.0524	0.0668	0.4322 $^{n.s}$	-2.3293	0.0767	0
Clay	-0.1028	0.0265	0.0001	-0.3241	0.0304	0
Peat	-0.2962	0.0265	0	-0.5295	0.0304	0
CQIN	0.0235	0.0008	0	0.0265	0.0009	0
invDEPTH	2.9668	0.0811	0	4.9804	0.0931	0
FETCHkm	-0.456	0.0189	0	-0.6109	0.0217	0
FMARSH	0.6319	0.0565	0	0.957	0.0649	0
resid. SE	*0.9475*		*1.088*			
d.f.	*1913*		*1913*			
R^2	*0.6125*		*0.7232*			

b. Regression including two-factor interactions

	turbidification switchpoint			clarification switchpoint		
	Value	Std.error	Pr(>|t|)	Value	Std.error	Pr(>|t|)
(Intercept)	0.4952	0.1101	0	-2.193	0.1132	0
Clay-	0.2547	0.0695	0.0003	-0.7475	0.0822	0
Peat	-0.6186	0.0695	0	-1.0349	0.0822	0
CQIN	0.0194	0.0019	0	0.0292	0.0015	0
invDEPTH	2.3666	0.1626	0	4.8943	0.1526	0
FETCHkm	-1.3417	0.0483	0	-1.4504	0.0572	0
FMARSH	1.1929	0.1449	0	1.7396	0.1715	0
Clay:CQIN	0.0018	0.0009	0.0386	0.0049	0.0010	0
Clay:invDEPTH	0.2675	0.0867	0.0021	0.654	0.1026	0
Clay:FETCHkm	-0.101	0.0202	0	-0.1687	0.0239	0
Clay:FMARSH	0.1348	0.0604	0.0258	0.1818	0.0715	0.011
Peat:CQIN	0.004	0.0009	0	0.0061	0.0010	
Peat:invDEPTH	0.6245	0.0867	0	0.8266	0.1026	0
Peat:FETCHkm	-0.2449	0.0202	0	-0.2407	0.0239	0
Peat:FMARSH	0.2748	0.0604	0	0.2357	0.0715	0.001
CQIN:invDEPTH	0.0068	0.0026	0.0097	–	–	n.s.
CQIN:FETCHkm	0.0039	0.0006	0	0.0052	0.0007	0
CQIN:FMARSH	-0.0058	0.0018	0.0018	-0.0133	0.0022	0
invDEPTH:FETCHkm	0.9209	0.0618	0	0.7701	0.0731	0
invDEPTH:FMARSH	-1.0252	0.1850	0	-0.7373	0.2189	0.0008
FETCHkm:FMARSH	0.3228	0.0430	0	0.2357	0.0509	0
residual SE	*0.8274*		*0.9789*			
d.f.	*1899*		*1899*			
R^2	*0.7067*		*0.7775*			

The critical load for turbidification is always higher than the one for clarification, except for the extremes where they may be equal.

Mechanisms involved

The hysteresis effect as shown by the simulations can be explained by several positive feedback mechanisms present in the model. The crux is that both the phytoplankton and the submerged macrophytes, directly or indirectly, promote their own favourite environmental conditions and deteriorate the conditions for the other, giving rise to two stable states in an intermediate range of the nutrient loading (see also chapter 2).

Light limitation is the main factor for aquatic macrophytes: they need clear water with light reaching the bottom. At the same time they keep the water clear, by several mechanisms: their specific light absorption is low (much lower than that of phytoplankton), they reduce resuspension by stabilizing the sediment, and they hamper phytoplankton growth by uptake of nutrients. Furthermore, they promote the top-down control of phytoplankton by favouring predatory fish and by hampering the feeding of benthivorous fish (being planktivorous as juveniles). Phytoplankton, on the other hand, wins the competition in darker or deeper waters, as it needs less light for growth. Once dominant, it keeps the water turbid because of its high light absorption and because it keeps the nutrients recycling in the water column. The unvegetated sediment is more subject to resuspension due to wind action (waves) and to stirring by benthivorous fish. So there are three main factors or pathways working together: light, nutrients and food web effects.

Other mechanisms have been demonstrated or suggested that may add to this picture, like the release of allelopathic substances by macrophytes that hamper algal growth, a shift towards bigger zooplankton species in clear water once relieved from predation, and others. Other mechanisms, on the contrary, may weaken the picture, such as a shift in clear lakes towards fish species that are better in feeding between the vegetation, or the development of defence mechanisms by phytoplankton to reduce grazing loss. These mechanism have not been included in the model, as they are considered of secondary importance and in order to keep the complexity within limits.

The effect of the different lake features can be understood from this picture. Increasing the fetch, to start with, causes lower critical loading values. (We recall that in the calibration dataset, fetch has been estimated as the square-root of the lake area.) The main slot for the factor fetch in the model is in the resuspension and settling equation: a larger fetch makes the resuspension rate increase and the settling rate of algae and suspended solids decrease, to mimick the greater influence of wind waves in larger lakes. So, a larger fetch may favour the ‘turbid state’ of a lake by two mechanisms, viz. an increased turbidity of the water and an increased release of nutrients from the sediment by physical action.

The effect of depth can partly be explained by the dependence of submerged macrophytes on the under-water light climate: the exponential decrease of light intensity with depth sets a limit to the depth where plants can survive. Also the lower sedimentation losses in deeper water favour phytoplankton, as well as the longer retention time (provided that the hydraulic loading does not change). On the other hand, the resuspension rate is lower in deeper lakes, as well as the impact of benthivorous fish, and the greater mixing depth for nutrients and suspended solids reduces the maximum algal concentrations. The net effect, as it appears from the model results, is a marked decrease of the critical loading with depth.

An increase of the hydraulic loading (or water inflow rate), keeping the nutrient load constant, increases the phytoplankton loss rate, thus reducing algal biomass and favouring the competitive power of macrophytes that are fixed to the bottom (increased critical loading values). On the other hand, the loss factor zooplankton grazing is also reduced. Another effect is a shift within the phytoplankton from the slow-growing cyanobacteria to the faster growing diatoms and 'other' ('green') algae, that can better compensate for the high dilution rate (Fig. 6.7). In practice, the hydraulic loading and nutrient loading are often partly correlated, but for this analysis, the factors have been dealt with independently.

The factor sediment type is of course a composite factor, made up of the porosity, organic and lutum fractions in the upper sediment; lutum is again linked to Fe and Al fractions (Table 4.5). Resuspension increases with porosity in the model, which may explain why life becomes harder for macrophytes going from sand to clay to peat lakes. The factor lutum acts in the same direction, as the higher lutum fracton in clay and peat sediments increases the amount of phosphorus that is retained in the system and recycled to the water column, promoting algal growth. The extra amount of organically bound nutrients in peat sediment also adds to the increased P availability.

The positive effect of a marsh zone can be attributed to several mechanisms in the model: the addition of an extra sedimentation area, uptake of nutrients by the marsh vegetation, extra opportunity for denitrification and the presence of a good habitat for predatory fish (modelled as a higher carrying capacity for this group). The first three are proportional to the marsh area, the latter one up to a marsh area of about 0.15. The fish factor has also been analysed apart from the other ones (Fig. 6.6, h): it turns out that this factor only affects the critical load for turbidification, not the one for restoration. This indicates that predatory fish mainly plays a role in maintaining the stability of the 'clear state', not so much in restoring it from the 'turbid state'.

6.4. Management implications

Lake management generally aims at maintenance or restoration of the macrophyte-dominated state. This is motivated by the fact that this state is often the historical reference situation, by a desire for a higher biodiversity, and/or by human functions such as recreational value or drinking water purposes. The results presented in the previous sections point to the possible role of the PCLake model when choosing a management strategy.

Clearly, the basic management strategy to restore a turbid lake back to the clear state is reduction of the external nutrient loading to a level lower than the threshold for restoration.

In many cases, however, this aim will not be easy to achieve. It will sometimes be possible to manipulate one of the intervening variables in order to increase the critical nutrient level of the particular lake. Options that can be derived from the simulations are:

- increasing the hydraulic loading rate and thus decreasing the water retention time (provided that the extra inflowing water has a lower P concentration than the lake)
- decreasing the wind effects on settling and resuspension, for instance by making sediment traps (deep areas) or by compartmentalisation
- decreasing the water depth, by water level manipulation
- improving the conditions for reestablishment of a marsh zone surrounding or connected to the lake. This may be enhanced by natural water level fluctuations.
- fishery management specifically removing planktivorous fish.
- Restoration can be enhanced by removing nutrient–rich sediment layers by dredging.

The critical nutrient levels may be influenced by the water temperature and hence by ongoing climate change, but this factor has not been investigated in this study.

In the intermediate range of nutrient loadings, where alternative stable states exist, additional in-lake management measures may sometimes be effective. A sufficient disturbance imposed on the system may make it switch between the two states. A practicable measure sometimes used to make a eutrophied, turbid lake switch back to the original macrophyte-dominated state is a drastic reduction in fish stock, known as biomanipulation (e.g. Gulati et al., 1990a).

This has been simulated by the PCLake model for the ‘average lake’ defined above. The lake was first brought from the clear into the turbid state by a high nutrient loading, above the threshold. The nutrient load was then moderately decreased, to the intermediate level of 1.5 mgP m^{-2} d^{-1}, with or without removal of the whitefish. The results indicated that biomanipulation can indeed make restoration of the clear state easier for intermediate loading values (Fig. 6.10), provided that the fish stock reduction is sufficient, and the loading is not too far above the ‘restoration switchpoint’. When the loading is close to or above the ‘turbidification switchpoint’, biomanipulation may only have a temporary effect and does not result in a long-term stable macrophyte-dominated state (Fig. 6.10). The model can be used to estimate the maximum loading for effectiveness of biomanipulation. Chapters 11-12 describe the simulation of a biomanipulation experiment that has been performed in reality. As will be discussed further in the following section, these findings are in line with lake restoration experiences so far (Meijer et al., 1999a).

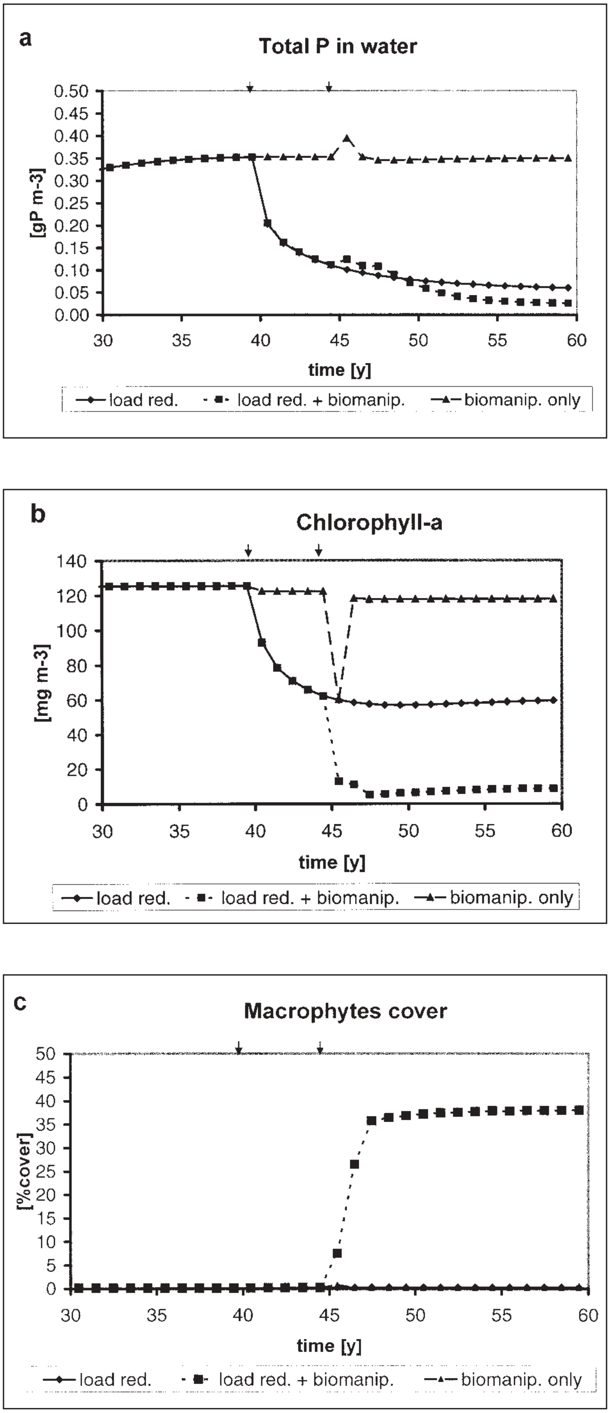


Fig. 6.10. *Simulations of several management options for an average shallow lake (see text) with a depth of 2 m. The lake was first brought from the clear into the turbid state by an increase in nutrient loading, followed by three options: (1) decrease in nutrient loading to the original, intermediate, level; (2) idem combined with biomanipulation five years later; (3) biomanipulation only, continuing the high nutrient loading.*
a, total phosphorus; b, chlorophyll-a; c, submerged vegetation.

6.5. Discussion

The model results are consistent with the existing evidence that shallow lakes may have two alternative states, a clear-water state dominated by macrophytes and a turbid state dominated by phytoplankton (Timms & Moss, 1984; Hosper, 1989; Scheffer, 1990, 1998; Moss, 1990; Jeppesen *et al.*, 1990, 1997, among others). Several factors determine which state prevails in a certain case. A general constraint is set by the external nutrient loading. At a very high loading, only the turbid state is stable, whereas the opposite is true for very low loadings. In the intermediate range, both states may exist and switches between the two states are possible. Because both states possess a number of self-stabilizing buffering mechanisms, the critical loading level at which a shift occurs is dependent on the initial state of the system: the shift from turbid to clear occurs at a much lower loading level than the opposite one (hysteresis).
The model simulations suggest that the values of the two switchpoints are affected by certain lake features, such as water depth, hydraulic loading rate, lake area, sediment type, fishery, and the presence of a marsh zone. The forward and the backward switchpoint are affected, according to the model, partly in a different way. These effects can be linked to certain mechanisms in the model system. To analyze this a little bit further, we now focus on the ecological mechanisms responsible for the thresholds.

Ecological mechanisms
Several authors described the events observed in a shallow lake during the course of eutrophication and oligotrophication (e.g. Scheffer, 1998, Hosper, 1997, and others). In a clear, oligo-mesotrophic lake, algal biomass is kept low due to nutrient limitation. A moderate increase of the external nutrient loading can be coped with by the macrophytes. The macrophytes keep the water clear, thereby favouring their own growth conditions. A further increase in loading gradually increases turbidity due to algal growth (planktonic and/or epiphytic species), until a certain turbidity is reached at which the macrophytes collapse. The algal biomass can increase somewhat further with the loading, until it levels off due to light limitation.
On the way back, as loading decreases, algal growth first shifts from light- to P-limitation and the biomass then gradually decreases with the loading, but less than proportionally: the chlorophyll/total-P ratio gradually increases (see Van Liere & Janse, 1992; Janse et al., 1992, chapter 10 of this thesis). Due to the absence of macrophytes, the water remains turbid. At a certain level, the transparency has increased enough as to allow a re-establishment of macrophytes, leading to a switch to the clear state and algae are kept low.

When trying to estimate the values of the two switchpoints in certain types of lakes, the factors on which they depend and the uncertainty in these values, it is important to consider:

- what are the buffering mechanisms of each of the two states
- how are these mechanisms affected by the nutrient loading
- how are these mechanisms affected by lake features and model parameters

The mechanisms primarily involved with the backward switch partly differ from those determining the forward switch. Therefore, the critical loading value for restoration is affected partly by other factors than the critical loading for turbidification.

The mechanisms modelled by PCLake can be roughly grouped around three aspects: nutrients (N), light (L) and food-web (F).

Mechanisms buffering the *clear* state, thus tending to *increase* the 'turbidification' switchpoint, as included in the model, are:

a) (N) macrophytes compete with algae for P and N
b) (N) macrophytes may promote N loss by denitrification (mediated by a more advantageous oxygen climate in the sediment)
c) (L+N) macrophytes reduce resuspension of sediment particles and nutrients, by stabilizing the sediment, thereby keeping transparency high enough to maintain their growth
d) (L+N) macrophytes hamper the feeding by benthivorous fish, thereby reducing bioturbation
e) (F) macrophytes promote the top-down control of algae, by promoting the growth of piscivorous fish (by providing shelter and habitat) and by providing some protection for zooplankton against predation by planktivorous fish.
f) (other:) (not modelled:) the release of allelopathic substances by macrophytes that are harmful to algae.

If one or more of these mechanisms weaken, the vegetation may collapse, probably mainly triggered by a deteriorated underwater light climate.

The model suggests that the most vulnerable parts of the year are the spring period, before the regrowth of the macrophytes after the winter, and the autumn period, when they start to 'retreat' in the sediment and partly die off. If phytoplankton succeeds in developing a short bloom in one of these periods, they have a chance to further increase in the next years (see example in chapters 11 and 12).

The buffering capacity of the mechanisms **a** and **b**, concerning nutrient availability, will become weaker as the nutrient loading increases. This also partly applies to the mechanisms **c** and **d**, when the 'time bomb' of the gradually increasing N and P concentrations in the sediment continues to tick. The model suggests that as long as the macrophytes are dominant, algal growth is limited by nitrogen rather than phosphorus (see also chapter 11). This is confirmed by experimental evidence in a number of cases (e.g. Van Donk & Gulati, 1995). This would suggest that a high nitrogen loading is potentially more harmful than phosphorus loading in this stage.

Also the buffer created by the top-down mechanism (**e**) is threatened indirectly by increasing nutrient loading, as the fish biomass generally increases with nutrient and food availability (Hanson & Leggett, 1982). Benthic feeding is thereby the most important, but increasing predation of the juveniles on zooplankton diminishes the grazing pressure on the algae. The importance of this mechanism depends on the lake's quality as a habitat for piscivorous fish: if the habitat is good, the piscivores are able to control the whitefish somewhat longer and the switchpoint is moved further to the right (viz. to a higher loading rate). As long as the lake is still clear, the increasing biomass of the benthivorous fish itself does not so much harm, according to the model, as the bioturbation is hampered by the vegetation. This has also to do with species differences: the fish species dominating in the clear state (e.g. tench) have other feeding habits and cause much less bioturbation than the turbid-water bream (this distinction is not included in the model, however). In the intermediate loading range, the model simulates a higher biomass of benthivores in the clear than in the turbid state, related to the higher zoobenthos biomass between the macrophytes due to the higher food availability (sediment organic matter and bottom algae). This is consistent with empirical evidence that both zoobenthos and benthivorous fish biomasses are higher in vegetated lakes (Diehl & Kornijów, 1998). At higher loading, however, the benthivores biomass is underestimated by the model. The food web relations are clearly much more complex than assumed in the model.

Mechanisms buffering the *turbid* state, thus tending to *decrease* the ‘clarification’ (‘restoration’) switchpoint, as included in the model, are:

a) (N) phytoplankton becomes more P efficient (higher biomass/P ratio) at relatively low P concentrations
b) (F+loss) dominance of cyanobacteria at relatively low P concentrations, which are poorly edible by zooplankton and have a lower settling rate
c) (L) high turbidity (by algae and/or dead suspended matter) hampers the growth of macrophytes and thus increases the competition strength of algae
d) (L+N) resuspension of sediment particles and nutrients from the unprotected sediments, keeping turbidity and nutrient release high
e) (L+N) biotic ‘resuspension’ caused by the feeding behaviour of benthivorous fish, also keeping turbidity and nutrient release high
f) (F) relatively lower grazing pressure on phytoplankton due to top-down effects (low piscivorous fish and high planktivorous fish biomass)
g) (N) (partly modelled:) algal blooms promote internal P loading, due to high pH and low sediment oxygen conditions (e.g. Hosper, 1997).

This last process (g) is, however, not confined to algal blooms only, but also to situations with high macrophyte densities (Barko & James, 1998; Søndergaard & Moss, 1998). In the model, the link is laid via the oxygen dynamics, the pH effect is left out.

As the nutrient loading decreases towards the backward switchpoint, the buffer created by the nutrient mechanisms (**a**, and possibly **g**) weakens, as the phytoplankton becomes more and more nutrient limited. Growth rates decrease, while inevitable loss processes remain unaltered. Algal biomass has to decline and the water transparency slowly increases, until a level is reached where macrophytes are able to take over. The model suggests that the most vulnerable part of the year is the late spring period (May), under natural conditions the ‘clear water phase’ caused by zooplankton grazing. If the water becomes clear long enough in spring so as to allow the macrophytes a good start, they have a chance to further increase in the next years (see example in chapters 11 and 12). Also Van Nes (2002) showed in a model study that the occurrence of a short period of clear water in late spring can promote the vegetation, but the effect was not strong and most marked in June.

The level of the 'turbidification' switchpoint is thus determined by the turbidity level at which the net algal growth (growth minus losses) exceeds the net macrophytes growth (growth minus losses), under conditions of low background turbidity. Likewise, the 'clarification' switchpoint is determined by the transparency level at which the net macrophyte growth exceeds the net algal growth, under turbid background conditions.

The great influence of the investigated lake features (depth, size, marsh area and type of sediment; see Fig. 6.9) confirm this picture: they all affect primarily the light climate and the nutrient availability. The hydraulic loading rate, by contrast, exerts its influence by increasing the phytoplankton loss rate. Top-down factors modify this picture. Unfortunately, the data on the higher trophic levels (food web) do not permit definite conclusions on their influence.
In the model, the food-web effects are more influential on the forward switchpoint than on the backward one. This applies to the maximum piscivorous fish stock (as influenced by the marsh area; can also be set independently in the model) and the fishery rate.

The model results thus suggest that nutrient and light factors are the most important for the switchpoint levels. The value of the backward switchpoint tends to be less variable (less uncertain) than the forward one, for a given lake type. Possible causes for this difference might be that near the backward switchpoint, all producers are (potentially) nutrient limited, so that growth rates are already low. Another cause might be that the forward switchpoint appears to be sensitive for more parameters than the backward one, especially for the fish-related parameters, leading to a higher uncertainty. This topic could be explored further by comparing more variations of the model parameters or structure. Especially in the food web relations there are many uncertainties, which could only partly be evaluated with the available data.

The model results do not proof, of course, that other mechanisms than the ones modelled might not be important as well. Despite the inclusion of many mechanisms, it is still possible to get 'the right results on the wrong grounds' (cf. Scheffer & Beets, 1994).

Comparison with empirical information: impact of lake features

– *Lake size*
The model predicts that smaller lakes are more favourable to macrophytes than larger ones, in agreement with observations in the field (e.g. Van Geest et al, 2003). The explaining mechanism in the model is higher settling and lower resuspension rates in small lakes (less wave action). Although the prediction is in agreement with observations, other mechanisms than this one may contribute to the impact of lake size. Wind or wave stress may hamper vegetation growth or survival directly as well. Other mechanisms are related to the generally greater relative shore length in small lakes (both variables are often strongly correlated). Small

lakes tend to have more shallow parts along the shores which are more favourable places for macrophyte colonisation that can then spread over the rest of the lake (Van den Berg, 1999). A greater shoreline, often partly overgrown with helophytes, may also favour top-down effects, by enhancing piscivorous fish (mainly pike) and by providing a refuge to zooplankton (Jeppesen et al., 1990a; Grimm, 1989). Finally, it has been suggested that natural winter fish kills due to oxygen depletion occur more frequently in small lakes (Jeppesen et al., 1990a), but the evidence for this cannot be derived from the paper; the fish kills might also be related to factors like shallowness or low water transport that are correlated with size. Also Van Geest el al. (2003) report more frequent fish kills in small lakes, but again, the relation with size is probably indirect as the fish kills were related to periods of low water level in summer. Anyway, the occurrence of fish kills acts as a natural biomanipulation experiment, that could certainly promote vegetation dominance in certain lakes. Van Geest et al (2003) conclude, from a cross-analysis study of shallow floodplain lakes in The Netherlands, that the colonisation argument and the top-down mechanisms are the most likely explanations for the negative impact of lake area on submerged macrophytes dominance.

– *Water depth:*

The dominating effect of the water depth, viz. a lower chance for the survival of submerged macrophytes with increasing depth, is consistent with well-documented empirical studies on the maximum colonisation depth of macrophytes as a function of water transparency (Spence, 1982; Chambers & Kalff, 1985; reviewed in Moss, 1988 and Scheffer, 1998, a.o.). These studies do not include very shallow and/or very turbid waters. The PCLake model predicts a sharp increase of the critical loadings at a water depth of 1 m or less (see sections 6.3 and 4.5), implying that these very shallow lakes have a high chance of maintaining their ‘clear’ state despite a rather high turbidity or nutrient level. The model seems a bit too optimistic in this respect, as compared to for instance studies in the Dutch Randmeren (Meijer et al., 1999b). A possible cause is that the model includes one prototypic macrophyte group, with the above-ground biomass equally distributed over depth and emerging in spring from overwintering parts. Species with other growth forms, like charophytes, that grow closer to the bottom, will be more vulnerable. Blindow (1992) showed that, although charophytes can grow to greater depths in clear water (due to their higher light affinity), angiosperms are in favour in more turbid water, as they have a greater part of their biomass near the surface.

– *Wetland zone:*

There are clear indications of a purifying effect of wetlands on adjacent lakes, see e.g. Johnston (1991), Mitsch (1995), Verhoeven & Meuleman (1999), among others. Richardson et al. (1997) conclude that natural wetlands may retain a phosphorus loading of up to 1-2 gP m^{-2} y^{-1}. Artificial wetlands may perform even better, depending on their construction and management. The example of the Kis-Balaton wetland system (Somlyódy, 1998), which was used to protect Lake Balaton (Hungary) by purifying the water of a river before it entered the lake, showed a considerable purifying effect, but at the same time demonstrated deteriorating effects of eutrophication on natural wetlands themselves.

The model results comply with the general evidence that wetland zones should cover an extensive area to have a significant impact on water quality. Quantitative data about natural systems are rare, but the loss of former wetland areas and flood plains around for instance the Friesian lakes (in the north of The Netherlands) is suspected to have enhanced the shift of these lakes to the turbid state. These wetlands were the result of a naturally fluctuating water level, that has later been fixed by means of water engineering works (Waterschap Friesland, 1993; Klinge et al, 1995).

Comparison with empirical information: critical loadings

Several authors have derived critical nutrient loadings or (mostly) in-lake concentrations from empirical information. Direct empirical data on individual lakes shifting between the clear and turbid states are scarce, but some information can be derived from multi-lake data sets. As biomanipulation generally can be effective in the 'intermediate' P range only, biomanipulation experiments can also supply information about critical P levels.

Hosper (1997, chapter 3) used an approach based on a critical relative Secchi depth (SD/z; SD = Secchi depth, z = mixing depth of the water) for the breaking of a cyanobacterial dominance of 0.6 [-], derived from a euphotic depth z_{eu} for phytoplankton as the depth where 1% of the light is left (Reynolds, 1984) and a Poole-Atkins coefficient (the product of extinction coefficient and Secchi depth) of 1.8 [-]. By means of empirical *maxima* of Chla versus inverse Secchi depth (Chla = 58/SD – 13) and Chla versus TP in a data set of Dutch lakes, this value was converted into critical TP *concentrations* of 0.055 gP m^{-3} for lakes with a depth of 1 m and 0.023 gP m^{-3} for depth = 2 m. These values thus relate to the 'backward' switchpoint. The maximum ratios were comparable to those derived in a similar way by Lijklema et al (1989) and Portielje & Van der Molen (1999). Hosper (1997) adds that still lower TP values are required if non-algal turbidity is high. These conclusions show already that the critical P values are dependent on water depth and other lake features.

Jeppesen et al (1990b, 1991) concluded from a multi-lake study on Danish lakes that shallow lakes > 3 ha were generally macrophyte-dominated at TP levels < ca 0.05 gP m^{-3} and turbid at levels > ca 0.125 gP m^{-3}, with alternative states possible at intermediate levels. In small lakes (< 3 ha) the upper limit could be substantially higher (the highest data point with macrophytes was 0.65 mgP m^{-3}). The fish stock increased with TP, but piscivores made up a substantial fraction of the total fish stock only up to TP levels of ca 0.10 mgP m^{-3}. In contrast to the Dutch lakes, the low-TP lakes were generally dominated by green algae instead of cyanobacteria. The authors suggest a relation with the generally higher winter and spring temperatures in The Netherlands; it could possibly also be related to a generally longer retention time. From these findings, together with the results of several whole-lake biomanipulation experiments, the authors conclude that the threshold level for long-term effects of biomanipulation in lakes > 10 ha (not severely limited by nitrogen) is ca 0.10 (0.08 - 0.15) gP m^{-3}. For the Danish situation, this corresponds to loadings of 0.5 – 2.0 gP m^{-2} y^{-1}, depending on lake morphometry and flushing rate. The authors state that values between 1 and 2 gP m^{-2} y^{-1} refer to lakes with a high flushing rate, but this is not further quantified. They add that in small lakes (< 3 ha) the threshold level may be higher because of more favourable conditions for submerged macrophytes and piscivorous fish. The same values are mentioned by Jeppesen et al. (1991), but based on some more biomanipulation experiments in later years, Jeppesen et al. (1997) reduce the threshold TP concentration somewhat to 0.050 – 0.10 gP m^{-3}. In case of nitrogen limitation, the threshold P level is higher.

These findings agree with the results of Benndorf (1987, 1990), also based on biomanipulation experiments, who reported a critical loading of 0.5-1.0 gP m^{-2} y^{-1} (for lakes shallower than 7 m) for biomanipulation to be effective.

Also Perrow et al. (1999) find distinct changes in composition and size distribution of the zooplankton at comparable phosphorus levels.

Biomanipulation experiments in The Netherlands were less conclusive at this point (Meijer et al., 1994, 1999a; Meijer, 2000), although there was a tendency that the chance for long-term success of a biomanipulation measure decreased with higher P levels. P and N *loadings* were not systematically assessed in the biomanipulated lakes. The biomanipulation itself also contributed to a decrease in P level. Other factors than P loading seemed to be more important to explain the success or failure of biomanipulation, like the percentage of fish that was indeed removed: this had to be > 75% for a longer-lasting effect (at least a few years). The authors conclude that in the initial phase of the restoration, zooplankton grazing, once relieved from fish predation, plays a key role in getting clear water in spring. If vegetation then develops, its stability depends on other factors, like its resistance to herbivory and nitrogen limitation of the phytoplankton. Also piscivorous fish plays a role in maintaining the clear state, not so much in provoking it. (See also chapters 11-12, describing a PCLake simulation of one of these biomanipulation case studies).

Also Van Geest et al. (2003) find in their study of shallow floodplain lakes in The Netherlands that a high macrophyte coverage may sometimes coincide with TP concentrations much higher than 0.1 g m^{-3}, even up to 0.4 g m^{-3}. In their data set, submerged macrophyte cover decreased significantly with the surface area, depth and age of he lakes. There was no significant relation with TP or TN concentrations or land use. Their data set was dominated by rather small lakes (range 0.01 - 45 ha, median 0.7 ha, 75% percentile 2.1 ha). The impact of morphometry probably overshadows the potential impact of nutrient status in this range. In some of these lakes the clear state seems to be transient, caused by fish kills after periodic drawdown of the lake.

Following a different approach, based on an empirical relation between TP concentration and total fish biomass, and an estimate of maximum *piscivorous* fish biomass, Klinge et al. (1995) derive a maximum P concentration for a clear, mesotrophic, vegetation-dominated lake in which pike is the main predator, of 0.1–0.2 mg/l. Above this limit, the balance between bottom-up and top-down forces is disturbed and the lake shifts to the turbid state void of vegetation.

For a limited number of cases, i.e. lakes that have switched in the past between the clear and the turbid state, estimates have been made of their critical loading, based on available information.

The Swedish lakes Takern and Krankesjön (average depth 1.0 and 1.5 m, resp.) both shifted several times between both states in the course of the last century, probably due to the direct or indirect effects of water level fluctuations (> 0.5 m). Both lakes had low TP concentrations: L. Takern 0.031 mgP/l, L. Krankesjön 0.02 – 0.06 mgP/l (Blindow, 1992; Blindow et al., 1993).

Lake Botshol in The Netherlands, a small peat lake made up of a mosaic of small water bodies and narrow stretches of land, also switched a few times between clear and turbid state. In its ‘clear’ periods, it is dominated by charophytes. The cause of the switches has been reported as differences in nutrient leaching from the surrounding peatland between wet winters (high leaching) and dry winters (lower leaching) (Ouboter, 1997). Based on the nutrient budgets, the critical loading of the lake was estimated as 0.3 gP m^{-2} y^{-1} (= 0.8 mg P m^{-2} d^{-1}); the data do not allow a conclusion about a possible difference between forward and backward switchpoints. The PCLake model calculates somewhat higher values of 2.3 (forward) and 1.3 (backward) mg P m^{-2} d^{-1} (section 4.5).

Lake Veluwe, which belongs to the Randmeren, also in The Netherlands, originates from embankment of a former estuary in the 1950s. The lake started in the clear state, switched to the turbid state in the 1960s as a result of eutrophication, and was restored to the clear state in the 1990s due to a combined management strategy (phosphorus diversion, flushing, fishery). It was reconstructed that the TP level at the start of the turbid period had been *ca* 0.15 mgP/l and the loading exceeded 1.5 à 2 gP m^{-2} y^{-1}, while the switch back started when the TP level had decreased below *ca* 0.10 mgP/l (Hosper, 1997; Meijer et al., 1999b; Scheffer et al., 2001). Based on these data, combined with water and nutrient budgets, a model study and other ecological information, Meijer et al. (1999b) estimate the critical TP *concentration* for a stable clear-water state at 0.10-0.15 mgP/l and the critical loading at about 1.0 gP m^{-2} y^{-1} (= 2.7 mg P m^{-2} d^{-1}). The tentative values of 3.4 (forward) and 1.6 (backward) mg P m^{-2} d^{-1} calculated by PCLake (see section 4.5) are in the same range.

Based on historical reconstructions of the former ‘clear state’ and other ecological studies in the Dutch Zuidlaardermeer (Klinge et al., 2000), Klinge (unpubl. results) estimates the maximum permissible loading for restoration of this lake at 0.7 gP m^{-2} y^{-1} (= 1.9 mg P m^{-2} d^{-1}) in summer, and 1.0-1.5 gP m^{-2} y^{-1} (= 2.7 - 4.1 mg P m^{-2} d^{-1}) in winter (when retention is lower). This is lower than the restoration threshold derived by PCLake of 6.1 mg P m^{-2} d^{-1} (section 4.5). The non-algal turbidity of the inflowing stream water has possibly been underestimated in this calculation.

In some cases, one can only speculate about the causes of a (periodical) switch of a particular lake (Scheffer, 1998). For some lakes, it might even be an intrinsic feature caused by internal mechanisms: a gradual accumulation of nutrients in the vegetated state until the system can no longer absorb them, followed by a switch to the turbid state, a gradual wash-out of the nutrients due to the lower retention, until nutrient limitation makes the phytoplankton collapse again, followed by a switch back to the clear state. This is of course a theoretical speculation, the plausibility of which and the ranges of its possible occurrence could be explored by means of PCLake simulations.

Comparison with other models

Several types of other models have been developed that cover aspects of the eutrophication of lake ecosystems. It is interesting to compare the approach and assumptions of these models and the type of questions they can answer, and to place PCLake in this context.

Models can be divided in (a) static models, based on statistical relations, and (b) dynamic models, based on ecological processes, which can be divided in different types. This distinction is not absolute, as also dynamic models often contain elements based on statistical relationships.

An early contribution was made by the empirical regression models relating the external nutrient loading to, among others, TP and TN concentrations, chlorophyll-*a* levels and transparency, based on multi-lake data sets. For reviews of this type of models see for instance Reckhow & Chapra (1983) and Hosper (1997). A ‘worst case variant’ of this approach are the empirical models relating maximum chlorophyll levels to TP or TN concentrations (Lijklema et al., 1998; Hosper, 1997; Portielje & Van der Molen, 1997). These models remain very useful to give an estimate of the trophic state and possible algal biomass of a lake, but they are essentially not apt for predictions for situations where aquatic macrophytes play a role.

The PCLake simulations for total phosphorus and chlorophyll-*a* are, in general, within realistic ranges when compared with these empirically derived relations.

Later, many dynamic, process-oriented, eutrophication models were developed, differing in complexity and in the factors and variables included (for overviews see for instance Chapra & Reckhow, 1983; Jørgensen, 2001). All of these models describe phytoplankton and phosphorus, most of them also nitrogen. They may include one or several species / functional groups of phytoplankton, they may include constant or variable stoichiometry, they may or may not explicitly cover the sediment (if so, with one or multiple layers), and they may assume a mixed water column or explicitly consider vertical and/or horizontal spatial gradients. A model applied in several Dutch lakes is DBS (Delwaq-BLOOM-Switch), based on a mixed water column, 2-4 sediment layers and three phytoplankton groups (Van der Molen et al., 1993). A recent phytoplankton model called PROTECH (Reynolds et al., 2001) describes up to eight functonal groups of phytoplankton. Mostly, elaboration of one aspect of the ecosystem coincides with a more simplified description of other aspects. Some of the models include zooplankton, some of them also fish and/or other food web components. It seems that, after a period of disappointment about the results of complex models including food webs, a certain re-appraisal of this approach can be observed. The availability of better analysis tools and much faster computational facilities have produced more insight in the systems behaviour through application of such complex models (e.g. Omlin et al., 2001; Krivtsov et al., 2002).

Macrophyte models are relatively scarce as compared to algal models (e.g. Best, 1991), and only very few models, besides *PCLake*, contain both phytoplankton and macrophytes. Contributions were made by the International Biological Programme around 1970, e.g. a model developed by C.J. Walters and R.A. Park (Le Cren & Lowe-McConnell, 1980, ch. 5). Voinov & Tonkikh (1987) proposed a qualitative model of eutrophication in macrophyte lakes. Recently developed models including both components are presented by Muhammetoglu & Soyupak (2000) and Hakanson & Boulion (2002). The latter model, called LakeWeb, is a dynamic model, partly relying on regression equations between, for instance, TP and the biomass production of several biota. This model excludes nitrogen.

A specific type of models are the structural dynamic models, that may adapt their parameter setting dynamically based on the optimization of an objective function such as the so-called 'exergy' (Jørgensen, 2001). Jørgensen & De Bernardi (1998) presented the effects of biomanipulation on the phyto- and zooplankton parameters in a lake model of this type. The appropriateness of the exergy as objective function, however, is questionable in this case.

An interesting kind of models are the so-called 'minimal models' or 'minimodels', dynamic models designed to explore and to generate hypotheses about a single (general) aspect of an (eco)system. They typically contain two state variables. Among the early examples were the Lotka-Volterra predator-prey models. Scheffer (1989, 1990, 1993, 1997, 1998) performed a series of studies with minimal models, each covering a subsystem of the lake ecosystem while keeping the surroundings fixed. These studies showed that different feedback mechanisms may give rise to alternative equilibria in a part of their parameter space. This was shown for the algae-zooplankton system with fish imposed, the macrophytes-algae competition via light, the competition green algae-cyanobacteria, and the bream-pike system. All models showed a dependency, in a direct or indirect way, on the trophic state of the system, alternative equilibria being possible in an intermediate range. This range could however not be quantified by this type of models.

Another approach are the 'individual-based' models, giving more emphasis on population structure and variation in individual traits. These models contain more realism on these aspects, but are computationally very demanding. A variant of this type are models in which individuals are aggregated in cohorts or the like (sometimes called 'super-individuals', Scheffer et al., 1995). This type of models have been successfully applied to fish dynamics (Van Nes, 2002). Also a spatially explicit model of two groups of water plants, *Chara* and *Potamogeton*, called Charisma (Van Nes et al., 2002) can be placed in this category. Using this model, the authors showed alternative equilibria in a range of turbidity values, and hysteresis in the switch between the two species. Factors such as the differences in seasonal cycle of the plant groups (e.g. overwintering strategy) and spatial aspects (e.g. depth gradients) were important in explaining the outcome of the competition.

The results obtained with *PCLake* are generally in line with predictions from minimal models and from individual-based models focussing on submerged plant growth, and are also in line with lake restoration experiences so far. This congruence does of course not proof that the models are 'true'; it might be that the same, but possibly wrong, mechanisms are represented in all models. On the other hand, it shows that the overall picture is robust against assumptions about numerous details in different models.

The *PCLake* results show that the conclusions from the minimal models, which each focus on a specific mechanism, are still valid if they are combined into one model and are embedded in a description of the nutrient cycles. The overall results appear to be quite robust to parameter variations.

The ***contribution of PCLake*** can be seen as threefold:

- estimation of the critical loading levels for shallow lakes, and the relative importance of different factors for those levels, by using a model in which the ecological mechanisms are coupled to the framework of the nutrient cycles.
- an evaluation of the combined impact of several input factors and lake features on lake eutrophication and restoration.
- an evaluation of the importance of different ecological mechanisms, including a comparison of model variants (*i.e.* a more structural uncertainty analysis).

Hence, the model may take an intermediate position between the existing simple modelling tools for the analysis of subsystems, the more detailed eutrophication models and the individual-based models. The best way to unravel what drives these ecosystems and to predict critical nutrient loadings is probably to combine the results of different modelling approaches, also combined with observations and experiments.

The model analyses also stress the close interrelationship between the nutrient cycle on the one hand and the biological structure on the other. The competition between the different primary producers, phytoplankton and macrophytes, is related to both light climate, nutrient availability and food web interactions. Changes in trophic state may cause changes in food web structure, while the latter may influence the system's (resistance to) response to nutrient loading. Cascading effects in the food web may be analyzed also in terms of changes in nutrient cycles (*cf* Carpenter *et al.*, 1992), while the overall trophic state of the system acts as a general boundary condition. These structural differences may also be related to aspects of biodiversity, as mesotrophic lakes often have the highest biodiversity (Dodson et al., 2000; Leibold, 1999; Chase & Leibold, 2002; Declerck et al., in press), and because functional and structural diversity are related (Tilman et al., 1997). Also other modelling studies show that a combination of a thorough consideration of the hydrological and nutrient budgeting and nutrient cycles (N, P, Si), together with a representation of complex ecological dynamics, is beneficial or even indispensable for the models's predictive value (Krivtsov et al., 2001, 2002; Jayaweera & Asaeda, 1996; Asaeda & Van Bon, 1997; Muhammetoglu & Soyupak, 2000). In many cases, feedbacks between the (bottom-up) nutrient regulation of phytoplankton growth and other biotic components (zooplankton, fish, macrophytes) were shown to be important (e.g. Carpenter et al., 1992, Jeppesen et al., 1990, Van Donk et al., 1993, Moss, 1990).

At the same time, it seems worthwile to investigate what simplifications of the model are possible, while maintaining its scope and structure. Some less sensitive parameters or processes might be lumped or simplified. The variable stoichiometry might be modelled more simply, thereby decreasing the simulation time. This would provide more time for an extensive sensitivity and uncertainty analysis. Another idea might be to handle the relatively fast and the relatively slow ecosystem processes in a distinctive way (Reed-Andersen et al., 2001). These modifications could be considered in future work.

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 & Omlin, 1997; Omlin & 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 & Mangel, 1997). Modern sensitivity analysis tools are indispensable for parameter selection. The Bayesian approach, of which an application is illustrated in chapter 4, 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.

7. Setting critical nutrient values for ditches using the eutrophication model PCDitch

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Abstract

Critical nutrient loads to prevent duckweed dominance loads in polder ditches were assessed using the eutrophication model PCDitch. In this article the ecological target was set at 50% duckweed coverage. This may be very high for ditches with a nature function, but is not unreasonable for ditches in agricultural areas, with upwelling nutrient rich groundwater, run-off and drainage. Since the change from a ditch with submersed vegetation to duckweed coverage is often a sudden shift, the choice of the amount of duckweed coverage does not influence the calculated loading very much. The main topic of the paper is to present a method to calculate critical loads of nutrients when ecological targets have been set.

Sediment type, residence time and water depth influenced the critical loading rates. The calculated critical phosphorus load ranged from 1.8 - 10.2 g P m^{-2} $year^{-1}$, while the calculated critical nitrogen load stretched from 12.1- 43.8 g N m^{-2} $year^{-1}$. The concentration ranges that were derived from the loading rate were 0.19 - 0.42 mg P l^{-1} and 1.3 - 3.3 mg N l^{-1}. Since PCDitch does not distinguish between *Lemna* spp. and *Azolla* spp., no definite conclusions were drawn concerning the effects of nitrogen reduction.

In a model situation a pristine ditch was loaded with phosphorus, which resulted into complete duckweed coverage during summer within a few years. When reducing the phosphorus load, it took 10 years before the original situation was reached again. Dredging would accelerate the process of recovery significantly, because the water depth would increase and the phosphorus release from the sediments in summer would decrease.

Introduction

Drainage ditches are small, linear water bodies, usually less than 1.5 m depth and ranging from 1 m to several meters wide. The main task of ditches in the Netherlands is to discharge superfluous water from agricultural areas. The hydraulic residence time is days to weeks. Many ditches serve as a water transport system to agricultural areas during dry spells. Next to these hydrological functions ditches are important as a source of cattle drinking water, and they provide an important habitat for plants and animals. Because of their shallowness ditches are often dominated by macrophytes, needing periodical maintenance (mowing the waterplants) to facilitate the waterflow. The physical-chemical status of the surface water is of paramount importance for the composition of the vegetation in ditches. When nutrient concentrations are low, water is clear and both submerged plants and helophytes arise with a spring bloom of phytoplankton (De Groot *et al.*, 1987, Veeningen, 1982, Higler, 1989, 2000; Nijboer, 2000). Eutrophication is the greatest menace in Dutch ditches (Nijboer, 2000, Arts et al., 2001). Run-off and seepage of nutrients from agricultural areas and aerobic degradation of peat are the most important sources, next to the (at present) less extensive point sources; and in some cases inlet water and upward seepage of nutrient rich groundwater (van Liere *et al.*, 2002). Moderate increase of nutrients will result in higher growth of submerged macrophytes. This higher amount of macrophytes induces self shading and light energy limited growth, causing a shift from species with a vertical growth strategy to species with a horizontal growth strategy (Sand-Jensen and Søndergaard, 1981). At still higher nutrient loading growth of filamentous and/or epiphytic algae may occur. The endpoint of the eutrophication process in ditches is a complete dominance of duckweeds (*Lemnaceae*) (Portielje and Roijackers, 1995, Nijboer, 2000, Arts et al., 2001). Because duckweed, as a floating plant, hampers re-aeration and releases the produced oxygen to the air compartment, while decomposition in the water phase uses the oxygen, the water underneath duckweed becomes often anoxic (Veeningen, 1982). When the phosphorus load is higher in comparison with the nitrogen load nitrogen limited growth occurs, which may result in a shift to *Azolla* spp.. These species grow in symbiosis with *Anabaena azollae*, a cyanobacterium which is able to fix nitrogen. At present duckweed dominance is fairly common in the Netherlands (van der Does and Klink, 1991, Nijboer, 2000).

It is generally assumed that phosphorus limits growth of phytoplankton and macrophytes in oligotrophic to mesotrophic freshwaters in the temperate climate zone (Corell, 1998; Newton and Jarell, 1999). In many eutrophic systems, such as ditches, an excess of phosphorus is present due to storage in plants and especially in the sediment. Nitrogen has a faster cycle, and a significant amount of it is lost by denitrification. It is hypothesized here that recovery from *Lemna* dominance is more efficient when phosphorus is reduced or when co-reduction of phosphorus and nitrogen occurs. As stated above, nitrogen reduction alone may result in a shift to *Azolla* spp. In shallow lakes it has been widely accepted that phosphorus is the main nutrient to be reduced. With nitrogen reduction alone the dominant cyanobacteria may be replaced by other (nitrogen fixing) ones (Zevenboom and Mur, 1980).

In this paper the results are presented of simulations with the ecological eutrophication model

PCDitch in order to assess critical loads and critical concentrations of phosphorus and nitrogen. Furthermore the effects of a simulated dredging experiment are shown.

Material and methods

Description of the eutrophication model PCDitch

The eutrophication model PCDitch includes the water column and the upper sediment layer of a ditch, both assumed to be well mixed. The model may be regarded as a competition model between several functional groups of water plants, coupled to nutrient cycles (Figure 1). The model describes the cycling of dry weight (DW), phosphorus (P), nitrogen (N) and oxygen (O_2). All biotic components as well as detritus are modelled in these components. This is done to close the nutrient cycles within the model system, and to account for variability of the nutrient ratios of water plants depending on the loading rate. The 'target variables' are biomass of plant groups, and concentrations of nutrients and dissolved oxygen. The abiotic and biotic components and the processes relevant in calculating effects of eutrophication are depicted in Figure 1. Zooplankton, macrofauna and fish have been left out, as they are considered not to be very important for the prediction of the target components in ditches.

The in- and outflow of water and the external nutrient loading to the ditch system should be given by the user or calculated by other models. The initial water depth, thickness of the

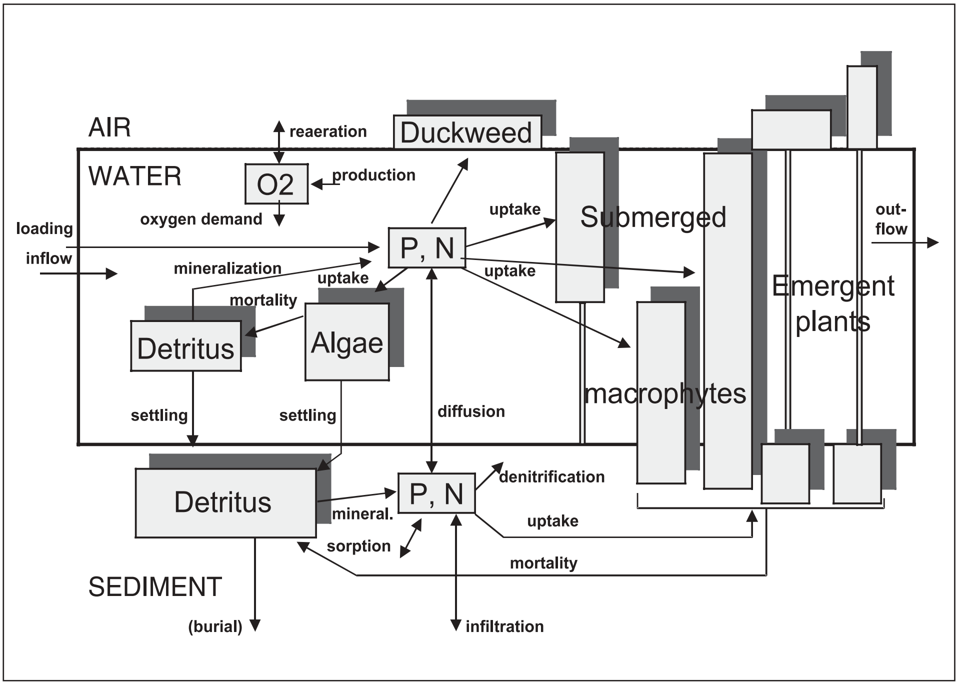


Figure 1. PCDitch model structure. Respiration fluxes are not shown.

sediment layer and the sediment type (defined by its density, porosity, lutum content and (initial) organic matter content) are input parameters.

Many of the formulations were derived from the lake eutrophication model PCLake (Janse & Aldenberg, 1990; Janse, 1997), but more types of macrophytes were distinguished. Properties of the aquatic plants were extracted from literature data. In the model, the competition between plant groups is mainly determined by the factors light, temperature, nutrients and - for algae and optionally for duckweed - outflow. The freely floating group duckweed is not limited by light, but is confined to the water column for its nutrient uptake. Duckweed hampers the growth of submerged vegetation due to light interception. The latter group is spit into plants that are able to use the sediment nutrient pool and plants that are not. Both nymphaeids and helophytes may take considerable amounts of nutrients from the sediment, while the first group also is a light interceptor. In field situations, helophytes are often removed once or twice a year because of ditch management. In the model all plants can be mowed once or twice a year (default once every autumn). PCDitch was calibrated with experimental ditches with sand and clay bottom (Portielje and Roijackers, 1995) that were exposed to various nutrient loads. Since phosphorus exchange in PCDitch is related with iron, aluminium, and lutum content as well as porosity and organic matter content, it is presumed that the calibration is also valid for peat ditches. Calibration and validation with field datasets are at hand. A complete description of the model is published in Janse (1998).

Simulation

The eutrophication model PCDitch version 1.22 (Janse, 1998) was used to calculate the coverage of duckweed and submersed aquatic plants as a function of phosphorus and nitrogen loading. Combinations of depth (0.25 – 1.5 m), hydraulic loading rate (q, ranging from 10 to 70 mm day^{-1}), and type of sediment (sand, peat, and clay) were used. The sediment type was defined in terms of porosity, organic matter and lutum content. When analysing phosphorus load (0.006 – 0.040 g P m^{-2} day^{-1}) nitrogen was kept in surplus to avoid nitrogen limitation of plant growth. When studying nitrogen, phosphorus was kept in surplus. An ‘average ditch’ was defined as a ditch with a depth of 0.5 m, a q of 30 mm day^{-1} and a clay sediment. For simplicity, the nutrient load was kept constant over the year (in field situations, the loading is often somewhat higher in winter than in summer, dependent on the local situation). The temperature and photosynthetic radiation were set sinusoidal as in an average year, vegetation was mowed every autumn, depth was kept constant and duckweed was not transported to or from the ditch. Previous simulations showed that equilibrium with the imposed nutrient load occurs normally within 10 years; to be certain that the equilibrium was reached a period of 20 years was calculated by the model.

As an indication for recovery of eutrophication 50% of duckweed coverage was assumed to be critical. This value is chosen arbitrarily. It seems high, certainly in ditches in natural areas, in which duckweed should hardly be present if external nutrient load is low. Most of the ditches are situated in agricultural areas, and in the Netherlands a large part of these ditches have been dug in areas in which nutrient rich upwelling waters are important. The differences in these situations demands for regionally differentiated settings of standards. In this paper a method is presented which can be used to set these standards. The method is applicable to any chosen relative duckweed coverage.

The various combinations gave rise to 1296 runs of PCDitch per nutrient. The simulations took about 6 hours on a PC with an Intel Pentium 4 processor. It took, however, several years to construct the model.

Results and discussion

Simulations of the summer-averaged duckweed cover as a function of phosphorus loading rate for different combinations of sediment types, hydraulic loading rate and water depth, are given in Figure 2. PCDitch simulates a rather steep S-shaped curve with a 'critical load' which, when it is exceeded, results in complete dominance of duckweed and disappearance of submerged plant growth. Since the slope of the simulated nutrient vs. duckweed coverage is often very steep it does not matter very much in critical load whether 20, 50 or 90 % duckweed coverage is chosen as the critical value. This choice has still to be made. In general, a shift to duckweed dominance occurs in sand ditches at a lower rate as compared to clay or peat ditches. The critical loading generally increases with flow rate, while its relation with water depth is more complex: in some ranges the critical load increases with water depth, but in other ranges there is no effect. The depth effect shows interaction with other factors and parameters and might in some instances vanish or even be opposite. An impression of the critical values in the 'average' ditch and their range as a function of depth, q and sediment type is given in Table 1 (for phosphorus and nitrogen) and for phosphorus only in Figure 3. Critical nutrient loads are more reliable than critical nutrient concentrations, as in the latter case an important part of the nutrients is present in primary producers and sediment. However, a disadvantage of nutrient loads is that they can only be modelled, or measured in experimentally managed systems. Loading cannot be measured in uncontrolled field situations. Both critical loads and critical concentrations are presented in Table 1. The range of critical values for phosphorus is somewhat wider than for nitrogen; the slope of the curve of nitrogen is much less steep as compared with phosphorus (results not shown). This might be due to the larger forcing function of phosphorus in controlling duckweed. It is difficult to draw precise conclusions with respect to nitrogen reduction, since PCDitch does not distinguish between *Lemna* and *Azolla*.

In mesocosm experiments, clay sediment with a top layer of gyttja, a depth of 0.8 m, but an unknown flow rate, (Arts *et al.*, 2002) recovery of eutrophication to a level of clear water with submerged plants and a duckweed coverage less than 5% within two years was simulated by reduction of the phosphorus load. It was found that the target was met at a load of 2 to 3 g P m^{-2} $year^{-1}$. From Figure 2 it can be estimated that 5% coverage of duckweed is calculated to be reached at about 6 g P m^{-2} $year^{-1}$. The difference is explicable because of different chosen targets. Non data were found in the literature of ditches in which recovery from eutrophication has been studied quantitatively.

Table 1. An overview of critical values for P and N in ditches calculated with PCDitch. The average ditch in this table is defined with a depth of 0.5 m, a hydraulic loading rate q of 30 mm day^{-1}, and clay sediment. The critical value of 50% duckweed coverage was arbitrarily chosen.

‘Critical values’ (50% duckweed coverage)	Minimum		‘Average-ditch’		Maximum	
	P	N	P	N	P	N
Load (g P m^{-2} year^{-1}) per surface area	1.8		4.7		10.2	
Load (g N m^{-2} year^{-1}) per surface area		12.1		21.9		43.8
Simulated nutrient concentration (mg l^{-1}, summer average)	0.19	1.3	0.23	1.4	0.42	3.3

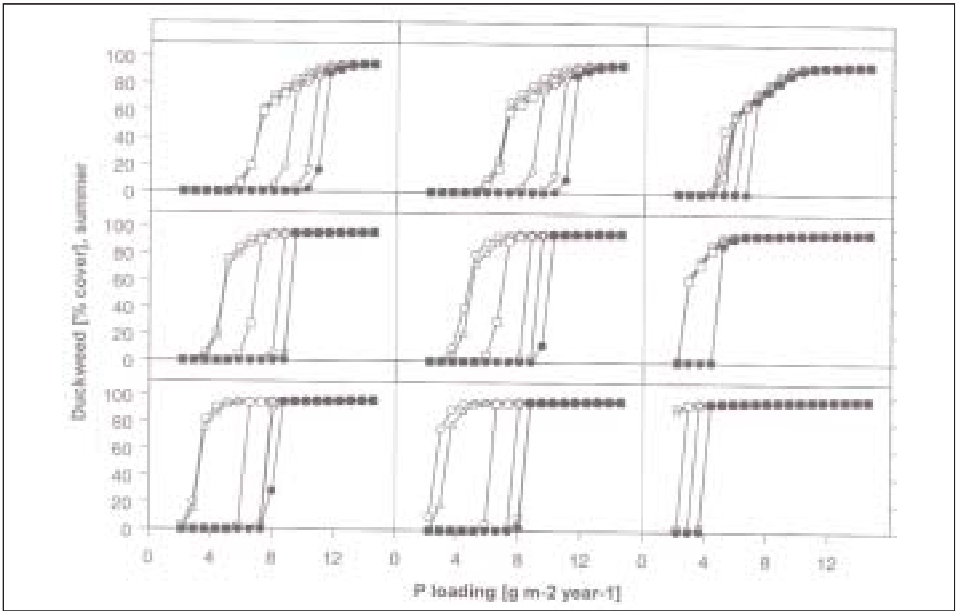


Figure 2. Results of PCDitch simulations for summer-averaged duckweed coverage with all combinations of P-load, sediment type, hydraulic loading rate (q), and water depth.
Symbols depicting water-depth: ○ 0.25 m, ∆ 0.5 m, □ 0.75 m, ◊ 1 m, ∇ 1.25 m, and ● 1.5 m.

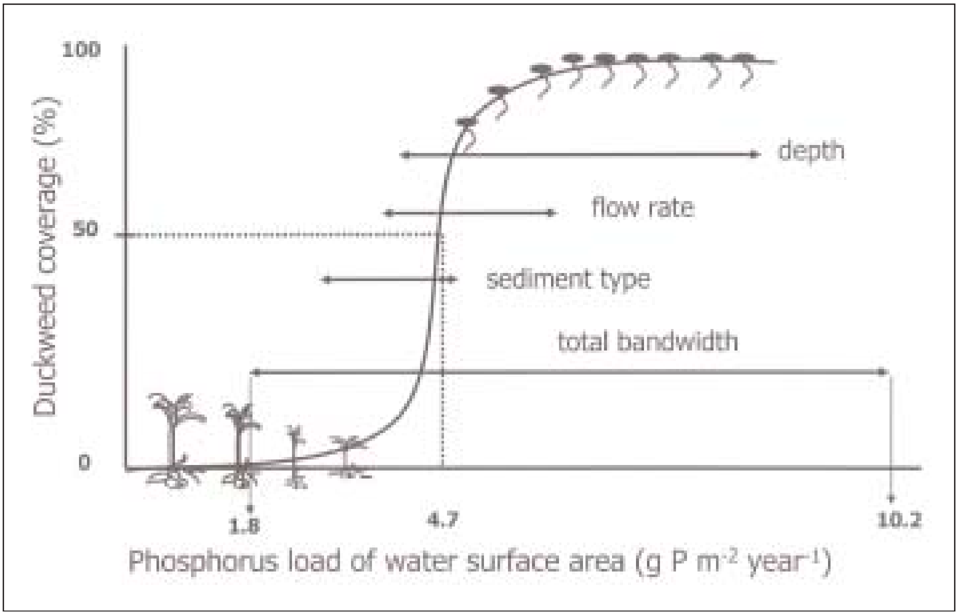


Figure 3. *Variation of critical phosphorus loading of ditches as function of depth, flow rate and sediment type. It is assumed that 50% coverage of duckweed is accepted to be a desired ecological status. However, this choice still has to be singled out. The 'average' ditch has been defined with a depth of 0.5 m, a hydraulic loading rate q of 10 mm day*$^{-1}$ *and clay sediment. The variation with depth and flow rate (hydraulic loading rate q) depicted in the figure are those calculated in the case of clay ditches. Sediment (described using lutum content) varies between sandy sediment on the left hand side of the arrow, and peat on the right hand side. The total bandwidth includes all depths, hydraulic loading rates and sediment types.*

PCDitch predicts duckweed coverage within a few years after increasing the phosphorus load to 11 g P m^{-2} year^{-1} to a pristine ditch with a loading of 1.3 g P m^{-2} year^{-1} (Figure 4a). A loading of 9 g P m^{-2} year^{-1} resulted in eutrophication in experimental ditches, see Arts et al., 2001. It takes almost 15 years for the system to return to its original state after a reduction of the phosphorus load to the original low value of 1.3 g P m^{-2} year^{-1} (Figure 4a). The system clearly reveals resilience, among others because of adsorption to sediment and concomitant release. Dredging also influences the system: it increases water depth, such as to allow for a higher load (Figure 2), and it removes sediment rich in phosphorus, thereby accelerating restoration. Dredging of the ditch (increasing the water depth with 50 cm) without reduction of the phosphorus load (Figure 4a, first part of the curve) would have no effect on the duckweed coverage (results not shown), because the phosphorus loading (11 g P m^{-2} year^{-1}) is too high. However, if simultaneously with dredging the phosphorus load is reduced to its original low value (1.3 g P m^{-2} year^{-1}) the time of recovery is some 2 years instead of 15 (Figure 4b compared with Figure 4a).

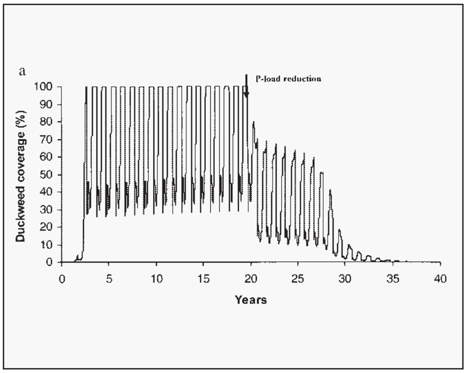
There exists also a threshold phosphorus load below which dredging results in an improvement of ditch quality. It is important to determine or find out this threshold loading from experiments and further modelling.

Conclusions

In The Netherlands there are no standards set for nutrient concentrations in ditches. As a precaution critical concentrations of 0.15 mg P l^{-1} and 2.2 mg N l^{-1} (summer average) are used for all water in the Netherlands. These values are derived from standards in shallow lakes, and are not related to duckweed coverage in ditches.

It is evident that it is not practicable to set critical nutrient loads or concentrations in ditches on a national scale, because of the rather large bandwidth for the various ditches (Figure 3). Regionally there are better possibilities for standardization, since depth and other features of ditches are generally within narrower ranges.

According to the European Framework Directive (European Commission, 2000) a Good Ecological Status has to be defined for all water bodies. Critical nutrient values should be derived from this status as precondition. The presented method for ditches in this paper is suitable for this operation. Depth, flow rate and type of sediment should be taken into account, since they too guide the ecological quality in ditches. It is also possible to attain a Good Ecological Status by performing other water management measures than nutrient reduction alone. Obviously this cannot be done above a certain threshold of nutrient loading. Therefore, reduction of nutrients still remains the most important measure in combating eutrophication.



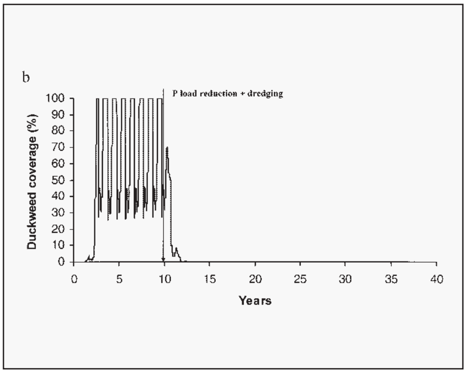


Figure 4a. *Duckweed coverage as a function of phosphorus loading. Starting from a pristine ditch (1.3 g P m^{-2} $year^{-1}$) the phosphorus load was increased (11 g P m^{-2} $year^{-1}$) and after 20 years the loading was reduced to its original low loading rate.*

Figure 4b. *Start as in Figure 4a. However, after 10 years the depth of the ditch was increased with 50 cm by dredging while simultaneously the high phosphorus loading was reduced to its original low rate.*

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Chapter 8

MODELLING PHOSPHORUS FLUXES IN THE HYPERTROPHIC LOOSDRECHT LAKES

J.H. JANSE and T. ALDENBERG

KEYWORDS: model; eutrophication; phosphorus; P/C ratio; lake ecosystem

ABSTRACT

A dynamic, deterministic model is presented to simulate the phosphorus cycle and plankton growth in the shallow, hypertrophic Loosdrecht Lakes (The Netherlands) before and after restoration measures. Besides inorganic phosphorus (SRP) in both the surface water and the interstitial water, the model comprises three algal groups, zooplankton, fish, detritus, zoobenthos and upper sediment (all modelled both in carbon and in phosphorus). Within the model system, the phosphorus cycle is completely closed. Carbon and phosphorus are described independently, so that the dynamics of the P/C ratios can be modelled. Sediment processes are described in a simplified form.

Simulated values are largely within the range of observed ones. The detrital fraction of the seston (= phytoplankton + detritus) varies from 50-60% in summer to about 90% in winter. SRP in the surface water is very low during most of the year. Sensitivity for external phosphorus input is larger for algal and detrital P than for algal and detrital C and chlorophyll-*a*. So the P/C ratio of the seston decreases following restoration measures, as is observed in the lakes, while the much higher P/C ratios of zooplankton and fish remain constant. Phosphorus mobilisation from the sediment decreases with decreasing external input. Adaptation of the model system to the reduced loading takes place within about two years.

Sources of uncertainty in the model include the limited knowledge on selective grazing as well as on mortality and mineralisation processes.

INTRODUCTION

Like many other Dutch shallow lakes, the Loosdrecht Lakes (Fig. 1) severely suffer from eutrophication, caused by the heavy nutrient loadings affecting the lakes for many decades. This process has led to an undesirable bloom of cyanobacteria with summer chlorophyll-*a* concentrations of 150-200 $\mu g.l^{-1}$ and more, disappearance of aquatic vegetation and fauna and replacement of other fish species by bream. A detailed description of the lakes system can be found in VAN LIERE *et al.*, 1984. During the 1970s and '80s, measures have been taken to reduce the external phosphorus loading, mainly by diversion and treatment of sewage water and, since 1984, by changing the source of inlet water and by dephosphatising the inlet water before it enters the lake. External loading decreased from about 1.1 $g.m^{-2}.y^{-1}$ in 1983 to 0.3 - 0.4 $g.m^{-2}.y^{-1}$ from 1984 onwards (ENGELEN *et al.*, 1988; BUIJSE, 1989). This reduction has not led to a substantial improvement of water quality, although some changes in the lake ecosystem are observed. An extensive research project is being performed, the WQL project (Water Quality research Loosdrecht Lakes), which is a cooperation of 8 institutions and which started fully in 1983. Its aim is to qualify and quantify the effects of phosphorus load reduction on the structural and functional aspects of the lake ecosystem and to contribute to (additional) water management measures.

The contribution of the RIVM (National Institute

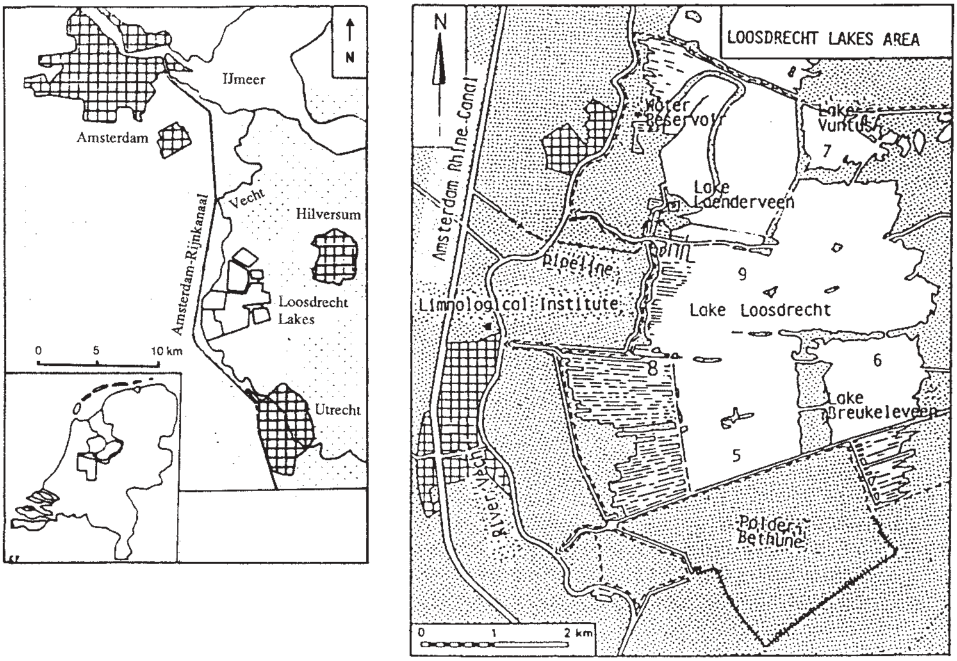

Fig. 1. Location of the Loosdrecht Lakes. (from: ENGELEN and KAL, 1985 and GULATI *et al* 1987.)

of Public Health and Environmental Protection) within the WQL project consists of the development of a mathematical model of the ecosystem which can provide a better insight in the functioning of the system and predict the effects of possible measures. The 'first step' in the modelling process has been described by KOUWENHOVEN and ALDENBERG (1986). The present paper describes the general concepts, formulation and results of the 'second step' model, called *PCLoos* (version 2.4). Main questions within the WQL project are: why did the water quality hardly improve following the restoration measures? Is any delayed reaction still to be expected? Will a further decrease in loading be succesful? Although the present model can not give a definite answer to these questions, it can explain some of the behaviour shown by the system.

GENERAL CONCEPTS OF THE MODEL

Model making starts with a *system definition* and with choosing the minimally required complexity. Such a choice is of course a subjective matter. A model should not be too complex, because uncertainty in the results rapidly increases with the number of state variables and parameters (process rates etc.). On the other hand, a too simple model does not give an adequate description of a system, because processes known to be important are overlooked and useful predictions are not possible. The relation between complexity and reliability of models exhibits an optimum, which depends on the objective of the model, the available ecological knowledge on the system and the available data for calibration (see *e.g.* AUER and CANALE, 1986; JØRGENSEN, 1980; STRASKRABA and GNAUCK, 1986).

Our model takes the simplest structure which is assumed to have retained enough realistic value and uses a maximum of information provided by the other WQL projects. It includes the main processes determining the present hypertrophic state of the system. The model system comprises the water phase and the well-mixed, 'active' first 2 cm of the sediment (mass fluxes within the deeper sediment are considered as less important for water quality). In the water phase, we have modelled soluble reactive phosphorus (SRP) and phytoplankton, as well as detritus (which makes up on average two-thirds of total seston) and two higher trophic levels, zooplankton and fish. The latter component is included because it contains more than half of the phosphorus in the system (VAN LIERE *et al.*, 1989, 1990). The phytoplankton has been split up into three groups (diatoms, greens and blue-greens (cyanobacteria)), of which the latter only is important at present. In the active layer of the sediment two phosphate fractions are modelled, a (degradable) organic one and an inorganic one, as well as the zoobenthos which is an important food source for fish.

The second basis concept is *a closed phosphorus cycle* within the model system. Therefore the sediment has been explicitly included in the model. But also in the water system the importance of this aspect cannot be stressed enough. It is known that at higher levels in the food chain, the phosphorus content of the organisms, related to biomass or carbon, increases. The P/C ratio of the seston can be highly variable and is quite low in the Loosdrecht Lakes (about 1% or less), whereas this ratio is much higher for the zooplankton (2.3%) and zoobenthos (2.0 - 2.5%) and still higher for fish (*ca.* 5.7%). So the zooplankton possesses feedback mechanisms to maintain a high (and more or less constant) P/C ratio, also when its food is poor in phosphorus. The same is true for fish with respect to its food organisms. These mechanisms can involve the uptake of phosphorus from the food, the excretion of phosphorus by the animal and/or its carbon respiration (see next paragraph). In many existing aquatic models, this problem is not adequately dealt with (*e.g.* THOMANN, 1977; DI TORO *et al.*, 1975; DI TORO and MATYSTIK, 1980; JØRGENSEN, 1980). In any model with different P/C ratios per compartment, one or more of the P/C ratios should be dynamical to maintain a closed P balance (ALDENBERG and PETERS, 1988).

In *PCLoos*, a closed phosphorus cycle at any time is achieved by modelling all compartments in two units: both in carbon and in phosphorus, making all P/C ratios dynamical. There is one exception: for thr SPR compartments, there is no equivalent C compartment; CO_2 is not included, because it is not growth-limiting for the phytoplankton. Another restriction is that only one nutrient, phosphorus, is modelled, because management policy is focussing on this nutrient.

In short, the model is composed of 18 state variables, 13 of which form the water phase and 5 the sediment phase. There are 10 phosphorus fractions and 8 carbon fractions. For every state variable a differential equation is formulated. The state variables are linked by a number of processes (mass fluxes), which form the terms in the differential equations. Figs. 2 and 3 depict the C and the P cycle, respectively. Many arrows in the P model, *e.g.* mortality of organisms and sedimentation of particles, are simply proportional to the corresponding C processes and require no extra information. In some cases, however, corresponding processes are independent. For instance as is the case with the assimilation of food by the different animal species and the P uptake and growth of the algae. The relative rate of these processes depends on the actual P/C ratio of the species. All processes in the phosphorus cycle are internal, except for the external loading and the losses from the system by dilution, fisheries and losses to the deeper sediment. In the next section, the main process formulations are given.

PROCESS FORMULATIONS

It is not the purpose of this paper to fully document all the process formulations in the model (for a complete description see JANSE and ALDENBERG, 1990), but the main items will be discussed. An overview of the equations and parameters is to be found in the Appendix.

Primary production of phytoplankton is defined as the fixation of carbon integrated over a 24 h period. For sake of simplicity, this term is considered equivalent to growth, though this is strictly speaking not correct since growth is the balanced production of all cell components. The growth rate is dependent on ambient temperature, available light and phosphorus.

The phosphorus dependency is modelled as a two-step process. Firstly, phosphorus uptake occurs which leads to increase of the internal P content ('cell quota', *Q*). The uptake rate increases with the external SRP concentration up to a maximum rate, determined by the cell quota (the minimum cell quota giving the highest maximum uptake rate). Unlike in a Monod-type function and in accordance with observations in cell cultures (RIEGMAN, 1985), however, the initial slope (initial affinity) is constant. Secondly, growth (increase in carbon) occurs depending on cell quota, according to the relation given by DROOP, 1974. Above the minimum cell quota, the growth rate increases asymptotically with cell quota until the maximum growth rate is reached.

The light dependency is described with a Steele equation (for blue-greens) or a Monod-type equation (for greens and diatoms), integrated with respect to depth and averaged over the day. The extinction coefficient appearing in the equation equals the sum

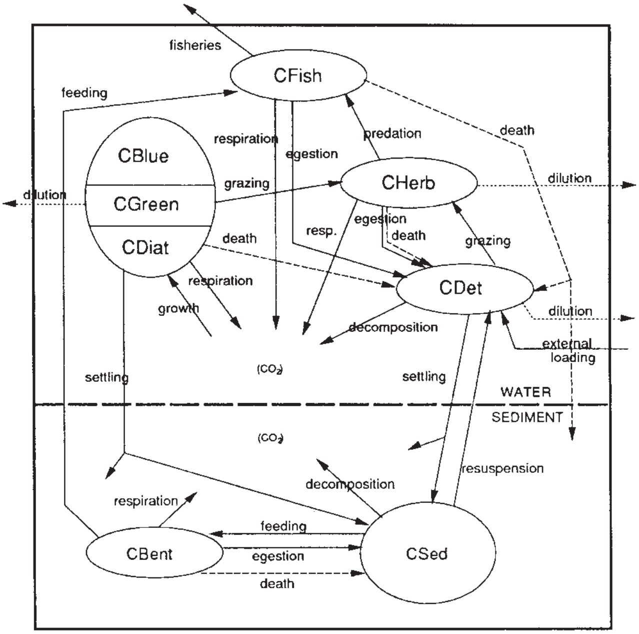

Fig. 2. The carbon cycle.

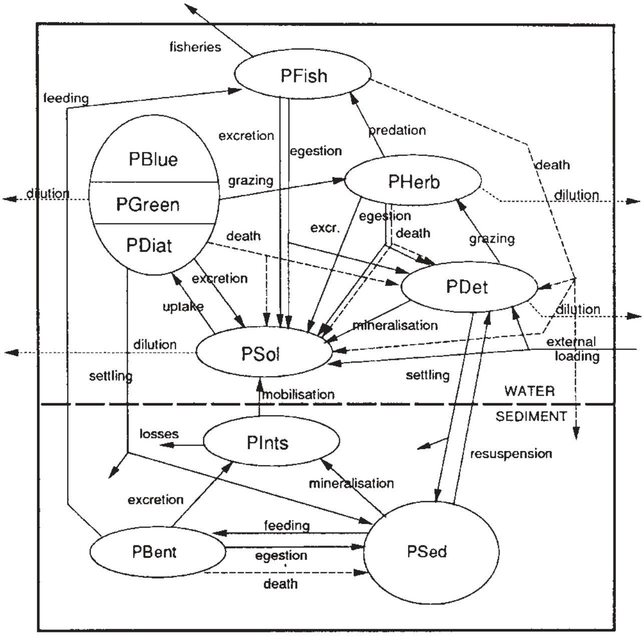

Fig. 3. The phosphorus cycle.

of the background extinction of the water and the contributions of algae and detritus, thus accounting for the self-shading effect. Temperature dependency of greens and blue-greens is described by the commonly used Arrhenius function: $f(T) = \exp(\ln\Theta\cdot(T-T_{ref}))$, in which Θ is a constant being somewhat greater than 1.0 and T_{ref} = 20°C. For the diatoms, however, an optimum function is used.

In the final calculation of the growth rate, the three functions (reduction factors) are multiplied with each other and with the maximum growth rate. Whether light and nutrient functions really can be regarded as independent can be discussed. It is generally agreed that when multiple nutrients are considered, for instance phosphorus and nitrogen, the effects are best described by the minimum law of Liebig, *i.e.*, only one of them is limiting at a time. The effect of temperature is generally reported as independent of other factors. Concerning light, neither of the two options seems entirely satisfactory and we followed the common modellers' view that light and nutrients affect photosynthesis independently. There are some indications, however, that these factors influence each other when both are low ('double limitation'), leading to an extra decrease in growth rate (RIEGMAN, 1985). Incorporation of such effects in a field model (with light intensity under water decreasing with depth) is complicated and needs further study. The growth rate (in day^{-1}) multiplied with the algal concentration gives the gross primary production (in $\mathrm{mg\ C.l^{-1}.d^{-1}}$).

The three algal groups in the model differ in their parameter values. The blue-greens have a higher phosphate and light affinity and maximum phosphate uptake rate than the other groups, but a much lower maximum growth rate. At high light intensity, growth inhibition occurs. The greens have a lower temperature parameter (making them less sensitive for temperature changes), while the diatoms display, as mentioned, an optimum temperature curve with an optimum at 15°C.

Grazing activity of zooplankton is described as a Monod-like function of the seston concentration, which is equivalent to a sharply hyperbolic curve of the specific filtration rate (*e.g.* GULATI *et al.*, 1982; GULATI, 1989). A selection factor is included for each food species to account for preference of the zooplankton for certain kinds of food. The selection factor is 1.0 for diatoms and greens, much lower (0.1) for blue-greens which are not easily handled by most filter feeders, see *e.g.* GLIWICZ (1980) and intermediate (0.25) for detritus. Only a part of the consumed food is actually assimilated by the animals. This fraction, the assimilation efficiency, is constant and quite low (30%) for carbon, but variable (dependent on the P/C ratio of the food) and therefore mostly higher for phosphorus.

Fish predation on zooplankton and zoobenthos is modelled as proportional to the fish concentration, with the predation coefficient depending linearly (in the case of zoobenthos) or in a sigmoid way (zooplankton) on prey density. The phosphorus assimilation efficiency is again dependent on the P/C ratio of the food organisms.

Natural mortality of all the biota is described as a first-order process. The rate constant for fish displays a unique seasonal pattern with most of the mortality taking place between May and July (E. LAMMENS, Limnol. Inst., pers. comm.). During the mortality process, a small part of the phosphorus immediately becomes available in soluble form, the rest in detrital form. The scales and bones of died fish are lost from the system. Also the phosphorus in non-assimilated food, which is egested by zooplankton and fish, is divided in a detrital and a soluble fraction. Respiration and P excretion are normally first-order processes, but especially the animals can adapt the rates of these processes to their P/C ratio (*e.g.* extra respiration and/or reduced P excretion in case of P shortage). Feedback of algal P excretion on cell quota is limited. Algal loss takes place by settling, at a constant, low, species dependent rate. All growth and loss processes (except algal settling and fish mortality) include the temperature function (Arrhenius function) of the respective organisms.

Detritus is the central compartment in the model. It is formed by many different processes, as mentioned above. Due to decomposition/mineralisation (first-order, temperature dependent) it disappears and the P fraction is remobilized. Detritus has an extensive exchange with the organic matter in the upper sediment by means of settling and resuspension. These processes are modelled as first-order processes, not influenced by temperature. A small part (5%) of the settled material is assumed to be buried in the sediment and is thus removed from the system. The remainder forms the organic pool in the upper sediment (*CSed* and *PSed*).

This quantity can be regarded as the exchangeable and degradable material in the upper 2 cm of the sediment, the layer we assume to be important for the nutrient recycling in the lake ecosystem. Other sediment fractions, like the phosphorus chemically bound in humic substances etc. which can amount about 1.1 $\mathrm{mgP.g^{-1}}$ dry weight at a dry weight content of 90 $\mathrm{g.l^{-1}}$ (BOERS *et al.*, 1984), are not modelled explicitly. Mineralisation is described as a first-order process with a strong temperature dependency. The

SRP formed can diffuse from the pore water to the surface water (mobilisation). A small part of the SRP (10%) is lost to deeper layers due to the net effect of adsorption processes and (probably the most important) downward seepage. The zoobenthos feeds on the organic sediment and can adjust its P/C ratio by means of a more efficient P assimilation or a reduced excretion. The sediment submodel resembles those of JØRGENSEN (1980) and KAMP-NIELSEN (1975).

Resuspension is, at average wind velocity, estimated as 5% of the sediment surface of the lake per day over a depth of a few centimeters (GONS, 1987). However, up to 90% of the resuspendable material (the 'epipelon') consists of coarse particles of peaty origin that settle again within a few hours and which are not modelled. Resuspension of 'true' detritus would then be about 1.25 $gC.m^2.d^{-1}$ or 0.01 $gP.m^{-2}.d^{-1}$. This amount is of course greatly affected by wind, ice cover and animal activity, but is described in the present model as a constant fraction of the upper sediment. Resuspension causes also an important horizontal transport of particles within the lake, but spatial inhomogeneities are not taken into account. The lake is assumed to be completely mixed which is a valid assumption regarding the very small variations between the two sampling stations in Lake Loosdrecht.

IMPLEMENTATION AND CALIBRATION

Parameter values (listed in the Appendix) have been derived from experimental data provided by other WQL working groups, from data in the literature and from calibration. Experimental data from the Loosdrecht Lakes are available mainly on the algal growth, the zooplankton filtration rate and the phosphorus mobilisation. Concerning fish, estimates have been made about stocks, mortality rate and fisheries activity. Very little information is available on selective grazing, mortality processes, predation rate, settling rates and mineralisation. For calibration we have made use of so-called 'minimodels' of parts of the system, *e.g.* the sediment subsystem, and of steady state analyses with summer averages. We calibrated on the average values of 1985-'87, without performing a (time-consuming) formal parameter estimation. This will be done in the near future when better tools are available.

Field data for calibration were collected by the Municipal Water Works of Amsterdam and (from 1983 on) by the Limnological Institute at Nieuwersluis. Unfortunately, phytoplankton and detritus can not be measured seperately. The sum of them was measured as seston < 150 µm of which, among others, dry weight and C, P and chlorophyll-*a* content were measured. Zooplankton was measured as the seston > 150 µm. Other measurements used were SRP, total P, sediment P and transparency, as well as the above mentioned process measurements.

Model calculations were performed by means of the simulation program FAME, developed at our institute under the Turbo Pascal programming language. A 5th order Runge-Kutta integration scheme was used with a variable step size. This program is apt to use for all kinds of dynamical models. For information about the program we refer to WORTELBOER and ALDENBERG (1989). Prior to a simulation, the model was allowed to equilibrate for a simulated period of two years. Simulation took about 15-45 minutes per simulated year, depending on the type of (AT) computer.

Input values for the model are measured water temperatures, daily radiation (data from KNMI, read in as two-week moving averages), water inflow and total phosphorus input. The latter two were read from the water and P balance models made by the Free University of Amsterdam (ENGELEN *et al.*, 1988; BUIJSE, 1989). These balances were made on a monthly base for the Loosdrecht Lakes system as a whole as well as for each lake separately from 1982 on. We assumed a constant factor (10%) of the phosphorus entering the lake in a soluble form, the remainder in organic form. This percentage reflects the average value in the inflowing water.

RESULTS

Fig. 4 depicts the external P loading of the largest lake in the system, Lake Loosdrecht, with a

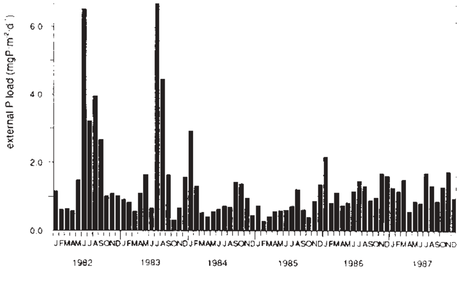

Fig. 4. Lake Loosdrecht, external phosphorus loading, 1982-1987. (data: Institute of Earth Sciences, Free University of Amsterdam.)

water area of 989.1 ha, a depth of 1.91 m and an average water residence time of 290 days (data from BUIJSE (1989)). Before 1984, in summer high loadings were observed as caused by inlet of heavily polluted supply water from the River Vecht. After restoration measures have been taken, these peak loadings have disappeared, but during the rest of the year loadings remained the same or even increased. These loadings originate for a great deal from the surrounding polders.

Simulations of the chlorophyll-*a* concentration, transparancy and the main carbon and phosphorus fractions in Lake Loosdrecht for the years 1982 to 1987, are depicted in Figs. 5-11, together with the data (sampling station 9). For chlorophyll-*a* (fig. 5B), both data and simulations display a seasonal variation with summer maxima around 200 $\mu g.l^{-1}$, which decrease a little over the years. The blue-greens are the dominant group of algae during most of the year (Fig. 6), but in spring, other groups succeed also in building up a significant biomass. The larger part of the seston $<$ 150 μm (about 60% in summer, up to 90% in winter) consists of detritus. This result is consistent with estimates by GONS (1987) of an average detrital fraction of two-thirds. The seasonal variation is somewhat underestimated. Also the summer maxima in later years are below the measured values, but one must keep in mind that the dynamics of wind-dependent resuspension has not been modelled. Moreover there are indications that resuspension has increased in the later years and that some data might be biased by storm events. The zooplankton, generally having its maximum in late spring, decreased a little following the load reduction (Fig. 7A). The exact seasonal pattern is not reproduced by the model. For that purpose, the model formulation is apparently too general, while the zooplankton, due to its position as 'middle' trophic level, is quite sensitive to parameter changes. The simulated fish stock (Fig. 7B) also decreases a little until 1.5-1.8 mgC.l^{-1}, being a little higher than the value recently established in the field of 300 kg fish.ha^{-1}, corresponding to about 1.2 mgC.l^{-1}.

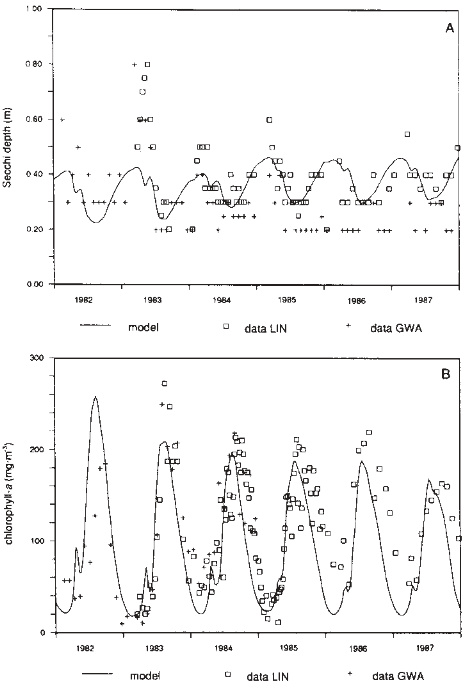

Fig. 5. Lake Loosdrecht, simulations compared with measurement, 1982-1987.
A, Secchi depth; B, Chlorophyll-*a* .

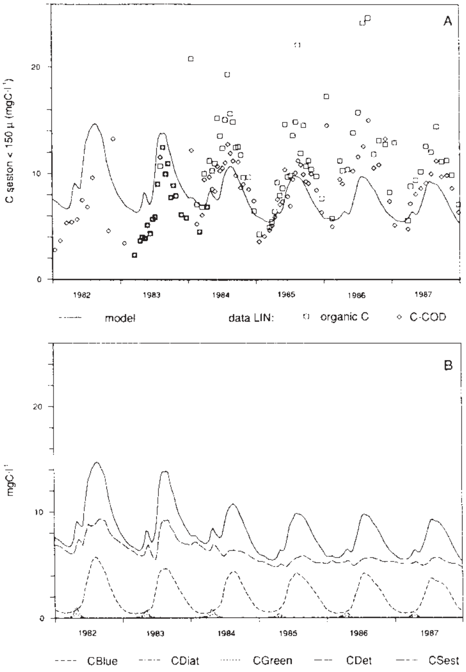

Fig. 6. Lake Loosdrecht, seston $<$ 150 μm, carbon fractions; 1982-1987.
A, CSest, simulations compared with measurements;
B, simulations of CSest and its constituents: CBlue, CDiat, CGreen and CDet.

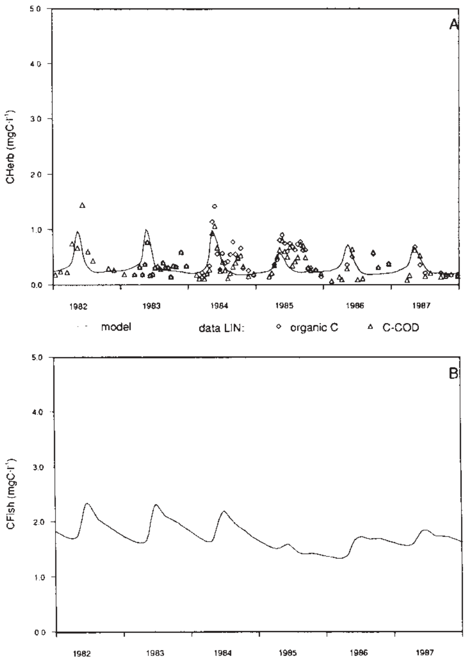

Fig. 7. Lake Loosdrecht, higher trophic levels, carbon; 1982-1987.
A, CHerb, simulations compared with measurements;
B, CFish, model simulation.

The simulated phosphorus present in phytoplankton and detritus, as well as total P, give a stronger response to the decreased phosphorus input than the corresponding carbon fractions (Fig. 8, B-D). Also the total P measurements show a decreasing tendency, although there is a lot of unexplained variations in the data. The simulated P/C ratio of the seston decreases gradually, a tendency also observed in the lake (Fig. 10, B-C). The P/C ratio of the zooplankton does not change, due to regulation mechanisms of the animals (Fig. 10A). The measurements show quite much variation, though, indicating that these mechanisms are not as perfect as assumed in the model. Also the P/C ratio of fish remains constant at 5.7% (data not shown). The phosphorus pool present in fish, being about 80-100 $\mu gP.l^{-1}$ (Fig. 9B), approximately equals the amount in all other compartments together, as is found in most hypertrophic lakes (VAN LIERE *et al.*, 1989, 1990). The SRP values (Fig. 8A) are very low during most of the year, like in the field, because of the high phosphate affinity of the algae. The model implicates that in winter, when algal growth is low, the cells can

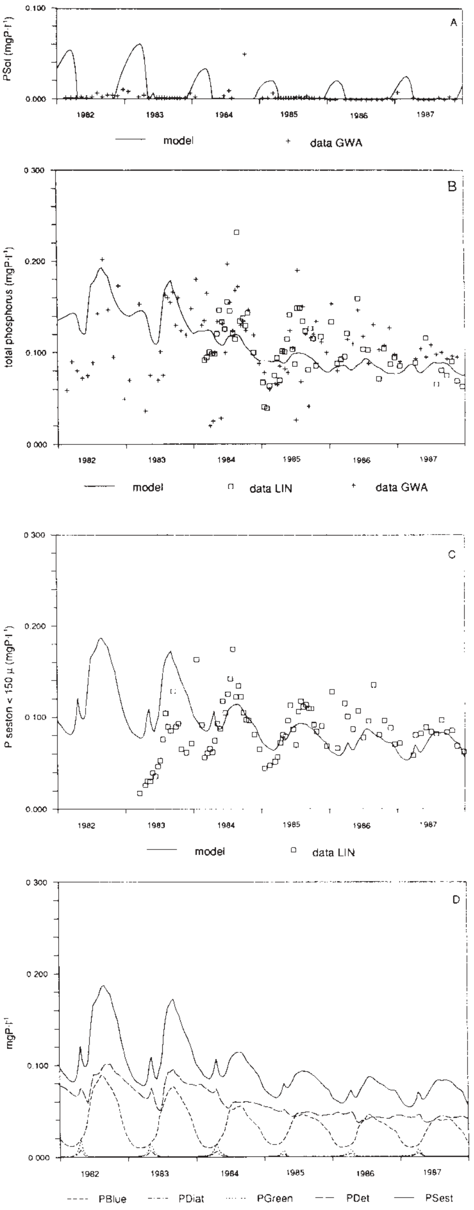

Fig. 8. Lake Loosdrecht, phosphorus fractions; 1982-1987.
A, SRP; B, PTot; C, PSest (all: simulations and measurements);
D, simulations of PSest and its constituents: PBlue, PDiat, PGreen and PDet.

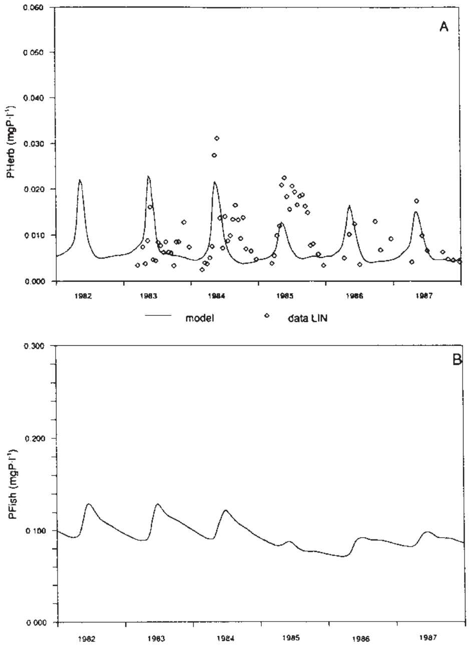

Fig. 9. Lake Loosdrecht, higher trophic levels, phosphorus; 1982-1987.
A, PHerb, simulations compared with measurements;
B, PFish, model simulation.

saturate themselves with phosphorus (*cf.* Fig. 10C). They can do this, however, only up to the maximum cell quota, and the surplus SRP is found as a winter peak in the simulations.

Concerning the upper sediment layer, the simulated phosphorus concentrations show a delayed response to the load reduction (Fig. 11, A-B.) The seasonal variation in the pore water concentration is considerable, because of the strong temperature dependency of the mineralisation. The zoobenthos (not shown) increases following the decrease in fish biomass and approximates (from 1986 on) the average measured density of 1 $gC.m^{-2}$ or 20 mg $P.m^{-2}$. A particularly interesting process with respect to the sediment, the phosphorus mobilisation (or internal loading), is shown in Fig. 11C. The mobilisation is within the range of values observed in column experiments (BOERS and VAN HESE, 1988; ACHTERBERG, 1988) and decreases with some time lag in response to the decreased external loading.

The characteristic response time of the model system to a change in loading seems to be about 2 years. Thus no further reactions of the system on the restoration measures are to be expected, unless additional measures will be taken. Preliminary scenario calculations with the model showed that a further reduction of P loading with 50 percent would indeed, after a lag time of 2-3 years, lead to a permanent improvement of the water quality. Total P concentration would be about half the present value, seston

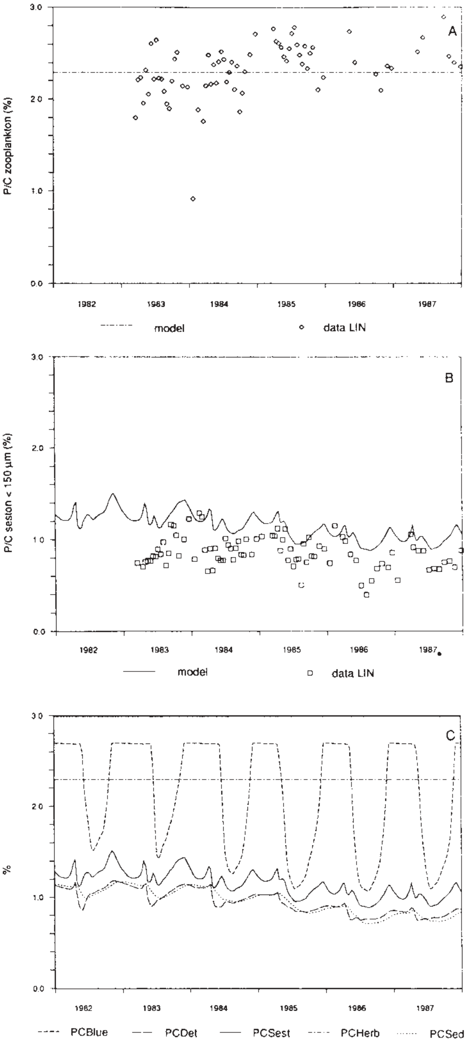

Fig.10. Lake Loosdrecht, P/C ratios, 1982-1987.
A, P/C ratio of zooplankton; B, P/C ratio of seston < 150 µm (both: simulations and measurements); C, P/C ratios of blue-greens, detritus, seston < 150 µm, zooplankton and upper sediment (model simulations).

<150 µm and chlorophyll-*a* about two-thirds the present values and, consequently, transparency would increase with 50%. Another 50% reduction would give a further improvement (see Fig. 13). Measures with a unique character, like removing 80% of the fish at once without changing external P input, would have only a temporary effect. However, the model is not yet fexible enough to draw any conclusions at this point, because the possibility of structural changes in the ecosystem following such measures (return of submerged vegetation, for example) is not included in the model.

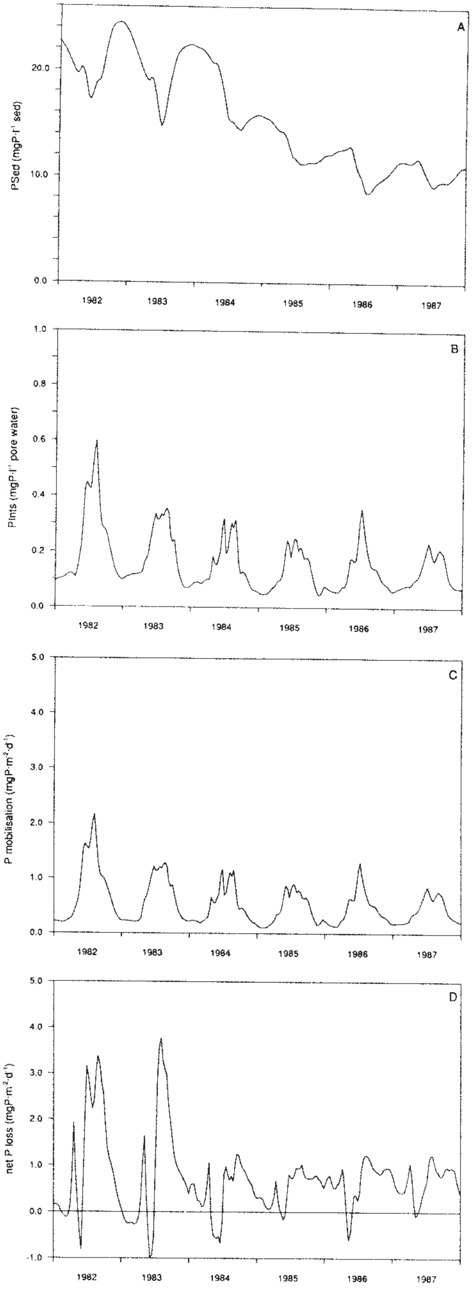

Fig.11. Lake Loosdrecht, upper sediment, simulations of phosphorus fluxes and concentrations, 1982-1987.
A, PSed; B, Plnts; C, Pmobilisation; D, Net P loss to the sediment.

DISCUSSION

The results obtained by modelling can give some insight in the phosphorus fluxes within the system and in their response to a changing external P loading. At the same time, they can be related to more empirically based indicators of the system's behaviour.

An important aspect is the net retention of phosphorus in the lake sediments, which is calculated in the model by means of the equation:

Net P loss = sedimentation − resuspension − mobilisation + fish bone sedimentation − fish feeding

$[mgP.m^{-2}.d^{-1}]$

Fig. 11D shows that the sediment continues to function almost always as a net sink of phophorus since sedimentation is higher than mobilisation and

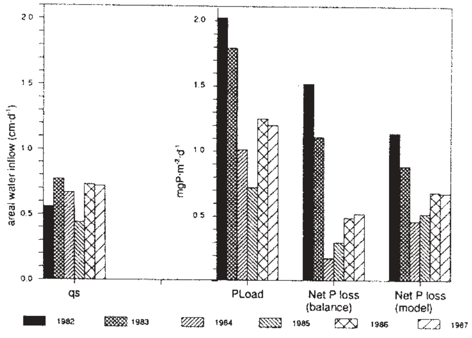

Fig.12. Lake Loosdrecht, net phosphorus loss to the sediment, year averages 1982-1987; simulations compared with balance derived data.
(qs = areal water inflow ($cm.d^{-1}$); PLoad = external P loading ($mgP.m^{-2}.d^{-1}$).

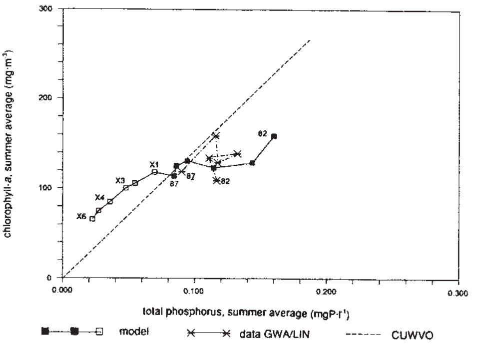

Fig.13. Lake Loosdrecht, relation between summer averaged chlorophyll-*a* and total phosphorus. Simulations and measurements of the years 1982-1987, and simulations at an additional reduction in P loading to 0.6 mgP.m^{-2}.d^{-1} in the years x1 - x3 and 0.3 mgP.m^{-2}.d^{-1} in the years x4 - x6.

resuspension together. The net effect of fish processes diminishes the net P loss a little, so one could say that fish is responsable for a small extra P flux from the sediment to the water. The year-averaged value of the net P loss can be compared with the value derived from the total phosphorus balance of the lake:

Net P loss = external P loading – P outflow [mgP.m^{-2}.d^{-1}]

Both the balance-derived and the model-derived averages for the years 1982-1987 are given in Fig. 12. It can be seen that the amount of phosphorus retained decreases with decreasing external loading and that the dynamical model and the balance model show the same trend, although the values are not identical. The fraction retained of the external loading, the retention coefficient *R*, averages 0.58 (balance-derived) or 0.54 (model-derived) over the six years studied. These values might be expected from the lake depth and water retention time (LIJKLEMA *et al.*, 1988; CUWVO, 1987). A fairly rapid adaptation of internal loading to a changing external loading was also observed in a number of recovering European lakes studied by IMSA (SAS, 1989).

In the range considered, the sensitivity for changes in phosphorus input is quite high for the sediment, algal and detrital P, and lower for the algal and detrital C and chlorophyll-*a*. This difference in sensitivity is reflected in the commonly used empirical relation between summer averaged chlorophyll-*a* and total phosphorus (Fig. 13). The lakes have not escaped from the cluster of data points around 100 µg.l^{-1} total P and 125 µg.l^{-1} chlorophyll-*a*. The straight line in the figure is the empirical upper limit for lakes where cyanobacteria are dominant, as established by the CUWVO from a database of Dutch lakes (LIJKLEMA *et al.*, 1988; CUWVO, 1987).

The above behaviour is related to the observed decrease of the P/C ratio of both the phytoplankton and the total seston <150 µm. The simulated summer averages decrease from 1.3% to less than 1.0% for total seston and from 2.1% to 1.5% for the blue-greens, following the load reduction. At the same time the maximum initial phosphate uptake rate is rising from about 0.25 to 0.5 mgP.mgC^{-1}.d^{-1}, which is also observed in experimental tests (BURGER-WIERSMA and BAARD, 1987). Both observations indicate that phosphorus limitation of the phytoplankton is becoming more severe (HEALEY, 1978; RIEGMAN, 1985). Apparently the phytoplankton can cope more and more efficiently with phosphorus or, in other words, it can maintain a high biomass also with less available phosphorus. This efficient growth applies especially to the cyanobacteria. The simulated P/C ratios of the other phytoplankton groups are always lower in summer, because of their lower phosphate affinity. Parallel with the decreasing P/C ratio of the seston the egestion of phosphorus from unused food by the zooplankton is decreasing, because more of the consumed phosphorus is retained by the animals when the food becomes phosphorus poorer.

The modelled phosphorus flow through the system, averaged over the summer months (April-September) of 1987, is depicted in Fig. 14. The direct phosphorus uptake by the phytoplankton is calculated as 4.3 mgP.m^{-2}.d^{-1}. External loading contributes still significantly to this amount (about 25%, organic and inorganic P loading together), while the contribution of mobilisation from the sediment is about 15%. About 30% becomes available by recirculation via the zooplankton (egestion, excretion, mortality) and some 10% via fish. The remaining 20% is recirculated directly by mortality and subsequent mineralisation of algal cells or by excretion of phosphorus. The SRP shows a very fast turnover. The zooplankton is the most dynamical biotic compartment in the model with a net turnover rate (P/B ratio) of more than 8% per day, while the fish compartment, where the turnover rate is only 0.3% per day, is the most stable. The phytoplankton (5.7% per day) and zoobenthos (3% per day) are in-between. Some of the phosphorus flows in the lakes, as derived from experimental and field research were reported by VAN LIERE *et al.*, (1989, 1990). The values they give for 'primary production' (8 µgP.l^{-1}.d^{-1}) and for grazing are considerably higher than those given in Fig. 14, but the relative importance of the various 'phosphorus

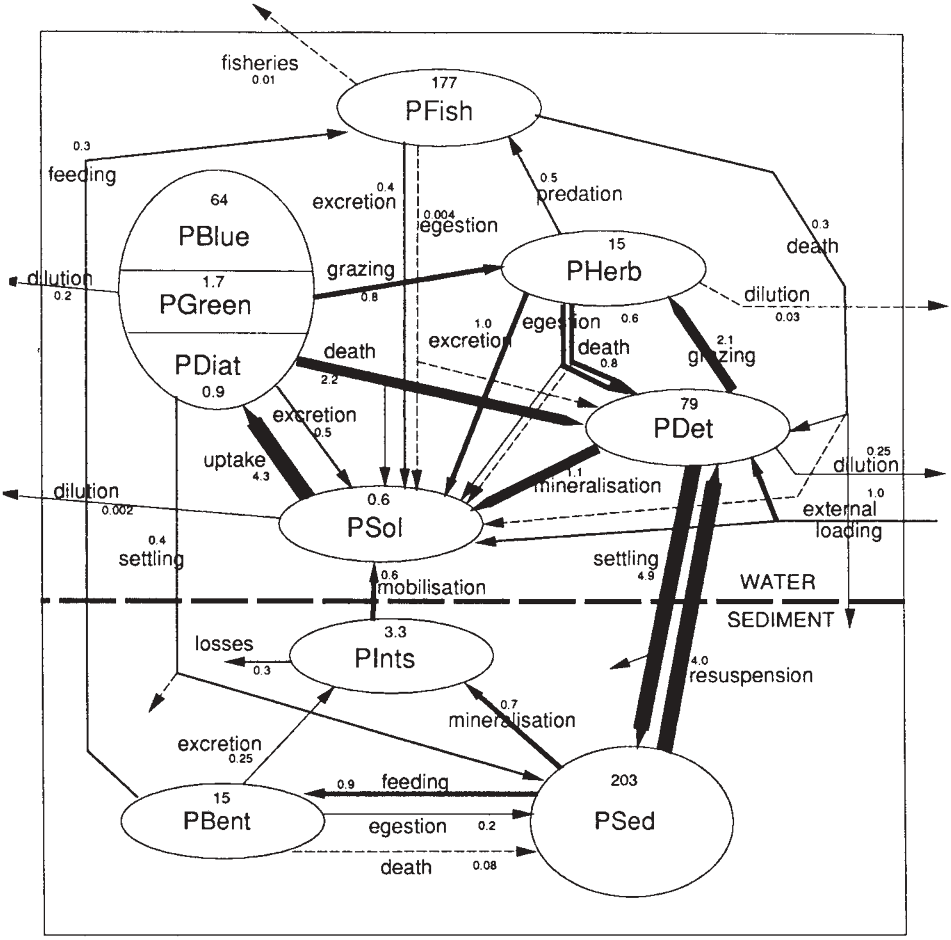

Fig.14. Simulated phosphorus flow diagram, averaged over the summer months (April-September) of 1987. Fluxes are given in mgP.m^{-2}.d^{-1}, (bio)masses in mgP.m^{-2}.

▬▬▬	> 2.5	mgP·m^{-2}·d^{-1}
━━━	1.0 - 2.5	mgP·m^{-2}·d^{-1}
───	0.5 - 1.0	mgP·m^{-2}·d^{-1}
───	0.25 - 0.5	mgP·m^{-2}·d^{-1}
───	0.1 - 0.25	mgP·m^{-2}·d^{-1}
- - - -	< 0.1	mgP·m^{-2}·d^{-1}

sources' is the same. The question is to what extent their figures can be compared with ours, because of differences in system description (for instance the compelled pooling of phytoplankton and detritus). Nevertheless the model and the field data stress the importance of the internal nutrient cycling. A relatively great part of the phosphorus remains in the lower trophic level, while the higher trophic levels play only a modest role in the phosphorus cycling.

In short, it can be concluded that both the internal loading and the dynamics of the P/C ratios can contribute to the observed resiliency of the ecosystem in its response to a decrease of the external P loading. The internal phosphorus recycling is important for the maintenance of the high seston mass. However, the system seems to adapt itself within a fairly short time (about 2 years) to the changed loading conditions.

A lot of problems, however, are not yet solved and many reactions of the system cannot be explained by the present model. For instance, the low chlorophyll-*a* concentration in Lake Loosdrecht in 1982, when loading was high, is difficult to explain. Possibly, the chlorophyll-*a* content of the algae might have been regulated by other factors. The species composition was not significantly different from the one in later years (BOESEWINKEL-DE BRUYN *et al.*, 1988). Seasonal dynamics of the detritus mass is somewhat underestimated by the model. In fact, total seston <150 μm follows more closely the changes in chlorophyll-*a*. Direct recycling and mineralisation within the water column might be more important than assumed. Also (seasonal) dynamics in resuspension could markedly influence seston dynamics, but one would expect this effect to have an overall moderating influence on the variation. In general, resuspension is more important in winter (except for ice periods) than in summer. These aspects will be further explored. Concerning zooplankton, adequate predictions are not possible without more information on selective grazing as well as on fish predation. This is a major source of uncertainty in the model. The zooplankton is very sensitive to food quality, i.e., the amount of well-edible algae, which depends on the phosphorus availability.

Another uncertainty lies in the long-term behaviour of the phosphorus retained in the deeper sediment. If this fraction would be released later this would cause an extra resiliency against restoration. However, recent analyses revealed that only 10% of the estimated total phosphorus loading of the past 50 years is found back in the upper 10 cm of the sediment. The remainder could have been washed out by downward seepage (KEIZER and BUYSMAN, 1990). Finally, direct adsorption of phosphorus to detrital particles and subsequent slow release could be an extra resiliating factor by creating an extra phosphorus pool in the system (RIJKEBOER *et al.*, 1988). Also these aspects deserve attention during further development of the model.

Despite shortcomings the model based on a closed phosphorus cycle with dynamical P/C ratios has shown its value. It can explain how a system can react in different ways to a change in phosphorus input in terms of carbon (or biomass) or in terms of phosphorus. It also gives some insight in turnover rates and can be related to much simpler models and empirical relations. However, for wider application it needs a more thorough validation against data of other lakes with a wider range of loadings and hydrological characteristics. This validation, together with uncertainty analysis and adaptations in some of the submodels, will be undertaken and described in a future paper.

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APPENDIX: MODEL EQUATIONS AND PARAMETERS

Differential equations

$$\frac{d[CPhyt(i)]}{dt} = \left\{\mu_i - k_{resp(i)}(T) - k_{mort(i)}(T) - \frac{velo_i}{H} - \alpha_i \cdot Filt \cdot CHerb - Dil\right\} \cdot CPhyt(i) + $$

$$+ \frac{f_{phyt(i)}(in) \cdot PLoad}{Q_{phyt}(in) \cdot H} \qquad \text{Phytoplankton species } i \ [\mathrm{mgC} \cdot \mathrm{l}^{-1} \cdot \mathrm{d}^{-1}]$$

$$\frac{d[PPhyt(i)]}{dt} = \frac{f_{phyt(i)}(in) \cdot PLoad}{H} + v_i \cdot CPhyt(i) + \{-k_{excr(i)}(T) - k_{mort(i)}(T) - \frac{velo_i}{H} + $$

$$- \alpha_i \cdot Filt \cdot CHerb - Dil\} \cdot PPhyt(i) \qquad \text{Phytoplankton species } i \ [\mathrm{mgP} \cdot \mathrm{l}^{-1} \cdot \mathrm{d}^{-1}]$$

$$\frac{d[CHerb]}{dt} = \left\{CEff_H \cdot \sum_j [\alpha_j \cdot CFood(j)] \cdot Filt - k'_{resp(H)}(T) - k_{mort(H)}(T) - Dil\right\} \cdot CHerb + $$

$$- Pred_{HF} \cdot CFish + \frac{f_{herb}(in) \cdot PLoad}{PCHerb_{ref} \cdot H} \qquad \text{Zooplankton } [\mathrm{mgC} \cdot \mathrm{l}^{-1} \cdot \mathrm{d}^{-1}]$$

$$\frac{d[PHerb]}{dt} = PEff_H \cdot \sum_j [\alpha_j \cdot PFood(j)] \cdot Filt \cdot CHerb + \{-k_{excr(H)}(T) - k_{mort(H)}(T) - Dil\}$$

$$\cdot PHerb - PCHerb \cdot Pred_{HF} \cdot CFish + \frac{f_{herb}(in) \cdot PLoad}{H} \qquad \text{Zooplankton } [\mathrm{mgP} \cdot \mathrm{l}^{-1} \cdot \mathrm{d}^{-1}]$$

$$\frac{d[CFish]}{dt} = \{CEff_{HF} \cdot Pred_{HF} + CEff_{BeF} \cdot Feed_{BeF} - k'_{resp(F)}(T) - k_{mort(F)} - k_{harv(F)}\} \cdot CFish$$

Fish $[\mathrm{mgC} \cdot \mathrm{l}^{-1} \cdot \mathrm{d}^{-1}]$

$$\frac{d[PFish]}{dt} = \{PEff_{HF} \cdot PCHerb \cdot Pred_{HF} + PEff_{BeF} \cdot PCBent \cdot Feed_{BeF}\} \cdot CFish + $$

$$+ \{-k_{excr(F)}(T) - k_{mort(F)} - k_{harv(F)}\} \cdot PFish \qquad \text{Fish } [\mathrm{mgP} \cdot \mathrm{l}^{-1} \cdot \mathrm{d}^{-1}]$$

$$\frac{d[CDet]}{dt} = \frac{f_{det}(in) \cdot PLoad}{PCDet(in) \cdot H} + \sum_i [k_{mort(i)}(T) \cdot CPhyt(i)] + k_{mort(H)}(T) \cdot CHerb + $$

$$+ (1 - CEff_H) \cdot \sum_j [\alpha_j \cdot CFood(j)] \cdot Filt \cdot CHerb - \alpha_D \cdot CDet \cdot CHerb + $$

$$+ \{(1 - CEff_{HF}) \cdot Pred + (1 - CEff_{BeF}) \cdot Feed\} \cdot CFish + $$

$$+ (1 - f_{bones(C)}) \cdot k_{mort(F)} \cdot CFish + \left\{-k_{dec(D)}(T) - \frac{velo_D}{H} - Dil\right\} \cdot CDet + $$

$$+ f_{fg} \cdot k_{resu(D)} \cdot \frac{z_s}{H} \cdot CSed \qquad \text{Detritus } [\mathrm{mgC} \cdot \mathrm{l}^{-1} \cdot \mathrm{d}^{-1}]$$

$$
\begin{aligned}
\frac{d[PDet]}{dt} = {} & \frac{f_{det}(in) \cdot PLoad}{H} + \sum_i [(1-\zeta_i) \cdot k_{mort(i)}(T) \cdot Phyt(i)] + (1-\zeta_H) \cdot k_{mort(H)}(T) \cdot PHerb + \\
& + (1-\rho_H) \cdot (1-PEff_H) \cdot \sum_j [\alpha_j \cdot PFood(j)] \cdot Filt \cdot CHerb - \alpha_D \cdot PDet \cdot CHerb + \\
& + (1-\rho_F) \cdot \{(1-CEff_{HF}) \cdot PCHerb \cdot Pred + (1-CEff_{BeF}) \cdot PCBent \cdot Feed\} \cdot CFish + \\
& + (1-\zeta_F) \cdot (1-f_{bones(P)}) \cdot k_{mort(F)} \cdot PFish + \left\{ -k_{\min(D)}(T) - \frac{velo_D}{H} - Dil \right\} \cdot PDet + \\
& + f_{fg} \cdot k_{resu(D)} \cdot \frac{z_s}{H} \cdot PSed
\end{aligned}
$$

Detritus $[\mathrm{mgP} \cdot \mathrm{l}^{-1} \cdot \mathrm{d}^{-1}]$

$$
\begin{aligned}
\frac{d[PSol]}{dt} = {} & \frac{f_{sol}(in) \cdot PLoad}{H} - \sum_i [v_i \cdot CPhyt(i)] + \sum_i [k_{excr(i)}(T) \cdot PPhyt(i)] + \\
& + \sum_i [\zeta_i \cdot k_{mort(i)}(T) \cdot PPhyt(i)] + \{k_{excr(H)}(T) + \zeta_H \cdot k_{mort(H)}(T)\} \cdot PHerb + \\
& + \rho_H \cdot (1-PEff_H) \cdot \sum_j [\alpha_j \cdot PFood(j)] \cdot Filt \cdot CHerb + \\
& + \rho_F \cdot \{(1-PEff_{HF}) \cdot PCHerb \cdot Pred + (1-PEff_{BeF}) \cdot PCBent \cdot Feed\} \cdot CFish + \\
& + \{k_{excr(F)}(T) + \zeta_F \cdot (1-f_{bones(P)}) \cdot k_{mort(F)}\} \cdot PFish + k_{\min(D)}(T) \cdot PDet - Dil \cdot PSol + \\
& + \frac{\left\{ k_{diff(IS)} / \left(\frac{z_s}{2} \right) \right\} \cdot (PInts - PSol) \cdot Por}{H}
\end{aligned}
$$

PSol $[\mathrm{mgP} \cdot \mathrm{l}^{-1} \cdot \mathrm{d}^{-1}]$

$$
\begin{aligned}
\frac{d[CSed]}{dt} = {} & \frac{(1-f_r) \cdot \left(\sum_i [velo_i \cdot CPhyt(i)] + velo_D \cdot CDet \right)}{z_s} + \{-f_{fg} \cdot k_{resu(D)} - k_{dec(Se)}(T)\} \cdot CSed + \\
& + \frac{\{-CEff_{SeBe} \cdot k_{eat(SeBe)}(T) + k_{mort(Be)}(T) \cdot CBent\} \cdot CBent}{z_s}
\end{aligned}
$$

Upper sediment $[\mathrm{mgC} \cdot \mathrm{l}^{-1}\mathrm{sed.} \cdot \mathrm{d}^{-1}]$

$$
\begin{aligned}
\frac{d[PSed]}{dt} = {} & \frac{(1-f_r) \cdot \left(\sum_i [velo_i \cdot PPhyt(i)] + velo_D \cdot PDet \right)}{z_s} + \{-f_{fg} \cdot k_{resu(D)} - k_{\min(Se)}(T)\} \cdot PSed + \\
& + \frac{\{-PEff_{SeBe} \cdot k_{eat(SeBe)}(T) + k_{mort(Be)}(T) \cdot CBent\} \cdot PBent}{z_s}
\end{aligned}
$$

Upper sediment $[\mathrm{mgP} \cdot \mathrm{l}^{-1}\mathrm{sed.} \cdot \mathrm{d}^{-1}]$

$$
\frac{d[CBent]}{dt} = \{CEff_{SeBe} \cdot k_{eat(SeBe)}(T) - k'_{resp(Be)}(T) - k_{mort(Be)}(T) \cdot CBent\} \cdot CBent - Feed_{BeF} \cdot \frac{CFish}{H}
$$

Zoobenthos $[\mathrm{gC} \cdot \mathrm{m}^{-2} \cdot \mathrm{d}^{-1}]$

$$\frac{d[PBent]}{dt} = \{PEff_{SeBe} \cdot k_{eat(SeBe)}(T) - k_{excr(Be)}(T) - k_{mort(Be)}(T) \cdot CBent\} \cdot PBent +$$

$$-PCBent \cdot Feed_{BeF} \cdot \frac{CFish}{H}$$

Zoobenthos $[\mathrm{gP} \cdot \mathrm{m}^{-2} \cdot \mathrm{d}^{-1}]$

$$\frac{d[PInts]}{dt} = \frac{k_{\min(Se)}(T) \cdot CSed}{Por} + \frac{k_{excr(Be)}(T) \cdot PBent}{z_s \cdot Por} - \frac{\left\{k_{diff(IS)} / \left(\frac{z_s}{2}\right)\right\} \cdot (PInts - PSol)}{z_s} - k_{prec(I)} \cdot PInts$$

Interstitial SRP $[\mathrm{mgP} \cdot \mathrm{l}^{-1} \text{pore water} \cdot \mathrm{d}^{-1}]$

Rates and other equations
(a) phytoplankton

$$v_i = \frac{PSol}{\frac{1}{A_{0(i)}} + \frac{PSol}{v_{\max(i)}(T) \cdot \{(Q_{\max(i)} - Q_i)/(Q_{\max(i)} - Q_{\min(i)})\}}}$$

algal P uptake $[\mathrm{mgP} \cdot \mathrm{mgC}^{-1} \cdot \mathrm{d}^{-1}]$

$$Q_i = \frac{PPhyt(i)}{CPhyt(i)}$$

P/C ratio of algal species *i* $[\mathrm{mgP} \cdot \mathrm{mgC}^{-1}]$

$$\mu = \mu_{\max(i)}(T) \cdot f(I_0) \cdot \left(\frac{Q_{\max(i)}}{Q_{\max(i)} - Q_{\min(i)}}\right) \cdot \left(1 - \frac{Q_{\min(i)}}{Q_i}\right)$$

algal growth rate $[\mathrm{d}^{-1}]$

$$\varepsilon = \varepsilon_{water} + \sum_i [k_{\varepsilon(i)} \cdot CPhyt(i)] + k_{\varepsilon(D)} \cdot CDet$$

extinction coeff. $[\mathrm{m}^{-1}]$

$$f(I_0) = \frac{f_l}{\varepsilon \cdot H} \ln\left(\frac{1 + I_0/k_I}{1 + I_0/k_I \cdot \exp(-\varepsilon \cdot H)}\right)$$

light function diatoms and greens [-]

$$f(I_0) = \frac{e \cdot f_l}{\varepsilon \cdot H} \cdot \left(e^{-I_0/I_{opt} \cdot \exp(-\varepsilon \cdot H)} - e^{-I_0/I_{opt}}\right)$$

light function blue-greens [-]

$$f_l = 0.5 - 0.2 \cdot \cos\left(2 \cdot \pi \cdot \frac{Time + 11}{365}\right)$$

daylight fraction [-]

$$I_0 = (1 - f_{refl}) \cdot I_{out}$$

light intensity at depth 0 $[\mathrm{W} \cdot \mathrm{m}^{-2}]$

$$Chla = 1000 \cdot \sum_i [ChlC_i \cdot CPhyt(i)]$$

chlorophyll-*a* $[\mathrm{mg} \cdot \mathrm{m}^{-3}]$

$$k_{excr(i)} = \frac{Q_{\max(i)} + k_{hexcr(i)}}{Q_{\max(i)}} \cdot \frac{Q_i}{k_{hexcr(i)} + Q_i} \cdot k_{resp(i)}(T)$$

algal excretion rate $[\mathrm{d}^{-1}]$

(b) zooplankton

$$Filt = \mathrm{MIN}\left[Filt_{con}(T), Filt_{con}(T) \cdot \frac{k_{filt} + CHold}{k_{filt} + CSest}\right]$$

filtration rate $[\mathrm{l} \cdot \mathrm{mgC}^{-1} \cdot \mathrm{d}^{-1}]$

$Dil = (q_s - q_{evap})/H$	dilution rate [d^{-1}]
$f_{det}(in) = 1 - f_{sol}(in) - \sum_i [f_{phyt(i)}(in)] - f_{herb}(in)$	detrital fraction of ext. P loading [-]
$CSest = CBlue + CGreen + CDiat + CDet$	C seston < 150 μ [$mgC \cdot l^{-1}$]
$PSest = PBlue + PGreen + PDiat + PDet$	P seston < 150 μ [$mgP \cdot l^{-1}$]
$PTot = PSest + PHerb + PSol$	total phosphorus [$mgP \cdot l^{-1}$]
$Secchi = PACoef/\varepsilon$	transparancy [m]

Symbols and parameters

$A_{0(i)}$	initial affinity of algal species *i* for external phosphorus	*B*: 20 [$l \cdot mgC^{-1} \cdot d^{-1}$] *Di/G*: 6 [$l \cdot mgC^{-1} \cdot d^{-1}$]
α_j	selection factor of food type *j* for zooplankton grazing	*B*: 0.1 [-] *Di/G*: 1.0 [-] *D*: 0.25 [-]
-B	suffix: denotes Bluegreen algae	
-Be	suffix: denotes zoobenthos	
$CEff_{BeF}$	C ass. eff. of fish for zoobenthal food	0.5 [-]
$CEff_H$	C assimilation efficiency of zooplankton	0.3 [-]
$CEff_{HF}$	C ass. eff. of fish for zooplankton food	0.4 [-]
$CEff_{SeBe}$	C assimilation efficiency of zoobenthos	0.25 [-]
$CFood(j)$	food type *j* for zooplankton	[$mgC \cdot l^{-1}$]
$ChlC_i$	chlorophyll-*a* content of algal species *i* [mg chlorophyll-*a*·mgC^{-1}]	*B*: 0.045 *Di*: 0.025 *G*: 0.050
$CHold$	seston concentration below which filtration rate is maximal (*i.e.* $Filt_{con}$)	1.0 [$mgC \cdot l^{-1}$]
-D	suffix: denotes detritus	
-Di	suffix: denotes diatoms	
ε_{water}	background extinction of the water	1.2 [m^{-1}]
-F	suffix: denotes fish	
$f_{bones(C)}$	fraction of *CFish* fixed in scales and bones	0.35 [-]
$f_{bones(P)}$	fraction of *PFish* fixed in scales and bones	0.5 [-]
f_{fg}	fine-granuled fraction of upper sediment	0.4 [-]
$f_{herb}(in)$	average fraction of external P loading in zooplankton	$5 \cdot 10^{-4}$ [-]
$f_{phyt(i)}(in)$	average fraction of external P loading in algal species *i*	*all*: 0.01 [-]
f_r	fraction of settled particles which is buried in the deeper sediment	0.05 [-]
f_{refl}	fraction of light reflected at the water surface	0.2 [-]
$f_{sol}(in)$	average SRP fraction of external P loading	0.10 [-]
$Filt_{con}$	maximum specific filtration rate at 20 °C (reached below *CHold*)	2.9 [$l \cdot mgC^{-1} \cdot d^{-1}$]
-G	suffix: denotes green algae	
H	water depth	1.91 [m]
-H	suffix: denotes zooplankton (herbivores)	

$-I$	suffix: denotes interstitial water	
(i)	index: denotes algal species *i* (*i.e.*: greens, diatoms or blue-greens)	
I_{opt}	optimum light intensity	*B*: 100 [W·m^{-2}]
I_{out}	average daily light intensity	[W·m^{-2}]
(j)	index: denotes food type *j* for zooplankton (*i.e.*: greens, diatoms, blue-greens or detritus)	
$k_{dec(D)}$	decomposition const. of detritus at 20 °C	0.02 [d^{-1}]
$k_{dec(Se)}$	decomp. const. of upper sediment at 20 °C	0.005 [d^{-1}]
$k_{diff(IS)}$	diffusion constant of SRP from interstitial to surface water	$4{\cdot}10^{-5}$ [m^2·d^{-1}]
$k_{eat(low)(Be)}$	feeding constant per unit sediment of zoobenthos at 20 °C	$5{\cdot}10^{-4}$ [l sed.·mgC^{-1}·d^{-1}]
$k_{eat(max)(Be)}$	(max.) feeding coeff. of zoobenthos at 20 °C	0.21 [d^{-1}]
$k_{\varepsilon(D)}$	specific extinction of detritus	0.25 [m^2·mgC^{-1}]
$k_{\varepsilon(i)}$	specific extinction of algal species *i*	*B/G*: 0.35 [m^2·mgC^{-1}] *Di*: 0.25 [m^2·mgC^{-1}]
$k_{feed(BeF)}$	feeding coeff. of fish on zoobenthos at 20 °C	0.008 [m^2·gC^{-1}·d^{-1}]
k_{filt}	half-saturating food concentration for filtration	0.25 [mgC·l^{-1}]
$k_{harv(F)}$	daily harvested fraction of fish	Oct-Mar: $6{\cdot}10^{-4}$ [d^{-1}] May-Oct: $6{\cdot}10^{-5}$ [d^{-1}]
$k_{hexcr(i)}$	correction parameter for algal P excretion	*all*: 0.0027 [mgP·mgC^{-1}]
k_I	half-saturating light intensity	*Di/G*: 25 [W·m^{-2}]
$k_{min(D)}$	mineralisation const. of detritus at 20 °C	0.02 [d^{-1}]
$k_{min(Se)}$	mineral. const. of upper sediment at 20 °C	0.005 [d^{-1}]
$k_{mort(Be)}$	mortality parameter of zoobenthos at 20 °C	0.01 [m^2·gC^{-1}·d^{-1}]
$k_{mort(F)(max)}$	maximum mortality rate of fish (reached mid June)	$3{\cdot}10^{-3}$ [d^{-1}]
$k_{mort(F)(min)}$	minimum mortality rate of fish (Aug - April)	$3{\cdot}10^{-4}$ [d^{-1}]
$k_{mort(H)}$	mortality constant of zooplankton at 20 °C	0.08 [d^{-1}]
$k_{mort(i)}$	mortality constant of algal species *i* at 20 °C	*all*: 0.04 [d^{-1}]
$k_{prec(I)}$	loss constant of interstitial P	0.1 [d^{-1}]
$k_{pred(HF)}$	half-saturating *CHerb* for fish predation	1.5 [mgC·l^{-1}]
$k_{resp(Be)}$	respiration constant of zoobenthos at 20 °C	0.02 [d^{-1}]
$k_{resp(F)}$	respiration constant of fish at 20 °C	0.003 [d^{-1}]
$k_{resp(H)}$	respiration constant of zooplankton at 20 °C	0.10 [d^{-1}]
$k_{resp(i)}$	respiration constant of algal species *i* at 20 °C	*B*: 0.01 [d^{-1}] *Di/G*: 0.03 [d^{-1}]
$k_{resu(D)}$	resuspended fraction of upper sediment	0.05 [d^{-1}]
k_{temp}	temp. interval for a factor 2 change in rate const.	*Di*: 10 [°C]
(m)	index: denotes animal group *m* (*i.e.*: zooplankton, fish or zoobenthos)	
$\mu_{max(i)}$	maximum growth rate of algal species *i*	*B*: 0.5 [d^{-1}] *Di*: 1.5 [d^{-1}] *G*: 1.7 [d^{-1}]
(n)	index: denotes model compartment *n* (*i.e.*: greens, diatoms, blue-greens, zooplankton, fish, detritus, zoobenthos or upper sediment)	

$-I$	suffix: denotes interstitial water	
(i)	index: denotes algal species i (*i.e.*: greens, diatoms or blue-greens)	
I_{opt}	optimum light intensity	B: 100 [W·m^{-2}]
I_{out}	average daily light intensity	[W·m^{-2}]
(j)	index: denotes food type j for zooplankton (*i.e.*: greens, diatoms, blue-greens or detritus)	
$k_{dec(D)}$	decomposition const. of detritus at 20 °C	0.02 [d^{-1}]
$k_{dec(Se)}$	decomp. const. of upper sediment at 20 °C	0.005 [d^{-1}]
$k_{diff(IS)}$	diffusion constant of SRP from interstitial to surface water	$4\cdot10^{-5}$ [m^{2}·d^{-1}]
$k_{eat(low)(Be)}$	feeding constant per unit sediment of zoobenthos at 20 °C	$5\cdot10^{-4}$ [l sed.·mgC^{-1}·d^{-1}]
$k_{eat(max)(Be)}$	(max.) feeding coeff. of zoobenthos at 20 °C	0.21 [d^{-1}]
$k_{\varepsilon(D)}$	specific extinction of detritus	0.25 [m^{2}·mgC^{-1}]
$k_{\varepsilon(i)}$	specific extinction of algal species i	B/G: 0.35 [m^{2}·mgC^{-1}] Di: 0.25 [m^{2}·mgC^{-1}]
$k_{feed(BeF)}$	feeding coeff. of fish on zoobenthos at 20 °C	0.008 [m^{2}·gC^{-1}·d^{-1}]
k_{filt}	half-saturating food concentration for filtration	0.25 [mgC·l^{-1}]
$k_{harv(F)}$	daily harvested fraction of fish	Oct-Mar: $6\cdot10^{-4}$ [d^{-1}] May-Oct: $6\cdot10^{-5}$ [d^{-1}]
$k_{hexcr(i)}$	correction parameter for algal P excretion	*all*: 0.0027 [mgP·mgC^{-1}]
k_{I}	half-saturating light intensity	Di/G: 25 [W·m^{-2}]
$k_{min(D)}$	mineralisation const. of detritus at 20 °C	0.02 [d^{-1}]
$k_{min(Se)}$	mineral. const. of upper sediment at 20 °C	0.005 [d^{-1}]
$k_{mort(Be)}$	mortality parameter of zoobenthos at 20 °C	0.01 [m^{2}·gC^{-1}·d^{-1}]
$k_{mort(F)(max)}$	maximum mortality rate of fish (reached mid June)	$3\cdot10^{-3}$ [d^{-1}]
$k_{mort(F)(min)}$	minimum mortality rate of fish (Aug - April)	$3\cdot10^{-4}$ [d^{-1}]
$k_{mort(H)}$	mortality constant of zooplankton at 20 °C	0.08 [d^{-1}]
$k_{mort(i)}$	mortality constant of algal species i at 20 °C	*all*: 0.04 [d^{-1}]
$k_{prec(I)}$	loss constant of interstitial P	0.1 [d^{-1}]
$k_{pred(HF)}$	half-saturating *CHerb* for fish predation	1.5 [mgC·l^{-1}]
$k_{resp(Be)}$	respiration constant of zoobenthos at 20 °C	0.02 [d^{-1}]
$k_{resp(F)}$	respiration constant of fish at 20 °C	0.003 [d^{-1}]
$k_{resp(H)}$	respiration constant of zooplankton at 20 °C	0.10 [d^{-1}]
$k_{resp(i)}$	respiration constant of algal species i at 20 °C	B: 0.01 [d^{-1}] Di/G: 0.03 [d^{-1}]
$k_{resu(D)}$	resuspended fraction of upper sediment	0.05 [d^{-1}]
k_{temp}	temp. interval for a factor 2 change in rate const.	Di: 10 [°C]
(m)	index: denotes animal group m (*i.e.*: zooplankton, fish or zoobenthos)	
$\mu_{max(i)}$	maximum growth rate of algal species i	B: 0.5 [d^{-1}] Di: 1.5 [d^{-1}] G: 1.7 [d^{-1}]
(n)	index: denotes model compartment n (*i.e.*: greens, diatoms, blue-greens, zooplankton, fish, detritus, zoobenthos or upper sediment)	

PACoef	Poole-Atkins coefficient	1.2 [-]
PCAnim(m)	P/C ratio of animal group *m* (*i.e.*: zooplankton, fish or zoobenthos)	$[mgP \cdot mgC^{-1}]$
$PCBent_{ref}$	reference P/C ratio of zoobenthos	0.0225 $[mgP \cdot mgC^{-1}]$
PCDet(in)	average P/C ratio of detritus in inflow	0.01 $[mgP \cdot mgC^{-1}]$
$PCFish_{ref}$	reference P/C ratio of fish	0.057 $[mgP \cdot mgC^{-1}]$
$PCHerb_{ref}$	reference P/C ratio of zooplankton	0.023 $[mgP \cdot mgC^{-1}]$
PFood(j)	food type *j* for zooplankton	$[mgP \cdot l^{-1}]$
PLoad	external P loading per m^2 lake area	$[gP \cdot m^{-2} \cdot d^{-1}]$
Por	porosity of upper sediment	0.91 $[l\ water \cdot l^{-1}\ sed.]$
$PrMax_{HF}$	max. predation coeff. of fish on zoopl.	0.15 $[d^{-1}]$
q_{evap}	areal evaporation from lake surface	$[m \cdot d^{-1}]$
$Q_{(i)}$	phosphorus content of algal species *i*	$[mgP \cdot mgC^{-1}]$
$Q_{max(i)}$	maximum phosphorus content of algal species *i*	*all*: 0.027 $[mgP \cdot mgC^{-1}]$
$Q_{min(i)}$	minimum phosphorus content of algal species *i*	*all*: 0.0054 $[mgP \cdot mgC^{-1}]$
$Q_{phyt}(in)$	phosphorus content of algae in inflow	0.0125 $[mgP \cdot mgC^{-1}]$
q_s	areal hydraulic loading (= water flow into the lake per m^2 lake area)	$[m \cdot d^{-1}]$
ρ_F	soluble P fraction of by fish egested food	0.25 [-]
ρ_H	soluble P fraction of by zooplankton egested food	0.25 [-]
-Se	suffix: denotes upper sediment	
T	water temperature	[°C]
T_{opt}	optimum temperature	*Di*: 15 [°C]
T_{ref}	reference temperature	20 [°C]
Time	time after the start of the year (1. Jan.)	[d]
Θ_{Be}	temperature constant of zoobenthos	1.07 $[(e^{^{\circ}C})^{-1})]$
Θ_D	temperature constant of detrital mineralisation	1.12 $[(e^{^{\circ}C})^{-1})]$
Θ_F	temperature constant of fish	1.07 $[(e^{^{\circ}C})^{-1})]$
Θ_H	temperature constant of zooplankton	1.10 $[(e^{^{\circ}C})^{-1})]$
Θ_i	temperature constant of phytoplankton species *i*	*B*: 1.07 $[(e^{^{\circ}C})^{-1})]$ *G*: 1.05 $[(e^{^{\circ}C})^{-1})]$
Θ_{Se}	temp. constant of mineral. of upper sediment	1.12 $[(e^{^{\circ}C})^{-1})]$
$v_{max(i)}(T)$	max. phosphate uptake rate of algal species *i*	*B*: 1.0 $[mgP \cdot mgC^{-1} \cdot d^{-1}]$ *Di/G*: 0.5 $[mgP \cdot mgC^{-1} \cdot d^{-1}]$
$velo_D$	settling velocity of detritus	0.12 $[m \cdot d^{-1}]$
$velo_i$	net settling velocity of algal species *i*	*B*: 0.01 $[m \cdot d^{-1}]$ *Di/G*: 0.04 $[m \cdot d^{-1}]$
z_s	depth of upper sediment layer	0.02 [m]
ζ_F	soluble fraction of P in died fish (excl. scales and bones)	0.10 [-]
ζ_H	soluble fraction of P in died zooplankton	0.10 [-]
ζ_i	soluble fraction of P in died algae of species *i*	*all:* 0.10 [-]

Chapter 9

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Modelling the eutrophication of the shallow Loosdrecht Lakes

J. H. Janse and T. Aldenberg

Introduction

Restoration of the water quality of hypertrophic lakes by reduction of the external phosphorus loading often has not the desired result because of resiliating or retarding mechanisms in the ecosystem itself. This is also the case in the shallow (2 m) Loosdrecht Lakes (The Netherlands), a series of interconnected hypertrophic lakes with an undesirable bloom of filamentous bluegreen algae. A description of the lakes can be found in VAN LIERE et al. (1984). Since 1984 the external P loading has been reduced from about 3.0 to 1.0 $mgP \cdot m^{-2} \cdot day^{-1}$ by dephosphatising summer inlet water (ENGELEN et al. 1988, BUIJSE 1989). This has not led to a decrease of algal biomass, although some changes in the lake ecosystem are observed (GONS et al. 1986, VAN LIERE et al. 1989, 1990). In the present paper, the reactions of the lake ecosystem are analysed by means of mathematical modelling. The paper describes some aspects of the eutrophication model PC Loos (version 2.4), currently being developed within the framework of the WQL project (Water Quality research Loosdrecht lakes). One of the 'precursors' of this model is the 'first step' model by KOUWENHOVEN & ALDENBERG (1986). Aim of the modelling effort is to provide a tool for a better understanding of the lake ecosystem and to predict the effects of possible (additional) measures.

Model structure

The model is based on two main concepts. The first one concerns the *system definition* and *system boundaries:* the model should give an adequate description of the lake system (it should include the most important biotic and abiotic compartments and processes that determine the present state of the lake), without becoming too complex (thus reducing uncertainty; see e.g. AUER & CANALE 1986, JØRGENSEN 1980). The present model comprises the water phase and the upper layer (2 cm) of the sediment. In the water phase phytoplankton (divided into three groups, abbreviated Diat, Green and Blue), detritus (Det), zooplankton (Herb), planktivorous fish (Fish) and soluble reactive phosphorus (SRP) (PSol) are modelled, and in the sediment: Organic material (Sed), zoobenthos (Bent) – an important food source for fish – and SRP in the interstitial water (PInts). The sediment subsystem is modelled in a much simplified way (cf KAMP-NIELSEN 1975 and JØRGENSEN 1980) and is included mainly because of the need to describe dynamically the phosphorus fluxes across the sediment-water interface. The model is restricted to only one nutrient, phosphorus, and is zero-dimensional in space.

The second basic concept is *a closed phosphorus cycle* within the model system at any time. In this way, our model differs from many existing models (e.g. DI TORO et al. 1975, THOMANN 1977, DI TORO & MATYSTIK 1980, JØRGENSEN 1980). It is well-known that at higher levels in the food chain the phosphorus content of the organisms, related to biomass or carbon, generally increases. The P/C ratio of the phytoplankton and detritus can be highly variable and is quite low in the Loosdrecht Lakes (about 1 % or less), whereas this ratio is much higher (2.3 %) and more or less constant for the zooplankton and still higher (5.7 %) for fish. This means that these animals possess feedback mechanisms to maintain a high P/C ratio, also when their food is poor in phosphorus. These mechanisms can involve a higher assimilation efficiency for phosphorus than for carbon, a lowered excretion and/or a forced carbon respiration. In a model with different P/C ratios per compartment, at least one of them (primarily the ratio for detritus) should be dynamical in order to maintain a closed P cycle (ALDENBERG & PETERS 1990). In PCLoos, all organic compartments, both biotic and abiotic, are modelled in two units, carbon and phosphorus, thus bringing the number of state variables at 18. By including the upper sediment, the P cycle is also closed at the sediment side.

Figs. 1 and 2 depict the C and the P cycle, respectively. A number of processes in the P cycle, like mortality of organisms and settling of particles, are simply proportional to the corresponding C processes. Some processes, however (namely: Algal growth and P uptake, the assimilation of food by animals and respiration / P excretion) have been uncoupled and thus contribute to the dynamics of the P/C ratios; their relative rate depends on the actual P/C ratio of the species. Losses from the system are: Outflow, fisheries, settling of refractory material (including fish bones) and loss of pore water P to the deeper sediment. For a full documentation of the process formulations and parameter values see JANSE & ALDENBERG (1990 a, 1990 b). One detail should be mentioned: The formulation of algal P uptake. This process is modelled as a modified Michaelis-Menten function with the maximum uptake rate depending on cell quota, but with a constant initial affinity, in accordance with observations in cell cultures (RIEGMAN 1985) (Fig. 3).

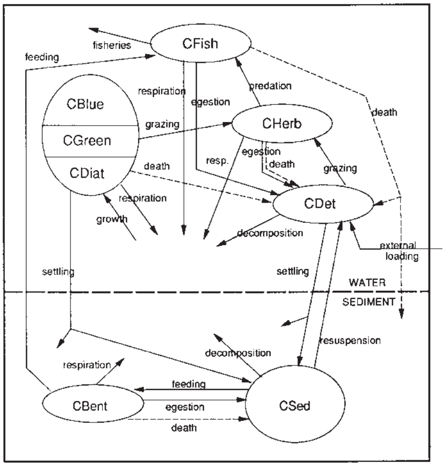

Fig. 1. The carbon cycle.

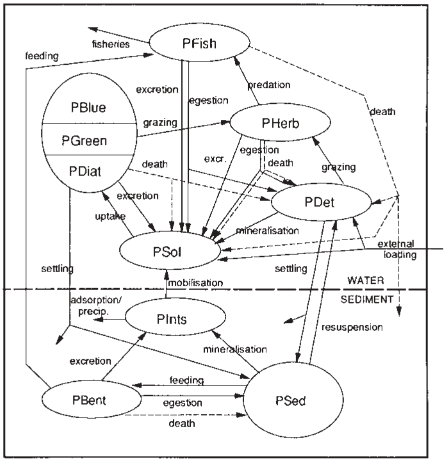

Fig. 2. The phosphorus cycle.

P dependent algal growth is then described by the well-known Droop equation (Droop 1974).

The model parameters have been derived from experimental work by other WQL groups, from data in the literature and, finally, from calibration on field data. Sources of uncertainty are the limited information available on selective grazing, mortality of plankton organisms, predation rate, settling rates and mineralisation.

The model thus consists of 18 linked differential equations and is solved numerically by means of the computer program FAME (see Wortelboer & Aldenberg 1989). For comparison with measurements, we assume that the sum of phytoplankton and detritus can be compared with the measured seston $< 150\,\mu m$ and the zooplankton with the seston $> 150\,\mu m$. Measurements have mainly been performed by the Limnological Institute at Nieuwersluis (LIN) and by the Municipal Waterworks of Amsterdam (GWA).

Results

Simulations have been carried out with the input data for Lake Loosdrecht, the largest lake in the system (water area 989 ha, mean depth 1.9 m, aver-

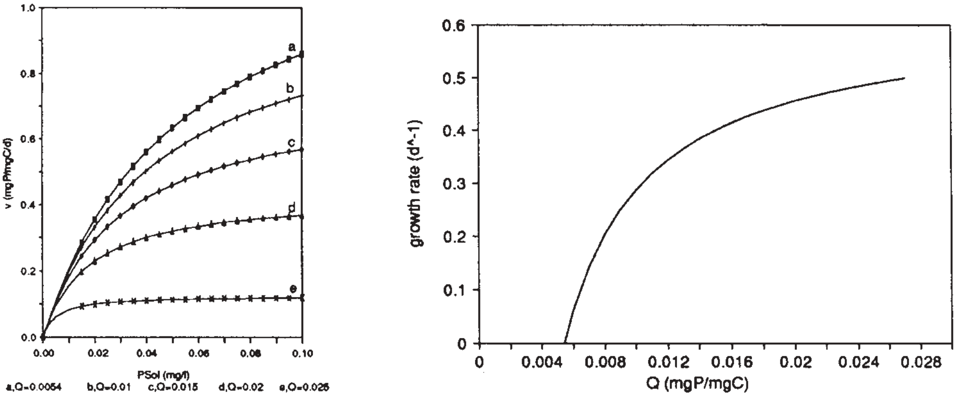

Fig. 3. Left: Phosphorus uptake functions for different values of algal cell quota (Q). Right: P dependent growth function according to Droop (1974).

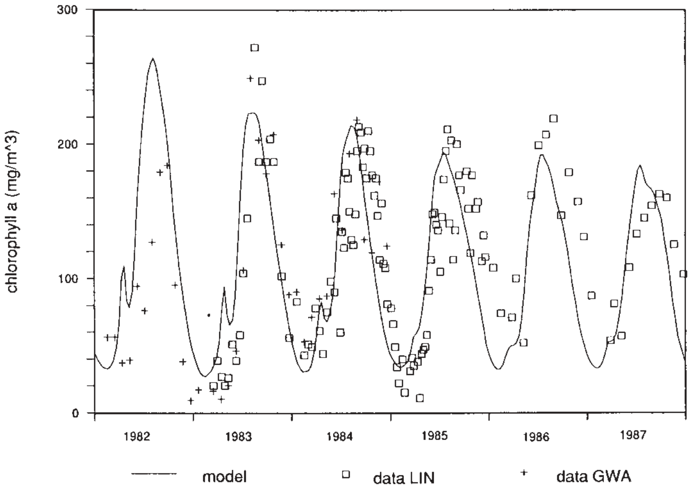

Fig. 4. Chlorophyll-*a*.

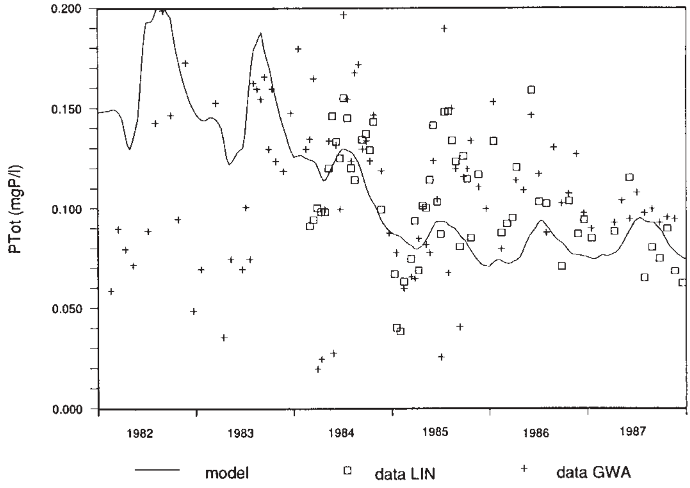

Fig. 5. Total phosphorus.

age water retention time 290 days) for the years 1982 to 1987. Annual external phosphorus loading was 2.01, 1.78, 1.00, 0.71, 1.24 and 1.19 mg $P \cdot m^{-2} \cdot day^{-1}$, respectively, the higher loadings in the first two years being due to a high summer peak (BUIJSE 1989). Figs. 4 and 5 depict the results for chlorophyll-*a* and total phosphorus. At a first glance on the data, not much seems to have happened in response to the load reduction. The bluegreens remain the dominating algal group. Chlorophyll-*a* levels remain very high and tend to decrease but a little over the years. A somewhat stronger decrease can be observed in total phosphorus levels, although the data show quite a lot of unexplained variation. The model predicts the sensitivity for changes in phosphorus input being

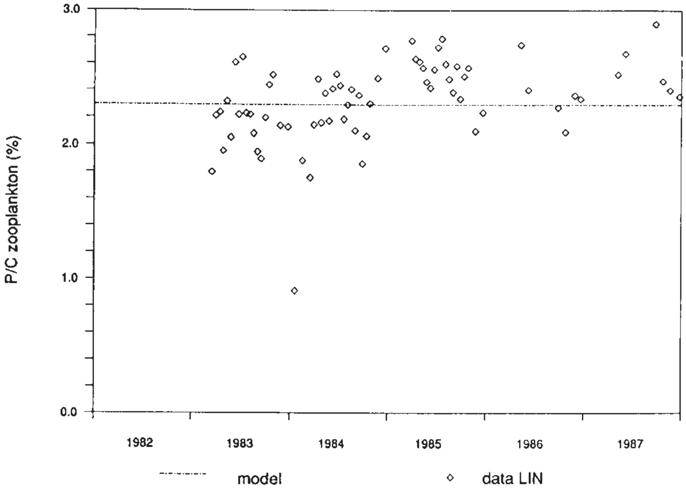

Fig. 6 A. P/C ratio of zooplankton.

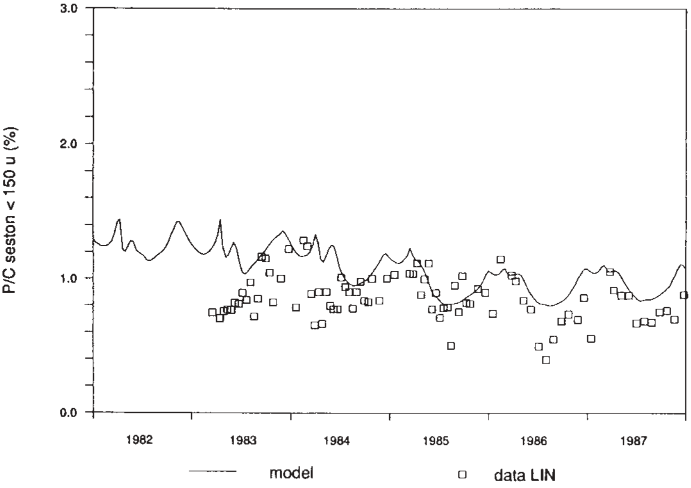

Fig. 6 B. P/C ratio of seston > 150 μm.

larger for sestonic (and total) phosphorus than for sestonic carbon (and chlorophyll-*a*). This is reflected in a slow but gradual decrease of summer P/C ratios of the phytoplankton, detritus and total seston (Fig. 6), as is observed in the field (SIEWERTSEN 1988). The model implicates that in winter, when algal growth is low, the cells can save phosphorus (up to a certain maximum) which they spend again in summer. The simulated P/C ratio of the zooplankton remains constant (and much higher), due to the regulation mechanisms already mentioned. The variation in the measurements shows, however, that these mechanisms are less stabilising than assumed in the model. Zooplankton biomass itself decreases a little in the later years (data not shown), the model reflecting guite some uncertainty on the subject. Other observations are the importance of detritus, which

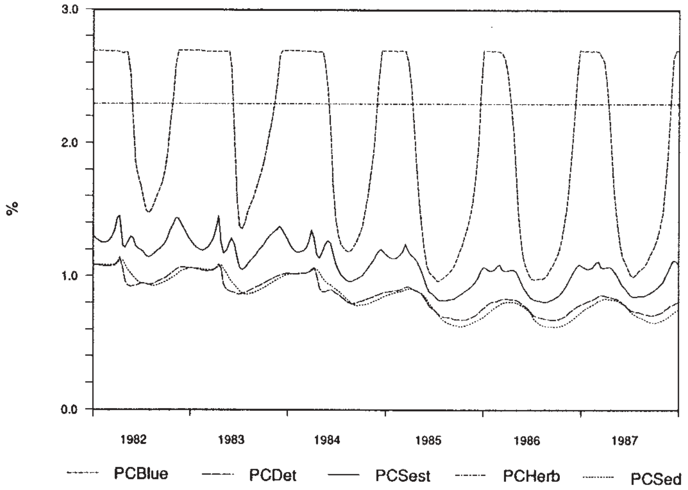

Fig. 6 C. P/C ratios of bluegreens, detritus, seston > 150 μm, zooplankton and upper sediment.

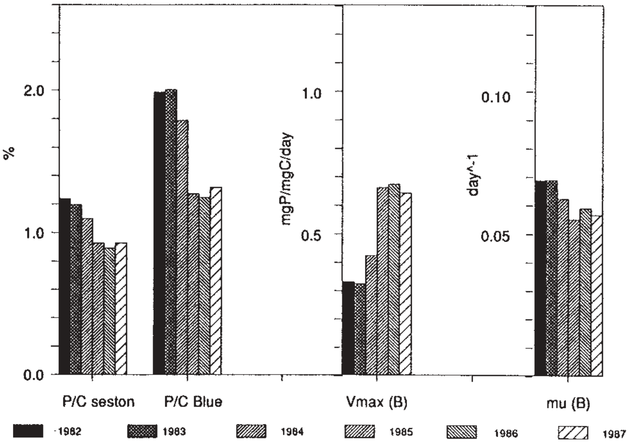

Fig. 7. Summer averaged growth parameters of the phytoplankton, model-derived.

makes up 60 – 90 % of simulated total seston (in accordance with estimates by Gons 1987), very low SRP concentrations during most of the year and a P/C ratio of the upper sediment that approximates the one of detritus.

Discussion

An interesting aspect of the model calculations is to look at the simulated trend in the P/C ratio of phytoplankton and total seston in view of physiological indicators of phosphorus limitation. Simulated summer averaged P/C ratios of total seston and bluegreen algae are depicted in Fig. 7, together with the maximum phosphate uptake rate (v_{max}) and growth rate (μ) of this (dominating) algal group. Together with a decreasing P/C ratio, an increase of v_{max} and a small decrease of μ is observed. Healey (1978) considers an algal cell quota of 10 μg P $\cdot$ mg^{-1} dry weight, equivalent to a P/C ratio of 2.0 %, indicative for a moderate P deficiency and half this value as an indicator for an extreme P deficiency. Also a $v_{max} > 0.2\,\mu mol\,P \cdot mg^{-1}$ dry weight $\cdot\, h^{-1}$ (= $0.3\,mg\,P \cdot mg\ C^{-1} \cdot day^{-1}$) is considered as an indicator for P limitation: Algae under phosphorus stress increase their uptake ability when they are offered more phosphorus. About the same value is used by Riegman (1985) and Burger-Wiersma & Baard (1987). The simulations suggest that the bluegreen algae in the Loosdrecht lakes are P deficient from 1984 on and that deficiency is becoming more stringent. Measurements of v_{max} sustain this conclusion: In 1983 values were often around or below the limit of $0.3\,mg\,P \cdot mg\,C \cdot day^{-1}$, while from 1985 on, they increase until $1.5-2\,mg\,P \cdot mg\,C^{-1} \cdot day^{-1}$ or higher. Average growth rate equals $0.1 \cdot day^{-1}$ or less (Burger-Wiersma & Baard 1987).

Both the model and experimental data show that the dynamics of algal P/C ratios can be an important factor in the resilience of the ecosystem towards changes in phosphorus loading. Simulations suggest that the system adapts itself within two years to a decreased load reduction and that without any further reduction no further changes in the system will occur. One needs to be very careful, however, to make predictions of the effects of possible measures, because of the uncertainty in a number of processes (especially those concerning the higher trophic levels and those in the sediment). Adaptation might further be retarded by some slow processes in the sediment or by adsorption of SRP to detritus, as suggested by Rijkeboer et al. (1988). The present model has still only a limited application range. For wider application, it needs a more thorough validation against data of other lakes, with a wider range of loadings and hydrological characteristics. Still, the model's basic concept, a closed phosphorus cycle within the system with dynamical P/C ratios, has shown its value and seems promising for future analyses.

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Chapter 10

Hydrobiologia **233**: 119–136, 1992.
L. Van Liere & R.D. Gulati (eds), Restoration and Recovery of Shallow Eutrophic Lake Ecosystems in The Netherlands. 119

A mathematical model of the phosphorus cycle in Lake Loosdrecht and simulation of additional measures

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Key words: model, simulation, eutrophication, phosphorus, P/C ratio, lake ecosystem

Abstract

The phosphorus cycle in the ecosystem of the shallow, hypertrophic Loosdrecht lakes (The Netherlands) was simulated by means of the dynamic eutrophication model PCLOOS. The model comprises three algal groups, zooplankton, fish, detritus, zoobenthos, sediment detritus and some inorganic phosphorus fractions. All organic compartments are modelled in two elements, carbon and phosphorus. Within the model system, the phosphorus cycle is considered as completely closed. Carbon and phosphorus are described independently, so that the dynamics of the P/C ratios can be modelled. The model has been partly calibrated by a method based on Bayesian statistics combined with a Range Check procedure.

Simulations were carried out for Lake Loosdrecht for the periods before and after the restoration measures in 1984, which reduced the external phosphorus loading to the lake from *ca.* 2 mgP m^{-2} d^{-1} to 1 mgP m^{-2} d^{-1}. The model outcome was largely comparable with the measured data. Total phosphorus has slowly decreased from an average 130 μgP l^{-1} to *ca.* 80 μgP l^{-1}, but chlorophyll-*a* (*ca.* 150 μg l^{-1}, summer-averaged) and seston concentrations (8–15 mgC l^{-1}) hardly changed since the restoration measures. About two-thirds of the seston consisted of detritus, while the phytoplankton remained dominated by filamentous cyanobacteria. The P/C ratio of the seston decreased from *ca.* 1.0% to 0.7%, while the P/C ratios of zooplankton, zoobenthos and fish have remained constant and are much higher. The system showed a delayed response to the decreased phosphorus loading until a new equilibrium was reached in *ca.* five years. Major reasons for the observed resilience of the lake in responding to the load reduction are the high phosphorus assimilation efficiency of the cyanobacteria and the high internal recycling of phosphorus. A further reduction of nutrient loading, perhaps in combination with additional measures like biomanipulation, will be the most fruitful additional restoration measure.

Introduction

Like many other shallow lakes in the Netherlands the Loosdrecht lakes have become highly eutrophic due to heavy nutrient loadings for the last forty years or so. This has led to almost permanent blooms of filamentous cyanobacteria with mean summer chlorophyll-*a* concentrations of 150–200 μg l^{-1}, high primary production and seston concentrations and loss of biological diversity (Hofstra & Van Liere, 1992). In order to reduce the algal growth, several measures have been taken to reduce the external phosphorus loading. From 1984 onwards, the source of summer inlet water, the polluted River Vecht, has been replaced by dephosphorized canal water.

This has resulted in a decrease in the average external phosphorus loading to the main lake from *ca.* 2 mg P m^{-2} d^{-1} in 1983 to 1 mg P m^{-2} d^{-1} from 1984 onwards (Engelen *et al.*, 1992; Buyse, 1988). This has, however, not led to a decrease of the seston concentration (Van Liere *et al.*, 1990).

The Water Quality research Loosdrecht lakes project (WQL) was carried out to assess and quantify the effects of reduction in phosphorus load on the lake ecosystem and to recommend additional water management measures (Van Liere *et al.*, 1984). A mathematical model, called PCLOOS, was developed at the National Institute of Public Health and Environmental Protection (RIVM), one of the participants in the WQL project. The aim of the model is to provide a better insight into the functioning of the system by integrating the results of the WQL project and to predict the effects of different restoration measures.

Several phosphorus models have been reported elsewhere, ranging from very simple to very complex ones. The most simple models, the so-called empirical or 'black box' models (OECD, 1982; Reckhow & Chapra, 1983; Sas, 1989), relate the in-lake total phosphorus concentration to the external loading and the water retention time and describe statistically the relationship between algal biomass and total P concentration. A second group are the dynamic models which describe phytoplankton growth as function of nutrient availability (see overview in Straskraba & Gnauck, 1985). Some of these models do, others do not include nutrient cycling in the sediment. The third group are detailed, multi-species models of the trophic web in aquatic ecosystems (*e.g.* Patten *et al.*, 1975).

The empirical models are, in fact, one-compartment models which cover the processes of inflow, dilution and net retention in the sediment. Such models are not sophisticated enough for the present study for two reasons. Firstly, in a shallow lake like Loosdrecht, with a very intense contact between water and sediment due to continuous mixing, the net retention is likely to decrease following the restoration measures (Sas, 1989). This implies that we need to include the upper sediment layer explicitly in the model. Secondly, the relationship between total phosphorus on one hand and algal biomass and total seston on the other hand is not unequivocal, so that a static description of this relationship is not sufficient. In the WQL project a dynamic model is needed, with a distinction between algal biomass and algal phosphorus and a variable ratio between them. Furthermore, detritus has to be considered as a separate compartment, also expressed in two units. Some dynamic phytoplankton models (*e.g.* Lehman *et al.*, 1975; Bierman & Dolan, 1981) use, in fact, a variable stoichiometry approach, but they either lack a sediment module or the description of the food web does not match the needs of the present study.

Apart from the algal growth in response to the phosphorus load we were also interested in the phosphorus exchange with higher trophic levels, especially zooplankton and fish. This required some modifications in the modelling of the phosphorus cycle. A basic feature of the PCLOOS model is that the phosphorus cycle is completely closed, except for external loading to and losses from the lake. This feature is important not only for describing algal growth or the exchange between water and sediment, but also for considering the phosphorus flow through the food web. It has been observed that at higher levels in the food chain the weight-specific phosphorus content of the organisms increases due to accumulation of phosphorus. The P/C ratio of the seston can be highly variable and is quite low in the Loosdrecht lakes (less than 1%; Gulati *et al.*, 1991), whereas this ratio is much higher for the zooplankton (2.0–2.5%; Gulati *et al.*, 1991) and zoobenthos (2.0–2.5%; Dr. J. Vijverberg, Pers. Comm.) and still higher for fish (*ca.* 5.5%; Dr. E. H. R. R. Lammens, Pers. Comm.). These differences can be maintained only if the animals have mechanisms to regulate their P/C ratio irrespective of the P/C ratio of their food. These mechanisms can involve a more efficient assimilation of phosphorus from the food and/or a reduced phosphorus excretion rate. In this respect, our model differs from several existing ones (*e.g.* Di Toro *et al.*, 1975; Di Toro & Matystik, 1980; Jørgensen, 1980). Aldenberg & Peters (1990) have stated that in a model in which the P/C ratios of the trophic levels differ, the P/C ratios of one or more compartments should be variable in order to maintain a closed P balance. In their model, only the detritus has a variable P/C ratio while the other compartments, phytoplankton and zooplankton, have a fixed one.

The PCLOOS model, version 2.4 (Janse & Aldenberg, 1990a, b, 1991) is based on the model by Aldenberg & Peters (1990), but extended with a sediment module, a more complete food web including zoobenthos and fish and variable P/C ratios of all the biotic and organic compartments. The model presented in this paper is PCLOOS version 2.5. It differs from the previous version in the incorporation of chemical adsorption, an improved modelling of some sediment processes and a number of minor changes in the phytoplankton, fish and zoobenthos growth equations. Moreover, the model was extended with a calibration routine based on Range-Check and Bayesian statistics.

Description of the lake

The model has been applied to the Loosdrecht lakes, a system of interconnected shallow lakes which originate from peat digging, located between Amsterdam and Utrecht, The Netherlands. A detailed description of the lakes system can be found in Gulati *et al.* (1990). The main lake, Lake Loosdrecht, has a water area of 989.1 ha, a mean depth of 1.91 m and an average water residence time of 0.7 years. Downward seepage averages 1.5 mm d^{-1} (Engelen *et al.*, 1992). The bottom consists of peat covered by a layer of loose organic matter of variable thickness. The lake is very much exposed to the wind and can be regarded as completely mixed.

Model structure

General features

The model comprises both the water column and the upper sediment layer (Fig. 1). The model is zero-dimensional in space: the lake is assumed to be completely mixed, a reasonable assumption regarding the high correlation of the data from the two sampling stations in Lake Loosdrecht, as can be derived from Breebaart *et al.* (1989). Carbon is used as the unit of biomass. The model is composed of eight organic compartments, modelled both in carbon and in phosphorus units, indicated as two partly overlapping boxes, and four inorganic phosphorus compartments, making twenty state variables altogether. Inorganic carbon is not included in the model: decomposition and respiration losses of CO_2 go to an 'outside' pool of dissolved inorganic carbon (DIC), from which CO_2 for algal growth is withdrawn. This assumption seems reasonable, because the phytoplankton growth in the lakes is not carbon-limited. For analogous reasons, other nutrients than phosphorus are not considered.

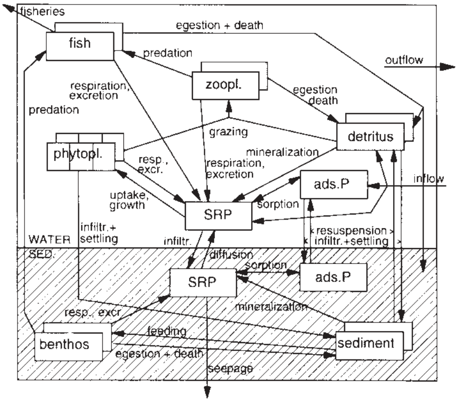

Fig. 1. Overview of the PCLOOS model. Compartments modelled in two units are indicated by two boxes behind each other. The algal compartment is composed of three functional groups: cyanobacteria, diatoms and green algae. The arrows in the figure denote both the carbon and the phosphorus fluxes. Some minor arrows have been lumped or left out for the sake of clarity.

Inorganic phosphorus is modelled both in the surface water and in the interstitial water. In both phases, a distinction is made between soluble reactive phosphorus (SRP), which is assumed to be biologically available, and adsorbed inorganic phosphorus. The organic matter in the lake, which is rich in iron, has a high adsorption capacity for phosphorus (Otten *et al.*, 1992).

The organic compartments of the model are: three functional groups of phytoplankton, detritus, zooplankton, sediment detritus, macrozoobenthos and fish. Of the three groups distinguished in the phytoplankton, diatoms, green algae and filamentous cyanobacteria, only the last-named is important at present. The term 'zooplankton' refers to the herbivorous filter feeders, mainly consisting of Crustacea. The fish mainly consists of bream and represents an important phosphorus pool in the lake. The macrozoobenthos, mainly *Chironomidae* larvae, is an important food source for the fish besides zooplankton. The functional groups of organisms are not split any further to avoid further complexity of the model. The bacteria are modelled implicitly in the decomposition processes.

For each state variable a differential equation is formulated, made up of the processes (mass fluxes) linking them (Fig. 1). Although the model has a complex structure with many parameters, it is not as complex as it might look at first sight. Phosphorus fluxes related to natural mortality, sedimentation or outflow, among others, simply equal the corresponding C fluxes times the actual P/C ratio of the compartment. These processes do not affect the compartment's P/C ratio. In other cases, however, corresponding fluxes are independent: for instance, the P/C ratio of food assimilated by animals may differ from the ratio of food egested; similarly, the carbon and phosphorus uptake by algae may be in a different proportion from the availability of these elements. These processes determine the P/C ratio of the species and are themselves controlled by it. The main process formulations in the model will be discussed briefly. A complete description of the version 2.4 model can be found in Janse & Aldenberg (1990a, b); a description of the version 2.5 model can be obtained from the authors.

Processes in the water

The external phosphorus loading to the lake occurs mainly as detrital, adsorbed or dissolved phosphorus; the inflow of P in biota is assumed to be very small. The total phosphorus input is divided over the different fractions according to the estimated average values. For detritus and the biota, the external carbon input is calculated by dividing the phosphorus input by constant, estimated P/C ratios. The detritus in the input flows directly to the detritus pool in the lake and is thus assumed to react in the same way. All compartments in the water, except fish, are subject to dilution due to water inflow into the lake, corrected for evaporation. As we assume a constant volume, the same amount of water leaves the lake as flows into it, the greater part of it by surface outflow. This water has the same composition of dissolved and particulate substances as the lake water. The same applies, except for the zooplankton component, for the water that leaves the lake by infiltration to the sediment.

The inorganic phosphorus can be present as dissolved phosphorus (SRP) or can be chemically adsorbed onto detrital particles. This is modelled as a, fast, chemical equilibrium between the two states, modifying the phosphorus flows which are due to the, relatively slow, biological processes (Di Toro, 1976). The adsorbed phosphorus is assumed to be subject to sedimentation, infiltration and grazing at the same rates as detritus, but not to other biological processes.

Primary production of phytoplankton is defined in the model as the integral carbon fixation in a 24 h period. For simplicity, the carbon fixation is assumed to equal growth. Algal biomass is calculated as a carbon concentration; the growth rate depends on temperature, available light and phosphorus. The light dependent growth of cyanobacteria and diatoms is described according to Di Toro & Matystik (1980), using Steele's equation integrated with respect to depth and time (1 day). This equation implies growth inhibition at high light intensities. For green algae, a similar equation is based on a Monod-type equation, assuming no light inhibition. The available light is determined by the light intensity at the water surface and its extinction in the water column. The extinction coefficient equals the sum of the background extinction of the water and the contributions of algae and detritus to it, thus accounting for the self-shading effect. The temperature does not affect the initial light affinity, but it does affect the maximum growth rate that can be reached. This dependence is described using an optimum function, *viz.* a modified Gauss' curve, normalized to 1.0 at 20 °C.

The phosphorus dependence is modelled as a two-step process. The first one is phosphorus uptake, increasing the internal P/C ratio or 'cell quota' *Q*. The uptake rate increases with increasing external SRP concentration up to a maximum. The initial affinity, *viz.* the slope of the curve at low external SRP concentrations, is taken as constant, according to the results of cultures studies by Riegman (1985). The maximum uptake rate, however, is determined by the cell quota: the minimum cell quota gives the highest maximum rate (Janse & Aldenberg, 1991). The second process is growth, taken as increase in carbon, depending on *Q* according to the Droop (1974) equation: above the minimum cell quota, the growth rate increases asymptotically with *Q* until the maximum growth rate is reached.

The actual growth rate is calculated by multiplying the maximum growth rate with the combined reduction functions for light and temperature and for phosphorus (Table 1). Whether light and nutrient functions operate independent of one another in reality is discussable. It is generally agreed that the effects of multiple nutrients, for instance phosphorus and nitrogen, are best described by the minimum law of Liebig, *viz.* only one of them is limiting at a time. The effect of temperature is generally reported as independent of nutrient availability. Concerning light, neither of the two options seems entirely satisfactory. We have followed the common assumption by modellers that light and nutrients affect photosynthesis independently. There are some indications that these factors might influence each other when both are low (Riegman, 1985), but we did not incorporate this for sake of simplicity. The chlorophyll-*a* content of the phytoplankton, a derived variable in the model, decreases with temperature and increases with the degree of light limitation (Riegman, 1985). The growth rate [d^{-1}] multiplied by the algal concentration gives the gross primary production [$mgC\,l^{-1}\,d^{-1}$].

Counteracting algal growth are the loss processes respiration, sedimentation and zooplankton grazing. Respiration is the sum of maintenance respiration, taken as a percentage of the biomass [d^{-1}], and growth respiration, a relatively small fraction of the daily growth. During respiration the algae excrete also phosphorus, the relative amount of which is controlled by their actual P/C ratio. Sedimentation is defined as gross sedimentation, the rate of which is slightly depending on temperature. We have assumed that settled algae die instantaneously on reaching the bottom and contribute to the bottom detritus, which can be resuspended into the water column. Phytoplankton death is thus modelled indirectly.

The parameter values of the three algal groups in the model differ. The cyanobacteria have a higher affinity both for phosphorus and light as well as a higher maximum uptake rate than the other groups. On the other hand, they have a much lower maximum growth rate and a stronger sensitivity to temperature. The diatoms have a lower temperature optimum, while the green algae are not inhibited by high light intensities. Both these groups have higher growth rates, but also higher loss rates through settling and zooplankton grazing.

The zooplankton feeds on both phytoplankton and detritus. Grazing is described as a Monod-like function of the seston concentration, the specific filtering rate decreasing hyperbolically with increasing seston concentration (Gulati *et al.*, 1982; Gulati *et al.*, 1985). A selectivity constant is used for each food species to account for preference of the zooplankton for certain kinds of food: 1.0 for green algae, 0.5 for diatoms, *ca.* 0.1 for filamentous cyanobacteria, which are not easily handled by most filter feeders (Gliwicz, 1980) and 0.3 for detritus. The assimilation efficiency for the consumed food is constant and quite low (0.3) for carbon (Gulati *et al.*, 1985), but variable (depending on the P/C ratio of the food) and, therefore, mostly higher for phosphorus. This is one of the mechanisms by means of which the differences in P/C ratio between the trophic levels are maintained. The egested material becomes detritus, but from this about half of the phosphorus 'leaks out' and enters the SRP pool. Losses of zooplankton include, besides egestion of the unutilised food, respiration, P excretion, natural mortality and fish predation. The P excretion is related to the respiration, but is reduced in times of P shortage.

Fish feeds, besides on zooplankton, also on the zoobenthos (midge larvae). Both predation processes are modelled as a so-called 'type III' response (Holling, 1965): the predation rate depends on prey density and this relation is described by a sigmoid curve. Selectivity between the two food species has not been included. The phosphorus assimilation efficiency, like for zooplankton, depends on the P/C ratio of the food. Also fish can reduce its P excretion rate with respect to the respiration rate in order to save phosphorus. Natural mortality of fish varies seasonally, being the highest after spawning in May–July (Dr. E. H. R. R. Lammens, Pers. Comm.). The scales and bones of the dead fish are lost from the system. The softer body parts become detritus, besides a small part of the phosphorus which immediately becomes available in dissolved form. Only small amounts of fish are removed by active fisheries.

Detritus is an important compartment in the model. It has an extensive exchange with the sediment detritus, the organic matter in the upper sediment, by means of sedimentation and resuspension. Sedimentation is, like the sedimentation of algae, described as a first-order process, the velocity being slightly influenced by temperature. Detritus disappears due to decomposition and mineralization, a first-order, strongly temperature dependent process, and the dissolved P is released and enters the SRP pool.

Processes in the sediment

The sediment module is confined to the exchangeable, degradable material assumed to be important for the nutrient recycling in the lake ecosystem, according to Keizer & Sinke (1992). These authors found that only the recently sedimented organic fraction and 10–20% of the inorganic fraction in the upper 10 cm can be recycled. Together they amount to less than 1.0 gP m^{-2}. Other sediment fractions, like peat particles and the phosphorus chemically bound to humic substances etc. are considered as unimportant for the nutrient recycling (see *e.g.* Boström *et al.*, 1982) and are not included, although they can be in considerable amount. The total P concentration of the sediment is about 1.1 mgP g^{-1} dry weight, at a dry weight content of 90 g l^{-1} (Boers *et al.*, 1984), which equals nearly 10 gP m^{-2} in the upper 10 cm. The sediment has a very high porosity of 0.91.

The most important compartment in the sediment is the sediment detritus, originating from sedimentation (and infiltration) of seston from the water column. This material can be recycled back to the water column by resuspension, which is estimated to affect 10% of the sediment surface of the lake per day at average wind velocity (Gons & Van Keulen, 1989). The average total phosphorus flux by resuspension is estimated as 30–40 mgP m^{-2} d^{-1}, of which 10%, *viz.* 3–4 mgP m^{-2} d^{-1}, consists of 'true', fine-sized, detritus (Gons *et al.*, 1991). The other 90% of the resuspendable material, also called 'epipelon', consist of coarse particles of peaty origin which settle again within a few hours and which are not modelled. The resuspension flux is, of course, highly variable and greatly affected by wind speed, ice cover and also – to a lesser extent – by boating and by browsing activity of bream in the sediment. For simplicity, however, the flux is modelled as a constant amount of carbon per day (provided that the size of the sediment detritus pool is sufficient). The amount of phosphorus resuspended this way depends on the actual P/C ratio of the sediment detritus.

Mineralization of the sediment detritus is described as a first-order process with a strong temperature dependency. The dissolved phosphorus in the interstitial water is again assumed to be in chemical equilibrium with the adsorbed form. However, since the anoxic conditions in most of the sediment except in the upper few millimeters, the adsorption capacity of the sediment is less than that in the water (Keizer *et al.*, 1991). Dissolved phosphorus can diffuse from the pore water to the surface water or can get lost by downward seepage.

The macrozoobenthos is assumed to feed only on the sediment detritus. Its feeding rate has been modelled by a Monod-like function of the available food, a so-called 'Type II' functional response (Holling, 1965). Loss processes are respiration, mortality (first-order) and fish predation. Also the zoobenthos can regulate its P/C ratio to a level higher than that of the food ingested by means of a more efficient P assimilation or by a reduced P excretion rate.

Parameter estimation and calibration

The main input parameters for the model were: the measured water temperature, daily radiation, water inflow, evaporation and total phosphorus input. Radiation data from the meteorological station at De Bilt, about 20 km from the lakes, were obtained from the Royal Netherlands Meteorological Institute (KNMI) and were read in as weekly values of a two-week moving average, to smoothe the input and to reduce the number of data. Hydrological data and phosphorus loading were read from the monthly balance models (1982–1987) made by Buyse (1988) and Engelen *et al.* (1992), both for the Loosdrecht lakes together and for each lake separately. For 1988–1990, the balance models for 1986 were used. Other important input parameters were the water depth, infiltration rate, sediment porosity, background extinction and a number of process parameters. The sources of these parameters were: experimental data of WQL, literature data and calibration. Experimental data on the Loosdrecht lakes concerned the growth of cyanobacteria, the growth of crustacean zooplankton, settling and resuspension of seston and the phosphorus mobilisation. Also, good estimates were available of the phosphorus pools in the sediment and of stocks and mortality of fish. Data on zoobenthos, food selectivity in grazing, fish predation and mineralization in the water were scanty. Field data for calibration were collected by the Municipal Water Works of Amsterdam and by the Limnological Institute at Nieuwersluis. The sum of phytoplankton and detritus was measured as seston $< 150\,\mu m$ of which, among others, dry weight and C, P and chlorophyll-*a* content were measured. These measurements do not allow to separate algae from detritus; this was done with use of the chlorophyll-*a* data and estimated C:chlorophyll-*a* ratios of the phytoplankton (Gons & Van Keulen, 1989) and with use of biovolume data which were collected in some periods. Zooplankton was measured as the seston $> 150\,\mu m$. In this paper, the term 'seston' refers to the seston $< 150\,\mu m$. Other measurements used were SRP, total phosphorus and Secchi-depth transparency.

For calibration of the model, we first made use of so-called 'minimodels' of subsystems, *e.g.* the sediment subsystem, and of steady state analyses with summer averages. Secondly, a formal calibration procedure was developed, based on Bayesian statistics (Box & Tiao, 1973), combined with a Range-Check procedure. The aim of the method of Bayesian parameter estimation was to explore how the combined uncertainty in a large number of parameters affects the uncertainty in the model results, and to estimate the parameter values more accurately. An important feature of the method is that a number of parameters are observed together rather than separately. Because the method is quite computer time-consuming, it was applied to only a subset of 11 of the *ca.* 100 parameters together. The other parameters were kept at their nominal value. The choice of the 11 parameters was based on their high uncertainty, their sensitivity and because they appear in different modules of the model. For each of them, a range of possible values was established. At the same time, output ranges of all the state variables were established, based on data and estimates on Lake Loosdrecht. Next, a large number of model runs was performed with randomly chosen parameter combinations. In every run, the model results were first compared with the output ranges, using the values on August 1 of the first year for comparison. If the simulation fell beyond one or more of these ranges, the parameter combination was rejected, the run was stopped and a new combination was chosen. If the simulation was within the ranges, the run was allowed to continue. This Range-Check procedure saved a considerable amount of computing time spent otherwise on unproductive runs. The successful runs were subjected to Bayesian statistics. For every measurement the difference between measured and simulated values was calculated and then used to compute the sum of squares for the variable:

$$\text{SumOfSquares}_{\text{var}} = \sum_{t} (\text{obs}_{\text{var},t} - \text{model}_{\text{var},t})^2 ,$$

with t = time. The eight obtained sum of squares values, one for each measured variable, were used to calculate the marginal posterior density (Box, 1971):

$$\text{posterior density} = \prod_{\text{var}=1}^{8} (\text{Sum Of Squares}_{\text{var}})^{-\frac{1}{2}\cdot n_{\text{var}}} ,$$

in which n = number of measurements, which can be different for different variables. The parameter combination with the maximum posterior density gives the best fit of the model to the measurements. This combination was used in the simulations depicted.

The model calculations were performed on a SUN Sparc station or on a 80386 PC, by means of the simulation program ACSL, level 10B, developed by Mitchell & Gauthier Associates (1991). The integration routine used was Gear's Stiff algorithm, with a variable order and variable step size, which were adapted according to preset error criteria. For our model, which includes processes with highly different time constants, this algorithm proved to be considerably faster than others. A ten-years simulation took 5–10 minutes per run. Initial values of the state variables were estimated from the data. Prior to a simulation, the model was allowed to equilibrate for a simulated period of three years.

Results

Simulations

Simulations have been carried out for the period 1982–1990 for three lakes of the Loosdrecht system, but here only the results for the largest lake, Lake Loosdrecht, are described. In the years up to 1984, the average total phosphorus concentration in the inflowing water (*viz.* the external P loading divided by the water inflow) was very high in the summer months, due to the inlet of highly polluted supply water from the River Vecht (Fig. 2). After restoration measures in 1984, these peak loadings have disappeared, but the loading from other sources remains high (Buyse, 1989; Engelen *et al.*, 1992). On annual basis, the external loading has been reduced by a factor 2 (Van Liere & Janse, 1992).

During the calibration of the model, about one run out of every six was successful, *i.e.* the results fell within the established ranges for the state variables. 200–300 runs were sufficient to find the maximum posterior density: the natural logarithm of it was −503. Simulations, together with the data, show that total phosphorus (Fig. 3) has tended to decrease steadily following the restoration measures, although the unexplained variation in the data is high. The solid line is the 'best

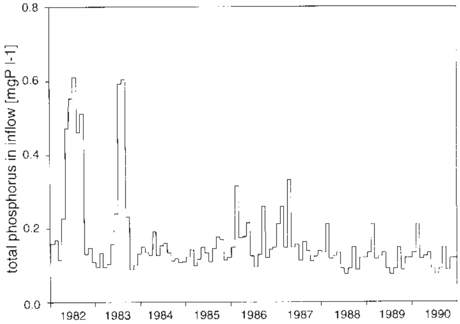

Fig. 2. Average total phosphorus concentration in the inflowing water to Lake Loosdrecht, 1982–1990. Based on data of Buyse (1988) and Engelen *et al.* (1992). The values for 1988–1990 are based on those of 1986.

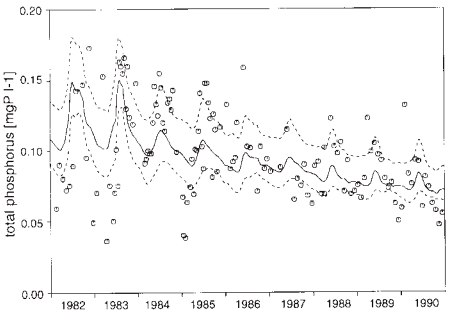

Fig. 3. Total phosphorus concentration in Lake Loosdrecht: simulation of nominal run (solid line), error bounds (dashed lines) and measurements (symbols), 1982–1990.

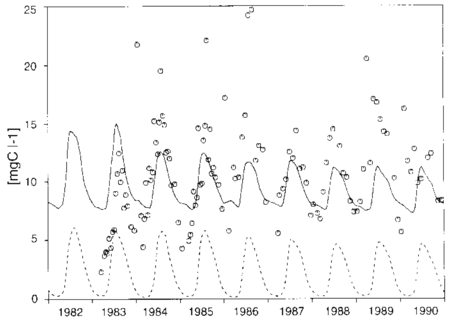

Fig. 5. Simulation of total seston (solid line) and cyanobacteria (dashed line) and measurements of total seston (symbols) in Lake Loosdrecht, in 1982–1990.

fit', the dashed lines indicate the ranges, due to variation of the 11 calibration parameters, of runs giving a natural logarithm of the posterior density higher than −520. A corresponding decrease in chlorophyll-*a* was, however, not observed (Fig. 4), nor in the total seston (Fig. 5) or Secchi depth, which still varies between 0.3 and 0.4 m. The cyanobacteria were the dominant group during most of the year, but in spring, also the diatoms developed a significant biomass, according to both the simulations and the field observations (Boesewinkel-De Bruyn *et al.*, 1988). Major part of the seston mass (*ca.* 60% in summer, >90% in winter) consists of detritus; this is consistent with estimates by Gons & Van Keulen (1989) of an average detrital fraction in the seston mass of two-thirds. The zooplankton (Fig. 6), zoobenthos and fish stock are not much affected by the reduced nutrient loading. The simulated densities of fish and zoobenthos are in the range of field estimates: fish 275 kg ha^{-1} (corresponding to about 2.8 gC m^{-2}) (Lammens *et al.*, 1992) and zoobenthos 1 gC m^{-2} on the average (Dr. J. Vijverberg, Pers. Comm.). Strikingly, the seston concentration if calculated as phosphorus gives a stronger response to the decreased phosphorus input than the corresponding carbon concentration. The simulated P/C ratio of the seston grad-

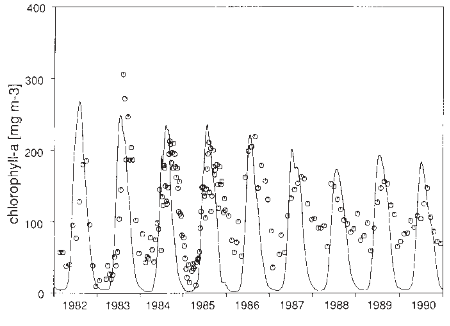

Fig. 4. Chlorophyll-*a* concentration in Lake Loosdrecht: simulation (line) and measurements (symbols), 1982–1990.

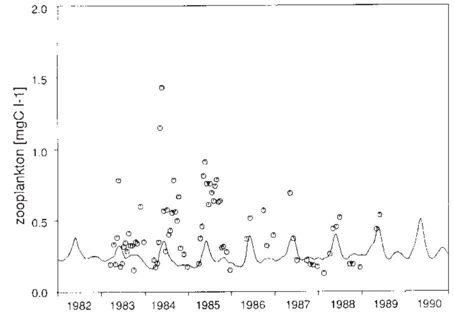

Fig. 6. Zooplankton concentration in Lake Loosdrecht: simulation (line) and measurements (symbols), 1982–1990.

ually decreases, both in the simulations and in the lake (Fig. 7), but those of the zooplankton, zoobenthos and fish do not change very much, because of the regulation mechanisms of the animals. The field zooplankton ratios also do not show a change (Gulati *et al.*, 1991). The phosphorus pool in fish, about 80 μg P l^{-1}, roughly equals the P in all the other compartments in the water phase together (Van Liere *et al.*, 1990), as found in many hypertrophic lakes. The SRP values (not shown) are very low during most of the year, according to both the model and the field data. As in the water phase, the simulated P concentration in the sediment (not shown) also decreases steadily because of the load reduction; although data are sparse, observations in the field seem to confirm this (Keizer & Sinke, 1992). The concentrations in the pore water vary considerably during the year, depending on the mineralization activity which is highly temperature dependent.

The characteristic response time of the model system to adapt itself to a decrease in nutrient loading is about five years. A new equilibrium, which has now been nearly reached, does not differ much from the one before the restoration measures, except for a decrease in phosphorus concentration, not accompanied by a corresponding decrease in chlorophyll-*a* and seston (Fig. 8). The shift to the left towards the maximum line based on a large number of Dutch lakes (CUWVO, 1987) clearly shows that the chlorophyll-*a*: total P ratio is among the highest recorded.

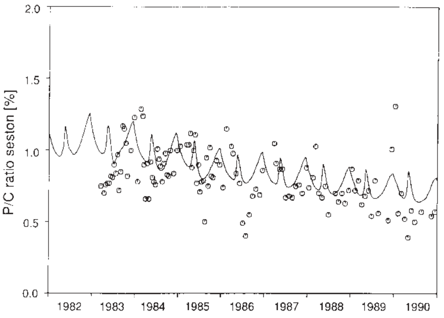

Fig. 7. P/C ratio of seston in Lake Loosdrecht: simulation (line) and measurements (symbols), 1982–1990.

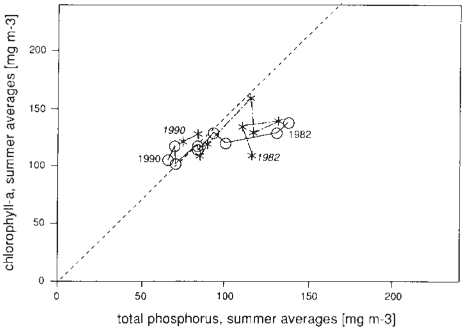

Fig. 8. Eutrophication diagram (summer-averaged chlorophyll-*a* against total phosphorus) in Lake Loosdrecht: simulation (circles) and measurements (asterisks), 1982–1990. The dashed line is the maximum ratio found in a database of Dutch lakes (Lijklema *et al.*, 1988).

The phosphorus turnover rates greatly differ for the different model compartments, as can be concluded from the simulated flow scheme, averaged for the summer of 1987 (Fig. 9). For the SRP compartment, which is very small in size, this rate is by far the highest (*ca.* 10 d^{-1}): SRP formed is taken up almost immediately by algae or, when these are saturated (for instance in winter), adsorbed onto iron-rich particles in the water. This pool of adsorbed phosphorus also has a high turnover rate (*ca.* 1 d^{-1}, on the average), due to rapid chemical exchange with the SRP pool. Of the organic compartments, the zooplankton has the fastest turnover, about 0.2 d^{-1}, the algae, detritus and zoobenthos have about 0.1 d^{-1} and the turnover rate of fish is only 0.02 d^{-1}. The compartment with the slowest turnover rate is the organic phosphorus in the sediment: about 0.01 d^{-1}. About 10% of the daily phosphorus needs of the phytoplankton is met, directly or indirectly, by the external loading, about 10% by desorption from the adsorbed P pool and only 3% by diffusion from the sediment. The larger part, *i.e. ca.* 75%, becomes available again by recycling via zooplankton, fish, detritus or the algae themselves. The phosphorus flow

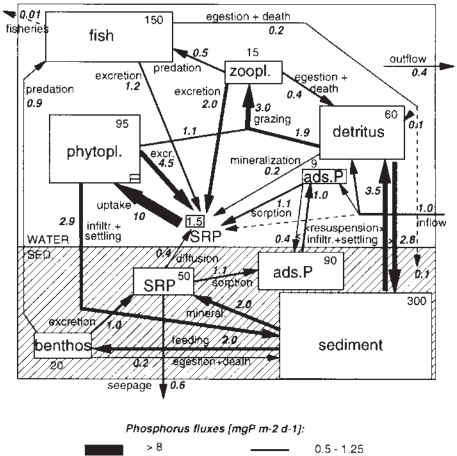

Fig. 9. Simulated phosphorus flow scheme of Lake Loosdrecht, summer average 1987. Concentrations in mgP m^{-2}, flows in mgP m^{-2} d^{-1}.

from the sediment to the water phase occurs mainly through resuspension; the flow due to fish feeding and the diffusive flux are much smaller. The modelled diffusive flux approximately equals the flux measured in sediment cores (Boers & Van Hese, 1988; Keizer *et al.*, 1991); it has decreased a little since the restoration measures (Figs. 9 and 10).

Simulation of additional measures

Because the achieved reduction in phosphorus loading of the lakes did not lead to a discernible improvement in the water quality, additional measures were considered by the regional water quality authorities (see also Van Liere & Janse, 1992). The possible effects of the following measures have been modelled, with the same parameter settings as established during the calibration:

(a) No further change in the present phosphorus loading (1.0 mgP m^{-2} d^{-1}).
(b) A further reduction in the phosphorus loading to 0.35 mgP m^{-2} d^{-1} (= 0.1 gP m^{-2} yr^{-1}), *i.e.* a reduction which is the maximum technically possible.
(c) Extra flushing with $1 \cdot 10^6$ m^3 dephosphorised water per month. This is the amount technically possible given the present hydrological

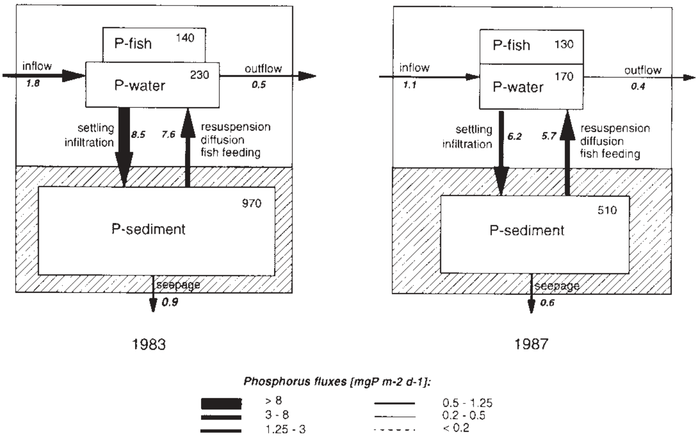

Fig. 10. Simplified phosphorus flow schemes of Lake Loosdrecht, yearly averages; concentrations in mgP m^{-2}, flows in mgP m^{-2} d^{-1}. (a) 1983. (b) 1987.

situation and the maximally allowed fluctuations in water level (Buyse, 1988).

(d) Removal, by dredging, of 80% of the organic material in the sediment top layer, carried out once. It is questionable whether this measure is technically possible in the Loosdrecht lakes (Van Liere & Janse, 1992).

(e) Reduction of the resuspension with 50% by deepening of the lake (Gons & Van Keulen, 1989).

(f) Biomanipulation, involving removal of 80% of the bream population, to be carried out once.

(g) Phosphorus load reduction (measure a), combined with biomanipulation, introduction of predatory fish and 80% reduction of resuspension, under the assumption that submerged vegetation will recolonize and survive.

The possible effects of the measures are presented as time series of the total P and seston concentrations (Fig. 11) and by means of the so-called AMOEBE method (Fig. 12). By this method, the state of an ecosystem is visualised, in an integrated way, with respect to a 'reference state'. This is a goal state, based on the state of the lakes in the period 1930–1950 (Hofstra & Van Liere, 1992). The results of the PCLOOS model for the present situation are comparable with those of the AMOEBE method. Fig. 12 shows the yearly averaged results of the various measures, six years after their application. The 'no change' scenario results in no further effects, because the system is now (nearly) in equilibrium with the prevailing phosphorus loading. A further reduction of phosphorus loading (measure b) would certainly lead to some permanent improvement of water quality, with total P concentration, seston and chlorophyll-*a* about half the present values and consequently, the transparency will increase. However, according to the simulations, the phytoplankton will probably still be dominated by cyanobacteria and the improvement will not be sufficient to reach the reference state. The same applies for resuspension reduction as a standalone measure (measure e). Biomanipulation (measure f) or removal of the top layer (measure d), without a concomitant reduction in phosphorus loading, will be effective only temporarily. Scenario (g), a combination of phosphorus load reduction and additional measures, seems to be promising. One must bear in mind, however, that this scenario is rather speculative, because it assumes the returning of aquatic macrophytes, which are not an explicit part of the model but are regarded as a boundary condition (see discussion section).

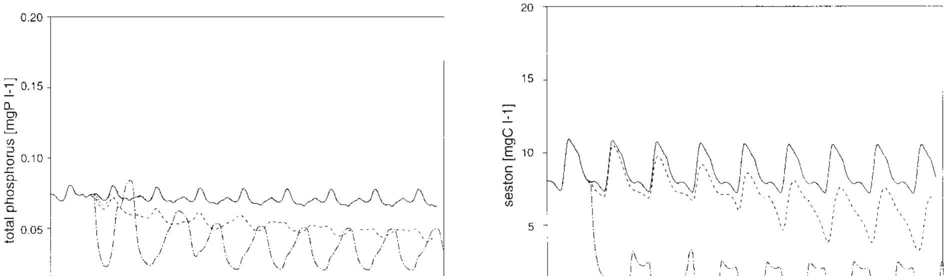

Fig. 11. Simulations of additional measures. (a) total phosphorus, (b) seston. Solid lines: 'no change' scenario (measure a); dotted lines: biomanipulation (measure f); dashed lines: P load reduction (measure b); dotted-dashed lines: P load reduction together with biomanipulation (measure g). For other details see text.

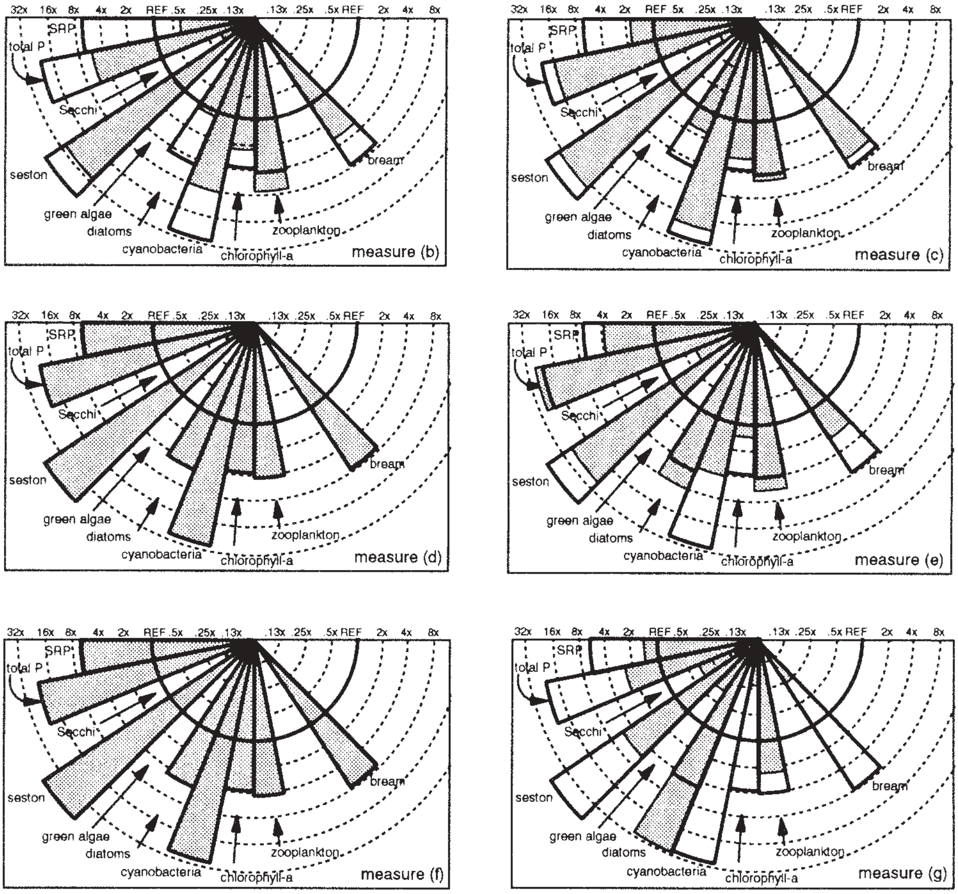

Fig. 12. Simulations of additional measures, depicted by means of the AMOEBE method (slightly adapted from Hofstra & Van Liere, 1992). Measure b: P load reduction. Measure c: flushing. Measure d: removal of top layer. Measure e: reduction of resuspension. Measure f: biomanipulation. Measure g: P load reduction together with biomanipulation. White slices: simulation of 1987; dark slices: simulations of additional measures (results after 6 years); solid circle: reference state. All values are based on yearly averages.

Discussion

The lake ecosystem

The overall behaviour of phosphorus in the system can be analysed from the simulated flow schemes (Fig. 10) based on the yearly averaged net fluxes between water and sediment. The flux from water to sediment is the sum of settling and infiltration, the opposite flux is the sum of resuspension, diffusion and fish feeding. It is obvious that the sediments act, on the average, as a net sink of phosphorus and that they continue to do so after load reduction. These schemes can be compared with 'empirical' lake parameters like the net retention coefficient, R, defined as the fraction of the input which is retained in the sediments

$$R = \frac{P_{\text{in}} - P_{\text{out}}}{p_{\text{in}}} \; [-],$$

with P_{in} denoting the phosphorus inflow and P_{out} the surface outflow of phosphorus. The retention coefficient has decreased from 0.7 to 0.6 after the load reduction, a phenomenon observed frequently in lakes under restoration and often attributable to an increased internal loading in the summer months (*e.g.* Ryding & Forsberg, 1977; De Pinto, 1981; Sas, 1989). In Lake Loosdrecht, where the direct phosphorus mobilisation due to diffusion is very small (Keizer *et al.*, 1991), the cause of the decreased retention lies in the high efficiency of phosphorus utilisation by the phytoplankton and in the high resuspension. The observed retention coefficients comply with empirical relations with lake depth and water retention time (OECD, 1982; Lijklema *et al.*, 1988; Sas, 1989). The decrease in phosphorus that does occur, follows the load reduction with a certain delay and a new equilibrium is reached after *ca.* five years. This 'characteristic time' of the system depends mainly on the processes which have the lowest specific rates, *i.e.* mainly processes in the sediment.

Apart from changes in the phosphorus flows, another important feature is the decrease of the P/C ratios of phytoplankton and seston, following the load reduction, both in the simulations and the field measurements (Fig. 7; see also Gulati *et al.*, 1991). The simulated summer averages decrease, between 1983 and 1990, from 1.0% (w/w) to 0.7% for total seston and from 2.1% to 1.6% for the cyanobacteria, while the growth rate remains the same at 0.11 d^{-1}. There is a concomitant rise in the maximum initial phosphate uptake rate from about 0.48 to 0.64 mgP mgC^{-1} d^{-1}, a trend also observed in experimental tests (Baard & Burger-Wiersma, 1991). Both phenomena indicate that phosphorus limitation of the phytoplankton is becoming more severe (Healey, 1978; Riegman, 1985). The phytoplankton, especially the cyanobacteria, apparently have increased their efficiency of utilising phosphorus and thus can maintain a high biomass despite a decrease in available phosphorus. Parallel with a decrease in P/C ratio of the seston the phosphorus assimilation efficiency of the zooplankton increases, in order to maintain a high P/C ratio when the food becomes poorer in phosphorus.

Although the general trends in the data are reproduced correctly by the model, there are differences between simulations and measurements, due to assumptions which may not always be true. The winter values of chlorophyll-*a* are often underpredicted, possibly because the phytoplankton can survive some days in the upper sediment layer (Otten *et al.*, 1992) and, if resuspended within that period, will be measured in the water again. The measured summer chlorophyll-*a* concentration in Lake Loosdrecht in 1982, when the loading was still high, is lower than simulated by the model and also lower than the concentration in 1983. It is not clear whether this difference is due to methodical aspects, as the measurements in 1982 have been done by another laboratory, or that some other factors might have reduced the algal biomass. The species composition was not significantly different from the one in later years (Boesewinkel-De Bruyn *et al.*, 1988).

The underestimation of the variations in the seston concentration, especially the detritus component, in the model, is partly due to the fact that the resuspension flux is assumed to be constant, *i.e.* its dynamics due to variation in wind speed and other factors, is not modelled. Some of the field data, however, might have been influenced by storm events, which increase the contribution of resuspended matter to the seston. This also includes peat-derived particles, which most often settle again within a few hours (Gons & Van Keulen, 1989). These particles have a much lower phosphorus content than the detritus, but a comparable carbon content, leading to a temporary increase in particulate carbon in the water, while particulate phosphorus is less affected. Apart from this variation, also the more or less regular seasonal dynamics of the seston concentration is underpredicted by the model. In fact, total seston follows the changes in chlorophyll-*a* more closely. The variation in the chlorophyll-*a* content of the algae might have been overestimated, or mineralization in the water column might have been more important than assumed.

The seasonal pattern of the zooplankton data is not adequately reproduced by the model; for that purpose, the model formulation is too much a generalisation, while the zooplankton, due to its position as intermediary trophic level, is quite sensitive to parameter changes. The zooplankton is especially sensitive to the food quality, determined by the ratio of well-edible to poorly-edible algae; the algal types in turn depend on light conditions and phosphorus availability. Unfortunately, the literature data on the food type selectivity in zooplankton grazing leave a lot of uncertainty.

Why, then, is the system so resilient in responding to the load reduction? One reason is that the reduction has been, on the average, only a factor two, *i.e.* less than that expected (Van Liere & Janse, 1992). But even so, the system seems to be resistant to react to P decrease. Three factors seem to be crucial for the continuation of the prevailing cyanobacterial dominance. Firstly, the large amount of sediment detritus, which can be easily resuspended in a wind-exposed, turbulent lake like Loosdrecht (Gons *et al.*, 1991). Secondly, the high phosphorus assimilation efficiency of the cyanobacteria, which go on forming new organic matter despite a decreased phosphorus input. For cyanobacteria, this input must be reduced further than for other algal types before their growth becomes phosphorus-limited (Riegman, 1985). Thirdly, the low grazing pressure on the seston, which makes that most of the phosphorus in the lake is recycled within the seston and that only a small amount is transferred to higher trophic levels (Van Liere *et al.*, 1990). Grazing pressure is low because of the poor edibility of cyanobacteria and also because of the dense population of bream predating selectively on the large-bodied zooplankton (Gulati, 1990). The bream population remains high because of the near lack of losses by harvesting or predators; the low light conditions which favour bream are unfavourable to predatory fish (Lammens *et al.*, 1992). The load reduction has not been sufficient to break through this complex of interconnected factors which tend to keep the system in the present state.

Additional measures

An extra load reduction is necessary to make a long-term recovery possible, because high nutrient loadings are the ultimate cause of the hypertrophic state of the system. However, a load reduction to 0.35 mgP m^{-2} d^{-1} alone (measure b) would probably not be sufficient to break the cyanobacterial dominance, because the turbidity will remain high enough to favour this group, due to the resuspension of sediment detritus. Measures like removal of the top layer (if technically possible) or biomanipulation, carried out once without a further reduction of the external input, will have only a temporary effect or will have to be repeated regularly, because the amount of organic material in the lake will be replenished rapidly, due to the high external nutrient load. Flushing is not well possible in Lake Loosdrecht within the given constraints.

Additional measures may thus only be effective combined with load reduction, as is done, for instance, in the scenario g, which involves phosphorus load reduction combined with biomanipulation, introduction of predatory fish and 80% reduction of resuspension, under the assumption that submerged vegetation will recolonize and survive (Figs. 11 and 12). In this scenario, improvement is achieved in three ways. Firstly, the zooplankton grazing pressure on the seston will increase because the bream population would be lowered by predatory fish; secondly, the seston concentration will decrease also because of the low external nutrient loading and thirdly, it will be replenished less because of the low resuspension. This result is still speculative, however, because it assumes that predatory fish, *e.g.* pike, will be able to survive. This implies the returning of aquatic macrophytes, which will reduce resuspension by stabilizing the sediment and which yield hiding and nesting sites for pike (Van Liere *et al.*, 1990). They are, however, not an explicit part of the model but are regarded as a boundary condition; possible effects of macrophytes on the nutrient cycling are not considered. Anyway, development of macrophytes will be only possible if a sufficiently long period of clear water can be achieved, which implies reduction of the formation of organic material in the system. Several authors (*e.g.* Moss, 1980) have shown that a lake ecosystem can have several stable equilibrium states, whereof two extrema are the hypertrophic phytoplankton-dominated state and the mesotrophic macrophytes-dominated state. Transition between these states as a function of a changing nutrient input is subject to hysteresis effects, which obstruct restoration of hypertrophic lakes. Scheffer (1989) has shown these effects in a two-compartment bream-pike model, where the 'attractability' of the clear, macrophytes-dominated, 'pike state' became less with increasing trophic state. A system already being in the 'pike state' could stand some eutrophication without being drawn back to the turbid 'bream state'. In Scheffer's model the effect is due to the way the equations describe the interaction between the two fish species. In PCLOOS, hysteresis effects occur as a result of the differences in parameter values between the phytoplankton species in the model, which can lead to a rapid transition, in the simulations, to a state dominated by green algae as soon as the system would pass a certain threshold. These aspects need to be investigated further when the model will be validated also on the data of other shallow lakes.

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Chapter 11

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MODELLING NUTRIENT CYCLES IN RELATION TO FOOD WEB STRUCTURE IN A BIOMANIPULATED SHALLOW LAKE

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KEYWORDS: Model; nutrients; macrophytes; biomanipulation; lakes.

ABSTRACT

The model *PCLAKE* describes the phosphorus and nitrogen cycles within a shallow lake ecosystem, including the sediment and a simplified biological food web. All components are modelled in a generalized way rather than a very detailed one. This model has been applied to Lake Zwemlust, a small biomanipulated lake in The Netherlands. Formerly, this highly eutrophic lake was dominated by cyanobacteria and devoid of macrophytes. Biomanipulation was carried out in 1987 by pumping-out of the water, removal of all fish, and refilling of the lake with seepage water. The lake was restocked with some rudd, pike, zooplankton and seedlings of macrophytes, and then monitored up to 1992. Macrophytes developed rather quickly and reached their maximum biomass during the six-years period in 1989. Despite the continuously high nutrient (N and P) loading, algal biomass remained low due to nitrogen limitation, caused by competition with the macrophytes. From 1990 onwards, the macrophytes declined again and a species shift occurred, following an increase of herbivorous birds on the lake and the development of herbivorous fishes.

Model simulations grossly reproduced the observed developments in Lake Zwemlust before and after the biomanipulation measures. The existence of multiple steady states at the same trophic state and the possible shift between them could be simulated well. This study also demonstrates the interrelation between system structure and the distribution and cycling of nutrients. It is concluded, that within general boundary conditions set by the trophic state of the system, the food web structure determines the actual nutrient flows and the occurrence of nutrient limitations of the primary producers. It is shown that both aspects can be integrated in one mathematical model. The long-term stability of the macrophyte dominance in the lake is discussed.

INTRODUCTION

During recent decades, many shallow lakes in The Netherlands have become hypertrophic due to high nutrient loadings. Many of them are now characterized by dense algal blooms dominated by cyanobacteria, low transparency, loss of vegetation and predominance of bream. Although these effects were caused by high nutrient loadings, restoration of the water quality often could not be achieved by reduction of external load alone (SAS, 1989; VAN LIERE *et al.*, 1990). Eutrophic lakes show resistance to recovery, which means that the system, indicated by, for instance, the algal biomass, is relatively insensitive to changes in nutrient input (CARPENTER *et al.*, 1992b). Possibly, a given system may have two (or more) stable states for the same trophic status, a clear one, dominated by macrophytes, and a turbid, phytoplankton-dominated state (MOSS, 1990; SCHEFFER, 1990). The switch from a clear to a turbid state is not reversible, because the structure of the system has changed. Several mechanisms are involved, put together in the 'trophic cascade' hypothesis (PAINE, 1980). Not only biological mechanisms directly related to ecosystem structure play a role, but also the nutrient fluxes through the system are related to its structure and contribute to the observed effects (CARPENTER *et al.*, 1992a; COOKE *et al.*, 1993).

Based on this hypothesis, food-web management (also called biomanipulation) is sometimes considered as an additional measure in lake restoration programmes, mostly in combination with nutrient load reduction (see GULATI *et al.* (1990) for an overview). In Lake Zwemlust, a small, highly eutrophied shallow lake in The Netherlands, biomanipulation was carried out as a stand-alone measure, because a reduction of the external nutrient loading was not feasible; the main nutrient sources are seepage water from a river nearby as well as atmospheric deposition (VAN DONK *et al.*, 1993).

Mathematical models are a useful tool to evaluate the effects of restoration measures (load reduction, food web management or combinations). Most existing models dealing with the eutrophication problem (*e.g.* LOS, 1982; VAN DER MOLEN *et al.*, 1994; AMBROSE *et al.*, 1988; AALDERINK, 1993; see also overview in STRAŠKRABA and GNAUCK (1985)) are restricted to the 'nutrient side' of the lake system, *i.e.* the 'bottom up' effects of nutrient loading on algal biomasss and transparency. Other models describe the (biological) interactions between two or more system components, *e.g.* phytoplankton – zooplankton or two species of fish. This group includes detailed, population-based models, and so-called minimodels which describe these interactions or subsystems in a semi-quantitative way (*e.g.* SCHEFFER, 1990). The model MC^2, which has also been applied to Lake Zwemlust (BAKEMA *et al.*, 1990), offers a method to construct a balanced food web description (based on the flow of organic matter) for a system, combining all the available data. However, this model is not suitable for non-steady state situations, while nutrient cycles are not taken into account at all.

In the present study, the model *PCLAKE* (JANSE *et al.*, 1992; 1993) is used. This model combines the food web approach with the phosphorus and nitrogen cycles, in order to integrate, at a general level, bottom-up and top-down effects, without describing all the components in detail. Its objective is to get insight into the overall nutrient cycling in shallow lakes and to explore the conditions under which restoration measures might have effect. The model is applied to the case of Lake Zwemlust, with two objectives in mind. Firstly, to explore the value of the model, and secondly, to get a better insight into the processes playing a role in this biomanipulated lake.

LAKE DESCRIPTION

Lake Zwemlust is a small, isolated water body (1.5 ha) with a mean depth of 1.5 m and a maximum depth of 2.5 m, located in the province of Utrecht (The Netherlands). For a detailed description see VAN DONK *et al.* (1989). Apart from precipitation, the lake is mainly fed by nutrient-rich seepage water from the polluted River Vecht running nearby. The main loss is by infiltration to the ground water. The average water retention time is about 10 months, the nitrogen loading 9.6 g N m^{-2} y^{-1} (of which 5.3 g from atmospheric deposition and the rest from the seepage water) and the phosphorus loading 2.4 g P m^{-2} y^{-1} (mainly from seepage) (VAN DONK *et al.*, 1993). The estimated atmospheric deposition of N corresponds with data from RIVM (1991). Before the biomanipulation, the lake was highly turbid in summer due to the high biomass of the cyanobacterium *Microcystis aeruginosa* Kütz. The Secchi depth was about 0.3 m and the chlorophyll-*a* concentration was about 250 µg l^{-1}. The aquatic vegetation had disappeared almost completely and the fish community (about 800 kg ha^{-1}) was dominated for 75% by bream (*Abramis brama* L.). Because a reduction of the nutrient loading was not possible, a biomanipulation experiment was carried out.

BIOMANIPULATION

The experiment was carried out in March 1987. The lake was emptied by pumping out the water, all fish was removed and after the lake was refilled by seepage, in *c.* 3 days, it was restocked with 1600 juvenile pike (*Esox lucius* L.), 140 rudd, a stock of *Daphnia*, roots of *Nuphar lutea* L. and 'seedlings' of charophytes. Thus, a complete shift in fish species was attained. Details are given by VAN DONK *et al.* (1989). The development of the main chemical and biological components was studied during six years following the measures.

SUMMARY OF FIELD DATA

The results of the biomanipulation experiment have been described by VAN DONK (1991), VAN DONK *et al.* (1989; 1990; 1993; 1994), GULATI (1989; 1990), OZIMEK *et al.* (1990) and KORNIJOW *et al.* (1990). Only the main topics are repeated here. Despite the continuously high nutrient loadings to the lake, the structure of the ecosystem changed markedly. The blooms of *Microcystis aeruginosa* disappeared, the mean summer chlorophyll-*a* concentration decreased from 250 to 5-13 µg l^{-1} and the transparency (measured as Secchi depth) often reached the lake bottom. Small algae from various groups were present in the phytoplankton. Occasionally, a temporary bloom of filamentous green algae occurred. The submerged macrophytes redeveloped rapidly. In 1987 5% of the lake bottom (6 g DW m^{-2}) was covered, in 1988 70% (87 g DW m^{-2}) and in 1989 almost 100% (200 g DW m^{-2}) (all data are summer averages). Up to 1989, the rooted species *Elodea nuttallii* was the dominant species in summer, comprising 70-80% of the biomass. This plant is edible by herbivorous birds and fishes. In spring, also other species were important. From 1990 onwards, the vegetation biomass declined to 57 g DW m^{-2} and a shift towards the non-rooted and non-edible *Ceratophyllum demersum* was observed in summer. Zooplankton averaged around 1 g DW l^{-1} in spring and summer. The rudd population, stocked in 1987, gradually increased to 395 kg ha^{-1} in 1990, followed by a decline to 300 kg ha^{-1} in 1991. The pike population was variable, but finally increased up to 44 kg ha^{-1} in 1990 and 1991. No other fish species developed. The biomass of the macrozoobenthos increased and averaged 26-66 g FW m^{-2} (KORNIJÓW *et al.*, 1990). From the winter 1989/1990 onwards, herbivorous birds (mainly coots) were present on the lake during winter in densities of *c.* 70 (maximum 120) birds per ha.

Before the biomanipulation, the N and P in the lake (excluding the sediment) were stored in the phytoplankton, fish and in dissolved form. In the first year after the measures, most of the nutrients

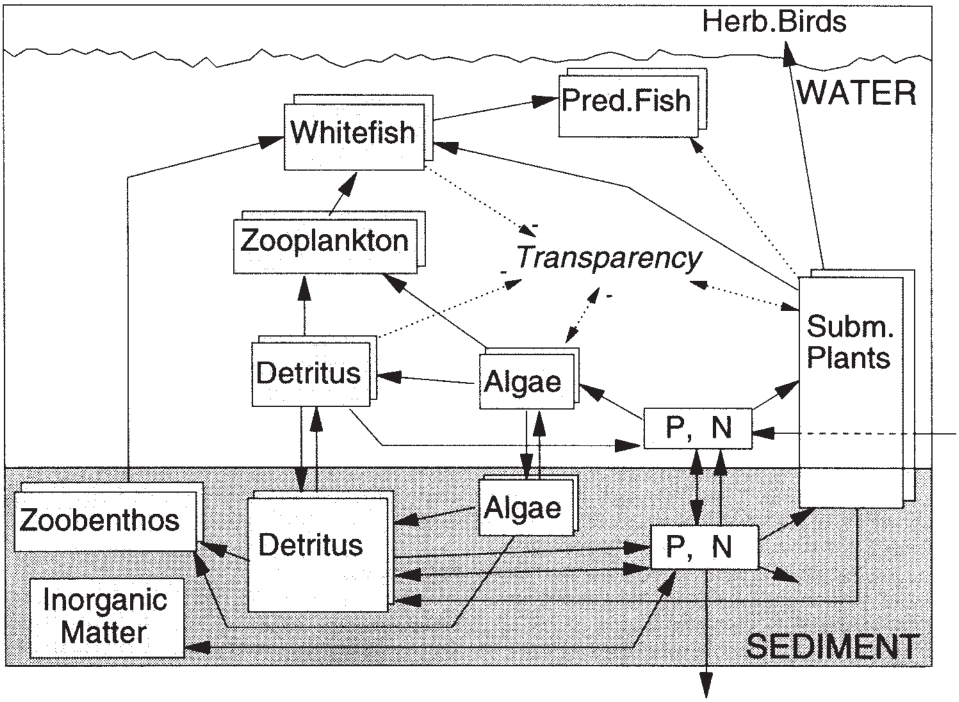


Fig. 1. *PCLAKE* model structure. Doubled blocks denote compartments modelled in both dry weight and nutrient units. Three functional groups of phytoplankton are distinguished: cyanobacteria, diatoms and other small edible algae. The macrophytes are divided in two groups: rooted, edible and non-rooted, non-edible plants, resp. Also, two groups of whitefish are distinguished, the first group ('bream') feeding on zooplankton and zoobenthos, the second one ('roach') on zooplankton and macrophytes. Arrows with solid lines denote mass fluxes (*e.g.* food relations), arrows with dotted lines denote 'empirical' relations (minus sign denotes negative influence, otherwise positive influence). Egestion and mortality fluxes of animal groups and respiration fluxes are not shown.

were present in dissolved form. During the following years, the SRP concentration remained high, whereas the concentrations of NO_3-N and NH_4-N dropped to very low levels in summer. Most of the nutrients were stored in the macrophytes during summer, and the phytoplankton was nitrogen limited (VAN DONK, 1991). In summer 1990, only 30% of the N and P was found in the macrophytes, while *c.* 30% was stored again in phytoplankton and fish (VAN DONK *et al.*, 1993).

THE *PCLAKE* MODEL

Structure

The *PCLAKE* model has been developed to describe the nutrient cycling in shallow lakes (JANSE *et al.*, 1992). It comprises both the water column and the upper sediment layer. The model has been applied to several lakes in The Netherlands, most of them being phytoplankton-dominated (JANSE *et al.*, 1992; 1993; ZAMUROVIĆ, 1993; ALDENBERG *et al.* 1994). It has been adapted for use on macrophytes-dominated lakes as well. Fig. 1 gives an overview of the model structure. For a detailed description see JANSE and ALDENBERG (1990, 1995). At the base of the model are the water and nutrient budgets (in- and outflow). The physico-chemical module describes the exchange of particles and nutrients between sediment and water. Processes included are sedimentation, resuspension, diffusion, burial and chemical adsorption. Mineralization processes are described both in the water column and the sediment. The trophic structure of the ecosystem is modelled on the basis of functional groups and is kept as simple as possible in view of the purpose of the model (Fig. 1). These groups are phytoplankton, detritus, zooplankton, macrozoobenthos, whitefish, predatory fish and submerged macrophytes.

The phytoplankton has been split into three subgroups, *i.e.* cyanobacteria, small edible algae and diatoms, because of their different characteristics concerning their function in the ecosystem and because of management's interests. For the modelling of the algal processes see JANSE *et al.* (1990). The macrophytes are modelled by a depth-integrated production function analogous to the one for algae. Some formulations are based on the models by VAN DIJK and JANSE (1993), WORTELBOER (1990) and SCHEFFER *et al.* (1993). Two groups of macrophytes are distinguished, rooted and non-rooted. The rooted plants may extract nutrients from both the water and the sediment pore water, the non-rooted only from the water. Except for the initial growth phase, it is assumed that the vegetation is homogeneously distributed over depth. It is realized that this might be an oversimplification in case of the non-rooted plants. Decline of the macrophytes is modelled as both natural mortality, taking place each year from a preset date, and, optionally, grazing losses to herbivorous birds and fishes. These grazing processes are assumed to affect the rooted plants only.

The animal groups are modelled according to TRAAS and ALDENBERG (1992). The growth formulations follow the logistic growth equation combined with a food limitation function and a correction to maintain a closed mass balance. It is assumed that the zooplankton feeds on phytoplankton and detritus, with a preference increasing in the sequence 1) cyanobacteria, 2) detritus, 3) diatoms and other small algae. Two groups of whitefish have been distinguished, the first one feeding on zooplankton and zoobenthos, the second one on zooplankton and macrophytes. The overall nutrient cycles are described as completely closed, except for external inputs and losses. This description was done by modelling all nutrient-to-dry-weight ratios dynamically (as indicated by the doubled blocks in Fig. 1). Mechanisms were included to cope with the often observed increase of the weight-specific nutrient contents of the organisms at higher trophic levels and the often observed changes in algal nutrient contents (ALDENBERG and PETERS, 1990; JANSE and ALDENBERG, 1990). It should be stressed that all the organisms are considered as dependent, directly or indirectly, on the nutrients that are available in the lake or the lake sediment.

Apart from mass fluxes (*e.g.* food relations), some 'empirical relations' are included in the model, such as the resuspension rate which is positively affected by the amount of bottom-feeding fish and negatively by the vegetation density, and the vegetation which is assumed to have a positive impact on the growth of predatory fish.

Implementation

The model has been implemented in the simulation package ACSL, version 10 (MGA, 1991). The model has been programmed in modules to allow some flexibility in structure. Most parameter values were taken from earlier studies with the model on phytoplankton-dominated lakes (JANSE *et al.*, 1992; 1993; ALDENBERG *et al.*, 1994). These values were derived from experimental and field research in Dutch lakes, from literature data and from calibration on the combined data of several lakes. The parameters for the 'cyanobacteria' group were based on those of *Microcystis*, the dominant species before the measures. The macrophytes parameters were taken from the macrophytes models mentioned in the previous paragraph and from literature on the two dominant species, while some of them were adjusted during calibration. For the rooted group, a root fraction of 0.05 was taken. It is assumed that only the rooted group is subject to grazing, whereas the natural decay starts earlier in the year for the non-rooted group. The calibration has not been exhaustive, as the model's aim is to analyse the general trends rather than trying to reproduce every single peak in the data.

Input parameters of the model were the inflow of water and nutrients, mean water depth, measured water temperatures, total irradiation (as bi-weekly moving averages) and the number of coots feeding in the lake in winter (from VAN DONK *et al.* (1994)). Because of the small size of the lake, wind influence on sedimentation and resuspension was assumed to be negligible. A final 'input' to the model was, of course, the biomanipulation measure carried out in 1987.

Output variables are the concentrations or densities of all modelled compartments and the fluxes between them, as well as a number of derived variables like total P, total N, chlorophyll-*a* and water transparency. Simulations were done for the period 1986-1992.

SIMULATION RESULTS

Food web changes

The *PCLAKE* simulations grossly followed the trend in the observations during the modelled period (Figs. 2 a-h); they did not reproduce, however, the exact field data. A problem for the comparison of simulations and field data is that for most variables, the data for 1986 are relatively scarce. Starting in 1986 with a stable turbid system, dominated by cyanobacteria and bream, it changed, within the two years following the biomanipulation measures, into a clear system with low chlorophyll-*a* concentrations, high Secchi depth in summer and well-developing macrophytes. This change is simulated well, although the macrophytes developed quicker in the model system than in reality. From 1990 on, following the development of rudd and the presence of herbivorous birds during winter, the rooted, edible plants were gradually replaced by the non-rooted, non-edible group. Although the total density declined, the macrophyte dominance persisted and the phytoplankton concentration remained low (Figs. 2 a and b). This trend is also observed in the field data, but with a lower macrophyte density and higher chlorophyll-*a* concentration in late summer.

On the average, the simulated total seston concentration (Fig. 2c) and Secchi depth (Fig. 2d) were in the range of the measured values, except for 1992. Peaks of zooplankton mostly followed within a month those of the edible algae (Fig. 2e). The rudd biomass increased within a few years up till about 6 g DW m^{-2} in 1990 (assuming a DW/FW ratio of 0.15), and decreased again later. The simulated pike density followed with a time lag (slower than observed) until a maximum of 0.5 g DW m^{-2} and declined later as well (data not shown).

The modelled SRP concentration (Fig. 2f) was underestimated during the cyanobacteria-dominated period (1986), but stayed always high after the biomanipulation. Both NH_4-N (Fig. 2g) and NO_3-N concentrations (Fig. 2h) were high in winter and spring (the NO_3-N peaks were overestimated), but near-zero during mid-summer from 1988 onwards. According to the model results, the phytoplankton growth was limited by both light and nitrogen before the biomanipulation. Shortly after the measures, the nitrogen availability was high, but after some time, a strong nitrogen limitation developed and remained. The simulations gave no indication for a phosphorus limitation.

Nutrient distribution

The distribution of the nutrients N and P among the various components of the system changed markedly over the years, like in the field data. Model and data are compared for the summer periods (May-August) of 1986 (Fig. 3a) and 1989 (Fig. 3b). The field data were taken from VAN DONK *et al.* (1993), completed with some unpublished results. Some compartments were pooled. If no summer averages were available, August values were taken. No field data were available on the sediment. The simulated total N and P concentrations (*viz.* the sum of all water compartments, including the macrophytes) roughly equal the observed ones, although differences remain in some compartments. In August 1986 most of the phosphorus was in the phytoplankton and fish compartments (Fig. 3a). The SRP pool at this time was underestimated by the model. The model indicated that the amount of phosphorus in the upper 20 cm of the sediment was much greater than the amount in the water compartments together, most of it in adsorbed, inorganic form. For nitrogen, the same overall conclusions hold true. Most of the nitrogen is bound in phytoplankton, fish

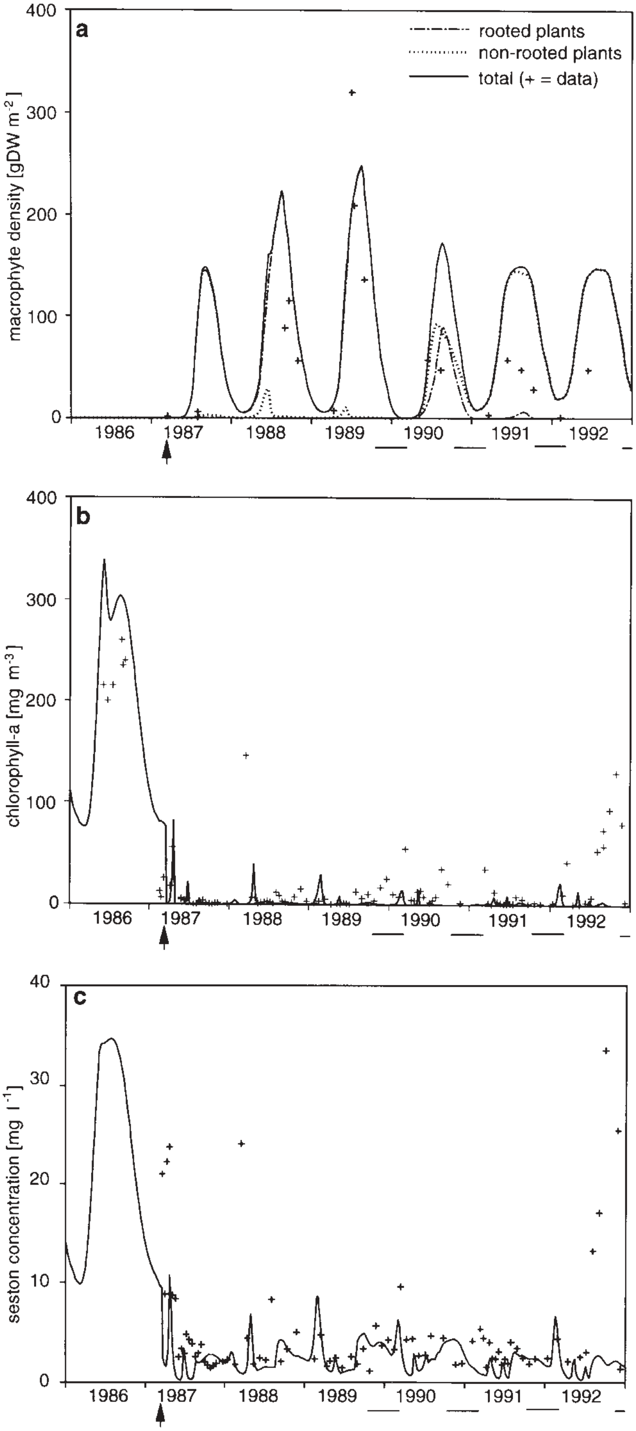


Fig. 2. Simulations for Lake Zwemlust, 1986-1992.

a, submerged macrophytes;

b, chlorophyll-*a*;

c, seston < 150 μm.

The arrow denotes the time of biomanipulation. The lines under the X-axis denote the periods during which herbivorous birds were present on the lake.

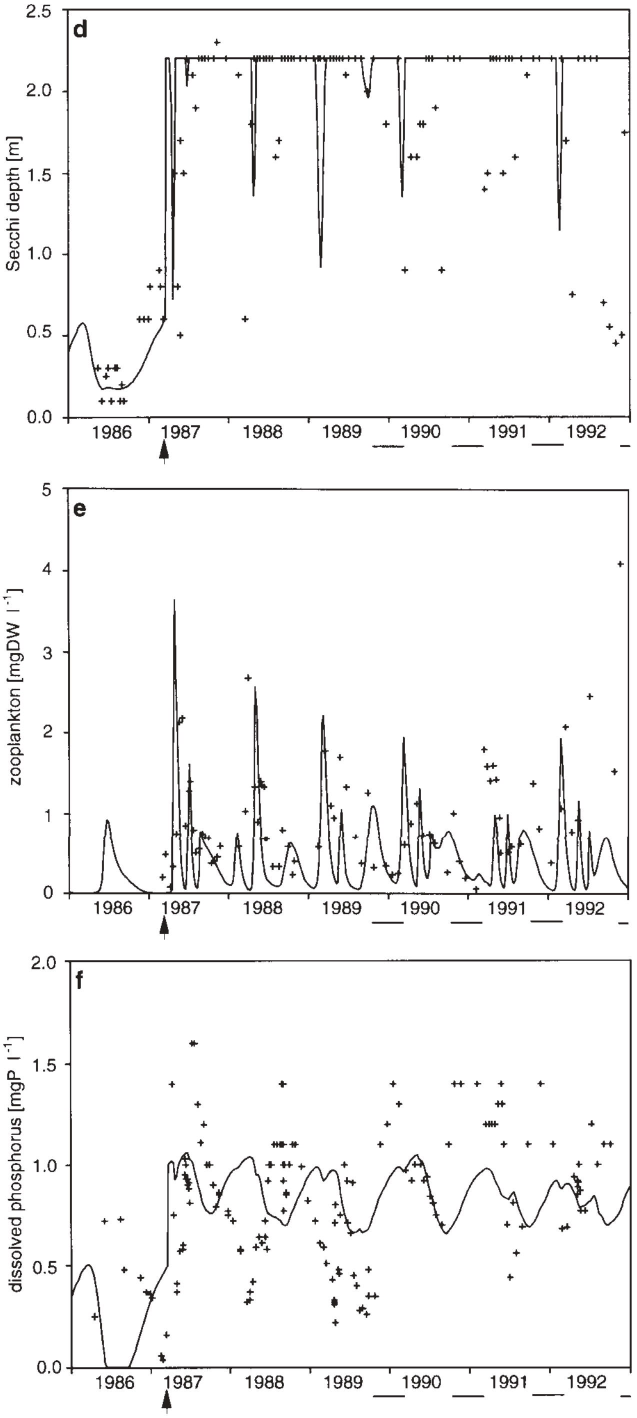


Fig. 2 Contd. Simulations for Lake Zwemlust, 1986-1992.

d, Secchi depth;

e, zooplankton;

f, SRP.

The arrow denotes the time of biomanipulation. The lines under the X-axis denote the periods during which herbivorous birds were present on the lake.

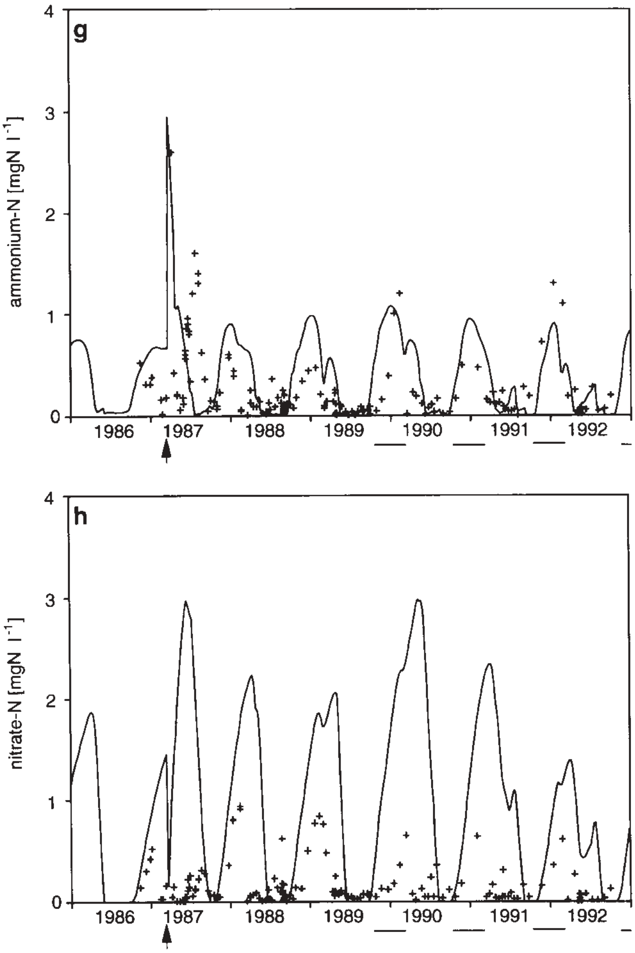


Fig. 2 Contd. Simulations for Lake Zwemlust, 1986-1992.

g, NH_4-N;

h, NO_3-N.

The arrow denotes the time of biomanipulation. The lines under the X-axis denote the periods during which herbivorous birds were present on the lake.

and organic matter in the sediment. The detritus compartment in the model is only partly comparable to the one in the field data, the latter probably including a pool of refractory detritus, which has no equivalent in the model.

In the summer of 1989, the phosphorus was mainly incorporated in the macrophytes and dissolved in the water, besides an amount present in fish (Fig. 3b). Also the sediment pool remains important. Concerning nitrogen, ammonia and nitrate pools were negligible, respectively, from May to August, and from June on (Fig. 2 g-h). (The high summer average of nitrate is explained by some high values in May.) The generally low levels of soluble nitrogen in summer contrast with the high concentrations of soluble phosphorus.

DISCUSSION

Evaluation of the model results

From an overall comparison of model simulations and field observations, it can be concluded that a generalized shallow lake model like *PCLAKE* is able to reproduce the main developments observed in the Lake Zwemlust case. Firstly, the existence of two different stable states, and the possible occurrence of a switch between them as a result of management options, is clearly demonstrated. Apparently, the main trigger to this switch is a sudden improvement of the underwater light climate. Secondly, this study demonstrates the close relation between nutrient dynamics and food web structure of a lake system. Despite the high nitrogen loadings to the lake, a nitrogen limitation of the phytoplankton is observed, in both model and field data. This limitation is because of competition with the macrophytes for the available nitrogen. In Lake Zwemlust nitrogen becomes the main limiting nutrient, because of the relatively low N/P ratio of 4 (w/w) in the external input. For most lakes in The Netherlands, the N/P ratio of the external loading is about 10 or higher (CUWVO, 1987). The nitrogen limitation might still be underestimated due to underestimation of the denitrification rate. An enhanced denitrification is often observed in macrophyte-dominated systems, but this aspect was not taken into account. Denitrification might be the cause of the too high simulated nitrate concentrations in spring.

After 1989, the grazing pressure on the macrophytes was increased, in winter by the presence of herbivorous birds and in summer by the increased biomass of herbivorous fishes (rudd). The birds were attracted from elsewhere by the newly developed vegetation and were imposed as an external factor in the model, whereas the fish is one of the model's state variables. As a result of this grazing pressure, a shift occurred from the edible (*Elodea*) to the non-edible (*Ceratophyllum*) macrophytes group. By introducing this extra mechanism in the model, the decline of the macrophytes could be prevented, as in reality (VAN DONK *et al.*, 1994), and the clear state of the system showed to be stable. However, the total macrophyte density was overestimated in the simulations after the shift had occurred. This overestimation might be due to competition with other plant species like *Potamogeton,* which are known to occur in the lake in spring and early summer, but were not included in the model, and/or to competition with periphytic algae.

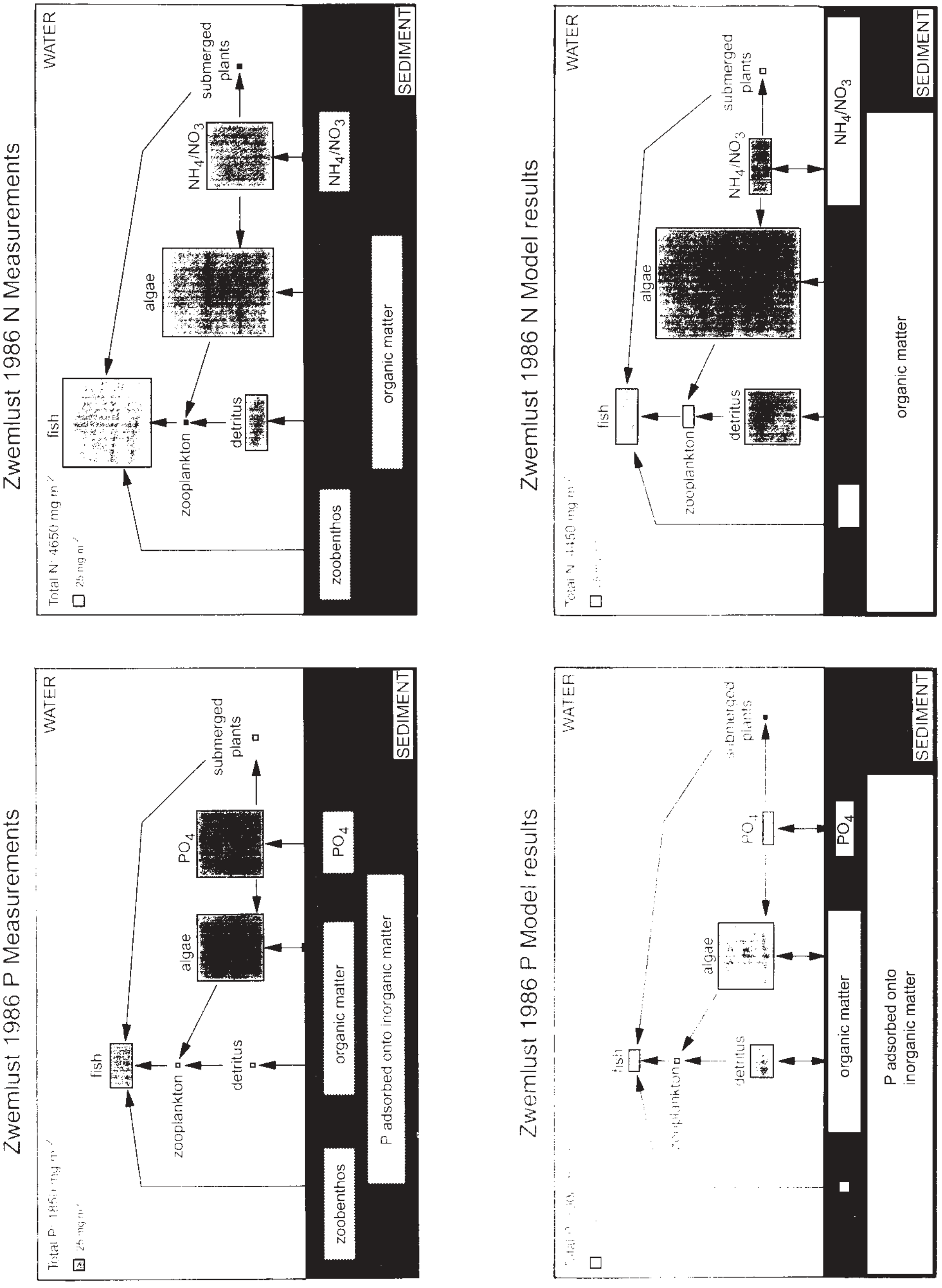
Although the model results are presented as single-run simulations, they should be interpreted in a probabilistic rather than a deterministic way. The results are dependent on a lot of parameter settings, many of which are more or less uncertain due to natural variability or other reasons. By means of statistical tools, such as Bayesian uncertainty analysis (ALDENBERG *et al.*, 1994), the resulting uncertainty in the results as a function of the combined uncertainty in the parameters should be established. In this way, the model results can be expressed as the *chance* to long-term recovery of a lake given the actual nutrient loading and management options and in view of local circumstances.

This study thus supports the view that shifts in the structure of a system may be analyzed also in terms of changes in nutrient cycles (*cf.* CARPENTER *et al.*, 1992 a,b), within the limits set by the overall trophic state of the system as a general boundary condition (see COOKE *et al.*, (1993)). It is shown to be useful to integrate those aspects in one mathematical model in order to evaluate the combined effects of bottom-up and top-down control. This approach may be complementary to the existing modelling tools for the analysis of two-compartment systems (*e.g.* SCHEFFER, 1990; SCHEFFER *et al.*, 1993; VAN DIJK and JANSE, 1993) and to more detailed water quality models.

Long-term stability

The model may be also helpful to evaluate under what circumstances the clear water state in biomanipulated lakes is stable or not (GULATI *et al.*, 1990). On both theoretical grounds and from experience in other lakes, it would be argued that a long-term stable clear situation is not compatible with high nutrient loadings (BENNDORF, 1990). Our model shows the central role of the macrophytes in the stability of the system, both through their role in the nutrient cycle and as habitat factor for pike. If the macrophytes decline, as a result of increased loss processes, to below a certain limit, the stability of the system might be threatened and the phytoplankton might increase again. In Lake Zwemlust, such loss processes are the grazing pressure by the newly attracted herbivorous birds and by herbivorous fish. Extinction of the macrophytes was impeded by the observed shift from edible to non-edible plant species, but the biomass became lower. Another potentially destabilising phenomenon might be competition for light and/or nutrients with filamentous green algae, which are developing occasionally in the lake (OZIMEK *et al.*, 1990) or with periphyton, which are not included in the model. Although the pike population contributed indirectly, through the 'trophic cascade', to keeping algal biomass low, it is itself dependent on the presence of macrophytes.

Several circumstances might act in favour of the success of the biomanipulation of Lake Zwemlust. Firstly, wind-induced resuspension of sediment material is negligible in this case because of the small area of the lake. From several biomanipulation studies in The Netherlands the picture arises that, while the measures had some success in small



Zwemlust 1986 N Measurements

Zwemlust 1986 N Model results

Zwemlust 1986 P Measurements

Zwemlust 1986 P Model results

Fig. 3a. Measured (VAN DONK *et al.* 1993) and modelled (*PCLAKE*) distribution of nitrogen (N) and phosphorus (P) among the [illegible] system compartments in summer 1986 (May-August), before the biomanipulation measures. The surface of the blocks denotes the average pool size. The totals refer to all compartments except for the sediment. Compartments which have not been measured are shown [illegible]

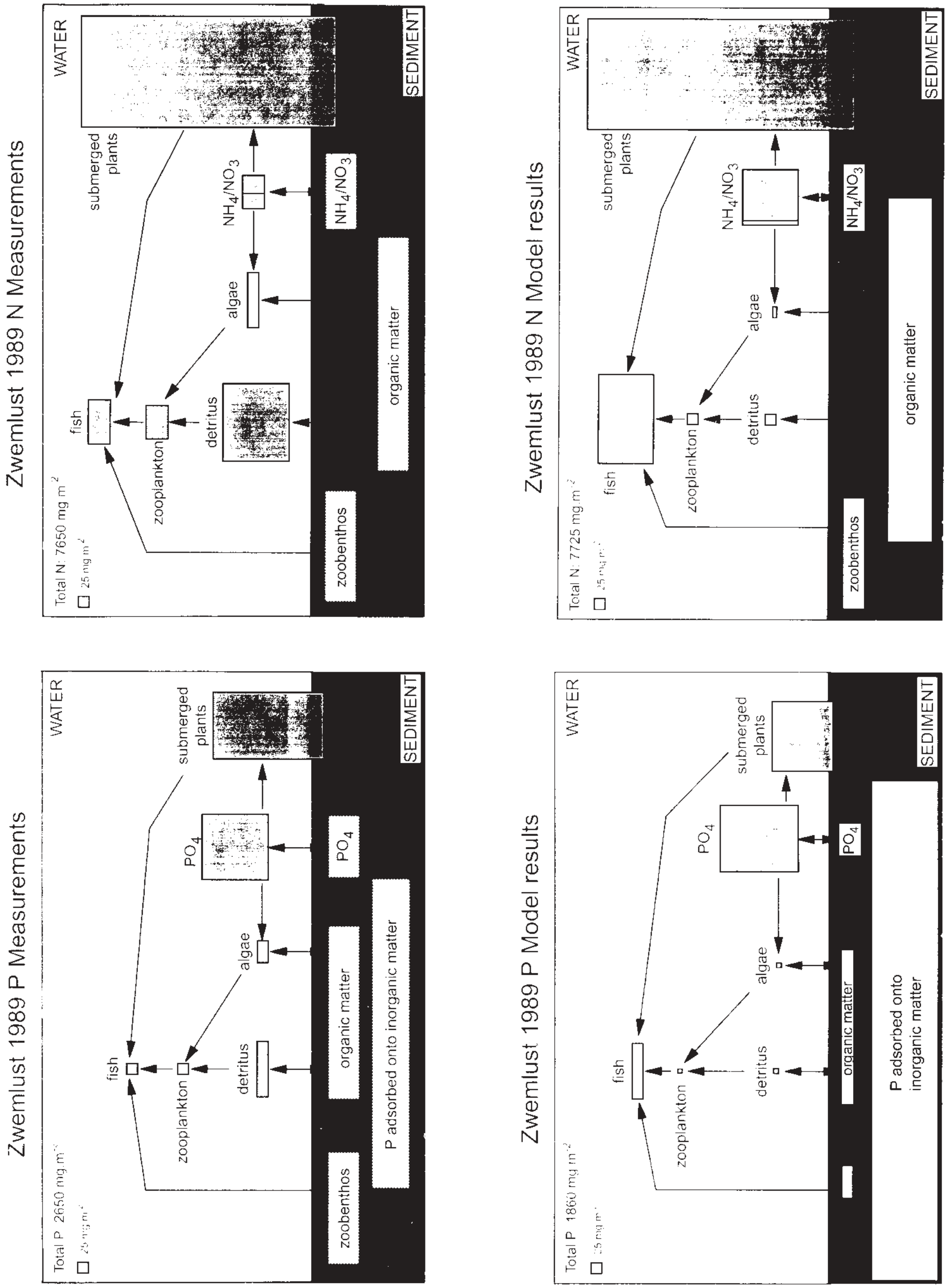


Fig. 3b. Measured (VAN DONK *et al.*, 1993) and modelled (*PCLAKE*) distribution of nitrogen (N) and phosphorus (P) among the main system compartments in summer 1989 (May-August), after the biomanipulation measures. Further details as in Fig. 3a.

lakes, they had not in larger lakes, where recovery of the vegetation was impeded by turbulence and deterioration of the light climate due to resuspension (GONS *et al.*, 1991; VAN DIJK and VAN DONK, 1991). This phenomenon can be reproduced by the *PCLAKE* model. Secondly, because of the rigorous way the biomanipulation experiment was carried out in Lake Zwemlust, benthivorous fish (bream) could be removed for 100% and due to the isolated character of the lake, it did not recolonize the lake. If it did (there would be ample food supply), it might be able cause deterioration of the light conditions again due to its browsing in the sediment. In a simulation experiment with re-introduction of benthivorous fish, a decrease in transparency was, indeed, observed (results not shown). Thirdly, the fact that nitrogen and not phosphorus becomes limiting might further reduce the competitive advantages of cyanobacteria compared with edible algae. There is some ecophysiological evidence that cyanobacteria are relatively good competitors for phosphorus, but less so for nitrogen (SCHREURS, 1992). This aspect might be further explored by means of simulation experiments with different nutrient loadings. Fortunately, blooming of nitrogen-fixing algae, a problem that occurred in some other lakes where algae were nitrogen-limited, did not occur in Lake Zwemlust. The cause for this is not known, but possible hypotheses are an iron or molybdenum limitation (two elements for which N-fixing organisms have a high need (PAERL, 1990) or allelopathic effects.

Nevertheless, in Lake Zwemlust the stability of the clear state is probably less than would be the case at a much lower nutrient loading. So, in view of this high loading, regularly repeated food web management might probably be required.

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Chapter 12

A MODEL STUDY ON THE STABILITY OF THE MACROPHYTE-DOMINATED STATE AS AFFECTED BY BIOLOGICAL FACTORS

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Abstract—The transition of shallow lake ecosystems between the clear-water, macrophyte-dominated state and the turbid state dominated by phytoplankton depends on both physico-chemical and biological factors. In this study, the impact of some of these interactions on the stability of the macrophyte-dominated state of a lake are studied by means of the integrated eutrophication model *PCLake*. The model describes phytoplankton, macrophytes and a simplified food web, within the framework of closed nutrient cycles. The aim of the study is to evaluate the impact of herbivory by birds and fish on the transition from clear to turbid state, including the influence of variability in other biological parameters. The model was applied to the data of a small, biomanipulated lake, dominated by macrophytes, showing signs of a transition back to the turbid state. Simulations were carried out for the lake as well as for an experimental situation where herbivory was impeded. A parameter variation study was performed for 10 parameters, affecting the zooplankton, fish and macrophytes behaviour, to determine the sensitivities and the model uncertainty. The model reproduced adequately the transition of the lake from phytoplankton dominance before the biomanipulation, via dominance of rooted perennial plants in the first years after it, to a state characterized by turion-forming plants in early summer and phytoplankton in autumn. It is shown that the probability of the transition back to phytoplankton dominance is mainly enhanced by herbivory by birds. This caused a shift towards inedible plant species with a shorter natural growing season, allowing the return of a phytoplankton bloom in autumn. If herbivory was impeded, this shift did not occur and phytoplankton remained low due to nitrogen limitation. The model results were quite sensitive to the zooplankton filtering rate and, in the presence of herbivory only, to the macrophytes growth parameters. The impact of the fish parameters showed to be less important. The model may be used to evaluate the relative importance of different assumptions or factors in the success of biomanipulation measures in lakes.

Key words—biomanipulation, herbivory, hysteresis, lake ecosystem, Lake Zwemlust, macrophytes, model, phytoplankton, sensitivity analysis, uncertainty analysis

INTRODUCTION

It is now generally realized that shallow lakes may have two alternative states, a clear-water state dominated by macrophytes and a turbid-water state dominated by phytoplankton (Moss, 1990; Scheffer, 1990; Jeppesen *et al.*, 1990). Several factors determine which state prevails in a certain case. A general constraint is set by the external nutrient loading. At a high loading, only the turbid state is stable, whereas the opposite is true for a low nutrient loading. In the intermediate range, both states may exist and switches between the two states are possible. Because both states possess a number of self-stabilizing buffering mechanisms, the critical loading level at which a shift occurs is dependent on the initial state of the system: the shift from turbid to clear occurs at a much lower loading level than the opposite one (hysteresis). In the intermediate range, a shift may be invoked by a natural or anthropogenic disturbance of the system (Scheffer, 1990). For example, a shift from turbid water to clear water might be induced by a natural fish kill or by a biomanipulation measure: removal of benthivorous and zooplanktivorous fish (Cooke *et al.*, 1993).

The probability of a switch at a certain nutrient loading depends on both physico-chemical and biological factors. The former include lake characteristics like depth, size, sediment type, water retention time, etc. Biological factors involve the ecophysiological properties of the organisms in the system, like their life cycle, growth and loss parameters. Growth parameters determine the competition between the different primary producers for environmental factors like nutrients and light. Loss factors include, besides natural mortality, zooplankton grazing on algae and the consumption of macrophytes by her-

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bivores. Both are affected by the ecosystem structure, e.g. dependent on "cascading effects" through the food web. This paper focuses on the role of these biological factors on the probability of a transition to the turbid state.

This topic is approached by means of the simulation model *PCLake*, an integrated eutrophication model describing phytoplankton, macrophytes and a simplified food web, within the framework of closed nutrient cycles (see "Model description"). The model gives the opportunity to evaluate the impact of different assumptions on ecological interactions (as derived, for instance, from ecophysiological knowledge). The *PCLake* model has been used to simulate the bistability of shallow lakes in a range of nutrient loadings and the hysteresis phenomenon frequently observed in this respect (Janse, 1997). The aim of the present study is to evaluate the impact of herbivory on the transition from clear to turbid state, including the influence of variability in a number of other biological parameters, concerning zooplankton, macrophytes and fish. As a case study, the model is applied to the data of Lake Zwemlust, a lake with a high nutrient loading which shifted between the two states in the past few years (Van Donk and Gulati, 1995). In an earlier study, the model has been applied to simulate the shift from the turbid to the clear-water state in Lake Zwemlust, triggered by a biomanipulation measure (Janse *et al.*, 1995). It was concluded that the clear-water state was mainly stabilized by the macrophytes themselves, by means of nitrogen competition. This paper deals with the transition to the turbid state observed six years later.

FIELD DATA

Summary of developments in the lake

The field data used are from Lake Zwemlust, a small (1.5 ha), shallow (mean depth 1.5 m), isolated lake in the Netherlands. The lake is fed by precipitation and by seepage water from a nearby river. The nitrogen loading to the lake averages $9.6\ \mathrm{g\,m^{-2}\,y^{-1}}$, the phosphorus loading $2.4\ \mathrm{g\,m^{-2}\,y^{-1}}$ and the water retention time *ca.* 10 months. The developments occurring in the lake have been described in detail by, among others, Van Donk *et al.* (1989, 1990, 1993) and Van Donk and Gulati (1995). At the end of the 1960s, the macrophytes that were previously present disappeared, due to increased eutrophication (M. de Ruiter, pers. comm.) and the use of herbicides (Van Donk *et al.*, 1989), and the lake turned into a turbid state dominated by the cyanobacterium *Microcystis aeruginosa*. This lasted until March 1987, when a rigorous biomanipulation measure (temporary drawdown of the lake and removal of all zooplanktivorous/benthivorous fish) reestablished a macrophytes-dominated state (Van Donk *et al.*, 1989). Three years later, a species shift occurred from *Elodea* via *Ceratophyllum* to *Potamogeton*, possibly triggered by increased herbivory. This was followed by a gradual decline of the macrophytes biomass and return of phytoplankton blooms in autumn, a sign of a transition in the direction of the turbid state (Van Donk and Gulati, 1995).

Cage experiments

In order to study the impact of herbivory by birds and fishes on the macrophytes development, exclosure experiments were carried out. They have been described by Van Donk and Otte (1995). Iron cages with a mesh-width of 1 × 1 cm were placed on the lake bottom All cages started with a mixed macrophytes community with *Elodea* as the dominant component. Birds and fishes were excluded from the cages, whereas some cages were additionally stocked with rudd. In contrast to the observations in the lake itself, the macrophytes biomass (mainly *Elodea*) remained high in all cages. The densities were somewhat lower in the cages including rudd. It was concluded that herbivory, especially by birds, was an important factor in explaining the species shift mentioned above.

MODEL DESCRIPTION

Model structure

The model used, *PCLake*, is a general eutrophication model of shallow lake ecosystems. It combines a description of the nutrient cycles and the development of phytoplankton and submerged water plants with a food web approach. The main components and processes considered as important for the development of algae and submerged macrophytes have been included, without going in too much detail. The food web has been included to account for the effects of food web structure on primary producers and nutrient cycles, and to simulate the effects of food web management on algal biomass. For an extensive description of the model see Janse and Aldenberg (1997). The model describes a well-mixed water body and comprises both the water column and the upper sediment layer. The nutrient cycles are closed within the model system (except for external inflow, outflow and denitrification); therefore, most components were modelled in multiple units (Janse and Aldenberg, 1990, 1997).

The components in the model are (Fig. 1): inorganic nutrients (both in water and pore water), detritus, sediment detritus, phytoplankton, submerged macrophytes, zooplankton, zoobenthos, whitefish and predatory fish. All biota are modelled as functional groups. The model configuration is flexible and may be adapted according to model objectives and available data. Concerning the phytoplankton, the default distinction in three groups, *viz.* cyanobacteria, diatoms and other edible algae, has been

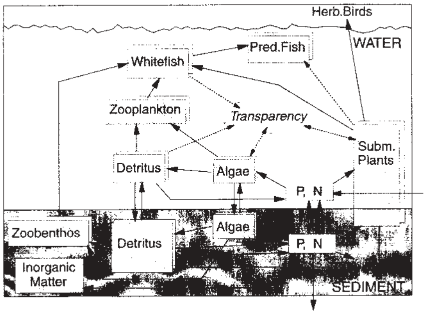

Fig. 1. *PCLake* model structure. Doubled blocks denote compartments modelled in both dry weight and nutrient units. Three functional groups of phytoplankton are distinguished: cyanobacteria, diatoms and other small edible algae. The macrophytes are divided into three groups, *viz.* rooted perennials, non-rooted plants and turion-formers. Also, two groups of whitefish are distinguished, *viz.* planktivorous/benthivorous group and a planktivorous/herbivorous group. Arrows with solid lines denote mass fluxes (e.g. food relations), arrows with dotted lines denote "empirical" relations (minus sign denotes negative influence, otherwise positive influence). Egestion and mortality fluxes of animal groups and respiration fluxes are not shown.

maintained. Epiphytic algae have not been modelled separately. For this study, three macrophyte groups have been distinguished, *viz.* rooted perennials, rooted turion-forming plants and non-rooted plants (Table 1), and two groups of whitefish, *viz.* planktivorous/benthivorous fish (represented by bream) and planktivorous/herbivorous fish (represented by rudd). The predatory fish is mainly represented by pike. Finally, herbivorous birds have been defined as an external factor: the period of their presence (mid-September until mid-March, from 1989 on) and their maximum density (*ca.* 100 birds ha^{-1}) is taken from visual observations (Van Donk and Otte, 1995). Thus, the same model configuration as in a previous paper on Lake Zwemlust (Janse *et al.*, 1995) was used, except for the inclusion of the turion-forming plants.

Processes and assumptions

General processes include mineralization, (de)nitrification, phosphorus adsorption, sediment-water exchange of nutrients, and settling of phytoplankton and detritus. Wind-induced resuspension has been neglected, because of the small size of the lake (1.5 ha). Phytoplankton production has been assumed dependent on the light climate and the internal nutrient concentrations; losses may occur by settling, mortality and grazing. The cyanobacteria have a lower growth rate, but also lower loss rates and a lower grazing pressure by zooplankton than the other algae. Also the growth of macrophytes is described as dependent on their internal nutrient content as well as the light climate, assuming a homogeneous distribution of the vegetation over the water column. The differences between the three macrophyte groups are summarized in Table 1. The root fraction of each group is assumed fixed. All plants may extract nutrients from the water column, and the two rooted groups also from the interstitial water. Natural mortality is assumed to start on a pre-set date towards the end of the growing season: for the perennial group mid-August, for the turion-formers early July, the time reallocation of biomass to the turions starts on the average (Van Wijk, 1988). The turions germinate again the next spring, giving rise to above-ground biomass. Apart from this difference in life cycle, the plant groups differ in their vulnerability to herbivores. The rooted perennials are considered as edible to both herbivorous birds and planktivorous/herbivorous fish, the non-rooted plants only (but not as their preferred food) to birds, and the turion-formers only to fish (Van Donk and Otte, 1995).

The zooplankton grazes upon phytoplankton and detritus, with a lower preference for cyanobacteria than for other algae. Possible effects of vegetation on zooplankton have been neglected. Concerning fish, the "bream group" is assumed to feed on zooplankton and zoobenthos, the "rudd group" on zooplankton and the two macrophytes already mentioned, and the predatory fish on both of the other fish groups. The herbivorous birds, if present, feed on the rooted perennials and a little on the non-rooted plants. Two "non-food relations" are to be mentioned: the "bream group" is assumed to cause some "stirring up" of sediment material when feeding (Breukelaar *et al.*, 1994), and the predatory fish

Table 1. Characteristics of the macrophyte groups in the model

	Macrophyte group		
Characteristic	Rooted perennials	Non-rooted plants	Turion-formers
Root fraction	0.05 [–]	0.0 [–]	0.15 [–]
Nutrient uptake	water and sediment	water column only	water and sediment
Formation of turions	no	no	yes, in early summer
Start of mortality	mid-August	mid-July	early July
Edibility for birds (coots)	yes	partial (low preference)	no
Edibility for fish (rudd)	yes	no	yes, partial
Example	*Elodea*	*Ceratophyllum*	*Potamogeton*

is dependent on the presence of vegetation for its growth and survival (Grimm, 1989).

Parameter values were derived from literature data and partly by calibration on data on a number of shallow Dutch lakes, used in earlier studies with the model (see Janse, 1997). The cyanobacteria parameters were based on those of *Microcystis*, the dominant species in the lake before the biomanipulation. A limited number of parameters, mainly of the macrophytes, have been calibrated on the Lake Zwemlust data within the ranges found in the literature.

Input and output of the model

The main output variables calculated by the model are the concentrations or densities of the different groups of phytoplankton and submerged macrophytes, chlorophyll-a, transparency, zooplankton and fish biomass, and the distribution and fluxes of the nutrients N and P. Inputs to the model are: water flow, nutrient loading, lake depth, temperature, light and sediment characteristics, as well as initial values of the state variables.

SIMULATION METHODS

Simulations

The model has been implemented in the program ACSL®, version 10. Firstly, simulations were done for the period 1986–1994, i.e. from the year before the biomanipulation until seven years after. The actual loading data were used as an input, but for light and temperature, sine functions were used. The biomanipulation measures in March 1987 were modelled the same way as in Janse *et al.* (1995): removal of the bream, removal of most of the phyto- and zooplankton (as the lake was temporarily drawn down), and restocking with some rudd, pike, zooplankton and macrophytes (all in very small densities). Secondly, simulations of the abovementioned cage experiments (*viz.* excluding herbivory by birds and fishes) were performed. They differed from the lake simulations in that the bird density was set to zero and the fish was assumed unable to feed on the macrophytes. The cage simulations started with the *Elodea*-dominated situation in 1989. (Actually, the cage experiments in the field were performed in 1992–93, but the initial conditions in the cages were comparable to the ones used in the simulations.) For comparison, an additional simulation was performed for a cage stocked with rudd, thus excluding herbivory by birds but including herbivory by fishes.

Uncertainty and sensitivity analysis

The simulations were combined with an uncertainty and sensitivity analysis, as it is realized that parameter values have a natural variability. The model results can thus be interpreted in a probabilistic way. Parallel simulations were done for the "lake" and the "cage" situations. Apart from the runs with the nominal parameter values, 200 Monte Carlo runs were performed for each situation. Ten parameters, dealing with the zooplankton, fish and growth of macrophytes (listed in Table 2), were sampled within predefined ranges (for most parameters ± 20% of the nominal value), assuming no correlations, according to the Latin Hypercube technique (Janssen *et al.*, 1992). This may be regarded as a "sparse grid" method, taking one sample in each "row" and one in each "column". All other parameters were kept constant, most of them equal to the nominal value. Results were written monthly for the fifth year of the simulations and the distribution of the output variables was analyzed. Multiple linear regression analysis was performed on the sampled parameters for a number of response variables (listed in Table 3) by means of the "Stepwise" method in the program SPSS®. The regression coefficients and relative sensitivity coefficients of the response variables to the different parameters were calculated for the combined results as well as for the "lake" and "cage" simulations separately.

RESULTS

Nominal simulations

The results of the nominal simulations for the lake and the fish-free cage are shown in Fig. 2(a)–(d), together with the data measured in the open lake (" + " signs). In these graphs, the time of the

Table 2. List of parameters used in the regression analysis

Symbol	Description	Unit	Mean value	SD
θ_0	Herbivory: 0 = no herbivory ("cage conditions"), 1 = herbivory included ("lake conditions")	[–]	–	(0.50)
θ_1	Maximum filtering rate of zooplankton	[$\mathrm{l\ mg^{-1}\ d^{-1}}$]	2.0	0.23
θ_2	Preference factor for cyanobacteria for zoopl. grazing	[–]	0.25	0.03
θ_3	Zooplankton mortality rate	[$\mathrm{d^{-1}}$]	0.04	0.005
θ_4	Max. growth rate of non-rooted plants	[$\mathrm{d^{-1}}$]	9.0	1.04
θ_5	Max. growth rate of rooted turion-forming plants	[$\mathrm{d^{-1}}$]	10.0	1.16
θ_6	Pref. factor for non-rooted plants for bird grazing	[–]	0.2	0.06
θ_7	Max. growth rate of whitefish	[$\mathrm{d^{-1}}$]	0.02	0.002
θ_8	Half-saturating food density for whitefish	[$\mathrm{g\ m^{-2}}$]	2.0	0.23
θ_9	Max. growth rate of predatory fish	[$\mathrm{d^{-1}}$]	0.02	0.002
θ_{10}	Half-saturating food density for predatory fish	[$\mathrm{g\ m^{-2}}$]	1.0	0.12

Table 3. List of response variables used in the regression analysis

Variable	Description	Unit	SD
Chlorophyll-a	Phytoplankton chlorophyll-a	[mg m^{-3}]	11.1
Rooted peren.	Rooted perennial plants	[g DW m^{-2}]	53.3
Non-rooted	Non-rooted plants	[g DW m^{-2}]	20.9
Turion-form.	Turion-forming plants	[g DW m^{-2}]	2.2
Macroph. total	Macrophytes, total	[g DW m^{-2}]	51.4
Zooplankton	Zooplankton	[g DW m^{-3}]	1.4

biomanipulation is indicated by an arrow and the periods with birds by bars under the x axis. The cage simulations started at the open square. The lake simulations (solid lines) are described first. The simulated macrophyte density [Fig. 2(a)] changed from near-zero before the biomanipulation to over 250 g m^{-2} in 1989, followed by a decline to about 100 g m^{-2}. The same was observed in the data. In 1988–1989, the rooted perennials were the dominant group in the simulations, whereas from 1990 on, they were replaced by the rooted turion-forming group [Fig. 2(b)]. The intermediate codominance of non-rooted plants observed in the data was not reproduced by the model (see below). The phytoplankton chlorophyll-a concentration [Fig. 2(c)] changed from high values throughout the year (about 300 mg m^{-3} in summer) before the measures to generally low values in 1988–1989 with only a bloom in the spring period. From 1991 on, also an autumn bloom appears, like in the field data, although its magnitude is underpredicted. The zooplankton [Fig. 2(d)], being very low before the measures, in general follows the algal peaks; the peaks are often overpredicted. Planktivorous/benthivorous fish was present only before the biomanipulation, while planktivorous/herbivorous fish reached densities between 5 and 7 g DW m^{-2} from 1990 on, comparable to the in-lake measurements (Van Donk and Otte, 1995) (data not shown). The calculated density of predatory fish reached values around 0.2 g DW m^{-2}, compared to 0.6 g DW m^{-2} in reality. The system seems to reach a new dynamic steady state (with constant seasonal fluctuations) from 1993 on.

The simulations of the cage experiments [Fig. 2(a), (c), (d), dotted lines] showed that the macrophyte density remained high [Fig. 2(a)] and dominated by the rooted perennials, in contrast to the shift observed in the lake simulations. The peaks of phytoplankton chlorophyll-a in the cage simulations shifted in time somewhat compared to the lake simulation, while the autumn bloom was nearly absent in the cage simulations [Fig. 2(c)]. Also the zooplankton peaks shifted in time. The zooplankton concentration in summer was lower in the cage simulations compared to the lake, while it was higher in autumn [Fig. 2(d)]. The simulated fish densities were near-zero. The simulations of the cage containing fish differed only slightly from those of the one without fish; the macrophyte density was a little bit lower (results not shown).

Monte Carlo simulations

The results of the Monte Carlo simulations, for the autumn of the fifth year after the start of the cage simulations, are shown in Figs 3 and 4 and Tables 4 and 5. For the analysis, the presence or absence of herbivory has been put in the discrete "herbivory parameter" θ_0: a value of 0 corresponds to the absence of herbivory ("cage conditions"), a value of 1 to its presence ("lake conditions"). The rooted perennial plants always have a high density in the absence of herbivory; their density varies between 75 and 130 g DW m^{-2} depending on the values of the other ten parameters [Fig. 3(a)]. When herbivory occurs, this plant group is absent in all model runs. The group is thus negatively correlated with herbivory (as indicated by the regression line). The opposite is true for the other two plant groups: without herbivory they are absent in all runs, with herbivory one of the two (or both) may be present [Fig. 3(b)–(c)]. The density of the turion-formers is always low, a reflection of the fact that they are present only a small part of the year. Also phytoplankton chlorophyll-a is positively correlated with herbivory: high values occur more frequently if plant-eating animals are present [Fig. 3(d)]. The zooplankton results are widely scattered, but the overall correlation between θ_0 and zooplankton turns out to be negative [Fig. 3(e)]. These results could also be interpreted in terms of percentiles or as the probability to exceed a certain value. The probability of the autumn chlorophyll-a concentration exceeding 20 mg m^{-3}, for instance, increases to 30% if herbivorous animals are present, in contrast to only 2% in absence of them [Fig. 3(d)]. The scatter plots [Fig. 4(a)–(c)] reveal some of the correlations between the output variables: a high density of rooted perennial plants most often coincides with a low chlorophyll-a concentration [Fig. 4(a)], while a high concentration is most often seen in conjunction with a relative dominance of turion-formers [Fig. 4(b)]. The relation between chlorophyll-a and zooplankton is mainly negative, but highly different for the two situations [Fig. 4(c)]. The differences may be explained by indirect effects, e.g. an increased formation of detritus (also food for zooplankton) in the period of macrophytes decline.

Multiple linear regression analysis revealed the impact of the different parameters on these distributions (Tables 4 and 5). The regression coefficients are given as is (Table 4) and in standardized form,

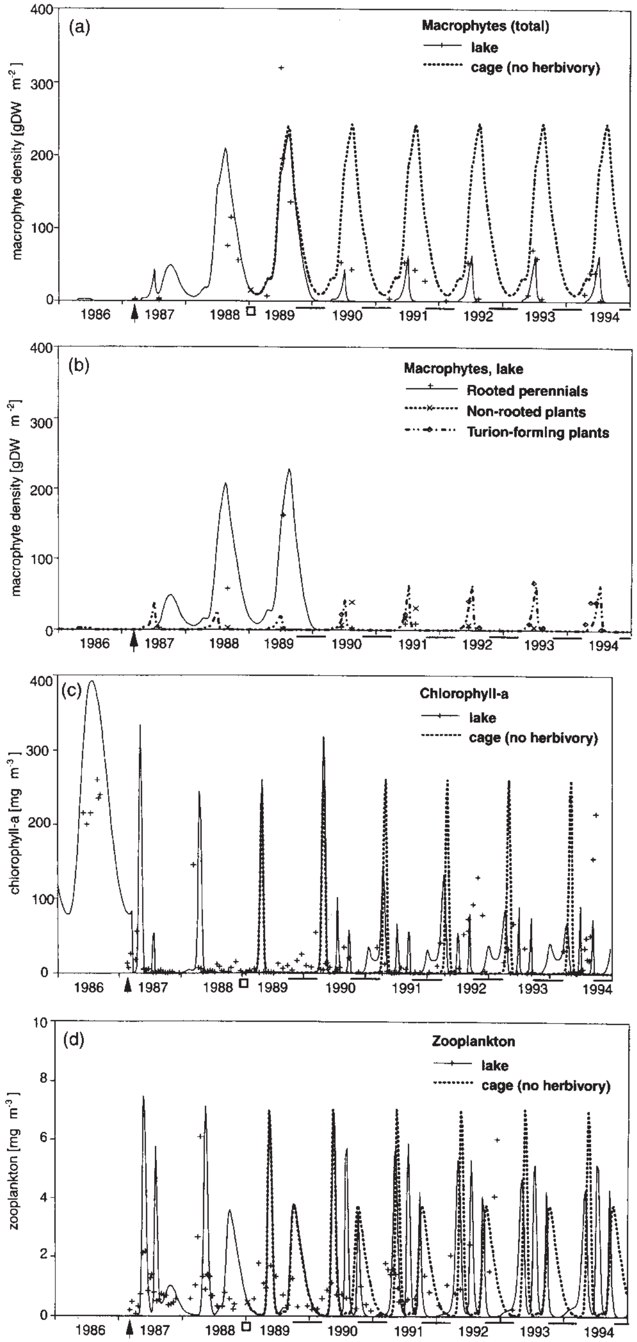

Fig. 2. Simulations for Lake Zwemlust for the period 1986–1994, and simulations of a cage experiment (excluding birds and fish) starting under the 1989 conditions. Arrow: time of biomanipulation measures (March 1987); bars under the *x* axis: periods with birds present on the lake; square: start of the cage simulations. In (a), (c) and (d), solid lines denote the lake simulations, dotted lines the cage simulations, and " + " signs the measured values in the lake. In (b), lake simulations only are depicted.

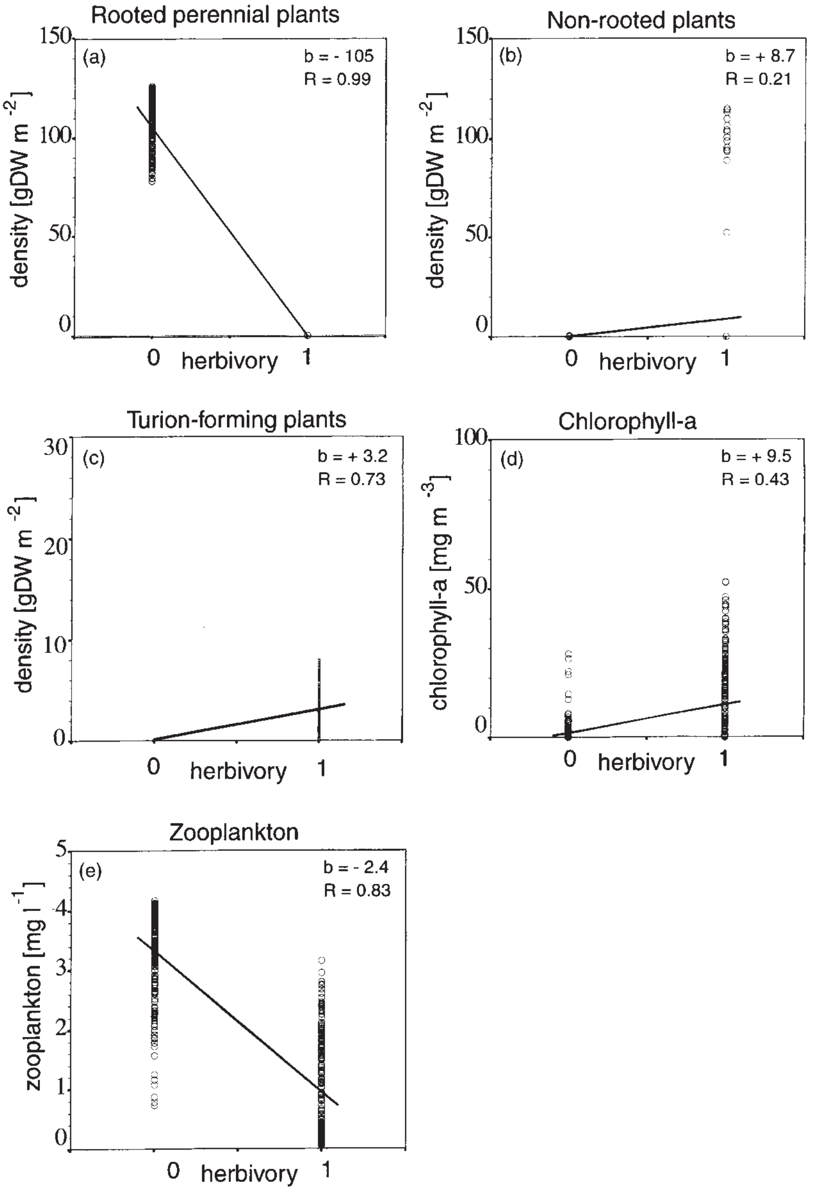

Fig. 3. Effects of herbivory on some model variables, including variation due to a ±20% variation of 10 process parameters. Results are for the autumn of the fifth year of the simulations. Herbivory = 0: cage simulations (excluding birds and fish); herbivory = 1: lake simulations. Please note that overlapping values show up as one circle in the graph. Solid lines are the linear regression lines, *b* = linear regression coefficient, *R* = correlation coefficient. (a), Rooted perennial plants; (b), Non-rooted plants; (c), Turion-forming plants; (d), Chlorophyll-a; (e), Zooplankton.

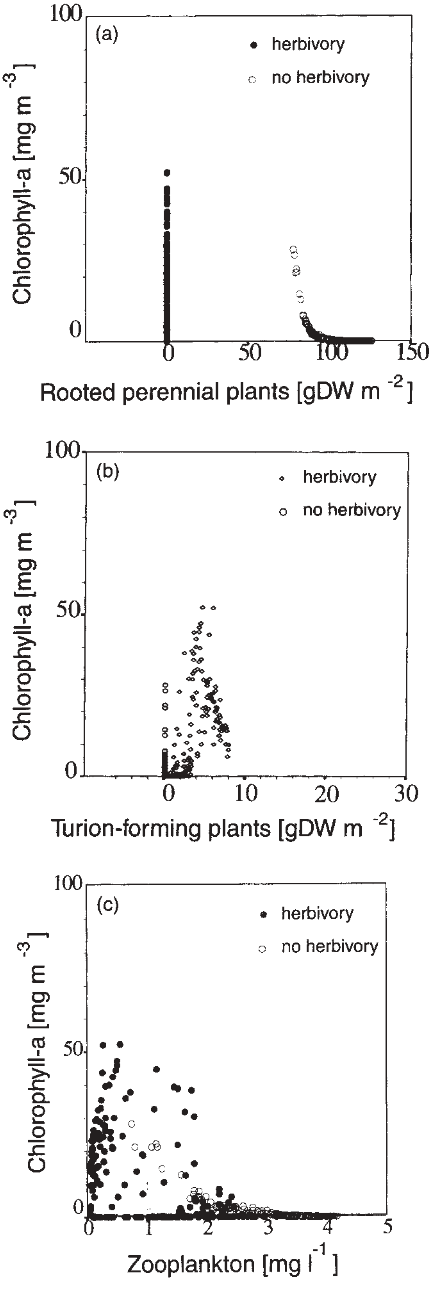

Fig. 4. Scatterplots of some model variables. Results are for the autumn of the fifth year of the simulations. Please note that overlapping values show up as one circle in the graph. (a) Chlorophyll-a against rooted perennial plants; (b) Chlorophyll-a against turion-forming plants; (c) Chlorophyll-a against zooplankton.

i.e. corrected for the standard deviations of parameter and variable (Table 5); the latter correspond to the relative sensitivity coefficients. All coefficients are given for the complete set of results as well as for both subsets; only significant relations are shown. For the combined results, the herbivory factor is the most sensitive parameter for most variables. Most variables are also quite sensitive to the zooplankton filtering rate (θ_1), especially in the cage simulations (i.e. if $\theta_0 = 0$). Phytoplankton chlorophyll-a and zooplankton are also affected by the zooplankton mortality rate (θ_3). The maximum growth rates of the non-rooted plants (θ_4) and the turion-formers (θ_5) have a significant positive impact on the biomass of the respective groups as well as (for θ_5) on the phytoplankton chlorophyll-a concentration, but only in the lake simulations ($\theta_0 = 1$). Apparently, the impact of these parameters is masked in the absence of herbivory. The parameters describing the growth of whitefish and of predatory fish (only relevant in the lake simulations) were less important.

DISCUSSION

The model indicates that the simulated lake system shifted from a stable turbid state before the biomanipulation, via a state dominated by rooted perennial plants in 1988–1990, to a state dominated by turion-forming macrophytes in summer and phytoplankton in autumn, from 1992 on. In general, the trend in the model simulations is in accordance with the one in the data, as described by Van Donk and Gulati (1995). All three states are dynamically stable, with constant seasonal fluctuations. The state dominated by rooted perennial plants was disturbed by herbivorous birds before it could reach stability. Without these birds, the lake would probably have remained in this state, as indicated by the results of the cage experiments and simulations. It thus can be concluded that herbivory decreases the stability of the macrophyte-dominated clear-water state of a lake, and increases the probability of returning phytoplankton blooms. In the simulations, the turion-forming plants could become the dominant group from 1992 on because of the inclusion in the model of two advantageous characteristics: they are not eaten by birds and they sprout quicker than the other groups in spring. Because of their die-off relatively early in the season, however, they leave the opportunity for a subsequent phytoplankton bloom. With these assumptions about differences in life cycle and edibility between the plant groups, as included in the model, the model is thus able to reproduce the observed shifts. This does not exclude other explaining hypotheses, though. Van Donk and Gulati (1995) mention a higher sensitivity of the turion-forming plants to epiphytic algae as a complementary factor causing an early decline of these

Table 4. Results of multiple regression of some response variables on the herbivory factor (θ_0) and 10 sampled parameters (θ_1–θ_{10})

	c	θ_0	θ_1	θ_2	θ_3	θ_4	θ_5	θ_6	θ_7	θ_8	θ_9	θ_{10}	R^2
Total results													
Chlorophyll-a	−29.7	+9.5	−9.2		+308		+3.7						0.39
Rooted peren.	+59.8	−105	+26.1		−174								0.99
Non-rooted	−45.1	+8.7	+14.9			+5.4		−79.2		−8.4			0.20
Turion-form.	−7.3	+3.2				−0.14	+0.81	+2.1					0.73
Macroph. total	(+6.7)	−93.1	+41.1			+5.3		−77.6		−8.1			0.88
Zooplankton	+2.6	−2.4	+1.1		−23.5	+0.11	−0.11	−1.7					0.74
Lake results only: including herbivory ($\theta_0 = 1$)													
Chlorophyll-a	−62.4	n.a.	−9.4		+468		+7.3						0.45
Macroph. total	−75.8	n.a.	+30.1			+10.2		−154		−16.8			0.32
Zooplankton	+5.1	n.a.	−0.82			+0.19	−0.23	−3.2	−63.1				0.26
Cage results only: no herbivory ($\theta_0 = 0$)													
Chlorophyll-a	+13.8	n.a.	−9.1		+148								0.28
Macroph. total	+8.1	n.a.	+52.4	+9.2	−350	+0.47							0.98
Zooplankton	−1.18	n.a.	+2.94		−34.4								0.83

The results are based on the simulated values in autumn after five years of simulation. Variables and parameters are explained in Tables 2 and 3. Results are shown for all simulations together (N = 400), as well as for the "lake" and the "cage" simulations separately (N = 200). The figures in the θ_i columns are the linear regression coefficients (unit of variable per unit of parameter); only significant values are shown; n.a. = not applicable. c = intercept. R^2 = fraction of the variance explained by the regression.

plants. Another possibility might be allelopathic effects among aquatic plants. These factors were not tested in the model. Anyhow, the results are in accordance with the conclusions of Meijer *et al.* (1994) that deterioration of the water quality starts with increasing phytoplankton concentrations in late summer and autumn.

Although the overall fit between model and data is reasonable, there are also differences. The simulated early development of turion-formers in 1986 is not realistic, and is probably due to the over-simplified description of the sprouting of turions in the model. The development of the macrophytes after the biomanipulation was more slowly in reality than in the simulations. The temporary (co)dominance of non-rooted plants (i.e. *Ceratophyllum)* in the lake, observed in 1990–1991, between the periods of *Elodea* and *Potamogeton* dominance, was not reproduced by the model. If the latter group would be neglected in the model, the non-rooted group would take over after the disappearance of the rooted perennials (Janse *et al.*, 1995), but it loses the competition if both groups are included, as in the current study. The outcome of this competition is, however, dependent on the actual combination of parameter values, as indicated by the Monte Carlo study: both groups draw profit from the decline of the rooted perennials [Fig. 3(b)–(c)]. Finally, in the years after 1991, with macrophytes in summer and phytoplankton in autumn, the autumn chlorophyll-a concentration is underestimated by the model. Whether this situation will be stable in the long run in reality is not yet clear. From the gradually increasing chlorophyll-a concentrations in autumn as reflected by the data one might expect that one day, the bloom will become permanent again and development of macrophytes in the next year will be impeded.

The results of the parameter variation study indicate that among the parameters tested, those affecting the grazing pressure on both macrophytes and phytoplankton, as well as the growth rates of the

Table 5. Same as Table 4, but the figures in the θ_i columns are now the standardized regression coefficients, β (dimensionless)

	θ_0	θ_1	θ_2	θ_3	θ_4	θ_5	θ_6	θ_7	θ_8	θ_9	θ_{10}
Total results											
Chlorophyll-a	+0.43	−0.19		+0.13		+0.39					
Rooted peren.	−0.99	+0.11		−0.02							
Non-rooted	+0.21	+0.16			+0.27		−0.22		−0.09		
Turion-form.	+0.73				−0.06	+0.42	+0.05				
Macroph. total	−0.91	+0.18			+0.11		−0.09		−0.04		
Zooplankton	−0.83	+0.17		−0.08	+0.08	−0.09	−0.07				
Lake results only: including herbivory ($\theta_0 = 1$)											
Chlorophyll-a	n.a.	−0.16		+0.15		+0.62					
Macroph. total	n.a.	+0.24			+0.38		−0.32		−0.14		
Zooplankton	n.a.	−0.22			+0.23	−0.31	−0.21	−0.17			
Cage results only: no herbivory ($\theta_0 = 0$)											
Chlorophyll-a	n.a.	−0.51		+0.16							
Macroph. total	n.a.	+0.98	+0.02	−0.13	+0.04						
Zooplankton	n.a.	+0.90		−0.21							

macrophytes, had a significant impact on the competition between the two primary producers. The grazing by birds (occurring in autumn and winter) is more important than the grazing by fish (in summer), as is also supported by experimental evidence. The macrophytes are probably more sensitive to the effects of herbivory during periods when their biomass is already low and their natural mortality high, compared to the more favourable summer conditions. The model results were less sensitive to the fish parameters, indicating that indirect effects via the "top down" route (the "trophic cascade") had less impact on the competition between the primary producers. Of course, only conclusions can as yet be drawn about the parameters or hypotheses that were included in the model analysis.

It may be concluded from this study that the presented model, with the ecological assumptions as described, is able to reproduce the main shifts between functional groups that have been observed in the lake and in the exclosures. Apparently, the observed shifts are possible within the general constraints set by the lake characteristics and the availability of nutrients. The shift following the biomanipulation measures could be explained by the assumptions on zooplankton grazing, the impact of benthivorous fish on the light climate, and the nutrient competition between phytoplankton and water plants (see also Janse *et al.*, 1995). To explain the shifts in 1990 and later years, additional key factors appear to be the presence of herbivorous birds, as well as differences in life cycle and edibility between the plant groups. At the same time, this leaves the possibility of alternative or modified hypotheses about the functioning of the system being valid as well. A flexibly structured model like the one used here makes it easy to evaluate the impact of different ecological hypotheses on the chosen output variables. Incorporation of these hypotheses (in the form of parameters) in an ecosystem model allows assessment of their influence (expressed as sensitivity coefficients) within the general ecological framework, and allows comparison of the explanatory power of different hypotheses. The model thus might be a valuable tool in determining the importance of different factors in, for example, the long-term success of biomanipulation measures. The results of this will probably be partly different among lakes.

The Monte Carlo simulations showed that a variation of 20% in 10 parameters, a variation that is probably rather under- than overestimated, already may cause a wide range in the model output. If the parameter ranges are considered as realistic, i.e. reflect a naturally occurring variability, the range of output values should be interpreted as a probability distribution. A possible outcome of the model would be, for instance, the probability of a system shift after certain measures, without giving an exact forecast. For a more complete picture of this, the analysis should be extended with the inclusion of additional parameters and model assumptions. This way of looking at model results resembles the approach of the "ecological risk assessment" often used for toxic substances. This procedure could best be combined with a calibration step, i.e. narrowing of the parameter range based on comparison of model output and data (cf. Aldenberg *et al.*. 1995).

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Chapter 13

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A Model Study on the Role of Wetland Zones in Lake Eutrophication and Restoration

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Shallow lakes respond in different ways to changes in nutrient loading (nitrogen, phosphorus). These lakes may be in two different states: *turbid*, dominated by phytoplankton, and *clear*, dominated by submerged macrophytes. Both states are self-stabilizing; a shift from turbid to clear occurs at much lower nutrient loading than a shift in the opposite direction. These critical loading levels vary among lakes and are dependent on morphological, biological, and lake management factors. This paper focuses on the role of wetland zones. Several processes are important: transport and settling of suspended solids, denitrification, nutrient uptake by marsh vegetation (increasing nutrient retention), and improvement of habitat conditions for predatory fish. A conceptual model of a lake with surrounding reed marsh was made, including these relations. The lake-part of this model consists of an existing lake model named PCLake[1]. The relative area of lake and marsh can be varied. Model calculations revealed that nutrient concentrations are lowered by the presence of a marsh area, and that the critical loading level for a shift to clear water is increased. This happens only if the mixing rate of the lake and marsh water is adequate. In general, the relative marsh area should be quite large in order to have a substantial effect. Export of nutrients can be enhanced by harvesting of reed vegetation. Optimal predatory fish stock contributes to water quality improvement, but only if combined with favourable loading and physical conditions. Within limits, the presence of a wetland zone around lakes may thus increase the ability of lakes to cope with nutrients and enhance restoration. Validation of the conclusions in real lakes is recommended, a task hampered by the fact that, in the Netherlands, many wetland zones have disappeared in the past.

KEY WORDS: shallow lakes, eutrophication, nutrients, nitrogen, phosphorus, wetlands, model, lake restoration

DOMAINS: freshwater systems, environmental sciences, ecosystems management, modeling, environmental modeling, networks

INTRODUCTION

As a result of high nutrient loadings during the past decades, many shallow lakes have become highly eutrophic. They are now characterized by dense algal blooms of cyanobacteria, high turbidity, absence of vegetation, and a fish community dominated by bream. Although these effects were caused by high nutrient loadings, restoration of the former macrophyte-dominated clearwater state often could not be achieved by external load reduction alone; eutrophic lakes often show resistance to recov-

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ery. Apparently, once the system has switched from a clear to a turbid state, this switch cannot simply be reversed[2,3,4,5]. Several, often interacting, mechanisms for this resistance have been proposed. Firstly, a prolonged internal loading from nutrient-rich sediments may delay the response[6,7]. Secondly, an increase of the nutrient utilization efficiency of the phytoplankton makes them produce the same biomass with less nutrient[8,9]. Thirdly, the grazing pressure on the phytoplankton is low, both because of the poor edibility of cyanobacteria and the strong predation by bream[10]. Finally, the large amount of detritus accumulated in the system, combined with wind/wave action and bioturbation by benthivorous fish, keeps the water turbid and impedes the return of vegetation[11]. Clearly, both direct effects of nutrients and indirect effects through the food web may contribute to the often observed resistance to recovery. Therefore, additional measures are sometimes considered apart from, or combined with, nutrient load reduction[10].

On the other hand, the clearwater state of shallow lakes, dominated by submerged macrophytes, shows a certain resistance to such external forcings as a moderate increase in nutrient loading[12]. Several stabilising mechanisms may play a role. Nutrient uptake by macrophytes may suppress algal growth due to nutrient limitation[13]; they may also provide favourable conditions for predatory fish and reduce wind-induced resuspension by stabilising the sediment.

This paper focuses on the role of wetland zones around lakes and their response to a change in nutrient loading. A number of studies[14,15,16,17] indicate that wetlands, both natural and constructed, may increase the retention of nutrients and other pollutants. Several relations between pelagic and wetland zones may be important in this respect, such as transport and settling of suspended solids, nutrient uptake by the marsh vegetation, and enhanced denitrification, processes all increasing the retention of nutrients. Another type of relation is the role of wetland zones as spawning and nursery areas for predatory fish[18]. A conceptual model of a lake with a surrounding reed marsh was made, which includes these relations in a simplified way (Fig. 1).

The relative area of lake and marsh can be varied in the model, equivalent to the variations in water level occurring in real life.

METHODS AND PROCEDURES

The study has been performed with a simulation model with two coupled compartments: open water and wetland (Fig. 1). The processes in the coupled model include:

- Transport of particles and nutrients
- Uptake and release of nutrients by the wetland vegetation
- Denitrification
- Relation between wetland zone and predatory fish

PCLake[1] is used as a basis for the open water part, because this model combines a description of the most important biological components (viz. phyto- and zooplankton, fish, and submerged macrophytes) with a description of the nutrient cycles in a shallow lake ecosystem, in both water and top-layer sediment. The model occupies an intermediate space between many eutrophication models, which focus mainly on the nutrient cycle, on the one hand, and more detailed biological models on the other. The model also differs from so-called minimodels[19] in that it is based on closed nutrient cycles, allowing a more quantified analysis.

The structure of the lake model is illustrated in Fig. 2. For a description of PCLake, the model for the lake part, we refer to Janse[1,20]. In short, the model describes the growth of phytoplankton and submerged macrophytes, as well as a simplified food web, coupled to a description of the nitrogen and phosphorus cycles in the water column and the sediment top layer. The nutrient cycles are closed within the model system.

The wetland part of the coupled simulation model is composed of a simplified growth model for reed[21,22,23] coupled

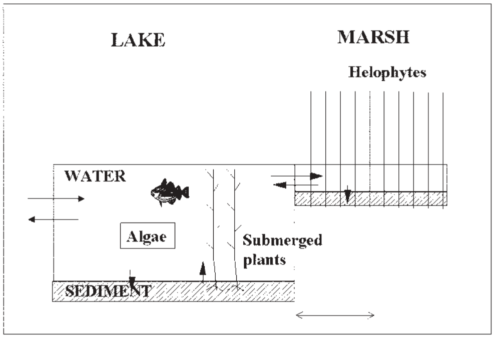

FIGURE 1. Lake-wetland system.

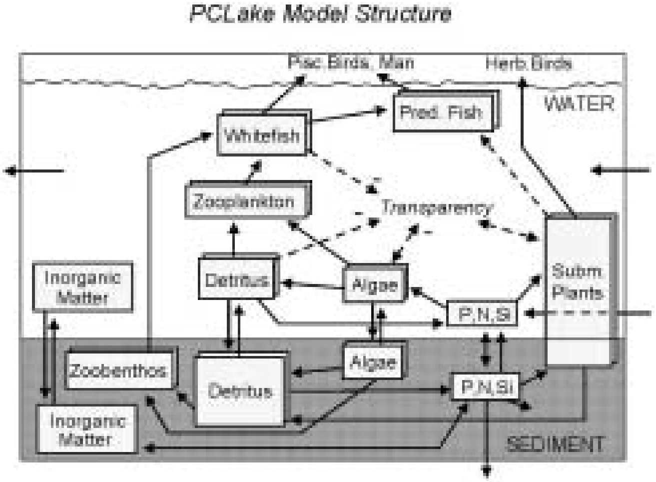

FIGURE 2. Model structure of PCLake.

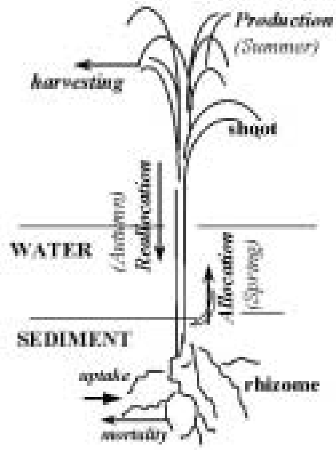

FIGURE 3. Model of wetland vegetation.

to a description of the nutrient processes in the water column and the sediment top layer of the marsh zone[15, 24] (Fig. 3). A description with references of the processes and the parameter values used is given by Van Tol[25] and will be published elsewhere. The main features are described here.

The biomass of the marsh vegetation is divided into root and shoot fractions. The seasonal development is modelled as allocation of a part of the root biomass to the shoots in spring, photosynthetic growth during summer, and partial reallocation back to the roots in autumn. Summer growth is assumed to be dependent on the marsh water depth, N and P in the sediment top layer, daylight, and temperature. Nutrients are taken up from the sediment top layer only. Optionally, regular mowing of the vegetation can be taken into account (in the current study, mowing is not included).

The substances and process descriptions are analogous to those in the lake model, except that the water depth is much lower (default 0.5 m), settling velocities are higher due to the absence of wind action, and resuspension is assumed to be zero. Phytoplankton is assumed not to grow in the shadow of the reed vegetation.

Mixing between the water columns of the lake and the wetland is described by a dispersion-like equation across the contact zone:

$$F = k_{exch} * A/L * (c_{lake} - c_{marsh})$$
$$\approx k_{exch} * D_{marsh}/(0.5 * fMarsh) * (c_{lake} - c_{marsh})$$

in which F is the mass flux between lake and marsh (g day^{-1}), k_{exch} the exchange coefficient, comparable to a dispersion coefficient (m^2 day^{-1}), A the interfacial area (m^2), L the mixing length (m), D_{marsh} the marsh water depth (m), fMarsh the relative marsh area (–), and c_{lake} and c_{marsh} the concentrations (g m^{-3}) of a substance in the lake and the marsh water, respectively. The exchange coefficient is by default set to 10^5 m^2 day^{-1}, corresponding to efficient mixing. Lower coefficients have also been used in the simulations, however (see below).

The relation between the wetland zone and fish population is simplified to the role as spawning and nursery area for predatory fish. It is assumed that the maximum possible biomass of these fish increases, within certain limits, with the relative area of wetland vegetation[18]:

$$B_{max} = \text{MIN}\ [B_{max,\ min} + B_{rel} * 100 * fMarsh,\ B_{max,\ max}]$$

in which B_{max} is the maximum stock (carrying capacity) of predatory fish, $B_{max,\ min}$ and $B_{max,\ max}$ the minimum (4 kg fish ha^{-1}) and maximum (75 kg ha^{-1}) carrying capacity, respectively, and B_{rel} the relative increase of B_{max} per % marsh. This last parameter amounts to about 5 kg ha^{-1} %$^{-1}$, or 7 in case submerged plants are also abundant in the lake.

The model has been implemented in the simulation package ACSL/Math v. 2.4 (which includes ACSL v. 11). So far, the lake model has already been used for several scenario analyses. These include studies on nutrient load reduction[20], biomanipulation[26], and combinations of these with dredging[27,28,29]. A partial calibration study on a multilake data set using Bayesian statistics has also been carried out[30]. The coupled lake-wetland model has not yet been calibrated on observed data.

With this coupled model, the question is studied: how is the water quality in shallow lakes (expressed as nutrient concentrations, Secchi depth, and chlorophyll-*a*) influenced by the presence and relative size of a wetland area along the lake?

The simulations have been carried out with starting conditions typical for Western European shallow lakes, i.e., turbid water, sediments heavily loaded with nutrients, and a fish stock dominated by benthivorous and zooplanktivorous fish. The most important assumptions in the simulations are:

- Depth of the lake: 2 m.
- Lake surface area: 200 ha.
- Water depth in the wetland zone: 0.5 m.
- A constant (i.e., not variable in time) water and nutrient influx to the lake. The water influx was set to 10 mm day^{-1}, i.e., a retention time of just over 0.5 year.
- Influx to the marsh zone takes place via the lake only.
- No mowing of the wetland vegetation.

The following input factors were varied in the simulations:

- The size of the wetland area relative to that of the lake (called fMarsh) was varied between 0 and 1 (–).
- The amount of nutrient loading was also varied. The nominal total N loading was set at 0.024 g m^{-2} day^{-1} and the P loading at 0.0022 g m^{-2} day^{-1}. For the sensitivity analysis, the N loading was varied between 0.009 and 0.029 g m^{-2} day^{-1}, with the P loading 20% of these values (making nitrogen the limiting nutrient).
- Three levels of mixing rate between the open water and the water in the wetland part were used: besides intensive mixing (exchange coefficient = 10^5 m^2 day^{-1}), the nominal setting, lower values of 10^4 and 10^3 (m^2 day^{-1}) were used.

The simulations have been carried out for a period of 10 years with a variable time step of integration. Weather conditions in this period (temperature, daylight) are assumed to follow sine curves, with the average ranges taken from the period 1961–1990. Additional simulations were done excluding the wetland-fish relation in order to compare the contributions of the different processes.

RESULTS AND DISCUSSION

Simulations of the development over time over time of some important variables, for different sizes of the wetland area and with nominal values for loading and mixing, are shown in Figs 4, 5, 6, 7, 8, and 9. For each figure, N loading = 0.024 g m^{-2} day^{-1}, P loading = 0.0022 g m^{-2} day^{-1}, and k_{exch} = 10^5 m^2 day^{-1}.

The aboveground marsh vegetation (g d.w. m^{-2}; Fig. 4) gradually increases over the years. The biomass per m^2 reached is somewhat lower when the wetland area increaes, due to nutrient dilution effects; the total biomass marsh vegetation in the area (biomass per m^2 times the area) is, of course, much larger. For nutrient concentrations (total N: Fig. 5; total P: Fig. 6), the model shows a substantial decrease of both nutrient concentrations at increasing wetland area.

As you can see in Fig. 7, a substantial decrease of summer peaks in chlorophyll-*a* occurs only at wetland areas of 0.5 times the lake area or more. A substantial increase in submerged vegetation (Fig. 8) only occurs at areas of 0.5 times the lake area or more. At a relative area of 1.0, a stable macrophyte development is simulated, while at a value of 0.5 the development is still unstable.

In agreement with the model assumptions, a reasonable wetland size (>10% of the lake) as breeding habitat is essential for the development of a substantial stock of predatory fish (Fig. 9).

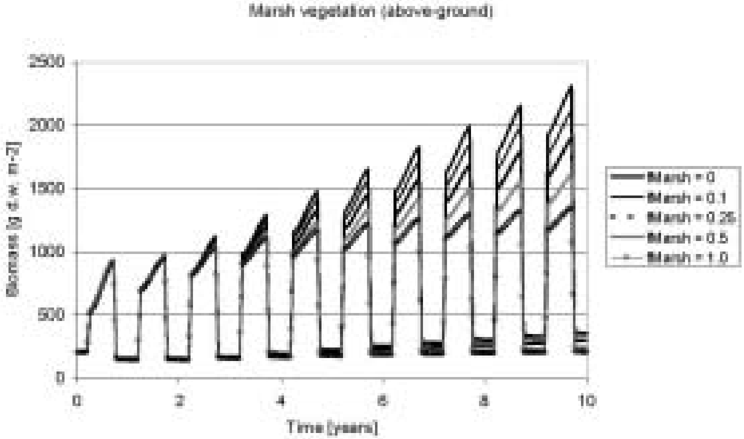

FIGURE 4. Marsh vegetation.

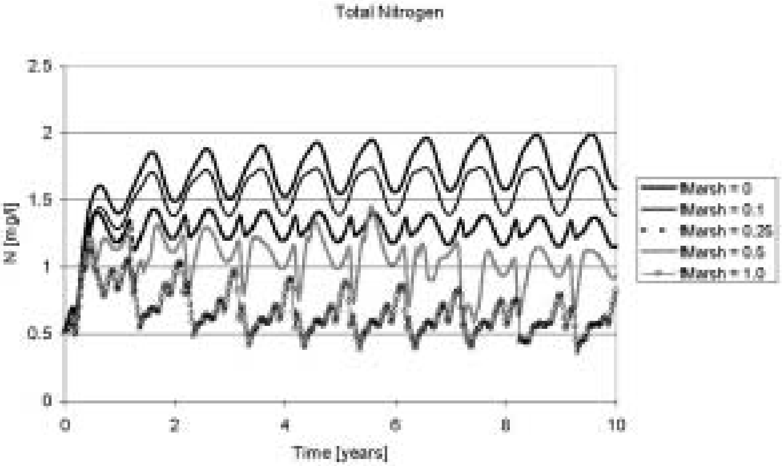

FIGURE 5. Total N.

At large marsh areas, the stock again decreases because of nutrient dilution effects.

The relative importance of the predatory fish relations (i.e., the wetland as breeding habitat) in the model was demonstrated by additional simulation runs with this relation omitted from the model. For a relative wetland area of 0.5 times the lake area, for instance, the slowly starting macrophyte development as shown in Fig. 8 vanishes and the chlorophyll-*a* concentration remains high if this relation is omitted (graph not shown), showing that the fish relation indeed contributes to the effect.

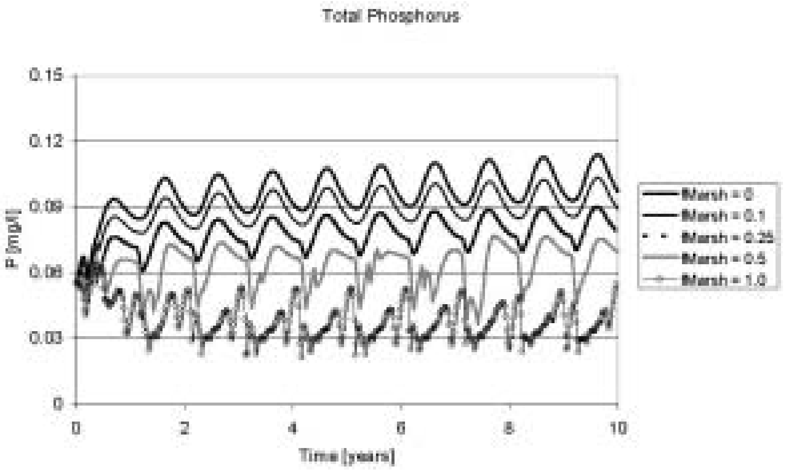

FIGURE 6. Total P.

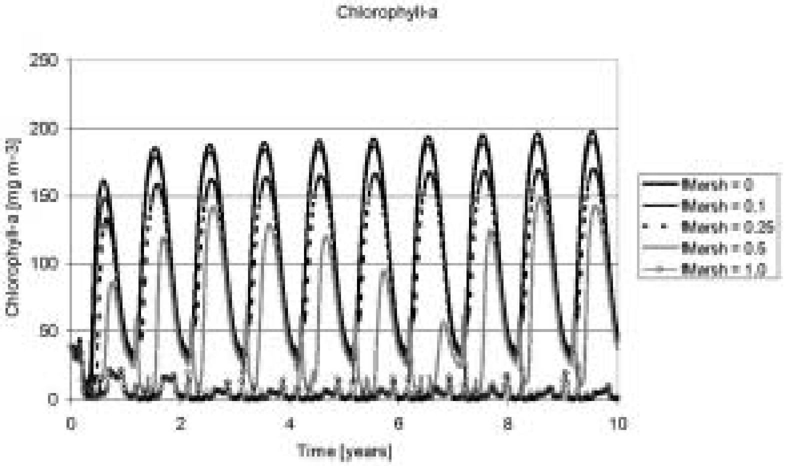

FIGURE 7. Algal biomass.

The effects of increasing marsh area shown in Fig. 4–9 are observed only if the nutrient loading is not too high (Fig. 10a–c). The critical nitrogen loading level increases with increasing wetland area. Comparable results are obtained for the phosphorus loading if this nutrient, rather than nitrogen, is made limiting. Furthermore, the effects are clearly dependent on the mixing rate between lake and marsh water. While at the high value of the exchange coefficient of 10^5 m^2 day^{-1} clear effects of the marsh are observed (Fig. 10a), they become less apparent or even disappear in case of intermediate (10^4; Fig. 10b) or low (10^3; Fig. 10c) mixing rates. At the high value of 10^5, there

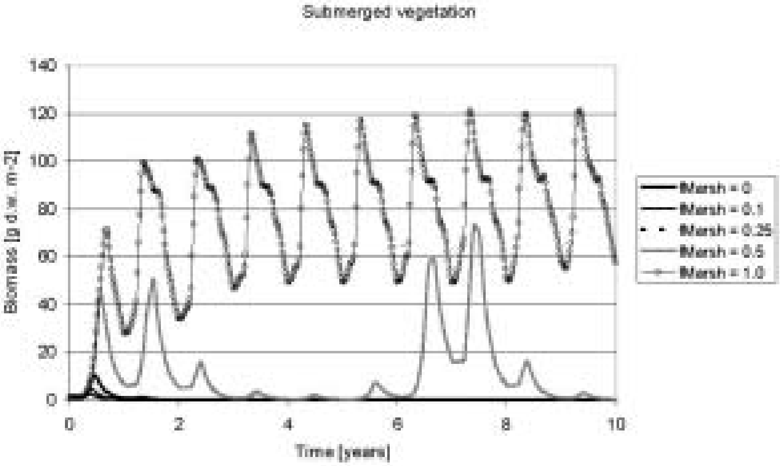

FIGURE 8. Submerged vegetation.

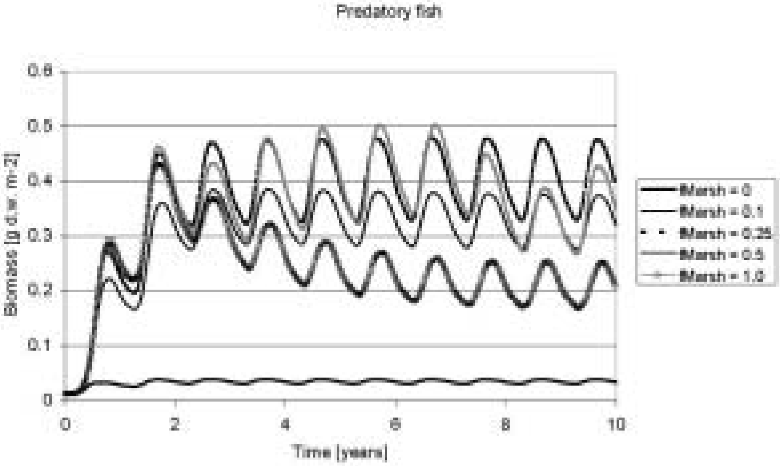

FIGURE 9. Predatory fish biomass.

is little difference in the simulated concentrations of substances between the water columns in the lake and the marsh.

Comparing the simulated year-average N and P concentrations with the nutrient input, for the nominal run, the retention of nitrogen in the system increases from 25% in the lake without marsh, to 34, 47, 58, and up to 76% for the largest marsh area. For phosphorus, the retention started higher (52%) in the lake proper, and increased somewhat less with the marsh area: 57, 62, 69, and up to 83%. This is for an N/P ratio in the input of >10 (g/g); for other ratios and loading levels, the percentages differ, but the trend remains. The extra retention of nitrogen by the marshland relative to phosphorus is probably due to the extra contribu-

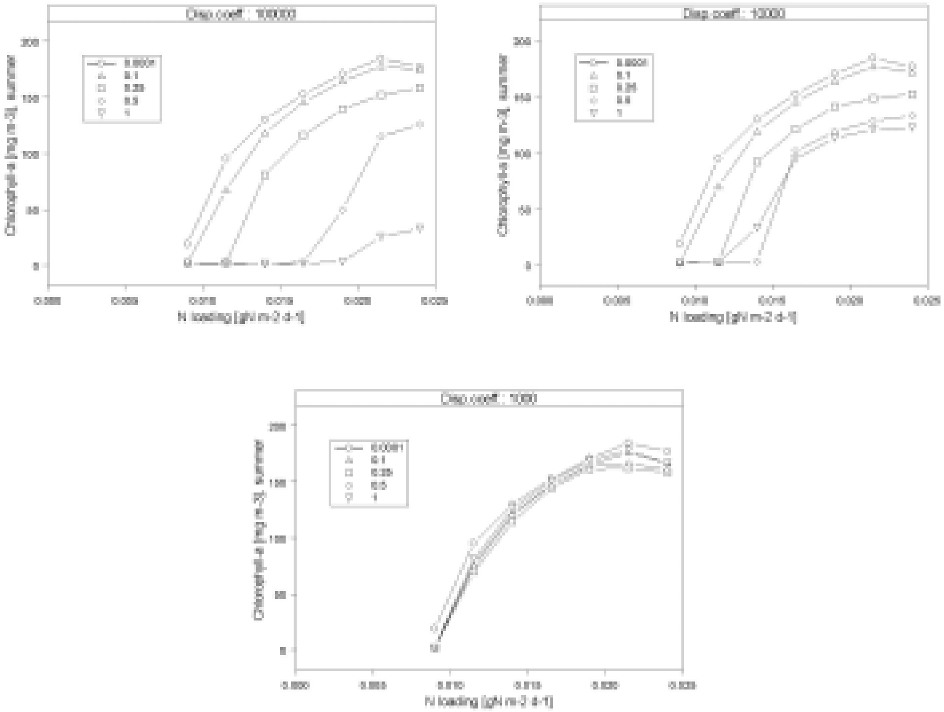

FIGURE 10. Simulated average chlorophyll-*a* concentrations as a function of nitrogen loading and marsh area, for three values of the exchange coefficient.

tion of denitrification in the wetland area. The annual amounts of nutrients retained are in the range of 1 to 10 g N m^{-2} year^{-1} and 0.1 to 1 g P m^{-2} year^{-1}, depending on the input settings. The study indicates that the modelled wetland system could play a significant role in lake restoration only if the area is relatively large, the water exchange is good, and the nutrient loading to the lake is not too high.

The retention values are in the range of those reported[15] or modelled[31] in many studies for natural wetlands, although lower and higher values are also found[15,32]. The values for different systems are often difficult to compare because of large differences in loading, physical characteristics, and hydrological regime. Values are generally higher for constructed wetlands[14,15,33] where dimensions are set to be optimal for water purification.

Translation of the simulated effects to those in real-world lake systems cannot be done automatically. In specific situations, one should verify the assumptions made in relation to the actual circumstances. For instance, the systems' response may differ in case of fluctuating water tables, or if the marsh is an instream wetland. Finally, one should of course find a balance between the use of natural wetlands for lake purification, and the risk of possible damage to the actual ecological values of the wetlands[34].

CONCLUSIONS

The simulations clearly show the extra purification effect of a lake with a substantial wetland zone as compared to lakes without such a zone. There is a positive relation between nutrient removal and the size of the wetland area. The switch from phytoplankton-dominated systems to lakes with submerged vegetation is easier with wetlands present, but only if the size of the marshes is substantial, the nutrient loading is moderate, and sufficient mixing is present. Transport and sedimentation processes seem to be the most important processes, but the food-web relations via predatory fish also play an important role, especially at intermediate nutrient conditions. The model takes a stabilisation time of several years, especially for the development of emergent vegetation.

The overall performance of the model is promising. Calibration of the model has been possible up to now mainly with data from rather eutrophied situations. Expansion of the available data set with time series from mesotrophic lakes is essential. Validation with an independent data set is foreseen.

Besides the mere wetland size, the effects of variations in hydrologic regime and water tables both in the lake and in the wetland area should also be studied. A more extensive sensitivity analysis on model parameters and lake characteristics also has to be carried out. With these additional analyses on the behaviour of lake-wetland systems, the model may play a role in the development of more integrated lake and catchment management strategies.

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A MODEL OF DITCH VEGETATION IN RELATION TO EUTROPHICATION

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ABSTRACT

A functional model of a ditch ecosystem has been developed, aimed at describing the relation between nutrient input and water quality and dominant vegetation in drainage ditches. Its aim is the derivation of the 'critical nutrient loading' for a shift from submerged vegetation to duckweed dominance. The model, called *PCDitch*, describes the competition between several functional groups of macrophytes, as well as algae. The macrophyte groups were defined according to the layer(s) in which they grow: submerged, floating or emergent, rooted or non-rooted. The model also includes the cycling of nutrients within the water, the sediment top layer and the vegetation. The model has been applied to the data of 8 experimental ditches located at Renkum (The Netherlands), which received different levels of nutrient loading during 4 years. The controls and the low- and medium-loaded ditches remained dominated by submerged plants, while in the high-loaded ones a dense cover of duckweed developed. In the sand ditches, submerged biomasses were lower than in the respective clay ditches. An optimization study has been performed for a number of sensitive parameters, minimizing the total sum of squared differences between simulated and measured values for all ditches, resulting in a set of parameter values that gives the best overall fit. The parameters included the maximum growth rates, the minimum phosphorus contents and the overwintering fraction of the plant groups. The model simulations by *PCDitch* were grossly comparable to the field observations, with duckweed in the high-loaded ditches and submerged plants in the other ones. The fit for algae and charophytes remained poor. Further calibration as well as testing the model in field situations are recommended to improve the model's predictive value. © 1998 IAWQ. Published by Elsevier Science Ltd

KEYWORDS

Ditch; duckweed; eutrophication; macrophytes; model; phosphorus; nitrogen; nutrients

INTRODUCTION

Drainage ditches are small, linear water bodies, with as a main task the discharge of surplus water from lowland agricultural areas. They form the link between the farmland and larger waters such as lakes and canals. Many ditches also serve to transport water *to* the fields during periods of shortage, mainly in summer. With a total length of about 300,000 km, ditches are a common water type in the western and northern parts of The Netherlands. They are found in lowland parts of other countries as well. Besides their hydrological functions, ditches have an important ecological function, providing a habitat for many plant and animal species. The water depth is typically less than 1.5 m. Because of their shallowness, ditches are often dominated by macrophytes, besides epiphytic, benthic and filamentous algae. Most ditches require yearly maintenance (removal of the vegetation and/or the detrital layer).

Many ditches are strongly affected by eutrophication and by pesticides. Agricultural run-off is usually the dominant source of nutrients in these waters. Eutrophication generally causes a shift from a submerged vegetation with a vertical growth strategy, to a vegetation with a horizontal growth strategy (Bloemendaal & Roelofs, 1988). The extreme of this is a surface layer of pleustophytic plants, such as duckweed (Lemnaceae) or floating fern (*Azolla*). This shift coincides with a deterioration of the oxygen household in the water and loss of biodiversity. This is a common phenomenon in The Netherlands; in the region Hollands Noorderkwartier (about 2500 km^2), for instance, about 30% of the ditches is dominated by duckweed (data from Water Board of Hollands Noorderkwartier, published by Janse & Van Puijenbroek, 1997).

An important question is at what level of nutrient input this shift occurs. De Groot et al. (1987) showed by means of regression analysis that duckweed cover in a set of ditches was positively related to the nitrogen dosage to the adjacent fields and to the phosphorus concentration in the water. Some other authors found a high duckweed cover often to coincide with high nutrient concentrations (e.g. Barendrecht & Wassen, 1989; Van der Does & Klink, 1991; STOWA, 1993; BKH, 1995), but the correlations were not always clear, while other factors, such as BOD, pH and chloride, sometimes showed a high correlation with duckweed as well. Boeyen et al. (1992) found a negative relation of duckweed cover with the water depth, while duckweed is also negatively related to the dilution rate. Dynamical models, because they include a number of explaining processes, potentially have a higher predictive value (e.g. Best, 1990), but few models which include duckweed have been made so far. The BKH model (STOWA, 1992) describes duckweed growth and management, but excludes the nutrient cycles. The NUSWA model (Drent et al., 1997) includes both, but neglects the competition between duckweed and other plants. In the current study, we integrated those aspects by the development of the dynamical model *PCDitch*. The model describes the relation between the external nutrient loading, the nutrient concentrations and the dynamics of the dominant vegetation types in ditches: submerged plants, algae, duckweed and helophytes. Its aim is to assess the 'critical level' of nutrient loading above which undesired effects are likely to occur, and the main factors influencing this level. Intended applications are the derivation of loading standards and, together with run-off models, agricultural scenario analyses. The model is confined to the ditch ecosystem itself; the relation between land use and nutrient run-off is not included.

MODEL DESCRIPTION

The *PCDitch* model (Janse & Van Puijenbroek, 1997) includes the water column and the upper sediment layer of a ditch, both assumed to be well mixed. The model may be regarded as a competition model between several functional groups of water plants, coupled to a description of the nutrient cycles. The model describes the cycling of four 'substances': dry weight (DW), phosphorus (P), nitrogen (N) and oxygen (O_2). All biotic components as well as detritus are modelled in both DW, N and P units. This is done to achieve closed nutrient cycles within the model system, and to account for variability of the nutrient ratios of water plants, e.g. depending on the loading level (e.g. Wetzel, 1983; Gerloff & Krombholz, 1966). The main 'goal variables' of the model are the biomasses of the different plant groups, as well as the phosphorus, nitrogen and oxygen concentrations. Plant biomasses are also converted to cover percentages.

The components of the model are (Fig. 1): Inorganic nutrients (PO_4, adsorbed P, NH_4, NO_3), both in the water column and in the sediment pore water; Oxygen in the water (O_2); Suspended detritus; Sediment detritus; Algae; and six functional groups of water plants, described below. Animal groups such as zooplankton, macrofauna and fish have been left out, as they are considered as generally not very important

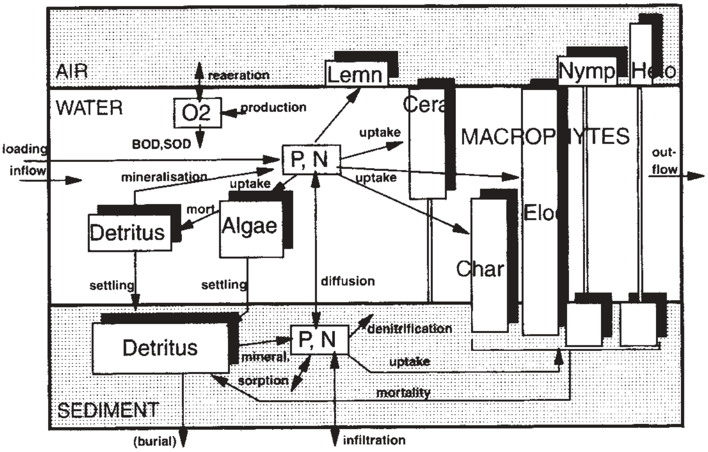

Figure 1. *PCDitch* model structure. Abbreviations of macrophyte groups are explained in the text. Shaded blocks denote components modelled in both dry-weight and nutrient units. Respiration fluxes are not shown.

The in- and outflow of water and the external nutrient loading to the ditch system should be given by the user or calculated by other models. The user should also provide the water depth, the (initial) thickness of the sediment layer and the sediment type, defined by its density, porosity, lutum content and (initial) organic matter content. These parameters influence the amount and bio-availability of nutrients in the system, by affecting, among others, phosphorus adsorption and the nutrient transport between sediment and water. Other general processes included are: (net) settling (resuspension was neglected), burial, mineralisation of detritus, nitrification and denitrification. The formulations were mostly derived from the lake eutrophication model PCLake (Janse & Aldenberg, 1990; Janse, 1997). Most of the oxygen processes were linked to the respective organic matter processes, such as mineralisation and primary production. Reaeration is assumed to be hampered by duckweed (Marshall, 1981; Portielje & Lijklema, 1995).

The water plants were divided into six functional groups, besides one functional group of algae. The definition of the plant groups is primarily based on the layer(s) in which they grow and the layer(s) where they get their nutrients from. The classification into 16 growth forms given by Den Hartog & Segal (1964) and Den Hartog & Van der Velde (1988) has been used as a template. Several groups were lumped, while others were left out because they are not common in ditches. The groups are defined by the relative size of emergent, floating, submerged and root fractions, and their vertical distribution. These fractions are assumed as constant in time; the average summer values were chosen. The number and the definition of the plant groups has been made flexible. The currently defined groups and their characteristics are (Fig. 1):

1. Submerged plants, divided into:
    a. Rooted submerged angiosperms (abbreviated as '*Elod*'). This group comprises the elodeid and potamid growth forms. Assumed to be present in the entire water column, nutrient uptake from both water and sediment. Root fraction estimated as 0.05.

   b. Non-rooted submerged angiosperms ('*Cera*'). Canopy-formers, confined to the upper half of the water column. Nutrient uptake from the water only.
   c. Charophytes ('*Char*'). Confined to the lower half of the water column. Root fraction estimated as 0.05. They were distinguished because of their special character as macro-algae.
2. Non-rooted, floating plants: duckweed ('*Lemn*'). This group includes floating fern (*Azolla*) as well. Nutrient uptake from the water only.
3. Rooted plants with floating or emergent leaves
   a. Floating-leaved plants: Nymphaeids ('*Nymp*'). Nutrient uptake from the sediment, root fraction estimated as 0.75.
   b. Emergent plants: helophytes ('*Helo*'). Nutrient uptake from the sediment, root fraction estimated as 0.5.

The modelled processes are basically the same for each plant group and they are described here in short; for a complete description see Janse & Van Puijenbroek (1997).

For each group, the general differential equation for the biomass [gDW m^{-2}] is:

$dx/dt = production - respiration - mortality\ (-\ migration)$; all terms in [gDW m^{-2} d^{-1}],

and a separate differential equation is used for the amount of nutrients in the plants, y [e.g. gP m^{-2}], in order to describe dynamically the nutrient-to-dry-weight ratios (Janse & Aldenberg, 1990):

$dy/dt = uptake - excretion - mortality\ (-\ migration)$; all terms in [gP m^{-2} d^{-1}] or [gN m^{-2} d^{-1}].

The production is described as:

$production = \mu max(T) * DayLength * f_L * \mathrm{MIN}(f_P, f_N) * x - \varphi * r/K * x^2$ [gDW m^{-2} d^{-1}]

with:

f_L = light function [-] = $(1-s) * 1/(e * Depth) * \mathrm{LOG}\{(1 + L0/Lref(T)) / (1 + Lb/Lref(T))\}$ for submerged plants; $f_L = 1$ for floating and emergent plants.
f_P = phosphorus function [-] = $(1 - cPDmin/rPD) * cPDmax / (cPDmax - cPDmin)$
f_N = nitrogen function [-]: analogous

in which x is the biomass of a plant group [gDW m^{-2}], μmax the maximum growth rate [d^{-1}], T the water temperature [°C], s the fraction of the water surface covered by floating plants [-], $Depth$ the water depth [m], $L0$ and Lb the light intensities at the top and the bottom of the vegetation layer, respectively [W m^{-2}], $Lref$ the half-saturating light intensity [W m^{-2}] and rPD, $cPDmin$ and $cPDmax$ the actual, minimum and maximum P content of the plants, respectively [gP g^{-1}DW]. The production is thus a function of the water temperature, day length, underwater light climate (for submerged plants) and the nutrients P and N.

The uptake of nutrients has been modelled separately from the biomass production, following the formulations for phytoplankton derived by Droop and adapted by Riegman (Riegman & Mur, 1984). The specific uptake rate v [gP g^{-1} DW d^{-1}] increases with the PO_4 concentration [mgP l^{-1}] in the medium (water or pore water) with slope (affinity) α [m^3 g^{-1}DW d^{-1}], up to a maximum rate $vmax^*$, which depends on the actual P content of the plants:

$vmax^* = vmax(T) * (cPDmax - rPD) / (cPDmax - cPDmin)$ [gP g^{-1} DW d^{-1}]
$v = vmax^* * PO_4 / (vmax^*/\alpha + PO_4)$ [gP g^{-1} DW d^{-1}]
$uptake = v * x$ [gP m^{-2} d^{-1}]

Respiration and nutrient excretion are modelled as first order processes, with excretion relatively lower than respiration. Regarding mortality, a simple phenomenological approach was chosen, following Scheffer *et al.*, 1993) and Wortelboer (1990). It is assumed that the mortality is low in spring and summer, and increases from a certain, predefined date at the start of autumn, causing die-off of the vegetation until a certain surviving fraction is left over which is available again at the start of the next growing season. This may include formation of, and subsequent germination from, overwintering organs. Mortality may also include mechanical removal of vegetation for management purposes. The equation is:

$$mortality = kmort * (x - fHiber*x_e) + (1-\varphi)*r/K*x^2 \quad [\mathrm{gDW\ m^{-2}\ d^{-1}}]$$

with *kmort* the mortality constant [$\mathrm{d^{-1}}$], x_e the biomass at the end of the growing season [$\mathrm{gDW\ m^{-2}}$] and *fHiber* the fraction of this biomass being available again the next spring [-]. During the growing season, the first term reduces to: $kmortmin * x$.

The quadratic terms in the production and mortality functions, based on the logistic growth equation, denote the effect of the plant biomass already present (Traas & Aldenberg, 1992). For macrophytes, it mainly comprises competition for space in a particular layer: at a high biomass, growth is hampered and mortality increases. K is the maximum biomass [$\mathrm{gDW\ m^{-2}}$], φ a distribution factor and r [$\mathrm{d^{-1}}$] the intrinsic rate of increase, i.e. the net rate of increase without nutrient limitation but including inevitable losses:

$$r = \mu max(T) * DayLength * f_L - kresp(T) - kmortmin \quad [\mathrm{d^{-1}}]$$

For duckweed only, passive migration has been added as a possible additional loss factor, with the migration rate coupled to the water outflow rate. This process is negligible for the application described in this paper. A number of the duckweed parameters have been derived from STOWA (1992).

The algae have been modelled as in the lake model *PCLake* (Janse & Aldenberg, 1990; Janse, 1997), but were lumped into one group. The formulations resemble those for the non-rooted submerged plants, with mortality and sedimentation as first order loss processes.

The competition between the plant groups is mainly determined, in the model, by the factors light, space, nutrients and - for algae and duckweed - outflow. The freely floating group (duckweed) are not limited by light, but are confined to the water column for their nutrient uptake. They hamper the growth of the submerged vegetation due to light interception. The submerged groups compete for light, nutrients and space. An important factor is whether they are able to use the sediment nutrient pool or not. Both Nymphaeids and helophytes may take considerable amounts of nutrients from the sediment, while the first group also is a light interceptor and competes with duckweed for space. In field situations, helophytes are often removed once or twice a year because of ditch management.

SITE DESCRIPTION

System characteristics

The experimental ditches, located at Renkum, the Netherlands, were constructed in 1987-1988; they have been described extensively by Portielje (1994). All ditches are 0.5 m deep in the middle, 1.6 m wide at the bottom and 40 m long and have a gravel bank with a slope of 30°. Four of the ditches have a lightly clayish sediment, four others a sandy sediment. The water retention time was in the order of 1 year. All ditches were left undisturbed for one year, followed by a nutrient treatment period from 1989 up to 1992. Each series consisted of a control ditch and three levels of nutrient addition (denoted as 'low', 'middle' and 'high'). The 'low-loaded' ditches received 0.52 gP m^{-2} y^{-1}, divided into two equal doses yearly. The 'middle-loaded' ditches received 1.64 gP m^{-2} y^{-1} and 6.2 gN m^{-2} y^{-1} in the same way.The two highly-loaded ditches received 14 gP m^{-2} y^{-1} and 85 gN m^{-2} y^{-1}, in ten doses yearly. Besides these nutrient additions, all ditches (including the 'controls') received dry and wet atmospheric deposition, estimated as 0.11 [gP m^{-2} y^{-1}] and 3.3 [gN m^{-2} y^{-1}]. The N load from this latter source is considerable. The additions were chosen so as to produce a P concentration of 0.15 mgP l^{-1} (the Dutch summer standard for lakes) in the low-treated ditches, about 3 times this value in the middle-treated and about 25 times in the high-treated ones. The total N loadings were about 6 times the P loadings; in the low-treated ditches it was somewhat higher because of the atmospheric load. No ditch management has been performed.

The sediment characteristics and the initial values of the model variables were derived from the measurements given in Table 1 (from Portielje, 1994).

Table 1. Sediment characteristics of the ditches

Variable	Unit	Clay ditches	Sand ditches
Lutum (<2 μm)	[%]	10.3 ± 0.4	1.2 ± 0.1
Porosity (below 1 cm)	[-]	0.4	0.3
Bulk density (idem)	[g m^{-3} sed.]	$1.5 \cdot 10^6$	$1.7 \cdot 10^6$
Organic matter	[% of DW]	0.75 (0.7-0.8)	0.13 (0.1-0.2)
Extractable P	[mgP g^{-1} DW]	0.25 (0.22-0.29)	0.10 (0.10-0.11)
Total N	[mgN g^{-1} DW]	0.50 (0.41-0.60)	0.05 (0.04-0.07)
Total Fe	[mgFe g^{-1} DW]	11 (10-12)	1.7 (1.6-1.8)
Oxalate-extractable Fe	[mgFe g^{-1} DW]	3.0	0.07
Extractable Al	[mgAl g^{-1} DW]	0.001	0.00032
$CaCO_3$	[% of DW]	0.4 (0.3-0.6)	< 0.1

We assumed a relevant sediment layer of initially 5 cm. An important difference between the two sediment types is thus that the clay ditches contain about 5 times as much organic matter, twice as much phosphorus and about 6 times as much nitrogen as the sand ditches. In the clay ditches, the phosphorus is mainly in organic form and adsorbed on iron, while in the sand ditches aluminum is the main adsorbent (Portielje, 1994).

Summary of field data

The vegetation succession in the ditches has been described by Portielje (1994) and Eugelink et al. (1997). In short, the charophytes in the clay ditches gradually disappeared, the higher the loading the faster. They were replaced by submerged plants (mainly *Elodea* species, besides *Potamogeton gramineus* and *Ranunculus circinatus*), the density of which was a function of the loading level. In the middle-loaded ditch they declined again in 1994. Occasionally, blooms of filamentous and/or planktonic algae were observed. Also helophytes developed in some of the ditches. The highly-loaded ditch was dominated by duckweed from 1991 on. In later years, the duckweed, after a rapid development, declined dramatically from June on due to grazing by lepidopteran larvae. In the untreated sand ditch hardly any plant life was seen at all. The low-treated ditch showed some benthic algae, together with some elodeids from 1993 on. The middle-treated ditch was dominated by algae (benthic, filamentous and planktonic) with some elodeids from 1995 on, while the highly-loaded was soon dominated by duckweed, like the respective clay ditch. Lepidopteran larvae were not observed.

SIMULATION METHOD

The simulations started in May 1989, with measured densities, i.e. a charophyte vegetation in the clay ditches and no macrophytes present in the sand ditches. It seemed most reasonable to start with these densities as initial values, as processes likely to affect initial colonisation of a new water body, such as migration and germination ecology, were not modelled. Alternatively, simulations were performed starting a few years beforehand, allowing the model to equilibrate to the control conditions. Inorganic matter in the water column was arbitrarily set at 1.0 g m^{-3} and the initial SRP concentration in the water at 0.01 mgP l^{-1} (about the value in the control ditches), while the sediment parameters were set as in Table 1. All process parameters were the same for all ditches. A number of sensitive parameters (listed in Table 2) were selected for an optimization study, calibrating against the vegetation monitoring data (coverage percentages) of all 8 ditches. The duckweed data of the high-loaded clay ditch were corrected as if no herbivory by lepidopteran larvae had taken place, as these larvae were not included in the model. As yet, also the algal data have been left out because of inconsistencies. The initial parameter ranges (see Table 2) were estimated from literature data. The fit criterion to be minimized (maximum likelihood) was the sum of squared differences between model and data for all data points in all ditches for all vegetation groups. In this way, the method seeks for that parameter combination that gives the best overall fit regarding all ditches, rather than the best fit for one ditch while leaving a poor fit for the others. The optimum was searched by means of the Simulated Annealing method (Aarts & Van Laarhoven, 1989).

RESULTS

The results of the optimization study with respect to the model parameters are shown in Table 2. The simulation results, using the calibrated values for the Table 2 parameters and the nominal values for all others, are depicted in Fig. 2, together with the measured data (from Eugelink et al., 1987). Only the figures for the control clay ditch and the high-loaded sand ditch are shown. Generally speaking, the dominance of submerged vegetation in the control, low- and medium-loaded ditches, and the shift towards duckweed dominance after two years in the heavily-loaded ones, is modelled reasonably well (Fig. 2b, d). The modelled densities of submerged vegetation in the sand ditches are much lower than in the respective clay ditches, which is in accordance with the monitoring data. The disappearance of the charophytes from all clay ditches is reproduced by the model, although the rate is overestimated for the control ditch (Fig. 2a). The algal densities are generally underestimated (Fig. 2c), as well as the helophytes in the control ditch (not shown). The absence of non-rooted plants and nymphaeids from all ditches is simulated well. The simulated dissolved PO_4 concentrations in the water were generally low (about 0.02 mgP l^{-1}) in the control ditches, showed short peaks at the times of dosage in the low- and middle-loaded ditches and increased to very high values (> 10 mgP l^{-1}) during the loading period in the high-loaded ditches. This is grossly in the range of measured concentrations, with some overestimation for the high-loaded ditches.

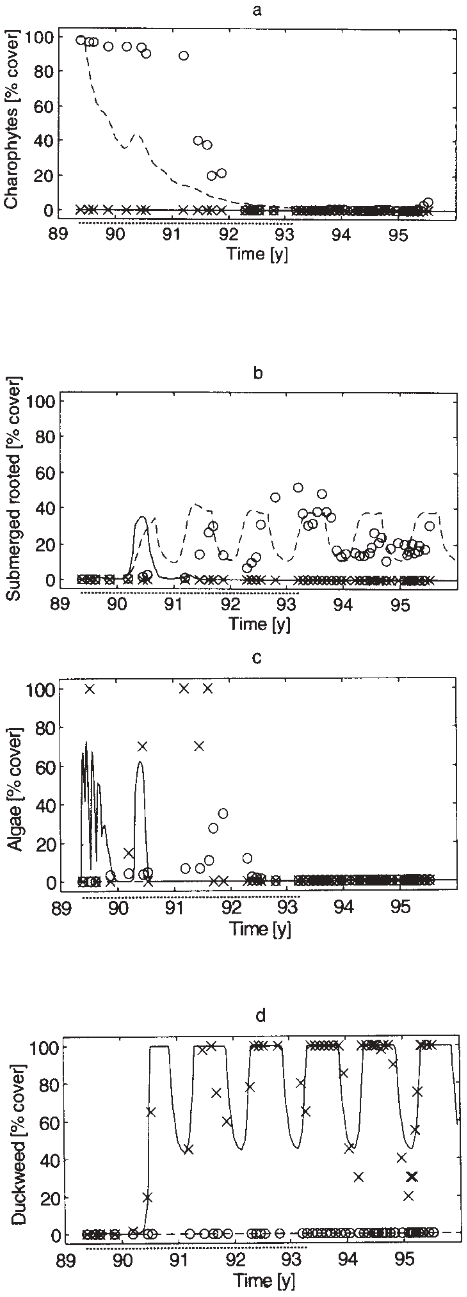

Figure 2. Simulations (lines) and monitoring data (symbols) for four vegetation groups for the control clay ditch (solid lines, x) - and the high-loaded sand ditch (dashed lines, o). The loading period is indicated by dotted line under the x-axis. a, charophytes; b, submerged rooted plants; c, algae; d, duckweed. Helophytes are not shown, non-rooted submerged plants and nymphaeids were not present. Plant densities are expressed in coverage percentages.

Alternative simulations, starting after 3 years of equilibration of the model, showed comparable results for all plant groups, except that the charophytes had disappeared already during the equilibration period.

Table 2. Parameters used in the optimization study

Parameter	Unit	Description	Range	Value
μMaxElod	[d^{-1}]	max. growth rate of submerged rooted plants	0.2 - 0.5 (0.8)	0.29
μMaxChar	[d^{-1}]	max. growth rate of charophytes	0.2 - 0.5	0.20
μMaxCera	[d^{-1}]	max. growth rate of non-rooted submerged plants	0.2 - 0.4	0.21
μMaxLemn	[d^{-1}]	max. growth rate of duckweed	0.2 - 0.4	0.40
μMaxNymp	[d^{-1}]	max. growth rate of nymphaeids	0.03 - 0.10	0.033
μMaxHelo	[d^{-1}]	max. growth rate of helophytes	0.03 - 0.10	0.043
μMaxAlgae	[d^{-1}]	max. growth rate of algae	1.0 - 2.0	1.90
LrefElod	[$W\ m^{-2}$]	Monod constant for light	20 - 50	31.6
LrefChar	[$W\ m^{-2}$]	Monod constant for light	10 - 50	18.6
LrefCera	[$W\ m^{-2}$]	Monod constant for light	20 - 50	39.1
LrefAlgae	[$W\ m^{-2}$]	Monod constant for light	10 - 30	10.2
cPDminElod	[$mgP\ mg^{-1}\ DW$]	min. P content	0.0005 - 0.002	0.0008
cPDminChar	[$mgP\ mg^{-1}\ DW$]	min. P content	0.0005 - 0.002	0.0012
cPDminCera	[$mgP\ mg^{-1}\ DW$]	min. P content	0.0005 - 0.002	0.0012
cPDminLemn	[$mgP\ mg^{-1}\ DW$]	min. P content	0.004 - 0.006	0.0041
cPDminAlgae	[$mgP\ mg^{-1}\ DW$]	min. P content	0.001 - 0.005	0.0020
fHiberElod	[-]	overwintering fraction	0.2 - 0.8	0.21
fHiberChar	[-]	overwintering fraction	0.6 - 1.0	0.91
fHiberCera	[-]	overwintering fraction	0.2 - 0.8	0.71
fHiberLemn	[-]	overwintering fraction	0.1 - 0.4	0.13
fHiberHelo	[-]	overwintering fraction	0.2 - 0.5	0.43
kdPAdsIMS	[$m^3\ g^{-1}\ DW$]	affinity constant for P adsorption	0.001 - 0.015	0.0074

DISCUSSION

The model reproduces correctly a dominance of submerged vegetation at phosphorus input concentrations up to 0.45 mgP l^{-1}, and a rather rapid shift to duckweed dominance at an input concentration of 3.5 mgP l^{-1}. The simulated submerged biomass (or coverage) is related to the nutrient loading level (up to 0.45 mgP l^{-1}) and to the sediment type (clay or sand). The results are in accordance with the hypothesis that eutrophication of shallow water bodies causes a shift in the vegetation towards more surface-oriented plants (Bloemendaal & Roelofs, 1988). This shift occurs, in the simulations, as soon as the availability of nutrients exceeds the uptake capacity of the submerged vegetation.

The initial dominance of charophytes in the clay ditches was not a stable situation, in view of the fact that they were replaced after a few years by elodeid plants in the untreated ditch as well. This succession in the pioneer phase is probably co-regulated by other (not-modelled) factors (Eugelink et al., 1997) and could not be reproduced well. This did, however, not influence the overall results, as the simulations with the pre-equilibrated model were almost identical for the later years. The simulation of the algal dynamics was poor. This is partly due to the fact that the algal data were not yet used for the calibration. Comparison of simulations and data is hampered by the need of estimating conversion factors from biomass to cover percentages. Continuation of the calibration on more data, including the nutrient concentrations, and using a broader set of parameters, is likely to further improve the model fit. This will also facilitate interpolation of the results to intermediate loading levels.

The aim of the model, to describe the relation between nutrient run-off, water quality and vegetation in ditches in a general way, makes extrapolation of the results to field situations necessary. The model application on the experimental ditches as described here is likely to be useful for this purpose, because both the input and the response variables are rather well defined. The representativeness of these ditches for real-world situations is limited, however, as they are nearly stagnant and are not subjected to vegetation management. In field situations, a number of additional intervening variables need to be accounted for. These include, among others, water depth and water level fluctuations, hydrological variables (water retention time, infiltration, seepage), the interconnection of ditches in drainage patterns, and yearly vegetation management. A field validation will be necessary to be able to derive the 'critical' loading levels for undesired ecological effects in different situations. In view of the remaining uncertainty in the model structure and parameters after calibration, these loading levels will be defined in a probabilistic way.

CONCLUSIONS

The *PCDitch* model reproduces reasonably the shift from a submerged vegetation to a duckweed dominance in semi-stagnant ditches, when increasing the external nutrient loading from low to very high. Further calibration as well as testing the model in field situations are necessary to improve the model's predictive value in a variety of ditch systems.

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Chapter 15

ELSEVIER

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ENVIRONMENTAL
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Effects of eutrophication in drainage ditches

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Abstract

Eutrophication of drainage ditches by over-fertilization with nitrogen and phosphorus causes a shift from a mainly submerged aquatic vegetation to a dominance of duckweed. This causes anoxic conditions, loss of biodiversity and hampering of the agricultural functions of the ditches. Simulations with the model *PCDitch*, previously calibrated on experimental ditches, indicate that this switch may occur as soon as a certain threshold nutrient loading level is exceeded. This level tends to increase with the water depth. It is recommended to validate the model predictions in field situations.

Keywords: Ditch; duckweed; eutrophication; nitrogen; phosphorus; macrophytes; model

Introduction

Drainage ditches are small, linear water bodies, usually less than 1.5 m deep and several meters wide. With a total length of about 300,000 km, they are a common water type in the lowland parts of the Netherlands, where their main task is the discharge of excess rainwater from agricultural areas. They form the link between the farmland and larger water bodies such as lakes and canals (Fig. 1). The water transport from the lowland polder areas is often mediated by pumping stations (formerly by windmills). Many ditches also serve to transport water to the fields during dry periods. Besides their hydrological functions, ditches have an important ecological function, providing a habitat for many plant and animal species. They are also important as a source of drinking water for cattle. Because of their shallowness, ditches are often dominated by macrophytes. Most ditches require yearly maintenance (removal of the vegetation and/or the detrital layer) to ensure water flow.

Many ditches are strongly affected by eutrophication due to agricultural nutrient losses. This has a number of adverse effects on the quality and functioning of the ditches, i.e. related to duckweed coverage and oxygen household. This paper summarizes these effects. For policy purposes, such as derivation of nutrient loading standards and the evaluation of agricultural scenarios, it is desirable to know how the probability of adverse effects depends on the N and P losses from the fields. In order to analyze this topic quantitatively, the mathematical model *PCDitch* has recently been developed (Janse and Van Puijenbroek, 1997; Janse, 1998). This paper describes some applications of this model for average ditches.

Summary of eutrophication effects

The vegetation structure in moderately eutrophic ditches is often characterised by a dominance of submerged vegetation, besides emergent species (helophytes) and often a phytoplankton bloom in spring (De Groot et al., 1987; Veeningen, 1982). Yearly mowing usually hampers a further natural succession to helophyte dominance. Several tens of plant species may occur, together with a rich fauna of, among others, insect larvae and amphibians. Moderate enrichment with nutrients causes an increase of submerged vegetation biomass. Further eutrophication often stimulates the blooming of

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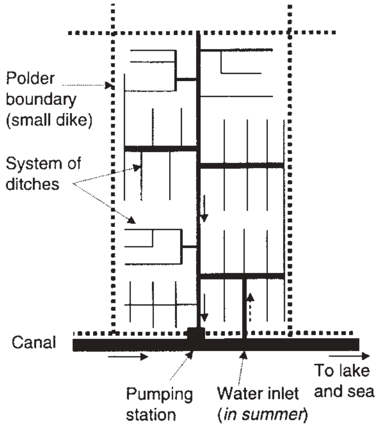

Fig. 1. Schematic drawing of the water system in the lowland parts of The Netherlands. The area is divided into polders where a certain water level is maintained; most polders are situated below sea level. If precipitation exceeds evapotranspiration, excess water is discharged by means of a network of ditches, and (usually) a pumping station, to a canal and further to lakes and sea. In dry periods, water can be let in from the canal.

filamentous and/or epiphytic algae. Decreased light conditions cause a shift from species with a vertical growth strategy to those with a horizontal growth strategy (Sand-Jensen and Søndergaard, 1981; Bloemendaal and Roelofs, 1988) and the species diversity diminishes. At very high nutrient loading, the vegetation becomes dominated by a surface layer of pleustophytic plants only, such as duckweed (Lemnaceae) or floating fern (*Azolla*), while submerged plants have disappeared (Portielje and Roijackers, 1995; Eugelink et al., 1998). Several adverse effects are related to this shift to duckweed. Because the oxygen produced is released into the atmosphere instead of the water and reaeration is hampered, while decomposition continues to extract oxygen from the water, the water becomes often anoxic and mineralization occurs mainly anaerobically (Veeningen, 1982; Marshall, 1981; Portielje, 1994). This leads to loss of aerobic life in the ditch. Because of health effects and/or a bad taste, the water becomes unsuitable as drinking water for cattle (Hovenkamp-Obbema, 1998). Water passages and pumping stations are obstructed by duckweed. In some regions, duckweed is removed by man, thus increasing management costs (STOWA, 1997).

Duckweed dominance is a fairly common phenomenon in the Netherlands (e.g. Van der Does and Klink, 1991; STOWA, 1992; BKH Adviesbureau, 1995). In the region Hollands Noorderkwartier (ca. 2500 km^2, situated north of Amsterdam), 30% of ca. 350 investigated ditches has a duckweed coverage of more than 25% in summer (Fig. 2). The mean summer nutrient concentrations in the ditches in this area are 3.4 mg N l^{-1} (range: 1.0–19.6) and 1.1 mg P l^{-1} (range: 0.05–7.9). The mean P concentration is somewhat higher in the duckweed-dominated ditches than in the other ones, but there is only little difference in mean N concentration (data from Water Board USHN). Several authors showed a positive correlation between duckweed cover on one hand, and nitrogen and phosphorus concentrations in the water or the nitrogen fertilizing level on the adjacent fields on the other (De Groot et al., 1987; Van der Does and Klink, 1991; STOWA, 1993; BKH Adviesbureau, 1995), but the correlations were often obscured by (all positive) correlations with other factors, such as BOD, conductivity and pH (Van der Does and Klink, 1991). Also transport processes are known to be important, while Boeyen et al. (1992) found duckweed cover to decrease with increasing water depth.

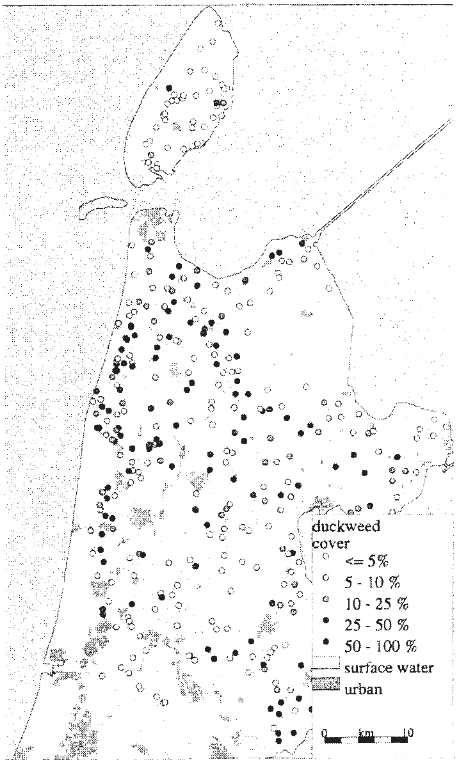

Fig. 2. Average duckweed cover in July-September at the monitoring stations in ditches in the region Hollands Noorderkwartier (data from Water Board USHN).

Model description and simulation method

The *PCDitch* model (Janse and Van Puijenbroek, 1997; Janse, 1998) describes the relationships between the external nutrient loading, the in-ditch nutrient concentrations and the dynamics of the dominant vegetation types in ditches: submerged plants, algae, duckweed and helophytes. Its aim is to assess the 'critical level' of nutrient loading above which shifts in vegetation are likely to occur, and to assess the main influencing factors. The model is confined to the ditch ecosystem itself (Fig. 3a); the relation between land use and nutrient leaching is covered by other models (e.g. Meinardi and Van den Eertwegh, 1995; Groenendijk and Kroes, 1997), the results of which are used as input. The model structure is shown in Fig. 3b. The main N and P flows in the system (water and sediment) are described, combined with different functional groups of vegetation. The division into vegetation groups is a simplification of the system of Den Hartog and Van der Velde (1988) and is based on the layers in which the plants grow and take up nutrients. Duckweed, algae and non-rooted submerged plants are confined to the water column for their nutrient uptake, while helophytes take nutrients from the sediment only and rooted submerged plants are able to use both pools. Alternatively, duckweed hampers the growth of submerged plants by light interception at the water surface.

The ranges of the model parameters were first derived from literature (for duckweed e.g. STOWA, 1992), whereas a number of them were calibrated against the data from a series of experimental, semi-stagnant ditches, collected during a research project of the Wageningen Agricultural University and the Winand Staring Centre (Portielje and Roijackers, 1995; Eugelink et al., 1998). The *PCDitch* model was able to reproduce the dominance of submerged plants at a low N and P loading (up to 9.5 g N m^{-2} ditch area $year^{-1}$ and 1.7 g P m^{-2} $year^{-1}$) and of duckweed at a very high loading (88 g N m^{-2} $year^{-1}$ and 14 g P m^{-2} $year^{-1}$) (Janse and Van Puijenbroek, 1987; Janse, 1998). The model has not yet been validated in field situations.

Using this model, calculations were performed over a 20-year period for a 'representative' clay ditch of, on the average, 0.8 m deep and 3 m wide (water surface area 300 m^2), at different levels of nitrogen loading. A constant water discharge rate was assumed of 10 m^3 d^{-1}, derived from a precipitation surplus of 1.0 mm d^{-1} and 3% of the total area consisting of ditches (the average figure in Hollands Noorderkwartier). Similar simulations were performed for water depths of 0.6, 1.0 and 1.2 m. In order to exclude phosphorus limitation of the vegetation, a relatively high phosphorus loading was assumed of 0.5 times [g/g] the N loading. The simulations were performed both with and without regular maintenance, consisting of 80% removal each autumn of the submerged and emergent vegetation by mowing. All simulations started with a nutrient-poor sediment and absence of vegetation.

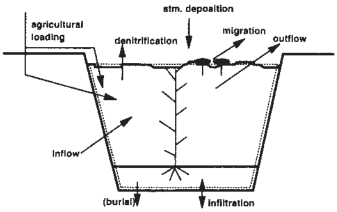

Fig. 3a. System boundary of the *PCDitch* model. The dotted line denotes the model boundary, the arrows the flows of water and/or nutrients that go into or out of the system. Submerged plants and duckweed are shown schematically.

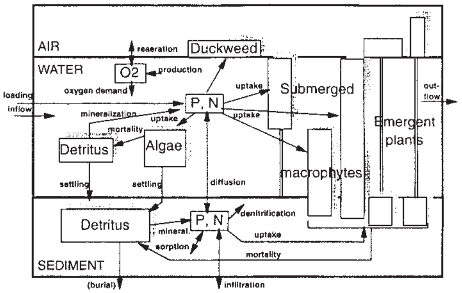

Fig. 3b. *PCDitch* model structure. Blocks denote the state variables of the model, those with a shadow are modelled both in dry-weight, N and P units. The arrows represent the modelled fluxes.

Results

At a low loading level of 10 g N d^{-1}, equivalent to an input concentration of 1 g N m^{-3} (Fig. 4a), the theoretical ditch with a depth of 0.8 m became (and remained) dominated by submerged vegetation in the simulations. Some algae were present in the first 10 years, while duckweed did not develop at all. Helophytes developed but very slowly in the case of yearly maintenance, while they became co-dominant after 8–10 years in the absence of mowing (not shown). By contrast, at a 3 times higher nutrient loading (Fig. 4b), the initially developing submerged vegetation collapsed after 5 years, and duckweed took over. It reached a biomass of over 150 g d.m. m^{-2}, which usually implies a 100% coverage of the water surface. The algal density in the first five years was higher than at low loading. In the absence of mowing, the helophytes, emerging after 8 years, reached a higher biomass as well (not shown).

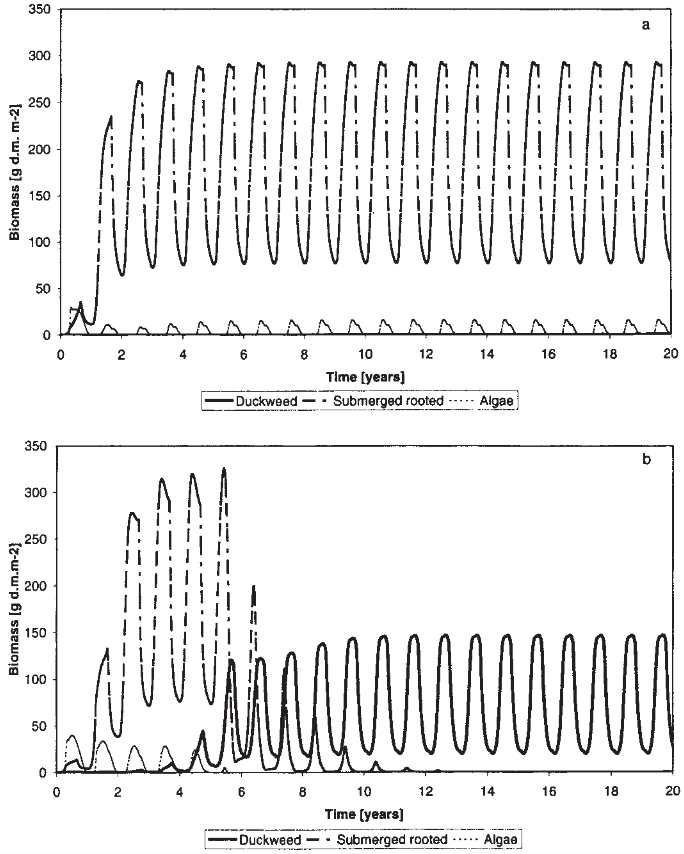

Fig. 4. Simulated biomass of submerged rooted vegetation, algae and duckweed in an average clay ditch of 0.8 m deep and 3 m wide (surface area 300 m^2) and a water discharge of 10 m^3 d^{-1}. (a) Low nutrient loading (10 g N d^{-1}); (b) high nutrient loading (30 g N d^{-1}).

By combining the results of simulations for a wide range of loading levels, a 'dose–effect relationship' of duckweed biomass as a function of the N loading was derived (Fig. 5). The duckweed biomass is given as an average for July to September of the 20th year of the simulations. The relationship is shown for different values of the water depth. It appears that as soon as a certain threshold nutrient level is exceeded, duckweed biomass easily reaches a high level (100% coverage of the water surface). The threshold nutrient level generally increases with the water depth. Only in very shallow ditches (0.6 m), the relationship between nutrient loading and duckweed biomass is less steep, with a lower biomass at intermediate loading levels. The relationship between loading level and submerged rooted plants (not shown) is more or less opposite to the one for duckweed: a high biomass at low and intermediate loading levels, and absence at high ones. The highest algal biomass is predicted at intermediate loading levels.

Discussion

The results of the simulations are consistent with the hypothesis that eutrophication of shallow water bodies causes a shift towards plants with a horizontal growth strategy, the extreme of which is duckweed (Bloemendaal and Roelofs, 1988). This result could be achieved by combining basic assumptions on the nutrient uptake and light dependency of the main functional groups of water

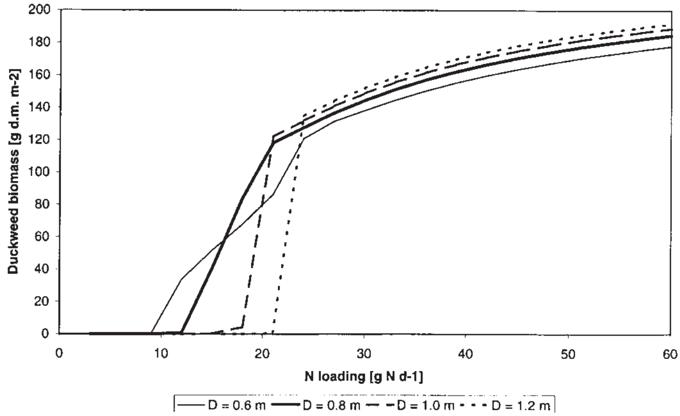

Fig. 5. Simulated duckweed biomass in summer (July–September) of the 20th simulated year as a function of the nitrogen loading, in average clay ditches (3 m wide, surface area 300 m^2) and a water discharge of 10 m^3 d^{-1}, at different water depths.

plants with general nutrient flow equations. Submerged rooted plants are favoured at low nutrient loading, as their minimum nutrient content for growth is relatively low (Gerloff and Krombholz, 1966), and because they are able to use two sources: water and sediment pore water. If the nutrient loading level is moderately increased, the competitive power of algae increases because of the higher nutrient concentrations in the ditch water and because of competition for light. In nature, the algal community may, besides filamentous algae, also consist of epiphytic species (Sand-Jensen and Søndergaard, 1981). If the nutrient loading increases to such an extent that a surplus of dissolved nutrients is left in the water column, duckweed may profit from this. Duckweed has a much higher need for nutrients, both phosphorus and nitrogen, which it has to take up from the water column (STOWA, 1992). As soon as duckweed develops, it may outcompete submerged plants, and also algae, completely, at least in late summer, because of light interception.

The model indicates shifts in vegetation at nitrogen loading levels of several tens of grammes per day, equivalent to input concentrations of several milligrams per liter. These concentrations are exceeded frequently in many Dutch polder areas (Meinardi and Van den Eertwegh, 1995). Observed nitrogen concentrations in ditches (De Groot et al., 1987; Van der Does and Klink, 1991; BKH Adviesbureau, 1995; data USHN) are often in this same range, but the simulated relationship between nitrogen and duckweed could not be compared directly with these literature data, among others because of the many other intervening factors. These were not always measured, while also in the simulations only a few factors were varied. The availability of monitoring data covering more environmental factors would facilitate a comparison between model and data.

The results indicate that deeper ditches are somewhat less sensitive to nutrient loading than shallow ones. This is consistent with the results of field studies by Boeyen et al. (1992) and could be explained by a stronger dilution of nutrients in deeper ditches. This implies that deepening could be useful as a management measure in moderately eutrophied ditches. Only in very shallow ditches (0.6 m), submerged plants may survive a somewhat higher nutrient loading, if the advantage of the higher light intensity under water outbalances the disadvantage of the higher nutrient concentrations in the water.

Comparable results as shown for nitrogen were obtained from simulations with varying phosphorus loading, avoiding nitrogen limitation (Janse and Van Puijenbroek, 1997). This indicates that both nitrogen and phosphorus are important to explain shifts in vegetation. These findings should, however, be compared with measurements and models of nutrient leaching, in order to draw conclusions on the relative importance of either element in field situations. At this stage of the model development, no absolute significance can be attached to the calculated threshold values. The model needs to be validated in 'real-life' situations. This is done in a follow-up research project that is being carried out, in cooperation with several Water Boards and other institutions.

Conclusions

Eutrophication of drainage ditches causes a shift from a mainly submerged aquatic vegetation to a dominance of duckweed. Simulations with the model *PCDitch*, previously calibrated on experimental ditches, indicate that this switch may occur as soon as a certain threshold nutrient loading level is exceeded. This level tends to increase with the water depth, except for very shallow ditches. It is recommended to validate these results in field situations.

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16. Conclusions

The *PCLake* model predicts that shallow lakes (depth up to *ca* 4 m) may switch between a clear, macrophyte-dominated state and a turbid, phytoplankton-dominated state as a function of changed nutrient loading. The response may take many years, dependent on the sediment history of the lake. This change is difficult to reverse: because both states can be stable in an intermediate range of loadings, the switches show a hysteresis effect. The critical loading rate for the switch from the turbid to the clear state is lower than for the opposite switch. Hence, restoration of a lake is difficult once it has become turbid. This complies with other existing evidence. The model predicts that the critical loading rates depend on lake type: they decrease with water depth and lake size, increase with hydraulic loading rate and relative marsh area, and depend on the type of sediment (highest for sand, lowest for peat, clay in-between). For the most common lake types in The Netherlands, the critical loading for 'turbidification' is calculated as about 2–5 mgP m^{-2} d^{-1}, and the value for 'clarification' (or 'restoration') as 0.6–1.0 mgP m^{-2} d^{-1}. The concomitant critical total-phosphorus concentrations for restoration are in the range of 0.03 - 0.1 mgP/l. These simulated threshold values are in reasonable ranges in view of empirical information. Based on a Bayesian identification and uncertainty analysis, the uncertainty in the predictions of the 'restoration' switchpoint may be estimated as a factor 2, and for the 'turbidification' switchpoint somewhat higher. Sensitivity analyses suggest that in the model light- and nutrient-related processes are the most important for the stability of both states, whereas foodweb mechanisms particularly affect the stability of the 'clear' state.

The structure of the model integrates water and nutrient budgets, biogeochemical cycles and ecological feedbacks via both bottom-up and top-down processes. This encompasses the range of mechanisms thought to be crucial in determining the critical load for either macrophytes or phytoplankton dominance. This allows to compare the impact of different mechanisms and fluxes. On the other hand, the resulting complexity inevitably has a cost in terms of uncertainty.

From the application point of view, the important contribution of the model is that it allows an integrated assessment of the combined effects of several management strategies, and of the impact of lake type and other autonomous factors. The following management options can be evaluated using *PCLake* (cf Fig. 2.3):

(a) Catchment management:

- increase or reduction in nutrient (P, N) loading
- hydrological measures, flushing
- wetland restoration
- water level, water level fluctuations

(b) Local factors or management:

- biomanipulation
- fishery
- birds
- mowing

- dredging
- reducing fetch
- sediment traps (local pits)

(c) Autonomous factors

- type of sediment
- water temperature, climate change. (Note: climate change is likely to affect other factors as well, like water levels, retention time and nutrient loading.)

The model *PCDitch*, describing eutrophication effects in ditches, predicts that, above a certain critical nutrient loading, the ecosystem may switch from a dominance of submerged vegetation to a floating mat of duckweed. The predicted critical loading ranges from *ca* 2-10 gP m^{-2} y^{-1} for common ditch types, with concomitant total phosphorus concentrations of 0.2-0.4 mgP l^{-1}, and varies among others with depth, hydraulic loading rate and sediment type. Besides, vegetation management usually carried out yearly in ditches affects the response. The uncertainty of the model has yet to be assessed. According to the model, the response time for a shift from duckweed to submerged vegetation is much longer than for the opposite one. The model suggests that dredging can enhance restoration only if the loading is below the critical level. Also *PCDitch* can be used to evaluate combined management strategies made up of catchment measures (loading, hydrology, water level) and local measures (dredging, mowing).

The models may be used in an explorative way, to select possible key factors and promising management strategies for specific lake or ditch types. If the model is to be applied in specific cases, one should be aware that part of the relations and parameters are based on general regressions, average of experimental results, or partly qualitative estimates that may be less reliable in a specific case. Strategies to improve the quality of predictions may be to adapt parameters to local knowledge, to use Monte Carlo simulations to account for remaining parameter uncertainty, or to use a ‘submodel’ by fixing some variables.

The outcome of both models may be expressed as, for instance, the chance for recovery of a lake or ditch type under different circumstances or with different management options, or in terms of the minimum load reduction to be achieved. This approach resembles the ecological risk assessment adopted for toxic substances and other environmental issues. The calculation of the critical loading values, although with a considerable uncertainty, may be helpful for the underpinning of ecological standards for water quality. Perhaps most importantly, the models indicate how sensitivity to nutrient loading may differ between water bodies. This allows the development of differentiated protection standards. The modelling approach presented here, coupling biological structure and nutrient cycle, is regarded a useful tool for the design of nutrient regulations and water management strategies.

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Appendix:
Model description of *PCLake* and *PCDitch*

1. *PCLake*

This section describes *PCLake*, as well as the equations common to *PCLake* and *PCDitch*.

1.1. Nomenclature

The model variables have been named according to an easy-to-read system of nomenclature, so that the type, unit and meaning of a variable can be derived directly from its name. This system is used throughout this chapter and in the model code. The basic system is as follows:

type + element + process + component + layer (+ suffix)

– State variables: s + element + compartment + layer (+ 0)
(state) (D/P/N/Si/O2) (IM/Det/PO4/NH4/Phyt/Zoo/etc.) (W/S) (-/IC)
- Processes (fluxes): t/w + element + process + compartment + layer
(flux) (D/P/N/Si/O2) (Set/Min/etc.) (IM/Det/PO4/NO3/Phyt/etc.) (W/S)

The abbrevations are listed here:

Substances, elements:
D- = dry weight
P- = phosphorus
N- = nitrogen
Si- = silica
O2- = oxygen
Q- = water flow
L- = light
Tm = temperature
Chla, Ch- = chlorophyll-a

Layers:
– W = water column
– S = sediment top layer
– T = total
– M = marsh zone
– WM = water column in marsh zone
– SM = sediment top layer in marsh zone

Components:
– IM = inorganic matter
– Det = detritus
– Hum = humus
– PO4 = phosphate, -NH4 = ammonium,
-NO3 = nitrate
– Diss = (total) dissolved,

Processes:
Load = external loading
Dil = dilution
Ev = evaporation
Outfl = surface outflow
Inf = infiltration/seepage
Eros = erosion
Exch = exchange lake <-> marsh
Set = settling, sedimentation
Resus = resuspension
Bur = burial
Dif = diffusion
Nitr = nitrification
Deit = denitrification
Sorp = ad-/desorption
Min = mineralization
Upt = uptake (of nutrients)
Ass = assimilation
Prod = production
Cons = consumption
Eges = egestion
Resp = respiration (DW)
Excr = excretion (nutrients0
Graz = grazing
Pred = predation
Mort = natural mortality

– AIM = adsorbed onto inorganic matter
– Phyt = (total) phytoplankton
-Diat = diatoms
-Blue = blue-greens
-Gren = small edible algae
-OM = total organic matter
-Zoo = zooplankton
-Fish = whitefish
-FiAd = adult whitefish
-FiJv = juvenile whitefish
-Pisc = predatory fish
-Bent- = zoobenthos
-Tot = total
-Veg = submerged vegetation
-Phra = reed vegetation
s...0 = initial value of state variable
d- = derivative
t- = transfer (flux, process) per area [g/m^2/d]
w- = flux (transfer, process) per volume of water [g/m^3/d]
v- = volume change per area [m/d]
r- = (dynamical) ratio [gA/gB]
o- = concentration [m/g/l]
a- = other auxiliary
c- = constant (general)
k- = rate constant [d-1]
h- = half-saturation constant
f- = fraction [–]
b- = derived constant
u- = (derived) input variable, or derived constant
m- = measurement, read variable
i-, j- = counters (integers)
n- = numbers (integers)
kd- = partitioning coefficient (used in sorption equations) [(gX/gDW)/(gX/m^3)]=[m^3/g]

Loss = phytopl. grazing loss (in case food web not included
Harv = harvesting
Man = management, mowing
Dred = dredging

Tran = total transport flux
Abio = total flux from abiotic module
Prim = total flux from algae module
Bed = total flux from vegetation module
Web = total flux from food web module
Mars = total flux from marsh module
Ext = total external flux (for mass balance)

Prefixes:
s- = state variable
Suffixes:
-Max = maximum
-Min = minimum
-In = incoming
-Bot = bottom
-mg = in milligrammes
-Sp = specific (’’per unit of biomass’’)

Other abbreviations:
-Fun- = function, dependence
-C(o)r- = corrected, modified
-Iso = adsorption isotherm
-Ext = extinction
-V- = velocity [m/d]
-Mu- = grwoth rate [d-1]
-Carr- = carrying capacity, maximum biomass [gDW/m^2 or gDW/m^3]
-Secchi = transparencym, Secchi dept [m]

1.2. Model structure

1.2.1. General structure and components

The model describes a homogeneous and well mixed shallow (non-stratifying) lake. The model comprises both the water column and the sediment top layer, with the most important biotic and abiotic components. Spatial differences within the lake are not taken into account, but optionally, a wetland zone with marsh vegetation may be included (Fig. 1). Moreover, the model can be used in a spatial setting, in conjunction with the water transport model DUFLOW (STOWA, 1998, 1999).

This model description is based on PCLake version 5.08 (2004). The model structure is made flexible so that the user may lump, split or leave out certain groups, but the default configuration is described here.

Mathematically, the model is composed of a number of coupled differential equations, one for each state variable, as listed in table 1. The structure of the lake model is shown in Fig. 2, that of the marsh module in Fig. 3. All biota are modelled as functional groups. Besides mass fluxes (food relations etc.), the model also contains some ‘empirical’ or indirect relations between components, such as the impact of fish and macrophytes on resuspension (see below). The water depth (sDepthW) is a state variable, while the thickness of the sediment top layer (cDepthS) is assumed constant (default 0.1 m). Both layers are considered as well mixed. All components in the water are modelled as concentrations [g m^{-3}], in the sediment as the amounts in the top layer [g m^{-2}].

The overall nutrient cycles for N, P and Si are described as completely closed (except for

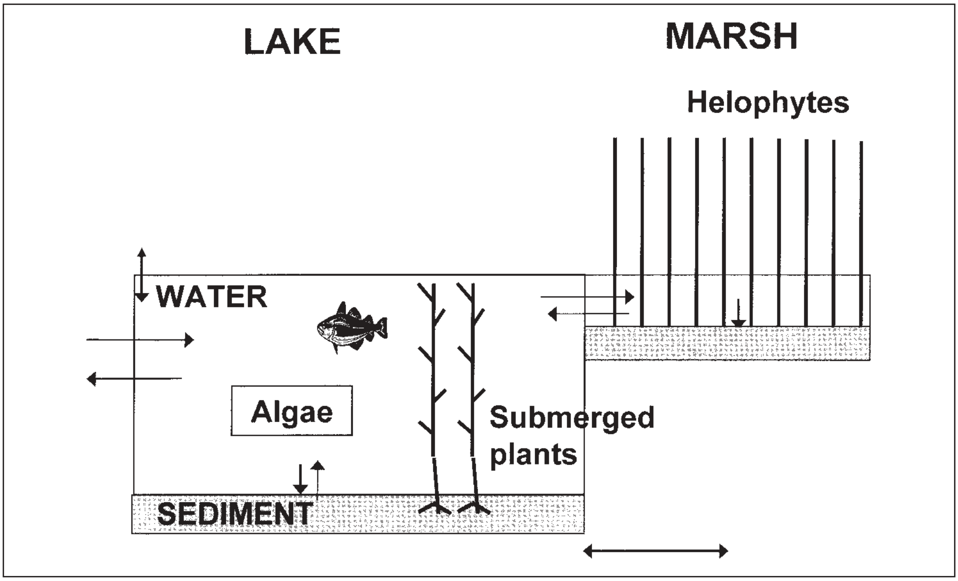

Fig. 1. *Schematic model structure of PCLake.*

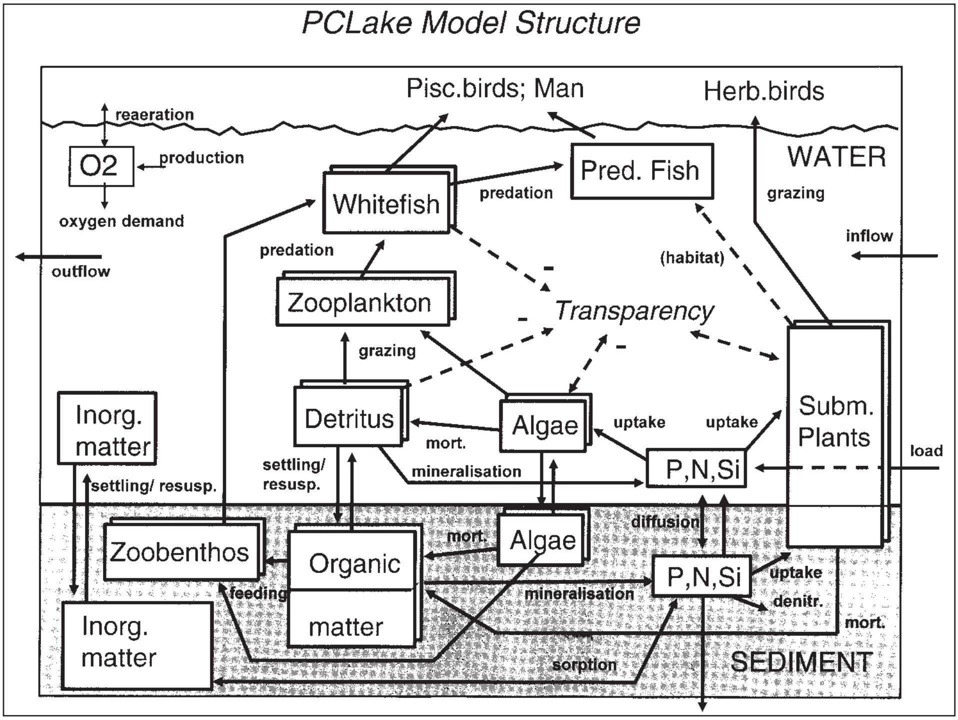

Fig. 2. *PCLake model structure (lake part).*

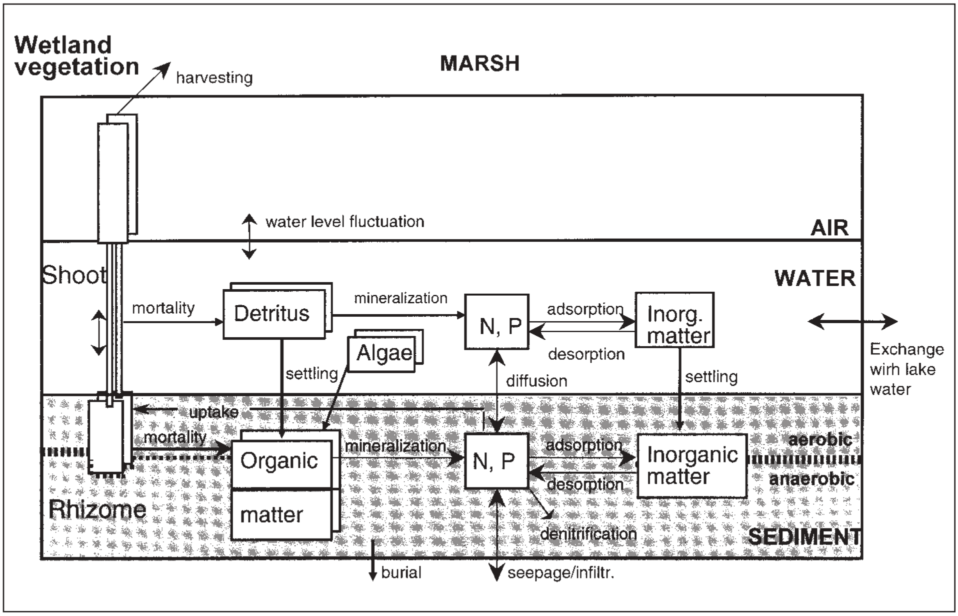

Fig. 3. *Model structure of the wetland module*

Table 1. State variables in PCLake. Abbreviations: s- = state variable, D = dry-weight, P = phosphorus, N = nitrogen, Si = silica, O_2 = oxygen.

Description	Unit	As water	As dry-weight (D)	As phosphorus (P)	As nitrogen (N)	As silica (Si)	As oxygen (O_2)
Water depth	[m]	sDepthW	–	–	–	–	–
Abiotic comp. in water column							
Inorganic matter	[g m^{-3}]		sDIMW	–	–	–	–
Detritus	[g m^{-3}]		sDDetW	sPDetW	sNDetW	sSiDetW	–
Inorg. nutrients	[g m^{-3}]		–	sPO$_4$W, sPAIMW	sNH$_4$W, sNO$_3$W	sSiO2W	–
Oxygen[g m^{-3}]			–	–	–	–	SO$_2$W
Abiotic comp. in sediment:							
Inorganic matter	[g m^{-2}]		sDIMS	–	–		–
Humus	[g m^{-2}]		sDHumS	sPHumS	sNHumS	–	–
Detritus	[g m^{-2}]		sDDetS	sPDetS	sNDetS	sSiDetS	–
Inorg. nutrients	[g m^{-2}]		–	sPO$_4$S, sPAIMS	sNH$_4$S, sNO$_3$S		–
Phytoplankton[1] in water column:							
Diatoms	[g m^{-3}]		sDDiatW	sPDiatW	sNDiatW	(oSiDiatW)	–
Small edible algae	[g m^{-3}]		sDGrenW	sPGrenW	sNGrenW		–
Blue-greens	[g m^{-3}]		sDBlueW	sPBlueW	sNBlueW		–
Settled phytoplankton[1]:							
Diatoms	[g m^{-2}]		sDDiatS	sPDiatS	sNDiatS	(aSiDiatS)	–
Small edible algae	[g m^{-2}]		sDGrenS	sPGrenS	sNGrenS		–
Blue-greens	[g m^{-2}]		sDBlueS	sPBlueS	sNBlueS		–
Vegetation:							
Submerged vegetation[2]	[g m^{-2}]		sDVeg	sPVeg	sNVeg		–
Animal groups[3]:							
Zooplankton	[g m^{-2}]		sDZoo	sPZoo	sNZoo		–
Zoobenthos	[g m^{-2}]		sDBent	sPBent	sNBent		–
Juvenile whitefish	[g m^{-2}]		sDFiJv	sPFiJv	sNFiJv		–
Adult whitefish	[g m^{-2}]		sDFiAd	sPFiAd	sNFiAd		–
Piscivorous fish	[g m^{-2}]		sDPisc	(aPPisc)	(aNPisc)		–
Marsh vegetation[4]:							
Reed shoots	[g m^{-2}]		sDShootPhra	sDRootPhra	sNShootPhra		–
Reed rhizomes	[g m^{-2}]		sDRootPhra	sPRootPhra	sNRootPhra		–

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[1] Optionally, the phytoplankton may be lumped into one group, sDPhyt.

[2] Optionally, several groups of macrophytes may be defined rather than one. The submerged vegetation may be split into several groups: rooted (sDElod), non-rooted (sDCera) and charophytes (sDChar), and/or floating-leaved plants (sDNymp) may be added. The vegetation can also be left out completely, if desired.

[3] The food-web module optionally can be left out.

[4] The wetland module is optional. IM, organic matter, nutrients, oxygen and phytoplankton are defined in the water and sediment of the wetland zone as well.

external fluxes such as in- and outflow and denitrification). This was done by modelling most components in three elements (as indicated by the ‘shadowed’ blocks in the pictures), viz. dry-weight (abbreviated as D), nitrogen (N) and phosphorus (P), detritus also in silica (Si). Inorganic carbon (CO_2) is not explicitly modelled. The nutrient-to-dry-weight ratios are thus variable. The total mass balances per element are dynamically checked during the calculations. ‘Day’ was chosen as a uniform time unit for all processes (but the simulation time can be chosen as variable); however, the relevant time scale for the output is about weeks to 1 month.

1.2.2. List of differential equations

The differential equations are listed per compartment. The naming conventions explained in § 1.1 are applied: state variables are denoted by *s*-, derivatives by *d*-, other variables by *a*-, concentrations by *o*-, and processes by *t*- (if expressed per area) or *w*- (if expressed per volume). The listed processes are described in detail in the next paragraphs.

The transport processes are typeset in the normal way, the *abiotic and microbial processes (as well as burial and dredging) in italics*, the **algal processes in bold**, the ***macrophyte processes in bold italics***, the food-web processes are underlined and the *processes in the marshland are in italics and underlined*.

Many equations apply to both *PCLake* and *PCDitch*. Most important differences are:

- the definition of three (*PCLake*) versus one (*PCDitch*) algal group
- the definition of one (*PCLake*) versus six (*PCDitch*) macrophyte groups.
- the food web and marsh modules apply to *PCLake* only, not to *PCDitch*. (Zooplankton grazing on algae is then replaced by a first-order loss processs of the algae, abbreviated as ‘Loss’.)
- the silica cycle is modelled in *PCLake* only (related to the diatoms).

Other differences are explained in § 2.

If there is more than one algal group, as default in *PCLake*, the abbreviation -Phyt- denotes the total phytoplankton. Likewise, in *PCDitch*, -Veg- denotes the sum of the vegetation groups.. The abbreviation ‘sDepthW’ means the water depth [m].

a. Water depth

dDepthW = ((uQin – cQinf – uQev – uQOut) / 1000) / (1.0 + fMarsh) + *vDeltaW* + *vDredDepthW*
= inflow – infiltration – evaporation – outflow + burial correction + dredging || Water depth [m/d]

b. Organic and inorganic matter

dDIMW = uDLoadIM/sDepthW - wDDilIM + *(uDErosIMW - tDSetIM + tDResusIM) / sDepthW - aRelDeltaW * sDIMW* – *wDExchIM* || Inorganic matter in water [mgD/l/d]
= loading – dilution + erosion – settling + resuspension – burial correction – marsh exchange

dDDetW = uDLoadDet/sDepthW - wDDilDet *(- tDSetDet + tDResusDet) / sDepthW - wDMinDetW* **+ wDMortPhytW + *(tDMortVegW + tDEgesBird) / sDepthW*** - wDConsDetZoo + wDEgesZoo + wDMortZoo + (tDEgesFish + tDMortFishDet + tDEgesPisc + tDMortPiscDet) / sDepthW - *aRelDeltaW * sDDetW – wDExchDet*
|| Detritus in water [mgD/l/d]

dPDetW = uPLoadDet/sDepthW - wPDilDet *(- tPSetDet + tPResusDet) / sDepthW - wPMinDetW* **+ wPMortPhytDetW + *(tPMortVegDetW + tPEgesBirdDet) / sDepthW*** - wPConsDetZoo + wPEgesZooDet + wPMortZooDet + (tPEgesFishDet + tPMortFishDet + tPEgesPiscDet + tPMortPiscDet) / sDepthW - *aRelDeltaW * sPDetW – wPExchDet*
|| Detritus in water [mgP/l/d]

dNDetW = uNLoadDet/sDepthW - wNDilDet *(- tNSetDet + tNResusDet) / sDepthW - wNMinDetW* **+ wNMortPhytDetW + *(tNMortVegDetW + tNEgesBirdDet) / sDepthW*** - wNConsDetZoo + wNEgesZooDet + wNMortZooDet + (tNEgesFishDet + tNMortFishDet + tNEgesPiscDet + tNMortPiscDet) / sDepthW - *aRelDeltaW * sNDetW – wNExchDet*
|| Detritus in water [mgN/l/d]
= loading - dilution - settling + resuspension - mineralisation + algal mortality + part of macrophyte mortality in water + birds egestion – zooplankton detritus consumption + zooplankton egestion and mortality + whitefish egestion and mortality + pred.fish egestion and mortality – burial correction – marsh exchange

dSiDetW = uSiLoadDet/sDepthW - wSiDilDet *(- tSiSetDet + tSiResusDet) / sDepthW - wSiMinDetW* **+ wSiMortDiatW** + wSiConsDiatZoo - *aRelDeltaW * sSiDetW – wSiExchDet* || Detritus [mgSi/l/d]
= loading - dilution - settling + resuspension – mineralisation + diatoms mortality + zooplankton diatoms consumption – burial correction – marsh exchange

dDIMS = *uDErosIMS* + *tDSetIM* - *tDResusIM* - *tDBurIM*- *tDDredNetIMS*
= erosion + settling – resuspension – burial – dredging
|| Sediment inorg. matter [gD m^{-2} d^{-1}]

dDHumS = *uDErosOM + fRefrDetS * tDMinDetS – tDMinHumS - tDBurHum - tDDredNetHumS*
Sediment humus [gD m^{-2} d^{-1}]

dPHumS = *uPErosOM + fRefrDetS * tPMinDetS – tPMinHumS - tPBurHum - tPDredNetHumS*
Sediment humus [gP m^{-2} d^{-1}]

dNHumS = *uNErosOM + fRefrDetS * NDMinDetS – tNMinHumS - tNBurHum - tNDredNetHumS*
Sediment humus [gN m^{-2} d^{-1}]
= erosion + humification– mineralisation – burial – dredging

dDDetS = *tDSetDet* - *tDResusDet* - *tDMinDetS* - *tDBurDet* – tDDredDetS **+ tDMortPhytS** +

tDMortVegS - tDConsDetBent + tDEgesBent + tDMortBent || Sediment detritus [gD m^{-2} d^{-1}]

dPDetS = *tPSetDet* - *tPResusDet* - *tPMinDetS* - *tBurDet* – tPDredDetS **+ tPMortPhytDetS** + ***tPMortVegDetS*** - tPConsDetBent + tPEgesBent + tPMortBent || Sediment detritus P [gP m^{-2} d^{-1}]

dNDetS = *tNSetDet* - *tNResusDet* - *tNMinDetS* - *tNBurDet* – tNDredDetS **+ tNMortPhytDetS** + ***tNMortVegDetS*** - tNConsDetBent + tNEgesBent + tNMortBent

|| Sediment detritus [gN m^{-2} d^{-1}]

= settling – resuspension - mineralisation - burial - dredging + sed. algal mortality + macrophyte mortality in sed. – zoobenthos detritus consumption + zoobenthos egestion and mortality

dSiDetS = *tSiSetDet* - *tSiResusDet* - *tSiMinDetS* - *tSiBurDet* – tSiDredDetS + **tSiMortDiatS** + tSiConsDiatBent || Sediment detritus Si [gSi/m2/d]

= settling – resuspension - mineralisation - burial - dredging + sed.diatoms mortality – zoobenthos diatoms consumption

c Inorganic nutrients

dPO4W = uPLoadPO4/sDepthW - wPDilPO4 + *cPBackLoad* + *wPMinDetW* - *wPSorpIMW* + *(tPDifPO4 + tPResusPO4 - tPInfPO4W) / sDepthW* **- wPUptPhyt + wPExcrPhytW + wPMortPhytPO4W + *(- tPUptVegW + tPExcrVegW + tPMortVegPO4W + tPEgesBirdPO4) / sDepthW*** + wPExcrZoo + wPEgesZooPO4 + wPMortZooPO4 + (tPExcrFiJv + tPExcrFiAd + tPEgesFishPO4 + tPMortFishPO4 + tPExcrPisc + tPEgesPiscPO4 + tPMortPiscPO4) / sDepthW - *aRelDeltaW* * *sPO4W* - *wPExchPO4*

|| PO_4 in water [mgP/l/d]

= loading - dilution + background loading + mineralisation – sorption + diffusion from sediment + resuspension - infiltration - algal uptake + algal excretion + part of algal mortality - macrophyte uptake from water + macrophyte excretion in water + part of macrophyte mortality + egestion by birds + zooplankton excretion and part of egestion and mortality + whitefish excretion and part of egestion and mortality + pred.fish excretion and part of egestion and mortality – burial correction – marsh exchange

dPAIMW = uPLoadAIM/sDepthW - wPDilAIM + *(tPResusAIM – tPSetAIM) / sDepthW* + *wPSorpIMW* - *aRelDeltaW* * *sPAIMW* *– wPExchAIM* || Adsorbed P in water [mgP/l/d]

= loading - dilution + resuspension - settling + sorption – burial correction – marsh exchange

dPO4S = *tPInfPO4W* - *tPInfPO4S* + *(1.0-fRefrDetS)* * *tPMinDetS* + *tPMinHumS* - *tPSorpIMS* - *tPResusPO4* - *tPDifPO4* - *tPDifGroundPO4* - *tPChemPO4* - *tPBurPO4* **+ tPExcrPhytS + tPMortPhytPO4S - *tPUptVegS* + *tPExcrVegS* + *tPMortVegPO4S*** + tPExcrBent + tPEgesBentPO4 + tPMortBentPO4 || PO_4 in pore water [gP m^{-2} d^{-1}]

= infiltration from water - infiltration to groundwater + detritus and humus mineralisation – sorption – resuspension - diffusion to water and groundwater - immobilisation - burial +

excretion and part of mortality of sed. algae - macrophyte uptake from sediment + macrophyte excretion in sediment + part of macrophyte mortality + excretion and part of egestion and mortality of zoobenthos.

dPAIMS = *tPSetAIM - tPResusAIM + tPSorpIMS - tPBurAIM - tPDredAIMS*

= settling – resuspension + sorption – burial – dredging || Adsorbed P in sediment [gP m^{-2} d^{-1}]

dNH4W = uNLoadNH4/sDepthW - wNDilNH4 + *cNBackLoad* + *wNMinDetW* - *wNNitrW* - *tNInfNH4W / sDepthW* + *(tNDifNH4 + tNResusNH4) / sDepthW* **- wNUptNH4Phyt + wNExcrPhytW + wNMortPhytNH4W –** ***(tNUptNH4VegW + tNExcrVegW + tNMortVegNH4W + tNEgesBirdNH4) / sDepthW*** + wNExcrZoo + wNEgesZooNH4 + wNMortZooNH4 + (tNExcrFiJv + tNExcrFiAd + tNEgesFishNH4 + tNMortFishNH4 + tNExcrPisc + tNEgesPiscNH4 + tNMortPiscNH4) / sDepthW - *aRelDeltaW* * *sNH4W* - *wNExchNH4* || ammonium in water [mgN/l/d]

= loading - dilution + background loading + mineralisation – nitrification in water - infiltration + diffusion from sediment + resuspension - algal uptake + algal excretion + part of algal mortality - macrophyte uptake from water + macrophyte excretion in water + part of macrophyte mortality + egestion by birds + zooplankton excretion and part of egestion and mortality + whitefish excretion and part of egestion and mortality + pred.fish excretion and part of egestion and mortality – burial correction – marsh exchange.

dNO3W = uNLoadNO3/sDepthW - wNDilNO3 + *wNNitrW* - *wNDenitW* + *(tNDifNO3 + tNResusNO3 - tNInfNO3W) / sDepthW* **- wNUptNO3Phyt -** ***tNUptNO3VegW / sDepthW*** - *aRelDeltaW* * *sNO3W* - *wNExchNO3* || Nitrate in water [mgN/l/d]

= loading - dilution + nitrification in water – denitrif. in water + diffusion from sediment + resuspension – infiltration - algal uptake - macrophyte uptake from water – burial correction – marsh exchange.

dNH4S = *tNInfNH4W* - *tNInfNH4S* + *(1.0-fRefrDetS)* * *tNMinDetS* + *tNMinHumS* - *tNResusNH4* - *tNDifNH4* - *tNDifGroundNH4* - *tNNitrS* - *tNBurNH4* + **tNExcrPhytS + tNMortPhytNH4S** ***- tNUptNH4VegS + tNExcrVegS + tNMortVegNH4S*** + tNExcrBent + tNEgesBentNH4 + tNMortBentNH4 || Pore water ammonium [gN m^{-2} d^{-1}]

= infiltration from water - infiltration to groundwater + detritus and humus mineralisation– resuspension - diffusion to water and groundwater - nitrification in sediment - burial + excretion and part of mortality of sed. algae - macrophyte uptake from sediment + macrophyte excretion in sediment + part of macrophyte mortality + excretion and part of egestion and mortality of zoobenthos.

dNO3S = *tNInfNO3W* - *tNInfNO3S* + *tNNitrS* - *tNDenitS* - *tNResusNO3* - *tNDifNO3* - *tNDifGroundNO3* - *tNBurNO3* ***- tNUptNO3VegS*** || Pore water nitrate [gN m^{-2} d^{-1}]

= infiltration from water - infiltration to groundwater + nitrification in sed. - denitrification in sed. – resuspension - diffusion to water and groundwater - burial - macrophyte uptake from sediment

dSiO2W = uSiLoadSiO2/sDepthW - wSiDilSiO2 + *wSiMinDetW* + *(1.0 - fRefrDetS)* * *tSiMinDetS / sDepthW* **- wSiUptDiat** + **wSiExcrDiatW + tSiExcrDiatS / sDepthW** - *aRelDeltaW * sSiO2W - wSiExchSiO2*
|| dissolved silica in water [mgSi/l/d]
= loading - dilution + mineralisation in water and sediment – diatoms uptake + diatoms excretion in water and sed. – burial correction – marsh exchange.

d Dissolved oxygen

dO2W = wO2Inflow - wO2Outfl + *tO2Aer / sDepthW* - *wO2MinDetW* - *wO2NitrW* - *(tO2MinDetS + tO2NitrS) / sDepthW* + **wO2ProdPhyt - wO2RespPhytW + wO2UptNO3Phyt** + (***tO2ProdVegW - tO2RespVegW + tO2UptNO3VegW) / sDepthW*** - *aRelDeltaW * sO2W* - *wO2Exch* || oxygen in water [gO2/m3/d]
= inflow - outflow + reaeration - mineralisation - nitrification - sediment oxygen demand + algal production - algal respiration + nitrate uptake by algae + macrophyte production - macrophyte respiration + nitrate uptake by macrophytes) – burial correction – marsh exchange

e. Algae / phytoplankton:

In *PCLake*, these equations are defined for each of the three groups: Blue, Gren and Diat.
If the food web is not modelled, as in *PCDitch*, grazing ('-ConsZoo-') is replaced by '-Loss-'.

dDPhytW = uDLoadPhyt/sDepthW - wDDilPhyt + **wDAssPhyt - wDRespPhytW - wDMortPhytW (- tDSetPhyt + tDResusPhyt) / sDepthW** - wDConsPhytZoo - *aRelDeltaW * sDPhytW – wDExchPhyt*
= loading - dilution + production - respiration – mortality – settling + resuspension – grazing – burial correction – marsh exchange. || Algae in water column [mgD/l/d]

dPPhytW = uPLoadPhyt/sDepthW - wPDilPhyt + **wPUptPhyt - wPExcrPhytW - wPMortPhytW (- tPSetPhyt + tPResusPhyt) / sDepthW** - wPConsPhytZoo - *aRelDeltaW * sPPhytW – wPExchPhyt*
= loading - dilution + uptake – excretion – mortality – settling + resuspension – grazing – burial correction – marsh exchange. || Algae in water column [mgP/l/d]

dNPhytW = uNLoadPhyt/sDepthW - wNDilPhyt + **wNUptPhyt - wNExcrPhytW - wNMortPhytW (- tNSetPhyt + tNResusPhyt) / sDepthW** - wNConsPhytZoo - *aRelDeltaW * sNPhytW – wNExchPhyt*
= loading - dilution + uptake – excretion – mortality – settling + resuspension – grazing – burial correction – marsh exchange. || Algae in water column [mgN/l/d]

dDPhytS = **tDSetPhyt - tDResusPhyt – tDMortPhytS - tDRespPhytS** - tDConsPhytBent – *tDDredPhytS* || Sediment algae [gD/m2/d]

dPPhytS = **tPSetPhyt - tPResusPhyt – tPMortPhytS - tPExcrPhytS** - tPConsPhytBent – *tPDredPhytS* || Sediment algae [gP/m2/d]

dNPhytS = **tNSetPhyt - tNResusPhyt – tNMortPhytS - tNExcrPhytS** - tNConsPhytBent – *tNDredPhytS* || Sediment algae [gN/m2/d]
= settling – resuspension – mortality – respiration or excretion – zoobenthos consumption - dredging

f. Water plants:

In *PCDitch*, these equations are defined for the plant groups Elod, Cera, Char, Lemn, Nymp and Helo.

dDVeg = ***tDProdVeg - tDRespVeg - tDMortVeg (+ tDMigrVeg) - tDGrazBird – tDManVeg*** - *tDDredVeg* || Macrophytes [gD m^{-2} d^{-1}]
= production - respiration - mortality (± migration) - bird grazing – mowing – dredging

dPVeg = ***tPUptVeg - tPExcrVeg - tPMortVeg (+ tPMigrVeg) - tPGrazBird – tPManVeg*** - *tPDredVeg*
= uptake – excretion - mortality (± migration) - bird grazing – mowing – dredging
|| [gP m^{-2} d^{-1}]

dNVeg = ***tNUptVeg - tNExcrVeg - tNMortVeg (+ tNMigrVeg) - tNGrazBird – tNManVeg*** - *tNDredVeg*
= uptake – excretion - mortality (± migration) - bird grazing – mowing – dredging
|| [gN m^{-2} d^{-1}]

g. Animal groups (in *PCLake* only)

dDZoo = ukDil * (cDZooIn - sDZoo) + wDAssZoo - wDRespZoo - wDMortZoo - tDConsFiJv / sDepthW - *aRelDeltaW * sDZoo* – *wDExchZoo* || Zooplankton [mg/l/d]
= inflow–dilution + assimilation - respiration – mortality – fish predation – burial corr. – marsh exchange

dDBent = tDMigrBent + tDAssBent - tDRespBent – tDMortBent - tDConsFiAd – *tDDredBent*
= migration + assimilation - respiration – mortality – fish predation – dredging || Zoobenthos [gD/m2/d]

dDFiJv = tDMigrFiJv + tDReprFish - tDAgeFish + tDAssFiJv - tDRespFiJv - tDMortFiJv - tDConsFiJvPisc || Juvenile whitefish [gD/m2/d]
= migration + reproduction – ageing + assimilation - respiration – mortality –predation

dDFiAd = tDMigrFiAd - tDReprFish + tDAgeFish + tDAssFiAd - tDRespFiAd - tDMortFiAd - tDConsFiAdPisc – tDHarvFish || Adult whitefish [gD/m2/d]
= migration - reproduction + ageing + assimilation - respiration – mortality –predation - harvesting

dDPisc = tDMigrPisc + tDAssPisc - tDRespPisc - tDMortPisc - tDHarvPisc || Predatory fish [g/m2/d]
= migration + assimilation - respiration – mortality - harvesting

These differential equations are, *mutatis mutandis*, defined in terms of P and N as well, except for predatory fish which is assumed to have constant nutrient ratios. For nutrients, the term ‘excretion’ is used parallel to ‘respiration’.

h Wetland zone (in *PCLake* only)
dDepthWM = vTranDepthW / 1000 *+ vDeltaWM* || Water depth [m/d]

Marsh vegetation:
dDShootPhra = ***tDProdShootPhra - tDRespShootPhra – tDMortShootPhra + tDAllPhra - tDRealPhra – tDManShootPhra*** || biomass shoot reed [gD/m2/d]
= production – respiration – mortality + allocation – reallocation - mowing
dDRootPhra = ***tDProdRootPhra - tDRespRootPhra - tDMortRootPhra - tDAllPhra + tDRealPhra***
= production – respiration – mortality - allocation + reallocation || biomass root reed [gD/m2/d]
dPShootPhra = ***tPUptShootPhra - tPMortShootPhra + tPTransPhra - tPRetrPhra – tPManShootPhra***
= uptake – mortality + translocation – retranslocation - mowing || P in shoot reed [gP/m2/d]
dPRootPhra = ***tPUptRootPhra - tPMortRootPhra – tPTransPhra + tPRetrPhra***
= uptake – mortality - translocation + retranslocation || P in root reed [gP/m2/d]
and comparable equations for N.

Other components in marsh water and sediment:
(equations, with mostly abiotic and microbial processes, are grossly the same as given above, with suffix
‘–M’ for ‘marsh’.)
dDIMWM = *- tDSetIMM/sDepthWM + wDExchIMM - aRelDeltaWM * sDIMWM* || IM in water [gD/m3/d]
dDIMSM = *tDSetIMM - tDBurIMM* || Inorg. matter in sediment [gD/m2/d]
dDHumSM = *fRefrDetS * tDMinDetSM - tDMinHumSM – tDBurHumM* || sed. humus [gD/m2/d]
and comparable equations in terms of P and N.
dDDetWM = ***tDMortShootPhra/sDepthWM*** *- tDSetDetM/sDepthWM – wDMinDetWM + wDExchDetM - aRelDeltaWM * sDDetWM* || Detritus in water [gD/m3/d]
and comparable equations in terms of P, N and Si.
dDDetSM = ***tDMortRootPhra*** *+ tDSetDetM - tDMinDetSM + tDSetPhytM - tDBurDetM*
|| Detritus in sediment [gD/m2/d]
and comparable equations in terms of P, N and Si.

dO2WM = *tO2AerM / sDepthWM - wO2MinDetWM - wO2NitrWM - (tO2MinDetSM + tO2NitrSM) / sDepthWM + wO2ExchM - aRelDeltaWM * sO2WM*

dPO4WM = *- tPInfPO4WM / sDepthWM + tPDifPO4M / sDepthWM + wPMinDetWM - tPEvPO4WM / sDepthWM - wPSorpIMWM + wPExchPO4M - aRelDeltaWM * sPO4WM*

dPAIMWM = *- tPSetAIMM / sDepthWM+ wPSorpIMWM + wPExchAIMM - aRelDeltaWM * sPAIMWM*

dPO4SM = *tPInfPO4WM - tPInfPO4SM + tPEvPO4WM + (1.0-fRefrDetS) * tPMinDetSM + tPMinHumSM - tPSorpIMSM - tPDifPO4M - tPDifGroundPO4M - tPChemPO4M -* ***tPUptPhraS*** *- tPBurPO4M*

dPAIMSM = *tPSetAIMM - tPBurAIMM + tPSorpIMSM*

dNH4WM = *tNDifNH4M/sDepthWM - wNNitrWM + wNMinDetWM - tNEvNH4WM/ sDepthWM - tNInfNH4WM/sDepthWM + wNExchNH4M - aRelDeltaWM * sNH4WM*

dNO3WM = *tNDifNO3M/sDepthWM + wNNitrWM - wNDenitWM - tNEvNO3WM/ sDepthWM - tNInfNO3WM/sDepthWM + wNExchNO3M - aRelDeltaWM * sNO3WM*

dNH4SM = *tNInfNH4WM - tNInfNH4SM + (1.0-fRefrDetS) * tNMinDetSM + tNMinHumSM - tNDifNH4M - tNDifGroundNH4M - tNNitrSM - tNBurNH4M -* ***tNUptNH4PhraS*** *+ tNEvNH4WM*

dNO3SM = *tNInfNO3WM - tNInfNO3SM + tNNitrSM - tNDenitSM - tNDifNO3M - tNDifGroundNO3M - tNBurNO3M -* ***tNUptNO3PhraS*** *+ tNEvNO3WM*

dSiO2WM = *wSiMinDetWM + tSiMinDetSM / sDepthWM + wSiExchSiO2M - aRelDeltaWM * sSiO2WM*

dDPhytWM = *wDExchPhytM - tDSetPhytM / sDepthWM - aRelDeltaWM * sDPhytWM*
and comparable equations in terms of P, N and Si.

dDZooM = *wDExchZooM - aRelDeltaWM * sDZooM*
and comparable equations in terms of P and N.

i Total mass balances:

Total fluxes in marsh module [g per m2 **lake** per day]:

tDMarsTotT = *(- tDBurTotM - wDMinDetWM * sDepthWM - (1.0 - fRefrDetS) * tDMinDetSM - tDMinHumSM +* ***tDProdPhra - tDRespShootPhra - tDRespRootPhra - tDManShootPhra*** *) * fMarsh*

tPMarsTotT = *(- tPInfPO4SM - tPDifGroundPO4M - tPBurTotM - tPChemPO4M -* ***tPManShootPhra*** *) * fMarsh*

tNMarsTotT = *(- tNInfNH4SM - tNInfNO3SM - tNDifGroundNO3M - tNDifGroundNH4M - tNBurTotM - wNDenitWM * sDepthWM - tNDenitSM -* ***tNManShootPhra*** *) * fMarsh*

tSiMarsTotT = *- tSiBurDetM * fMarsh*

Total fluxes [g per m2 lake per day]:

tDExtTotT = uDLoad - wDDilTot * sDepthW - *tDBurTot + cDErosTot - wDMinDetW * sDepthW - (1.0 - fRefrDetS) * tDMinDetS - tDMinHumS* + **(wDAssPhyt - wDRespPhytW) * sDepthW - tDRespPhytS** + ***tDMigrVeg + tDProdVeg - tDRespVeg - tDManVeg -***

tDAssVegBird - wDRespZoo * sDepthW + tDMigrFiJv + tDMigrFiAd + tDMigrPisc + tDMigrBent - tDRespFiJv - tDRespFiAd - tDRespPisc - tDRespBent - tDMortFishBot - tDMortPiscBot - tDHarvFish - tDHarvPisc + *tDMarsTotT* – *tDDredNetTot*
|| Total dry-weight mass balance [gD m^{-2} d^{-1}]

tPExtTotT = uPLoad - wPDilTot * sDepthW + cPBackLoad – *tPBurTot* + *uPErosOM* - *tPChemPO4* - *tPInfPO4S* - *tPDifGroundPO4* + ***tPMigrVeg - tPManVeg – tPAssVegBird*** tPMigrFiJv + tPMigrFiAd + tPMigrPisc + tPMigrBent - tPMortFishBot - tPMortPiscBot - tPHarvFish - tPHarvPisc + *tPMarsTotT* – tPDredNetTot
|| Total P mass balance [gP m^{-2} d^{-1}]:

tNExtTotT = uNLoad - wNDilTot * sDepthW + *cNBackLoad* - *tNBurTot* + *uNErosOM* - *tNDenitS* - *wNDenitW* * *sDepthW* - *tNInfNH4S* - *tNInfNO3S* - *tNDifGroundNO3* - *tNDifGroundNH4* + ***tNMigrVeg - tNManVeg – tNAssVegBird*** tNMigrFiJv + tNMigrFiAd + tNMigrPisc + tNMigrBent - tNMortFishBot - tNMortPiscBot - tNHarvFish - tNHarvPisc + *tNMarsTotT* – tNDredNetTot || Total N mass balance [gN m^{-2} d^{-1}]

tSiExtTotT = uSiLoad - wSiDilTot*sDepthW - *fRefrDetS* * *tSiMinDetS* - *tSiBurTot* + *tSiMarsTotT* – *tSiDredTot* || Total Si mass balance [gSi m^{-2} d^{-1}]

1.2.3. Coupling of dry-weight and nutrient cycles, and mass balances

An important feature of the present model is the basically independent modelling of the carbon cycle and the phosphorus cycle. The reason for this is as follows. It has been observed that the higher one gets within the trophic web, the higher the phosphorus content of the organisms. The average P/C (or P/D) ratio of the zooplankton is much higher than the ratio of its food (algae and detritus) and the same is true for fish with respect to the zooplankton and bottom organisms. In any food web model, this fact should be accounted for, in order to achieve a closed cycle for all modelled substances at any time. In many existing models, this topic is not adequately dealt with, often without mentioning it. In all models of the ‘Di Toro-type’ for instance (Di Toro et al. 1971, 1975, Thomann 1977, Di Toro & Matystik 1980), with phytoplankton chlorophyll, zooplankton C, detritus P and inorganic P as state variables, no closed phosphorus cycle is possible whatsoever, unless the P/C ratios of all compartments are equal (Aldenberg & Peters 1988). Jørgensen (1980) developed a multi-unit model (dry weight, C, N and P) with variable ratios between them, but also in this model no systematic differences in ratios between compartments can be achieved, because the underlying ecological and physiological mechanisms which are responsible for those differences, are not included; therefore, in steady state, all P/C ratios would become equal. In any model with basically different P/C ratios between compartments, one or more of the P/C ratios should be dynamical to maintain a closed P balance. In the ‘second step’ precursor of PCLake (Aldenberg 1987a,b, Aldenberg & Peters 1988), the P/C ratio of the detritus has been used for this purpose; the ratios of phyto- and zooplankton were kept constant. In PCLake 2.4 (at that time called PCLoos) the multi-elemental modelling has been extended to the phytoplankton, in view of empirically observed shifts in nutrient ratios, and to the animal groups, to increase the model’s robustness. In later versions including nitrogen and macrophytes, the same approach has been followed.

The PCLake model described here has maintained these basic features, i.e. closed phosphorus and nitrogen cycle at any time and differences in P/D and N/D ratios between compartments.
As may be seen from this table and from fig. 2, organic matter and all biota (except piscivorous fish) are modelled in multiple elements, viz. dry-weight, phosphorus and nitrogen (and water detritus also in silica; see below). This makes it possible to account for variations in the nutrient-to-dry-weight ratios of these groups. These ratios are simply calculated as (with *r*- being the prefix for ratios):

$rPDComp = sPComp / sDComp$	P/D ratio of component ‘Comp’ [gP/gD]
$rNDComp = sNComp / sDComp$	N/D ratio of component ‘Comp’ [gN/gD]

Only the equations for growth/nutrient uptake, respiration/excretion and assimilation/egestion are really different for dry-weight or nutrients. In this way, the nutrient ratios of algae and macrophytes may change during the model run. The nutrient ratio of detritus may vary because it is formed by a mixture of many sources, mainly algae and macrophytes after they die off. All other processes, such as settling, mortality and mineralisation, are described in the same way for nutrients as for dry-weight, and do not influence the ratios:

$$tPProcess = rPDComp * tDProcess$$
$$tNProcess = rNDComp * tNProcess$$

The only purpose of tripling these equations is to close the nutrient cycles. The model is thus much less complex than it may seem at first sight from the list of differential equations. For a quick impression of the model, it should be sufficient to have a look at the dry-weight differential equations as well as the equations for PO_4, NH_4 and NO_3.

Mass balance check

Please note that the cycles of all four elements are considered as closed within the sytem, apart from external fluxes. These are: external input and outflow, infiltration, burial, denitrification (for N), precipitation (for P) and migration. As dissolved carbon is not modelled, in contrast to dissolved N and P, growth and respiration by algae and macrophytes and decomposition, expressed as dry-weight, are considered as external fluxes as well. The corresponding nutrient processes of uptake and excretion are internal fluxes.
The external fluxes are reflected in the total mass balance equations. These consist of four additional differential equations, one for each element D, P, N and Si, describing the mass crossing the system boundaries. This amount should equal the difference between the total amount present in the system, i.e. the sum of all biotic and abiotic components, and the initial amount. This can be checked any time during the simulation. For P:

uPTotT0	initial amount of P in the system (= sum of all P components) [gP m^{-2}]
aPTotT	total amount of P in system [gP/m2]

tPExtTotT	sum of the fluxes entering or leaving the system [gP m^{-2} d^{-1}]
sPExtTotT = INTEG(tPExtTotT, uPTotT0)	total amount of P moved into or out from the system [gP m^{-2}]
aPError = aPTotT – sPExtTotT	P mass balance error [gP m^{-2}]

The equations for D, N and Si look similar. All four ‘mass balance errors’ [g m^{-2}] should be smaller than the accuracy of the integration method.

1.2.4. Software implementation

The model has a modular structure: the processes have been gathered in the following modules (### stands for the version number, i.e. 508):

1. *main module* (‘PCLk###.csl’): definition of the model components, initialisation, differential equations and overall mass balances, as well as burial and dredging.
2. transport module (‘PCLTran###.csl’): external transport of water and substances.
3. *abiotic and microbial module* (‘PCLAbio###.csl’): physical and chemical processes, water-sediment exchange, mineralisation processes.
4. **algal module** (‘PCLPrim###.csl ‘): growth and loss processes of phytoplankton.
5. ***vegetation module*** (‘PCLBed###.csl ‘): growth and loss processes of macrophytes.
6. food web module (‘PCLWeb###.csl’): zooplankton, zoobenthos and fish.

Optional: wetland module, consisting of:

7. *wetland water module* (‘PCLMarshwater###.csl’): marsh processes and exchange.
8. ***wetland vegetation module*** (‘PCLMarshveg###.csl’): emergent vegetation processes.

The transport module and the wetland water module are not included in the DUFLOW version.

The model has been implemented in ACSL/Math v. 11.8 (MGA, 2002) as well as in DUFLOW v. 3.5 (MX Systems, 2002).

For clarity reasons, in the ACSL version, the different modules (listed at the top of this chapter) are represented by different files (file names between brackets; ### = version number), which are automatically combined during the compilation step.

A number of options allow the user to deviate from the default model configuration. The following options are available:

- Lumping of the phytoplankton into one group, abbreviated as ‘Phyt’: set the flag (LOGICAL variable) ‘InclThreeAlg’ to 0 (= FALSE), give the state an initial value and set the initial values of the skipped subgroups to 10^{-33}.
- Definition of several vegetation groups rather than one: change the MACRO calls in the vegetation module and define appropriate initial values. It is possible to split the submerged vegetation into two or three groups and/or to include a separate floating-leaved group.
- Or, contrarily, leave out the entire vegetation module by setting ‘InclBed’ to 0.
- Leave out the food-web module and replace it by an extra phytoplankton loss process, by setting ‘InclWeb’ to 0.

The DUFLOW code can automatically be generated from the ACSL code by a translator programme (an MS-Word macro, written in Visual Basic). Because transport processes are incorporated already in DUFLOW itself, the transport module has been excluded when making the conversion.

1.3. Transport processes and water depth

Transport and loading

One of the basic processes in a lake (and most other surface waters) is the inflow and outflow of water with dissolved and particulate substances. The following mass balance is kept for each component in the water column:

$$dCV/dt = V\,dC/dt + C\,dV/dt$$

$$dC/dt = Q_{in}/V * (C_{in} – C) – Q_{out}/V * (C_{out} – C)$$

$$dV/dt = Q_{in}/V – Q_{out}/V$$

As C_{out} equals C for all outflows except evaporation (where the outflow concentration is zero), the differential equation for concentration reduces to:

$$dC/dt = Q_{in}/V * C_{in} – (Q_{in} – Q_{ev})/V * C$$

or

$$dC/dt = L/V – (Q_{in} – Q_{ev})/V * C$$

where Q_{in} is the sum of all water inflows and C_{in} the weighted average of the concentrations of the component in those inflows. The product $Q_{in} * C_{in}$ is the external loading, L. Note that the dilution effect on the concentration is caused by the water *inflow*, not by the outflow. In the model, all water flows and loadings are expressed per m^2 water by dividing by the lake area. Water flows are in [mm/d] (so, for practical reasons, a factor 1000 is introduced) and loadings in [g m^{-2} d^{-1}].

Evaporation is default described as a sinusoid; instead, it may be read in from a file.

$$uQEv = cQEvAve - cQEvVar * COS(2.0*Pi * (Time + 10 - cTimeLag) / 365) \qquad [mm/d]$$

The minimum is thus found at *cTimeLag* days after the shortest day of the year. The ‘time lag’ is chosen the same as the one for the water temperature (see below). In the Dutch situation, the average evaporation is about 1.5, the amplitude about 1.3 mm/d.

The resulting transport equations are, with PO_4 as an example:

tPTranPO4W = uPLoadPO4 / sDepthW – tPDilPO4 [gP m^{-2} d^{-1}]

in which:

uPLoadPO4	external loading with PO4 [gP m^{-2} d^{-1}]
sDepthW	water depth [m]
*tPDilPO4 = ukDil * sPO4W*	dilution of PO4 [gP m^{-3} d^{-1}]
ukDil = (uQIn - uQEv) / 1000 / sDepthW	dilution rate [d^{-1}]

These loading and dilution equations apply (mutatis mutandis) to the following components in the water column: dissolved nutrients (PO4, NH4 and NO3), oxygen, IM, adsorbed P, detritus, phytoplankton and zooplankton. So not to fish, water plants and zoobenthos; possible migration of these biota is defined separately (see below).

The total P load, N load and water inflow should be supplied by the user, either as time-series, as constants or as summer- and winter-averages. Evaporation values may be supplied as a time-series or approximated as a sinusoid function. In case of constants or seasonal averages, the fraction of the load entering in dissolved form (PO4, resp. NH4 and NO3) and bound in phytoplankton should be given as well; the remainder is in detrital form. Algal and detrital nutrient loading are converted to dry-weight loading by means of fixed conversion factors. External input of IM and SiO2 should be given as input concentrations [mg/l]. See the User Manual for details.

Water depth

The water depth is a state variable. It may vary due to two causes, viz. ‘at the top’ (due to water level changes) or ‘at the bottom’ (due to siltation). The differential equation is:

dDepthW = vTranDepthW + vDeltaW + vDredDepthW change in water depth [m/d]

with

vTranDepthW = (uQin – uQev – uQout) / 1000	water level change [m/d]
vDeltaW	change in water depth due to sedimentation [m/d]
vDredDepthW	change in water depth due to dredging [m/d]

Water level changes occur if water inflow and outflow + evaporation are not equal. In this case, the user should supply a separate time-series for the outflow rate *Qout* [mm/d]. The user should check that both time-series together reflect a realistic picture of the water level around the year.

The second contribution to (slow) changes in water depth is (net) sedimentation. Dredging can be explicitly modelled as well. These processes are mainly important in ditches, less so in lakes. They are discussed in the next § under ‘burial’ and ‘dredging’.

Note on the DUFLOW implementation

In the DUFLOW implementation of the model, the transport processes (i.e. the transport of the state variables defined as of type ‘WATER’ in DUFLOW) are calculated by DUFLOW itself already and are thus left out from the model code. This has been done done by excluding the transport module at the DUPROL translation step (see User’s manual).

Infiltration and seepage

Infiltration is defined as a water flux from the surface water to the groundwater, via the sediment top layer. If applicable, it is assumed that dissolved substances (PO4, NH4, NO3, SiO2) are transported with it: dissolved nutrients from the water column enter the pore water, while pore water nutrients are lost to the deeper ground water.

The opposite situation is seepage, a flux of water with dissolved nutrients from the groundwater via the upper sediment layer to the water column.

The infiltration / seepage rate *cQInf* is expresssed in [mm/d]; a positive value means infiltration, a negative one seepage, zero is none.

The dilution rate minus the infiltration rate is called the surface outflow rate:

ukOutfl = (uQIn - uQEv - cQInf) / 1000 / sDepthW surface outflow rate [d^{-1}]

The nutrient infiltration fluxes are described as (with PO4 as an example):

In case of infiltration (IF cQInf > 0):

*tPInfPO4W = cQInf / mmPerm * sPO4W*

infiltration of PO4 from water to pore water [gP/m2/d]

*tPInfPO4S = cQInf / mmPerm * oPO4S*

infiltration of interstitial PO4 to groundwater [gP/m2/d]

In case of seepage (IF cQInf < 0):

*tPInfPO4S = cQInf / mmPerm * cPO4Ground*

seepage of groundwater PO4 to pore water [gP/m2/d]

*tPInfPO4W = cQInf / mmPerm * oPO4S*

seepage of interstial PO4 to water column [gP/m2/d]

In this case, a user-defined groundwater concentration *cPO4Ground* [mgP/l] is used.

Background loading

Direct loading on the water surface, e.g. by atmospheric deposition, is defined separately in the model, apart from the transport processes. Average values for The Netherlands around 1990 approximate 0.0003 gP m^{-2} d^{-1} and 0.009 gN m^{-2} d^{-1}, they have since decreased (RIVM, div. years).

Erosion

Apart from loading via inflowing water, an input of soil material by erosion can be defined, which is directly added to the pools of organic and inorganic matter. A total erosion flux (*cDErosTot* [g/m2/d]) is defined, plus the organic fraction (*fDOrgSoil* [-]) and the P and N fractions in it (*cPDSoilOM* and *cNDSoilOM*). The parameters are taken from the soil composition in the surroundings. The inorganic matter is divided in an instantly sedimentating part (*fSedErosIM* [-]) and the remainder that is suspended in the water column. The organic matter goes to the sediment humus pool.

*uDErosIM = (1.0 - fDOrgSoil) * cDErosTot*	IM input from banks [gD/m2/d]
*uDErosIMS = fSedErosIM * uDErosIM*	IM input to sediment from banks [gD/m2/d]
uDErosIMW = uDErosIM - uDErosIMS	IM input to water column from banks [gD/m2/d]
*uDErosOM = fDOrgSoil * cDErosTot*	organic matter input from banks [gD/m2/d]

The corresponding organic P and N fluxes are calculated as *cPDSoilOM* resp. *cNDSoilOM* times the D flux.

1.4. Abiotic and microbial processes

1.4.1. Organic and inorganic components and initialisation

Water column

The abiotic components in the water column are: inorganic matter, detritus, adsorbed P and dissolved PO_4, NH_4 and NO_3 and SiO_2. It is assumed that the dissolved fractions are available for primary production. Humus is neglected in the water column, as it is assumed to settle out quickly.

They should be **initialised** as concentrations, as well as the initial P/D and N/D ratios of the detritus. Adsorbed P, usually a minor component in the water column, is initialised at 0 mgP/l; adsorption is calculated, however, during the run.

Derived variables (total seston, total P, etc.) in the water column are defined as:

DW variables:

oDPhytW = sDDiatW + sDGrenW + sDBlueW	total phytoplankton [mgD/l), see below.
oDOMW = sDDetW + oDPhytW	organic seston [mgD/l]
oDSestW = oDOMW + sDIMW	total seston [mgDW/l]

P variables:

oPPhytW = sPDiatW + sPGrenW + sPBlueW	total phytoplankton [mgP/l), see below.

oPOMW = oPPhytW + sPDetW	org.seston P, without adsorbed [mgP/l]
oPSestW = oPPhytW + sPDetW + sPAIMW	total seston P (incl. adsorbed [mgP/l]
oPInorgW = sPO4W + sPAIMW	inorganic P in water [mgP/l]
oPTotW = oPSestW + sPO4W	total P in water (excl. animals and vegetation) [mgP/l]

N variables:

oNDissW = sNO3W + sNH4W	SRN in water [mgN/l]
oNPhytW = sNDiatW + sNGrenW + sNBlueW	total phytoplankton [mgN/l], see below.
oNOMW = oNPhytW + sNDetW	org.seston N [mgN/l]
oNSestW = oNOMW	total seston N [mgN/l]
oNkjW = oNSestW + sNH4W	kjeldahl N in water [mgN/l]
oNTotW = oNkjW + sNO3W	total N in water (without animals and vegetation) [mgN/l]

Nutrient ratios:

rPDIMW = sPAIMW / sDIMW	P adsorbed to IM in water [gP/gD]
rPDDetW = sPDetW / sDDetW	P/D ratio of water detritus [gP/gD]
rNDDetW = sNDetW / sDDetW	N/D ratio of water detritus [gN/gD]
rSiDDetW = sSiDetW / sDDetW	Si/D ratio of water detritus [gSi/gD]
rPDOMW = oPOMW / oDOMW	P/D ratio of org.seston [mgP/mgD]

Sediment

The sediment top layer consists of particulate matter and a pore water fraction with as dissolved nutrients PO_4, NH_4 and NO_3. The particulate matter consists of inorganic (‘IM’) and organic (‘OM’) matter. The inorganic matter (sand or clay particles) does not take part in the biological cycling, but forms the basic structure of the sediment and determines its P adsorption capacity. The organic matter (usually given as fraction ash-free dry-weight, AFDW) has been split into refractory (‘humus’, abbreviated as ‘Hum’) and degradable OM or ‘detritus’ (‘Det’). Detritus is the organic matter that takes part in the biological cycling while its nutrients become available again at a time scale of months. The humus component may break down at a very slow rate, comparable the decomposition rate of peat. For simplicity, detritus is modelled as one component, although it may originate from various sources. Organic matter can also be expressed in carbon units by means of a fixed ratio, *cCPerDW* (default 0.4 gC per g dry weight).

The thickness of the top layer, *cDepthS* [m], is considered as fixed, with a default value of 0.1 m, following Lijklema (1993) and other models. This layer is assumed to contain all the nutrients taking part in the present nutrient cycle, thus being important for the water quality and bioproduction. Net increase of sediment material is counteracted in the model by *burial* of a small layer of sediment, equally thick as the layer that had been added to it. This process of ‘sediment dilution’ may change the composition of the sediment top layer and may constitute a nutrient sink (Lijklema, 1993). The burial calculation is given below.

As in the water column, inorganic phosphorus comprises dissolved P in the pore water and adsorbed P. Inorganic nitrogen comprises nitrate and ammonia in the pore water; the sum of these is called *NDiss*. Inorganic silica is not included in the pore water; the silica cycle is modelled more simply. Please note that all water fractions are expressed as concentrations [g m^{-3}], while the pore water fractions are expressed on an areal base [g m^{-2}]. Elemental units are used (so, g $N\text{-}NO_3$ and not g NO_3). The amounts are converted to concentrations in the pore water by dividing by the porosity and the sediment depth.

Initially, the dry-weight fraction (w/w), the fraction organic matter (w/w), the detritus fraction and the lutum fraction (= particles <16_) in the top layer, are given by the user. Data may be derived from measurements, databases or estimates. These values are used to calculate the initial amounts, in [g m^{-2}], of the sediment components, the initial bulk density of the sediment, and the porosity: the water content of the sediment on a volume base [m^3 water m^{-3} sediment]. To avoid unnecessary complexity, the porosity is further considered as constant. The porosity is used in various equations, such as the calculation of nutrient concentrations in the pore water, as well as diffusion fluxes and resuspension (see below).

fDTotS0	initial dry-weight fraction [g solid g^{-1} sediment]
fDOrgS0	initial fraction organic matter [g AFDW g^{-1} solid]
fLutum	fraction lutum (= particles <16_) in the inorganic matter [g g^{-1}]
fDDetS0	initial fraction detritus of the organic matter [g g^{-1}]

The solid density of the organic and inorganic fractions are taken as constant:
cRhoOM solid density of organic matter [g m^{-3} solid]
cRhoIM solid density of inorganic matter [g m^{-3} solid]
and
cRhoWat density of water = $1.0 \cdot 10^6$ [g m^{-3}]

Default values for these solid densities are $1.4 \cdot 10^6$ [g m^{-3} solid] for OM and $2.5 \cdot 10^6$ [g m^{-3} solid] for IM (Hendriks, 1991). Jørgensen (1991) gives values of 1.3 (1.2-1.4) for organic matter, 1.95 (1.7-2.2) for clay soil and 1.7 (1.4-2.0) for sandy soil (all $\cdot 10^6$ [g m^{-3} solid]).

$bRhoSolidS0 = fDOrgS0 * cRhoOM + (1 - fDOrgS0) * cRhoIM$
initial average density of solid material [g m-3 solid]
$bPorS = (1.0 - fDTotS0) * bRhoSolidS0 / cRhoWat / (fDTotS0 + (1.0 - fDTotS0) * bRhoSolidS0 / cRhoWat)$ porosity [m3 water m-3 sediment]
$bPorCorS = bPorS ** (bPorS + 1.0)$ sediment porosity, corrected for tortuosity [-]
$bRhoTotS0 = bRhoSolidS0 * (1.0 - bPorS)$
initial (apparent) bulk density of sediment [g solid m-3 sediment]

Based on this density, the initial values of the state variables are calculated:

bDTotS0	*= bRhoTotS0 * cDepthS*	initial total dry-weight in top layer [gD m-2]
sDHumS0	*= (1.0 - fDDetS0) * fDOrgS0 * bDTotS0*	initial humus in top layer [gD m-2]
sDDetS0	*= fDDetS0 * fDOrgS0 * bDTotS0*	initial detritus in top layer [gD m-2]
sDIMS0	*= bDTotS0 - sDHumS0 - sDDetS0*	initial inorganic matter in top layer [gD m-2]

Also the initial amounts of nutrients should be given by the user, in the form of P and N fractions in the organic matter [gP/gD and gN/gD], dissolved NH_4 and NO_3 and a fraction inorganic P [gP/gD]; the latter is divided in an adsorbed fraction *sPAIMS* (usually the bulk) and dissolved PO_4. It is important, though not always easy, to start with good estimates of all these initial values. It is recommended that these are derived from actual measurements. The default values are listed here.

sNH4S0 = 0.02	initial dissolved N-NH4 in interstitial water [gN/m2]
sNO3S0 = 0.002	dissolved N-NO3 in interstitial water [gN/m2]
cPDDet0 = 0.0025	initial P fraction in detritus [gP/gD]
cNDDet0 = 0.025	initial N fraction in detritus [gN/gD]
cSiDDet0 = 0.01	initial Si fraction in detritus [gSi/gD]
cPDHum0 = 0.005	initial P fraction in humus [gP/gD]
cNDHum0 = 0.05	initial N fraction in humus [gN/gD]
*sPHumS0 = cPDHum0 * sDHumS0*	initial sediment humus [gP/m2]
*sNHumS0 = cNDHum0 * sDHumS0*	initial sediment humus [gN/m2]
*sPDetS0 = cPDDet0 * sDDetS0*	initial sediment detritus [gP/m2]
*sNDetS0 = cNDDet0 * sDDetS0*	initial sediment detritus [gN/m2]
*sSiDetS0 = cSiDDet0 * sDDetS0*	initial sediment detritus [gSi/m2]

To comply with measurements, inorganic P is initialised as a fraction of the sediment dry-weight [gP g^{-1}D], and divided in an adsorbed (the bulk) and a dissolved part by a fixed fraction. (We refrained from an initialisation based on an ‘inverse’ Langmuir equation, which was considered as unnecessarily complex.)

fPInorgS0 = 0.0005	initial inorg. P fraction in sed. [gP/gD]
fPAdsS0 = 0.99	initial adsorbed fraction of inorg. P in sed. [-]

*sPAIMS0 = fPAdsS0 * fPInorgS0 * bDTotS0*
P adsorbed into inorg. matter in sediment [gP.m-2]
*sPO4S0 = (1.0 - fPAdsS0) * fPInorgS0 * bDTotS0*
initial amount of dissolved P in sediment [gP.m-2]

During the model run, all state variables are of course calculated dynamically, based on the various processes.

Besides, a number of **derived variables** (total N, total P, etc.) are calculated as these variables are useful output and/or used in process equations. These are, for the sediment (recall that the prefix *o-* stands for concentration [g m^{-3}]):

DW variables:
$aDTotS = sDIMS + sDHumS + sDDetS$
total sediment (excl. biota) [g/m2]
$aRhoTotS = aDTotS / cDepthS$
(apparent) bulk density of sediment [g solid m-3 sediment]
$aRhoSolidS = (sDIMS * cRhoIM + (sDHumS + sDDetS) * cRhoOM) / aDTotS$
average solid density [g m-3 solid]
$afDTotS = 1.0 / (1.0 + bPorS/(1.0-bPorS) * cRhoWat / aRhoSolidS)$
sediment dry-weight fraction [g solid g-1 sediment]
$afDOrgS = (sDHumS + sDDetS) / aDTotS$
total organic fraction of sediment DW [-]
$afDDetS = sDDetS / (sDHumS + sDDetS)$
detrital fraction of sediment organic DW [-]
$afDetTotS = sDDetS / (sDIMS + sDHumS + sDDetS)$
detrital fraction of total sediment DW [-]

P variables:
$aPInorgS = sPO4S + sPAIMS$ inorganic P in sediment [gP/m2]
$aPTotAvailS = sPDetS + aPInorgS + aPPhytS$
total P in sediment (excl. humus, animals and vegetation) [gP/m2]
$aPTotS = aPTotAvailS + sPHumS$
total P in sediment (excl. animals and vegetation) [gP/m2]
$afPInorgS = aPInorgS / aDTotS$ fraction inorganic P in sediment [gP/gD]
$afPTotS = aPTotS / aDTotS$ total P fraction in sediment [gP/gD]
$afPO4S = sPO4S / aPTotAvailS$ fraction dissolved P in sediment [-]
$oPO4S = sPO4S / cDepthS / bPorS$ conc. dissolved P in interstitial water [gP/m3]

N variables:
$aNDissS = sNH4S + sNO3S$ total dissolved N in pore water [gN/m2]
$aNkjAvailS = sNDetS + aNPhytS + sNH4S$
kjeldahl N in sediment, excl. humus [gN/m2]
$aNkjS = aNkjAvailS + sNHumS$ kjeldahl N in sediment [gN/m2]
$aNTotAvailS = aNkjAvailS + sNO3S$
total N in sediment, excl. humus [gN/m2]
$aNTotS = aNkjS + sNO3S$ total N in sediment [gN/m2]

$afNInorgS = aNDissS / aDTotS$ fraction inorganic N in sediment [gN/gD]
$afNTotS = aNTotS / aDTotS$ total N fraction in sediment [gN/gD]
$oNO3S = sNO3S / cDepthS / bPorS$
conc. dissolved N-NO3 in interstitial water [gN/m3]
$oNH4S = sNH4S / cDepthS / bPorS$
conc. dissolved N-NH4 in interstitial water [gN/m3]
$oNDissS = aNDissS / cDepthS / bPorS$ Dissolved N conc. in sediment [mgN/l]

Nutrient/DW ratios:
$rPDIMS = sPAIMS / sDIMS$ adsorbed P on sediment IM [gP/gD]
$rPDHumS = sPHumS / sDHumS$ P content of sediment OM [gP/gDW]
$rNDHumS = sNHumS / sDHumS$ N content of sediment OM [gN/gDW]
$rPDDetS = sPDetS / sDDetS$ P content of sediment detritus [gP/gDW]
$rNDDetS = sNDetS / sDDetS$ N content of sediment detritus [gN/gDW]
$rSiDDetS = sSiDetS / sDDetS$ Si content of sediment detritus [gSi/gDW]

Overview of processes

The modelled processe are: sedimentation (for IM and detritus) and resuspension (IM, detritus and nutrients), burial (IM, humus, detritus and nutrients), mineralisation (detritus and humus), denitrification (NO3), nitrification (NH4), diffusion (nutrients and O2), reaeration (O2), sorption (PO4) and immobilisation (PO4 in sediment), as well as dredging.

Formation of detritus or dissolved nutrients caused by mortality of phytoplankton, or macrophytes or by feeding by or mortality of animals, are discussed in the respective paragraphs.

Concerning nitrogen, adsorption and atmospheric release of NH_4 are neglected, as well as nitrogen fixation by blue-green algae or bacteria.

1.4.2. Sedimentation and resuspension

These counteracting processes are defined for the small-sized particles only, i.e. the lutum fraction of IM and detritus, as well as for phytoplankton. The sandy fraction of IM and humus particles are neglected, as they are assumed to settle down within a time scale of hours, shorter than the scope of the model.

These processes are modelled on an average base, neglecting the daily dynamics of wind and currents, but still including differences between lakes related to dimensions and type of sediment. The basic equation is:

$$dC/dt = tResus / Depth - (VSet / Depth) * C \quad [\mathrm{g\ m^{-3}\ d^{-1}}]$$

so resuspension is considered zero-order and settling first-order. The equilibrium solution (dC/dt = 0) is:

$$C = tResus / VSet \quad [\mathrm{g\ m^{-3}}]$$

The use of mechanistically based relations about wind-induced shear stress as a function of lake dimensions (e.g. Carper & Bachman, 19..; Partheniades & Krone, 19..) was considered as too detailed for the scope of the model. Instead, an empirical logistic relation between lake depth and seston concentration in a data set of 35 lakes was used, corrected for lake fetch. The fetch [m] is, roughly spoken, the length of the lake in the prevailing wind direction. The value should be provided by the user; as a first estimate the sqare root of the lake area [m^2] may be taken. As a reasonable guess, the effect of fetch is modelled as the square-root of the relative fetch (= fetch / 1000). The resulting ‘suspended matter function’ (called *aFunDimSusp* in the model, ‘Dim’ standing for lake dimensions) is made zero if the water is frozen. So:

```
IF uTm > 0.1
    aFunDimSusp = cSuspRef * ((cSuspMin + cSuspMax / (1.0 +
        EXP(cSuspSlope * (sDepthW - hDepthSusp)))) * SQRT(cFetch/ cFetchRef))
            empirical suspended matter function (logistic fit to data) [-]
ELSE
    aFunDimResus = 0
ENDIF
```

with:

cSuspRef = 0.5	‘reference’ suspended matter function [-]
cSuspMin= 6.1	minimum value of logistic function
cSuspMax = 25.2	maximum value of logistic function
cSuspSlope = 2.1	slope of logistic function
hDepthSusp = 2.0	‘half-sat. value’ of depth in logistic function
cFetchRef = 1000.0	‘reference’ fetch [m]

and

cFetch	fetch [m]

It is assumed that the effect of this function is partly reflected in the resuspension, partly (in the opposite way) in the settling velocity. This is done by taking the square-root of *aFunDimResus* for the resuspension, and *dividing* the settling velocity by the same square-root of *aFunDimResus*, so that together, they reconstitute the derived function. (Note: for the special case of values < 1.0, the value itself is taken in stead of the square-root.)

The resuspension rate is further adapted to the lutum content and the porosity of the sediment. It is assumed that the resuspension increases with the lutum content. As a reasonable guess, a factor equal to the square-root of the relative lutum fraction (= lutum fraction / 0.2, the value for sandy clay soils) is used. This implies, for instance, that the resuspension is reduced by a factor 2 if the lutum content drops from 0.2 to 0.05, and is increased by 1.4 for a lutum content of 0.4. The effect of the porosity is assumed to be linear: the resuspension from a loose sediment with a porosity of 0.9 is nearly twice the value from a rather stable sediment with a porosity of 0.5.

tDResusTauDead = MIN(aFunDimSusp, SQRT(aFunDimSusp))
** SQRT(fLutum / fLutumRef) * bPorS*
resuspension due to shear stress [gD/m2/d]
in which
fLutumRef = 0.2 'reference' lutum fraction [-]
and the abbreviation '*-Dead*' stands for non-living matter, i.e. IM and detritus.

Apart from physical action (wind, currents), another cause of resuspension is benthivorous fish when browsing for food. Empirical evidence shows resuspension to increase linearly with the biomass of benthivorous fish such as adult bream or carp (Meijer et al., 1990; Breukelaar et al., 1994). The latter authors derived from pond experiments a daily amount of sediment stirred up by adult bream of about 5 g per g fish-FW (~ 1 g g^{-1}D d^{-1}).
In *PCLake*, this linear relation is adopted, corrected for temperature by the same function as used for fish foraging (see below).

*tDTurbFish = (kTurbFish * uFunTmFish * sDFiAd)* fish bioturbation [g/m2/d]

Furthermore, the resuspension is affected by the macrophytes coverage. There is ample evidence that macrophytes reduce resuspension (James & Barko, 1990; Hamilton & Mitchell, 1996; Jeppesen et al., 1990, 1997; Van den Berg et al., 1997), although general quantitative relations are not easy to assess. The effect not only depends on the coverage or biomass but also on the species, growth form and spatial pattern of the vegetation, and is of course season-dependent. In the model, a linear decrease of the resuspension with vegetation biomass is assumed:

*aFunVegResus = MAX(1.0 - kVegResus * aDVeg, 0.0)*
vegetation dependence of resuspension [-]
with *kVegResus* in the order of 0.01 [(gD $m^{-2})^{-1}$].

The contributions of wind and fish, and the vegetation effect, are thus combined:
*tDResusDead = (tDResusTauDead + tDTurbFish) * aFunVegResus*
resuspension, corrected for vegetation effect [gD/m2/d]

The resuspension rate is divided over IM (lutum part only) and detritus according to their relative concentrations in the top layer:

*tDResusIM = fLutum * sDIMS / (fLutum * sDIMS + sDDetS) * tDResusDead*
IM resuspension [gD/m2/d]
*tDResusDet = sDDetS / (fLutum * sDIMS + sDDetS) * tDResusIM*
detrital resuspension [gD/m2/d]

The resuspension of phytoplankton is described in a slightly different way, as it is assumed that settled phytoplankton is not instantaneously mixed in the sediment. Phytoplankton resuspension is described as a fraction of the biomass present, equal to the estimated resuspension frequency (the part of the time that resuspension occurs), which is in turn based on an empirical relation between frequency and rate of resuspension for 10-years daily wind data.

kResusPhytMax = 0.25 max. phytoplankton resuspension [d-1]
cResusPhytExp = -0.379 exp. par. for phytopl. resuspension [(gD/m2/d)$^{-1}$]
*tDResusPhytTot = kResusPhytMax * (1.0 - EXP(cResusPhytExp * tDResusDead))*
** aDPhytS* phytoplankton resuspension [gD/m2/d]

This last flux is divided over the three phytoplankton species according to their presence on the sediment.
The total resuspension flux is:
tDResusTot = tDResusDead + tDResusPhytTot
total resuspension [gD/m2/d]

From these fluxes, the concomitant nutrient fluxes for detritus and adsorbed P are calculated by means of the actual nutrient ratios. It is assumed that resuspension also affects dissolved nutrients, as follows:

*tPResusPO4 = sPO4S / sDDetS * tDResusDet*
resuspension flux of dissolved P [gP/m2/d]

and comparable equatons for ammonium and nitrate.

Settling
Settling (sedimentation) is modelled by a commonly used first-order equation. The settling velocity is different for the different seston components and is made dependent on the lake’s dimensions as explained above. The settling of IM is also made dependent on its lutum content. All settling velocities are slightly influenced by temperature as well (Theta = 1.01) to account for the effect on the viscosity of water. The maximum settling rates are different for the different seston components: IM, detritus and the phytoplankton groups.

*tDSetIM = cVSetIM / sDepthW * MIN(1.0 / SQRT(aFunDimSus), 1.0) * cThetaSet*$^{Tm-20}$
** SQRT(fLutumRef / fLutum) * sDIMW* settling of IM [gD m^{-2} d^{-1}]
*tDSetDet = cVSetDet / sDepthW * MIN(1.0 / SQRT(aFunDimSus), 1.0) * cThetaSet*$^{Tm-20}$
** sDDetW* settling of detritus [gD m^{-2} d^{-1}]
The function for detritus is also used (with adapted parameter values) for the phytoplankton types.

The corresponding P, N and Si fluxes are simply calculated as the dry-weight flux times the actual nutrient ratios:

$tPSetAIM = sPAIMW / sDIMW * tDSetIM$ [gP m^{-2} d^{-1}]
$tPSetDet = rPDDetW * tDSetDet$ [gP m^{-2} d^{-1}]
$tNSetDet = rNDDetW * tDSetDet$ [gN m^{-2} d^{-1}]
$tSiSetDet = rSiDDetW * tDSetDet$ [gSi m^{-2} d^{-1}]

1.4.3. Burial

In order to keep a fixed sediment thickness and closed nutrient cycles at the same time, a process of burial is defined. A net increase of sediment material is counteracted in the model by burial of a small layer of sediment, equally thick as the layer that had been added to it. This material is considered as buried in the deeper sediment and lost from the system.

This thickness is calculated from the derivatives (excluding burial itself) of the three sediment components (resp. denoted as *tDIMS, tDHumS* and *tDDets*) (Van Drecht, pers. comm.):

$vDeltaS = (tDIMS / cRhoIM + (tDHumS + tDDetS) / cRhoOM)$
‘sediment turnover depth’ [m/d]

If its value is positive, as is the usual case, then the burial fluxes (‘*Bur*’) [gD m^{-2} d^{-1}] of the three components are:

$tDBurIM = ((tDHumS + tDDetS) + (cRhoOM / cRhoIM) * tDIMS) /$
$((sDHumS + sDDetS) / sDIMS + cRhoOM / cRhoIM)$
$tDBurOM = (sDHumS + sDDetS) / sDIMS * tDBurIM$

$tDBurDet = sDDetS / (sDHumS + sDDetS) * tDBurOM$
$tDBurHum = tDBurOM - tDBurDet$

and the total burial loss is:
$tDBurTot = tDBurIM + tDBurOM$

The corresponding nutrient fluxes are calculated according to the actual ratios and concentrations in the sediment, following the assumption of a mixed layer. For dissolved nutrients the equation is (with PO4 as an example):
$tPBurPO4 = sPO4S * (vDeltaS / cDepthS)$ [gP/m2/d]
Settled phytoplankton is assumed not to be buried.

In case of a ‘negative burial’, e.g. if resuspension temporarily exceeds sedimentation, it is assumed that the sediment thickness is maintained by addition of soil material from a deeper layer. It is assumed that the organic fraction equals the one in the surrounding soil (*fDOrgSoil* [-]) and consists of refractory material (humus), so no detritus. The correction fluxes are then calculated as:

$tDBurIM = ((tDHumS + tDDetS) + (cRhoOM / cRhoIM) * tDIMS) /$ &
$(fDOrgSoil / (1.0 - fDOrgSoil) + cRhoOM / cRhoIM)$
$tDBurOM = fDOrgSoil / (1.0 - fDOrgSoil) * tDBurIM$
$tDBurDet = 0.0$
$tDBurHum = tDBurOM$
$tDBurTot = tDBurIM + tDBurOM$

The corresponding nutrient fluxes are calculated using constant PO4, NO3 and NH4 concentrations in the groundwater, the same as used for seepage. Adsorbed P is neglected for simplicity.

Effect on water depth

A net rise of the sediment layer (*vDeltaS* [m/d]) as described above, is reflected in a decrease of the water depth, called *vDeltaW* [m/d]. In practice, this effect can often be neglected in lakes, unless the simulation period is very long. The effect may be partly counteracted by consolidation, which is not modelled. In ditches, this process cannot be neglected. The water depth can be maintained by dredging (described under *PCDitch*). A switch parameter (*ConstDepth*), with the value 0 or 1, is available in the model to switch this effect on or off:

IF (ConstDepth) THEN $vDeltaW = 0.0$
ELSE $vDeltaW = - vDeltaS$ change in water depth [m/d]

The *relative* water depth change due to sediment turnover and dredging is:
$aRelDeltaW = (vDeltaW + vDredDepthW) / sDepthW$ [d-1]

This (potential) volume change does not affect the *amounts* of dissolved and particulate substances in the water column, but it does affect their *concentrations*. Their derivatives are therefore corrected for this volume change; *e.g.*:
$dPO4W = \ldots - aRelDeltaW * sPO4W$ [gP m^{-3} d^{-1}]

1.4.4. Mineralisation, nitrification, denitrification and oxygen conditions

Mineralisation

Following many other water quality models, the mineralisation process has been described as simply as possible, by means of a first order, temperature dependent, rate. The temperature dependency follows the Arrhenius' equation: the rate increases exponentially with temperature. In the water:
$wDMinDetW = kDMinDetW * cThetaMin^{Tm-20} * sDDetW$ [gD m^{-3} d^{-1}]

In the sediment:
$tDMinDetS = kDMinDetS * cThetaMin^{Tm-20} * sDDetS$ [gD m^{-2} d^{-1}]

and analogous for PDet and NDet. The rates may differ for water and sediment, because the mechanisms may be different: usually mainly aerobic mineralisation in the water (except for very polluted situations), in contrast to a variety of electron acceptors in the sediment. The rates for nutrients are default set equal to the one for D. In the literature, wide ranges of mineralisation rates are often found. Calibration has been performed within these ranges. During mineralisation, the nutrients are released as PO_4, NH_4 or SiO_2, while the dry-weight is assumed to be lost from the system. PO_4 and NH_4 are added to the pore water pool, while, for simplicity, SiO_2 is assumed to be released to the water column directly.

Oxygen

The oxygen consumption related to these mineralisation fluxes are calculated by means of two conversion factors, O2/C and C/DW, and corrected for the available oxygen concentration (as the oxygen consumption comes to a halt if the oxygen concentration is very low). In the **water column**, where the oxygen concentration is modelled dynamically, we followed the common Michaelis-Menten-type correction used in classical (Streeter & Phelps) BOD models:

aCorO2BOD = sO2W / (hO2BOD + sO2W)
  correction of O2 demand in water at low oxygen conc. [-]
*wO2MinDetW = molO2molC * cCPerDW * aCorO2BOD * wDMinDetW*
  O2 flux due to mineralization of detritus [gO2/m3/d]
with
hO2BOD = 1.0
  half-sat. oxygen conc. for BOD [mgO2/l]
molO2molC = 2.6667 = 32/12 [gO2/gC], ratio of mol.weights
cCPerDW = 0.4 C content of organic matter [gC/gDW]

The variable *aCorO2BOD* is also used in the equations for denitrification, nitrification and phosphorus adsorption in the water column (see below).

In the **sediment**, the oxygen conditions are modelled by an equilibrium equation, as the time scale of the oxygen dynamics in the sediment is that small (order of minutes) that a dynamic description is not useful (Lijklema, 1993). Following Lijklema (1993) and other models (Smits & Van der Molen, 1993; Asaeda & Van Bon, 1997; cf also Van Straten, 1982), the thickness of the aerobic sediment layer is described as a function of the oxygen concentration in the water, the oxygen diffusion rate and the sediment oxygen demand *per volume* of sediment:

*aDepthOxySed = (2.0 * sO2W * akO2DifCor / tSOD) ** 0.5*
  oxygen penetration depth [m]
with
*akO2DifCor = kO2Dif * uFunTmDif * cTurbDifO2 * bPorCorS*
  corrected O2 diffusion coefficient [m2/d]
and
*tSOD = (molO2molC * cCPerDW * (1.0 - fRefrDetS) * tDMinDetS +*

*O2PerNH4 * molO2molN * kNitrS * uFunTmNitr * sNH4S) / cDepthS*
sediment oxygen demand [gO2/m3/d]

in which:

molO2molN = 2.2857 = 32/14 [gO2/gN]	ratio of mol.weights
molNmolC = 1.1667 = 14/12 [gN/gC]	ratio of mol.weights
kO2Dif = 2.6D-5	mol. O2 diffusion constant [m2/d]
cThetaDif = 1.02	temperature coefficient for diffusion [$1/e^{oC}$]
cTurbDifO2 = 2.0	bioturbation factor for O2 diffusion [-]
bPorCorS = bPorS $^{(bPorS + 1)}$	corrected porosity [-] (explained below under 'diffusion')
kNitrS = 1.0	nitrification rate constant in sediment [d^{-1}]
cThetaNitr = 1.08	temperature coefficient of nitrification [$1/e^{oC}$]
O2PerNH4 = 2.0	mol O2 used per mol NH4+ nitrified [-]
cDepthS = 0.1	sediment depth [m]

The SOD is thus estimated as the sum of the main potential oxygen-demanding processes, i.e. the mineralisation of organic matter and the nitrification of NH4 to NO3. This allows to relate the size of the aerobic layer to the amount of degradable organic matter and to allow for seasonal variation (aerobic layer is smaller in summer tha in winter). This formulation, although a bit pragmatic in nature, results in a thickness of a few millimeters to centimeters, which is reasonably in line with observations in lake sediments.

The thickness of the aerobic layer is divided by the (fixed) thickness of the sediment top layer to get the 'proportion aerobic sediment':
afOxySed = aDepthOxySed / cDepthS
proportion aerobic sediment [-]

It is assumed that this proportion of the mineralisation occcurs aerobically; the oxygen consumption is again based on the conversion factors O2/C and C/DW:
*tO2MinDetS = molO2molC * cCPerDW * afOxySed * (1.0 - fRefrDetS) * tDMinDetS*
oxygen consumption by mineralisation in sediment [gO2/m2/d]

It is assumed that a small part *fRefrDetS* [-] (default 15%) of the decomposed material in the sediment is transformed into humus.
The humus component itself may be subject to (further) mineralisation if exposed to oxygen, although at a very low rate *kDMinHum* in the order of 10^{-5} [d^{-1}] (Hendriks, 1991):
*tDMinHumS = kDMinHum * uFunTmMinS * afOxySed * sDHumS*
decomposition of upper sediment humus [gDW/m2/d]
and parallel equations for P and N.

The same variable *afOxysed* is used in the equations for denitrification, nitrification and phosphorus adsorption in the sediment, processes that are highly dependent on the oxygen conditions.

This description is a simplification to avoid the – rather complicated and calculation time consuming - description of several sediment layers, with vertical transport between them, as is done in many sediment models (e.g. Smits & Van der Molen, 1993). Typically, going from top to bottom, one encounters a small aerobic layer, a small denitrication layer, a sulphate reduction layer and a methanogenic layer, depending on the type of elektron acceptor for mineralisation. The formulation in *PCLake* is based on an 'aerobic fraction' of the sediment top layer for those processes where this is needed, maintaining the assumption of a mixed top layer as far as possible, without defining exact 'layers'. Arguments in favour of this approach are the fact that, in shallow lakes, the sediment top layer is often disturbed, and the observation that aerobic and anaerobic processes are not always neatly located in layers but rather in intertwined 'hot spots' (e.g. Van Luin, 1997).

Denitrification

Denitrification is an important process by which nitrogen is lost from the system. It comprises the transformation of nitrate into volatile substances like molecular nitrogen, which is lost into the atmosphere. It occurs when nitrate is used as elektron acceptor for mineralisation of organic matter. The process is thus anaerobic and needs the presence of both organic carbon and nitrate; as a microbial process, it is temperature-dependent (Van Luin, 1997; Soetaert et al., 1995).
In *PCLake*, denitrification is coupled to the of anaerobic part of the mineralisation process. The nitrate dependency is described as a sigmoid function, with a half-saturation value estimated at 1-2 mgN-NO_3/l. Soetaert et al. (1995) report a value of 0.4 mg/l for Michaelis-Menten kinetics.

In the water:
*wNDenitW = NO3PerC * molNmolC * cCPerDW*
    ** sNO3W**2.0 / (hNO3Denit**2.0 + sNO3W**2.0)*
    ** (1.0 – aCorO2BOD) * wDMinDetW*
    Denitrification flux [gN.m-3.d-1]

In the sediment:
*tNDenitS = NO3PerC * molNmolC * cCPerDW*
    ** oNO3S**2.0 / (hNO3Denit**2.0 + oNO3S**2.0)*
    ** (1.0 - afOxySed) * (1.0 - fRefrDetS) * tDMinDetS*
    Denitrification flux [gN.m-2.d-1]

The process normally is significant in the sediment layer only, but it may also play a role in the water column if the oxygen concentration drop to a very low value.

Nitrification

Nitrification is a microbial process involving the transformation of ammonia to nitrate. Obviously, this process is aerobic. It is modelled as a first order function of the ammonium concentration, dependent on temperature and corrected for the oxygen conditions. The nitrification constant is assumed to be much higher in the sediment than in the water as it is assumed that the density of nitrifying bacteria is higher. The corresponding oxygen consumption is calculated using a conversion factor of 2 mol O_2 per mol NH4$^+$ and the ratio of molecular weights.

$uFunTmNitr = cThetaNitr ** (uTm-20)$ temperature dependence [-]

In the water:

$aCorO2NitrW = sO2W ** 2.0 / (hO2Nitr ** 2.0 + sO2W ** 2.0)$

$wNNitrW = kNitrW * uFunTmNitr * aCorO2NitrW * sNH4W$

nitrification flux [mgN/l/d]

$wO2NitrW = O2PerNH4 * molO2molN * wNNitrW$

2 flux due to nitrification [gO2/m3/d]

In the sediment:

$tNNitrS = afOxySed * kNitrS * uFunTmNitr * sNH4S$

nitrification flux [gN/m2/d]

$tO2NitrS = O2PerNH4 * molO2molN * tNNitrS$

O2 flux due to nitrification [gO2/m2/d]

1.4.5. Sorption of phosphorus

Dissolved P may adsorb onto inorganic matter, especially when this consists of clay. This process acts as a ‘buffer’ for the availability of phosphorus for primary production. It is assumed that the adsorbed fraction is in reversible chemical equilibrium with the dissolved state. Although also adsorption of P onto organic matter has been described in some cases (e.g. Rijkeboer et al., 1991), this process is neglected in the model. The sorption process is defined in the model as an instantaneous, reversible binding of phosphorus to an adsorbent. In reality, it might be a lumped process involving a variety of different chemical processes, while in some cases, a part of the phosphorus binding might be explained by the activity of detritus-bound bacteria.

The equilibrium value is determined by the adsorption isotherm, defined as the relation between the dissolved P concentration and the amount of adsorbed P per gram adsorbent [gP/gD] at equilibrium. The total amount of adsorbed P, expressed as [gP m^{-2}] in the sediment or [gP m^{-3}] in the water, thus equals the product of the relative adsorption (as given by the isotherm) and the amount of adsorbent.

For the relative adsorption, the generally used Langmuir isotherm is used, which is a Monod-type equation: the relation is about linear at low phosphorus concentrations, while at higher concentrations, the curve flattens and approaches a maximum. The isotherm is defined by the

maximum adsorption capacity, *bPAdsMax* [gP/gD] and the affinity *aKPAds* [mgP/l]. (The affinity equals the reciprokal half-saturation value, which is the quotient of the maximum adsorption and the initial slope). The use of a linear adsorption isotherm would simplify the model, but is allowed only for substances always present in low concentrations, like micropollutants. Phosphorus concentrations in sediments can easily be so high that the maximum adsorption capacity is reached. This maximum mainly depends on the iron and aluminium contents of the adsorbent, as these are the main adsorbing elements (*e.g.* Lijklema, 1980). The adsorption is influenced by a number of environmental conditions, like the redox conditions and the pH: only oxidised forms of iron adsorb phosphorus. This is modelled by means of the aerobic fraction of the layer. The entire water column is in general aerobic, whereas the thickness of the aerobic sediment layer is often restricted to 1-2 mm.
In mathematical terms, these relations are expressed as follows:

In the water column:

$\mathit{aPAdsMaxW} = \mathit{cRelPAdsD} + \mathit{aCorO2BOD} * \mathit{cRelPAdsFe} * \mathit{fFeDIM} + \mathit{cRelPAdsAl} * \mathit{fAlDIM}$
max. P adsorption per g inorg. matter in water [gP/gD]
$\mathit{aKPAdsW} = (1.0 - \mathit{fRedMax} * (1.0-\mathit{aCorO2BOD})) * \mathit{cKPAdsOx}$
P adsorption affinity, corrected for redox conditions [m3/gP]
$\mathit{aPIsoAdsW} = \mathit{aPAdsMaxW} * \mathit{aKPAdsW} * \mathit{sPO4W} / (1.0 + \mathit{aKPAdsW} * \mathit{sPO4W})$
P adsorption isotherm onto inorg. matter in sediment [gP/gD]

$\mathit{aPEqIMW} = \mathit{aPIsoAdsW} * \mathit{sDIMW}$ equilibrium conc. [gP.m-3]
$\mathit{wPSorpIMW} = \mathit{kPSorp} * (\mathit{aPEqIMW} - \mathit{sPAIMW})$
sorption flux in water [gP.m-3.d-1]

In the sediment:

$\mathit{aPAdsMaxS} = \mathit{cRelPAdsD} + \mathit{afOxySed} * \mathit{cRelPAdsFe} * \mathit{fFeDIM} + \mathit{cRelPAdsAl} * \mathit{fAlDIM}$
max. P adsorption per g inorg. matter in sediment [gP/gD]
$\mathit{aKPAdsS} = (1.0 - \mathit{fRedMax} * (1.0-\mathit{afOxySed})) * \mathit{cKPAdsOx}$
P adsorption affinity, corrected for redox conditions [m3/gP]
$\mathit{aPIsoAdsS} = \mathit{aPAdsMaxS} * \mathit{aKPAdsS} * \mathit{oPO4S} / (1.0 + \mathit{aKPAdsS} * \mathit{oPO4S})$
P adsorption isotherm onto inorg. matter in sediment [gP/gD]

$\mathit{aPEqIMS} = \mathit{aPIsoAdsS} * \mathit{sDIMS}$ equilibrium amount [gP.m-2]
$\mathit{tPSorpIMS} = \mathit{kPSorp} * (\mathit{aPEqIMS} - \mathit{sPAIMS})$ sorption [gP.m-2.d-1]
with:
cRelPAdsD max. P adsorption per gram dry-weight[gP g^{-1}D]
cRelPAdsFe max. P adsorption per gram iron[gP g^{-1}Fe]
cRelPAdsAl max. P adsorption per gram aluminium[gP g^{-1}Al]

fFeDIM iron content of IM[gFe g^{-1}D]
fAlDIM aluminium content of IM[gAl g^{-1}D]
afOxySed proportion aerobic sediment[-]

1.4.6. Phosphorus immobilisation

The model provides the option of defining a maximum PO$_4$ concentration, *cPO4Max* [mgP/l], in the interstitial water, above which phosphorus is lost by irreversible chemical immobilisation. The equation is:

tPChemPO4 = MAX(0.0, *kPChemPO4 * (oPO4S - cPO4Max))*
chem. loss of dissolved P from pore water [gP m^{-2} d^{-1}]

in which *kPChemPO4* [d^{-1}] is a rate constant set at 0.03 and the maximum P concentration is set at 1 mgP/l.

1.4.7. Nutrient release

Dissolved inorganic phosphorus, ammonia and nitrate can move from the pore water to the water column by diffusion across the sediment-water interface. The diffusion fluxes can be upward (defined as positive in the model) or downward (negative). In most cases, however, phosphorus and ammonia diffuse upward, whereas nitrate diffuses downward. Upward diffusion means *release* of nutrients from the sediment.

The fluxes depend on the concentration gradient between the two compartments, which is approximated in the model by the difference in concentration divided by the diffusion distance, *aDepthDif* [m], defined at half the thickness of the modelled sediment layer. The equation for phosphorus is:

*tPDifPO4 = kPDifPO4 * uFunTmDif * cTurbDifNut * bPorCorS **
(oPO4S - sPO4W) / aDepthDif
diffusion flux of dissolved P from sediment to water [gP/m2/d]

The equations for ammonia and nitrate are analogous.

in which

kPDifPO$_4$	diffusion constant of dissolved P [m^2/d]
cThetaDif	temperature parameter $[(e–^{C})^{-1}]$
cTurbDifNut	bioturbation factor [-]
*aDepthDif = 0.5 * cDepthS*	diffusion distance [m]

*bPorCorS = bPorS ** (bPorS + 1.0)*
sediment porosity, corrected for tortuosity [-]

The latter equation includes a correction factor for the diffusion path in the sediment. This equation is used in stead of the usual formulation of porosity divided by the squared tortuosity, a parameter which is mostly unknown. The molecular diffusion constant is $7.2 \cdot 10^{-6}$ cm^2/s = $6.2 \cdot 10^{-5}$ m^2/d for PO4, $8.6 \cdot 10^{-5}$ m^2/d for NO$_3$ and $11.2 \cdot 10^{-5}$ m^2/d for NH$_4$.

1.4.8. Reaeration

Reaeration, the diffusion of oxygen across the water surface, is proportional to the oxygen deficit with respect to the saturation concentration, which is temperature dependent (Rich, 1973, ref. in Portielje & Lijklema, 1995):

$uO2Sat = 14.652 - 0.41022 * Tm + 7.991 \cdot 10^{-3} * Tm^2 - 7.7774 \cdot 10^{-5} * Tm^3$
oxygen saturation concentration [mgO_2/l]
$tO2Reaer = kReaer * (uO2Sat - sO2W) * uFunTmReaer * uFunLemnReaer$
reaeration flux of O2 into the water [$gO_2\ m^{-2}\ d^{-1}$]

The reaeration constant *kReaer* [m/d] depends on the temperature (*Tm*) and the wind speed (*uVWind*). The temperature influence is described as an exponential function with a σ of 1.024 [$1/e^{oC}$] (Downing & Truesdale, 1955). The wind influence is described using the empirical relation derived by Banks & Herrera (1977):

$kReaer = 0.727 * uVWind^{0.5} - 0.371 * uVWind + 0.0376 * uVWind^{2}$
reaeration coefficient [m/d]

The model uses default a constant wind speed of 5 m/s, giving a reaeration constant of 0.71 [m/d], but it is possible to use measured time-series of wind speed.

Reaeration is assumed to be hampered by a layer of duckweed (in *PCDitch*).

1.5. Phytoplankton

1.5.1. Overview

Three functional groups of phytoplankton are default distinguished in *PCLake*, viz.:

- cyanobacteria (also called ‘blue-green algae’)
- diatoms (*Bacillariophyta*)
- ‘other edible algae’, loosely referred to as ‘green algae’.

This distinction is made because of their different ecological features and because of management interests.

Phytoplankton is considered as homogeneously distributed over the water column.

As stated before, each group is modelled in three elements: dry-weight (D), P and N. The specific nutrient contents of the algae are modelled dynamically; nutrient uptake and production are modelled as separate processes. The nutrient-to-dry-weight ratios are simply given by:

$rPDSpec = sPSpec / sDSpec$	P/D ratio [gP/gD]
$rNDSpec = sNSpec / sDSpec$	N/D ratio [gN/gD]

Only the silica content of the diatoms is considered as fixed (default 0.15 gSi/gD).

The biomass of each group is described by the following differential equations:

dDSpecW/dt = production – respiration – mortality – settling + resuspension – grazing + transport [gD m^{-3} d^{-1}]
dPSpecW/dt = uptake – excretion – mortality – settling + resuspension – grazing + transport [gP m^{-3} d^{-1}]
dNSpecW/dt = uptake – excretion – mortality – settling + resuspension – grazing + transport [gN m^{-3} d^{-1}]

Because for the other seston components, viz. IM and detritus, sedimentation and resuspension are modelled separately, the same is done for the phytoplankton. This implies that also differential equations for the settled phytoplankton are needed, as follows:

dDSpecS/dt = – respiration – mortality + settling - resuspension – grazing [gD m^{-2} d^{-1}]
dPSpecS/dt = – excretion – mortality + settling - resuspension – grazing [gP m^{-2} d^{-1}]
dNSpecS/dt = – excretion – mortality + settling - resuspension – grazing [gN m^{-2} d^{-1}]

The settled phytoplankton is expressed as [g m^{-2}]. It is assumed that the settled phytoplankton is not active any more (no uptake and production), that respiration goes on, and that the mortality rate is higher. They are grazed by the zoobenthos rather than the zooplankton.

The algal processes thus are (Fig. 4):

- growth and nutrient uptake
- respiration and nutrient excretion
- settling and resuspension
- natural mortality
- grazing loss

These processes are described in the next sections, except grazing, which is described in the section ‘food web’. If no food web as included, zooplankton grazing is replaced by a first-order loss processs of the algae, abbreviated as ‘Loss’. (Note: not mentioned separately in the list in § 2.1.2). Although the processes are modelled in the same way for each functional group, differences in the parameter values give each group its specific functional characteristics.

1.5.2. Nutrient uptake

The modelling of the nutrient uptake is worked out here for *phosphorus*. The specific phosphorus uptake rate, that is the uptake rate per unit of biomass, is dependent on both the nutrient demand of the phytoplankton, defined by its actual nutrient content, and the availability of dissolved phosphorus in its environment. This is modelled as follows.

The *maximum* specific uptake rate is dependent on the actual nutrient content of the algae, the P/D ratio. If this ratio is low (close to the minimum value), the maximum uptake rate is high (close to the intrinsic maximum rate at the current temperature), while the rate drops to near-zero if the P/D ratio is close to its maximum value:

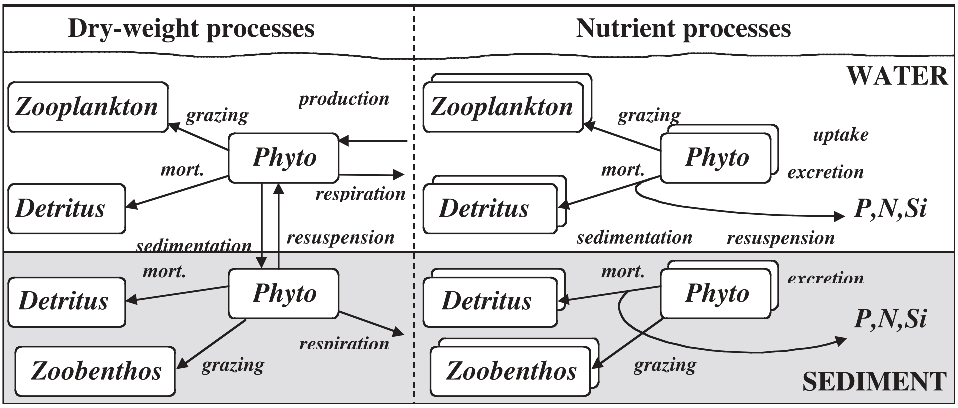

Fig. 4. Phytoplankton processes

$$aVPUptMaxCorSpec = cVPUptMaxSpec * uFunTmSpec * \frac{cPDSpecMax - rPDSpec}{cPDSpecMax - CPDSpecMin}$$

maximum P uptake rate [mgP/mgD/d]

with *cPDSpecMin* [gP g^{-1}D] and *cPDSpecMax* [gP g^{-1}D] the minimum and maximum phosphorus content of the plants, respectively.

The temperature function is modelled as an optimum curve, implemented as a Gaussian function, defined by an optimum temperature *cTmOpt* and a measure for
normalized to 1.0 at the reference temp. of 20 oC.

*uFunTmSpec = EXP(-0.5/cSigTmSpec**2 * ((uTm - cTmOptSpec)**2 - (cTmRef - cTmOptSpec)**2))*

temperature function of phytoplankton group [-]

The specific uptake rate is then described as a modified Monod-type function of the SRP concentration. The modification means that the phosphorus *affinity*, the slope of the curve when SRP is close to zero, is taken as constant for all values of V_{max}, in accordance with experimental data (Riegman & Mur, 1984). The specific uptake rate is:

$$aVPUptSpecW = aVPUptMaxCorSpec * \frac{SPO4W}{\frac{aVPUptMaxCorSpec}{cAffPUptSpec} + sPO4W}$$

specific P uptake rate [mgP/mgD/d]

This formulation implies that the half-saturating SRP concentration is not a constant, but is depending on V_{max}:

$ahPUptSpec = aVPUptMaxCorSpec / cAffPUptSpec$
half-saturating SRP concentration [mgP/l]

The resulting P uptake flux is the product of the specific uptake rate and the biomass:

$tPUptSpec = aVPUptSpec * sDSpecW$
P uptake flux [gP m^{-3} d^{-1}]

The uptake of *nitrogen* is modelled in the same way, with one extra feature, namely the form in which nitrogen is taken up, as nitrate or as ammonium. It is assumed that the plants have a strong preference for ammonium, because this is energetically more advantageous. The N uptake rates are based on total SRN in the water, and are then divided over the two N fractions according to the preference equation taken from the EPA WASP4 model (Ambrose et al., 1988). The fraction of the N uptake absorbed as ammonium, $afNH_4UptSpecW$ [-], equals:

$$afNH4UptSpecW = \frac{sNH4W * sNO3W}{(ahNUptSpec + sNH4W) * (ahNUptSpec + sNO3W)}$$

$$+ \frac{sNH4W * ahNUptSpec}{(sNH4W + \mathrm{sNO3W}) * (ahNUptSpec + sNO3W)}$$

This equation, however terribly looking, only states that nitrogen is absorbed preferably as ammonium. Only when the ammonium concentration drops to very low values, the plants switch to nitrate as nitrogen source. A technical advantage of this preference function is that it requires no extra parameters.

The relation between internal nutrient content and growth rate is described in the next paragraph.

1.5.3. Production

By production (or growth) is meant increase in biomass. It is expressed in grammes dry weight per m^2 per day. The production may also be expressed in g oxygen production per g total biomass; 1 g biomass assimilation is approximately equivalent to 1 g oxygen production. Growth respiration (photorespiration) is included in the definition, but maintenance respiration (dark respiration) is not; this is described as a separate process.

In the model, the production is a function of the following factors:

- maximum growth rate (defined at 20 °C)
- water temperature
- day length
- light interception at the water surface
- under-water light climate (extinction coefficient)
- P content (P/D ratio) of the plants, representing P limitation
- N content (N/D ratio) of the plants, representing N limitation

Maximum growth rate

The *maximum growth rate* is the maximum increase in biomass per gram total plant biomass per day, on an exponential base: *D(t) = EXP(cMuMax * t)*. The maximum growth rate is defined at a temperature of 20 °C.

Temperature

The temperature function is as described already: an optimum curve, implemented as a Gaussian function, defined by an optimum temperature *cTmOpt* and a measure for normalized to 1.0 at the reference temp. of 20 oC.

*uFunTmSpec = EXP(-0.5/cSigTmSpec**2 * ((uTm - cTmOptSpec)**2 - (cTmRef - cTmOptSpec)**2))*
temperature function of phytoplankton group [-]

Light function

The limitation factor for under-water light is modelled as a Monod-type P-I curve, integrated over the depth trajectory in which the plants grow, and averaged over 24 hrs. (Jørgensen, 1980). Light attenuation with increasing depth is described by the well known Lambert-Beer law:

*aLPAR(z) = uLPAR(0) * EXP(- aExtCoef * z)*
with
*uLPAR(0) = LOut * fPAR * (1 - fRefl)*

in which *LOut* [W m^{-2}] is the light intensity above the water surface, fPAR [-] the fraction photosynthetically active radiation, 0.48, *fRefl* [-] the fraction reflected at the surface (about 0.1), *uLPAR(0)* [W m^{-2} PAR] the light intensity just under the surface, *aLPAR(z)* [W m^{-2} PAR] the intensity at depth *z*, and *aExtCoef* [m^{-1}] the extinction coefficient. The extinction coefficient is the sum of the background extinction (the extinction of the water itself and dissolved substances) and the contributions of inorganic matter, detritus, algae and submerged water plants:

aExtCoef = cExtWat + aExtIM + aExtDet + aExtPhyt + aExtVeg
extinction coefficient [m^{-1}]

The contributions of the different components to the extinction are linearly related to their concentrations or submerged biomass density, the proportionality constant being the specific extinction, *cExtSpSpec* [m^2 g^{-1}]. For example:

*aExtSpec = cExtSpSpec * sDSpecW*
contribution of algal group to extinction coefficient [m^{-1}]

The contribution of submerged vegetation is based on the submerged shoots (see next section):

$aExtVeg = cExtSpVeg * aDSubVeg / sDepthW$

contribution of submerged vegetation to extinction coefficient [m^{-1}]

The specific extinction of macrophytes is much less than that of phytoplankton.

To reduce complexity, the extinction coefficient is based on the total biomass present in the water column, without accounting for a posssible inhomogeneous distribution of the vegetation. This might introduce a small inaccuracy in some cases regarding the light intensity encountered by certain plant groups, but the total light absorption is exactly the same with or without this simplification.

The extinction coefficient without the contribution of the macrophytes is called *aExtCoefOpen* [m^{-1}]. This variable is used for conversion to Secchi depth, as this variable is usually measured in open water:

$aSecchi = MIN(sDepthW, aPACoef / aExtCoefOpen)$ Secchi depth [m]

with *aPACoef* [-] the Poole-Atkins coefficient, which depends, in a certain range, negatively on the concentration of organic matter (= the sum of algae and detritus) in the water, *oDOMW* [mgD/l]. The slope parameter is called *hPACoef* :

$aPACoef = cPACoefMin + (cPACoefMax - cPACoefMin) * hPACoef / (hPACoef + aDOMW)$

Poole-Atkins coefficient [-]

The Secchi depth is merely an additional output variable of the model; calculations of production are based on the extinction coefficient itself.

For the ‘green algae’, the light limitation is described by an integral function based on a Monod-type production curve (thus neglecting possible light inhibition):

$aLimGren = 1.0 / (aExtCoef * sDepthW) * LOG((1.0 + uLPAR0 / uhLGren) / (1.0 + aLPARBot / uhLGren))$

Lehman light function [-]

with

$uLPAR0$ light at depth 0 [W m^{-2} PAR]

$aLPARBot = uLPAR0 * EXP(- aExtCoef * sDepthW)$

light at the bottom [W m^{-2} PAR]

$uhLGren = hLRefGren * uFunTmGren$

half saturating light intensity at current temp. [W m^{-2} PAR]

For cyanobacteria and diatoms, the function is based on the Steele equation, accountimg for photo-inhibition at high light intensiyy

$$aLLimSpec = EXP(1.0) / (aExtCoef * sDepthW) * (EXP(- aLPARBot / (cLOptRefSpec * uFunTmSpec)) - EXP(- uLPAR0 / (cLOptRefSpec * uFunTmSpec)))$$

with *cLOptRef* the optimum light intensity [W m^{-2}].

These functions include a ‘self-shading’ effect, as the extinction coefficient is partly dependent on the phytoplankton concentration itself.
Like the maximum growth rate, also the half-saturating light intensity is dependent on the temperature. This implies that temperature has only little impact as long as the in situ light intensity is very low. This generally found phenomenon can be explained by the fact that in this range, photochemical reactions predominate, while at light saturation, the rate is determined by enzymatic reactions (e.g. Wetzel, 1983, p. 354). This permits the plants to grow also in winter, when both light and temperature are low.
Averaging the production over the day takes places in a very simplified way, by multiplying the growth rate with the day length, *ufDay* [-], which is calculated according to a cosine function (with *Time* = time in days):

$ufDay = 0.5 - 0.3 * COS(2*\pi*(Time+10)/365)$ day length [h/24h]

The combined growth rate equation, including the influence of temperature and light, based on the entire biomass [d^{-1}], is described as:

$aMuTmLSpec = ufDay * (1.0 - afCovSurfVeg) * aLLimSpec * uFunTmSpec * cMuMaxSpec$
growth rate at current light and temp. [d-1]

Nutrient limitation
Nutrient limitation is modelled by means of the well-known Droop equation (see for instance Riegman & Mur, 1984), which describes the dependence of the growth rate on the nutrient content of algae. The growth rate rapidly increases above the minimum content. For phosphorus, the equation is:

$$aPLimSpec = \left(1.0 - \frac{cPDSpecMin}{rPDSpec}\right) * \frac{cPDSpecMax}{cPDSpecMax - cPDSpecMin}$$

Droop function (P) for growth rate of algal group “Spec” [-]

with *cPDSpecMin* [gP g^{-1}D] and *cPDSpecMax* [gP g^{-1}D] the minimum and maximum phosphorus content of the cells, respectively. The equation for nitrogen is analogous.
The growth of diatoms is also dependent on silica. This is modelled more simply, by a Monod equation of the external SiO_2 concentration, assuming a constant Si/D ratio cSiDDiat of the diatoms; default *cSiDDiat* = 0.15 [gSi/gD] (Mylius, 1992):

aSiLimDiat = sSiO2W / (hSiAssDiat + sSiO2W)
silica dependence of growth rate [-]

For the other groups, the silica function is set to 1.0.
It is assumed that the *minimum* of the nutrient equations determines the growth rate (Liebig's law), and that the nutrient limitation is multiplicative with the light reduction function:

aNutLimSpec = MIN [aPLimSpec, aNLimSpec, aSiLimSpec]
nutrient reduction function [-]
*aMuSpec = aNutLimSpec * aMuTmLSpec*
growth rate [d^{-1}]

Besides in dry-weight or nutrients, algal biomass may also be expressed as the concentration of chlorophyll-*a*. The chlorophyll-a content of the phytoplankton, a derived variable in the model, is assumed to be variable, being higher in case of a more severe light limitation (Riegman, 1985).
*rChDSpec = cChDSpecMax - (cChDSpecMax - cChDSpecMin) * aLLimSpec*
chlorophyll-a/DW ratio [mg/mg]

1.5.4. Respiration and nutrient excretion

In general, respiration can be divided in growth respiration (or photorespiration), which is related to growth, and maintenance respiration (also called 'dark respiration'), which denotes the energy required for maintenance. In *PCLake*, only maintenance respiration is explicitly modelled, because growth respiration is incorporated implicitly in the growth rate. The maintenance respiration is modelled as a temperature dependent first order process. The respiration rate of a plant species is often correlated with its maximum growth rate and, consequently, differs among species. This process is modelled identically for the water and the sediment algae.

*ukDRespTmSpec = kDRespSpec * uFunTmSpec*
maintenance respiration rate at current temperature [d^{-1}]
*tDRespSpec = ukDRespTmSpec * sDSpec*
maintenance respiration flux [gD m^{-3} d^{-1}]

Together with the respiration fluxes, nutrient fluxes are defined, called 'excretion'. It is assumed that they are proportional to the dry-weight fluxes if the nutrient content of the cells is high, but are relatively lower if the nutrient content is low: saving of sparse nutrients. The excretion process is modelled like this:

*wPExcrSpecW = rPDSpecW / (cPDSpecMin + rPDSpecW) * rPDSpecW * wDRespSpecW*
P excretion Algae in water [gP/m3/d]
and a comparable function for the sediment algae.

1.5.5. Settling, resuspension and mortality

Settling is described as a first-order process, the rate being the settling velocity [m/d] divided by the water depth. The rate is dependent on lake dimensions (wind function) identically to detritus (see above).
Resuspension of sediment algae has already been described.

Natural mortality is also described as a first-order process.
*wDMortSpecW = kMortSpecW * sDSpecW*
  mortality in sediment [g/m3/d]
*tDMortSpecS = kMortSpecS * sDSpecS*
  mortality in water [g/m2/d]
The rates have taken as higher for the settled algae than for algae in the water column.

The parameter values of the three algal groups in the model differ. The cyanobacteria have a higher light affinity (they are shade-adapted) as well as a higher phosphorus uptake rate than the other groups. On the other hand, they have a much lower maximum growth rate and a stronger sensitivity to temperature. The diatoms have a lower temperature optimum, while the other small algae are not inhibited by high light intensities. Both these groups have higher growth rates, but also higher loss rates through settling and zooplankton grazing (see below). The diatoms are the only group that might be limited by silica.

1.6. Water plants

1.6.1. Overview

As stated before, macrophytes are modelled in three elements: dry-weight (D), P and N, always in grammes per m^2. For comparison with field data, the biomass values are also converted to cover percentages by means of a fixed conversion factor, with a maximum of 100 % cover. The overall differential equations are:

For biomass:
dDVeg/dt = tDProdVeg - tDRespVeg - tDMortVeg ± tDMigrVeg (- tDGrazBird)
(= production - respiration - mortality ± migration (- bird grazing)) [gD m^{-2} d^{-1}]

For nutrients:
dPVeg/dt = tPUptVeg - tPExcrVeg - tPMortVeg ± tPMigrVeg (- tPGrazBird) [gP m^{-2} d^{-1}]
dNVeg/dt = tNUptVeg - tNExcrVeg - tNMortVeg ± tPMigrVeg (- tNGrazBird) [gN m^{-2} d^{-1}]
  (= uptake - excretion - mortality ± migration (- bird grazing))

By modelling the vegetation in three units, the specific nutrient contents of the plants are modelled dynamically. Hence, nutrient uptake and production are modelled as separate processes, equally to the phytoplankton. The nutrient-to-dry-weight ratios are simply given by:

rPDVeg = sPVeg / sDVeg P/D ratio of vegetation [mgP/mgD]
and
rNDVeg = sNVeg / sDVeg N/D ratio of vegetation [mgN/mgD]

These ratios refer to the plant as a whole; no distinction is made between different parts of the plant, like roots or leaves. It is assumed that the nutrients are distributed homogeneously over the whole plant (instantaneous reallocation).
It is assumed that the biomass is divided in an under-ground part (roots) (*afRootVeg*) and an above-ground part (shoots) (*afShootVeg*), and that the latter is homogeneously divided over the water column. Hence, the modelled vegetation mimicks plants with overwintering parts.

Seasonality is modelled in a simplified way by assuming a high root fraction in the winter period and a low one during the growing season (default 0.6 and 0.1, resp.). The switch between both values in spring and autumn mimicks germination, allocation and reallocation processes, which are not explicitly modelled. It is assumed that allocation of biomass to the shoots in spring starts when the water temperature exceeds a certain value (default 9 oC); the biomass is then gradually (default in 15 days) redistributed over roots and shoots untill the summer ratio is reached. The opposite takes in place at a predefined day in autumn, default mid-September. (This date can be set group-specific.) These functions have been designed as part of a sinusoid to make them work fluently.
The second seasonal aspect is a temporarily enhanced mortality in autumn, described below.

The modelled processes are (Fig. 5):

- nutrient uptake
- production
- respiration and nutrient excretion

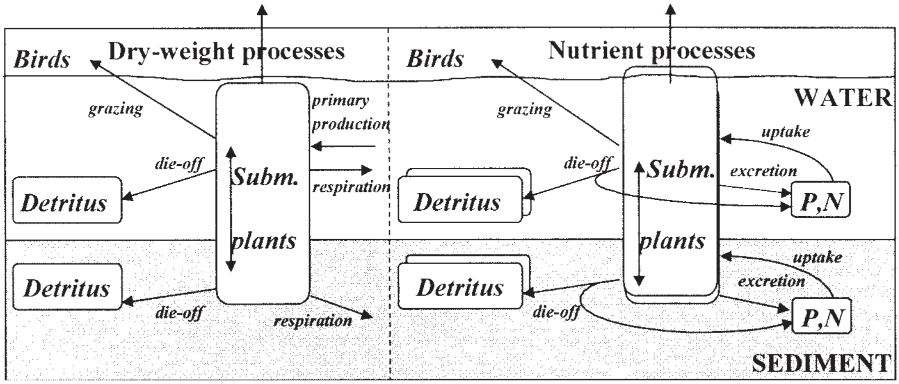

Fig. 5. *Processes of submerged vegetation*

- mortality
- (migration)
- grazing by birds
- management: mowing, dredging

These processes are described in the next sections.

Note: optionally, the user can split the vegetation into more than one functional group, like is done in *PCDitch*. In the description we sometimes anticipate on this by giving group-specific variants. However, most processes are modelled in the same way for each plant group, although with distinct parameter values.

1.6.2. Nutrient uptake

Nutrient uptake and production are modelled grossly analogously to the phytoplankton. Because of specific differences (as macrophytes have root and shoot fractions), the processe are described again.

It is assumed that macrophytes can take nutrients both from the water and from the pore water. The modelling of the nutrient uptake is again illustrated for phosphorus. The specific phosphorus uptake rate, that is the uptake rate per unit of biomass, is dependent on both the nutrient demand of the vegetation, defined by its actual nutrient content, and the availability of dissolved phosphorus in its environment. This is modelled as follows.

The *maximum* specific uptake rate is dependent on the actual nutrient content of the plants, the P/D ratio. If this ratio is low (close to the minimum value), the maximum uptake rate is high (close to the intrinsic maximum rate at the current temperature), while the rate drops to near-zero if the P/D ratio is close to its maximum value:

$$\mathit{aVPUptMaxCorSpec} = \mathit{cVPUptMaxSpec} * \mathit{cQ10ProdSpec}^{0.1*(Tm-20)} * \frac{\mathit{cPDSpecMax} - \mathit{rPDSpec}}{\mathit{cPDSpecMax} - \mathit{cPDSpecMin}}$$

maximum P uptake rate [mgP/mgD/d]

with *cPDVegMin* [gP g^{-1}D] and *cPDVegMax* [gP g^{-1}D] the minimum and maximum phosphorus content of the plants, respectively. The specific uptake rate is then described as a modified Monod-type function of the SRP concentration. The modification means that the phosphorus *affinity*, the slope of the curve when SRP is close to zero, is taken as constant for all values of V_{max}, in accordance with experimental data (Riegman & Mur, 1984). The specific uptake rate is calculated separately for uptake from the water and from the sediment pore water, as the SRP concentrations in both compartments will often markedly differ. The specific uptake rate from the *water* is:

$$aVPUptSpecW = aVPUptMaxCorSpec * \frac{sPO4W}{\frac{aVPUptMaxCorSpec}{cAffPUptSpec} + sPO4W}$$

specific P uptake rate by shoots [mgP/mgD/d]

This formulation implies that the half-saturating SRP concentration is not a constant, but is depending on V_{max}:

$ahPUptVeg = aVPUptMaxCorVeg / cAffPUptVeg$
half-saturating SRP concentration [mgP/l]

The resulting P flux from the water is the product of the specific uptake rate and the biomass of the submerged and floating parts:

$tPUptVegW = aVPUptVegW * (aDSubVeg + aDFloatVeg)$
P uptake from water [gP m^{-2} d^{-1}]

In the same way, the specific uptake rate from the *sediment* is:

$$aVPUptSpecS = aVPUptMaxCorSpec * \frac{oPO4S}{\frac{aVPUptMaxCorSpec}{cAffPUptSpec} + oPO4S}$$

specific P uptake rate by roots [mgP/mgD/d]

and the P uptake from the pore water is the product of this rate and the root biomass:

$tPUptVegS = aVPUptVegS * aDRootVeg$
P uptake from pore water [gP m^{-2} d^{-1}]

The total P uptake is the sum of water and sediment uptake:

$tPUptVeg = tPUptVegW + tPUptVegS$
total P uptake by the plant group [gP m^{-2} d^{-1}]

This formulation results in most phosphorus being absorbed from that compartment (water or sediment pore water) where it is most available, which is usually the pore water. Many other authors found that aquatic macrophytes take up the greater part of their nutrients from the sediment (e.g. Carignan, 1982; Moss, 1988). The formulation used here has the same effect, but is more robust within the framework of the nutrient cycle in *PCLake* than the empirical equation derived by Carignan (1982), which can be used as an alternative.

The uptake of *nitrogen* is modelled in the same way, with one extra feature, namely the form in which nitrogen is taken up, as nitrate or as ammonium. It is assumed that the plants have a strong preference for ammonium, because this is energetically more advantageous. The N uptake rates are based on total SRN in the water resp. pore water, and are then divided over the two N fractions according to the preference equation taken from the EPA WASP4 model (Ambrose et al., 1988). For the shoots, the fraction of the N uptake absorbed as ammonium, $afNH_4UptVegW$ [-], equals:

$$afNH4UptSpecW = \frac{sNH4W * sNO3W}{(ahNUptSpec + sNH4W) * (ahNUptSpec + sNO3W)}$$

and the ammonium fraction [-] of the N uptake by the roots:

$$afNH4UptSpecS = \frac{oNH4S * oNO3S}{(ahNUptSpec + oNH4S) * (ahNUptSpec + oNO3S)}$$

$$+ \frac{oNH4S * ahNUptSpec}{(oNH4S + oNO3S) * (ahNUptSpec + oNO3S)}$$

These equations are analogous to the one for phytoplankton and state a preference for ammonium uptake. Only when the ammonium concentration drops to very low values, the plants switch to nitrate as nitrogen source. A technical advantage of this preference function is that it requires no extra parameters.

The relation between internal nutrient content and growth rate is described in the next paragraph.

1.6.3. Production

By production (or growth) is meant increase in biomass. It is expressed in grammes dry weight per m^2 per day. The production may also be expressed in g oxygen production per g total biomass; 1 g biomass assimilation is approximately equivalent to 1 g oxygen production. Growth respiration (photorespiration) is included in the definition, but maintenance respiration (dark respiration) is not; this is described as a separate process (see next subsection).

In the model, the production is a function of the following factors:

- maximum growth rate (defined at 20 °C)
- water temperature
- light interception at the water surface (for submerged and floating plants)
- under-water light climate (extinction coefficient) (for submerged plants only)
- P content (P/D ratio) of the plants, representing P limitation
- N content (N/D ratio) of the plants, representing N limitation
- the plant biomass already present in the particular layer; this accounts for competition for space or other (unknown) density dependent factors.

Maximum growth rate

The *maximum growth rate* is the maximum increase in biomass per gram total plant biomass per day, on an exponential base: *D(t) = EXP(cMuMax * t)*. The root fraction (if present) does not contribute to the production. The maximum growth rate is defined at a temperature of 20 _C. In the literature, values between about 0.05 and 0.5, sometimes up to 1.0 [d^{-1}] are given, depending on the plant species. The lowest rates are found among the nymphaeids and helophytes, while many submerged plants and also duckweeds show rates in the range of 0.2 - 0.4 [d^{-1}]. These values are lower than those of most phytoplankton species.

Temperature

The effect of *temperature* (symbol: *Tm*) has been modelled by an exponential function (comparable to the well-known Arrhenius equation). It is based on the commonly used Q_{10} value (symbol: *cQ10Prod*), that is the factor by which the growth rate increases due to a 10 °C temperature increase.

$uMuMaxTmVeg = cMuMaxVeg * cQ10ProdVeg^{0.1 * (Tm - 20)}$

max. growth rate at current temperature [d^{-1}]

Actually, this relation only applies within a certain temperature range; most species have an optimum temperature, above which the growth rate decreases again. In stead of applying some kind of optimum curve, which have the disadvantage of using parameters which are less easy to derive from experimental data, we mimicked an optimum function by applying a similar temperature function for the maintenance respiration, but with a higher Q_{10} (symbol: $cQ_{10}Resp$). Typical Q_{10} values are between 1.5 and 2.5 for the production, and 2.0 - 3.0 for the respiration, depending on the plant species.

Light function

The *light function* applies to the submerged growing plants, not to floating or emergent plants. The formulation is made up of two parts, viz. the light interception by surface coverage, and the limitation factor for under-water light.

The fraction of the daylight intercepted at the water surface is calculated from the biomass of the floating, floating-leaved and emergent plants, with a maximum of 100 %. For the duckweeds, a single layer of fronds determines the percentage light interception. The equation is, per plant group:

$afCoverSurfVeg = MIN[1.0, MAX[aDFloatVeg / cDLayerVeg, aDEmergVeg / (fEmergVeg * cDCarrVeg)]]$

fraction of water surface covered by vegetation [-]

The total fraction of the water surface covered by plants, *afCoverSurfVeg* [-], is the sum of the fractions for each group, with a maximum of 1.0 (= 100 %). This part of the water area does not contribute to the submerged production.

It is assumed that the production of the floating and floating-leaved plants is hampered by light interception by the emergent plants.

The limitation factor for under-water light is modelled as a Monod-type P-I curve, integrated over the depth trajectory in which the plants grow, and averaged over 24 hrs. (Jørgensen, 1980). Light attenuation with increasing depth (Lambert-Beer law) and extinction coefficient are described already in the phytoplankton section. It is assumed that only the shoots are the productive part. The light limitation of the submerged production is calculated as:

$$aFunLSubSpec = \frac{1}{aExtCoef\ *\ sDepthW} * LOG\left(\frac{1+\frac{aLPAR1Spec}{uhLSpec}}{1+\frac{aLPAR2Spec}{uhLSpec}}\right)$$

light function of submerged growth [-]

with

$$aLPAR1Veg = uLPAR0 * EXP(- aExtCoefOpen * uDepth1Veg)$$

light at top of vegetation layer [W m^{-2} PAR]

$$aLPAR2Veg = aLPAR1Veg * EXP(- aExtCoef * (uDepth2Veg - uDepth1Veg))$$

light at bottom of vegetation layer [W m^{-2} PAR]

$$uhLVeg = hLRefVeg * uFunTmProdVeg$$

half-saturating light for vegetation production at current temp. [W m^{-2} PAR]

For the default assumption that the macrophytes are homogeneously distributed over the depth, this function equals the one for green algae.

Like the maximum growth rate, also the half-saturating light intensity is dependent on the temperature. This implies that temperature has only little impact as long as the in situ light intensity is very low. This generally found phenomenon can be explained by the fact that in this range, photochemical reactions predominate, while at light saturation, the rate is determined by enzymatic reactions (e.g. Wetzel, 1983, p. 354). This permits the plants to grow also in winter, when both light and temperature are low.
Averaging the production over the day takes places, as for phytoplankyton, by multiplying the growth rate with the day length, *ufDay*.

The combined growth rate equation, including the influence of temperature and light, based on the entire biomass [d^{-1}], is described as:

$$aMuTmLSpec = uMuMaxTmSpec * ufDay * \frac{ufSubSpec * (1.0 - afCoverSurfVeg) * aFunLSubSpec + fFloatSpec + fEmergSpec}{ufShootSpec}$$

max. growth rate at current temp. and light [g prod./g total biomass/d]

Hence, the growth rate of submerged plants [d^{-1}] depends on the temperature, the under-water light climate, the covered fraction of the water surface (*afCoverSurfVeg* [-]) and the day length (*ufDay*). Only the shoot fraction (*afShoot* [-]) contributes to the production.

Nutrient limitation

Nutrient limitation is, analogous to phytoplankton, modelled by means of the Droop equation (see for instance Riegman & Mur, 1984), which describes the dependence of the growth rate on the nutrient content of the plants. The growth rate rapidly increases above the minimum content. For phosphorus, the equation is:

$$aPLimSpec = \left(1.0 - \frac{cPDSpecMin}{rPDSpec}\right) * \frac{cPDSpecMax}{cPDSpecMax - cPDSpecMin}$$

Droop function (P) for growth rate of plant group “Veg” [-]

with *cPDVegMin* [gP g^{-1}D] and *cPDVegMax* [gP g^{-1}D] the minimum and maximum phosphorus content of the plants, respectively. The equation for nitrogen is analogous. It is assumed that the minimum of both equations determines the growth rate (Liebig’s law), and that, for submerged plants, the nutrient limitation is multiplicative with the light reduction function:

aNutLimVeg = MIN [aPLimVeg, aNLimVeg] nutrient reduction function [-]
*aMuVeg = aNutLimVeg * aMuTmLVeg* growth rate [d^{-1}]

Density dependence

Finally, the description of the growth rate is combined with a density-dependent correction. The assumption is that other factors than the ones explicitly modelled (*i.e.* phosphorus, nitrogen, light and temperature) might be limiting for the plant density that could maximally be achieved in a certain environment. This maximum biomass is expressed as the *carrying capacity*. This parameter appears in the logistic growth equation which is generally used in animal population models, and which is adapted here for vegetation. The general equation is:

$$\frac{dx}{dt} = r \cdot x \cdot \left(1 - \frac{x}{K}\right) = r \cdot x - \frac{r}{K} \cdot x^2$$

with *r* the intrinsic rate of increase and *K* the maximum biomass. The quadratic term in the equation represents the feedback caused by the (non-modelled) density-dependent factors. For water plants, one should primarily think of competition for *space*, and possibly for carbon dioxide. In general, the intrinsic rate of increase is the maximum growth rate minus the ‘inevitable losses’: respiration and mortality. Specifically for water plants, the ‘inevitable growth limitations’, *i.e.* temperature and light limitation, have been included in the definition of the growth rate, while the ‘inevitable losses’ have been defined as the sum of the respiration rate corrected for temperature, and the minimum mortality rate (see next paragraph).

So the intrinsic increase rate r, in our nomenclature $\mathit{akDIncrVeg}$, is defined as:

$$\mathit{akDIncrVeg} = \mathit{aMuTmLVeg} - \mathit{ukDRespTmVeg} - \mathit{bkMortVeg}$$

intrinsic net increase rate of vegetation [d^{-1}]

and the correction term $\mathit{tDEnvVeg}$ (“*Env*“ is an abbreviation for “*Environment*”) equals:

$$\mathit{tDEnvVeg} = \mathit{akDIncrVeg} / \mathit{aDCarrVeg} * \mathit{sDVeg}^2$$

logistic correction of vegetation [gD m-2 d-1]

The correction term $\mathit{tDEnvVeg}$ is divided between a reduction of the production and an increase of the mortality (Traas & Aldenberg, 1992). The partitioning is based on the degree of growth limitation (including nutrient limitation). This formulation leads to a correct handling of all mass fluxes, without a need for an extra parameter. Other assumptions are possible and might be more plausible, however.

The production reduction is described as:

$$\mathit{tDEnvProdVeg} = \mathit{aNutLimVeg} * \mathit{aLLimProdVeg} * \mathit{ufDay} * \mathit{tDEnvVeg}$$

logistic correction of production [gD m-2 d-1]

and thus the total production flux (per plant group) is:

$$\mathit{tDProdVeg} = \mathit{aMuVeg} * \mathit{sDVeg} - \mathit{tDEnvProdVeg}$$

vegetation production flux [gD m-2 d-1]

and the *submerged* production is, simply:

$$\mathit{tDProdSubVeg} = \mathit{ufSubVeg} * \mathit{tDProdVeg}$$

submerged production [gD m-2 d-1]

The remainder of the environmental correction:

$$\mathit{tDEnvMortVeg} = \mathit{tDEnvVeg} - \mathit{tDEnvProdVeg}$$

logistic correction of mortality [gD m-2 d-1]

is added to the mortality, as explained in paragraph 1.6.6.

1.6.4. Respiration and nutrient excretion

In general, respiration can be divided in growth respiration (or photorespiration), which is related to the plant’s growth, and maintenance respiration (also called ‘dark respiration’), which denotes the energy required for maintenance. Only maintenance respiration is explicitly modelled, because growth respiration is incorporated implicitly in the growth rate. The maintenance respiration is modelled as a temperature dependent first order process. The respiration rate of a plant species is often correlated with its maximum growth rate and, consequently, differs among species. An exponential temperature function is used, based on the Q_{10} value, the temperature interval that causes a doubling of the rate. This Q_{10} value is in general higher than the one for growth. Together, this leads to an optimum curve for the net growth rate.

$ukDRespTmVeg = kDRespVeg * cQ10RespVeg^{0.1*(Tm-20)}$
maintenance respiration rate at current temperature [d^{-1}]
$tDRespVeg = ukDRespTmVeg * sDVeg$
maintenance respiration flux of vegetation [$gD\ m^{-2}\ d^{-1}$]

Together with the respiration fluxes, nutrient fluxes are defined, called ‘excretion’. It is assumed that they are proportional to the dry-weight fluxes if the nutrient content of the cells is high, but are relatively lower if the nutrient content is low: saving of sparse nutrients. The excretion process is modelled like this:

$tPExcrVeg = rPDVeg / (cPDVegMin + rPDVeg) * rPDVeg * tDRespVeg$
P excretion by vegetation [$gP\ m^{-2}\ d^{-1}$]

The P and N excretion fluxes are partitioned between sediment and water column according to the root/shoot ratio of the plant group:
$tPExcrVegS = fRootVeg * tPExcrVeg$
$tPExcrVegW = tPExcrVeg - tPExcrVegS$

1.6.5. Mortality

In general, the natural mortality of water plants is low during spring and summer, and increases in autumn. The factors responsible for this increased mortality are only poorly understood. Decreasing day length probably is one of the triggers, others might be temperature changes, ageing of leaves, or investment in the formation of overwintering structures. Because the causal relationships between these factors are poorly known, a simple phenomenological approach was chosen to model the mortality. In spring and summer, a first-order equation is used with a low mortality constant (*kMortVegSum* [d^{-1}]). At a certain, predefined date (*cDayWinVeg*), default mid-September, the same day as the reallocation starts, the mortality rate is increased, and the vegetation dies off until a certain fraction (*fWinVeg* [-]) of the biomass is left over. This surviving fraction is available again at the start of the next growing season. (This is not completely true, because production and respiration will not stand still completely during winter). The start and length of the “autumn period”, as well as the surviving fraction, can be defined by the user. They may, of course, differ among plant groups.

The equations are:

```
IF (Day .LT. cDayWinVeg) THEN
    bkMortVeg = kMortVegSum
        low mortality constant [d-1]
ELSE
    IF (Day .LT. cDayWinVeg + cLengMort) THEN
        bkMortVeg = - LOG(fWinVeg) / cLengMort
            high mortality constant (autumn) [d-1]
    ELSE
        bkMortVeg = kMortVegSum
            low mortality constant [d-1]
      ENDIF
ENDIF
```

The mortality is always extended with the environmental correction tDEnvMortVeg, as explained above:

tDEnvMortVeg = tDEnvVeg - tDEnvProdVeg

logistic correction of mortality [gD m^{-2} d^{-1}]

The total mortality flux then is:

*tDMortVeg = bkMortVeg * sDVeg + tDEnvMortVeg*

The corresponding N and P mortality fluxes are proportional to the dry-weight fluxes. To account for autolysis, it is possible to define a fraction of the nutrients (*fDissMortVeg*) released directly in dissolved form (as PO_4 or NH_4).

The remainder of the mortality flux, the particulate fraction, is divided between the suspended detritus (a small part, *fDetWMortVeg*, of the shoot mortality) and the sediment detritus (the remainder). This seems reasonable, as a relatively large proportion of died leaves etc. will settle to the bottom quite fast.

1.6.6. Grazing by birds

Optionally, grazing of the vegetation by herbivorous birds can be included. The birds are considered as an ‘external’ component and are not modelled dynamically. The user can define the bird density and, if applicable, the period of the year that they are present on the lake. It is assumed that a fixed amount per bird is consumed, with a fixed assimilation efficiency. A Monod factor is included to ensure that no more is eaten than is there. The egested part returns as detritus, the assimilated part is considered as lost from the system.

```
IF( (Time .GE. cYearStartBirds * DaysPerYear) .AND.
    (Day .GE. cDayStartBirds) .AND. (Day .LE. cDayEndBirds) ) THEN
```

```
    tDGrazVegBird = cPrefVegBird * sDVeg / (hDVegBird + sDVeg)
        * cBirdsPerha / m2Perha * cDGrazPerBird
    biomass loss due to grazing of birds [g/m2/d]
    (Note: preference = edibility)
ELSE
    tDGrazVegBird = 0.0
ENDIF
```

1.6.7. Migration

A small migration flux, transport of plant biomass into or out of the lake, has been assigned to all plant groups, mainly for computational reasons: it prevents state variables from approaching zero and thereby slowing down the model calculations. The migration constant *kMigrVeg* has been chosen arbitrarily at the low rate of 10^{-5} d^{-1} and the external plant density *cDVegIn* at 1.0 gD m^{-2}. The general equation is:

*tDMigrVeg = kMigrVeg * (cDVegIn - sDVeg)* [gD m-2 d-1]

The equations for P and N are analogous.

1.7. Food web

1.7.1. General

The food web module is kept as simple as possible and comprises zooplankton, macrozoobenthos, whitefish (juvenile and adult) and predatory fish. The general equations for the animal groups are (zooplankton in g m^{-3} d^{-1}, others groups in g m^{-2} d^{-1}):

as D: *dx/dt = (consumption – egestion) – respiration – mortality – predation*

as N and P: *dy/dt = (consumption – egestion) – excretion – mortality - predation*

The P/D and N/D ratios of all groups, except piscivorous fish, are modelled dynamically.
The suffix *–Spec* in the description denotes that the equation is used for all groups; in the model, *-Spec* is replaced by the respective suffix *–Zoo, -Bent, -FiJv, -FiAd* or *–Pisc*.
All assimilation and mortality rates are combined with a density-dependent correction, derived from the logistic growth equation explained already in § 1.6 (Hallam et al., 1983; Traas, 2004). This stands for all non-modelled (i.e. not food-related) factors. The carrying capacities have been set to high values. The effect of this correction is that the biomass cannot become higher than the carrying capacity.
It is assumed that zooplankton feeds on phytoplankton and detritus in the water, zoobenthos on phytoplankton and detritus in the sediment, juvenile whitefish on zooplankton, adult whitefish on zoobenthos, and predatory fish on both juvenile and adult whitefish.
The temperature effect is always modelled as an optimum function:

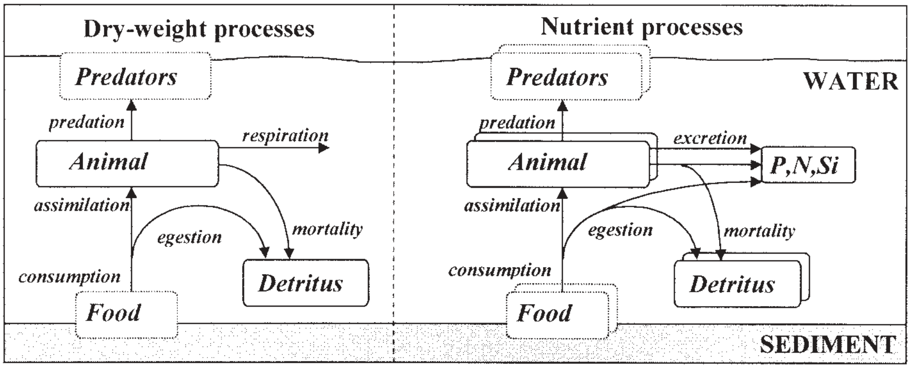

Fig. 6. *Processes of animal groups.*

A part of the consumption flux, the assimilation efficiency (*fDAssSpec*), is used for growth of the animals, the remainder is egested and becomes detritus: Consumption – egestion = assimilation. The nutrient to biomass ratios generally increase with the trophic level. In order to maintain these differences and to close the mass balances, some parallel processes were uncoupled, i.e. made dependent on the actual nutrient ratios. Three mechanisms were included:

1 phosphorus is assimilated with a greater efficiency than carbon;
2 phosphorus excretion is relatively lower than respiration (phosphorus is retained in the body);
3 an increased respiration (extra utilisation of carbohydrates) when P content becomes too low.

ad 1: The assimilation efficiencies for P and N are made dependent on the P/D or N/D ratios of the food. Hence, the P and N assimilation efficiencies are higher than the D assimilation efficiencies. The general equations are, for phosphorus:

*afPAssSpec = MIN(1.0, cPDSpecRef / rPDFoodSpec * fDAssSpec)*
P assimilation efficiency of group “Spec” [-]

in which *cPDSpecRef* is the ‘reference’ P/D ratio of the animals (the ratio they need for their functioning and which try to maintain), *rPDFoodSpec* the P/D ratio of the food, and *fDAssSpec* the D assimilation efficiency [-].

For nitrogen:
*afNAssSpec = MIN(1.0, cNDSpecRef / rNDFoodSpec * fDAssSpec)*
N assimilation efficiency of group “Spec” [-]

ad 2: The relative excretion rates are related to the respiration rate constant as follows:
*akPExcrSpec = rPDSpec / cPDSpecRef * kDRespSpec*
P excretion rate of group “Spec” [d-1]
*akNExcrSpec = rNDSpec / cNDSpecRef * kDRespSpec*
N excretion rate of group “Spec” [d-1]

ad 3: The respiration rate is multiplied by the following factor:
aCorDRespSpec = MAX(cPDSpecRef / rPDSpec, cNDSpecRef / rNDSpec)
correction factor of respiration for P and N content [-]

The second and third mechanisms do not apply to piscivorous fish, as they are assumed to have constant nutrient ratios.

1.7.2. Zooplankton

Zooplankton feeds on both phytoplankton and detritus. The consumption (or ingestion) of food by filter feeders is commonly described by means of the specific filtering rate.

The actual 'functional response' of the zooplankton is described by the way in which the specific filtering rate depends on the food concentration and other environmental factors. Several formulations can be found in literature (see J›rgensen, 1980, chapter 3 and Scavia & Robertson, 1979 for a review). We adopted the formulation by Gulati et al. (1982, 1985) as well as Canale (1976) who found the filtering rate to decrease hyperbolically with seston concentration and to increase with temperature.

Apart from the concentration of food particles, another important factor is its *composition*. The seston is composed of four components: detritus, diatoms, green algae and blue-green algae. Differences in seston composition are known to affect specific consumption rate. Notably, most zooplankton species have much difficulty in handling filamentous bluegreen algae. This is caused by an interference of the long trichomes with the filtering apparatus of the animals and possibly also by a direct toxic effect (Gliwicz, 1980; Davidowicz et al., 1988). Lyche (1984) found a striking difference in specific consumption rate of *Daphnia longispina*, depending on the algal species offered as food. Differences were primarily related to cell shape: two small spherical or disk-like species (the cyanophyte *Synechococcus sp*. and the diatom *Cyclotella pseudostelligera*, resp.) were eaten est, the filamentous cyanophyte *Oscillatoria agardhii* was eaten poorly (ingestion rate about 10 % of the former species) and three 'intermediate' species, viz. the chlorophyte *Selenastrum capricornutum* ('sausage-shaped'), the cryptophyte *Rhodomonas sp*. ('drop-shaped') and the 2-4 cell colony forming chlorophyte *Scenedesmus quadricauda*, were in-between (30 - 50 % of the former species). Comparable differences in specific consumption rates were found by Arnold (1971) for *Daphnia pulex*.

These differences are modelled by introducing a selection step in the filtering process. Each kind of food is attributed a preference factor (*cPref*) [-]. This factor denotes what fraction of the amount of the particular food component present in the filtered water is actually ingested by the animal. The remainder (if any) is rejected. So, the selectivity constants rank: 'other' algae > diatoms > detritus > cyanobacteria.

The equations are:

*oDFoodZoo = cPrefDiat * sDDiatW + cPrefGren * sDGrenW + cPrefBlue * sDBlueW + cPrefDet * sDDetW* food for zooplankton [mgD/l]

uFunTmZoo = EXP(-0.5/cSigTmZoo**2 * ((uTm-cTmOptZoo)**2 - (cTmRef-cTmOptZoo)**2))
temp. function of zooplankton [-]
aFilt = cFiltMax * uFunTmZoo * hFilt / (hFilt + oDOMW) filtering rate [ltr/mgDW/d]
ukDAssTmZoo = fDAssZoo * cFiltMax * uFunTmZoo * hFilt
max. assimilation rate of zooplankton, temp. corrected [d-1]
aDSatZoo = oDFoodZoo / (hFilt + oDOMW) food saturation function of zooplankton [-]
ukDRespTmZoo = kDRespZoo * uFunTmZoo respiration constant of zooplankton [d-1]
ukDIncrZoo = ukDAssTmZoo - ukDRespTmZoo - kMortZoo
intrinsic rate of increase of zooplankton [d-1]

wDEnvZoo = MAX(0.0, ukDIncrZoo / cDCarrZoo * sDZoo**2)
environmental correction of zooplankton (cannot be negative.) [mg/l/d]
wDAssZoo = aDSatZoo * (ukDAssTmZoo * sDZoo - wDEnvZoo)
assimilation of zooplankton [mg/l/d]
wDConsZoo = wDAssZoo / fDAssZoo consumption of zooplankton [mg/l/d]
wDConsDetZoo = cPrefDet*sDDetW / oDFoodZoo * wDConsZoo
detritus consumption by zooplankton [mg/l/d]
wDConsDiatZoo = cPrefDiat*sDDiatW / oDFoodZoo * wDConsZoo
diatoms consumption by zooplankton [mg/l/d]
wDConsGrenZoo = cPrefGren*sDGrenW / oDFoodZoo * wDConsZoo
greens consumption by zooplankton [mg/l/d]
wDConsBlueZoo = cPrefBlue*sDBlueW / oDFoodZoo * wDConsZoo
blue-greens consumption by zooplankton [mg/l/d]
wDConsPhytZoo = wDConsDiatZoo + wDConsGrenZoo + wDConsBlueZoo
phytoplankton consumption by zooplankton [mg/l/d]
wDEgesZoo = wDConsZoo - wDAssZoo egestion of zooplankton [mg/l/d]

The P/C or P/D ratio of the zooplankton is much higher than that of the seston which serves as food. Moreover, this ratio is fairly constant (P/C = *ca* 2.3 %), both throughout the year as between different lakes, in spite of sometimes large variations or differences in the P/C ratio of the food (Gulati, 1990, 1991). Zooplankton seems to possess mechanisms to maintain its phosphorus content within narrow ranges, also under varying external conditions. We therefore included the mechanisms mentioned above. Although We assume that all mechanism may be important, but unfortunately, little experimental work has been done on this subject. Our interest is in the effect of these mechanisms on the phosphorus flows in the ecosystem, without going to deep into the physiological backgrounds.
The egested material becomes detritus, but a considerable part of the nutrients are released in inorganic form.

Respiration, nutrient excretion and mortality are modelled as first-order processes. The dependence on the nutrient ratios are as described above,

1.7.3. Zoobenthos

Zoobenthos is assumed to feed on sediment detritus and a bit on settled algae, also by a Monod-type (or ‘type II’) functional response. It is also assumed to be able to ‘accumulate’ P from its food comparable to zooplankton. The P/C ratio of the organisms is estimated as 2.0 - 2.5 % The equations are analogous.

1.7.4. Fish

Juvenile whitefish feeds on zooplankton, adult whitefish on zoobenthos, and predatory fish on both classes of whitefish.

All fish predation processes are modelled as a so-called ‘type III’ response (Holling, 1965): the predation rate depends on prey density according to a sigmoid curve. Besides, a vegetation dependence is included as it is assumed that the feeding, especially sediment feeding, is less efficient in dense vegetation (a part of the food is ‘overlooked’ by the fish). As exact data on this are not available, we assumed a linear decrease.

aFunVegFiJv = MAX(0.0, 1.0 - cRelVegFiJv * aCovVeg)
vegetation dependence of young fish feeding [-]
aDSatFiJv = (aFunVegFiJv * sDZoo * sDepthW) **2 / (hDZooFiJv **2 + (aFunVegFiJv * sDZoo * sDepthW) **2) food limitation function of young fish [-]

aFunVegFiAd = MAX(0.0, 1.0 - cRelVegFiAd * aCovVeg)
vegetation dependence of adult fish feeding [-]
aDSatFiAd = (aFunVegFiAd * sDBent) **2 / (hDBentFiAd **2 + (aFunVegFiAd * sDBent) **2)
food limitation function of adult fish [-]

Spawning is simulated as the transfer, every May, of a small proportion of the adult biomass to the juvenile biomass. At the end of each year, half the juvenile biomass becomes ‘adult’.

```
IF (Day .GE. cDayReprFish .AND. Day .LT. cDayReprFish + 1.0) THEN
    tDReprFish = fReprFish * sDFiAd
        Reproduction flux [gD m-2 d-1]
ELSE
    tDReprFish = 0.0
ENDIF
```

```
IF (Day .GE. 364.0) THEN
    tDAgeFish = fAgeFish * sDFiJv
        Ageing [gD m-2 d-1]
ELSE
    tDAgeFish = 0.0
ENDIF
```

Also the whitefish is assumed to have a relatively higher phosphorus assimilation efficiency, as the internal P content of fish is again much higher than that of its food organisms (Kitchell et al., 1975).
The effect of adult whitefish on water turbidity has been explained under ’resuspension’.

Predatory fish is assumed to be dependent on the presence of vegetation. Its carrying capacity can be made dependent on the size of the marsh zone connected to the lake.
In case of no marsh zone:
aDCarrPisc = MAX(cDCarrPiscMin, MIN(cDCarrPiscMax, cDCarrPiscBare))
If there is a marsh zone:

```
IF (aCovVeg .LT. cCovVegMin) THEN
    aDCarrPisc = MAX(cDCarrPiscMin, MIN(cDCarrPiscMax,  &
        fMarsh * (1.0/PerCent) * cRelPhraPisc))
    ELSE
        aDCarrPisc = MAX(cDCarrPiscMin, MIN(cDCarrPiscMax,  &
        fMarsh * (1.0/PerCent) * (cRelPhraPisc + cRelVegPisc)))
    Carrying capacity of Pisc of lake with marsh zone [$gD.m^{-2}$]
ENDIF
```

aFunVegPisc = aDSubVeg / (hDVegPisc + aDSubVeg)
vegetation dependence of Pisc growth rate [-]
*aDSatPisc = aDFish**2 / (hDFishPisc**2 + aDFish**2)*
food limitation function of Pisc [-]

Fishery (on adult whitefish and piscivorous fish), by man and/or by piscivorous birds, can be implemented as a first-order rate constant, which can be different for summer and winter. For adult whitefish:

```
IF(COS(2.0 * Pi * Time / DaysPerYear) .GT. 0.1) THEN
    ukHarvFish =  kHarvFishWin
ELSE
    ukHarvFish = kHarvFishSum                fish harvesting constant [d-1]
ENDIF
tDHarvFish   = ukHarvFish * sDFiAd           harvesting of fish [gD/m2/d]
```

and analogous equations for piscivorous fish.

Respiration, excretion, mortality and harvesting are modelled as first-order processes. After dying of fish, the scales and bones, consisting of undecomposable material, settle to the bottom and remain there. In this way, 35% of the biomass and 50% of the phosphate of a died fish is permanently removed from the lake system. The ‘flesh’ flows to the detritus pool, except for a small phosphate fraction which is released in soluble form.

1.8. Wetland module

This module describes the vegetation in relation to water quality in the wetland zone around the lake by modelling the nitrogen and phosphorus cycle. The wetland zone is described as a system built of the two environmental compartments sediment and surface water (*Fig. 3*). The water depth is variable, with a default initial value of 0.5 m. The anaerobic and aerobic proportion of the sediment is modelled analogous to the lake sediment. Mixing between the water in the wetland zone and the lake water is described by a dispersion-like equation across the contact zone.

The wetland module includes the components: emergent vegetation (divided in shoot and rhizome), detritus, inorganic nutrients (nitrogen and phosphorus) and inorganic matter. The components are in terms of mass per volume (water) or per square meter (sediment and vegetation shoot and rhizome) (*Table 2*).

All abiotic and microbial processes (adsorption, desorption, settling, diffusion, mineralization, nitrification, denitrification) are described similar to those in the lake as much as possible. Resuspension is set to zero and settling rates are assumed not to be affected by wind stress.

Also, the exchange of water and components between marsh and lake is described.

Phytoplankton is assumed not to grow in the wetland zone, but it exchanges with the water and can settle in the wetland zone.

Processes related to the vegetation

The basic assumption for modelling the marsh vegetation is reed vegetation (Phragmites australis). The description of the processes related to the reed vegetation is divided into a shoot and a rhizome fraction. Both components are in terms of biomass (D), nitrogen (N) and phosphorus (P). The processes related to biomass are modelled for both shoot and rhizome. The following text elucidates the equations that describe the processes for the shoot. The description of nitrogen and phosphorus in the vegetation is comparable. The following equations related to nutrients are worked out for nitrogen.

Table 2 *Components of the wetland module*

Components	**Unit**		**As (bio)mass**	**As nitrogen**	**As phosphorus**
	Water	**Sedim.**			
Vegetation: Shoot	[g m^{-2}]	–	sDShootPhra	sNShootPhra	sPShootPhra
Veg.:Rhizome	–	[g m^{-2}]	sDRootPhra	sNRootPhra	sPRootPhra
Detritus	[g m^{-3}]	[g m^{-2}]	sDDet(WM/SM)	sNDet(WM/SM)	sPDet(WM/SM)
Humus	–	[g m^{-2}]	sDHumSM	sPHumSM	sPHumSM
Inorg. matter	[g m^{-3}]	[g m^{-2}]	sDIM(WM/SM)	–	–
Inorg. nutrients	[g m^{-3}]	[g m^{-2}]	–	sNH4(WM/SM), sNO3(WM/SM)	sPO4(WM/SM), sPAIM(WM/SM)

During plant growth nutrients continuously move between shoot and rhizome, while the concentration of the nutrients fluctuates. It is assumed the nutrients are equally spread in the vegetation and are continuously moving to the places where they are needed.

The biomass development of the shoot depends on the allocation in spring (tDAllPhra), production in summer (tDProdShootPhra), mortality (tDMortShootPhra), respiration (tDRespShootPhra) and reallocation in autumn (tDRealPhra) and, possibly, mowing (*Fig. 7*).

dDShootPhra = tDProdShootPhra - tDRespShootPhra – tDMortShootPhra + tDAllPhra - tDRealPhra – tDManShootPhra
Biomass shoot reed vegetation [gD m^{-2} d^{-1}]

The nitrogen in the shoot depends on the translocation in spring (tNTransPhra), uptake (tNUptShootPhra), mortality (tNMortShootPhra), retranslocation in autumn (tNRetrPhra) and mowing:

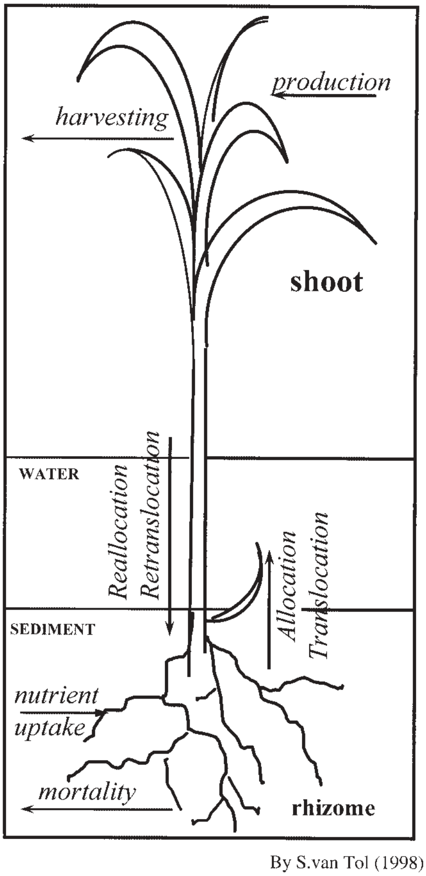

Figure 7. Model of wetland vegetation

$dNShootPhra = tNUptShootPhra - tNMortShootPhra + tNTransPhra - tNRetrPhra - tNManShootPhra$
Nitrogen in shoot reed vegetation [gN m^{-2} d^{-1}]

A comparable equation is defined for phosphorus.

The root biomass [gD m^{-2} d^{-1}] is described as follows:
$dDRootPhra = tDProdRootPhra - tDRespRootPhra - tDMortRootPhra - tDAllPhra + tDRealPhra$

and N in the roots [gN m^{-2} d^{-1}] as:
$dNRootPhra = tNUptRootPhra - tNMortRootPhra - tNTransPhra + tNRetrPhra$
with again a comparable equation for P.

The growing season exists of two phases, the initial growth and the productive growth. During the last growing season clones are formed, these sprout in the initial growing phase. Therefore the vegetation uses carbohydrate in the rhizomes. When shoots reach the water surface, carbohydrate is produced by photosynthesis. At that time the productive growth starts and biomass is increasing.

Allocation and reallocation

Not the full carbohydrate supply in the rhizomes is being used during the initial growth. The allocated carbohydrate supply is modelled as a constant fraction of the subterranean roots (fDAllPhra) at the start of the growing season (t0). The temperature determines this point in time.
$tDAllPhra = kDAllPhra * aDAllPhra$
Allocation of biomass, per day [gD m^{-2} d^{-1}]
$aDAllPhra = fDAllPhra * sDRootPhra(t0)$
Available biomass [gD m^{-2}]

The allocation ends when the total carbohydrate fraction is replaced to the aboveground parts of the vegetation.

At the end of the growing season, reallocation takes place. Then when autumn begins, biomass is being moved from shoot to the rhizome. This process is modelled similar to allocation with this difference that the available biomass equals the biomass of the shoot at the beginning of autumn.

Translocation and retranslocation

Allocation and reallocation are coupled with translocation and retranslocation respectively. The amount of nutrients replaced at the beginning and end of the growing season, is related to the N/D-ratio and P/D-ratio of the subterranean and aboveground biomass of the vegetation respectively. The translocation of nitrogen at the beginning of the growing season is calculated as follows:

$tNTranPhra = rNDRootPhra * tDAllPhra$

Translocation of nitrogen [gN m^{-2} d^{-1}]

Production

The moment the sprouts reach the water surface determines the start of the productive growth. The success or otherwise of sprouts reaching the water surface is depending on the water depth and the length of the stem. The length of the stem equals the quotient of the actual biomass of the shoot and the product of the weight of one stem and the density of stems.

$$aHeightShootPhra = \frac{sDSHootPhra}{cDStemPhra * cDensShootPhra}$$

Stem height during initial growth [m]

The growth rate, actual biomass and growth limitation due to factors related to density, determine the biomass production of the vegetation.

$tDProdPhra = aMuPhra * sDShootPhra – tDDensProdPhra$

Production of the vegetation [gD m^{-2} d^{-1}]

The production of the shoot is calculated by multiplying the biomass production of the vegetation with the biomass shoot/vegetation ratio (i.e. sDShootPhra / (sDShootPhra + sDRootPhra)).

The growth rate equals the product of the maximum growth rate and the nutrient limitation.

$aMuPhra = aMuPhraMax * aNutLimPhra$

Growth rate [d^{-1}]

The maximum growth rate is described by a Monod-type function which depends on temperature, daylength en the maximum growth rate specific for the type of vegetation.

$aMuPhraMax = cMuPhraMax * uTmProdPhra * ufDay$

Maximum growth rate at a certain temperature and daylength [d^{-1}]

Temperature is modelled as an exponential function based on the factor Q_{10}. This factor denotes the increase of the growth rate by an increasing temperature of 10° C.

$uTmProdPhra = cQ10ProdPhra^{0.1*(Tm-cTmRef)}$

Temperature function [° C]

The day length has been described earlier.

The available nutrients in the environment sustain the growth. If there is not enough phosphorus available for the growth of the vegetation, the biomass will not increase, even when there is enough nitrogen available. Than the production is limited by phosphorus. Nitrogen can also be limited. Limitation by nutrients is described by the Droop-function (*see equation*), where the growth rate depends on the nutrient content in the vegetation. While nitrogen and phosphorus can both limit the growth it is assumed the minimum of both functions (N and P Droop-function) equals the growth rate.

$aNutLimPhra = MIN\,(aNLimProdPhra, aPLimProdPhra)$
Nutrient reduction function [-], where:

$$aNLimProdPhra = \left(1 - \frac{cNDPhraMin}{rNDPhra}\right) * \frac{cNDPhraMax}{cNDPhraMax - cNDPhraMin}$$

Nitrogen Droop-function for growth rate [-]

The maximum biomass that can be reached, also depends on the maximum density of the vegetation. The growth of clones determines this maximum density and depends on genetic characteristics and environmental circumstances like availability of nutrients in the last growing season.

Competition for space between plant species and damage by animals are examples of environmental factors affecting the density of the vegetation that are not taken into account in this version of the wetland module. The avifauna responsible for damage of the vegetation will be modelled in a later stage.

The population-dynamic commonly uses the following equation for growth:

$$\frac{dD}{dt} = r * D * \left(1 - \frac{D}{K}\right) = r * D - \frac{r}{K} * D^2$$, where:

D = biomass,
K = maximum biomass and
r = intrinsic increasing rate.

The quadratic term represents the growth reduction as consequence of density factors. The biomass of the vegetation can not infinitely increase, but is limited by the maximum density in terms of biomass (K). The intrinsic increasing rate is usually defined by the maximum growth rate subtracted with losses by respiration and mortality. For vegetation these losses are defined by respiration rate corrected for temperature and the minimum mortality rate (*see equation*). The density correction of the vegetation production is described as follows:
$tDDensProdPhra = aNutLimPhra * ufDay * tDDensPhra$
Density correction of the vegetation production [gD m^{-2} d^{-1}], with:

$$tDDensPhra = \frac{akDIncrPhra}{cDPhraMax} * sDPhra^2$$

Density correction [gD m^{-2} d-1], where:

$$\mathit{akDIncrPhra} = \mathit{aMuPhraMax} - \mathit{ukDRespTmPhra} - \mathit{kMortPhraMin}$$
Intrinsic increasing rate [d^{-1}]

Mortality
The rate of mortality is small in spring and summer. In autumn, when vegetation blooms and produces seed, mortality is increasing. This seasonal variation is not explicated. The day length possibly influences (might be a controlling factor) the mortality at the end of the growing season. Mortality is modelled by the average age of the shoot and rhizome, 1 and 7 years respectively (Haslam, 1973). This mortality rate is multiplied with the biomass at the start of autumn:

$$\mathit{tDMortShootPhra} = \mathit{kDMortShootPhra} * \mathit{sDShootPhraAut}$$
Dying shoot biomass [gD m^{-2} d^{-1}]

The loss of nutrients due to mortality is proportional to the dying biomass. For nitrogen:

$$\mathit{tNMortShootPhra} = \mathit{rNDShootPhra} * \mathit{tDMortShootPra}$$
Dying shoot biomass [gN m^{-2} d^{-1}]

Respiration
Analysis of growth rate mostly does not carry out respiration measurements.
Respiration in light is not modelled separately because it is already included in the production data (growth rate). Maintenance respiration indicates the vital energy of the vegetation. Maintenance respiration is modelled as a first order process at a rate of 1.75 mg O_2 g^{-1} AFDW h^{-1} (Van Dijk and Janse, 1993).

$$\mathit{tDRespShootPhra} = \mathit{ukDRespTmPhra} * \mathit{sDShootPhra}$$
Maintenance respiration of the shoot [gD m^{-2} d^{-1}], with:

$$\mathit{ukDRespTmPhra} = \mathit{kDRespPhra} * \mathit{cQ10RespPhra}^{0.1*(\mathit{Tm} = \mathit{cTmRef})}$$
Maintenance respiration at a certain temperature [d^{-1}]

Management
Experiences in the cultivation of reed show that mowing in the summer leads to less vital vegetation. Therefore reed is usually mowed in the winter. Mowing in wintertime works out badly for the removal of nutrients because a part of the nutrients in the shoot retanslocates to the rhizomes in this period. The moment of mowing determines the percentage of the nutrient removal by management. This point of time is flexible. The removal of biomass due to management (mowing) is modelled as a once-only removal of a part of the actual shoot biomass.

$aDManShootPhra = fDManPhra * aDShootPhra$

Biomass removal by management [gD m^{-2}]

$aNManShootPhra = rNDShout * aDManShootPra$

Nitrogen removal by management [gN m^{-2} d^{-1}]

Nutrient uptake

The basic assumption for modelling the nitrogen uptake is the total available nitrogen in the sediment. The distinguishing characteristics of the uptake of ammonia and nitrate are not taken into account. The uptake of nitrogen is determined by the uptake rate and the rhizome biomass:

$tNUptPhra = aVNUptPhraS * sDRootPhra$

Nitrogen uptake by vegetation [gN m^{-2} d^{-1}]

The amount of nitrogen taken up by the vegetation is equally distributed over the shoot and rhizome. The nutrient uptake rate is determined by the maximum nutrient uptake rate, the available nutrients in the sediment and the affinity of the vegetation for the nutrients.

$$aVNUptPhra = aVNUptMaxPhra * \frac{aNDissS}{ahNUptPhra + aNDissS}$$

Nitrogen uptake rate (rhizome) [mgN mgD^{-1} d^{-1}]

The nutrient uptake rate depends on the need of nutrients by the vegetation, the maximum nutrient uptake rate of the vegetation and the availability of the nutrients in the sediment.
The maximum nitrogen uptake rate is descriped as a Monod-type function depending on temperature and corrected for the availability of the nutrients in the sediment.

$$aVNUptMaxPhra = cVNUptMaxPhra * uTmProdPhra * \frac{cNDPhraMax - rNDPhra}{cNDPhraMax - cNDPhraMin}$$

Maximum nitrogen uptake rate at a certain temperature [mgN mgD^{-1}d^{-1}]

The terms cNDPhraMin [gN gD^{-1}] and cNDPhraMax [gN gD^{-1}] mean the minimum and maximum amount of nitrogen the vegetation can hold respectively.

The affinity for nutrients by vegetation equals the rate at which the vegetation responds to changes in environmental circumstances. This parameter is of significance when the concentration of nutrients becomes very low. However, this never happens in the Netherlands. The affinity for nutrients by vegetation is kept constant for all values of the maximum uptake rate (Vmax.). This matches experimental data for alga (Riegman en Mur, 1984). The affinity for nutrients by vegetation is put in terms of half-saturation constant:

$$ahNUptPhra = \frac{aVNUptMaxPhra}{aAffNUptPhra}$$

Half-saturation constant N concentration in sediment [gN m^{-3}]

Exchange with the lake

Mixing between the water columns of the lake and the wetland is described by an exchange coefficient (representing both dispersive transport and transport due to water level changes) multiplied by the concentration difference. The maximum exchange coefficient *kExchMaxM* has default been set to 1.0 [d^{-1}], but should be adapted for a specific situation. *hfMarsh* has arbitrarily been set to 0.1 [-] to prevent unrealistically high exchange rates if the wetland zone is small.

*akExchM = kExchMaxM * hfMarsh / (hfMarsh + fMarsh) + vTranDepthW / sDepthWM*
marsh water exchange coefficient [m3.m-3 marsh_water.d-1]
*wDExchIMM = akExchM * (sDIMW - sDIMWM)*
IM exchange fluxes for marsh water (“M”) [g m-3 marsh_water d-1]:
(Note: positive flux = lake -> marsh, negative is opposite.)

The effect of the exchange on concentrations in the lake are calculated as follows:
*afVolMarsh = fMarsh * sDepthWM / sDepthW*
relative marsh volume [m3 marsh.m-3 lake]
*akExchL = akExchM * afVolMarsh*
lake water exchange coefficient [m3.m-3 lake_water.d-1]
*wDExchIM = akExchL * (sDIMW - sDIMWM)*
IM exchange fluxes for lake [g m-3 lake_water d-1]:
(Note: positive flux = lake -> marsh, negative is opposite.)

2. PCDitch

2.1. Model structure and components

The model components are listed in the next table. Please recall that state variables are denoted by s-, and that ‘D’ is the abbreviation for dry-weight.

In the following description, only the differences with PCLake are described.

The phytoplankton comprises in reality both planktonic, epiphytic and filamentous species, the latter often being dominant in biomass. For simplicity, they have been lumped into one group (which may be split if desired, however). The competition between the plant groups is mainly determined, in the model, by the factors light, temperature, N and P and - for algae and possibly duckweed – in- and outflow. For all groups, a logistic correction term based on a maximum

Description	Unit	As dry-weight (D)	As phosphorus (P)	As nitrogen (N)	As oxygen (O_2)
Water depth	[m]	sDepthW			
Abiotic comp. in water column					
Inorganic matter	[g m^{-3}]	sDIMW	–	–	–
Detritus (org. matter)	[g m^{-3}]	sDDetW	sPDetW	sNDetW	–
Inorg. nutrients	[g m^{-3}]	–	sPO_4W, sPAIMW	sNH_4W, sNO_3W	—
Oxygen	[g m^{-3}]	–	–	–	sO_2W
Abiotic comp. in sediment:					
Inorganic matter	[g m^{-2}]	sDIMS	–	–	–
Org. matter: humus	[g m^{-2}]	sDHumS	sPHumS	sNHumS	–
Org. matter: detritus	[g m^{-2}]	sDDetS	sPDetS	sNDetS	–
Inorg. nutrients	[g m^{-2}]	–	sPO_4S, sPAIMS	sNH_4S, sNO_3S	–
Algae:					
Algae	[g m^{-3}]	sDPhytW	sPPhytW	sNPhytW	–
Vegetation:					
Submerged, rooted	[g m^{-2}]	sDElod	sPElod	sNElod	–
Charophytes	[g m^{-2}]	sDChar	sPChar	sNChar	–
Submerged, non-rooted	[g m^{-2}]	sDCera	sPCera	sNCera	–
Duckweed	[g m^{-2}]	sDLemn	sPLemn	sNLemn	–
Nymphaeids	[g m^{-2}]	sDNymp	sPNymp	sNNymp	–
Helophytes	[g m^{-2}]	sDHelo	sPHelo	sNHelo	–

carrying capacity has been included, which represents all non-modelled factors, for instance space. Duckweed, algae and non-rooted submerged plants are confined to the water column for their nutrient uptake, while helophytes take nutrients from the sediment only and rooted submerged plants are able to use both pools. Duckweed hampers the growth of submerged plants by light interception at the water surface. Most processes are described analogously to the *PCLake* model. The water depth (usually much lower than in lakes) can be made variable. Resuspension can ususally be neglected. Reaeration (exchange of oxygen with the atmosphere) is assumed to be hampered by duckweed (Marshall, 1981; Portielje & Lijklema, 1995). Default, yearly vegetation management in autumn is defined, as occurs in practice. For long-term management, a sediment dredging frequency can be set.

2.2. Abiotic and microbial processes

Sedimentation and resuspension

Resuspension has default been set to zero, and settling is not affected by a wind function like in lakes. This is done by setting the fetch to zero or a very low value.

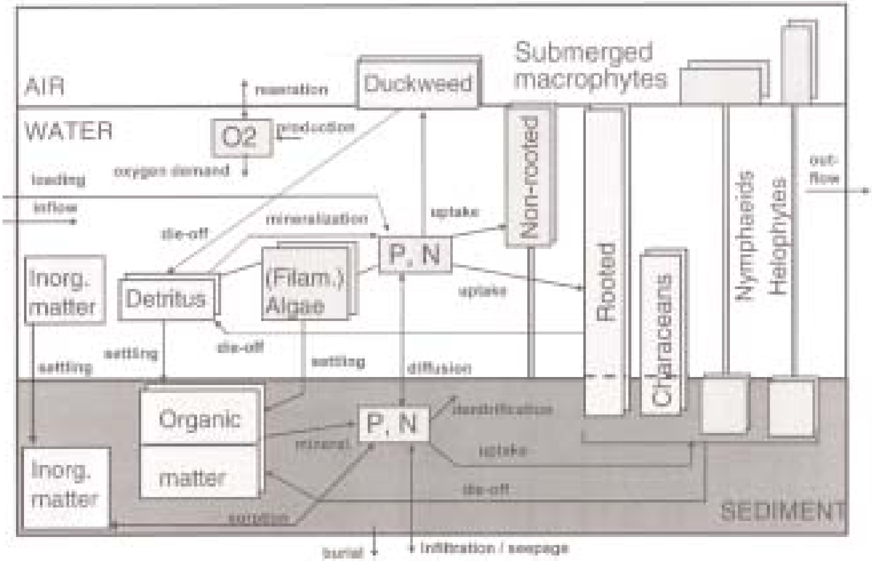

Fig. 8. PCDitch model structure.

Direct sediment N loading by artificial fertilizer

It sometimes happened that ditches received a direct loading of artificial fertilizer, due to spill or drift during the application of fertilizer on the adjacent fields. Although measures have now been taken to avoid this, the option to include it has remained in the model, to allow for historical or scenario runs:

*tNH4LoadS = fNH4LoadS * cNLoadS* NH4 load to sediment from artificial fertilizer
tNO3LoadS = cNloadS - tNH4LoadS NO3 load to sediment from artificial fertilizer

Dredging

Optionally, it is possible to include periodical dredging of the ditch every x years (given by the parameter *cDredInterval* [y]). A part of the sediment, including the water plants, is then removed, to re-establish a user-defined water depth (*cDepthRef)*. A dredging efficiency *fEffDred*, default 0.95 [-], can be set. The material removed is replaced by ‘clean’ soil material.

```
IF (Time .GE. cDredStart * DaysPerYear) THEN
    bTimeDred = (INT(TimeYears/cDredInterval) * cDredInterval) * DaysPerYear
        dredging time (every nth year) [d]
ELSE
    bTimeDred = -9999.999
ENDIF

IF (Time .EQ. bTimeDred) THEN
    update dredged layer
```

```
    aDepthStart = sDepthW
ELSE
aDepthStart = aDepthStart
ENDIF

IF( (Time .GE. bTimeDred) .AND. (Time .LT. bTimeDred + cLengDred) .AND.
    (aDepthStart .LE. cDepthRef - cDepthS) ) THEN
        dredging occurs between 0 and cLengDred days after each dredging time,
            provided that depth < reference depth minus sediment depth.

akDredDepth = (LOG(cDepthRef / aDepthStart)) / cLengDred
    rate constant of deepening [d-1]
    akDred = (- LOG(1.0 - fEffDred)) / cLengDred
        rate constant of dredging (exponential function) [d-1]
    akDredBent = (- LOG(1.0 - fEffDredBent)) / cLengDred
        rate constant of dredging for zoobenthos [d-1]
    akDredLemn = (- LOG(1.0 - fEffDredLemn)) / cLengDred
        rate constant of dredging for duckweed [d-1]
ELSE
    akDredDepth = 0.0
    akDred = 0.0
      akDredBent = 0.0
akDredLemn = 0.0
ENDIF
```

Rates:
*vDredDepthW = akDredDepth * sDepthW* [m/d]
*tDDredDetS = akDred * sDDetS* [gD/m2/d]
and analogous for the other components.

2.3. Algae

The algae are modelled as one lumped group, abbreviated as ‘Phyt’. In stead of grazing, a first-order, temperature dependent loss factor, called ‘Loss’, is included; the loss constant is set to zero or a low value, however, as filamentous algae that are often dominant in ditches are not heavily grazed. Settling rate is assumed not to be reduced by wind fetch influence.

2.4. Water plants

The water plants were divided into six functional groups, besides one functional group of algae.

The definition of the plant groups is primarily based on the layer(s) in which they grow and the layer(s) from which they take up nutrients. The classification into 16 growth forms given by Den Hartog & Segal (1964) and Den Hartog & Van der Velde (1988) has been used as a template. Several groups were lumped, while others were left out because they are not common in ditches. Duckweed and submerged plants were of course included; the latter were split into rooted and a non-rooted group, with charophytes (also rooted) as macro-algae as a special group. Helophytes (emergent plants) and floating-leaved plants are included because of their role in the nutrient household and light interception. (In practice, the natural succession to helophytes is impeded by regular ditch management.) The groups are defined by the relative size of emergent, floating, submerged and root fractions, and their vertical distribution. The number and the definition of the plant groups has been made flexible. The default configuration and their characteristics are:

1. Submerged plants, divided into:
   a. Rooted submerged angiosperms (abbreviated as '*Elod*'). This group comprises the elodeid and potamid growth forms. Assumed to fill the entire water column, nutrient uptake from both water and sediment. Root fraction set to 0.1 in summer, 0.6 in winter.
   b. Charophytes ('*Char*'). Confined to the lower half of the water column. Root fraction set to 0.05 in summer, 0.1 in winter. They were distinguished because of their special character as macro-algae.
   c. Non-rooted submerged angiosperms ('*Cera*'). Canopy-formers, confined to the upper half of the water column. Nutrient uptake from the water only.
2. Non-rooted, floating plants: duckweed ('*Lemn*'). This group includes floating fern (*Azolla*) as well. Nutrient uptake from the water only.
3. Rooted plants with floating or emergent leaves
   a. Floating-leaved plants: Nymphaeids ('*Nymp*'). Nutrient uptake from the sediment, root fraction set to 0.75 in summer, 0.95 in winter.
   b. Emergent plants: helophytes ('*Helo*'). Nutrient uptake from the sediment, root fraction set to 0.5 in summer, 0.8 in winter.

The total vegetation is denoted by -*Veg*-.
Each group is defined by the fractions of the biomass that are present in the sediment (the

Parameter	Elod	Char	Cera	Lemn	Nymp	Helo
fRoot summer	0.1	0.05	0	0	0.75	0.5
fRoot winter	0.6	0.1	0	0	0.95	0.8
Proportion of shoots:						
emergent	0	0	0	0	0	1
floating	0	0	0	1	1	0
submerged	1	1	1	0	0	0
Distribution of submerged	water column	lower half	upper half	n.appl.	n.appl.	n.appl.

roots), in the water column (submerged part), on the water surface (the floating part), and above the water (the emergent part). Their sum is, of course, always 1.0. Optionally, the submerged fraction (if existing) can be assumed homogeneously distributed over the water column, or restricted to only a part of it. For the current model with six plant groups, these parameters are summarized in the next table.

Migration

The only plant group that really migrates is that of the duckweeds (“Lemn”). Because these plants are freely floating on the water surface, thay can be moved into or out of the ditch by the water flow. The migration of duckweeds is also affected by wind. On the other hand, obstructions like small dams hamper the migration. The local situation may thus result in a complicated pattern of migration of duckweeds, which can only be simulated using a network approach. In the current zero-dimensional model, the process is approximated by an outward migration rate, coupled to the outflow rate of dissolved and suspended substances, *ukOutfl* [d^{-1}], but corrected for an ‘obstruction factor’ *fObstrLemn* [-]:

$kMigrLemn = (1 - fObstrLemn) * ukOutfl$ migration rate of duckweeds [d^{-1}]

Vegetation management

Optionally, management (mowing) of the vegetation can be defined once or twice a year, with a defined efficiency. Default, the vegetation is assumed to be managed once a year in early autumn, with an efficiency of 40 % for duckweed and 80 % for the other plants.

3. Parameter listing

The next table lists all the default model parameters with their units for *PCLake* (v. 5.08) and *PCDitch* (v. 1.24). A distinction is made in process parameters, input factors and initial values. The last two categories are case-specific.

Please note that the parameters of ‘Veg’ apply to PCLake, those for the plant groups to PCDitch. Likewise, the parameters for ‘Phyt’ apply to PCDitch, those for ‘Diat’, ‘Gren’ and ‘Blue’ to PCLake, like those for the animal groups and the wetland zone (‘Phra’).

Configuration settings

BeginTime [0.0] day ;begintime
InitCalc [1.0] ; If T, skip calculation of initial values; used in case of REINIT command.
ConstDepth [1.0] ; If T, water depth kept constant by “daily dredging”.
Lake [1.0] ;
Ditch [0.0] ;
InclTran [1.0] ;
InclPrim [1.0] ;
InclThreeAlg [1.0] ;
InclPhytS [1.0] ;
InclBed [1.0] ;
InclSixVeg [0.0] ;
InclWeb [1.0] ;
InclMarsh [1.0] ;
DUFLOW [0.0] ; Set F in ACSL version, T in DUFLOW version.
Marsh [0.0] ; Used in DUFLOW version only: if T, section is marsh section.
UseWindFunc [0.0] ; FALSE = no wind function for shear stress,
ReadTemp [0.0] ; If TRUE use measured time-series of temperature, otherwise sinus
ReadLOut [0.0] ; If TRUE use measured time-series of light, otherwise sinus
ReadVWind [0.0] ; If TRUE use measured time-series of wind, otherwise constant
RewindInput [0.0] ; Only important if time-series are being used.
YearZero [0.0] ; Note: also Dayno 1 = 1. Jan. of this year.

Optional input tables

mTemp [0.0] ;
mLOut [0.0] ;
mVWind [0.0] ;
mQIn [0.0] ;
mQOut [0.0] ;
mQEv [0.0] ;
mPLoad [0.0] ;
mPLoadPO4 [0.0] ;
mPLoadOrg [0.0] ;
mPLoadPhytTot [0.0] ;
mNLoad [0.0] ;
mNLoadNH4 [0.0] ;
mNLoadNO3 [0.0] ;
mNLoadOrg [0.0] ;
mDLoadDet [0.0] ;
mDLoadIM [0.0] ;

Input factors

cFetch [1000.0] m ; wind fetch
fMarsh [0.0] m2 marsh m-2 lake ; relative marsh area
fLutum [0.1] - ; lutum content of inorg. matter
fFeDIM [0.01] gFe/gD ; Fe content of inorg. matter
fAlDIM [0.01] gAl/gD ; Al content of inorg. matter
cTmAve [12.0] oC ; average water temperature
cTmVar [10.0] oC ; annual temperature variation
cTimeLag [40.0] day ; time lag for temperature

cVWind [5.0] m/s ; average wind speed
cQInf [0.0] mm/day ; infiltration rate
cPBackLoad [0.0] ; background P loading (0.00016)
cNBackLoad [0.0] ; background N loading (0.009)
cLDayAve [10000000.0] J/m2/day ; annual average radiation
cLDayVar [8000000.0] J/m2/day ; annual variation in radiation
cfDayAve [0.5] - ; average day length
cfDayVar [0.2] - ; annual variation in day length
fRefl [0.2] ; 0.1
cExtWat [0.5] m-1 ; background extinction
cDredInterval [9999000.0] y ; dredging interval
cDredStart [9999000.0] y ; first dredging year (should be n times cDredInterval)
cDepthRef [0.0] m ; reference water depth for dredging
cLengDred [10.0] day ; length of dredging period
fEffDred [0.95] - ; dredging efficiency (<1.0)
fEffDredBent [0.5] - ; dredging efficiency for zoobenthos (<1.0)
fEffDredLemn [0.5] - ; dredging efficiency for duckweed (<1.0)

ReadQIn [0.0] ; If TRUE, use measured time-series of inflow, otherwise constant
ReadQOut [0.0] ; If TRUE, use measured time-series of inflow, otherwise constant
ReadQEv [0.0] ; If TRUE, use measured time-series of inflow, otherwise constant
ReadPLoad [0.0] ; If TRUE, use measured time-series of P loading, otherwise constant
ReadNLoad [0.0] ; If TRUE, use measured time-series of N loading, otherwise constant
ReadNutFrac [0.0] ; If TRUE, use measured time-series of loading with diff. nutrient fractions,
ReadPLoadPhyt [0.0] ; If TRUE, use measured time-series of DDet loading, otherwise constant
ReadDLoadDet [0.0] ; If TRUE, use measured time-series of DDet loading, otherwise constant
ReadDLoadIM [0.0] ; If TRUE, use measured time-series of DIM loading, otherwise constant
UseSeasonLoad [0.0] ; If TRUE, use different inflow and loading for summer and winter periods.
UsePulseLoad [0.0] ; If TRUE, use a pulse-wise nutrient loading.
cQIn [20.0] mm/day ; standard water inflow if not measured
cQInSum [20.0] mm/day ; summer water inflow if not measured
cQInWin [20.0] mm/day ; winter water inflow if not measured
cQInExtraApril1 [0.0] mm/day ; extra inflow at start of summer
cQInExtraOct1 [0.0] mm/day ; extra inflow at start of winter
cQOutExtraApril1 [0.0] mm/day ; extra outflow at start of summer
cQOutExtraOct1 [0.0] mm/day ; extra outflow at start of winter
cQEvAve [1.5] mm/day ; standard average evaporation
cQEvVar [1.3] mm/day ; standard variation in evaporation
cPLoad [0.005] gP/m2/day ; standard P loading if not measured
cPLoadSum [0.005] gP/m2/day ; summer P loading if not measured
cPLoadWin [0.005] gP/m2/day ; winter P loading if not measured
fPO4In [0.5] - ; fraction PO4 in input (if PO4 input not measured)

fPhytInWin [0.02] - ; minimum algal fraction in organic P input
fPhytInSum [0.1] - ; maximum algal fraction in organic P input
fDiatPhytIn [0.33] - ; diatoms fraction of algal input
fGrenPhytIn [0.34] - ; greens fraction of algal input
fBluePhytIn [0.33] - ; blue-greens fraction of algal input
cNLoad [0.05] gN/m2/day ; standard N loading
cNLoadSum [0.05] gN/m2/day ; summer N loading
cNLoadWin [0.05] gN/m2/day ; winter N loading
cNPLoadMeas [7.0] gN/gP ; N/P loading if P is measured and N not
cNPPhytIn [7.0] gP/gD ; N/P ratio of algal input
cNPDetIn [7.0] gP/gD ; N/P ratio of detrital input
fNH4DissIn [0.5] - ; NH4 fraction of dissolved N load (if NH4 not measured)
cNDPhytIn [0.07] gN/gD ; N/day ratio of algal input
cNDDetIn [0.07] gN/gD ; N/P ratio of detrital input
cDIMIn [5.0] mgD/l ; IM conc. in inflow
cO2In [10.0] mgO2/l ; O2 conc. in inflow
cSiO2In [3.0] mgSi/l ; SiO2 conc. in inflow
cSiDDetIn [0.05] gSi/gD ;
cDZooIn [0.1] mgD/l ; zoopl. conc. in inflowing water
cDayApril1 [91.0] day ; April 1
cDayOct1 [273.0] day ; October 1
cLengChange [10.0] day ; length of season change
PulseWidth [1.0] day ;
cNLoadS [0.0] gN/m2/day ; N fertilizer to sediment
fNH4LoadS [0.5] - ; NH4 fraction of N fertilizer to sediment
cDErosTot [0.1] g/m2/day ; Erosion input (tentative)
fSedErosIM [0.95] - ; instantly sedimentating fraction of IM
fDOrgSoil [0.1] - ; fraction soil organic matter
cPDSoilOM [0.001] gP/gD ; P/D ratio of soil organic matter
cNDSoilOM [0.01] gN/gD ; N/D ratio of soil organic matter
cPO4Ground [0.1] mgP/l ; PO4 cone in groundwater
cNH4Ground [1.0] mgN/l ; NH4 cone in groundwater
cNO3Ground [0.1] mgN/l ; NO3 cone in groundwater

(vegetation:)
fObstrLemn [1.0] - ; obstructed fraction of duckweed outflow
cDayManVeg1 [-9999000.0] day ; first mowing day (default: non-existent)
cDayManVeg2 [-9999000.0] day ; second mowing day (Note: 259 = 16 Sep)
fManVeg [0.0] - ; Fraction removed by management , for submerged plants
fManLemn [0.0] - ; Fraction of duckweed removed by management
fManHelo [0.0] - ; Fraction of helophytes and nymphaeids removed by management
cLengMan [10.0] day ; length of mowing period

cYearStartBirds [0.0] y ; first year of birds' presence

cDayStartBirds [46.0] day ; yearly first day of birds' presence

cDayEndBirds [288.0] day ; yearly last day of birds' presence

cBirdsPerha [0.0] n/ha ; number of birds per ha vegetated lake (Default = 0)

(food web:)

cDBentIn [0.01] gD/m2 ; external zoobenthos density

kMigrBent [0.001] day-1 ; zoobenthos migration rate

kMigrFish [0.001] day-1 ; fish migration rate

cDFiJvIn [0.005] gD/m2 ; external fish density

cDFiAdIn [0.005] gD/m2 ; external fish density

kHarvFishWin [0.0] ; fish harvesting fraction in winter

kHarvFishSum [0.0] ; fish harvesting fraction in summer

cDPiscIn [0.001] gD/m2 ; external Pisc density

kMigrPisc [0.001] day-1 ; Pisc migration rate

kHarvPiscWin [0.0] ; Pisc harvesting fraction in winter

kHarvPiscSum [0.0] ; Pisc harvesting fraction in summer

(wetland:)

kExchMaxM [1.0] m3.m-3 marsh_water.day-1 ; maximum dispersive marsh water exchange coefficient

hfMarsh [0.1] - ; rel. marsh area where exchange is 50%

cDayManPhra [255.0] day ; time of management

fManPhra [0.0] - ; fraction biomass loss by management

kDManShootPhra [1.0] 1/day ; rate of management

Initial values

sDIMW0 [5.0] mgDW/l ; water IM

sDDetW0 [2.0] mgDW/l ; water detritus

sO2W0 [10.0] mgO2/l ; oxygen in water

sPO4W0 [0.01] mgP/l ;

sPAIMW0 [0.0] mgP/l ; adsorbed on IM in water

sNO3W0 [0.1] mgN/l ; NO3 in water

sNH4W0 [0.1] mgN/l ; NH4 in water

sNH4S0 [0.02] gN/m2 ; dissolved N-NH4 in interstitial water

sNO3S0 [0.002] gN/m2 ; dissolved N-NO3 in interstitial water

sSiO2W0 [3.0] mgSi/l ; dissolved silica in water

sDPhytW0 [1.0] mgDW/l ; phytoplankton

sDDiatW0 [0.5] mgDW/l ; Diatoms in water

sDGrenW0 [0.5] mgDW/l ; Green algae in water

sDBlueW0 [3.0] mgDW/l ; Blue-greens in water

sDPhytS0 [0.001] gDW/m2 ; sediment algae

sDDiatS0 [0.001] gDW/m2 ; Sediment diatoms

sDGrenS0 [0.001] gDW/m2 ; Sediment greens

sDBlueS0 [0.001] gDW/m2 ; Sediment blue-greens
sDVeg0 [1.0] gDW/m2 ; Vegetation
sDElod0 [1.0] gD/m2 ;
sDChar0 [1.0] gD/m2 ;
sDCera0 [1.0] gD/m2 ;
sDLemn0 [1.0] gD/m2 ;
sDNymp0 [1.0] gD/m2 ;
sDHelo0 [1.0] gD/m2 ;
sDZoo0 [0.05] mgDW/l ; Zooplankton
sDFiJv0 [0.5] gDW/m2 ; Juvenile whitefish
sDFiAd0 [2.0] gDW/m2 ; Adult whitefish
sDPisc0 [0.01] gDW/m2 ; Predatory fish
sDBent0 [1.0] gDW/m2 ; Zoobenthos
fDTotS0 [0.3] g solid g-1 sediment ; initial dry-weight fraction in sediment
fDOrgS0 [0.1] g/g ; initial organic fraction of sediment DW
fDDetS0 [0.05] g/g ; initial detritus fraction of sediment organic matter
fPInorgS0 [0.0005] gP/gD ; initial inorg. P fraction in sed.
fPAdsS0 [0.99] - ; initial adsorbed fraction of inorg. P in sed.
cPDDet0 [0.0025] gP/gDDet ; initial P fraction in detritus
cNDDet0 [0.025] gN/gDDet ; initial N fraction in detritus
cSiDDet0 [0.01] gSi/gDDet ; initial Si fraction in detritus
cPDHum0 [0.005] gP/gDDet ; initial P fraction in humus
cNDHum0 [0.05] gN/gDDet ; initial N fraction in humus
cPDPhyt0 [0.01] gP/gD ; initial P fraction in algae
cNDPhyt0 [0.1] gN/gD ; initial N fraction in algae
cPDDiat0 [0.01] gP/gD ; initial P fraction in diatoms
cNDDiat0 [0.1] gN/gD ; initial N fraction in diatoms
cPDGren0 [0.01] gP/gD ; initial P fraction in green algae
cNDGren0 [0.1] gN/gD ; initial N fraction in green algae
cPDBlue0 [0.01] gP/gD ; initial P fraction in blue-green algae
cNDBlue0 [0.1] gN/gD ; initial N fraction in blue-green algae
cPDVeg0 [0.002] gP/gD ; initial P fraction in veg.
cNDVeg0 [0.02] gN/gD ; initial N fraction in veg.
cPDElod0 [0.002] gP/gD ; initial P fraction in Elod.
cNDElod0 [0.02] gN/gD ; initial N fraction in Elod.
cPDChar0 [0.002] gP/gD ; initial P fraction in Char.
cNDChar0 [0.02] gN/gD ; initial N fraction in Char.
cPDCera0 [0.002] gP/gD ; initial P fraction in Cera.
cNDCera0 [0.02] gN/gD ; initial N fraction in Cera.
cPDLemn0 [0.005] gP/gD ; initial P fraction in Lemn.
cNDLemn0 [0.05] gN/gD ; initial N fraction in Lemn.
cPDNymp0 [0.002] gP/gD ; initial P fraction in Nymp.

cNDNymp0 [0.02] gN/gD ; initial N fraction in Nymp.
cPDHelo0 [0.002] gP/gD ; initial P fraction in Helo.
cNDHelo0 [0.02] gN/gD ; initial N fraction in Helo.
(wetland)
fDTotSM0 [0.3] g solid g-1 sediment ; initial dry-weight fraction in sediment
fDOrgSM0 [0.1] g AFDW g-1 solid ; initial organic fraction of sed.
fDDetSM0 [0.05] g/g ; initial detritus fraction of sediment organic matter
fPInorgSM0 [0.0005] gP/gD ; initial inorg. P fraction in sed.
sDepthWM0 [0.5] m ; marsh water depth
sNO3SM0 [0.01] gN/m2 ; NO3 in sediment
sNH4SM0 [1.0] gN/m2 ; NH4 in sediment
sDShootPhra0 [1000.0] gD/m2 ; shoot biomass
sDRootPhra0 [5000.0] gD/m2 ; root biomass
cPDPhra0 [0.002] gP/gD ; initial P/day ratio of reed
cNDPhra0 [0.02] gN/gD ; initial N/day ratio of reed

Parameters
fPAR [0.48] - ; fraction photosynthetically active radiation (PAR)
cExtSpDet [0.15] m2/gDW ; specific extinction detritus
cExtSpIM [0.05] m2/gDW ; specific extinction inert matter

cSiDDiat [0.15] mgSi/mgDW ; Si/D ratio of diatoms
cPDZooRef [0.01] mgP/mgDW ; reference P/D-ratio herb. zooplankton
cNDZooRef [0.07] mgN/mgDW ; reference N/D-ratio herb. zooplankton
cPDBentRef [0.01] mgP/mgDW ; reference P/D ratio of zoobenthos
cNDBentRef [0.07] mgN/mgDW ; reference N/D ratio of zoobenthos
cPDFishRef [0.022] mgP/mgDW ; reference P/D ratio of Fish
cNDFishRef [0.1] mgN/mgDW ; reference N/D ratio of Fish
cPDPisc [0.022] mgP/mgDW ; reference P/D ratio of Pisc
cNDPisc [0.1] mgN/mgDW ; reference N/D ratio of Pisc

cDepthS [0.1] m ; sediment depth
cCPerDW [0.4] gC/gDW ; C content of organic matter
cRhoIM [2500000.0] g/m3 solid ; density of sediment IM
cRhoOM [1400000.0] g/m3 ; density of sediment detritus
cTmRef [20.0] oC ; reference temperature
cAerRoot [0.727] ; coefficient for VWind^0.5
cAerLin [-0.371] s/day ; coefficient for VWind (is negative.)
cAerSquare [0.0376] ; coefficient for VWind^2
cThetaAer [1.024] 1/e^oC ; Temperature coeff. for reaeration
kLemnAer [0.01] m2/gD ;
cVSetIM [1.0] m/day ; max. sedimentation velocity of inert org. matter

cVSetDet [0.25] m/day ; max. sedimentation velocity of detritus
cThetaSet [1.01] 1/e^oC ; temp. parameter of sedimentation
cSuspMin [6.1] ;
cSuspMax [25.2] ;
cSuspSlope [2.1] ;
hDepthSusp [2.0] ;
cFetchRef [1000.0] ;
fLutumRef [0.2] ;
cSuspRef [0.5] ;
kVegResus [0.01] m2/gDW ; rel. resuspension reduction per g vegetation
kTurbFish [1.0] g/g fish/day ; relative resuspension by adult fish browsing
kResusPhytMax [0.25] d-1 ; max. phytopl. resuspension
cResusPhytExp [-0.379] {gD/m2/day)-1 ; exp. par. for phytopl. resuspension
cThetaMinW [1.07] - ; expon. temp. constant of mineralization in water
kDMinDetW [0.01] day-1 ; decomposition constant of detritus
hO2BOD [1.0] mgO2/l ; half-sat. oxygen conc. for BOD
O2PerNO3 [1.5] - ; mol O2 formed per mol NO3- ammonified
cThetaMinS [1.07] - ; expon. temp. constant of sediment mineralization
kDMinDetS [0.002] day-1 ; decomposition constant of sediment detritus
fRefrDetS [0.15] - ; refractory fraction of sed. detritus
hNO3Denit [2.0] mgN/l ; quadratic half-sat. NO3 conc. for denitrification
NO3PerC [0.8] - ; mol NO3 denitrified per mol C mineralised
kDMinHum [0.00001] day-1 ; maximum decomposition constant of humus material
kNitrW [0.1] day-1 ; nitrification rate constant in water
kNitrS [1.0] day-1 ; nitrification rate constant in sediment
cThetaNitr [1.08] ;
O2PerNH4 [2.0] - ; mol O2 used per mol NH4+ nitrified
hO2Nitr [2.0] mgO2/l ;
kPDifPO4 [0.000072] m2/day ; mol. PO4 diffusion constant
kNDifNO3 [0.000086] m2/day ; mol. NO3 diffusion constant
kNDifNH4 [0.000112] m2/day ; mol. NH4 diffusion constant
kO2Dif [0.000026] m2/day ; mol. O2 diffusion constant
cThetaDif [1.02] ; Temperature coefficient for diffusion
fDepthDifS [0.5] - ; nutrient diffusion distance as fraction of sediment depth
cTurbDifNut [5.0] - ; bioturbation factor for diffusion
cTurbDifO2 [5.0] - ; bioturbation factor for diffusion
kPSorp [0.05] day-1 ; P sorption rate constant not too high -> model speed
cRelPAdsD [0.00003] gP/gD ; max. P adsorption per g DW
cRelPAdsFe [0.065] gP/gFe ; max. P adsorption per g Fe
cRelPAdsAl [0.134] gP/gAl ; max. P adsorption per g Al
cKPAdsOx [0.6] m3/gP ; P adsorption affinity at oxidized conditions
fRedMax [0.9] - ; max. reduction factor of P adsorption affinity

coPO4Max [2.0] mgP/l ; max. SRP conc. in pore water
kPChemPO4 [0.03] day-1 ; chem. PO4 loss rate
cPACoefMin [1.5] - ; minimum Poole-Atkins coefficient
cPACoefMax [2.5] ;
hPACoef [3.0] g/m2 ; decrease constant for P.A. coeff. with DOMW
cSecchiPlus [0.0] m ; maximum Secchi depth above water depth
cEuph [1.7] - ; conversion constant Secchi depth -> euphotic depth

(algae:)
cCovSpPhyt [2.0] % per gD/m2 ; specific coverage
cTmOptLoss [25.0] oC ; optimum temp. for grazing
cSigTmLoss [13.0] oC ; temperature constant of grazing (sigma in Gaussian curve)
fDissMortPhyt [0.2] - ; soluble nutrient fraction of died Algae
fDissLoss [0.25] - ; dissolved nutrient fraction of grazing loss
cMuMaxPhyt [1.9] day-1 ; maximum growth rate algae
cTmOptPhyt [25.0] oC ; optimum temp. of algae
cSigTmPhyt [15.0] oC ; temperature constant greens (sigma in Gaussian curve)
cExtSpPhyt [0.25] m2/gDW ; specific extinction algae
UseSteelePhyt [0.0] ; ‘Flag’: 1 = use Steele function, 0 = use Lehman function
hLRefPhyt [10.2] W/m2 ; half-sat. PAR for algae at 20 oC (Lehmann function)
cLOptRefPhyt [1000.0] W/m2 ; optimum PAR at 20 oC (Steele function) Fake value
cChDPhytMin [0.01] mgChl/mgDW ; min. chlorophyll/C ratio algae
cChDPhytMax [0.02] mgChl/mgDW ; max. chlorophyll/C ratio algae
kDRespPhyt [0.1] day-1 ; maintenance respiration constant greens
kLossPhyt [0.0] - ; grazing loss rate for algae
kMortPhytW [0.01] day-1 ; mortality constant of algae in water
cVSetPhyt [0.1] m/day ; sedimentation velocity algae
kMortPhytS [0.05] day-1 ; mortality constant algae
cVPUptMaxPhyt [0.01] mgP/mgDW/day ; maximum P uptake capacity of algae
cAffPUptPhyt [0.2] l/mgDW/day ; initial P uptake affinity algae
cPDPhytMin [0.002] mgP/mgDW ; minimum P/day ratio algae
cPDPhytMax [0.015] mgP/mgDW ; max. P/day ratio algae
cVNUptMaxPhyt [0.07] mgN/mgDW/day ; maximum N uptake capacity of algae
cAffNUptPhyt [0.2] l/mgDW/day ; initial N uptake affinity algae
cNDPhytMin [0.02] mgN/mgDW ; minimum N/day ratio algae
cNDPhytMax [0.1] mgN/mgDW ; max. N/day ratio algae
hSiAssPhyt [0.0] mgSi/l ; half-sat. Si conc. for growth of algae = 0
cMuMaxDiat [2.0] day-1 ; maximum growth rate Diatoms
cTmOptDiat [18.0] oC ; optimum temp. diatoms
cSigTmDiat [20.0] oC ; temperature constant diatoms (sigma in Gaussian curve)
cExtSpDiat [0.25] m2/gDW ; specific extinction Diatoms
UseSteeleDiat [1.0] ; ‘Flag’: 1 = use Steele function, 0 = use Lehman function

cLOptRefDiat [54.0] W/m2 ; optimum PAR for Diatoms at 20 oC (Steele function)
hLRefDiat [1000.0] W/m2 ; half-sat. PAR at 20 oC (Lehmann function) Fake value
cChDDiatMin [0.004] mgChl/mgDW ; min. chlorophyll/C ratio Diatoms
cChDDiatMax [0.012] mgChl/mgDW ; max. chlorophyll/C ratio Diatoms
kDRespDiat [0.10] day-1 ; maintenance respiration constant diatoms (= 0.05 * MuMax)
kLossDiat [0.25] - ; grazing loss rate for Diatoms
kMortDiatW [0.01] day-1 ; mortality constant of Diatoms in water
kMortDiatS [0.05] day-1 ; mortality constant of sed. Diatoms
cVSetDiat [0.5] m/day ; sedimentation velocity Diatoms
cVPUptMaxDiat [0.01] mgP/mgDW/day ; maximum P uptake capacity of Diatoms
cAffPUptDiat [0.2] l/mgDW/day ; initial P uptake affinity Diatoms
cPDDiatMin [0.0005] mgP/mgDW ; minimum P/day ratio Diatoms
cPDDiatMax [0.005] mgP/mgDW ; max. P/day ratio Diatoms
cVNUptMaxDiat [0.07] mgN/mgDW/day ; maximum N uptake capacity of Diatoms
cAffNUptDiat [0.2] l/mgDW/day ; initial N uptake affinity Diatoms
cNDDiatMin [0.01] mgN/mgDW ; minimum N/day ratio Diatoms
cNDDiatMax [0.05] mgN/mgDW ; max. N/day ratio Diatoms
hSiAssDiat [0.09] mgSi/l ; half-sat. Si for diatoms
cMuMaxGren [1.5] day-1 ; maximum growth rate greens
cTmOptGren [25.0] oC ; optimum temp. of greens
cSigTmGren [15.0] oC ; temperature constant greens (sigma in Gaussian curve)
cExtSpGren [0.25] m2/gDW ; specific extinction greens
UseSteeleGren [0.0] ; ‘Flag’: 1 = use Steele function, 0 = use Lehman function
hLRefGren [17.0] W/m2 ; half-sat. PAR for green algae at 20 oC (Lehmann function)
cLOptRefGren [1000.0] W/m2 ; optimum PAR at 20 oC (Steele function) Fake value
cChDGrenMin [0.01] mgChl/mgDW ; min. chlorophyll/C ratio greens
cChDGrenMax [0.02] mgChl/mgDW ; max. chlorophyll/C ratio greens
kDRespGren [0.075] day-1 ; maintenance respiration constant greens (= 0.05 * MuMax)
kLossGren [0.25] - ; grazing loss rate for greens
kMortGrenW [0.01] day-1 ; mortality constant of Diatoms in water
kMortGrenS [0.05] day-1 ; mortality constant greens
cVSetGren [0.2] m/day ; sedimentation velocity of greens
cVPUptMaxGren [0.01] mgP/mgDW/day ; maximum P uptake capacity of greens
cAffPUptGren [0.2] l/mgDW/day ; initial P uptake affinity greens
cPDGrenMin [0.0015] mgP/mgDW ; minimum P/day ratio greens
cPDGrenMax [0.015] mgP/mgDW ; max. P/day ratio greens
cVNUptMaxGren [0.07] mgN/mgDW/day ; maximum N uptake capacity of greens
cAffNUptGren [0.2] l/mgDW/day ; initial N uptake affinity greens
cNDGrenMin [0.02] mgN/mgDW ; minimum N/day ratio greens
cNDGrenMax [0.1] mgN/mgDW ; max. N/day ratio greens
hSiAssGren [0.0] mgSi/l ; half-sat. Si conc. for growth of green algae = 0
cMuMaxBlue [0.6] day-1 ; maximum growth rate Bluegreens

cTmOptBlue [25.0] oC ; optimum temp. blue-greens
cSigTmBlue [12.0] oC ; temperature constant blue-greens (sigma in Gaussian curve)
cExtSpBlue [0.35] m2/gDW ; specific extinction Bluegreens
UseSteeleBlue [1.0] ; 'Flag': 1 = use Steele function, 0 = use Lehman function
cLOptRefBlue [13.6] W/m2 ; optimum PAR for blue-greens at 20 oC (Steele function)
hLRefBlue [1000.0] W/m2 ; half-sat. PAR at 20 oC (Lehmann function) Fake value
cChDBlueMin [0.005] mgChl/mgDW ; min. chlorophyll/C ratio Bluegreens
cChDBlueMax [0.015] mgChl/mgDW ; max. chlorophyll/C ratio Bluegreens
cCyDBlueMin [0.004] mgChl/mgDW ; min. c-phycocyanin/C ratio Bluegreens
cCyDBlueMax [0.06] mgChl/mgDW ; max. c-phycocyanin/C ratio Bluegreens
kDRespBlue [0.03] day-1 ; maintenance respiration constant blue-greens (= 0.05 * MuMax)
kLossBlue [0.03] - ; grazing loss rate for Blue-greens
kMortBlueW [0.01] day-1 ; mortality constant of blue-greens in water
kMortBlueS [0.2] day-1 ; mortality constant Bluegreens
cVSetBlue [0.06] m/day ; sedimentation velocity Blue-greens
cVPUptMaxBlue [0.04] mgP/mgDW/day ; maximum P uptake capacity of Bluegreens
cAffPUptBlue [0.8] l/mgDW/day ; initial P uptake affinity Bluegreens
cPDBlueMin [0.0025] mgP/mgDW ; minimum P/day ratio Bluegreens
cPDBlueMax [0.025] mgP/mgDW ; max. P/day ratio blue-greens
cVNUptMaxBlue [0.07] mgN/mgDW/day ; maximum N uptake capacity of Bluegreens
cAffNUptBlue [0.2] l/mgDW/day ; initial N uptake affinity Bluegreens
cNDBlueMin [0.03] mgN/mgDW ; minimum N/day ratio Bluegreens
cNDBlueMax [0.15] ; 0.12
hSiAssBlue [0.0] mgSi/l ; half-sat. Si conc. for growth of blue-greens = 0

(veg.)
cDGrazPerBird [45.0] gD/coot/day ; daily grazing of birds
hDVegBird [5.0] ; half-sat. vegetation biomass
fDAssBird [0.5] - ; birds assim. efficiency
fDissEgesBird [0.25] - ; fraction dissolved nutrient of coot egestion
fDissMortVeg [0.25] - ; fraction dissolved nutrients from died plants
cLengAllo [15.0] day ; duration of allocation and reallocation phase
cLengMort [15.0] day ; duration of autumn mortality period
fRootVegSum [0.1] g root / g veg ; root fraction outside growing season
fRootVegWin [0.6] g root / g veg ; root fraction outside growing season
fFloatVeg [0.0] g floating / g shoot ; floating fraction of shoot
fEmergVeg [0.0] g floating / g shoot ; emergent fraction of shoot
fDepth1Veg [0.0] - ; max. upper depth of submerged veget. layer, as fraction of water depth
fDepth2Veg [1.0] - ; max. lower depth of submerged veget. layer, as fraction of water depth
cDLayerVeg [0.0] gD/m2 ; biomass of a single layer floating leaves
cCovSpVeg [0.5] % cover per gD/m2 ; specific cover
kMigrVeg [0.001] day-1 ; vegetation migration rate

cDVegIn [1.0] gD/m2 ; “external vegetation density”
cTmInitVeg [9.0] oC ; temperature for initial growth
cDCarrVeg [400.0] gDW/m2 ; max. vegetation standing crop
cMuMaxVeg [0.2] g/g shoot/day ; maximum growth rate of vegetation at 20oC
cQ10ProdVeg [1.2] - ; temperature quotient of production
hLRefVeg [17.0] W/m2 PAR ; half-sat. light at 20 oC
cExtSpVeg [0.01] m2/gDW ; specific extinction
kDRespVeg [0.02] day-1 ; dark respiration rate of vegetation
cQ10RespVeg [2.0] - ; temperature quotient of respiration
kMortVegSum [0.005] day-1 ; vegetation mortality rate in Spring and Summer (low)
fWinVeg [0.3] - ; fraction surviving in winter
cDayWinVeg [259.0] day ; end of growing season = 16 Sep
fDetWMortVeg [0.1] - ; fraction of shoot mortality becoming water detritus
cPrefVegBird [1.0] - ; edibility for birds
cVPUptMaxVeg [0.01] mgP/mgD/day ; maximum P uptake capacity of vegetation
cAffPUptVeg [0.2] l/mgD/day ; initial P uptake affinity vegetation
cPDVegMin [0.0008] mgP/mg ; minimum P/day ratio vegetation
cPDVegMax [0.0035] mgP/mgD ; maximum P/day ratio vegetation
cVNUptMaxVeg [0.1] mgN/mgD/day ; maximum N uptake capacity of vegetation
cAffNUptVeg [0.2] l/mgD/day ; initial N uptake affinity vegetation
cNDVegMin [0.01] mgN/mgD ; minimum N/day ratio vegetation
cNDVegMax [0.035] mgN/mgD ; maximum N/day ratio vegetation
fRootElodSum [0.1] g root / g veg ; root fraction outside growing season
fRootElodWin [0.6] g root / g veg ; root fraction outside growing season
fFloatElod [0.0] g floating / g shoot ; floating fraction of shoot
fEmergElod [0.0] g floating / g shoot ; emergent fraction of shoot
fDepth1Elod [0.0] - ; max. upper depth of submerged veget. layer, as fraction of water depth
fDepth2Elod [1.0] - ; max. lower depth of submerged veget. layer, as fraction of water depth
cDLayerElod [0.0] gD/m2 ; biomass of a single layer floating leaves
cCovSpElod [0.5] % cover per gD/m2 ; specific cover Tent.
kMigrElod [0.00001] day-1 ; vegetation migration rate
cDElodIn [0.1] gD/m2 ; “external vegetation density”
cTmInitElod [10.0] oC ; temperature for start of season
cDCarrElod [500.0] gDW/m2 ; max. vegetation biomass
cMuMaxElod [0.32] ;
cQ10ProdElod [1.2] - ; temperature quotient of production
hLRefElod [32.0] W/m2 PAR ; half-sat. light at 20 oC
cExtSpElod [0.01] m2/gDW ; specific extinction
kDRespElod [0.024] day-1 ; dark respiration rate of vegetation
cQ10RespElod [1.5] - ; temperature quotient of respiration
cDayWinElod [259.0] - ; end of growing season = 16 Sep
kMortElodSum [0.005] day-1 ; vegetation mortality rate in Spring and Summer (low)

fWinElod [0.2] - ; fraction surviving in winter

fDetWMortElod [0.5] - ; fraction of shoot mortality becoming water detritus

cPrefElodBird [1.0] - ; edibility for birds

cVPUptMaxElod [0.005] mgP/mgD/day ; maximum P uptake capacity of vegetation

cAffPUptElod [0.1] l/mgD/day ; initial P uptake affinity vegetation

cPDElodMin [0.0008] ; 0.001

cPDElodMax [0.0035] ; Best, 1979

cVNUptMaxElod [0.05] mgN/mgD/day ; maximum N uptake capacity of vegetation

cAffNUptElod [0.1] l/mgD/day ; initial N uptake affinity vegetation

cNDElodMin [0.01] mgN/mgD ; minimum N/day ratio vegetation

cNDElodMax [0.035] ; 3 a 4 %, Best 1979

fRootCharSum [0.05] g root / g veg ; root fraction in growing season

fRootCharWin [0.10] g root / g veg ; root fraction outside growing season

fFloatChar [0.0] g floating / g shoot ; floating fraction of shoot

fEmergChar [0.0] g floating / g shoot ; emergent fraction of shoot

fDepth1Char [0.5] - ; max. upper depth of submerged veget. layer, as fraction of water depth

fDepth2Char [1.0] - ; max. lower depth of submerged veget. layer, as fraction of water depth

cCovSpChar [0.5] % cover per gD/m2 ; specific cover Tent.

cDLayerChar [0.0] gD/m2 ; biomass of a single layer floating leaves

kMigrChar [0.00001] day-1 ; vegetation migration rate

cDCharIn [0.1] gD/m2 ; “external vegetation density”

cTmInitChar [10.0] oC ; temperature for start of season

cDCarrChar [500.0] gDW/m2 ; max. vegetation biomass

cMuMaxChar [0.22] g/g shoot/day ; maximum growth rate of vegetation at 20oC

cQ10ProdChar [1.2] - ; temperature quotient of production

hLRefChar [19.0] W/m2 PAR ; half-sat. light at 20 oC

cExtSpChar [0.01] m2/gDW ; specific extinction

kDRespChar [0.025] day-1 ; dark respiration rate of vegetation

cQ10RespChar [1.2] - ; temperature quotient of respiration

cDayWinChar [259.0] - ; end of growing season = 16 Sep

kMortCharSum [0.005] day-1 ; vegetation mortality rate in Spring and Summer (low)

fWinChar [0.9] - ; fraction surviving in winter

fDetWMortChar [0.5] - ; fraction of shoot mortality becoming water detritus

cPrefCharBird [0.5] - ; edibility for birds

cVPUptMaxChar [0.005] mgP/mgD/day ; maximum P uptake capacity of vegetation

cAffPUptChar [0.1] l/mgD/day ; initial P uptake affinity vegetation

cPDCharMin [0.0012] mgP/mg ; minimum P/day ratio vegetation

cPDCharMax [0.0035] ; Best, 1979

cVNUptMaxChar [0.05] mgN/mgD/day ; maximum N uptake capacity of vegetation

cAffNUptChar [0.1] l/mgD/day ; initial N uptake affinity vegetation

cNDCharMin [0.01] mgN/mgD ; minimum N/day ratio vegetation

cNDCharMax [0.035] ; 3 a 4 %, Best 1979 fRootCeraSum [0.0] g root / g veg ; root fraction in growing season

fRootCeraWin [0.0] ; root fraction outside growing season

fFloatCera [0.0] g floating / g shoot ; floating fraction of shoot

fEmergCera [0.0] g floating / g shoot ; emergent fraction of shoot

fDepth1Cera [0.0] - ; max. upper depth of submerged veget. layer, as fraction of water depth

fDepth2Cera [0.5] - ; max. lower depth of submerged veget. layer, as fraction of water depth

cCovSpCera [0.5] % cover per gD/m2 ; specific cover Tent.

cDLayerCera [0.0] gD/m2 ; biomass of a single layer floating leaves

kMigrCera [0.00001] day-1 ; vegetation migration rate

cDCeraIn [0.1] gD/m2 ; “external vegetation density”

cTmInitCera [10.0] oC ; temperature for start of season

cDCarrCera [500.0] gDW/m2 ; max. vegetation standing crop

cMuMaxCera [0.21] g/g shoot/day ; maximum growth rate of vegetation at 20oC

cQ10ProdCera [1.5] - ; temperature quotient of production

hLRefCera [25.0] W/m2 PAR ; half-sat. light at 20 oC

cExtSpCera [0.01] m2/gDW ; specific extinction

kDRespCera [0.024] day-1 ; dark respiration rate of vegetation

cQ10RespCera [2.0] - ; temperature quotient of repiration

cDayWinCera [259.0] - ; end of growing season = 16 Sep

kMortCeraSum [0.005] day-1 ; vegetation mortality rate in Spring and Summer (low)

fWinCera [0.1] - ; fraction surviving in winter

fDetWMortCera [0.5] - ; fraction of shoot mortality becoming water detritus

cPrefCeraBird [0.0] - ; edibility for birds

cVPUptMaxCera [0.005] mgP/mgD/day ; maximum P uptake capacity of vegetation

cAffPUptCera [0.1] l/mgD/day ; initial P uptake affinity vegetation

cPDCeraMin [0.0012] mgP/mg ; minimum P/day ratio vegetation

cPDCeraMax [0.0035] ; Best 1979

cVNUptMaxCera [0.05] mgN/mgD/day ; maximum N uptake capacity of vegetation

cAffNUptCera [0.1] l/mgD/day ; initial N uptake affinity vegetation

cNDCeraMin [0.01] mgN/mgD ; minimum N/day ratio vegetation

cNDCeraMax [0.035] ; 3 a 4 %, Best 1979

fRootLemnSum [0.0] g root / g veg ; root fraction in growing season

fRootLemnWin [0.0] g root / g veg ; root fraction outside growing season

fFloatLemn [1.0] g floating / g shoot ; floating fraction of shoot

fEmergLemn [0.0] g emergent / g shoot ; emergent fraction of shoot

fDepth1Lemn [0.0] - ; max. upper depth of submerged veget. layer, as fraction of water depth

fDepth2Lemn [0.0] - ; max. lower depth of submerged veget. layer, as fraction of water depth

cCovSpLemn [1.0] % cover per gD/m2 ; specific cover Tent.

cDLayerLemn [100.0] gD/m2 ; biomass of a single layer floating leaves

cTmInitLemn [10.0] oC ; temperature for start of season

cDCarrLemn [575.0] gDW/m2 ; max. vegetation standing crop

cMuMaxLemn [0.30] g/g shoot/day ; maximum growth rate at 20oC cQ10ProdLemn [2.5] - ; temperature quotient of production

hLRefLemn [7.5] W/m2 PAR ; half-sat. light at 20 oC (n.a.)

cExtSpLemn [0.01] m2/gDW ; specific extinction (not appl.)

ckMigrLemn [0.00001] day-1 ; vegetation migration rate

cDLemnIn [0.1] gD/m2 ; “external vegetation density”

kDRespLemn [0.03] day-1 ; dark respiration rate of vegetation

cQ10RespLemn [3.0] - ; temperature quotient of respiration

cDayWinLemn [289.0] - ; end of growing season = 16 Oct

kMortLemnSum [0.02] day-1 ; vegetation mortality rate in Spring and Summer (low)

fWinLemn [0.2] - ; fraction surviving in winter

fDetWMortLemn [0.8] - ; fraction of shoot mortality becoming water detritus

cPrefLemnBird [0.0] - ; edibility for birds

cVPUptMaxLemn [0.005] mgP/mgD/day ; maximum P uptake capacity of vegetation

cAffPUptLemn [0.1] l/mgD/day ; initial P uptake affinity vegetation

cPDLemnMin [0.004] mgP/mg ; minimum P/day ratio vegetation

cPDLemnMax [0.026] mgP/mgD ; maximum P/day ratio vegetation

cVNUptMaxLemn [0.05] mgN/mgD/day ; maximum N uptake capacity of vegetation

cAffNUptLemn [0.1] l/mgD/day ; initial N uptake affinity vegetation

cNDLemnMin [0.04] ;

cNDLemnMax [0.1] ;

fRootNympSum [0.75] g root / g veg ; root fraction in growing season

fRootNympWin [0.95] g root / g veg ; root fraction outside growing season

fFloatNymp [1.0] g floating / g shoot ; floating fraction of shoot

fEmergNymp [0.0] g floating / g shoot ; emergent fraction of shoot

fDepth1Nymp [0.0] - ; max. upper depth of submerged veget. layer, as fraction of water depth

fDepth2Nymp [0.0] - ; max. upper depth of submerged veget. layer, as fraction of water depth

cCovSpNymp [0.5] % cover per gD/m2 ; specific cover Tent.

cDLayerNymp [100.0] gD/m2 ; biomass of a single layer floating leaves

kMigrNymp [0.00001] day-1 ; vegetation migration rate

cDNympIn [0.1] gD/m2 ; “external vegetation density”

cTmInitNymp [10.0] oC ; temperature for start of season

cDCarrNymp [500.0] gDW/m2 ; max. vegetation standing crop

cMuMaxNymp [0.1] g/g shoot/day ; maximum growth rate of vegetation at 20oC

cQ10ProdNymp [1.5] - ; temperature quotient of production

hLRefNymp [25.0] W/m2 PAR ; half-sat. light at 20 oC (n.a.)

cExtSpNymp [0.01] m2/gDW ; specific extinction (n.a.)

kDRespNymp [0.01] day-1 ; dark respiration rate of vegetation

cQ10RespNymp [2.0] - ; temperature quotient of respiration

cDayWinNymp [259.0] - ; end of growing season = 16 Sep

kMortNympSum [0.005] day-1 ; vegetation mortality rate in Spring and Summer (low)

fWinNymp [0.333] - ; fraction surviving in winter

fDetWMortNymp [0.25] - ; fraction of shoot mortality becoming water detritus

cPrefNympBird [0.0] - ; edibility for birds
cVPUptMaxNymp [0.005] mgP/mgD/day ; maximum P uptake capacity of vegetation
cAffPUptNymp [0.1] l/mgD/day ; initial P uptake affinity vegetation
cPDNympMin [0.001] mgP/mg ; minimum P/day ratio vegetation
cPDNympMax [0.0075] mgP/mgD ; maximum P/day ratio vegetation
cVNUptMaxNymp [0.05] mgN/mgD/day ; maximum N uptake capacity of vegetation
cAffNUptNymp [0.1] l/mgD/day ; initial N uptake affinity vegetation
cNDNympMin [0.01] mgN/mgD ; minimum N/day ratio vegetation
cNDNympMax [0.03] ; 3 a 4 %
fRootHeloSum [0.5] g root / g veg ; root fraction in growing season
fRootHeloWin [0.8] g root / g veg ; root fraction outside growing season
fFloatHelo [0.0] g floating / g shoot ; floating fraction of shoot
fEmergHelo [1.0] g floating / g shoot ; emergent fraction of shoot
fDepth1Helo [0.0] - ; max. upper depth of submerged veget. layer, as fraction of water depth
fDepth2Helo [0.0] - ; max. upper depth of submerged veget. layer, as fraction of water depth
cDCarrHelo [2000.0] gDW/m2 ; max. vegetation standing crop
cCovSpHelo [0.05] % cover per gD/m2 ; specific cover Tent.
cDLayerHelo [0.0] gD/m2 ; biomass of a single layer floating leaves
kMigrHelo [0.00001] day-1 ; vegetation migration rate
cDHeloIn [0.1] gD/m2 ; “external vegetation density”
cTmInitHelo [10.0] oC ; temperature for start of season
cMuMaxHelo [0.1] g/g shoot/day ; maximum growth rate of vegetation at 20oC
cQ10ProdHelo [1.5] - ; temperature quotient of production
hLRefHelo [25.0] W/m2 PAR ; half-sat. light at 20 oC (n.a.)
cExtSpHelo [0.01] m2/gDW ; specific extinction (n.a.)
kDRespHelo [0.01] day-1 ; dark respiration rate of vegetation
cQ10RespHelo [2.0] - ; temperature quotient of respiration
cDayWinHelo [259.0] - ; end of growing season = 16 Sep
kMortHeloSum [0.005] day-1 ; vegetation mortality rate in Spring and Summer (low)
fWinHelo [0.333] - ; fraction surviving in winter
fDetWMortHelo [0.25] - ; fraction of shoot mortality becoming water detritus
cPrefHeloBird [0.0] - ; edibility for birds
cVPUptMaxHelo [0.005] mgP/mgD/day ; maximum P uptake capacity of vegetation
cAffPUptHelo [0.1] l/mgD/day ; initial P uptake affinity vegetation
cPDHeloMin [0.001] mgP/mg ; minimum P/day ratio vegetation
cPDHeloMax [0.0075] mgP/mgD ; maximum P/day ratio vegetation
cVNUptMaxHelo [0.05] mgN/mgD/day ; maximum N uptake capacity of vegetation
cAffNUptHelo [0.1] l/mgD/day ; initial N uptake affinity vegetation
cNDHeloMin [0.01] mgN/mgD ; minimum N/day ratio vegetation
cNDHeloMax [0.03] ; 3 a 4 %

(food web)

cFiltMax [4.5] ltr/mgDW/day ; maximum filtering rate (when DOMW=0)
hFilt [1.0] mgDW/l ; half-sat. food conc. for filtering
cDCarrZoo [25.0] mg/l ; carrying capacity of zooplankton
cPrefDiat [0.75] - ; selection factor for Diatoms
cPrefGren [0.75] - ; selection factor for Greens
cPrefBlue [0.125] - ; selection factor for Bluegreens Cal.
cPrefDet [0.25] - ; selection factor for detritus
fDAssZoo [0.35] - ; DW-assimilation efficiency of herb. zooplankton
fDissEgesZoo [0.25] - ; soluble nutrient fraction of by herb.zoopl. egested food
kDRespZoo [0.15] day-1 ; maintenance respiration constant herb.zooplankton
kMortZoo [0.04] day-1 ; mortality constant herb.zooplankton
fDissMortZoo [0.1] - ; soluble nutrient fraction of died zooplankton
cTmOptZoo [25.0] oC ; optimum temp. zooplankton
cSigTmZoo [13.0] oC ; temperature constant zooplankton (sigma in Gaussian curve)
cDCarrBent [10.0] ; tentative
kDAssBent [0.1] day-1 ; maximum assimilation rate
hDFoodBent [200.0] g/m2 ; half-saturating food for zoobenthos
fDAssBent [0.3] - ; C ass. efficiency of zoobenthos
fDissEgesBent [0.25] - ; soluble nutrient fraction of by zoobenthos egested food
kDRespBent [0.005] day-1 ; maint. respiration constant of zoobenthos
kMortBent [0.005] day-1 ; mortality constant of zoobenthos
fDissMortBent [0.1] - ; soluble P fraction of died zoobenthos P
cTmOptBent [25.0] oC ; optimum temp. of zoobenthos
cSigTmBent [16.0] oC ; temperature constant of zoobenthos (sigma in Gaussian curve)
fDBone [0.35] - ; fraction of fish C fixed in bones and scales
fPBone [0.50] - ; fraction of fish P fixed in bones and scales
cDCarrFish [15.0] gDW/m2 ; carrying capacity of fish (= 100 gFW/m2)
fDissEgesFish [0.25] - ; soluble nutrient fraction of by fish egested food
fDissMortFish [0.1] - ; soluble nutrient fraction of died fish (excl. bones and scales
cTmOptFish [25.0] oC ; optimum temp. of fish
cSigTmFish [10.0] oC ; temperature constant of fish (sigma in Gaussian curve)
cDayReprFish [120.0] - ; reproduction date of fish = 1 May
fReprFish [0.02] - ; yearly reproduction fraction of adult fish
fAgeFish [0.5] - ; yearly ageing fraction of young fish
cRelVegFiJv [0.000] - ; decrease of young fish feeding per % vegetation cover (max. 0.01)
cRelVegFiAd [0.009] - ; decrease of adult fish feeding per % vegetation cover (max. 0.01)
kDAssFiJv [0.12] day-1 ; maximum assimilation rate of young fish
hDZooFiJv [1.25] g/m2 ; half-saturating zooplankton biomass for young fish predation
fDAssFiJv [0.4] - ; C assimilation efficiency of young fish
kDRespFiJv [0.01] day-1 ; maintenance respiration constant of young fish
kMortFiJv [0.00137] day-1 ; specific mortality of young fish (= 0.1 y-1)
kDAssFiAd [0.06] day-1 ; maximum assimilation rate of adult fish

hDBentFiAd [2.5] g/m2 ; half-saturating zoobenthos biomass for adult fish predation
fDAssFiAd [0.4] - ; C assimilation efficiency of adult fish
kDRespFiAd [0.004] day-1 ; maintenance respiration constant of adult fish
kMortFiAd [0.00027] day-1 ; specific mortality of adult fish (= 0.1 y-1)
cDCarrPiscMax [1.2] gDW.m-2 ; maximum carrying capacity of Pisc (=75 kg/ha)
cDCarrPiscMin [0.1] gDW.m-2 ; minimum carrying capacity of Pisc (=6 kg/ha)
cDCarrPiscBare [0.1] gDW.m-2 ; carrying capacity of Pisc for lake without marsh zone
cDPhraMinPisc [50.0] gD.m-2 ; min. reed biomass for Pisc
cCovVegMin [40.0] % ; min. subm.veg. coverage for Pisc
cRelPhraPisc [0.075] gD.m-2.%-1 ; rel. Pisc density per % reed if subm.veg. absent
cRelVegPisc [0.03] gD.m-2.%-1 ; extra rel. Pisc density per % reed if aCovVeg > cCovVegMin
kDAssPisc [0.025] day-1 ; maximum assimilation rate
hDVegPisc [5.0] g/m2 ; half-sat. vegetation biomass for Pisc growth
hDFishPisc [1.0] g/m2 ; half-saturating DFish for Pisc predation
fDAssPisc [0.4] - ; C ass. efficiency of Pisc
fDissEgesPisc [0.25] - ; soluble P fraction of by fish egested food
kDRespPisc [0.005] day-1 ; maint. respiration constant of Pisc
kMortPisc [0.00027] day-1 ; specific mortality of Pisc = 0.1 y-1
fDissMortPisc [0.1] - ; soluble nutrient fraction of died Pisc (excl. bones and scales
cTmOptPisc [25.0] oC ; optimum temp. of Pisc
cSigTmPisc [10.0] oC ; temperature constant of Pisc (sigma in Gaussian curve)

(wetland)
cDepthSM [0.1] m ; sediment depth
cDensStemPhra [61.5] m-2 ; density stem (+/- 13.9)
cTmInitPhra [8.0] °C ; temp.start initial growth
fDAllPhra [0.3] - ; allocation fraction
kDAllPhra [0.05] 1/day ; allocation rate
cDStemPhra [6.0] g/m ; average stem weight
cQ10ProdPhra [2.0] - ; temp. quotient of production
cMuPhraMax [0.030] 1/day ; maximum growth rate reed
cDShootPhraMax [3500.0] gD/m2 ; max. shoot biomass of reed
cCovSpPhra [0.1] % cover per gD/m2 ; specific coverage
cPDPhraMin [0.0008] - ; min.Phra P/day -ratio
cPDPhraMax [0.003] - ; max.Phra P/day -ratio
cNDPhraMin [0.008] - ; min.Phra N/day -ratio
cNDPhraMax [0.03] - ; max.Phra N/day -ratio
cAffNUptPhra [0.0002] l/mgD/day ; N uptake affinity reed
cAffPUptPhra [0.0002] l/mgD/day ; P uptake affinity reed
cVNUptPhraMax [0.1] mgN/mgD/day ; max. uptake rate N
cVPUptPhraMax [0.01] mgP/mgD/day ; max. uptake rate P
kDRespPhra [0.001] 1/day ; respiration rate of reed

cQ10RespPhra [2.5] 1/e^°C ; temp. quotient of respiration
fDayWin [0.52] ; Start autumn
fDRealPhra [0.85] - ; reallocated fraction day
kDRealPhra [0.05] 1/day ; reallocation rate day
kDMortShootPhra [0.0] 1/day ; mortality rate shoots
kDMortRootPhra [0.000391] 1/day ; mortality rate roots
cDayWinPhra [259.0] day ; begin autumn (16 sept.)
cLengMortShoot [42.0] day ; length of shoot mort. period

General conversion factors:
molO2molC = 2.6667; = 32/12 [gO2/gC], ratio of mol.weights
molO2molN = 2.2857; = 32/14 [gO2/gN], ratio of mol.weights
molNmolC = 1.1667; = 14/12 [gN/gC], ratio of mol.weights
cRhoWat = 1000000.0; density of water [g/m3]
Pi = 2.0*ASIN(1.0); Pi (approx. 3.14159) [-]
DaysPerYear = 365.0; [d/y]

Summary

Aquatic ecosystems all over the world heavily suffer from excess input of nutrients, especially phosphorus and nitrogen. This process, called eutrophication, causes the degradation or disappearance of natural plant and animal communities which are (or were) typical for our surface waters. Shallow, more or less stagnant waters like lakes, ponds and ditches are particularly vulnerable to eutrophication. The naturally occurring communities of these waters, mostly dominated by aquatic plants (macrophytes) as primary producers, can change dramatically upon nutrient loading. Besides a collapse of the macrophytes, the related communities of algae, invertebrates, fishes and other animals also change completely, and biodiversity as a whole generally decreases.

This study concentrates on eutrophication effects in *shallow lakes and ponds* on the one hand and in *ditches* (small water channels in agricultural areas) on the other. In shallow lakes (up to *ca* 4 m of depth), the clear-water community characterized by macrophytes is generally replaced by a dominance of phytoplankton and turbid water, while a diverse fish community including piscivores is transferred into a species-poor community dominated by bream. In ditches, eutrophication causes the typical, richly structured community of submerged macrophytes to be replaced by a monotonous layer of small floating plants, duckweeds. This leads, among other things, to an anaerobic environment and deterioration of aquatic life.

As these biotic effects are considered as undesirable, it is important to be able to *predict*, as far as possible in a quantitative way, at what degree of eutrophication these changes will occur, and whether they are reversible or not. Mathematical models are a useful tool to address such questions and support management decisions. This thesis describes two such mathematical model, a model for lakes and a model for ditches. The aim of both models is to answer the following questions:

a. At what nutrient loading the system changes from the natural state to the degraded state
b. How long does this take
c. Is this change reversible, i.e. how far should the nutrient loading be decreased to restore the natural state once the system is degraded
d. Why is the one lake/ditch more susceptible to eutrophication than the other, i.e. how do the critical loading levels depend on the type of lake/ditch
e. What are the key processes determining degradation and restoration
f. What is the effect of different management options for restoration of degraded ecosystems, or increasing the resilience of natural ecosystems
g. What is the uncertainty of these predictions

There are many types of mathematical models, of which several types have been applied to lake eutrophication in previous studies. These include: regression models relating e.g. chlorophyll levels to nutrient concentrations or loading, regression models linking species composition or biodiversity to nutrient concentrations, dynamic models of algal growth as a function of

nutrient loading, detailed biological species models and dynamic minimodels covering the interaction between two biotic groups. In this study, we developed two dynamic, functional-ecological models, covering explicitly the most important biotic groups and their interrelations, within the general framework of the nutrient cycles (chapter 2). Mathematically, they are composed of coupled differential equations. These models are meant to be an integrative evaluation tool, offering ‘slots’ and pathways to represent differences in system properties and to impose (combinations of) input or management factors. Moreover, they give the possibility of evaluating the impact of alternative ecological assumptions. An ecosystem may be better managed if we understand how it works. All these type of models have their proper ‘niche’, and the combined use of them, in connection to empirical data, is probably the best way to enhance our insight in the functioning of ecosystems.

The simulation model for shallow lakes, called *PCLake* (§ 2.3), describes what are considered to be 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 the nutrient cycles. 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 The sediment top layer is included because of its intensive interaction with the lake water, and to cope with the lake’s ‘history’ and reaction time. Inorganic nutrients and suspended solids are included for a proper modelling of the nutrient cycles and the water transparency. A simplified food web is included made up of zooplankton, zoobenthos, young and adult whitefish and piscivorous fish. The water level can be kept constant or be made variable. The lake is assumed to be homogeneous and well-mixed, but optionally, a wetland zone with marsh vegetation, and water exchange with the lake, can be included in the model. The model calculates chlorophyll-*a*, transparency, phytoplankton types, vegetation coverage and fish biomass, as well as the concentrations and fluxes of the nutrients N, P and Si and oxygen. 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 loading history (initial conditions). Policy and management options that can be evaluated, alone or in combination, include: reduction of nutrient loading, hydrological and morphological changes, climate change, dredging and biomanipulation.

Ditches are narrow canals designed for the drainage of lowland areas. Here, eutrophication usually leads to a shift from submerged plants to a floating mat of duckweed rather than phytoplankton dominance. Following the same principles as for lakes, a functional-ecological model, *PCDitch*, was developed (§ 2.5). The model describes the competition between several vegetation groups, coupled to the nutrient cycles in water and sediment top layer as in *PCLake*. The plant groups were characterized based on their growth form (e.g. the ‘layer’ in which they grow) and nutrient uptake strategy (from the water, the sediment or both): submerged rooted, submerged non-rooted, Charophytes, algae, floating, nymphaeid and emergent plants. The growth of the different plant groups is modelled as a function of light, temperature, phosphorus and nitrogen. Grazers and other animal groups were left out, but grazing can be considered as an external factor, like vegetation management (mowing) and dredging. Inputs to the model are again nutrient loading, hydrology, temperature and light, water depth, sediment properties and initial conditions.

Both models are strongly related, and may be characterized as relatively complex. The structure of a model is inevitably always a compromise between realism, and thus extrapolative power, and identifiability by data (chapters 3-4). The implication of the chosen model structure for *PCLake* is a large number of parameters (> 200), of which only a part can be derived from available data. It is not always possible to decide between different parameter values or even different structural variants. Moreover, parameters show a natural variation, which is reflected in an uncertainty (or variability) in the model results. In this study, the Bayesian principle for model validation is followed, accepting and making explicit use of this variability. The analysis is based on the likelihood, the degree of fit between the simulated and measured concentrations for real lakes, combined with prior knowledge on the model structure and parameters. This is a strategy to seek an optimal balance between accounting for uncertainty in the data and uncertainty in the model. Put another way, it is an attempt to have the best of both worlds: modelled knowledge of processes on the one hand, and observations of lake dynamics on the other.

A data set containing both input factors and measured data on over 40 lakes of different types and different ecological states, combining information from many sources, was used for the analysis. The likelihood function was based on the (quasi-)steady-state summer-averages of total-phosphorus, total-nitrogen, chlorophyll-a, Secchi depth and submerged vegetation coverage, for all lakes combined (chapter 4).

As a first step, a sensitivity analysis was performed, to select the most sensitive parameters and input factors. This was done by the Morris method (a ‘screening method’) and the FAST method (a variance-based method). Besides the sensitivity for the parameters and input factors of the output variables proper, e.g. chlorophyll-*a* concentration, the sensitivity of the likelihood was evaluated as well. The most sensitive parameters and input factors turned out to be (ranked): P loading, N loading, water depth, water inflow, resuspension parameters, zooplankton filtering rate and food preference factors, algal and detrital settling rates, max. growth rates of algae and macrophytes, growth rate of fish, infiltration rate, overwintering fraction of macrophytes, minimum nutrient content of algae, mineralisation rate.

To seek those parameter set(s) that would allow the model to fit well to the observation data, ten process parameters from this list were varied. With each parameter combination, simulations were performed for all lakes in the data set, and the likelihood of each run was determined. The ‘best run’ was used to choose the default parameter values. All ‘reasonable runs’ were used to estimate the variability of the model results. The simulations with the ‘tuned’ model (using the values for the best run) matched reasonably well, for most of the investigated lakes, with the observations for total P, chlorophyll-*a*, submerged macrophytes and relative euphotic depth (Secchi depth relative to the water depth), but somewhat less for total N. Furthermore, the simulated overall relationships between these variables complied with empirical relations derived elsewhere. This suggests that the model might well represent a reasonable description of key processes in these lakes.

To explore the model's behaviour systematically, long-term simulations were performed for a number of 'hypothetical lakes', subject to a broad range of nutrient loadings, while starting from either of two initial conditions: a turbid state with phytoplankton dominance or a clear state dominated by macrophytes (chapters 5-6). The simulated response (chlorophyll-a or submerged macrophytes coverage) as a function of the nutrient input was in general highly non-linear and showed hysteresis. The critical loading for restoration of the clear state was always lower than the switchpoint for 'turbidification'. This complies with evidence from many other recent theoretical and field studies, and can be explained by the fact that both states possess a number of self-stabilizing buffering mechanisms. The hysteresis thus pops up from the simulations as 'emerging property' of the model, resulting from the combination of mechanisms brought together.

An important aspect of the model is that it allows to estimate how critical loading levels depend on lake type, and gives a clue for the relative importance of different factors in certain lake types (chapter 6). The values of the two switchpoints in the model are dependent on lake characteristics such as water depth, hydraulic loading rate, lake area, sediment type, and the size of the marsh zone. For the most common lake types in The Netherlands, the critical loading for 'turbidification' is calculated as about 2–5 mgP m^{-2} d^{-1}, and the value for 'clarification' (or 'restoration') as 0.6–1.0 mgP m^{-2} d^{-1}, with concomitant total P concentrations of 0.03-0.1 mgP/l. About 2/3 of the lakes in the data set presented in chapter 4 had a phosphorus loading higher than the 'turbidification' switchpoint. The uncertainty in the prediction of the turbidification switchpoint appeared to be higher than that in the restoration switchpoint, as derived from the Bayesian likelihood calculations presented in § 4.5.

The model can also be used to address the possible effectiveness of management options for a particular (type of) lake. Biomanipulation, for instance, would, on the long term, be only effective if the nutrient load is reduced to a level well below the turbidification switchpoint. Overall, the predicted critical loading values were quite well in line with empirical information.

A comparable systematic analysis of critical nutrient loading limits was done for ditches using the *PCDitch* model (chapter 7). Specifically, critical loading rates for a switch from submerged plant dominance to duckweed dominance were calculated as a function of ditch characteristics and management. Water depth, retention time and the type of sediment were particularly influential to critical nutrient levels. Predicted critical loadings for a switch to duckweed dominance ranged from 2–10 gP m^{-2} y^{-1}, with concomitant total P concentrations of 0.2–0.4 mgP l^{-1}. Hysteresis was observable in the simulations in the sense that restoration of the submerged vegetation after load reduction took a longer time than the switch to duckweed dominance in the opposite situation. This was mainly due to the long time it takes to unload the sediments. There were also cases in which the duckweed dominated situation and the submerged plant dominated situation represented alternative stable states, but this is often obscured by vegetation and ditch management. The model suggests that dredging may help to combat duckweed dominance, provided that the external loading is not too high.

The *PCLake* model also proved to be able to mimick the observations in some case studies well, when it was used to zoom in to the dynamics in a more detailed way. For instance, the response of Lake Loosdrecht to P load reduction, viz. a high resilience of the turbid state, was simulated well (chapters 8-10). The resilience could be attributed to an increase of the P efficiency of the cyanobacteria (decreasing P/C ratio), the high internal recycling of phosphorus via resuspension and the high density of bream.
Also the effects of a biomanipulation experiment in a small lake, Lake Zwemlust, could be reproduced quite realistically (chapters 11-12). Following the fish removal, phytoplankton was replaced by macrophytes. Mechanisms involved were first top-down factors (relief of zooplankton from predation), later also bottom-up factors (nitrogen limitation of phytoplankton once macrophytes had established). The structural changes coincided with changes in nutrient distribution and fluxes. In this case, we ‘zoomed in’ a little bit further in the effect of macrophytes’ life strategies; a species shift (to less edible, but ‘weaker’ plants) caused by herbivorous birds that came in a few years after the measure, made the lake switch back to the turbid state. The external nutrient load of the system was high.
Concerning the positive effect of wetland zones on lake quality (chapter 13), the model results were well in line with the idea that transport and nutrient uptake processes, and improved conditions for piscivorous fish, may be key mechanisms. The model also suggested that the effect on nutrient dynamics only occurs if there is a good exchange of water between the lake and the marshland. In practice, this would be promoted by water level fluctuations as occurred in many lowland lakes in the past.

Also the ditch model *PCDitch* was applied in case studies in some detail. We used the well documented dynamics of a series of experimental ditches that were subjected to different levels of nutrient loading (chapter 14). The observed development of submerged macrophytes at low loading, an increase of algae at intermediate loading and a shift to a duckweed dominance at high loading, was simulated well. A further analysis of more natural field dynamics is now underway.

In conclusion, the modelling approach presented here, taking into account both the biological structure and the nutrient cycle, is a useful tool to aid in the development of nutrient regulations and water management strategies. It fills a niche between minimal (‘conceptual’) models that address mechanisms in a highly abstract lumped way and traditional eutrophication models that neglect important food web interactions and the role of macrophytes. The presented models can be used to explore the potential combined effects of catchment-scale management options and local measures, including the uncertainties in those estimates. Importantly, the models also allow an estimate of differences in sensitivity to eutrophication between different types of lakes and ditches. This allows the development of differentiated protection standards.

Samenvatting

Wereldwijd hebben aquatische ecosystemen ernstig te lijden van overbemesting, in het bijzonder door de nutriënten (voedingsstoffen) fosfor en stikstof. Dit proces, eutrofiëring genaamd, is de oorzaak van de aftakeling of het verdwijnen van de karakteristieke planten- en dierengemeenschappen die van nature in onze oppervlaktewateren voorkwamen. Ondiepe, min of meer stilstaande wateren zoals meren, plassen en sloten, zijn het meest gevoelig voor de effecten van eutrofiëring. De natuurlijke levensgemeenschappen van deze wateren, veelal gedomineerd door onderwaterplanten (makrofyten) als primaire producenten, storten volledig in. Met het verdwijnen van de waterplantenvegetatie veranderen ook de levensgemeenschappen van algen, invertebraten, vissen, enz., en de biodiversiteit (de verscheidenheid aan levensvormen) neemt af.
Deze studie richt zich op de effecten van eutrofiëring in *ondiepe meren en plassen* (minder dan *ca* 4 m diep) enerzijds en *sloten* anderzijds. In ondiepe meren verdwijnt door eutrofiëring de helderwatergemeenschap met waterplanten en wordt vervangen door troebel water met een hoge concentratie aan fytoplankton (algen). De visstand verandert van een soortenrijke gemeenschap met relatief veel roofvis in een soortenarme gemeenschap gedomineerd door brasem. In sloten is het effect van eutrofiering dat de karakteristieke, rijk-gestructureerde gemeenschap van ondergedoken waterplanten wordt vervangen door een kroosdek. Dit leidt onder andere tot een zuurstofarm milieu en het verdwijnen van veel aquatische organismen.

Daar deze ecologische effecten als ongewenst worden beschouwd, is het belangrijk om te kunnen voorspellen, zo veel mogelijk kwantitatief, bij welk niveau van eutrofiering deze veranderingen gaan optreden, en of zij omkeerbaar zijn of niet. Wiskundige modellen vormen een nutig instrument om zulke vragen te beantwoorden en om beheervragen te onderbouwen. Dit proefschrift beschrijft twee zulke modellen, een voor meren en een voor sloten. Beide modellen hebben tot doel om de volgende vragen te beantwoorden:

a. Bij welke nutriëntenbelasting verandert het systeem van de natuurlijke in de ongewenste toestand
b. Op welke tijdschaal gebeurt dat
c. Is die verandering omkeerbaar, ofwel hoe ver moet de nutriëntenbelasting worden verlaagd om de natuurlijke staat te herstellen wanneer het systeem reeds is gedegradeerd
d. Waarom is het ene water gevoeliger voor eutrofiëring dan het andere, ofwel hoe hangen de kritische grenswaarden voor de belasting af van het *type* meer of sloot
e. Wat zijn de belangrijkste processen die achteruitgang en herstel van wateren bepalen
f. Welke beheersmaatregelen zijn effectief om watersystemen te herstellen, of om de veerkracht van natuurlijke systemen te vergroten
g. Wat is de mate van onzekerheid in deze voorspellingen

Er bestaan verschillende typen wiskundige modellen die zijn toegepast in eerdere studies over eutrofiëring van meren. Hieronder vallen regressiemodellen die bijv. de algenconcentratie relateren aan de nutriëntenconcentraties of –belasting, regressiemodellen die de soortensamenstelling of biodiversiteit koppelen aan de nutriëntenconcentraties, dynamische modellen van de algengroei als functie van de nutriëntenbelasting, gedetailleerde biologische soortmodellen en dynamische minimodellen die de interactie tussen twee groepen organismen beschrijven. In deze studie zijn een tweetal dynamische, functioneel-ecologische modellen ontwikkeld die de belangrijkste biotische groepen en hun onderlinge relaties beschrijven, binnen het kader van de nutriëntenkringlopen in het systeem (hoofdstuk 2). Functioneel-ecologisch wil zeggen dat de organismen niet per soort worden beschreven maar per groep van soorten met ongeveer dezelfde plaats in het ecosysteem; dynamisch betekent dat veranderingen in de tijd worden berekend. Mathematisch gezien bestaan beide modellen uit een stelsel van gekoppelde differentiaalvergelijkingen. De modellen zijn bedoeld als een geïntegreerd evaluatie– en voorspellingsinstrument; zij bieden de mogelijkheid om het effect van verschillende (combinaties van) invoerfactoren en beheersmaatregelen door te rekenen voor watersystemen met verschillende eigenschappen. Bovendien bieden zij de mogelijkheid om de implicaties van verschillende ecologische aannamen of theorieën met elkaar te vergelijken. Een ecosysteem kan beter worden beheerd als we begrijpen hoe het functioneert. Alle genoemde typen modellen hebben hun voor- en nadelen en hun eigen werkdomein. Hun gecombineerde inzet, samen met empirische gegevens, is waarschijnlijk de beste manier om ons inzicht in het gedrag van ecosystemen te verhogen.

Het simulatiemodel voor ondiepe meren, *PCLake* (§ 2.3), beschrijft wat beschouwd wordt als de belangrijkste ecologische interacties die bepalen in welke toestand een ondiep meer terechtkomt: de troebele, algenrijke toestand of de heldere toestand met veel waterplanten. Zowel processen ‘van onderop’ (zoals algen- en plantengroei), ‘van bovenaf’ (zoals begrazing en predatie) als indirect van invloed zijnde processen (zoals de invloed van vegetatie op vissen) zijn in het model opgenomen, binnen de kringloop van nutriënten. De belangrijkste biotische groepen zijn fytoplankton, verdeeld in cyanobacteriën (blauwalgen), diatomeeën en overige algen, en ondergedoken waterplanten. De belangrijkste abiotische variabelen zijn de helderheid (zichtdiepte) van het water en de nutriënten fosfor, stikstof en silicium. De toplaag van het sediment (de waterbodem) wordt ook meegenomen vanwege zijn intensieve uitwisseling met het water en om rekening te kunnen houden met vroegere belasting van het meer en met de reactietijd op maatregelen. Anorganische nutriënten en zwevende stof (slibdeeltjes in het water) zijn opgenomen om de helderheid van het water en de nutriëntenkringloop correct te kunnen modelleren. Verder is een sterk vereenvoudigd voedselweb opgenomen, bestaande uit zoöplankton (watervlooien), zoöbenthos (kleine bodemdiertjes), jonge en volwassen witvis (die leeft van resp. zoöplankton en zoöbenthos) en roofvis (visetende vis). Het waterpeil van het meer kan constant gehouden worden, maar men kan het ook gedurende het jaar laten variëren. Het meer wordt verondersteld homogeen en goed gemengd te zijn, maar indien gewenst kan een zone met moerasvegetatie in het model worden opgenomen, waarvan het water uitwisselt met dat van het meer.

Het model berekent chlorofyl-a (‘bladgroen’, een maat voor de concentratie algen in het water), de helderheid (zichtdiepte), de verdeling over de drie algentypen, de bedekkingsgraad met onderwaterplanten en de hoeveelheid vis, naast de concentraties en fluxen van stikstof, fosfor, silicium en zuurstof. Als invoergegevens gebruikt het model: de toevoer en afvoer van water, de nutriëntenbelasting (de hoeveelheid voedingsstoffen die het meer inkomt), de watertemperatuur en hoeveelheid daglicht door het jaar heen, de diepte en oppervlakte van het meer, de grootte van de moeraszone (indien aanwezig), het bodemtype (bijv. zand, klei of veen) en de begincondities (die o.a. afhangen van de vroegere belasting van het meer). Beheer- en beleidsopties die, alleen of in combinatie, kunnen worden doorgerekend, zijn vermindering van de nutriëntenbelasting, hydrologische en morfologische veranderingen, klimaatverandering, baggeren en biomanipulatie.

Sloten zijn smalle, ondiepe kanalen die gegraven zijn voor de afvoer van water uit laaggelegen landbouwgebieden (poldergebieden); soms hebben ze ook een water*aanvoer*functie. Nederland telt naar schatting zo'n 300.000 km aan sloten, en ook in laaglandgebieden in andere landen komen ze voor. Behalve een landbouwfunctie hebben sloten ook een belangrijke natuurfunctie. Eutrofiëring leidt in sloten vaak tot een omslag van een onderwatervegetatie naar een drijflaag van kroos, in tegenstelling tot de fytoplanktondominantie in meren. Volgens dezelfde principes die voor meren gehanteerd zijn, is een functioneel-ecologisch model voor sloten ontwikkeld, genaamd *PCDitch* (§ 2.5). Het model beschrijft de competitie tussen verschillende groepen vegetatie (waterplanten), gekoppeld aan de kringlopen van nutriënten in water en bodemtoplaag zoals in *PCLake*. De plantengroepen zijn gebaseerd op hun groeivorm (met name de 'laag' waarin zij groeien: onder water, op het water en/of boven water) en op de zone waar zij hun voedingsstoffen uit betrekken: direct uit het water, via wortels uit de bodem, of uit beide. De plantengroepen zijn: ondergedoken wortelend, ondergedoken niet-wortelend, kranswieren, (draad)algen, kroos, drijfbladplanten en emergente planten. De groei van deze plantengroepen wordt gemodelleerd als functie van licht, watertemperatuur, fosfor en stikstof. Grazers en andere diergroepen zijn weggelaten, maar begrazing (herbivorie) kan worden meegenomen als een externe factor, evenals maaibeheer en baggeren. Invoergegevens voor het model zijn weer de nutriëntenbelasting, de hydrologie (toe- en afvoer van water), temperatuur en licht door het jaar heen, de waterdiepte, bodemtype en begincondities.

Beide modellen (die qua opzet vergelijkbaar zijn) hebben een relatief complexe structuur. De structuur van een model is onvermijdelijk altijd een compromis tussen realisme en daarmee voorspellend vermogen enerzijds en identificeerbaarheid aan de hand van meetgegevens anderzijds (hoofdstukken 3-4). De gekozen modelstructuur voor *PCLake* impliceert een groot aantal (>200) parameters, die slechts ten dele kunnen worden afgeleid uit beschikbare meetgegevens. Het blijkt niet altijd mogelijk om een beslissende keuze te maken tussen verschillende parameterwaarden of zelfs verschillende structuurvarianten. Bovendien vertonen veel parameters een natuurlijke variatie, die tot uiting komt in een onzekerheid (of variabiliteit) in de modeluitkomsten. In dit onderzoek wordt de Bayesiaanse benadering voor modelvalidatie gevolgd, die deze variabiliteit als gegeven accepteert en er expliciet gebruik van maakt. De analyse is gebaseerd op de mate van aannemelijkheid (*likelihood*), de mate van overeenkomst tussen de gesimuleerde en de waargenomen waarden voor een aantal onderzochte meren, gecombineerd met reeds vooraf beschikbare kennis over de modelstructuur en –parameters. Deze strategie beoogt een optimale balans tussen rekening houden met de onzekerheid in de gegevens en de onzekerheid in het model. Anders gezegd, er wordt naar gestreefd om het beste te halen uit twee werelden, gemodelleerde proceskennis enerzijds en waarnemingen aan reële meren anderzijds.

Een set met zowel invoer- als meetgegevens over ruim 40 meren van verschillende typen en met verschillende ecologische toestand (zowel ‘heldere’ als ‘troebele’), afkomstig uit verschillende bronnen, werd gebruikt voor de analyse van *PCLake*. De mate van overeenkomst tussen gesimuleerde en gemeten waarden, de *likelihood*-functie, werd gebaseerd op de meerjarige zomergemiddelden van totaal-fosfor, totaal-stikstof, chlorofyl-*a*, zichtdiepte en plantenbedekkingsgraad, waarbij de scores voor alle meren werden gecombineerd (hoofdstuk 4).

Als eerste stap werd een gevoeligheidsanalyse uitgevoerd om uit de complete set parameters en invoerfactoren de meest gevoelige te selecteren. Dit werd gedaan met de Morris-methode, een *screening*-methode, die een globale rangorde van het belang van de diverse parameters aangeeft, en de ‘FAST’ methode, die een meer kwantitatieve gevoeligheidsmaat geeft en die werd toegepast voor een subset van de parameters. De gevoeligheid voor de parameters werd zowel bepaald voor de uitvoervariabelen zelf (bijv. de chlorofyl-*a*-concentratie) als voor de mate van overeenkomst tussen gesimuleerde en gemeten waarden. De meest gevoelige parameters en invoerfactoren waren, in volgorde van belangrijkheid: fosforbelasting, stikstofbelasting, waterdiepte, watertoevoer, resuspensieparameters, filtratiesnelheid en voedselpreferentiefactoren van zoöplankton, sedimentatiesnelheden, maximale groeisnelheid van fytoplankton en waterplanten, groeisnelheid van vis, infiltratiesnelheid, overwinterende waterplantenfractie, minimum nutriëntengehalte van fytoplankton, mineralisatiesnelheid.

Om de parameterset(s) te vinden die goed aansluit(en) bij de meetgegevens werden tien procesparameters uit deze lijst gevarieerd. Met elk van de parametercombinaties werden simulaties uitgevoerd voor alle voorbeeldmeren, en de aannemelijkheid van elke *run* werd berekend. De beste *run* werd gebruikt voor de standaardwaarden van de parameters. Alle ‘redelijke’ *runs* samen werden gebruikt om de spreiding (variabiliteit) in de modeluitkomsten te schatten. De simulaties (met gebruik van de waarden van de ‘beste *run*’) kwamen voor de meeste voorbeeldmeren redelijk goed overeen met de gemeten waarden van totaal-fosfor, chlorofyl-*a*, waterplantenbedekking en relatieve zichtdiepte (= zichtdiepte in verhouding tot de waterdiepte), maar minder goed voor totaal-stikstof. Bovendien kwam het verband tussen deze variabelen gevonden in de simulaties redelijk overeen met elders afgeleide empirische relaties. Dit betekent dat het model een redelijke afspiegeling vormt van de belangrijkste processen in dit type meren.

Vervolgens is het gedrag van het model systematisch nagegaan door het uitvoeren van langjarige simulaties voor een aantal ‘hypothetische meren’ van verschillend type, die werden belast met verschillende hoeveelheden nutriënten, van laag tot hoog (hoofdstukken 5-6). Elke simulatie werd uitgevoerd voor twee begincondities, respectievelijk een troebele toestand gedomineerd door fytoplankton en een heldere toestand met veel onderwaterplanten. De gesimuleerde langetermijnuitkomst (chlorofyl-*a* of onderwaterplantenbedekking) als functie van de nutriëntentoevoer was in het algemeen sterk niet-lineair en vertoonde hysterese, hetgeen betekent dat de terugweg anders verloopt dan de heenweg. De kritische belasting voor herstel van de heldere toestand lag altijd lager dan het omslagpunt voor de omgekeerde weg (‘vertroebeling’). Dit resultaat komt overeen met aanwijzingen verkregen uit andere recente theoretische en veldstudies, en kan worden verklaard door het feit dat beide toestanden in het bezit zijn van een aantal zelf-stabiliserende buffermechanismen. De hysterese komt dus als ‘onverwachte’ modeleigenschap (‘*emerging property*’) tevoorschijn uit de simulaties, als resultante van de aannamen en mechanismen die in het model zijn samengebracht.

Het model maakt het mogelijk om in te schatten hoe de kritische belasting afhangt van het type meer, en geeft het relatieve belang aan van verschillende factoren in verschillende meertypen (hoofdstuk 6). De waarden van de twee omslagpunten in het model blijken afhankelijk van meereigenschappen zoals de waterdiepte, de watertoevoer of verblijftijd, de oppervlakte, het bodemtype en de omvang van de moeraszone. Voor de typen meren die in Nederland het meest voorkomen wordt een kritische belasting voor ‘vertroebeling’ berekend van ongeveer 2–5 mgP m^{-2} d^{-1}, en een kritische waarde voor ‘opheldering’ (herstel) rond de 0.6–1.0 mgP m^{-2} d^{-1}, met een bijbehorende totaal-P-concentratie van 0.03-0.1 mgP/l. Van de in hoofdstuk 4 beschreven voorbeeldmeren heeft ongeveer 2/3 een belasting die hoger ligt dan de kritische waarde voor ‘vertroebeling’. Uit de Bayesiaanse onzekerheidsanalyse beschreven in § 4.5 blijkt dat de onzekerheid (variabiliteit) in de voorspelling van het ‘vertroebelingspunt’ wat hoger is dan die in het omslagpunt voor herstel.
Het model kan ook worden gebruikt om de mogelijke effectiviteit van beheersmaatregelen in een bepaald type meer te onderzoeken. Biomanipulatie (actief biologisch beheer) bijvoorbeeld zou op de lange duur alleen effectief zijn indien de nutriëntenbelasting een stuk lager ligt dan het omslagpunt voor ‘vertroebeling’. In het algemeen zijn de voorspelde waarden voor de omslagpunten redelijk goed in overeenstemming met empirische informatie.

Een vergelijkbare systematische analyse van kritische nutriëntenbelastingsniveaus is uitgevoerd voor sloten met behulp van het model *PCDitch* (hoofdstuk 7). De kritische belasting voor een omslag van onderwaterplanten naar kroosdominantie is berekend als functie van slootype en beheer. Waterdiepte, verblijftijd en bodemtype waren in het bijzonder van invloed op het kritische belastingsniveau. De voorspelde kritische waarden voor een omslag naar een kroosdek liepen uiteen van 2–10 gP m^{-2} y^{-1}, met bijbehorende totaal-fosfor-concentraties tussen 0.2–0.4 mgP l^{-1}. Hysterese kwam in de simulaties meestal tot uiting in het feit dat herstel van de watervegetatie na reductie van de belasting veel langer duurde dan de omslag naar kroos na verhoging ervan. Dit is vooral toe te schrijven aan de vertraagde reactie van het sediment. Er waren ook gevallen waar de kroos- en de onderwatervegetatiegedomineerde situaties alternatieve stabiele evenwichtstoestanden vormden, maar door maai- en slootbeheer komt dit soms niet tot uiting. Het model suggereert dat baggeren kan helpen om kroosdominantie te bestrijden, mits de externe nutriëntenbelasting niet te hoog is.

Het model *PCLake* was ook in staat om de waarnemingen in enkele *case studies* te reproduceren, waarbij in meer detail op de dynamiek werd ingegaan. De reactie van de Loosdrechtse Plassen op een in de jaren 1980 uitgevoerde verlaging van de fosfaatbelasting bijvoorbeeld, te weten een hoge mate van veerkracht van de troebele toestand, kon goed door het model worden gesimuleerd (hoofdstukken 8-10). De veerkracht kon worden toegeschreven aan een verhoogde efficiëntie van het gebruik van fosfaat (een lagere P/C-verhouding) door de cyanobacteriën (‘blauwalgen’), de sterke interne kringloop van fosfaat via resuspensie en de grote hoeveelheid brasem. Deze mechanismen zorgden ervoor dat de Loosdrechtse Plassen in de troebele toestand bleven ondanks de genomen maatregel.
Ook de effecten van een biomanipulatie-experiment dat is uitgevoerd in het meertje Zwemlust (nabij Loenen) konden door het model redelijk worden gereproduceerd (hoofdstukken 11-12). Na de verwijdering van alle witvis uit de plas verdween de fytoplanktondominantie en namen waterplanten het rijk over. In het begin waren daarbij vooral factoren ‘van bovenaf’ van invloed (zoöplankton kon de algen de baas doordat het niet meer werd opgegeten door jonge witvis), later ook factoren ‘van onderop’ (stikstoflimitering van de algengroei nadat de waterplanten zich goed hadden ontwikkeld). De structurele veranderingen in het systeem gingen samen met veranderingen in de verdeling en de fluxen van nutriënten. In dit geval zoomden we wat nader in op de invloed van verschillen in levenscyclus tussen plantensoorten. Zo deed een verschuiving naar andere (oneetbare, maar ‘zwakkere’) plantensoorten na enkele jaren, veroorzaakt door de komst van plantenetende vogels, het meertje weer omslaan naar de troebele toestand. De nutriëntenbelasting van het systeem was hoog.
Het positieve effect van moeraszones op de waterkwaliteit in meren is wat verder uitgewerkt in hoofdstuk 13. De modelresultaten kwamen goed overeen met het idee dat transport en sedimentatie, nutriëntenopname door moerasvegetatie en verbeterde condities voor roofvis daarbij de belangrijkste mechanismen zijn. Het model suggereert ook dat het effect op de nutriëntendynamiek alleen optreedt indien er een goede uitwisseling van water is tussen de moeraszone en het meer. In de praktijk zou die bijvoorbeeld worden bevorderd door waterpeilfluctuaties, zoals die vroeger in veel Nederlandse laaglandmeren voorkwamen.

Ook het slotenmodel *PCDitch* werd in enkele *case studies* toegepast waarbij wat nader op de details werd ingegaan. Wij maakten gebruik van de goed gedocumenteerde gegevens over de waterplantenontwikkeling in een serie experimentele sloten die werden belast met verschillende hoeveelheden nutriënten (hoofdstuk 14). De waargenomen ontwikkeling van ondergedoken waterplanten bij lage belasting, een toename van algen bij matig hoge belasting en een omslag naar kroos bij hoge belasting, kon goed door het model worden gesimuleerd. Verdere analyse en simulatie van slootsystemen in het veld en toetsing van het model is gaande.

Concluderend kan worden gezegd dat de in deze studie gepresenteerde modelbenadering, gebaseerd op de combinatie van biologische structuur en nutriëntenkringloop, een bruikbaar instrument kan zijn bij het onderbouwen van het beleid ten aanzien van nutriënten (o.a. het mestbeleid) en van het waterbeheer. Het model neemt een plaats in tussen minimodellen die bepaalde ecologische mechanismen op een sterk geabstraheerde wijze analyseren, en traditionele eutrofiëringsmodellen, die echter belangrijke voedselwebinteracties en de rol van waterplanten verwaarlozen. De gepresenteerde modellen kunnen worden gebruikt om de potentiële gecombineerde effecten van (beleids)opties op stroomgebiedsniveau en meer lokale (beheers)maatregelen te kunnen inschatten, inclusief de onzekerheden in die schattingen. De modellen maken het ook mogelijk om verschillen in gevoeligheid voor eutrofiëring tussen verschillende typen meren of sloten aan te geven. Dit kan bijdragen aan de ontwikkeling van gedifferentieerde normen voor natuur- en milieubescherming.

Curriculum vitae

De auteur van dit proefschrift werd op 21 september 1955 geboren in Zoetermeer, in een agrarische familie. Na de vooropleiding gymnasium _ aan het Haags Montessori Lyceum in Den Haag volgde hij de studie biologie aan de Rijksuniversiteit Utrecht, waar hij in 1982 afstudeerde met als doctoraalrichtingen o.a. natuurbeheer (aquatische richting, bij de Landbouwhogeschool in Wageningen), biologische toxicologie en milieukunde. Veel van de gekozen onderwerpen hadden direct of indirect met water te maken. Naast de studie werkte hij enige jaren als student-assistent bij de vakgroep Milieukunde. Hij werkte een jaar bij het Zuiveringschap Amstel- en Gooiland aan een modelstudie over de Vechtplassen. Bij het Rijksinstituut voor Natuurbeheer (thans opgegaan in Alterra) verrichtte hij in opdracht van Rijkswaterstaat een literatuurstudie over de uiterwaardenplassen, ten behoeve van de ontwikkeling van ecologische doelstellingen. Daarna werkte hij bij de Landbouwuniversiteit Wageningen en voerde daar een landelijk onderzoek uit naar de eutrofiëring van meren en plassen, in opdracht van de Coördinatiecommissie Uitvoering Wet Verontreiniging Oppervlaktewateren. Sinds 1987 is hij verbonden aan het Rijksinstituut voor Volksgezondheid en Milieu, sector Milieu-onderzoek (thans Milieu- en Natuurplanbureau), eerst bij de afdeling Modellering van het Laboratorium voor Ecotoxicologie, Milieuchemie en Drinkwater, later het Laboratorium voor Water en Drinkwater, thans bij het team Natuur, Landschap en Biodiversiteit. Hij werkte mee aan het project Waterkwaliteitsonderzoek Loosdrechtse Plassen, een samenwerkingsverband van zeven instituten. In dit project werd de basis gelegd voor het model *PCLake*. Later werd dit model verder ontwikkeld en veralgemeniseerd tot een ecologisch model voor eutrofiëring en herstel van meren. In een parallel project werd ook een model voor eutrofiëringseffecten in sloten ontwikkeld. Bij beide projecten werd samengewerkt met verschillende instituten elders en met waterbeheerders. In dit kader werd ook deelgenomen aan een aantal internationale symposia. Daarnaast werkte de auteur mee aan de ontwikkeling van ecotoxicologische modellen ten behoeve van het toxischestoffenbeleid, in samenwerking met het Instituut voor Onderzoek van Bestrijdingsmiddelen in Wageningen (thans opgegaan in Alterra). De auteur werkte mee aan toegepaste projecten zoals ‘Onderbouwing normstelling oppervlaktewater’, ‘Evaluatie meststoffenwet’ en ‘Natuurlijke zuivering van oppervlaktewater’, in opdracht van het Ministerie voor Milieubeheer, en aan de nationale Milieu- en Natuurverkenningen, en aan meer theoretische zoals ‘Stabiliteit van ecosystemen’, samen met onder meer de Universiteit Wageningen. Hij nam deel aan een EU-project over ‘Biodiversiteit en menselijke beïnvloeding in ondiepe meren’, een samenwerkingsverband van instituten in België, Denemarken, Duitsland, Spanje en Nederland. De auteur was enige jaren bestuurslid van de Nederlands-Vlaamse Vereniging voor Aquatische Ecologie (thans opgegaan in de NecoV), en nam en neemt deel aan verschillende begeleidingscommissies en werkgroepen op het gebied van modellering, onderzoek of beheer van watersystemen.

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