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PCLoos: a eutrophication model of the Loosdrecht Lakes

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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. Both the water and the upper sediment layer are modelled. The model comprises three algal groups, zooplankton, fish, detritus, zoobenthos and upper sediment (all modelled both in carbon and in phosphorus) besides inorganic phosphorus (SRP) in both the surface water and the interstitial water. Within the model system, the phosphorus cycle is completely closed. Carbon and phosphorus are described independently, so that dynamics of 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. The 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 P/C ratios of zooplankton and fish remain constant and much higher. Phosphorus mobilisation from the sediment decreases with decreasing external input. Adaptation of the model system to the reduced loading takes place in about two years. This means that without additional measures no further changes in the system are to be expected. Further reduction of phosphorus loading will lead to an improvement of water quality.

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

Samenvatting

In dit rapport wordt een dynamisch, deterministisch model beschreven waarmee de fosfaatkringloop en planktongroei in de ondiepe, sterk ge-eutrofieerde Loosdrechtse Plassen kan worden gesimuleerd voor en na de uitgevoerde beheersmaatregelen. Zowel de waterfase als de bovenste sedimentlaag is gemodelleerd. Het model omvat drie fytoplanktongroepen, zoöplankton, vis, detritus en bodemdetritus (alle gemodelleerd in twee eenheden: koolstof en fosfor), alsmede opgelost reactief fosfaat (SRP) in zowel het oppervlaktewater als het poriënwater. De koolstof-en fosforcycli worden in principe onafhankelijk van elkaar beschreven, zodat de dynamiek van de P/C-ratio's kan worden gemodelleerd. De sedimentprocessen zijn opgenomen in vereenvoudigde vorm.

De simulatieresultaten voor de jaren 1982 t/m 1987 zijn in grote lijnen vergelijkbaar met meetgegevens in het veld. De detritusfractie van het seston (= fytoplankton + detritus) varieert van 50-60 % in de zomer tot ongeveer 90% in de winter. De concentratie opgelost reactief fosfaat in het water is gedurende het grootste deel van het jaar erg laag. De gevoeligheid voor de externe fosfaatbelasting is sterker voor fytoplankton- en detritus-fosfaat dan voor fytoplankton- en detritus-koolstof en chlorofyl a. Dit betekent dat de fosfaat/koolstof-verhouding (P/C ratio) van het seston lager wordt na de uitgevoerde beheersmaatregelen, zoals ook in het veld is waargenomen, terwijl de P/C ratio's van zoöplankton, zoöbenthos en vis constant blijven en bovendien veel hoger zijn. De mobilisatie van fosfaat uit het sediment neemt enigszins af met afnemende externe belasting. Het modelsysteem past zich in ongeveer twee jaar aan een veranderde fosfaatbelasting aan. Dit houdt in dat er zonder aanvullende beheersmaatregelen geen verdere veranderingen in het systeem te verwachten zijn. Verdere reductie van de fosfaatbelasting zal wèl tot een verbetering van de waterkwaliteit leiden.

Bronnen van onzekerheid in het model zijn met name de beperkte kennis op het gebied van sterfte- en mineralisatieprocessen, selectieve graas en de processen met betrekking tot vis.

1 Introduction

Within the framework of the interdisciplinary WQL project (Water Quality research Loosdrecht Lakes or WaterkwaliteitsOnderzoek Loosdrechtse Plassen), a cooperation of eight Dutch institutes and institutions, an extensive research programme is being performed in the shallow, hypertrophic Loosdrecht Lakes (The Netherlands). The aim of this programme, which started fully in 1983, is to describe and quantify the effects of phosphorus load reduction on the functional and structural aspects of the lake ecosystem and to contribute to water management measures.

One of the tools to achieve this goal is the development of a mathematical model of the lake ecosystem, a project being undertaken by the RIVM (National Institute of Public Health and Environmental Protection). The aims of this effort are:

- to contribute to a better understanding of the functioning of the aquatic ecosystem and to formulate gaps in our knowledge.
- to provide a predictive tool to evaluate the effects of possible recovery measures.

The model described in this report is called *PCLoos* version 2.4. It has been developed from mid 1987 until mid 1989 and is the result of successive revisions. It has been built largely from the ground up, but is based partly on the 'first step' model by Kouwenhoven & Aldenberg (1986), now called '*PCLoos* version 1'. Subsequent interim versions are documented upon by Aldenberg (1987a, 1987b), Janse (1987, 1988) and Aldenberg & Peters (1988). The current model will be extended and improved further in future versions.

After a brief introduction about the Loosdrecht Lakes system (Chapter 2), this report describes the basic principles of the model (Chapter 3), the model structure and process formulations (Chapters 4 and 5), calibration and implementation (Chapter 6) and the results of performed simulations (Chapter 7). In Chapter 8, the model results are discussed and implications for future model development as well as recommendations for experimental research are indicated.

2 The Loosdrecht Lakes system

An overview of the lake system is given by Van Liere et al. (1984) and Van Liere (1986); only a brief summary will follow here.

The Loosdrecht Lakes are a system of shallow lakes, situated between Amsterdam and Utrecht (The Netherlands) (Figure 1). Their origin is due to peat mining in the 17th century. The system consists of four interconnected lakes, of which the general characteristics are given in Table 1. (The Loenderveen Lakes are hydrologically isolated from the system.) The originally mesotrophic lakes, with clear water and a great diversity in flora and fauna, became rapidly eutrophic from about 1950 onwards due to increased nutrient loadings. These were mainly due to the inlet of nutrient-rich water from the river Vecht during summer, necessary to replenish the lakes when upward seepage of ground water diminished. This, in turn, is caused by the increased extraction of ground water in the nearby sandy hills of Het Gooi and the Utrechtse Heuvelrug.

Table 1. *General characteristics of the Loosdrecht Lakes (Data from Engelen et al., 1988 and Buijse, 1989)*

Lake	Water area	Total area	Mean depth	Volume	Average water residence time
	$10^6 m^2$	$10^6 m^2$	m	$10^6 m^3$	days
Lake Loosdrecht	9.891	11.035	1.91	18.892	290
Kievitsbuurt	2.106	2.649	2.48	5.223	250
L.Loosdr.+Kievitsb.	11.997	13.684	2.01	24.115	280
Lake Breukeleveen	1.572	2.365	1.45	2.279	140
Lake Vuntus	0.902	1.23	1.36	1.227	270
Total	14.471	17.280	1.91	27.621	250

The structure of the Loosdrecht ecosystem now reflects the one commonly found in hypertrophic shallow lakes (Van Liere et al., 1989a; Van Liere et al., 1989b). Aquatic plants disappeared and the lakes became dominated by filamentous blue-green algae, mainly *Oscillatoria limnetica* and the recently discovered prochlorophyte *Prochlorothrix hollandica*, but also other *Oscillatoria* species (Boesewinkel-de Bruyn et al., 1988). Transparancy as measured by a Secchi disk is about 0.30 m. Mean algal concentration increased to about 150 µg chlorophyll-*a* per liter in summer, total seston concentration to about 20 - 40 mg dry weight per liter; about 2/3 of this consists of dead particles (detritus). Also zooplankton increased, but to a much lesser extent as the seston: the zooplankton/seston ratio decreased from 0.38 to 0.04 - 0.07 between 1955 and 1987 (Van Liere, 1986; Siewertsen, 1988). Within the zooplankton, there has been a shift towards smaller species. The fish community mainly consists of Bream

(*Abramis brama*), feeding on the high stock of midge larvae (*Chironomus plumosus*) in the sediment. Fish contains nearly 50% of the phosphorus in the lake. Total phosphorus in the water (excl. fish) averages 100 - 130 µg/l in summer and total nitrogen about 1.5 - 3 mg/l. Ortho-phosphate is only present in very low concentrations.

Recently, external input to the lakes has been diminished by diversion and treatment of waste water from the surrounding villages (effected between 1970 and 1985) and by replacement of Vecht water supply by dephosphorised water from the Amsterdam-Rijn-kanaal, from 1984 onward. A phosphorus-oriented approach was expected to be most promising. Yearly-averaged phosphorus input to the system has decreased from 1 g $P/m^2/yr$ in 1983 to 0.3 g $P/m^2/yr$ in 1986 (Engelen et al., 1988); reduction took place only in summer, whereas in winter the loading gradually increased due to input from the surrounding polders. In the five years following restoration measures, water quality has hardly changed. However, phosphorus limitation of algal growth tends to become more stringent (Van Liere et al., 1988). Additional measures are being planned.

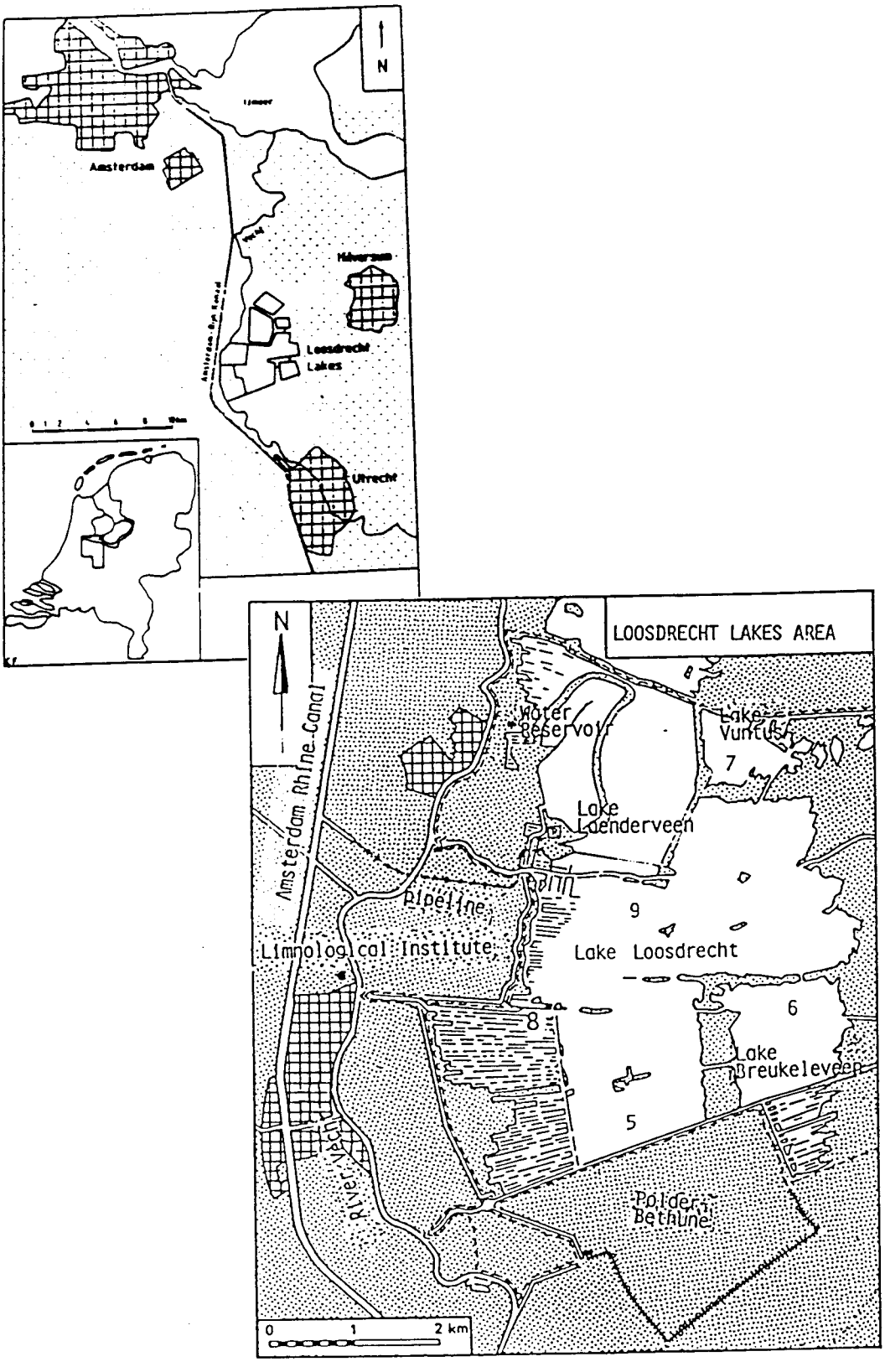
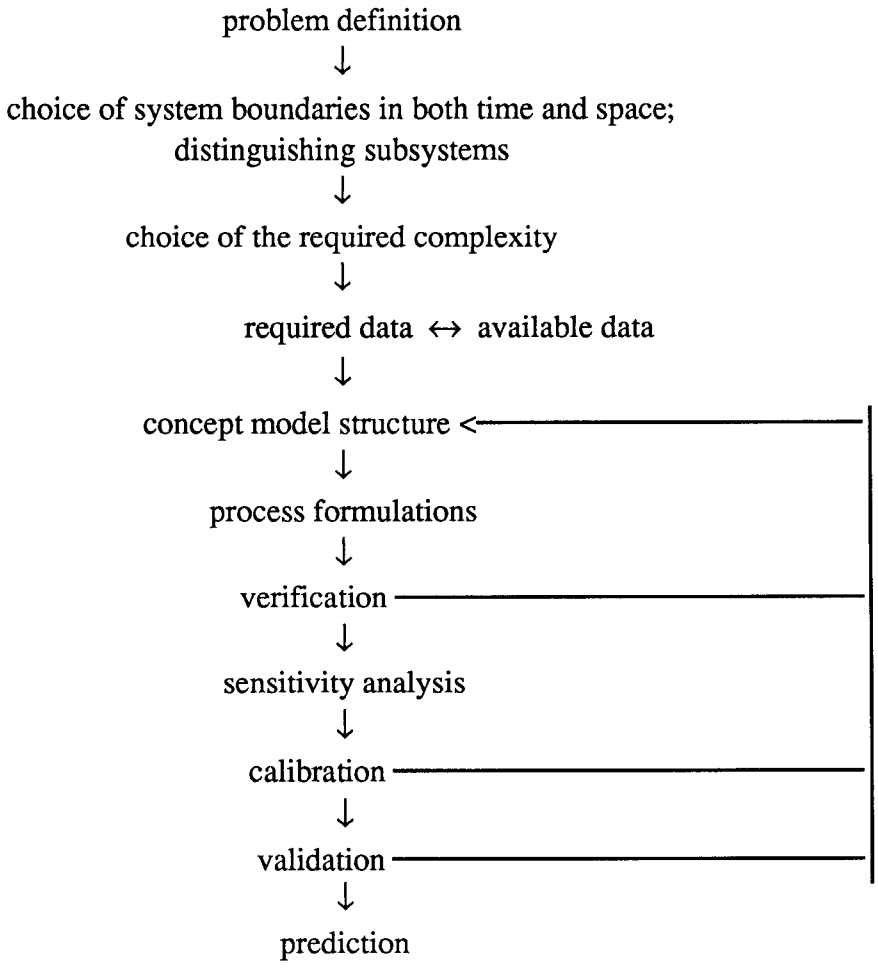


Fig. 1. The Loosdrecht Lakes.
(from Engelen and Kal, 1985 and Gulati *et al.*, 1987)

3 Model development

3.1 Introduction

Development of a model of an ecosystem is an iterative process, in which the following steps can be distinguished (after Jørgensen, 1980):



The problem definition is already clear from the objective of the WQL project: understanding the mechanisms of the eutrophication process and evaluating the effects of recovery measures. The second and third step in this scheme, the choice of subsystems and complexity, are discussed in the next paragraphs. On the fourth point, the availability of data, it can be said that within the frame of the WQL project a large amount of data are collected, which contribute to model development. There are, however, some gaps in the research programme; this matter is discussed in chapter 8. After the model structure and the process equations are formulated, a verification step reveals whether the gross behaviour of the model is correct. During sensitivity analysis, the effect of variations in certain parameters (input values or process rates) on the model output is tested. During calibration, some parameters are modified to improve model output and resemblance between model and data. Before a model is apt to make predictions, a validation step is needed, which means that the model is tested on a more or less identical

system which differs only in input (e.g. external P loading). Often this requirement is not fulfilled, because of the lack of such a system. Also the present model needs a more extensive validation procedure in the near future. Therefore, simulations of possible measures decribed in this report are only preliminary.

3.2 Choice of complexity

A standard ecosystem model is composed of a number of compartments (state variables), which are linked to each other by means of mass fluxes (processes). Compartments are for instance: phytoplankton, zooplankton, SRP, detritus, etc. The mass fluxes are calculated dynamically (varying in time) on an infinitesimal basis. Mathematically, this is performed by solving a set of linked differential equations. Since the early seventies, when the development of ecological models for water quality management started, a number of eutrophication models have been described. These models vary greatly in structure. Besides differences in the exact process equations and parameter values, the models may differ in two main aspects:

(1) the complexity of the trophic web in the model;
(2) the relation between the nutrient cycle and the carbon (or biomass) cycle. (This aspect is discussed in the next paragraph.)

The number of state variables in eutrophication models varies from 1 to about 40 (see Jørgensen, 1980 for an overview). Models differ for instance in the number of algal groups described, the number of zooplankton groups, inclusion of higher trophic levels or not, one or two detritus pools, the included nutrients (nitrogen, phosphorus and/or silicon), inclusion of chemical equilibria or not, inclusion of sediment compartments, etc. Furthermore, horizontal or vertical differences in the system may or may not be modelled. Parts of the system which are not modelled explicitly are considered as external. They are often taken as constants or described by measurements.

No general answer can be given to the question how complex a certain model should be, i.e. the question which subsystems should be included explicitly. The choice primarily depends on:

- the objective of the model
- the available ecological knowledge on the system
- the available data

There exists an optimum between model complexity and model reliability, of which the position depends on both the system under consideration and the objectives of the research project (see *e.g.* Auer & Canale, 1986; Jørgensen, 1980; Benndorf et al., 1985; Straskraba & Gnauck, 1986). But unfortunately, no one can tell where this optimum lies in general. The ecological system itself is of course extremely complicated. It has been argued that the more complex a model is, the better and the more reliable it should be able to image reality. This, however, is in general not true: expansion of a model implies a larger number of parameters (rate constants etc.) and therefore a greater uncertainty. Therefore, it is better to add or split compartments and processes only if there is enough knowledge about them. Benndorf et al. (1985) recommend to use a limited number of state variables and to put extra ecological knowledge in the complexity of the process equations linking them.

At the opposite side of the spectrum are the overly-simple models. They mostly fail to provide an adequate description of the system because processes or feedbacks known to be important are overlooked. The realistic and predictive values of such models are very limited and the uncertainty in the simulation results increases again. However, simple models of parts of the system (the most simple ones called 'minimodels') can be a valuable tool when building or calibrating a more complex model and can give a quick insight in the consequences of certain options. In this project, besides the main model we have also used submodels for the phytoplankton, the sediment system and the carbon cycle.

In the WQL project we have chosen the simplest model structure which is still assumed to retain enough realistic value. It includes the main processes which determine the present hypertrophic state of the lake system. The resulting model structure is necessarily a compromise. This matter has been discussed in the WQL working group on modelling.

Because our objective is a phosphate-eutrophication model, in any case it is necessary to consider the compartments phytoplankton, zooplankton, detritus and SRP. (Because nitrogen is at present not a limiting nutrient in the Loosdrecht Lakes, it is not taken into account within the WQL project as a whole.) The model includes a fish compartment, bearing in mind that fish (mainly Bream) contains more than 50 percent of the total phosphate pool of the system (Van Liere et al., 1988). Zoobenthos has been included because it is a major component in the diet of Bream. In order to be able to model possible shifts in species composition, phytoplankton has been split up in three functional groups: "blue-greens", "greens" and "diatoms", with different growth characteristics and loss coefficients. For the sake of simplicity, only one detritus pool is included in the model.

Within the frame of the WQL project, a lot of research is and has been done, providing information on the ecological relations in the system which is used in the model. Some subjects, however, are currently not covered by the research programme and this is reflected in great uncertainties in some of the model formulations. These include selective grazing by zooplankton, fish predation and mineralisation processes. Process-oriented research on these topics is needed.

3.3 The relation between phosphorus and carbon cycle

A very 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 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. When making a model, it is very important to keep this fact in mind in order to achieve a closed cycle for all modelled substances at any time.

In many existing models, this problem is not adequately dealt with, often even 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 (Aldenberg, 1987a). In the first version of the current model (*PCLoos* 2.1) (Aldenberg 1987b), which has (in steady state) been applicated to the Waterleidingplas (the "Reservoir" or Lake Middle Loenderveen) (Aldenberg & Peters 1988) and Lake Loosdrecht (Janse, 1987), the P/C ratio of the detritus has been used for this purpose; the ratios of phyto- and zooplankton were kept constant. This model therefore has as state variables: phytoplankton C, zooplankton C, detrital C, detrital P and SRP. The version being described in this report *(PCLoos* 2.4) has maintained the basic features of this model, i.e. a closed phosphorus cycle at any time and differences in P/C ratios between compartments. This means that for every C compartment a corresponding P compartment is present.

3.4 The sediment subsystem

In order to achieve a closed P cycle also in the sediment subsystem and to be able to model changes in internal nutrient loading, it is necessary to model at least two phosphate fractions in the sediment dynamically: an organically bound fraction and a fraction solved in the interstitial water. One biotic component, the zoobenthos, is also included. Only the upper layer of the sediment (2 cm) is modelled, which seems sufficient for the time being. Future extensions to the sediment submodel will be made in view of the sediment models being developed at the Institute of Inland Water Management and Waste Water Control (DBW/RIZA) (P.C.M. Boers, D.T. van der Molen, E. Achterberg), Delft Hydraulics (WL) (J. Bril) and the Limnological Institute (LIN) (A. Sinke, O. van Tongeren).

4 Model structure

4.1 State variables

The model (PCLoos 2.4) is composed of the following 18 state variables, 13 of which form the water phase and 5 the sediment phase; C denotes the carbon fraction and P the corresponding phosphorus fraction.

In the water phase we have:

CDiat [mgC/l]	;	*PDiat* [mgP/l]	diatoms
CGreen [mgC/l]	;	*PGreen* [mgP/l]	green algae
CBlue [mgC/l]	;	*PBlue* [mgP/l]	blue-green algae
CHerb [mgC/l]	;	*PHerb* [mgP/l]	zooplankton
CFish [mgC/l]	;	*PFish* [mgP/l]	fish
CDet [mgC/l]	;	*PDet* [mgP/l]	detritus
		PSol [mgP/l]	soluble reactive phosphorus (SRP)

and in the sediment phase:

CSed [mgC/l sed]	;	*PSed* [mgP/l sed]	organic material in upper sediment
CBent [gC/m^2]	;	*PBent* [gP/m^2]	zoobenthos
		PInts [mgP/l pore water]	soluble reactive phosphorus in the interstitial water

Please note: There are no corresponding compartments "*CSol*" and "*CInts*", because CO_2 is not included; carbon is assumed never to be growth limiting.)

4.2 Processes

The state variables are linked by the following processes (mass fluxes or, better, concentration effects), mostly expressed in mg/l/d. The corresponding C and P processes are always stated together.
An asterisk (*) denotes that C and P process are not linked; explanation follows later on.

Phytoplankton processes:

CInl(i) [mgC/l/d]	;	*PInl(i)* [mgP/l/d]	external loading and dilution of species *i*	
CAss(i) "	;	*PUpt(i)* "	growth and P uptake by species *i*	*
CResp(i) "	;	*PExcr(i)* "	respiration and P excretion by species *i*	*
CMort(i) "	;	*PMort(i)* "	mortality of species *i*	
CSett(i) [gC/m^2/d]	;	*PSett(i)* [gP/m^2/d]	sedimentation of species *i*	

Please note: These processes are defined for all three algal groups: diatoms (with suffix *-Di*), greens (with suffix *-G*) and blue-greens (with suffix *-B*). All algae together are denoted by the suffix *-Ph.*

Zooplankton processes

CInlH [mgC/l/d]	;	*PInlH* [mgP/l/d]	external loading and dilution	
CConsDiH "	;	*PConsDiH* "	consumption of diatoms by zooplankton	
CConsGH "	;	*PConsGH* "	consumption of greens by zooplankton	
CConsBH "	;	*PConsBH* "	consumption of blue-greens by zooplankton	
CConsDH "	;	*PConsDH* "	consumption of detritus by zooplankton	
CAssH "	;	*PAssH* "	assimilation of consumed food by zooplankton	*
CEgesH "	;	*PEgesH* "	egestion of unassimilated food by zooplankton	*
CRespH "	;	*PExcrH* "	respiration and P excretion by zooplankton	*
CMortH "	;	*PMortH* "	mortality of zooplankton	

Fish processes

CPredHF [mgC/l/d]	;	*PPredHF* [mgP/l/d]	predation of fish on zooplankton	
CFeedBeF "	;	*PFeedBeF* "	feeding of fish on zoobenthos	
CAssF "	;	*PAssF* "	assimilation of consumed food by fish	*
CEgesF "	;	*PEgesF* "	egestion of unassimilated food by fish	*
CRespF "	;	*PExcrF* "	respiration and P excretion by fish	*
CMortF "	;	*PMortF* "	fish mortality	
CHarvF "	;	*PHarvF* "	fish harvesting	

Processes involving detritus:

CInlD [mgC/l/d]	;	*PInlD* [mgP/l/d]	external loading and dilution	
CDecD "	;	*PMinD* "	decomposition and mineralisation	(*)
CSettD [gC/m^2/d]	;	*PSettD* [gP/m^2/d]	sedimentation of detritus	
CResuD "	;	*PResuD* "	resuspension of detritus	

Processes in upper sediment:

CDecSe [mgC/l sed./d]	;	*PMinSe* [mgP/l sed./d]	decomposition and mineralisation of upper sediment	(*)
		PPrecI [mgP/l pore water/d]	loss of interstitial SRP to deeper sediment	
		PDiffIS [gP/m^2/d]	diffusion of SRP to surface water	

Processes involving zoobenthos:

CEatSeBe [gC/m^2/d]	;	*PEatSeBe* [gP/m^2/d]	feeding of zoobenthos on sediment	
CAssSeBe "	;	*PAssSeBe* "	assimilation of consumed sediment by zoobenthos	*
CEgesBe "	;	*PEgesBe* "	egestion of unassimilated sediment by zoobenthos	*
CRespBe "	;	*PExcrBe* "	respiration and P excretion by zoobenthos	
CMortBe "	;	*PMortBe* "	zoobenthal mortality	

Although nearly all compartments and processes are represented twice (*i.e.* allow for separate modelling in two units: carbon and phosphorus), in most cases the corresponding C and P processes are directly linked. This means that the P process equals exactly the C process times the P/C ratio of the compartment. In some cases, however, corresponding processes are independent and can contribute to diffferences in P/C ratios between trophic levels etc. These are:

- growth and P uptake by algae
- assimilation and egestion of food by animals (different assimilation efficiencies for C and P); this is true for zooplankton, fish and zoobenthos.
- respiration and P excretion by the organisms (algae, zooplankton, fish and zoobenthos.
- during mortality of organisms: a (small) part of the P fraction in the died organisms is added to the SRP pool, due to autolysis, the remainder to the detritus P, thus changing the P/C ratio of the detritus.
- during egestion by zooplankton and fish, a part of the egested P becomes available in soluble form, the remainder becoming detrital P. This also changes the P/C ratio of the detritus.
- decomposition and mineralisation: in principle, different decay rates for C and P are possible; in the present version, however, they are taken identical.

4.3 Differential equations

The model is formed in the following way. For each state variable a differential equation is written down, the right side of which is the sum of the processes involving the particular state variable. Fluxes going into the state variable are added, fluxes going from it are subtracted. The set of 18 linked differential equations forms the model, which can be solved numerically. The differential equations are:

In the water phase:

$$\frac{d[CDiat]}{dt} = CInlDi + CAssDi - CRespDi - CMortDi - \frac{CSettDi}{H} - CConsDiH$$

Diatoms [mgC/l/d]

$$\frac{d[PDiat]}{dt} = PInlDi + PUptDi - PExcrDi - PMortDi - \frac{PSettDi}{H} - PConsDiH$$

Diatoms [mgP/l/d]

$$\frac{d[CGreen]}{dt} = CInlG + CAssG - CRespG - CMortG - \frac{CSettG}{H} - CConsGH$$

Greens [mgC/l/d]

$$\frac{d[PGreen]}{dt} = PInlG + PUptG - PExcrG - PMortG - \frac{PSettG}{H} - PConsGH$$

Greens [mgP/l/d]

$$\frac{d[CBlue]}{dt} = CInlB + CAssB - CRespB - CMortB - \frac{CSettB}{H} - CConsBH$$

Blue-greens [mgC/l/d]

$$\frac{d[PBlue]}{dt} = PInlB + PUptB - PExcrB - PMortB - \frac{PSettB}{H} - PConsBH$$

Blue-greens [mgP/l/d]

$$\frac{d[CHerb]}{dt} = CInlH + CAssH - CRespH - CMortH - CPredHF$$

Zooplankton [mgC/l/d]

$$\frac{d[PHerb]}{dt} = PInlH + PAssH - PExcrH - PMortH - PPredHF$$

Zooplankton [mgP/l/d]

$$\frac{d[CFish]}{dt} = CAssHF + CAssBeF - CRespF - CMortF - CHarvF$$

Fish [mgC/l/d]

$$\frac{d[PFish]}{dt} = PAssHF + PAssBeF - PExcrF - PMortF - PHarvF$$

Fish [mgP/l/d]

$$\frac{d[CDet]}{dt} = CInlD + CMortPh + CMortH + CEgesH - CConsDH + CEgesF + \\ + CMortFD - \frac{CSettD}{H} + \frac{CResuD}{H} - CDecD$$

Detritus [mgC/l/d]

$$\frac{d[PDet]}{dt} = PInlD + PMortPhD + PMortHD + PEgesHD - PConsDH + PEgesFD + \\ + PMortFD - \frac{PSettD}{H} + \frac{PResuD}{H} - PMinD$$

Detritus [mgP/l/d]

$$\frac{d[PSol]}{dt} = PInlS - PUptPh + PExcrPh + PMortPhS + PExcrH + PEgesHS + \\ + PMortHS + PExcrF + PEgesFS + PMortFS + PMinD + \frac{PDiffIS}{H}$$

Soluble reactive phosphorus [mgP/l/d]

In the sediment phase:

$$\frac{d[CSed]}{dt} = \frac{CSettToSe - CResuD}{z_s} - CDecSe - \frac{CEatSeBe - CEgesBe - CMortBe}{z_s}$$

Upper sediment [mgC/l sed./d]

$$\frac{d[PSed]}{dt} = \frac{PSettToSe - PResuD}{z_s} - PMinSe - \frac{PEatSeBe - PEgesBe - PMortBe}{z_s}$$

Upper sediment [mgP/l sed./d]

$$\frac{d[PInts]}{dt} = \frac{PMinSe}{Por} + \frac{PExcrBe}{z_s \cdot Por} - \frac{PDiffIS}{z_s \cdot Por} - PPrecI$$

Interstitial SRP [mgP/l pore water/d]

$$\frac{d[CBent]}{dt} = CEatSeBe - CFeedBeF \cdot H - CRespBe - CMortBe$$

Zoobenthos [gC/m^2/d]

$$\frac{d[PBent]}{dt} = PEatSeBe - PFeedBeF \cdot H - PExcrBe - PMortBe$$

Zoobenthos [gP/m^2/d]

Figures 2 and 3 give a schematic representation of the C and the P cycle in the model, respectively. In the surface water, there is a 'main cycle' (SRP → phytoplankton → detritus → SRP) with two 'subsidiary cycles', the first one via zooplankton and the second via zooplankton and fish. There is an exchange between detritus and upper sediment, while P mobilisation and fish feeding are fluxes from the sediment to the surface water.

Regarding the phosphorus cycle, the system boundary is the physical boundary of the lake, including the 'active' layer of the sediment. So the overall phosphorus balance is completely closed. The boundary of the carbon system is the boundary between organic and inorganic carbon: only the former is included in the model. Input-/output-terms of the model are: flow into the lake (dilution and external loading), losses to the 'deeper' sediment and fish harvesting; regarding carbon, also assimilation by algae, respiration by organisms and decomposition exceed the system boundary. All other processes are internal. All process formulations are discussed in the next chapter. A complete description of the model can be found in the appendix.

A final remark is that the model is spatially homogeneous: the lake is assumed to be completely mixed, both horizontally and vertically.

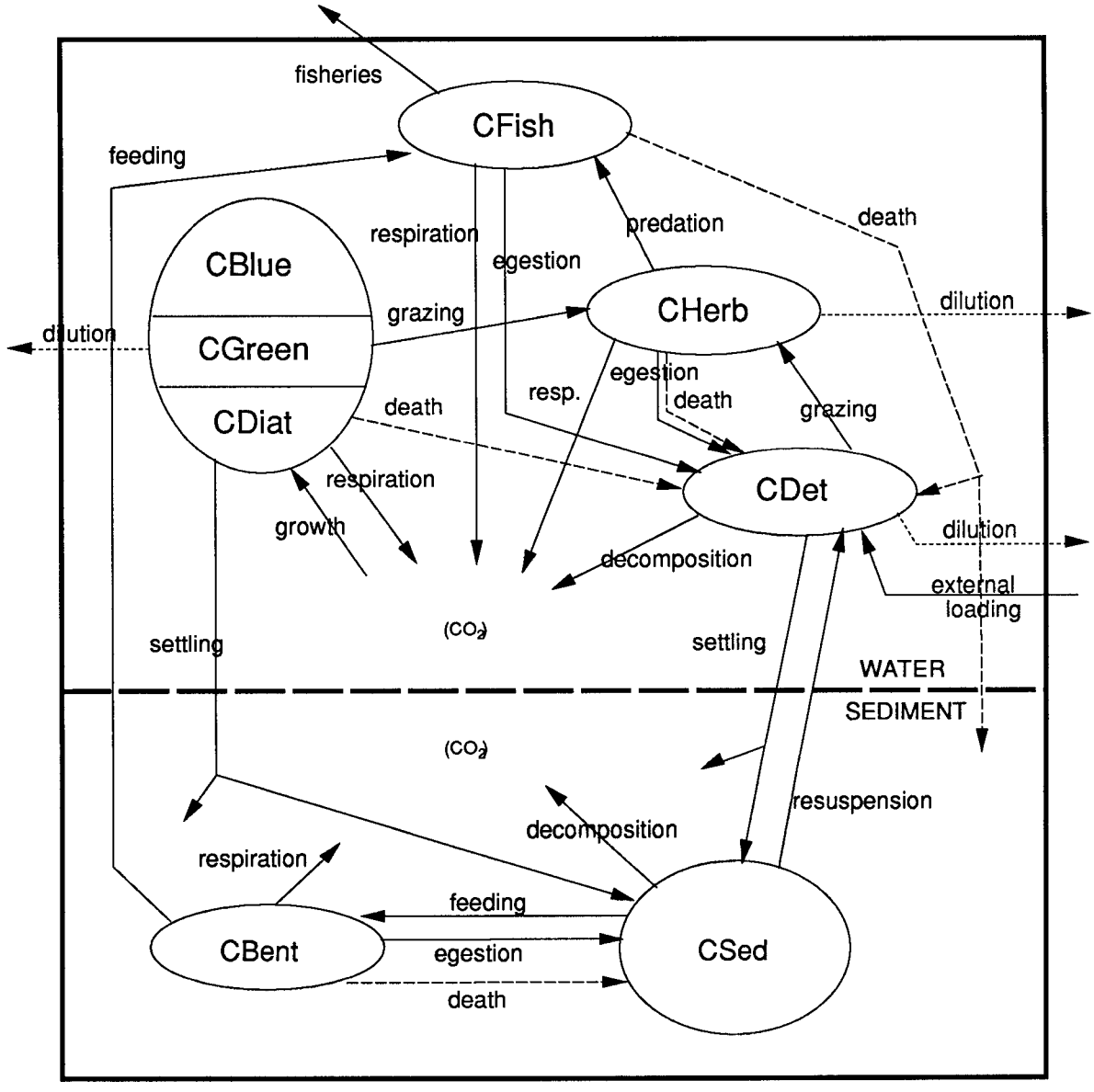


Fig. 2. The carbon cycle.

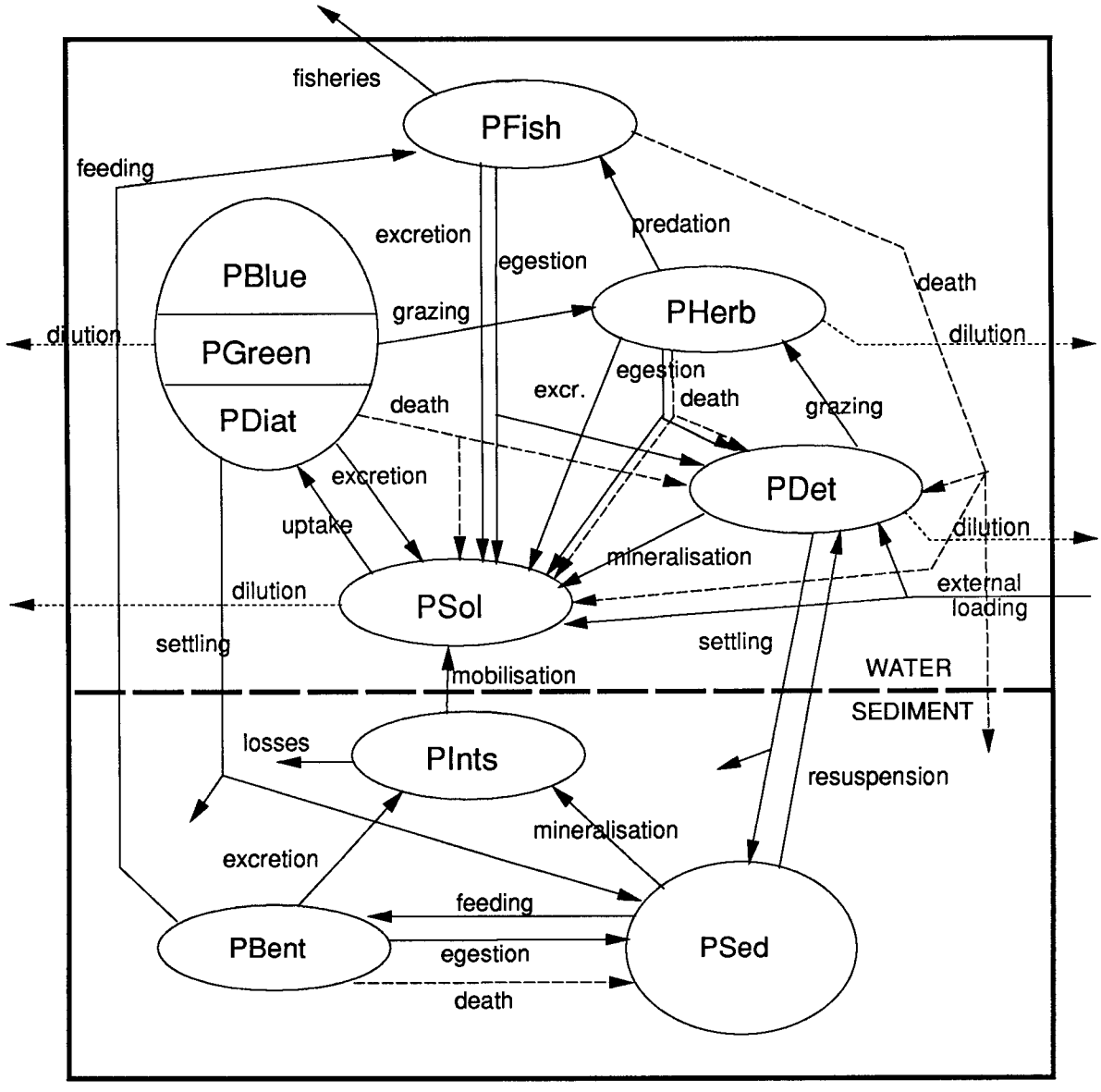


Fig. 3. The phosphorus cycle.

5 Description of processes

This chapter gives a detailed description of the processes included in the model.

5.1 External loading and dilution

In principle, all substances and particles are subject to the effects of external loading and dilution. For each one, the following mass balance should be matched at any time (with the assumption of a constant lake volume):

$$\frac{dC}{dt} = \frac{Q_{in(1)}}{V}\cdot(C_{in(1)}-C) + \frac{Q_{in(2)}}{V}\cdot(C_{in(2)}-C) + \ldots + \frac{Q_{in(n)}}{V}\cdot(C_{in(n)}-C) +$$

$$- \frac{Q_{out(1)}}{V}\cdot(C_{out(1)}-C) - \frac{Q_{out(2)}}{V}\cdot(C_{out(2)}-C) - \ldots - \frac{Q_{out(n)}}{V}\cdot(C_{out(n)}-C) \pm \qquad (5.1)$$

$$\pm \text{ in-lake processes}$$

with

$\frac{dC}{dt}$	change in concentration [mg/l/d]
$Q_{in(1)}, Q_{in(2)}, \ldots, Q_{in(n)}$	the different incoming water flows [m^3/d]
$C_{in(1)}, C_{in(2)}, \ldots, C_{in(n)}$	concentrations of the substance in the respective incoming flows [mg/l]
C	in-lake concentration [mg/l]
V	lake volume [m^3]
$Q_{out(1)}, Q_{out(2)}, \ldots, Q_{out(n)}$	the different water flows out of the lake [m^3/d]
$C_{out(1)}, C_{out(2)}, \ldots, C_{out(n)}$	concentrations of the substance in the respective outflows [mg/l]

As $Q_{in(n)} \cdot C_{in(n)} = L_n$, the loading from source n [g/d], this equation can be rewritten as:

$$\frac{dC}{dt} = \frac{L_1}{V} + \frac{L_2}{V} + \ldots + \frac{L_n}{V} - \frac{Q_{tot\text{-}in}}{V}\cdot C +$$

$$- \frac{Q_{out(1)}}{V}\cdot(C_{out(1)}-C) - \frac{Q_{out(2)}}{V}\cdot(C_{out(2)}-C) - \ldots - \frac{Q_{out(n)}}{V}\cdot(C_{out(n)}-C) \pm \qquad (5.2)$$

$$\pm \text{ in-lake processes}$$

The concentrations in all outflows, except the evaporation, are assumed equal to the in-lake concentration. As to the evaporation, the outflow concentration is zero. Now the equation reduces to:

$$\frac{dC}{dt} = \frac{L_1}{V} + \frac{L_2}{V} + \ldots + \frac{L_n}{V} - \frac{Q_{\text{tot-in}}}{V} \cdot C - \frac{Q_{\text{evaporation}}}{V} \cdot (-C) \pm \text{in-lake processes} \quad (5.3)$$

or

$$\frac{dC}{dt} = \frac{L_{\text{total}}}{V} - \frac{Q_{\text{tot-in}} - Q_{\text{evaporation}}}{V} \cdot C \pm \text{in-lake processes} \quad (5.4)$$

The first term in this equation denotes the external input of a given substance and the second term the dilution of it by the water flow through the lake. Together they are called *CInl(n)* (for carbon) or *PInl(n)* (for phosphorus) for every model compartment *n*. The entity $(Q_{\text{tot-in}} - Q_{\text{evaporation}})/V$ is called the *dilution rate* (*Dil*).

Actually, a simplification is being made with respect to the downward seepage, which amounts to an average 2 mm/d or 30 % of the total inflow minus evaporation. The outflow concentration in this water may not equal the in-lake concentration for all substances and a part of the substances removed in this way may be retained in the sediment.

The phosphorus load, water inflow and evaporation are read from the water and phosphate balance models developed by the Department of Earth Sciences of the Free University at Amsterdam (see Engelen et al., 1988 and Buijse, J.J., in press). These balances are made on a monthly base for the years 1982 t/m 1987 (the water balances from 1978 onward) for the four different parts of the Loosdrecht Lakes. The figures are recalculated in $mgP/m^2/day$ or mm/day and assumed constant within a given month.

Finally, the external phosphorus load should be divided over the different compartments (SRP, detrital P and biota) and the equivalent C load should be established. It is assumed that the inflow of biota (phytoplankton and zooplankton) is very limited; in fact, its main function is to prevent irreversible extinction of a species in the model. For zoobenthos and fish, external input and dilution are zero. The form in which phosphorus actually reaches the lakes is not known, but it is assumed that most of it is in particulate form. In the model, we have chosen arbitrarily 10 % soluble and about 87 % detrital phosphate. Together with the detrital (and biotic) phosphate input, an equivalent C input should be calculated. This is done by means of fixed P/C ratios of input: 0.0125 mg P/mg C for phytoplankton, 0.01 for detritus and 0.023 for zooplankton. The exact values of these parameters are not important for the model results.

5.2 Processes of the phytoplankton

5.2.1 P uptake and growth

In accordance with generally accepted theories, phosphate-dependent phytoplankton growth is modelled as a two-step process:

- phosphate uptake by the cells, dependent on both the actual phosphate content of the cell and the external SRP concentration.
- growth (defined here as the carbon fixation per 24 h), dependent on the actual phosphate content of the cell, besides light availability and temperature.

It is realised that this definition of growth is actually a simplification of reality, because growth involves not only carbon fixation but the balanced production of all cell components. However, for modelling purposes this definition seems sufficient.

Phosphorus uptake

Uptake rate as a function of external SRP concentration is often described as a Michaelis-Menten relation (e.g. Lehman et al., 1975; Jørgensen, 1980):

$$v = v_{max}(T) \cdot \frac{Q_{max} - Q}{Q_{max} - Q_{min}} \cdot \frac{PSol}{k_P + PSol} \tag{5.5}$$

in which

v	uptake rate	[mg P/mg C/d] (with 1 d = 24 h)
$v_{max}(T)$	maximum uptake rate	[mg P/mg C/d]
Q	phosphorus content of the cell or 'cell quota'	[mg P/mg C]
Q_{min}	minimum phosphorus content of the cell	[mg P/mg C]
Q_{max}	maximum phosphorus content of the cell	[mg P/mg C]
$PSol$	external SRP concentration	[mg P/l]
k_P	half-saturation constant	[mg P/l]

See (Figure 4a). However, research on the phosphate uptake by filamentous cyanobacteria like *Oscillatoria* learned that the initial uptake rate is independent of Q (Riegman, 1985) and that this equation needs to be modified. In the model, this is done by making the initial derivative of the above function a constant, called 'initial affinity', A_0 [l/mgC/d]. As

$$A_0 = \left.\frac{dv}{dPSol}\right|_{PSol=0} = \frac{v_{max}(T) \cdot \left(\frac{Q_{max} - Q}{Q_{max} - Q_{min}}\right)}{k_P} \tag{5.6}$$

this can be done by changing k_P into $\frac{v_{max}(T) \cdot \left(\frac{Q_{max} - Q}{Q_{max} - Q_{min}}\right)}{A_0}$. Rearrangement of terms yields:

$$v = \frac{PSol}{\frac{1}{A_0} + \frac{PSol}{v_{max}(T) \cdot \left(\frac{Q_{max} - Q}{Q_{max} - Q_{min}}\right)}} \tag{5.7}$$

In *Oscillatoria*, A_0 equals about 0.45 l/mgDW/h ≈ 20 l/mgC/d, v_{max} (at $Q = Q_{min}$) ≈ 0.9 µmol P/mg DW/h = 1.34 mgP/mgC/d, Q_{min} = 2.7 µg P/mgDW = 0.0054 mgP/mgC and $Q_{max} \approx 5 \times Q_{min}$ = 0.027 mgP/mgC (Riegman, 1985). (For greens and diatoms, the same function is used, with a lower affinity and v_{max}). Figure 4b gives a representation of this function. At the low SRP concentrations mostly met in the Loosdrecht Lakes, P uptake is almost proportional to the SRP concentration.

Finally, total phosphorus uptake equals:

$$PUpt(i) = v_i \cdot CPhyt(i) \qquad \text{[mgP/l/d]} \tag{5.8}$$

in which *CPhyt(i)* [mgC/l] stands for the algal species at concern.

As phosphorus uptake is defined as a flow of SRP to the phytoplankton, it cannot be negative; in case $Q \geq Q_{max}$, uptake will be zero. The opposite process P excretion, however, will increase in that case and will account for a net release of phosphorus from the cells (see next paragraph).

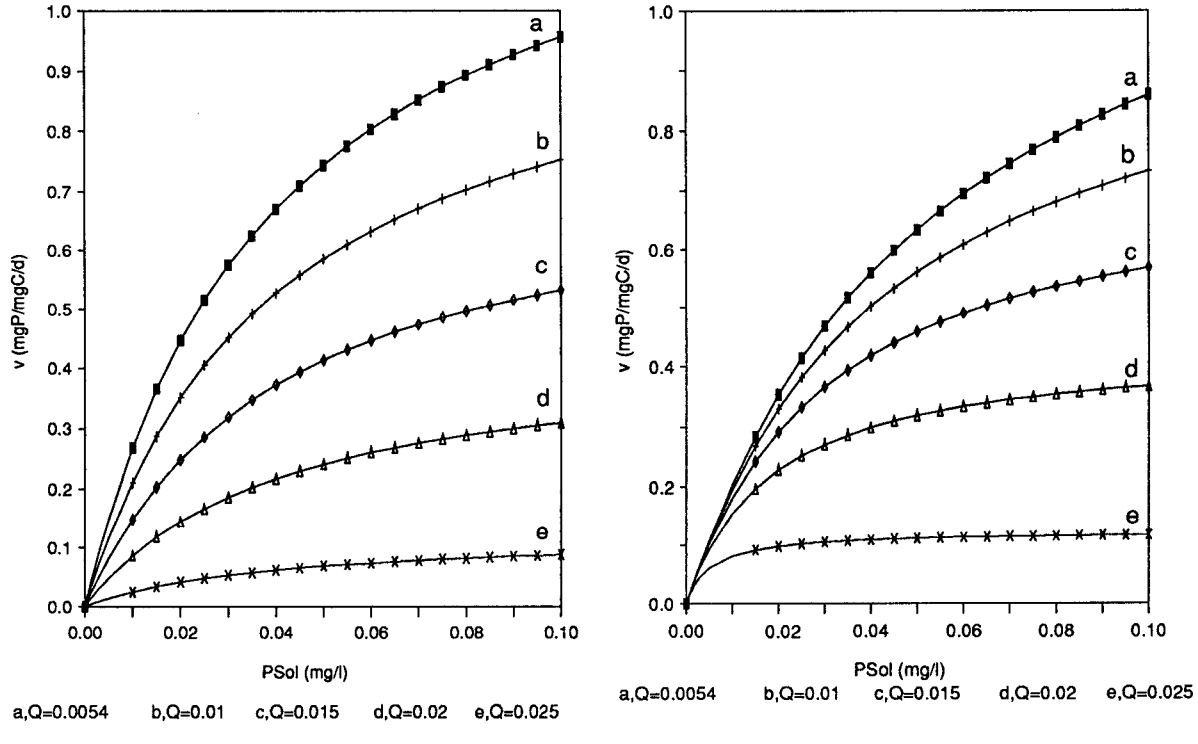


Fig. 4. Phosphorus uptake functions of phytoplankton.
a (left): Michaelis-Menten function. (k_P = 0.04 mgP/l; v_{max} = 1.34 mgP/mgC/d); Q_{min} = 0.0054 mgP/mgC; Q_{max} = 0.027 mgP/mgC)
b (right): Modified function, with constant initial affinity. (A_0 = 20 l/mgC/d)

Growth

Algal growth depends on cell quota by the following equation, originally described by Droop (1973) and modified by Droop (1974) (Figure 5):

$$\mu = \mu_{max} \cdot \left(\frac{Q_{max}}{Q_{max} - Q_{min}} \right) \cdot \left(1 - \frac{Q_{min}}{Q} \right) \tag{5.9}$$

in which μ growth rate [d^{-1}]
μ_{max} maximum growth rate [d^{-1}]

Maximum growth rate averages about 0.5 - 1 day^{-1} for filamentous blue-greens (Burger-Wiersma et al., 1987; Riegman, 1985), 1 - 2 d^{-1} for diatoms and 1.5 - 3 d^{-1} for green algae species (see *e.g.* Post *et al.*, 1985a,b; Jørgensen et al., 1979; Canale, 1976).

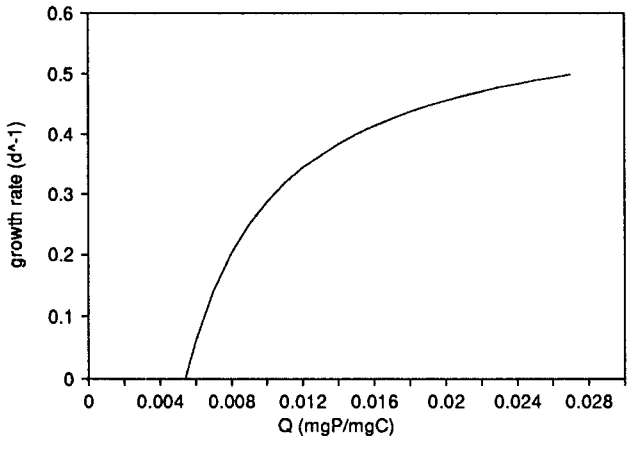


Fig. 5. Growth function according to Droop
(μ_{max} = 0.5)

Growth rate not only depends on cell phosphate quota, but also on temperature, available light and the availability of other nutrients like nitrogen. In the Loosdrecht Lakes, these other nutrients are currently assumed to be saturating and are left out of the model.
For the green and blue-green algae, the effect of *temperature* is reflected in the commonly used Arrhenius function:

$$\mu_{max}(T) = \mu_{max}(20°) \cdot \Theta^{T-20} \tag{5.10}$$

in which Θ [$e^{1/°C}$] is a constant slightly greater than 1.0. In this equation one assumes that the optimum temperature of the algae (about 25 - 30 °C) lies above the maximum temperature in the lake. For the diatoms, whose optimum temperature is known to be much lower, an optimum function is used:

$$\mu_{max}(T) = \mu_{max}(T_{opt}) \cdot \exp\left(\ln(0.5) \cdot \left| \frac{T - T_{opt}}{k_{temp}} \right|\right) \tag{5.11}$$

with T_{opt} optimum temperature [°C]
k_{temp} temperature interval for a factor 2 change in μ_{max} [°C]

The effect of *light* on algal growth is more difficult to model because of the differences between culture vessels and the in-lake situation. The relation between irradiation and growth rate in a culture vessel is given by a Steele, Smith or Monod-like equation. In the field, however, light intensity reduces rapidly with depth due to absorption of light in the water column, according to the Beer equation:

$$I(z) = I_0 \cdot \exp(-\varepsilon \cdot z) \tag{5.12}$$

with $I(z)$ light intensity at depth z [W/m^2]
I_0 light intensity just under the surface [W/m^2]
z current depth in the water column [m]
ε extinction coefficient [m^{-1}]

I_0 equals the outdoor light intensity, corrected for the reflection at the water surface by subtraction of a fixed percentage, which is about 20 - 25 % in Loosdrecht (WQL Basic data). The extinction coefficient depends on the density of particles (mainly: phytoplankton and detritus) in the water, the so-called self shading effect, according to:

$$\varepsilon = \varepsilon_{water} + k_\varepsilon(Diat) \cdot CDiat + k_\varepsilon(Green) \cdot CGreen + k_\varepsilon(Blue) \cdot CBlue + k_\varepsilon(Det) \cdot CDet \tag{5.13}$$

with ε_{water} background extinction of the water [m^{-1}]
$k_\varepsilon(j)$ specific extinction of component j [m^2/mgC]

The background extinction in Lake Loosdrecht equals the (rather high) value of 1.2 [m^{-1}] (Rijkeboer *et al.*, 1988). In the literature, specific extinctions values between 0.23 and 0.45 are found (Kouwenhoven and Aldenberg, 1986; Rijkeboer *et al.*, 1988; Jørgensen *et al.*, 1979); these values will be determined more precisely in a current research programme at the Limnological Institute.

An equation for the depth- and daytime-averaged growth rate, under phosphorus saturating conditions (i.e. $Q = Q_{max}$) is obtained by integrating the μ/I-curve over the depth and averaging over daytime. Using the Monod-type equation, one obtains:

$$f(I_0) = \frac{f_l}{\varepsilon \cdot H} \ln\left(\frac{1 + \frac{I_0}{k_l}}{1 + \frac{I_0}{k_l} \cdot \exp(-\varepsilon \cdot H)} \right) \tag{5.14}$$

with f_l daylight fraction [-]

H water depth [m]
k_I half-saturating light intensity [W/m^2]

This equation, also used by Jørgensen (1980) and by Aldenberg & Peters (1988), is used in the present model for the diatoms and green algae. For the blue-greens, where growth inhibition occurs at high light intensity, an integration of the Steele equation is used, like in most of the American modelling literature (e.g. DiToro & Matystik, 1980) and also in Kouwenhoven & Aldenberg (1986):

$$f(I_0) = \frac{e \cdot f_I}{\varepsilon \cdot H} \cdot \left(e^{-\frac{I_0}{I_{opt}} \cdot \exp(-\varepsilon \cdot H)} - e^{-\frac{I_0}{I_{opt}}} \right) \tag{5.15}$$

with I_{opt} optimum light intensity [W/m^2]

$e = \exp(1)$ base of natural logarithm (≈ 2.7)

(All light intensities are expressed as total radiation. In some literature, they are expressed as photosynthetically active radiation (PhAR), which is about 48 % of total radiation. This gives no problems, if I_0 and I_{opt} or k_I are expressed in the same way.) Parameter values are estimated from Post et al. (1985a,b), Riegman (1985), Burger-Wiersma and Baard (1987) and WQL Basic data.

Finally, the expressions for the effects of temperature, light and phosphorus content are combined as follows:

$$\mu = \mu_{max} \cdot \Theta^{T-20} \cdot f(I) \cdot \left(\frac{Q_{max}}{Q_{max} - Q_{min}} \right) \cdot \left(1 - \frac{Q_{min}}{Q} \right) \tag{5.16}$$

This means that the growth rate can be limited by both light and phosphorus at the same time. From laboratory experiments it is known that in case of 'double limitation' (which is likely to occcur in the turbid, SRP-poor Loosdrecht Lakes), the effects of light and phosphorus are not independent. For instance, the minimum cell quota in the Droop equation decreases in case of low light intensity (Riegman, 1985), giving rise to an extra reduction in growth rate. One can imagine that also the μ to I relation might be influenced by low phosphorus. Adaptations of this kind are easily performed when describing the behaviour of laboratory cultures, but cause difficulties in models of the field situation, as the resulting equations are not integratable with respect to depth. This subject will be discussed in a future paper; in the meantime we will adapt ourselves to the general modeler's view of independent light and nutrients effects.

The three algal groups which are distinguished in the model differ in the light and temperature functions (already mentioned) and in the parameter values. In short, the blue-greens have a higher phosphate affinity, a lower minimal phosphate content and a higher light affinity than the other groups. On the other hand, they are subject to photo-inhibition at

high light intensity, they have a lower maximal growth rate and are more severely influenced by temperature. Diatoms differ from greens primarily in their low temperature optimum and a lower maximum growth rate.

A final remark is that the chlorophyll-*a* concentration in the water is calculated from the phytoplankton carbon concentrations as an extra output variable, using fixed, but species-dependent chlorophyll-*a* to carbon ratios. Although these ratios can vary depending on the degree of light limitation (*e.g.* Post *et al.*, 1985a,b), the variation in the chlorophyll-*a* to carbon ratio of the Loosdrecht Lakes phytoplankton is quite small (Rijkeboer *et al.*, 1988).

5.2.2 Loss processes

Algal loss processes are: (C-)respiration, (P-)excretion, sedimentation, natural mortality and grazing by zooplankton. Grazing is discussed in the next paragraph.

Respiration and P excretion

Respiration means the combustion of carbohydrates by the living cells for physiological processes. The process is modelled as a first order process (a linear function of the concentration), temperature influencing it the same way as it affects growth:

$$CResp(i) = k_{resp(i)} \cdot \Theta_i^{T-20} \cdot CPhyt(i) \tag{5.17}$$

with

$CResp(i)$	respiration	[mgC/l/d]
$k_{resp(i)}$	respiration constant at 20 °C	[d^{-1}]

Living cells also excrete phosphorus. The amount excreted generally will not be exactly proportional to the respiration: we assume that algae display a (limited) feedback mechanism with repect to their phosphorus content. In times of severe P shortage, cells will try to retain their phosphorus by diminishing excretion, while in a (theoretical) case of oversaturation, with $Q \geq Q_{max}$, excretion will be higher. This is modelled as a Michaelis-Menten-type equation:

$$PExcr(i) = k_{excr(i)}(T) \cdot PPhyt(i) = \frac{Q_{\max} + k_{hexcr(i)}}{Q_{\max}} \cdot \frac{Q_i}{k_{hexcr(i)} + Q_i} \cdot k_{resp(i)} \cdot \Theta_i^{T-20} \cdot PPhyt(i) \tag{5.18}$$

with

$PExcr(i)$	P excretion	[mgP/l/d]
$k_{excr(i)}$	P excretion constant	[d^{-1}]
$k_{hexcr(i)}$	half-saturation constant for P excretion	[mgP/mgC]

Excreted phosphorus goes to the SRP compartment.

Sedimentation

In shallow lakes like the Loosdrecht Lakes, sedimentation of algae and other particles is not well understood. Each algal species has a specific sedimentation velocity, which can be several tens of centimeters per day (see Jørgensen et al. (eds.), 1979); for most blue-greens it is lower than for other species. These figures are often used in models of deep lakes. In shallow lakes, where the interaction between water and sediment is much more important, sedimentation is counteracted by the process of resuspension: due to wind action or animal activities, particles in the upper sediment (the 'epipelon') can return to the water column. This process is further discussed in paragraph 5.5.

As far as algal cells are concerned, it turns out that most of them can survive only a limited time in the sediment. Preliminary studies show that after a few days, only some diatoms and greens survive and almost none of the blue-greens (J. Otten, Limnological Institute, pers. comm.). This means that most algae die soon after their settling and become part of the 'bottom detritus' (of which a part will be resuspended). As a simplifying assumption, for the phytoplankton we only deal with the net settling, defined as the flux of algal material to the sediment detritus. This flux is modelled as a first order process:

$$CSett(i) = velo_i \cdot CPhyt(i) \tag{5.19}$$

with

$CSett(i)$	(net) settling of species i	[gC/m^2/d]
$velo_i$	(net) settling velocity of species i	[m/d]

To obtain the effect on the algal concentration, this term is divided by the water depth [m]. We assume that the particles do not loose or bind phosphorus during settling, so the corresponding P settling equals the cell quota times the C settling. The net settling velocities are assumed to be rather low (0.01-0.04 m/d).

Mortality

Natural mortality of algae is a somewhat obscure process on which only limited information is available. Direct loss of phytoplankton in the water column seems to be important, because the seasonal variations in the total seston concentration closely follow those in the chlorophyll-*a* concentration (*cf* Figs. 8B and 9A, 15A and C and 16A and C). Very little is known, however, about what happens when a cell dies off. Mortality might even be indistinguishable from other loss processes like sedimentation or grazing and sometimes it is argued that a separate formulation of it is unnecessary. In the model, we define mortality as a flux from living algae to detritus in the water; no statements are made about the exact mechanisms underlying this flux. The process is described as a first order process:

$$CMort(i) = k_{mort(i)} \cdot f(T) \cdot CPhyt(i) \tag{5.20}$$

with

$CMort(i)$	mortality of species i	[mgC/l/d]
$k_{mort(i)}$	mortality constant of species i	[d^{-1}]
$f(T)$	temperature function	[-]

The temperature function is quite a problem. As a first hypothesis the same temperature function as for the other phytoplankton processes is taken: a mortality rate increasing with temperature. Field observations, however, suggest a higher mortality in autumn than in spring, leading either to the conclusion that the *direction* of temperature change might be more important than the temperature itself, or to a stronger dependency on temperature of the mortality than the growth rate (for instance a higher Θ).

The corresponding P mortality equals Q times the C mortality. A small fraction (called ζ_i) of the phosphorus from the died algae is released in soluble form, the remainder goes to the detrital phosphorus compartment.

5.3 Zooplankton processes

5.3.1 Overview

The majority of the zooplankton, measured as 'seston > 150 μ', consists of 'filter feeders' or herbivorous zooplankton grazing on the algae and detritus. The most abundant species are *Bosmina longirostris*, *Bosmina coregoni*, *Daphnia cucullata* and *Chydorus sphaericus*, all Cladocerans, but filter feeders in other taxonomic groups are also found. In general, zooplankton species in the Loosdrecht Lakes are small-sized (Gulati et al., 1987). The *Bosmina* and *Daphnia* species together are responsible for 63 - 89 % of total filtration activity (Gulati, 1984).

In the model, growth of herbivores occurs as a result of grazing on algae and detritus. Part of the food is assimilated by the animals, the remainder is egested as detritus. The (other) losses are: (C-)respiration and (P-)excretion, natural mortality and predation by fish. Assimilation minus respiration is the net secundary production. Predation is discussed in paragraphs 5.4 and 5.5, respectively.

The P/C ratio of the zooplankton is much higher than that of the seston < 150 μ which serves as food; in the Loosdrecht Lakes it averages 2.3 % against 0.6 - 0.9 % (Siewertsen, 1988). Moreover, this ratio is fairly constant, both throughout the year as between different lakes, in spite of sometimes large variations or differences in the P/C ratio of the food (WQL Basic data; R.D. Gulati, pers. comm.). Zooplankton seems to possess mechanisms to maintain its phosphorus content within narrow ranges, also under varying external conditions. This implies that certain zooplankton processes must be dependent on the actual P/C ratio of the organisms. Theoretically, the following mechanisms are possible:

- phosphorus is assimilated with a greater efficiency than carbon;
- phosphorus excretion is relatively lower than respiration (phosphorus is retained in the body or stored in 'immobile' parts like an exoskeleton);
- an increased respiration (extra utilisation of carbohydrates) when P content becomes too low.

We assume that the first mechanism may be important, but unfortunately, little experimental work has been done on this subject. Concerning the second mechanism: although P excretion as measured in the Loosdrecht Lakes is low when compared to other lakes (R.D. Gulati, pers. comm.), it is still that high that it does not (or scarcely) contribute to a higher P/C ratio: average P excretion in the summer of 1987 was 2.4 μgP/l/d, whereas respiration is estimated as 10 - 15 % of biomass per day, i.e. 50 - 75 μgC/l/d at a biomass of 500 μgC/l. The P/C ratio of the egested material is therefore 2.4 - 3.6 %, equal to or even higher than that of the zooplankton itself (2.3 %). It is possible, however, that excretion is temporarily higher than the average. As to the fourth mechanism, there are indeed indications toward an increased respiration in case of phosphorus shortage. In short, all three mechanisms are included in the model; the relative importance of each one is determined by the parameter values. We focus on the effect of these mechanisms on the phosphorus flows in the ecosystem, without going to deep into the physiological backgrounds.

5.3.2 Grazing

Filtration and consumption

The consumption (or ingestion) of food by filter feeders is commonly described by means of the specific filtration:

$$CConsH = Filt \cdot CSest \cdot CHerb \tag{5.21}$$

in which:
- *CConsH* consumption (ingestion) of food by zooplankton [mgC/l/d]
- *Filt* specific filtration rate of the zooplankton (filtrated volume of water per unit zooplankton biomass per unit time) [l/mg CHerb/d] (Sometimes specific filtration rate is expressed in [ml/animal/day])
- *CSest* concentration of seston < 150 μ [mgC/l]

Specific consumption or 'daily ration', the daily consumption per unit of zooplankton, *CConsH / CHerb*, equals *Filt · CSest* [d^{-1}].

Specific grazing pressure or 'daily grazing', the fraction of the seston < 150 μ which is filtrated by the zooplankton, *CConsH / CSest*, equals *Filt · CHerb* [d^{-1}], sometimes multiplied by 100 and expressed as [%/d].

The actual 'functional response' of the zooplankton is described by the way in which the specific filtration rate *Filt* depends on the *food concentration* and other environmental factors. Several formulations can be found in literature (see Jørgensen, 1980, chapter 3 and Scavia & Robertson, 1979 for a review). Gulati et al. (1982) found the filtration rate to decrease hyperbolically with seston concentration and to increase with temperature. In accordance with this result is the equation of Canale (1976):

$$Filt = Filt_{\max} \cdot \Theta_H^{T-20} \cdot \frac{k_{filt}}{k_{filt} + CSest} \tag{5.22}$$

with
- $Filt_{max}$ maximum specific filtration rate at 20 °C [l/mg CHerb/d] (theoretically reached when *CSest* = 0)
- Θ_H temperature constant [$e^{1/°C}$]
- k_{filt} half-saturating food concentration (the food concentration at which the filtration rate is half of the maximal) [mgC/l]

Fitting of this function on the grazing measurements performed by the Limnological Institute leads to a very high maximum filtration rate of ca. 9 l/mg CHerb/d and a k_{filt} of 0.2 mgC/l. Is is perhaps more realistic, like many authors do, to 'chop off' this function at very low seston concentrations. (See Figure 6a). The function now becomes:

$$Filt = \mathrm{MIN}\left[Filt_{con} \cdot \Theta_H^{T-20}, Filt_{con} \cdot \Theta_H^{T-20} \cdot \frac{k_{filt} + CHold}{k_{filt} + CSest} \right] \tag{5.23}$$

with *CHold* seston concentration below which filtration rate is maximal (i.e. $Filt_{con}$) [mgC/l]

$Filt_{con}$ maximum specific filtration rate at 20 °C (reached below *CHold*) [l/mg CHerb/d]

In fact, at the high seston concentrations in the Loosdrecht Lakes (about 5 - 15 mgC/l), filtration rate never reaches its maximum and is only slightly influenced by changes in seston amount. However, setting a maximum to the filtration rate contributes to the stability of the model. For *CHold* the value of 1 mgC/l is chosen. At high seston concentrations, specific consumption approximates $Filt_{con}(T) \cdot (k_{filt} + CHold)$ [d^{-1}].

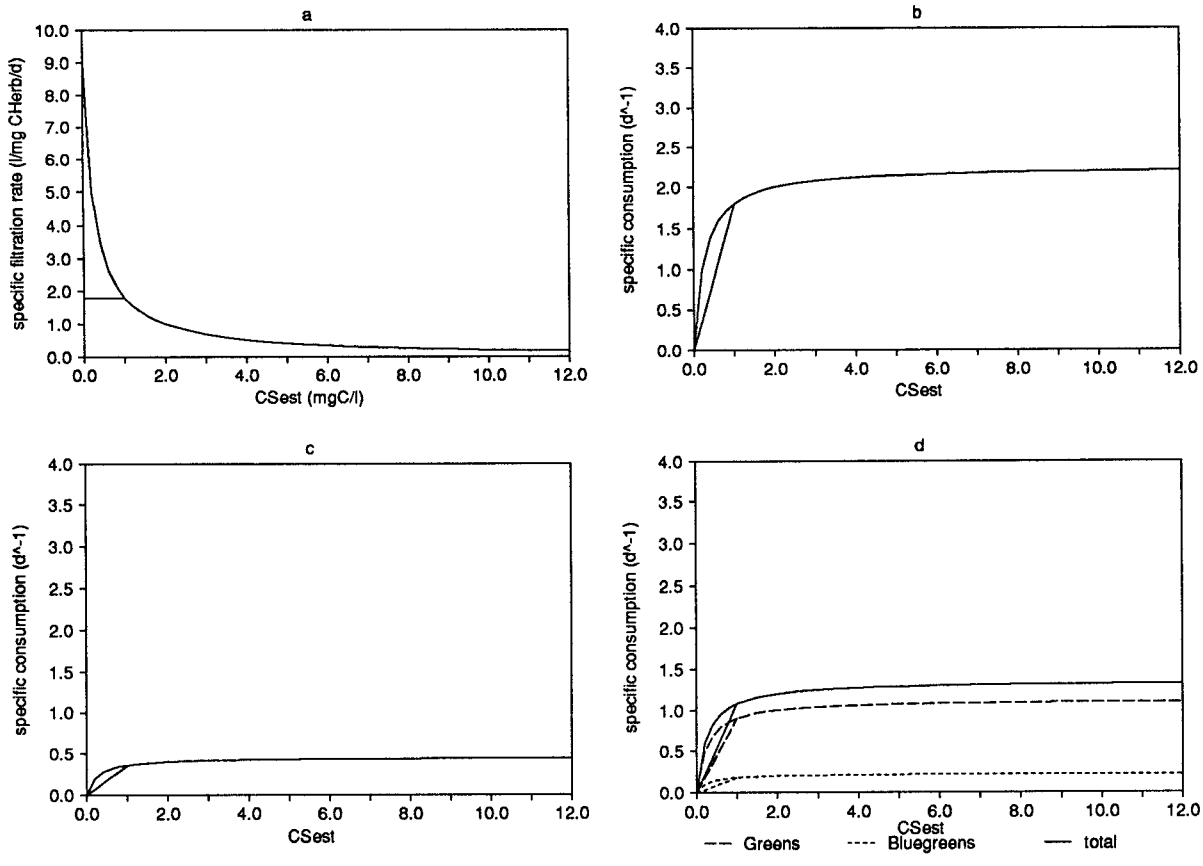


Figure 6. Functions for zooplankton filtration and consumption rates.
a: specific filtration rate; b-d: specific consumption rate.
b: only greens present (α_{Green}=1.0); c: only blue-greens present (α_{Blue}=0.1); d: seston consists of 50 % greens and 50 % blue-greens.

Apart from the concentration of food particles, another important factor is its *composition.* The seston < 150 µ is composed of four components: detritus, diatoms, green algae and bluegreen 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 disklike species (the cyanophyte *Synechococcus sp.* and the diatom *Cyclotella pseudostelligera*, resp.) were eaten best, the filamentous cyanophyte *Oscillatoria agardhii* was eaten poorly (ingestion rate about 10 % of the former species) and three 'intermediate' species, namely 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 / rejection* step as part of the filtration process. Each kind of food particle is attributed a selection factor α_j [-]. This factor denotes what fraction of the amount of the particular food component present in the filtrated water is actually ingested by the animal. The remainder (if any) is rejected. So the equations for the specific consumption of each food component become:

$$\frac{CCons(j)H}{CHerb} = \alpha_j \cdot Filt \cdot CFood(j) \cdot \tag{5.24}$$

in which for α_j [-] should be read α_{Diat} for diatoms, α_{Green} for greens, α_{Blue} for blue-greens and α_{det} for detritus. The selection factor causes a proportional shift of the specific consumption rate, without changing the shape of the curve (see Figure 6).

When describing single-species food situations, this formulation is identical to an adaptation of the maximum specific filtration rate. In a multi-species food situation, however, there is a difference: in a 'filtration-oriented' approach the consumption of species *i* would be affected by the presence of other species, which seems unlikely. In the formulation used here, food components do not affect each other's consumption.

The parameters α_j are, of course, difficult to determine and are in fact poorly known, although they are very important for modelling results. More information on 'selective grazing' is much needed. As a 'good guess' the values 1.0 for diatoms and greens, 0.1 for filamentous blue-greens and 0.25 for detritus are used. Especially the value for detritus (which makes up two-thirds of total food) is uncertain. The chosen fairly low value is based on the assumption that quite a large fraction of the detritus will be, directly or indirectly, of bluegreen algal origin. One should probably split up the detritus when modelling selective grazing, because there are many sources of detritus (including zooplankton grazing itself) giving rise to differences in particle size and composition. This goes, however, beyond the scope of the present model.

Total specific consumption by the zooplankton equals:

$$\frac{CCons(tot)H}{CHerb} = \sum_j CCons(j)H = \bar{\alpha} \cdot Filt \cdot CSest \tag{5.25}$$

with

$$\bar{\alpha} = \frac{\alpha_{Diat} \cdot CDiat + \alpha_{Green} \cdot CGreen + \alpha_{Blue} \cdot CBlue + \alpha_{det} \cdot CDet}{CSest} \tag{5.26}$$

When deriving the value for the maximum specific filtration rate from grazing experiments, one must keep in mind that the filtration rate measured in an experiment with total seston as food source, is comparable with the product $\bar{\alpha} \cdot Filt$ [l/mgC/d] in the model and that the daily ration approximates $\bar{\alpha} \cdot Filt \cdot CSest \approx \bar{\alpha} \cdot Filt_{con}(T) \cdot (k_{filt} + CHold)$ [d^{-1}]. Filtration rate, measured in 1983 and 1984, averages 0.1 - 0.2 l/mgC/d in summer at seston concentrations of 10-15 mgC/l, while the daily ration lies mostly between 1 and 1.5 d^{-1} [*see* WQL Basic data]. From these findings, and with $CHold$ = 1 [mgC/l], k_{filt} = 0.25 [mgC/l] and $\bar{\alpha} \approx 0.25$ [-], a value for $Filt_{con}$ between 3 and 6 [l/mgC/d] can be derived.

Assimilation and egestion

Once consumed, not all the food is actually assimilated by the animals. A fraction $CEff_H$ is assimilated , the remainder is egested:

$$CAssH = CEff_H \cdot CConsH \tag{5.27}$$

$$CEgesH = CConsH - CAssH \tag{5.28}$$

with

	$CAssH$	C assimilation [mgC/l/d]
	$CEgesH$	C egestion of unused food [mgC/l/d]
	$CEff_H$	C assimilation efficiency [-]

The C assimilation efficiency is modelled as a constant fraction, independent of the food concentration. There is some experimental evidence for the efficiency being different for different food components. Lyche (1984), in her study on *Daphnia* feeding behaviour, found assimilation efficiency to be lower for cyanophyta (40 - 50 %) than for the other algae studied (80 - 100 %). This would be related to the 'taste' (chemical composition of the cell wall) of the particular groups rather than to the cell shape, because the same was found for the spherical cyanophyte as for the filamentous one. On the other hand, zooplankton studies in Lake Vechten, dominated by diatoms and greens, revealed the same assimilation efficiency as in the blue-green-dominated Loosdrecht Lakes, namely about 40 % (range: 20 - 60 %) (Gulati et al., 1982 and WQL Basic data 1983 and 1984). Many modellers (all working on lakes with a diatom or green dominance) use a percentage of 60 - 65 (Di Toro, 1975; Di Toro & Matystik, 1980; Jørgensen, 1980). Kouwenhoven & Aldenberg (1986) apply a value of 45 % in the 'first step' Loosdrecht model. Grazing experiments might, however, give an overestimation of the figure (H.J. Gons, Limnological Institute, pers. comm.) which might be, in the field, not higher than 20 - 30 %. Moreover, in view of the demand for a closed phosphorus balance (see next paragraph), the carbon assimilation efficiency can not be much higher than about 30 %. In *PCLoos*, we used a constant efficiency of 30 %.

What happens to the particles that are ingested but not assimilated is not clear. Although algal cells sometimes seem to pass undamaged the filtering and digestive apparatus of the animal, most often they do not survive (Gliwicz, 1980). Therefore, in the model, all the undigested food is added to the detritus pool (as far as carbon is concerned).

Phosphorus

When a food particle is ingested by a herbivore, it carries its own P/C ratio. Therefore, the P consumption equals the C consumption times the P/C ratio of the food.

However, as the P/C ratio of the herbivores is mostly much higher than that of its food, the phosphorus assimilation efficiency is likely to be higher than the carbon assimilation efficiency and also variable: phosphorus will be extracted selectively from the food, dependent on the actual needs (see § 5.3.1). However, efficiency can never be higher than 100 %, of course: the organism can not extract more phosphorus than is present. P efficiency is modelled in the following way:

$$PEff_H = \mathrm{MIN}\left[1,\ \frac{PCHerb_{ref}}{PCFood} \cdot CEff_H\right] \tag{5.29}$$

in which $PCHerb_{ref}$ reference P/C ratio of zooplankton [mgP/mgC]
$PCFood$ weighted average P/C ratio of consumed food [mgP/mgC]

The actual physiological mechanism involved is left open. In fact, feedback will most likely take place on the phosphorus content of the animals itself in stead of that of the seston. But the above equation is more easily applied.
The P assimilation efficiency is used to model P assimilation and egestion:

$$PAss(i)H = PEff_{iH} \cdot PCons(i) \tag{5.30}$$

$$PEgesH = PConsH - PAssH \tag{5.31}$$

with $PAssH$ P assimilation [mgP/l/d]
$PEgesH$ P egestion [mgP/l/d]

In the Loosdrecht Lakes, the P egestion is always relatively lower than the C egestion. In most plankton models, all egested phosphorus is directed towards the detritus pool (*e.g.* Canale *et al.*, 1976; Jørgensen, 1980). There is some evidence, however, that part of it (sometimes estimated as high as 50 - 65 % (R.D. Gulati, pers. comm.)) is released in soluble form (SRP). This fraction is called ρ_H in the model and has been assigned the (rather arbitrary) value of 0.25.

5.3.3 Loss processes

Besides egestion the loss processes of the herbivores are: (C-)respiration and (P-)excretion, predation by fish and natural mortality. Predation is discussed in § 5.4.

Respiration and P excretion

Respiration is the combustion of carbohydrates by the living animals, necessary to perform their physiological activities. Normally, it is modelled as a simple first order process, by means of a respiration coefficient which only depends on temperature. When, however, the animals face a phosphorus shortage, extra respiration can occur in order to restore the reference P/C ratio. (The animal starts to 'combust itself' in times of P shortage). In mathematical terms:

$$CRespH = k'_{resp(H)} \cdot \Theta_H^{T-20} \cdot CHerb \tag{5.32}$$

$$k'_{resp(H)} = \frac{PCHerb_{ref}}{PCHerb} \cdot k_{resp(H)}$$

with

$CRespH$	respiration of zooplankton	[mgC/l/d]
$k_{resp(H)}$	respiration constant at 20 °C	[d^{-1}]
$k'_{resp(H)}$	idem, corrected for P/C ratio	[d^{-1}]

Under average summer conditions, the respiration constant is estimated as 0.10 - 0.15 d^{-1} (Gulati, 1989).

The corresponding P excretion (N.B.: This is another process than the egestion of phosphorus from unassimilated food) is normally related to respiration, but can be lowered in times of P shortage by selectivily retaining phosphorus. In reality, the physiological mechanism of this process may be quite complex, but in the model we only consider the effect on the net flux. The formulation is:

$$PExcrH = k_{excr(H)} \cdot \Theta_H^{T-20} \cdot PHerb \tag{5.33}$$

$$k_{excr(H)} = \frac{PCHerb}{PCHerb_{ref}} \cdot k_{resp(H)}$$

with

$k_{excr(H)}$	excretion constant at 20 °C	[d^{-1}].

Natural mortality

Natural mortality is modelled as simple as possible: as a first order process, only temperature dependent:

$$CMortH = k_{mort(H)} \cdot \Theta_H^{T-20} \cdot CHerb \tag{5.34}$$

$$PMortH = PCHerb \cdot CMortH \tag{5.35}$$

in which	*CMortH*	natural mortality of zooplankton [mgC/l/d]
	PMortH	natural mortality of zooplankton [mgP/l/d]
	$k_{mort(H)}$	mortality constant of zooplankton at 20 °C [d^{-1}]

When an animal dies, all the carbon is added to the detritus pool. Concerning phosphorus, a small fraction ζ_H (10 %?) is released in soluble form, the rest in detrital form. (In most models, the rapid release of soluble P is neglected or, in other words, ζ_H=0.)

5.4 Fish

5.4.1 Introduction

Fish is an important component of the Loosdrecht Lakes system. Biomass is high, about 300 kg/ha (E.H.R.R. Lammens, pers. comm.), which equals 15 mg/l fresh weight or 3 mg/l dry weight. The latter consists for 40 % of carbon (= 1.2 mg C/l) and for 2.3 % in phosphorus (= 70 µg P/l); P/C ratio is thus 5.7 %. This is considerably higher than that of its food, so also fish must have mechanisms for preserving phosphorus. The phosphorus pool in fish is nearly the same size as all the other pools together.

The main part of the fish stock consists of Bream (*Abramis brama*), which feeds mainly on zooplankton and benthal midge larvae (Lammens, 1988). The smaller fishes, up to about 20 cm, feed primarily on zooplankton, the larger ones on *Chironomidae* (Van Densen et al., 1986). Both size classes account for about 50 % of the biomass. Compared with other lakes, the bream population (when expressed in numbers per ha.) is dominated by relatively small individuals (< 25 cm) (Lammens, 1989). Natural enemies are nearly absent.

The following processes are incorporated in the model: growth of fish stock can take place by predation on zooplankton and zoobenthos; decrease by respiration and P excretion, natural mortality and harvesting (fisheries).

5.4.2 Predation

a) Predation on zooplankton

In accordance with generally accepted ideas, the predation of fish on zooplankton is supposed to increase with prey density in a sigmoidal way, approaching an upper limit at high prey density. This is a so-called 'type III' functional response, commonly seen with vertebrate predators. In mathematical form:

$$CPredHF = PrMax_{HF} \cdot \Theta_F^{T-20} \cdot \frac{CHerb^2}{k_{pred(HF)}^2 + CHerb^2} \cdot CFish \tag{5.36}$$

$$CAssHF = CEff_{HF} \cdot CPredHF \tag{5.37}$$

with

$CPredHF$	predation of fish on zooplankton	[mgC/l/d]
$PrMax_{HF}$	maximum predation coefficient	[d^{-1}]
$k_{pred(HF)}$	zooplankton density at which the predation coefficient is half-maximal	[mgC/l]
$CAssHF$	assimilation of zooplankton food	[mgC/l/d]
$CEff_{HF}$	carbon assimilation efficiency for zooplankton food	[-]
Θ_F	temperature constant	[$e^{1/°C}$]

The carbon assimilation efficiency is estimated as 0.4-0.5 (E.H.R.R. Lammens, pers. comm.). The non-assimilated food is egested as detritus.

Formulations on base of phosphorus are analogous, except that the P assimilation efficiency, $PEff_{HF}$, depends on the P/C ratio of the zooplankton:

$$PEff_{HF} = \mathrm{MIN}\left[1, \frac{PCFish_{ref}}{PCHerb} \cdot CEff_{HF}\right] \tag{5.38}$$

with $PCFish_{ref}$ reference P/C ratio of fish = 0.057 [mgP/mgC]
PCHerb P/C ratio of zooplankton [mgP/mgC]

Analogous to the formulation of the zooplankton phosphorus egestion (par. 5.3.2), it is assumed that a fraction ρ_F of 0.25 becomes immediately available in soluble form, the remainder in organic form.

b) Predation on zoobenthos.

Because not much is known quantitatively about the predation of fish on zoobenthos, it is modelled as simple as possible, namely by a Lotka-Volterra type equation. This means that the specific consumption is a linear function of prey density; the consumed amount is thus proportional to both prey and predator concentration. The predation coefficient is only dependent on water temperature:

$$CFeedBeF = k_{feed(BeF)} \cdot \Theta_F^{T-20} \cdot CBent \cdot CFish \tag{5.39}$$

with $CFeedBeF$ consumption of zoobenthos by fish [mgC/l/d]
$k_{feed(BeF)}$ feeding coefficient [m^2/gC/d]

The feeding coefficient is expressed in [m^2/gC/d] because of conversion from zoobenthos biomass (in grams per square meter) into fish biomass (in milligrams per liter). Carbon assimilation efficiency is rather high and has sometimes been observed to be as high as 0.8 (E. Lammens, pers. comm.). In the model, we assumed an efficiency of 0.5 in order to leave the fish the opportunity to maintain its high P/C ratio. The P/C ratio of zoobenthos is only 2.0 - 2.5 %, which implicates that the phosphorus assimilation efficiency will be close to 1.0.

Predation and feeding constants have mainly been assessed by calibration on summer averages. More field research on these topics is needed.

5.4.3 Loss processes

Loss processes are: respiration, P excretion, mortality and harvesting. The former two are modelled analogous to the respective processes of the zooplankton: as temperature dependent first-order processes with a correction in case of deviation from the reference P/C ratio. The respiration rate of fish is estimated as 0.005 d^{-1} (Kitchell et al., 1975).

Concerning natural mortality of fish populations, a characteristic seasonal pattern is found. After spawning, in the months of May, June and July, about 20 % of the population dies. During the rest of the year, mortality is low, except for calamities in severe winters (E. Lammens, pers. comm.). In the model, mortality is described as a first order process with a seasonally fluctuating proportionality constant.

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 ζ_F which is released in soluble form.

Commercial fisheries captures about 10% of total fish stock, mainly in winter (October - mid March), i.e. a loss rate of $6 \cdot 10^{-4}$ per day. The rest of the year only recreational fishermen operate, who have only a minor quantitative influence on fish stock.

5.5 Detrital processes

5.5.1 Introduction

Detritus (dead organic material) is the central compartment in the model (see Figures 1 and 2). In the preceding paragraphs, numerous detritus-forming processes have been mentioned and consequently, the detrital material is heterogenous with respect to origin and composition. However, in a hypertrophic lake with a high concentration of algae like the Loosdrecht Lakes, an important part of the detritus will be, directly or indirectly, of algal origin.

A complicating factor is that it is not possible, in measurements, to distinguish between live and dead algae. We do not know what percentage of the seston < 150 μ consists of algae and what percentage the detritus accounts for. In many lakes, more than 50 % of the seston is detritus (Aldenberg & Van der Vlugt, 1983). Gons (1987) has estimated the detrital fraction in seston of the Loosdrecht Lakes by two methods: by means of differences in chlorophyll-*a* content between algae, seston and epipelon, and by means of microscopic observations. Both methods give great fluctuations, but summer means are about 1/3 algae and 2/3 detritus.

Most detritus-forming processes have been discussed already: external input, mortality of all biota and egestion by all animal groups. Another one is resuspension of epipelon, the upper layer of organic material in the sediment. This process is discussed together with the sedimentation, one of the two detrital loss processes. The other one is decomposition / mineralisation.

5.5.2 Sedimentation and resuspension

In a shallow lake like Loosdrecht, both processes are counteracting in a complicated way, causing an extensive exchange between detritus in the water and detritus in the upper sediment or epipelon. Sestonic particles in the water settle to the bottom at a velocity primarily depending on their density (according to Stokes' law) but influenced by water turbulence. In general, dead particles settle faster than living ones. Temperature has only a minor influence (Straskraba & Gnauck, 1986). In mathematical terms:

$$CSettD = Velo_D \cdot CDet \tag{5.40}$$

with

CSettD	settling of detritus	[gC/m^2/d]
$Velo_D$	settling velocity of detritus	[m/d]

The settling velocity in the Loosdrecht Lakes seems to be quite low; in the model we assumed *ca* 0.1 m/d. A small portion (5 %) of the settled particles, called f_r, is buried permanently in the sediment. The greater part, however, is added to the organic pool in the upper sediment, called *CSed* and *PSed* in the model. This is the exchangeable and degradable material in the first 2 cm of the sediment, containing the phosphorus that takes part actively in the nutrient cycling within the lake ecosystem. (The more or less immobile phosphorus fractions in the sediment are left out; see § 5.6).

The upper sediment can partly be resuspended into the water column. This resuspension is primarily wind-driven, but also boating and bioturbation (especially feeding activity of fishes on bottom organisms) play a role (Gons, 1987). The amount of epipelon (resuspendable material) is estimated as 500 g dry matter per m^2 (Gons, 1987); at a sediment porosity of 0.91 (see § 5.6), this amount would form a layer of 0.6 cm. The epipelon consists of two fractions: a fine fraction ('true' detritus, originating from dead algae etc.), about 10 %, and a coarse fraction, mainly consisting of peat particles. The resuspended peat particles resettle within a day and are not important when discussing system behaviour on a larger time-scale; this fraction is left out of the model. The fine-granuled fraction remains much longer in the water before resettling. (However, shortly after a storm event both fractions are present in the water and can cause bias in seston measurements.) Resuspension of fine detritus is estimated as 2.5 g dry matter per m^2 per day, based on resuspension occurring at an average 5 % of the lake area per day during summer (Gons, 1987). (Recent measurements suggest that this figure might be an underestimation.) Assumed that one-third to one-half of the degradable organic material in the upper 2 cm of the sediment (*CSed* resp. *PSed*) consists of fine-granuled epipelon and that resuspension can be approximated as a linear function of the amount available, the process can be described as follows:

$$CResuD = k_{resu(D)} \cdot f_{fg} \cdot z_s \cdot CSed \tag{5.41}$$

$$PResuD = PCSed \cdot CResuD \tag{5.42}$$

with

CResuD	amount of resuspended carbon	[gC/m^2/d]
PResuD	amount of resuspended phosphorus	[gP/m^2/d]
CSed	organic C in upper sediment	[mgC/l sediment]
f_{fg}	fine-granuled fraction of *CSed*	[-]
$k_{resu(D)}$	frequency of resuspension	[d^{-1}]
z_s	depth of upper sediment layer	[m]
PCSed	P/C ratio of upper sediment	[mgP/mgC]

The resuspended fraction $k_{resu(D)}$ is taken constant in the present model, but can be made dependent on wind velocity, ice cover, fish activity and other factors. Resuspension and subsequent horizontal transportation of particles cause a substantial rearrangement of epipelon within the lake (Gons et al., 1986b). As the model is spatially homogeneous, this phenomenon is not discussed any further.

5.5.3 Decomposition and mineralisation of detritus

Decay of organic material (decomposition), together with mineralisation of organic phosphate, occurs in both the water phase and the sediment. It is difficult to quantify these processes. Both fauna and micro-organisms as bacteria and fungi play a role in the decomposition process. Decay rate depends on the chemical composition of the particles; often, the rate decreases after some time when only the poorly degradable substances are left. For plant and algal material, often no clear distinction can be made between mortality phase and decomposition phase; for

aquatic plants it is found that decomposition may start already in the productive phase. The decay rate (for carbohydrates or biomass) may differ from the mineralisation rate of phosphorus, the latter being a little higher. More process-oriented research is needed here.

With all these complex phenomena in mind, we have followed the common modellers' option of decomposition as a simple first order process, strongly influenced by temperature. For the values of the decomposition and mineralisation constants a wide range is found in literature (see *e.g.* Jørgensen et al., 1979), reflecting the limited knowledge on the subject, but several percents per day at 20 °C seems a reasonable guess. Temperature influence is mostly described by an Arrhenius function (an exponential increase with temperature), sometimes by a linear dependence. As a simplification, the decay rates of carbon and phosphorus have been taken equal. The currently used equations are:

$$CDecD = k_{dec(D)} \cdot \Theta_D^{T-20} \cdot CDet \tag{5.43}$$

$$PMinD = k_{min(D)} \cdot \Theta_D^{T-20} \cdot PDet \tag{5.44}$$

with

	$CDecD$	decomposition of detritus [mgC/l/d]
	$k_{dec(D)}$	decomposition rate of detritus C at 20 °C [d^{-1}]
	$PMinD$	mineralisation of detritus P [mgP/l/d]
	$k_{min(D)}$	mineralisation rate of detritus P at 20 °C [d^{-1}]
	Θ_D	temperature constant [$e^{1/°C}$]

5.6 Processes in the upper sediment layer

5.6.1 General

The sediment has been included in the model for two reasons: modelling the phosphorus mobilisation and, most important, closing the phosphorus cycle within the model system. This means that we are only interested in that part of the sediment phosphorus that comes into circulation again and takes part in the nutrient recycling in the lake ecosystem.

In most parts of the Loosdrecht Lakes a peaty soil is present, covered by a layer of loose, brown mud of varying thickness. Only in the eastern part of the area and near some of the islands, the lake bottom is sandy. The top layer (0 - 2 cm) has a very low content of dry matter: about 9 % (= 90 g/l sediment), of which about 270 mg/g is organic carbon and 1.1 mg/g is phosphorus (Boers et al., 1984; Boers & van Hese, 1988); the P/C ratio is thus 0.45 %. The phosphorus content of the interstitial water forms a profile with a maximum at 1-2 cm depth which is highest in summer (about 0.2 - 0.3 mgP/l). Sediment phosphorus is chemically bound in different ways: bound in complexes with iron or aluminium, in organic matter or in humic acids. Total amount of phosphorus in the sediment (including the deeper layers) is considerable: about 10-15 gP/m^2, which equals 50-100 times the amount in the water phase.

Concerning the phosphorus household of the sediment, the following processes are the most important:

- settling of organic material (algae and detritus)
- mixing of the upper sediment layer
- mineralisation of organic phosphate by bacteria and fungi and release of soluble phosphate into the interstitial water
- transportation of soluble phosphate (due to diffusion or advection) to deeper sediment or to the surface water (mobilisation)
- adsorption to Fe- and Al-compounds; usually a fast process
- (slow) precipitation of anorganic phosphate

Phosphorus release by the sediment is very low, compared to other lakes: between 1 and 2 $mgP/m^2/d$ (in one measurement up to 4 $mgP/m^2/d$) in the summers of 1983 and 1984, and less than 1 $mgP/m^2/d$ in later years. Balance studies carried out by Buijse (in press) indicate a summer phosphorus release not higher than 0.2 - 0.4 $mgP/m^2/d$ in recent years. Boers & van Hese (1988) found by means of column experiments mineralisation to be the principal driving force behind the phosphorus mobilisation. However, the mobilisation is a complicated process, influenced by many factors like the redox conditions, the pH and the iron household. Research on these factors is still in progress within the WQL project.

With respect to the mineralisation a zonation can be found in the sediment according to the type of electron acceptors used by the micro-organisms. In the aerobic layer (the upper 2 mm), oxygen and also nitrate is used, beneath this layer reduction of sulphate into sulphides occurs and further down, only CO_2 can be used as oxidator under formation of methane. The aerobic mineralisation is quantitatively the most important.

In the model, we consider the average mineralisation rate in the upper 2 cm, the layer that we assume to be important for the nutrient recycling in the lake ecosystem. What fraction of the material in this layer can be considered as the biologically degradable pool, important for the nutrient recycling in the lake, is not clear. Boers & Van Hese (1988) estimate this fraction as 40 % of the total phosphorus, *i.e.* a pool of 40 mgP/l sediment. Achterberg (1988) calculates with a pool of only 1 mgP/l. An indication can also be derived from the epipelon investigations: an average 70 % of the epipelon consists of ash (WQL Basic data). If the epipelon grossly corresponds to the upper sediment layer, one can estimate a percentage degradable material of 30 or a phosphorus pool of 30 mgP/l. The P/C ratio of the epipelon approximates 0.006, somewhat lower than that of the seston < 150 μ.

In the model, the state variables *PSed* [mgP/l sediment] and *CSed* [mgC/l sediment] correspond to the degradable organic material in the upper 2 cm. This layer is assumed to be completely mixed, due to bioturbation and wind influence. Changes in sediment volume are neglected. *PInts* [mgP/l pore water] is the SRP concentration in the interstitial water. Moreover, zoobenthos has been included, both in carbon (*CBent* [gC/m^2/d]) and in phosphorus (*PBent* [gP/m^2/d]) (see next paragraph).

This framework is comparable to those used by Jørgensen (1980) and Achterberg (1988), except that these authors do not include resuspension nor zoobenthos and do not bother about P/C ratios. A difference with Achterberg's model is that he works with a variable thickness (varying from *ca* 1-3 cm). In the current model, the fluxes between water and sediment (in grams per square meter per day), like the P mobilisation, are insensitive to the chosen sediment thickness. In fact, a model like ours, with a constant thickness of the active layer but a variable carbon concentration in that layer, could be rewritten in a form where the thickness is variable but its carbon content is fixed, without any change in the results.

5.6.2 Processes

Mineralisation is modelled as a first order process:

$$CDecSe = k_{dec(Se)} \cdot \Theta_{Se}^{T-20} \cdot CSed \tag{5.45}$$

$$PMinSe = k_{min(Se)} \cdot \Theta_{Se}^{T-20} \cdot PSed \tag{5.46}$$

with

$CDecSe$	decomposition of upper sediment	[mgC/l sed./d]
$k_{dec(Se)}$	decomposition constant of upper sediment at 20 °C	[d^{-1}]
Θ_{Se}	temperature constant	[e$^{1/°C}$]
$PMinSe$	mineralisation of upper sediment	[mgP/l sed./d]
$k_{min(Se)}$	mineralisation constant of upper sediment at 20 °C	[d^{-1}]

Boers & van Hese (1988) estimate the mineralisation constant, based on sediment oxygen demand measurements (about 0.6 g O_2/m^2/d) and also assuming a first order mineralisation, as lying between 0.0012 and 0.014 d^{-1}, averaged 0.006 d^{-1}, with a Q_{10} of about 3. The reported

sediment oxygen demand lies in the range found by many other authors (see Van Brummelen, 1988). To calculate the effect of mineralisation on interstitial P concentration, the flux is divided by the porosity (0.91 l pore water / l sediment).

In the model, the interstitial SRP that has been formed by the mineralisation process can go two ways: it can either be retained in the sediment (by adsorption to sediment compounds, precipitation and/or transport to deeper layers by downward seepage) or it can move to the surface water by diffusion. Advective transport is neglected. Loss to the deeper layers is again described as a first order process:

$$PPrecI = k_{prec(I)} \cdot PInts \tag{5.47}$$

with $PPrecI$ loss of interstitial P in the (deeper) sediment [mgP/l pore water/d]
$k_{prec(I)}$ daily fraction of interstitial P lost to the (deeper) sediment [d^{-1}]

Both Boers & van Hese (1988) and Achterberg (1988) estimate the loss constant (or 'precipitation constant') as 0.1 d^{-1}. Probably, downward seepage might be the principal long-term driving force causing this flux (Keizer and Buysman, 1990).

Finally, diffusion to the surface water, the phosphorus mobilisation itself, is described as a function of the *difference in SRP concentration* between pore water and surface water and the thickness of the active sediment layer:

$$PDiffIS = \frac{k_{diff(IS)}}{z_s/2} \cdot (PInts - PSol) \cdot Por \tag{5.48}$$

with $PDiffIS$ diffusion of interstitial P to the surface water [gP/m^2/d]
$k_{diff(IS)}$ diffusion coefficient [m^2/d]
Por porosity of upper sediment [l water/l sediment]

The effect on the interstitial P concentration is calculated by division of the flux by both the porosity and the thickness of the active layer, z_s. The diffusion coefficient might be somewhat higher than the effective diffusion constant of phosphorus (= $3 \cdot 10^{-5}$ m^2/d) due to bioturbation and other factors. Temperature has only a minor influence on the diffusion process (Jørgensen et al., 1975; Kamp-Nielsen, 1975) and the correction is neglected.

5.7 Processes of the zoobenthos

As stated earlier, zoobenthos is included in the model for its role as fish food, thereby creating an extra phosphate flux to the lake water system. Most of the zoobenthos consists of midge larvae (*Chironomidae*), especially large specimens of *Chironomus plumosus*. Density has been determined on ten dates throughout the years 1985, 1986 and 1987 and turned out to vary between 0.1 and 7.6 g dry matter per m^2, averaged 2.4 g dry matter per m^2 or 1.2 gC/m^2 (Limnological Institute, unpubl. res.). Average density is in the range reported in the literature for eutrophic lakes (Wetzel, 1982). The P/C ratio of the organisms is estimated as 2.0 - 2.5 % (Van Liere, Limn. Inst., pers. comm.).

Processes described with respect to the zoobenthos are: feeding on the sediment, predation by fish, respiration / excretion and mortality. Predation by fish has already been described in § 5.4.

Feeding on the sediment is described as a first order process, temperature dependent, assuming that the amount of sediment is normally not limiting growth (only at very low availability of food, which does never occur, a correction is made):

$$CEatSeBe = k_{eat(Be)} \cdot \Theta_{Be}^{T-20} \cdot CBent \qquad (5.49)$$

with

$CEatSeBe$	feeding of zoobenthos on sediment	[$gC/m^2/d$]
$k_{eat(Be)}$	feeding coefficient at 20 °C	[d^{-1}]
Θ_{Be}	temperature constant	[$(e^{°C})^{-1}$)]

A fraction $CEff_{Be}$ (C assimilation efficiency [-]) is assimilated, the remainder is egested and returned to the sediment pool. For phosphorus, an analogous equation is used, except that P assimilation efficiency, $PEff_{Be}$ [-], is adapted to the P/C ratio of the sediment, allowing the animals to keep their P/C ratio at its reference value of 2.25 %. Because the P/C ratio of the sediment is only about 0.6 %, the C efficiency is estimated as 0.25 [-]. On the feeding of bottom organisms not much is known experimentally. Beattie (1982) gives a figure for the *net* production of Diptera larvae of 5 y^{-1}. This would mean 0.02-0.03 d^{-1} in summer, an assimilation rate of 0.05-0.06 d^{-1} (accounting for losses by repiration and death) and an ingestion rate of 0.20-0.24 d^{-1}. This value approximates the ingestion rate needed by the zoobenthos to be able to remain its biomass under the given fish predation pressure. The temperature coefficient has been assigned the same value as the one for fish.

Natural mortality is modelled as a second order process (with a - rather arbitrary - rate constant of 0.01 $m^2/gC/d$) because this improves stability; not much is known of it. Respiration and P excretion are included for the sake of completeness, with a first-order rate constant of 0.02 d^{-1} (about 40 % of the carbon assimilation).

6 Calibration and implementation

The model contains a rather large number of rate constants and other parameters, that have to be assigned a numeric value. Parameter values (listed in Appendix A) have been derived from three sources: experimental data provided by other WQL working groups, data in the literature and, finally, 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. All these parameters are already mentioned in chapter 5. Very little information is available on selective grazing, mortality of plankton organisms, predation rate, settling rates and mineralisation. These unknown parameters have been assigned values found in the literature and/or calibrated on the data, within the ranges found.

With respect to the calibration, it must be kept in mind that a model parameter is not necessarily identical to a parameter derived from experiments. A state variable in the model will in general be a 'lumped' variable, consisting of several species or chemical fractions, and a process in the model will be composed of a number of subprocesses. Alternatively, difficulties often arise when applying results of experimental research in the field situation, because the latter is always more complex and more variable, both in time and in space. For these reasons, we consider it as allowed to change, to some extent, also *measured* parameters during the calibration. In the model, one builds an 'idealised' picture of the ecosystem to make sure that the flows of matter through the system are always consistent with one-another.

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. In previous versions of the model (see Janse, 1987, 1988) it was possible to perform a nearly-complete calibration of the 'missing' parameters from the measured ones in a steady state analysis (putting all derivatives to zero). The present model has become too complex for that, but some elements of the analysis are still useful. We calibrated on the average values in 1985-'87, without performing a (time-consuming) formal parameter estimation; this will be left for the near future when better tools are available.

We used the field data collected by the Municipal Water Works of Amsterdam and (from 1983 on) by the Limnological Institute at Nieuwersluis, especially those of Lake Loosdrecht itself (sampling stations 9 and 5). The data for Lake Vuntus (station 7) and Lake Breukeleveen (station 6) have only been used for comparison; no recalibration has taken place when applying the model to these lakes except for lake-dependent characteristics as depth, temperature and frequency of resuspension. As stated earlier (§ 5.5), phytoplankton and detritus can not be measured separately; the sum of them is measured as seston < 150 μ of which, among others, dry weight and C, P and chlorophyll-*a* content are measured. Zooplankton is measured as the seston > 150 μ. Other measurements used are SRP, total P, sediment P and transparency, as well as the above mentioned process measurements.

Input values for the model are: measured water temperatures (the average of stations 5 and 9 for Lake Loosdrecht, station 7 for Lake Vuntus and station 6 for Lake Breukeleveen), daily radiation (data from KNMI, station De Bilt, read in as two-week moving averages), water inflow and total phosphorus input. Temperature and radiation are interpolated when read in. Water inflow and phosphorus input are read from the balance models made by the Free

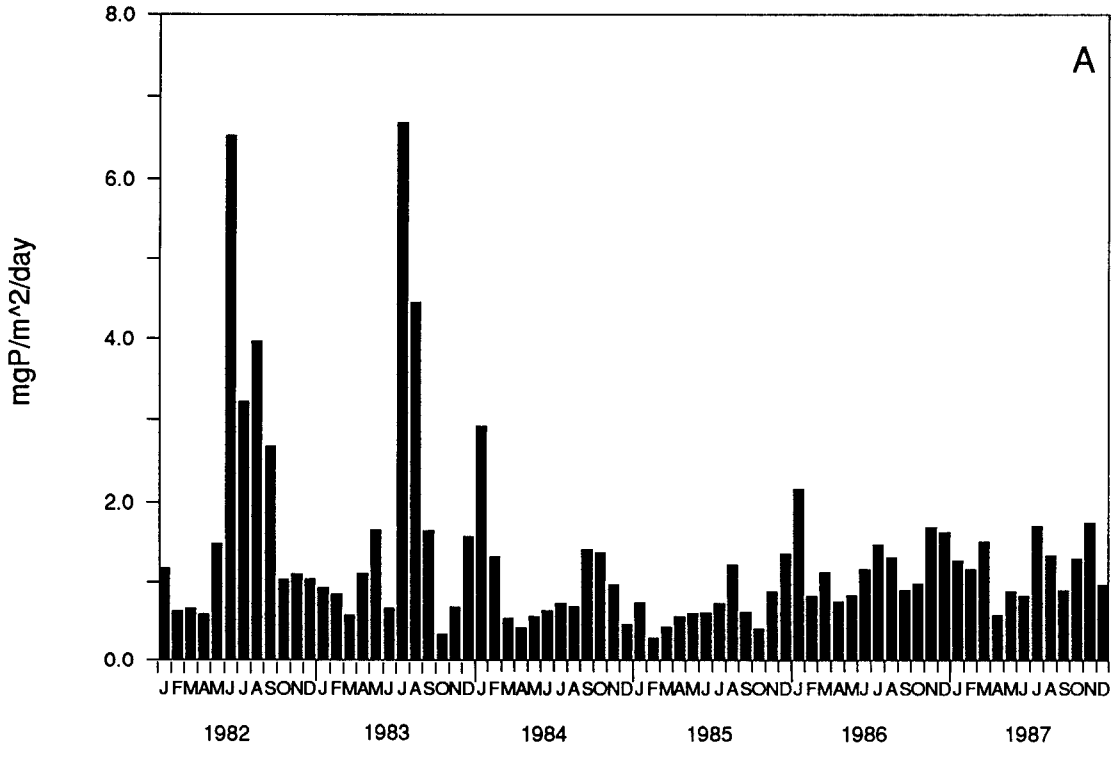
University of Amsterdam (Engelen *et al.*, 1988; Buijse, 1989). These balance are made, on a monthly base, for the Loosdrecht Lakes system as a whole as well as for each lake separately, from 1982 on. Values are read in as step functions: the value for January is valid from day 1 till day 31, etc. The water inflow is used minus the evaporation (see § 5.1), the phosphorus input minus the 'input' caused by storage differences between the start and the end of a month.

Model calculations are 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 is used with a variable step size. The 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 is allowed to equilibrate for a simulated period of two years with the input data for 1982; this means that the initial values at the start of 1982 are in agreement with those data. (The question rises whether this is correct for Lake Breukeleveen, where the external loading in 1980 and 1981 might have been higher than in 1982. Detailed balances are not available for those years, however). Simulation takes quite long: about 15-45 minutes per simulated year, depending on the type of (AT) computer.

7 Results

7.1 External phosphorus loading

Fig. 7 A-C depicts the external P loading (in mgP/m^2/d) of the three lakes in the system: Lake Loosdrecht, Lake Vuntus and Lake Breukeleveen, on a monthly base for the years 1982-1987 (data from Buijse, 1989). The data for Lake Loosdrecht exclude the Kievitsbuurt area, a system of ditches and small dikes at the west side of the lake. Part of the loading from the Vecht or Amsterdam-Rijn-kanaal is retained in this area and does not reach the main lake; in the balance model, assumptions have been made about these fractions. Before 1984, high loadings are observed in the summer months, 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 remain the same or even increase. These loadings originate for a great deal from the surrounding polders. The external loading of Lake Breukeleveen is in general somewhat higher than that of Lake Loosdrecht, except for the summer peaks in the first two years. The loading of (the most isolated) Lake Vuntus is lower and has hardly changed during the period concerned.



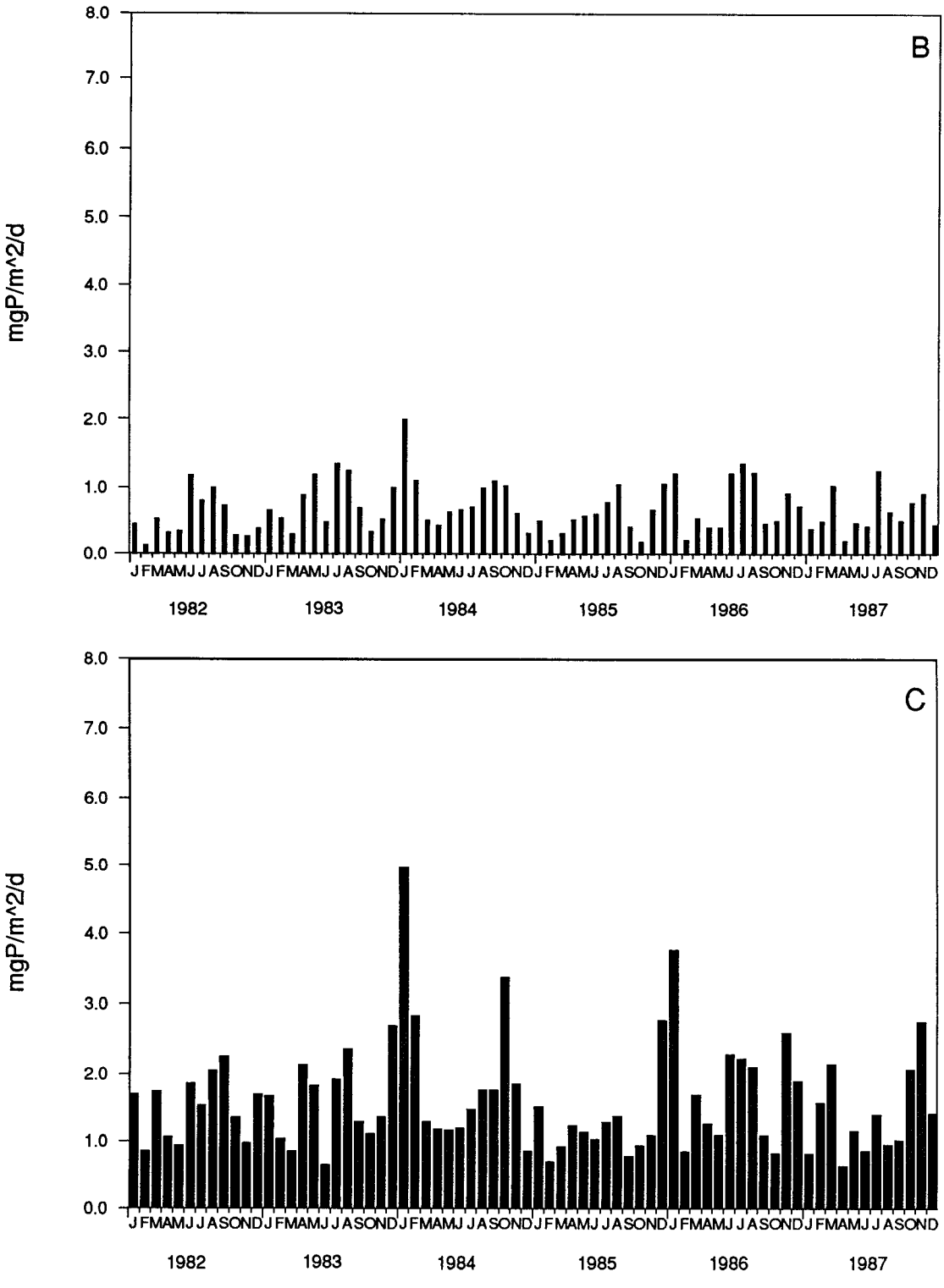


Fig. 7. External phosphorus loading of the Loosdrecht Lakes, 1982 - 1987 (without storage differences).
A, Lake Loosdrecht; **B**, Lake Vuntus; **C**, Lake Breukeleveen.
(data from Buijse, 1989).

7.2 Simulations 1982-1987

The results of model simulations are shown most extensively for the main lake, Lake Loosdrecht, with some examples of results for the smaller lakes. The simulated period is in all cases the years 1982 to 1987. The results for Lake Loosdrecht are depicted in Figs. 8-14, together with the data (sampling station 9). For chlorophyll-*a* (Fig. 8B), both data and simulations display a seasonal variation with summer maxima around 200 µg/l, which decrease a little over the years. Transparency averages 30 cm in summer and is somewhat higher in winter (Fig. 8A). The blue-greens are the dominant group during most of the year (Fig. 9), but in spring, also the other groups succeed in building up a significant biomass. The larger part of the seston < 150 µ (about 60 % in summer, up to 90 % in winter) consists of detritus. This is consistent with estimates by Gons (1987) of an average detrital fraction of two-thirds. The seasonal variation is somewhat underpredicted. 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 (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 the late spring, decreases a little following the load reduction (Fig. 10A). The exact seasonal pattern is not reproduced by the model; for that purpose, the model formulation is too much a generalisation, while the zooplankton, due to its position as 'middle' trophic level, is quite sensitive to parameter changes. The simulated fish stock (Fig. 10B) also decreases a little until 1.5-1.8 mgC/l, a little higher than the value recently established in the field (1.2 mg C/l, corresponding to 300 kg fish per ha).

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. 11, B-D). Also the total P measurements show a decreasing tendency, although there is a lot of unexplained variation in the data. The simulated P/C ratio of the seston is gradually decreasing, a tendency also observed in the lake (Fig. 13, B-C). The P/C ratio of the zooplankton does not change, due to regulation mechanisms of the animals (Fig. 13A). The measurements still show quite some 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, about 80-100 µgP/l (Fig. 12B), nearly equals the amount in all other compartments together, as is found in most hypertrophic lakes (Van Liere *et al.*, 1989a,b). The SRP values (Fig. 11A) 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 saturate themselves with phosphorus (*cf.* Fig. 13C). 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 phosphorus concentrations show a delayed response to the load reduction (Fig. 14, 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 mgP/m^2. A particularly interesting process with respect to the sediment, the phosphorus mobilisation (or

internal loading), is shown in Fig. 14C. The mobilisation is within the range of values observed in column experiments (Boers and Van Hese, 1988; Achterberg, 1988); it decreases (with some time lag) in response to the decreased external loading.

For most variables, the characteristic response time of the model system to a change in loading seems to be about 2 years.

The results for Lake Vuntus (Fig. 15, A-C) and Lake Breukeleveen (Fig. 16, A-C) are in agreement with the resp. lower and higher average phosphorus loading and the resp. lower (3 %) and higher (7 %) fraction of resuspension. Because of the smaller variation in phosphorus loading, the variation in the output is also smaller than in Lake Loosdrecht.

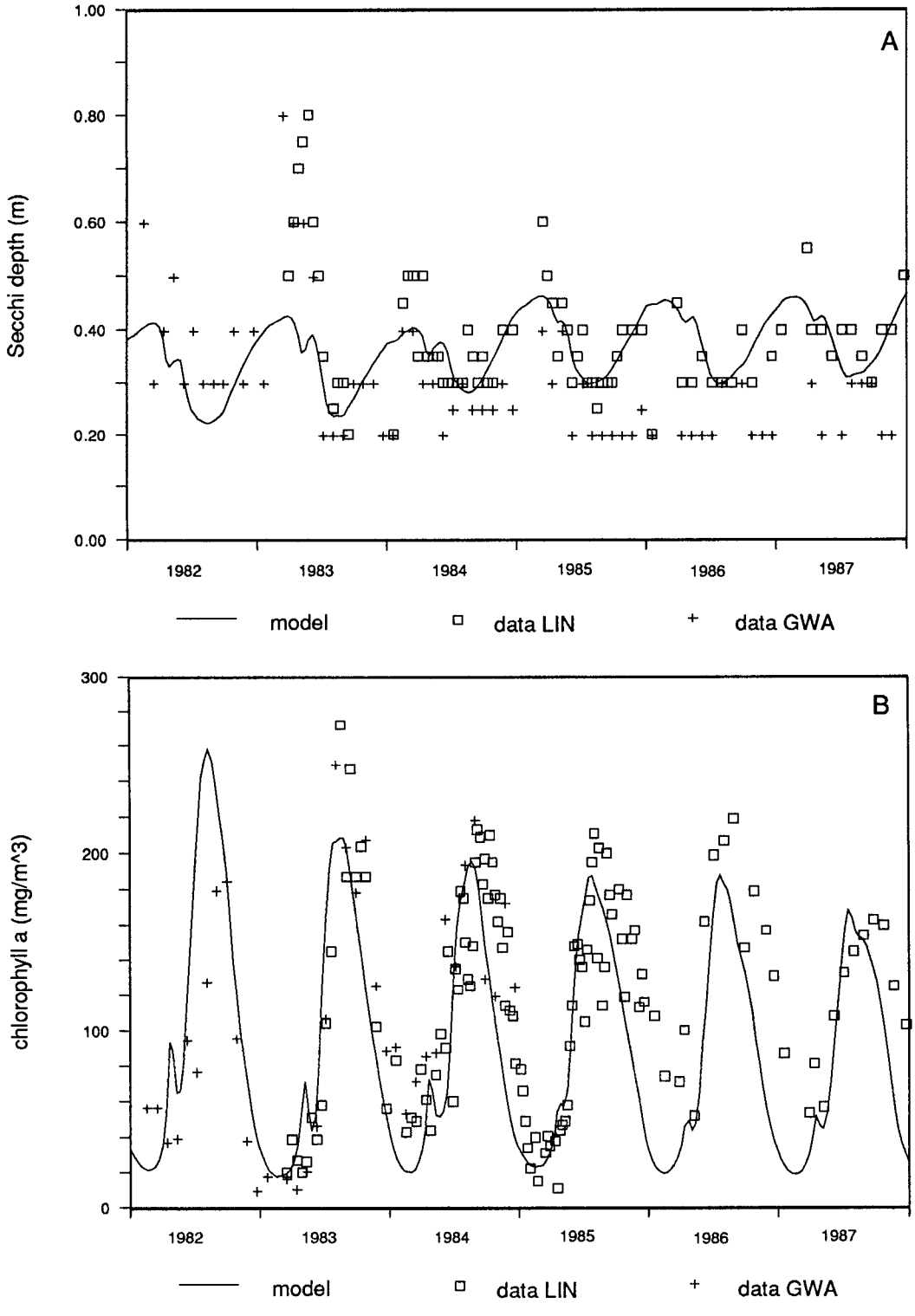


Fig. 8. Lake Loosdrecht, simulations compared with measurements, 1982 - 1987. **A**, Secchi depth; **B**, Chlorophyll-*a*.

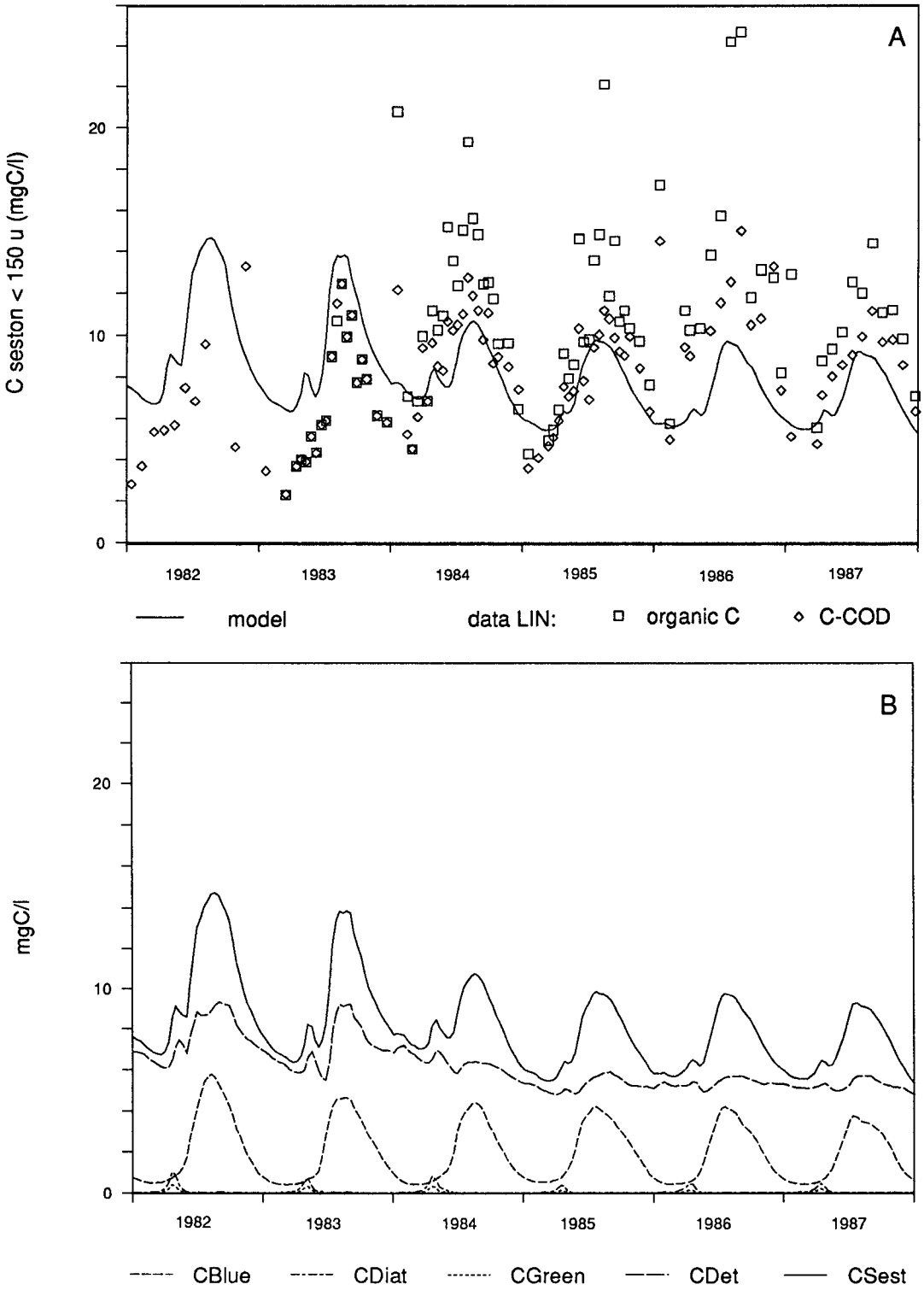


Fig. 9. Lake Loosdrecht, seston < 150 μ, carbon fractions; 1982 - 1987.
A, CSest, simulations compared with measurements;
B, simulations of CSest and its constituents: CBlue, CDiat, CGreen and CDet.

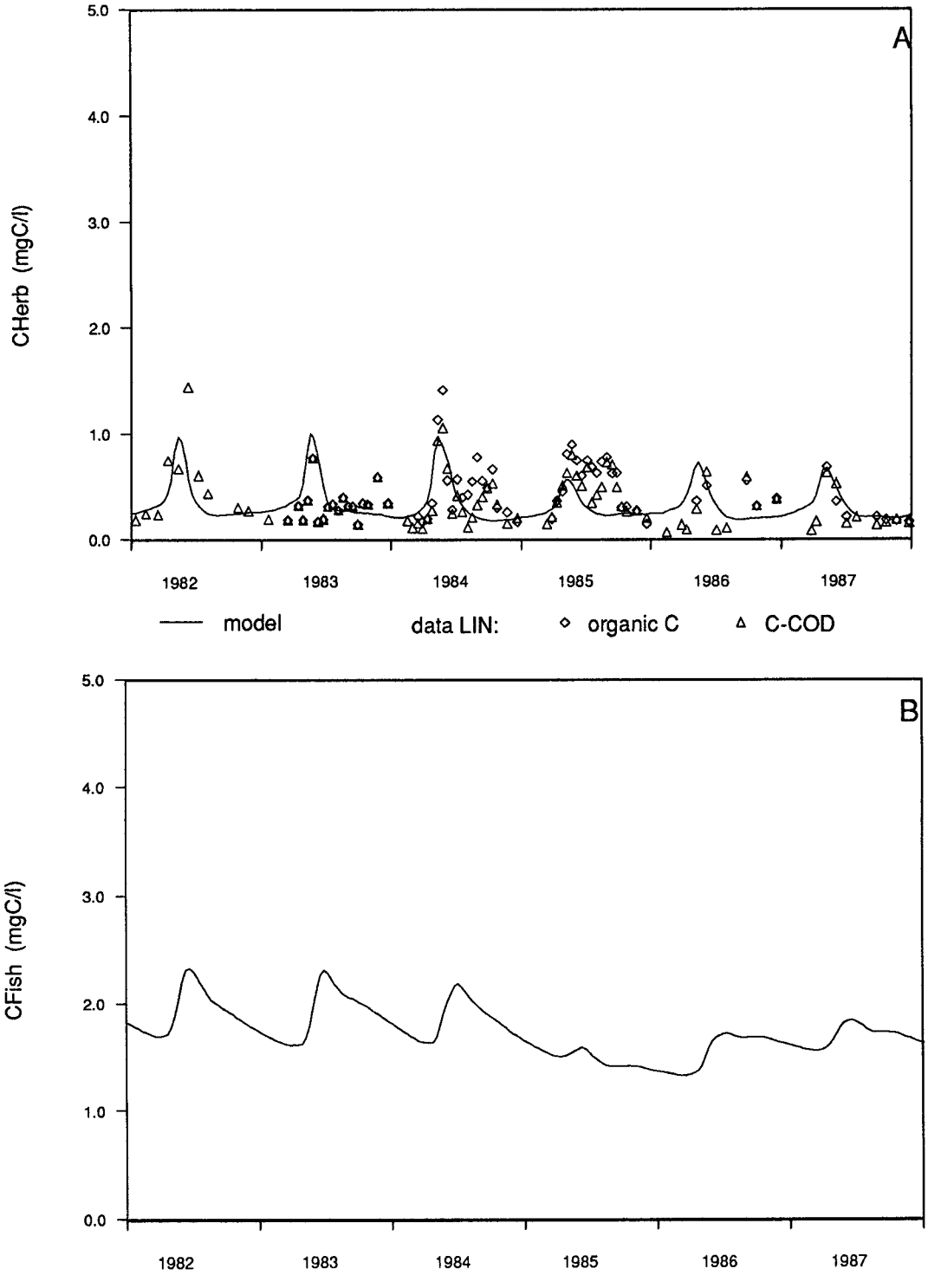
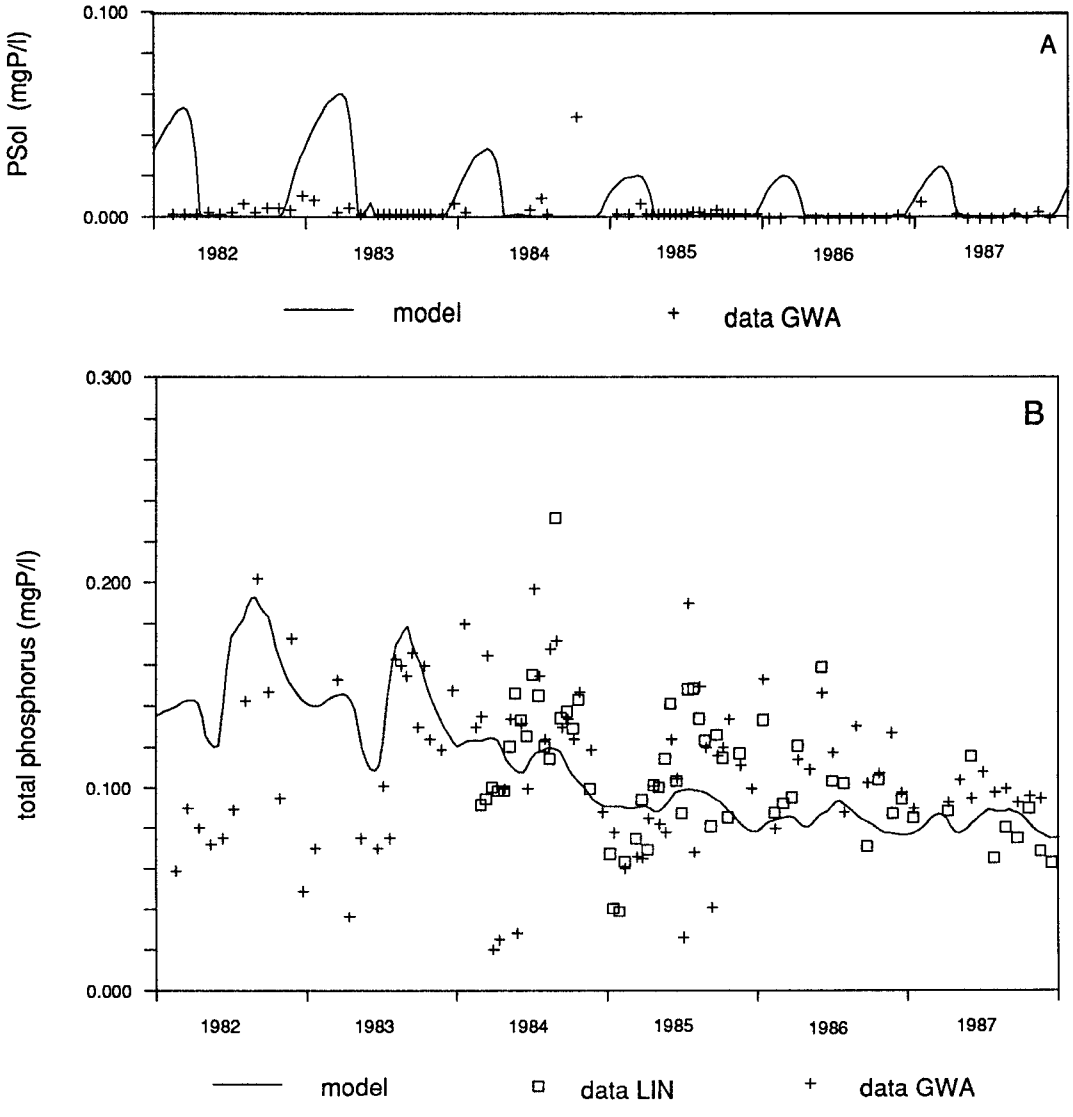


Fig. 10. Lake Loosdrecht, higher trophic levels, carbon; 1982 - 1987.
A, CHerb, simulations compared with measurements;
B, CFish, model simulation.


PSol (mgP/l)
0.100
0.000
A
1982
1983
1984
1985
1986
1987
model
data GWA
total phosphorus (mgP/l)
0.300
0.200
0.100
0.000
B
1982
1983
1984
1985
1986
1987
model
data LIN
data GWA

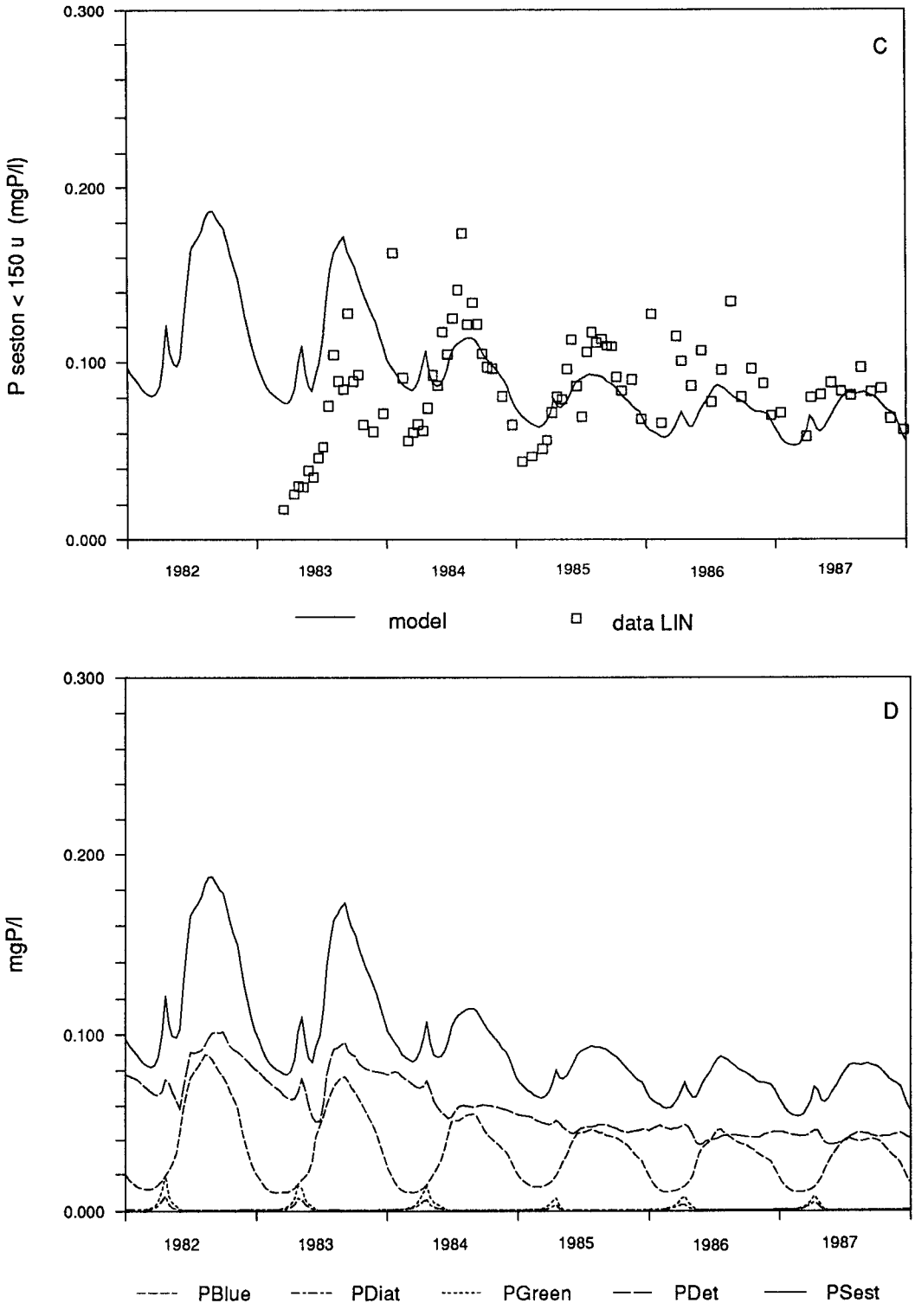


Fig. 11. Lake Loosdrecht, phosphorus fractions; 1982 - 1987.
A, SRP; **B**, PTot; **C**, PSest (all: simulations and measurements);
D, simulations of PSest and its constituents: PBlue, PDiat, PGreen and PDet.

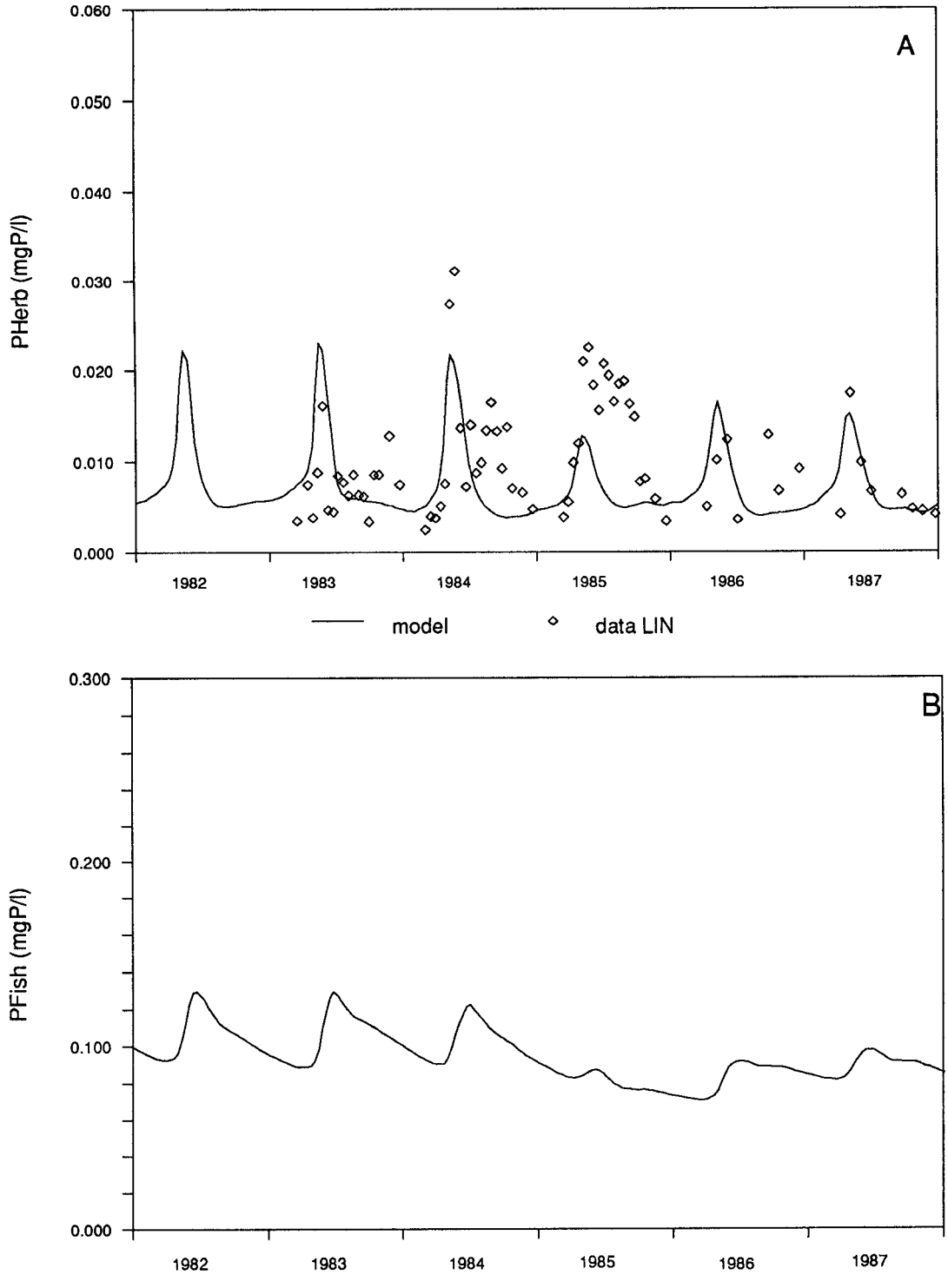
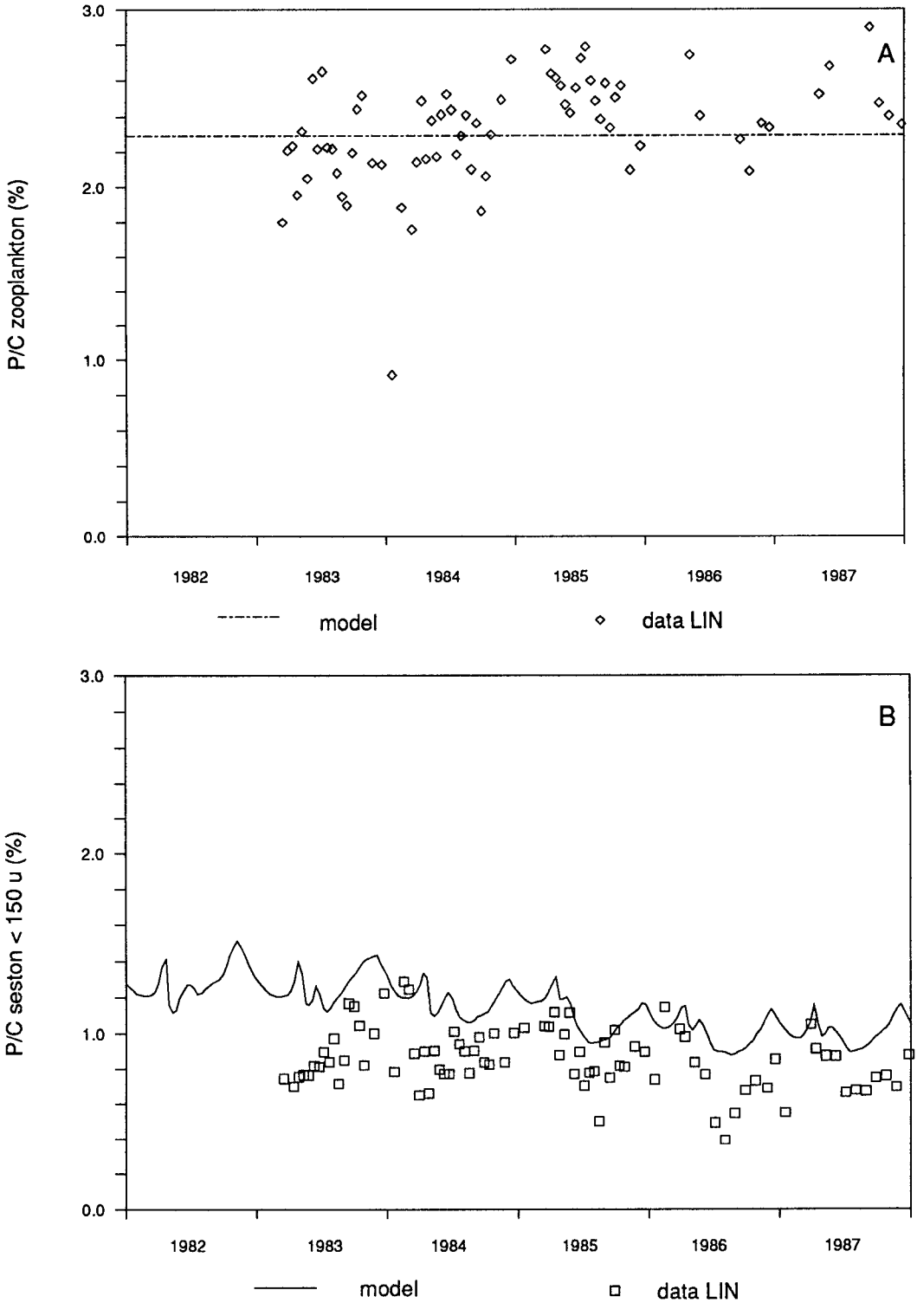


Fig. 12. Lake Loosdrecht, higher trophic levels, phosphorus; 1982 - 1987.
A, PHerb, simulations compared with measurements;
B, PFish, model simulation.


A
P/C zooplankton (%)
3.0
2.0
1.0
0.0
1982
1983
1984
1985
1986
1987
model
data LIN
B
P/C seston < 150 u (%)
3.0
2.0
1.0
0.0
1982
1983
1984
1985
1986
1987
model
data LIN

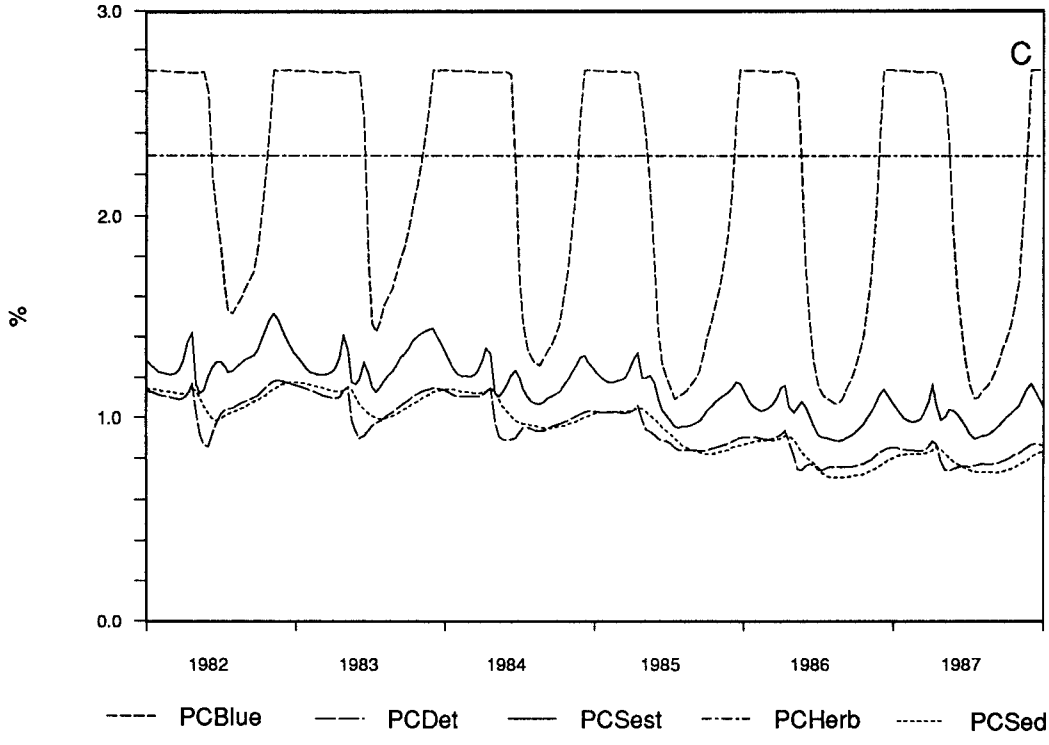
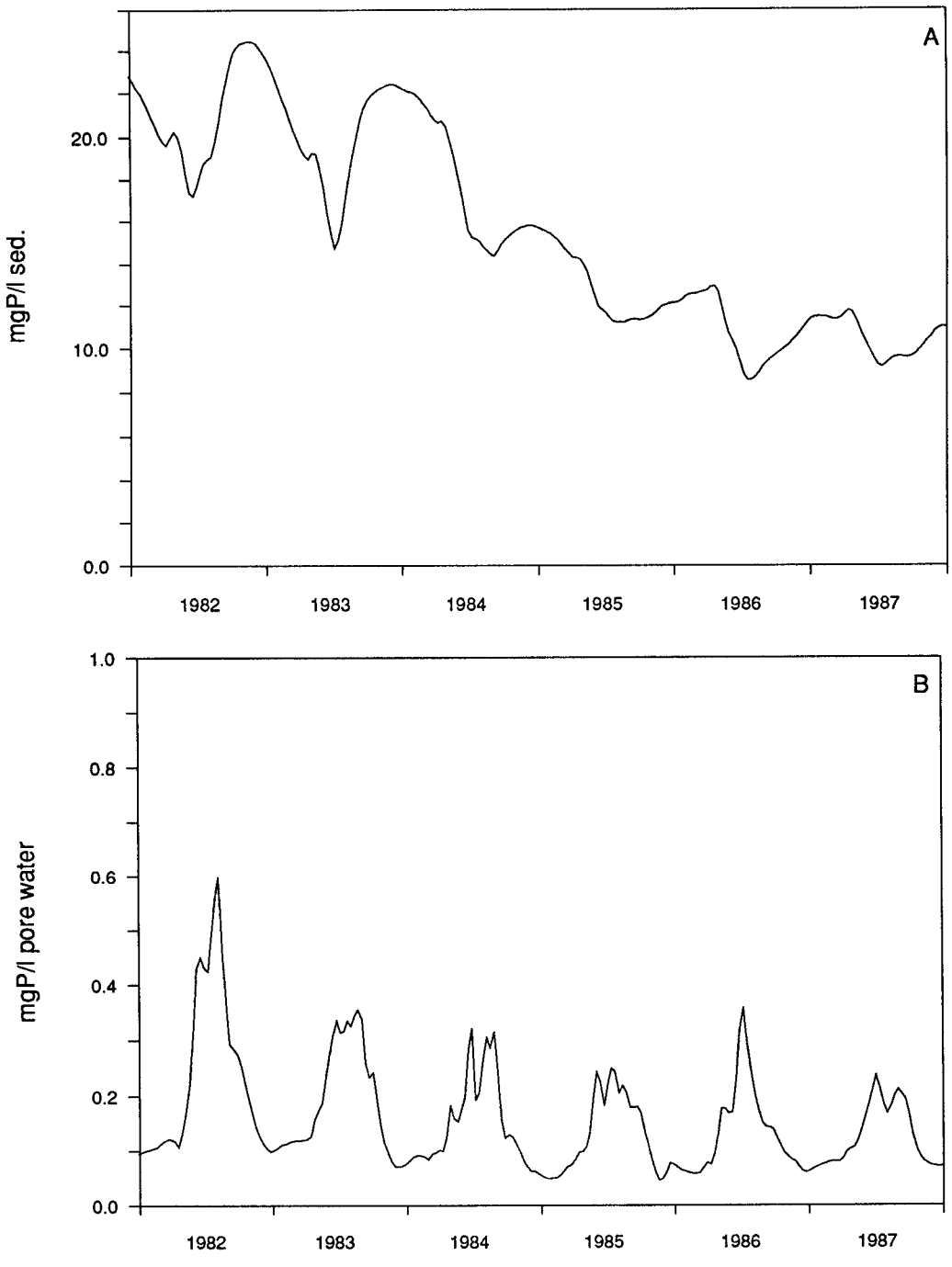


Fig. 13. Lake Loosdrecht, P/C ratios, 1982 - 1987.
A, P/C ratio of zooplankton; **B**, P/C ratio of seston < 150 μ (both: simulations and measurements); **C**, P/C ratios of blue-greens, detritus, seston < 150 μ, zooplankton and upper sediment (model simulations).


A
mgP/l sed.
20.0
10.0
0.0
1982
1983
1984
1985
1986
1987
B
mgP/l pore water
1.0
0.8
0.6
0.4
0.2
0.0
1982
1983
1984
1985
1986
1987

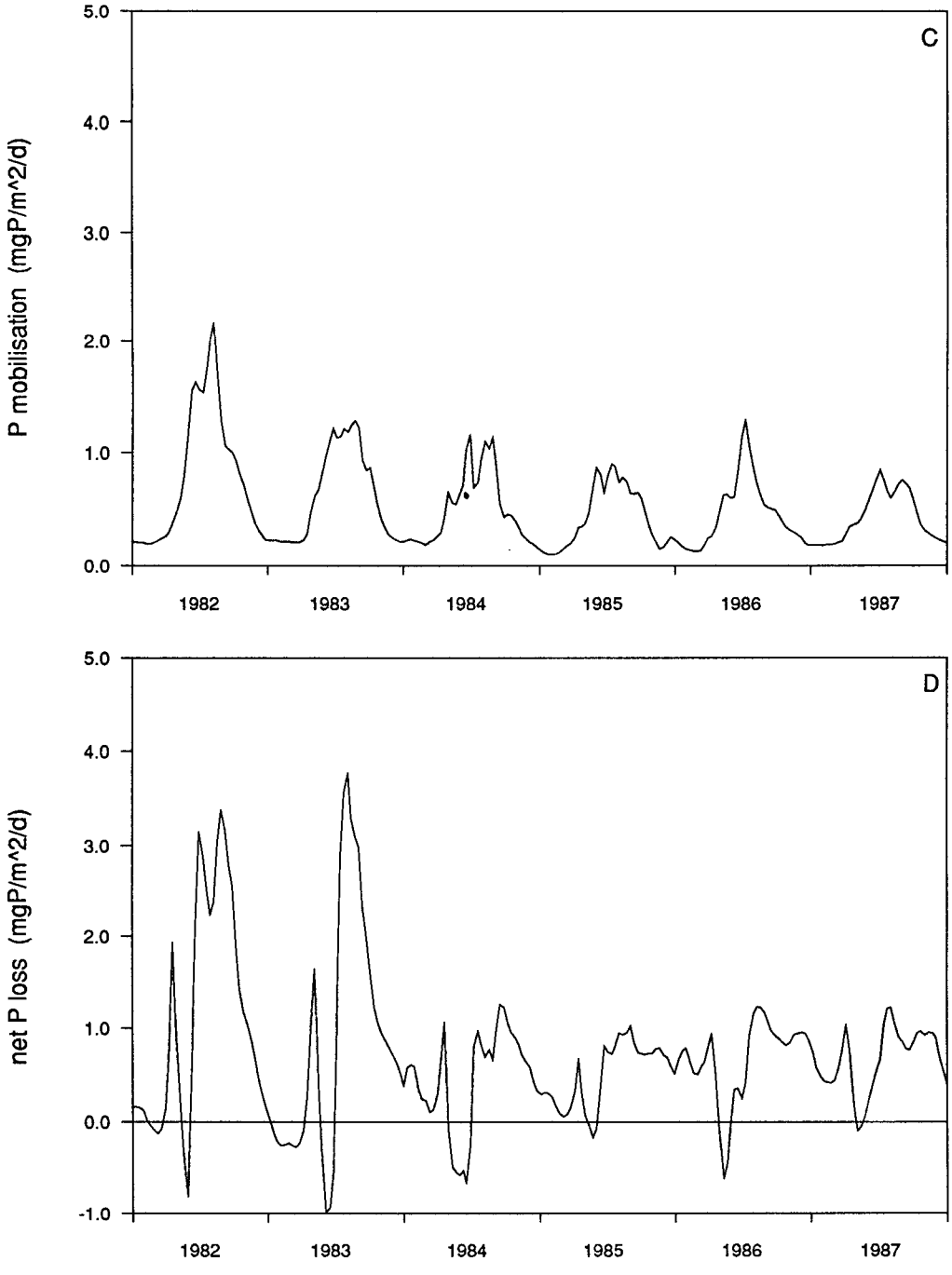
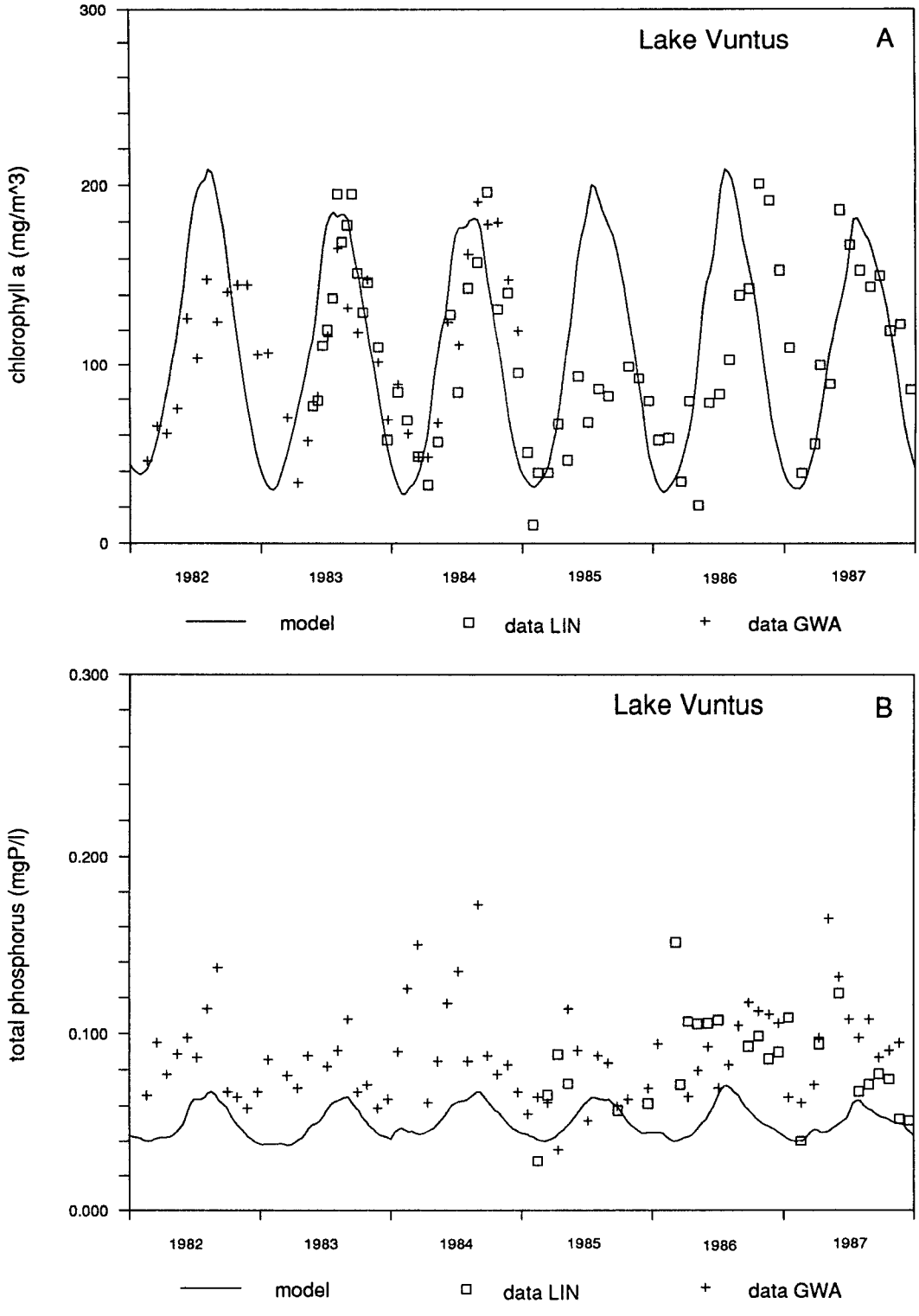


Fig. 14. Lake Loosdrecht, upper sediment, simulations of phosphorus fluxes and concentrations, 1982 - 1987.
A, PSed; **B**, PInts; **C**, P mobilisation; **D**, Net P loss to the sediment.


Lake Vuntus
A
chlorophyll a (mg/m^3)
300
200
100
0
1982
1983
1984
1985
1986
1987
model
data LIN
data GWA
Lake Vuntus
B
total phosphorus (mgP/l)
0.300
0.200
0.100
0.000
1982
1983
1984
1985
1986
1987
model
data LIN
data GWA

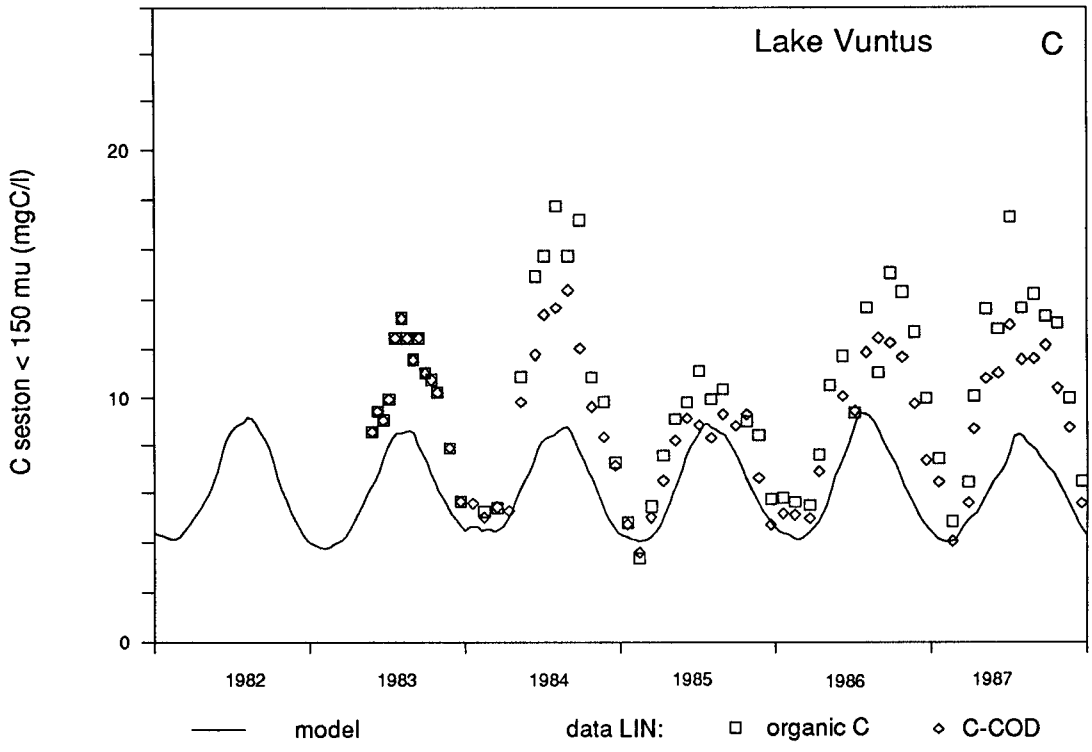
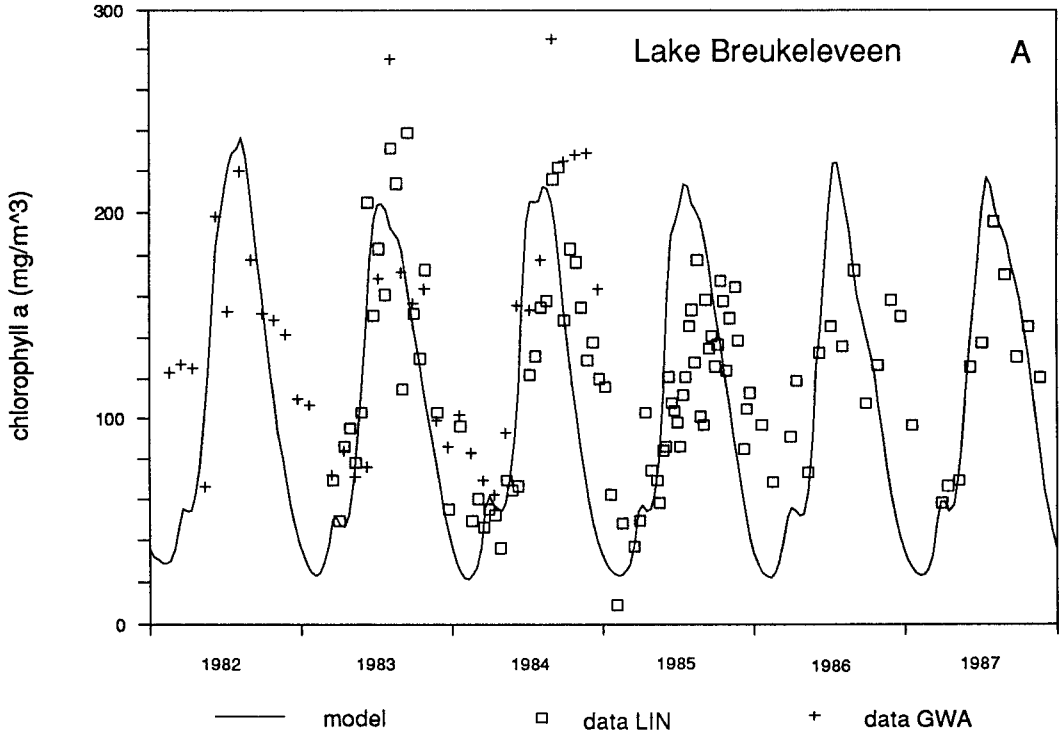
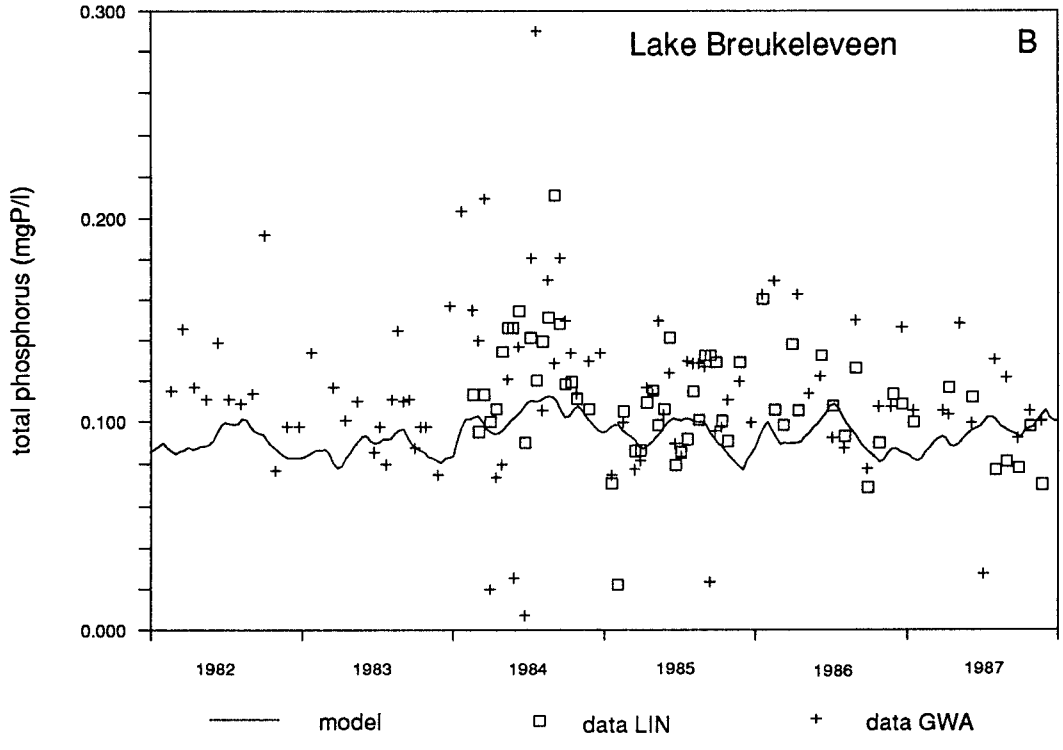


Fig. 15. Lake Vuntus, simulations and measurements, 1982 - 1987.
A, Chlorophyll-*a*; **B**, PTot; **C**, CSest.


Lake Breukeleveen
A
chlorophyll a (mg/m^3)
300
200
100
0
1982
1983
1984
1985
1986
1987
model
data LIN
data GWA


Lake Breukeleveen
B
total phosphorus (mgP/l)
0.300
0.200
0.100
0.000
1982
1983
1984
1985
1986
1987
model
data LIN
data GWA

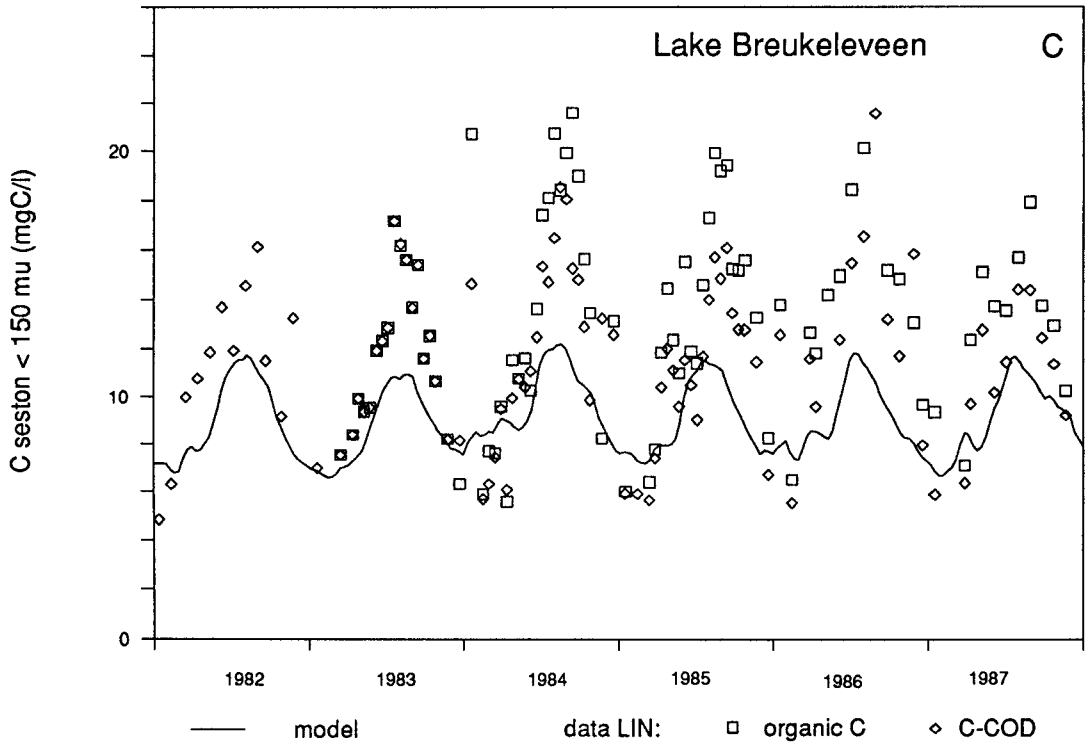


Fig. 16. Lake Breukeleveen, simulations and measurements, 1982 - 1987. **A**, Chlorophyll-*a*; **B**, PTot; **C**, CSest.

7.3 Future trends

The fact that the system shows a response time of about two years means that no further reactions of the system on the restoration measures in 1984 are to be expected (Figs. 17 and 18A). The 'no change' scenario has been calculated with standard sinusoidal inputs for temperature (12 ± 10 °C) and light (200 ± 150 W/m^2) and a constant phosphorus input of 1.2 $mgP/m^2/d$, the average value in 1986 and 1987. On the opposite, calculations with additional P reduction scenarios show that a further reduction of P loading with 50 percent would indeed, with a lag time of about 3 years, lead to a permanent improvement of water quality, with total P concentration about half the present value, seston < 150 µ and chlorophyll-*a* about two-thirds the present values and, consequently, also a 50% increased transparency. Another 50 % reduction of external phosphorus loading would give a further improvement (Figs. 17 and 18). There seems to be a limit to the mechanism of a decreasing P/C ratio of the seston as a resiliating factor.

Measures with a unique character, like removing 80 % of the fish at once without changing external P input, have only a temporary effect (Fig. 18C). The sudden decrease in fish stock gives rise to a strong increase of zooplankton and a subsequent decrease of seston < 150µ, but after half a year the system has re-adapted itself to its former equilibrium. However, the model is not yet flexible 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.

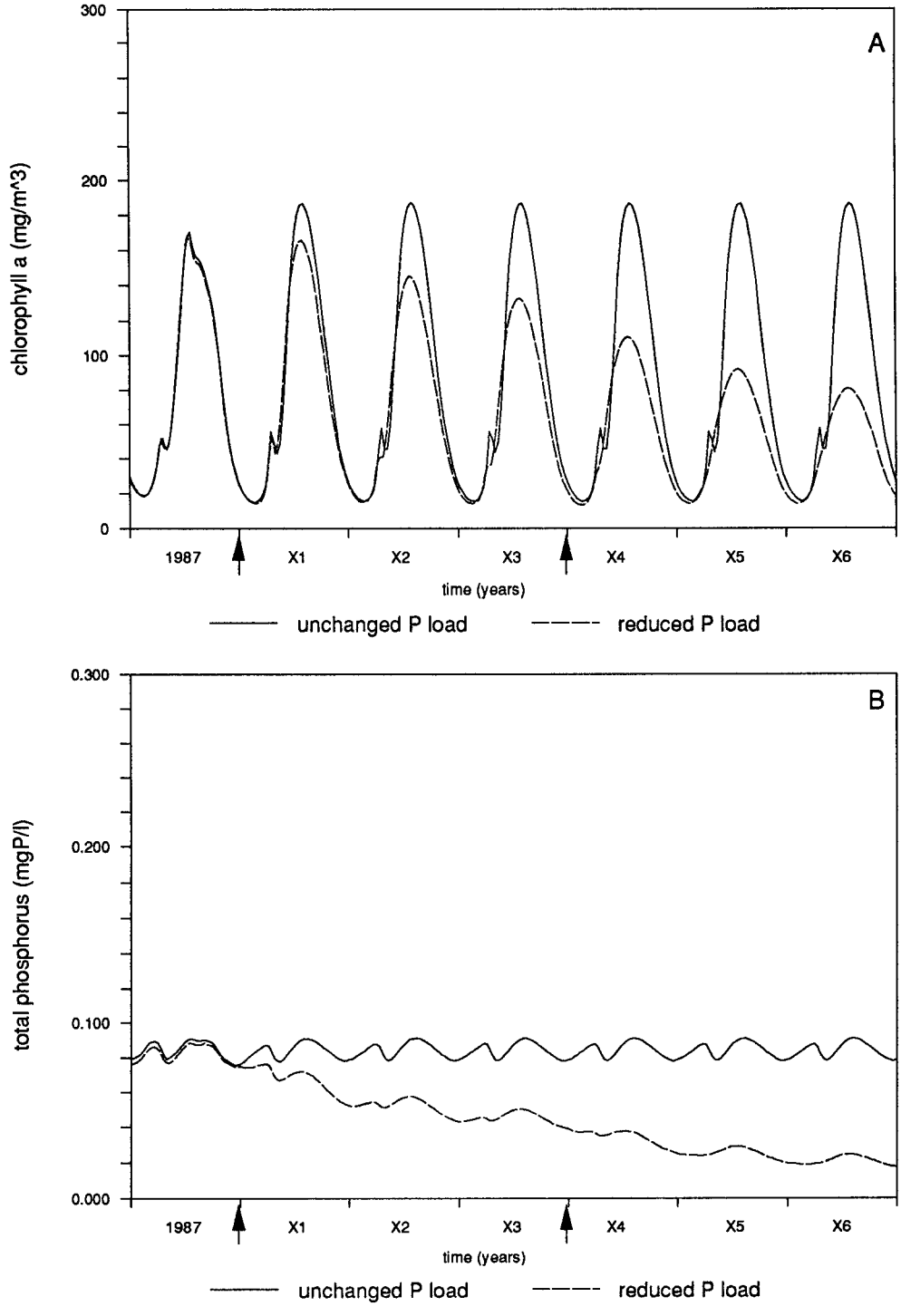
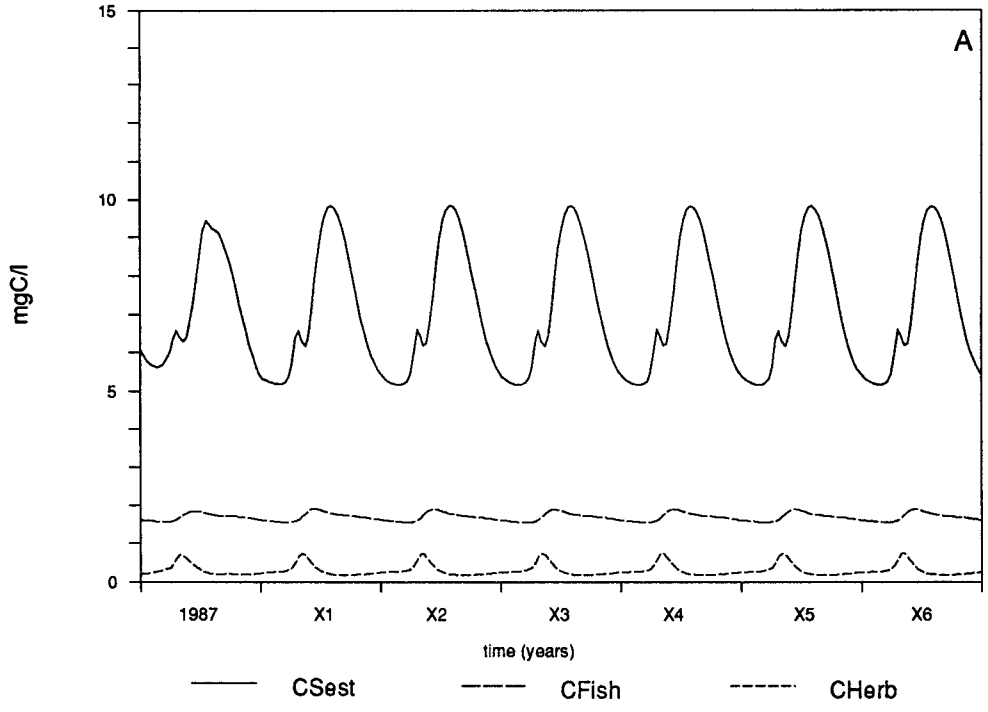
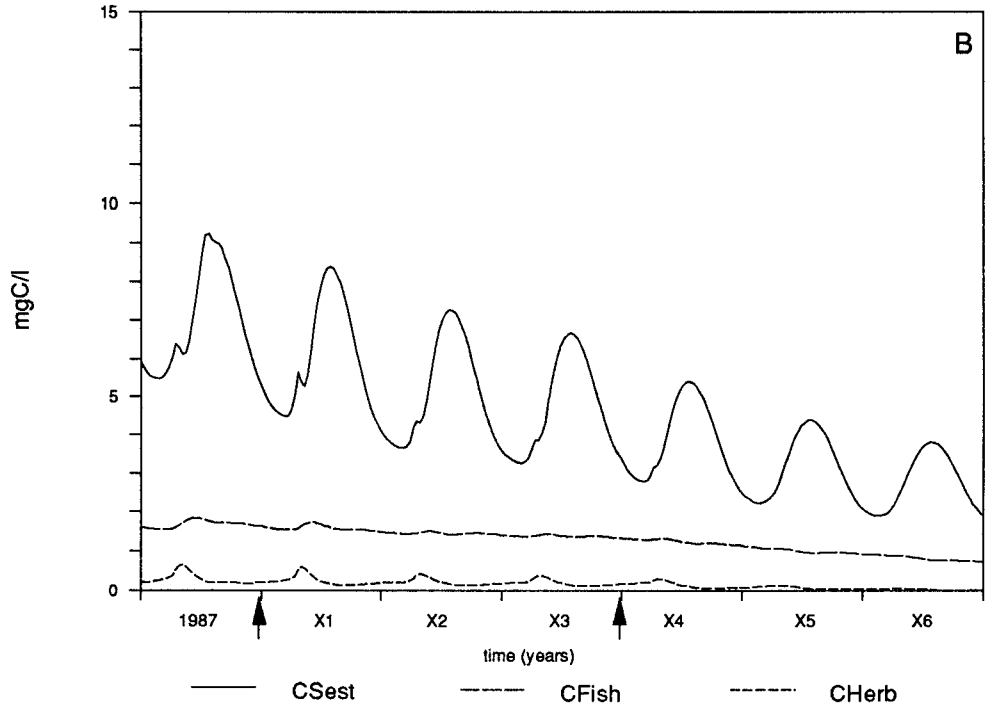


Fig. 17. Trend calculations with unchanged and reduced phosphorus loading, Lake Loosdrecht: **A**, Chlorophyll-*a*; **B**, PTot.
1987 with real input data, afterwards standard sinusoidal input for temperature and radiation and constant external P loading. Straigt lines: P loading = 1.2 mgP/m^2/d. Dashed lines: P loading = 0.6 mgP/m^2/d in the years X1-X3 and 0.3 mgP/m^2/d in the years X4-X6.


A
15
10
5
0
mgC/l
1987
X1
X2
X3
X4
X5
X6
time (years)
CSest
CFish
CHerb


B
15
10
5
0
mgC/l
1987
X1
X2
X3
X4
X5
X6
time (years)
CSest
CFish
CHerb

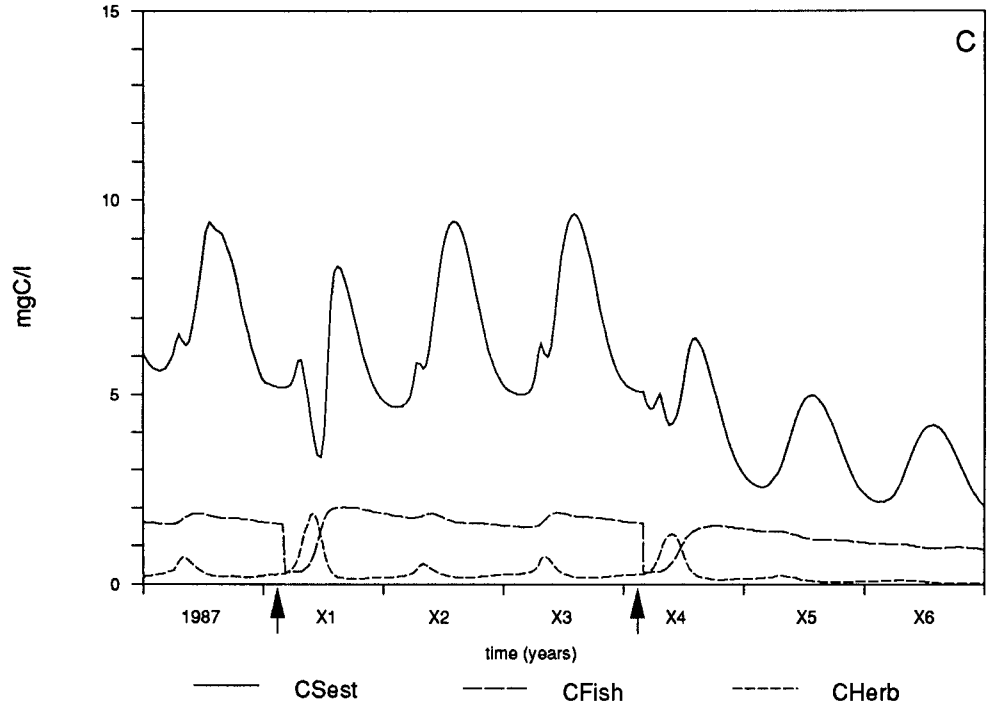


Fig. 18. Trend calculations with reduced phosphorus loading and fish removal, Lake Loosdrecht: CSest, CHerb and CFish.
1987 with real input data, afterwards standard sinusoidal input for temperature and radiation and constant external P loading.
A, P loading = 1.2 mgP/m^2/d.
B, P loading = 0.6 mgP/m^2/d in the years X1-X3 and 0.3 mgP/m^2/d in the years X4-X6.
C, P loading = 1.2 mgP/m^2/d in the years X1-X3 and 0.3 mgP/m^2/d in the years X4-X6, and biomanipulation (80 % fish removal) is carried out on 1. March of both the years X1 and X4.

8 Discussion

8.1 The system's behaviour

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:

$$\begin{aligned} Net\ P\ loss = {} & sedimentation - resuspension - mobilisation + \\ & + fish\ bone\ sedimentation - fish\ feeding \quad [\text{mgP/m2/d}] \end{aligned} \tag{8.1}$$

Fig. 14D shows that the sediment continues to function almost always as a net sink of phosphorus: sedimentation is higher than mobilisation and 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:

$$Net\ P\ loss = external\ P\ loading - P\ outflow \quad [\text{mgP/m2/d}] \tag{8.2}$$

Both the balance-derived and the model-derived averages for the years 1982 t/m 1987 are given in Fig. 19. It can be seen that the amount of phosphorus retained decreases with decreasing external loading and that the dynamical model and balance model show the same trend, although the values are not identical. The amount retained as fraction of the external loading, the retention coefficient R, averages 0.58 (balance-derived) or 0.54 (model-derived) over the six studied years, values which 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 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*. The different sensitivities for carbon and phosphorus in the seston is reflected in the commonly used empirical relation between summer averaged chlorophyll-*a* and total phosphorus (Fig. 20). The lakes have not escaped from the cluster of data points around 100 µg/l total P and 125 µg/l chlorophyll-*a*. The straight line in the figure is the empirical upper limit for lakes where filamentous cyanobacteria are dominant, as established by the CUWVO from a database of Dutch lakes (Lijklema *et al.*, 1988; CUWVO, 1987).

This behaviour is related to the observed decrease of the P/C ratio of both the phytoplankton and the total seston < 150 µ. It is interesting to look at this aspect in view of physiological indicators of phosphorus limitation. The simulated summer averaged P/C ratio 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/d), while the growth rate μ remains about 0.07 day^{-1} (Fig. 21). Healey (1978) considers an algal cell quota of 10 μgP/mg 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 μmolP/mg dry weight/h (= 0.3 mgP/mgC/day) 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 and baard (1987). The simulations suggest that the blue-green algae in the Looosdrecht Lakes are P deficient from 1984 on and that deficiency is becoming more stringent. Measurements of v_{max} support this conclusion: in 1983 values were often around or below the limit of 0.3 mgP/mgC/day, while from 1985 on, they increase until 1.5 - 2 mgP/mgC/day or even higher; average growth rate equals 0.1 day^{-1} or less (Burger-Wiersma and baard, 1987). These observations indicate that the phytoplankton can cope more and more efficiently with phosphorus or, in other words, that it can maintain a high biomass also with less phosphorus available. This 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 carbon and phosphorus flows through the system, averaged over the summer months (April through September) of 1987, are depicted in Figs. 22 and 23, respectively. The direct phosphorus uptake by the phytoplankton is calculated as 4.3 $mgP/m^2/day$. External loading still contributes 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 are also reported by Van Liere *et al.* (1989a,b) derived from experimental and field research. The values they give for 'primary production' (8 μgP/l/day) and for grazing are considerably higher than those given in Fig. 23, but the relative importance of the various 'phosphorus sources' is the same. Their figures often can not be compared directly with ours, because of differences in system description (for instance the compelled pooling of phytoplankton and detritus). Both the model and the field research stress, however, the importance of the internal nutrient cycling within the system: 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 within the system 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.

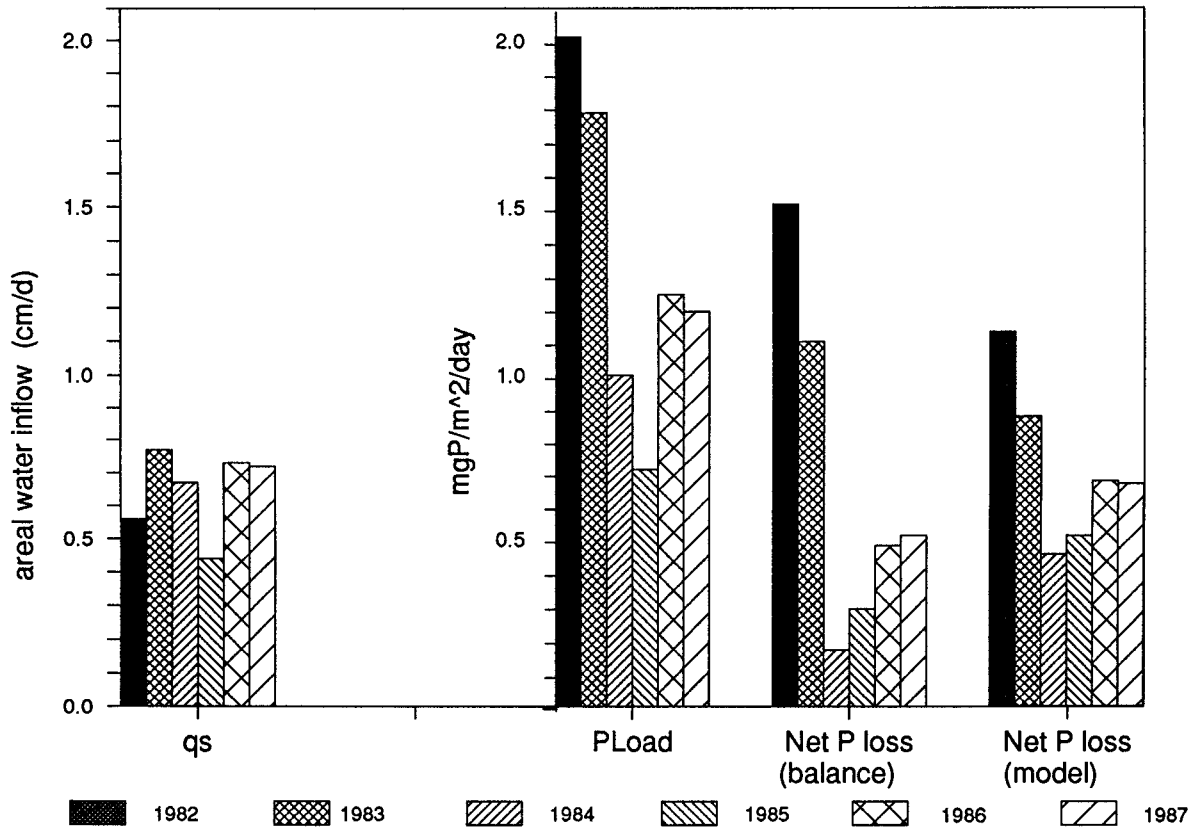


Fig. 19. Lake Looosdrecht, net phosphorus loss to the sediment, year averages 1982 - 1987; simulations compared with balance derived data.
(qs = areal water inflow [cm/d]; PLoad = external P loading [mgP/m^2/d])

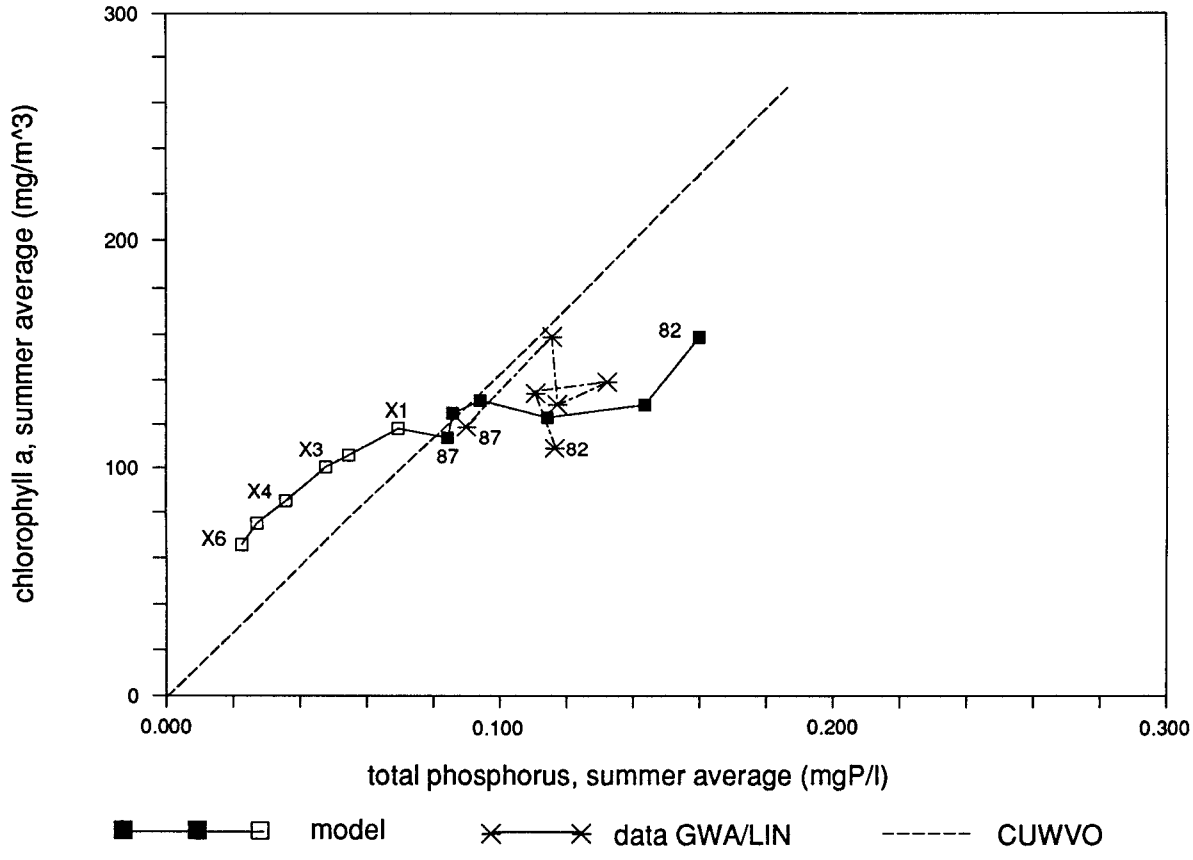


Fig. 20. Lake Loosdrecht, relation between summmer averaged chlorophyll-*a* and total phosphorus. Simulations and measurements of the years 1982 - 1987, and simulations at an additional reduction in P loading to 0.6 mgP/m^2/d in the years x1 - x3 and 0.3 mgP/m^2/d in the years x4 - x6.

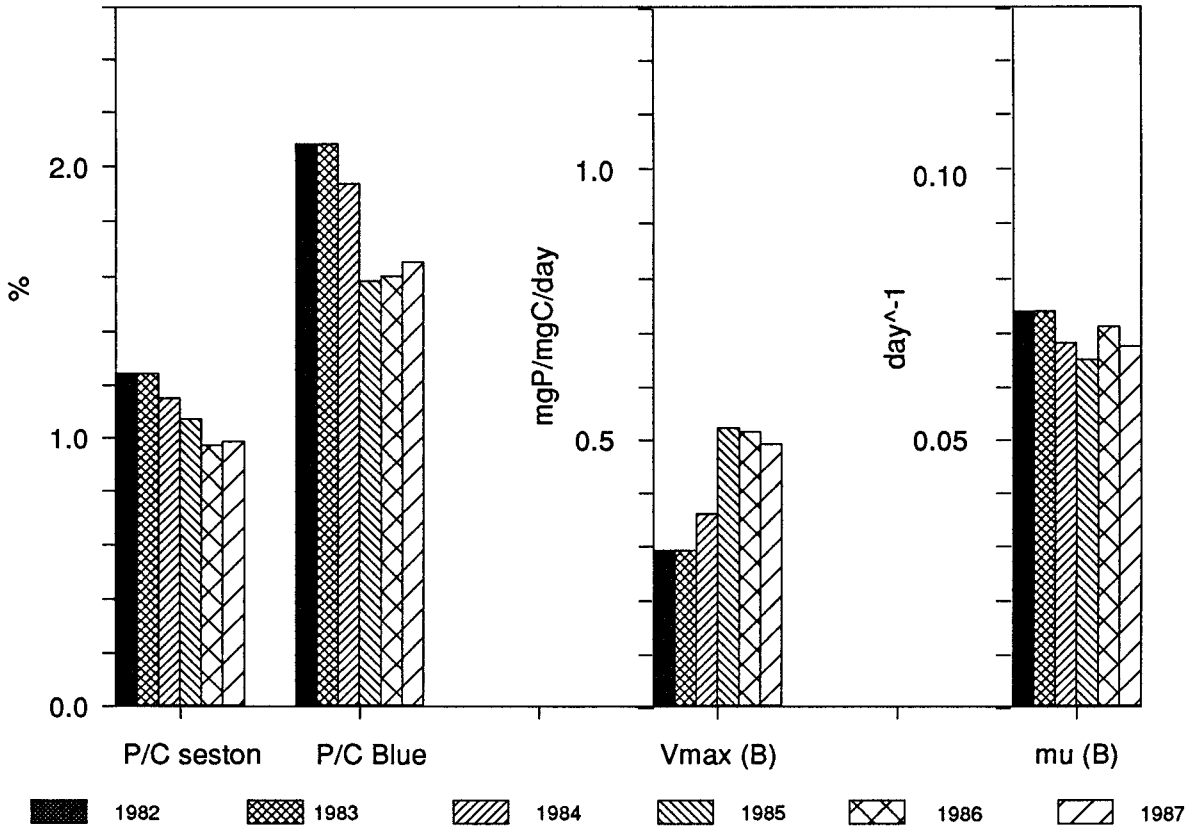


Fig. 21. Phytoplankton growth parameters, model-derived; summer averages, 1982 - 1987.

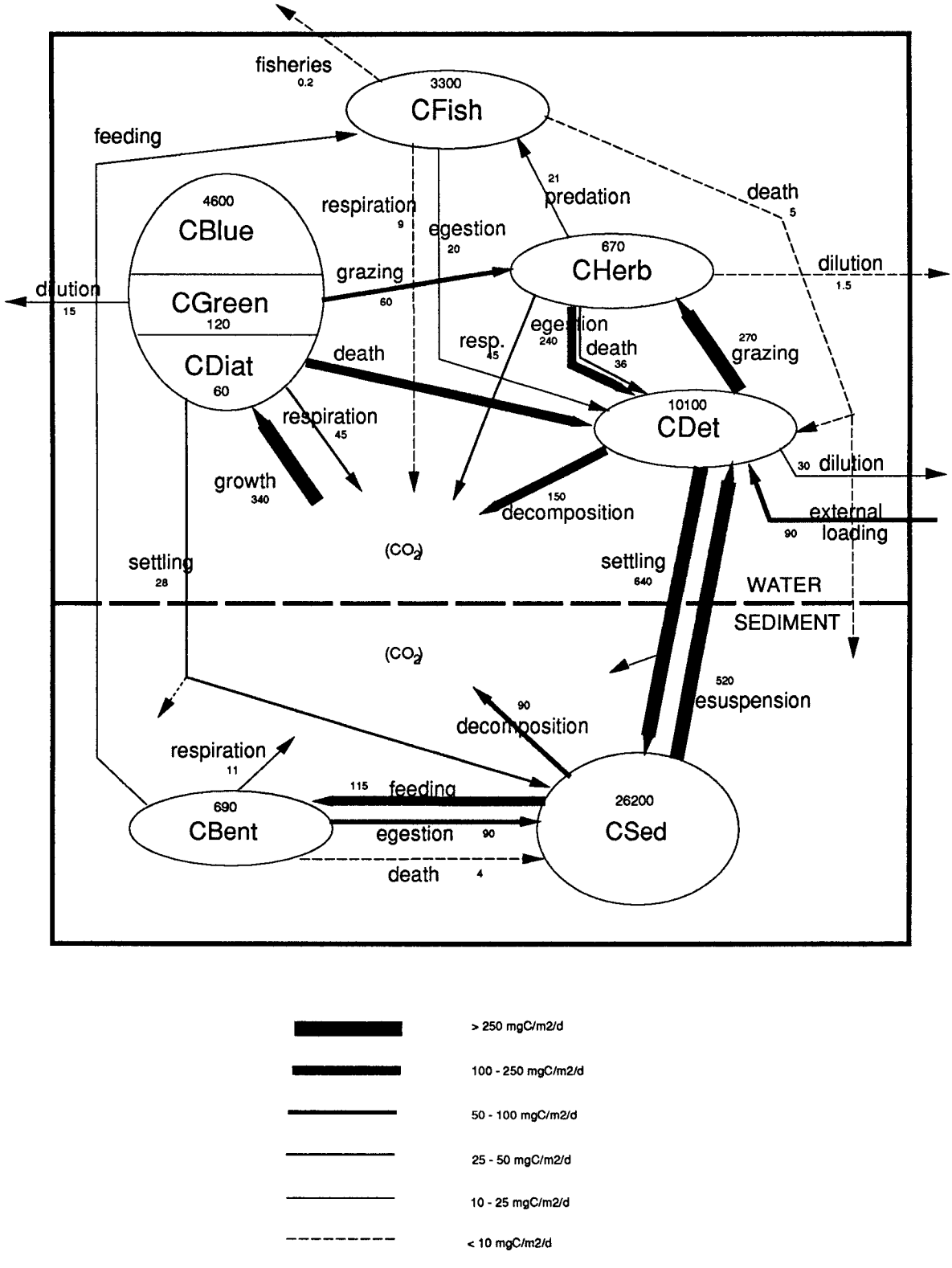


Fig. 22. Simulated carbon flow diagram, averaged over the summer months (April through September) of 1987. Fluxes are given in $mgC/m^2/d$, (bio)masses in mgC/m^2.

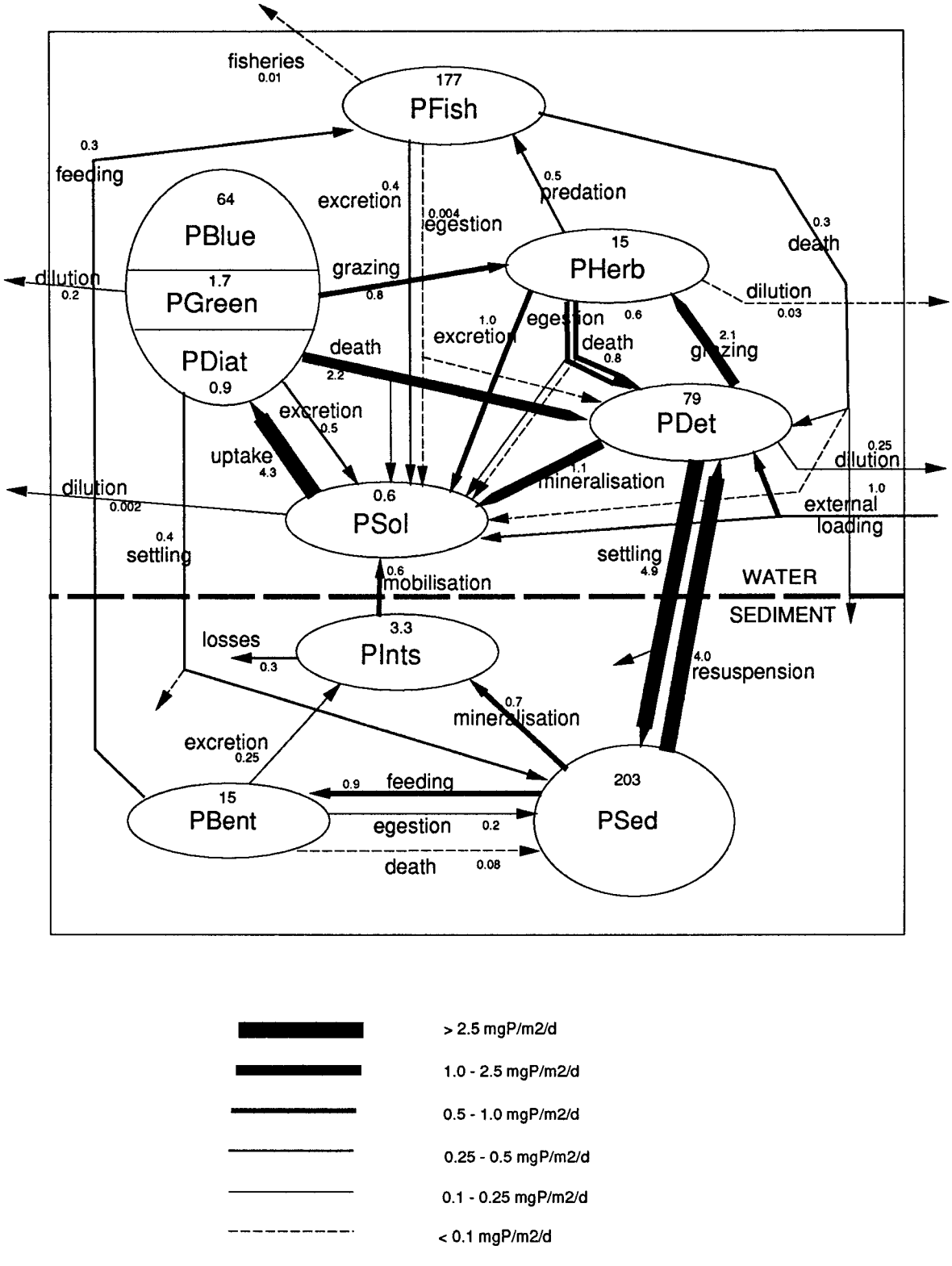


Fig. 23. Simulated phosphorus flow diagram, averaged over the summer months (April through September) of 1987. Fluxes are given in mgP/m^2/d, (bio)masses in mgP/m^2.

8.2 Uncertainties

In the above analysis, we have shown that both the adaptation of algal P/C ratios and the exchange between water and sediment can be important factors in the resilience of the lake ecosystem upon reduction of external phosphorus input. 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; posssibly, the chlorophyll-*a* content of the algae might have been lower in those years or other factors might have regulated growth. 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 μ 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 an overall moderating influence on the variation from this: in general, resuspension is more important in winter (except for ice periods) than in summer. These aspects will be further explored. The uncertainty in the detritus processes is, in general, higher than the one in the phytoplankton processes.

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 (especially the amount of well-edible algae, which is again dependent on the phosphorus availability). Another uncertainty lies in the long-term behaviour of the sediment: what will happen with 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 reveal that only 10% of the estimated total phosphorus loading into the lake during the past half a century 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). One could imagine that the soluble phosphorus that is released at the onset of winter, when most of the biomass dies off, is adsorbed by the detritus and released again in the next growing season, when the SRP concentration is low due to rapid uptake by the phytoplankton.

To reduce these uncertainties and to improve the model, more process oriented research on the topics mentioned in this paragraph is much needed.

8.3 Future model development

The model shows its value by means of The main concept on which it is based, namely a closed phosphorus cycle within the model system with dynamical P/C ratios. It can explain how a system can react in different ways on a change in phosphorus input, depending on whether it is observed from the carbon (or biomass) side or from the phosphorus side. It also gives some insight in turnover rates within the system and can be related to much simpler models and

empirical relations. However, 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. This validation, together with uncertainty analysis and adaptations in some of the submodels, will be performed in future model versions. One of the problems with the current model is the lacking of some kind of uncertainty analysis. Given the uncertainties in parameters and input values, the model output is, in fact, not a fixed answer but a 'probability that the answer will lie between x and y'. This uncertainty analysis will be included in the next model version, together with methods of formal parameter estimation by means of Bayesian statistics.

Another problem is that the model can not be used in case of significant changes in the ecosystem, for example the return of submerged vegetation or the occurrence of nitrogen limitation. When the long-term effects of biomanipulation are to be predicted, the model should be extended with formulations for water plants, piscivorous fish and probably the nitrogen cycle.

Third, a problem is, while validating the model, that the temporal and spatial variation in phosphorus loadings of the Loosdrecht Lakes in the period studied is not very high. Therefore, the model will be more thoroughly validated on the data of a number of other lakes, to test its applicability in a wider range of phosphorus loadings and hydrological characteristics.

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Appendix A Model equations and parameters

A.1 Differential equations

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

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

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

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

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

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

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

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

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

Fish [mgC/l/d]

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

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

$$\frac{d[CDet]}{dt} = \frac{f_{det}(\text{in}) \cdot PLoad}{PCDet(\text{in}) \cdot H} + \sum_i [k_{mort(i)}(T) \cdot CPhyt(i)] + k_{mort(H)}(T) \cdot CHerb +$$
$$+ (1 - CEff_H) \cdot \sum_j [\alpha_j \cdot CFood(j)] \cdot Filt \cdot CHerb - \alpha_D \cdot CDet \cdot CHerb +$$
$$+ \{(1 - CEff_{HF}) \cdot Pred + (1 - CEff_{BeF}) \cdot Feed\} \cdot CFish +$$
$$+ (1 - f_{bones(C)}) \cdot k_{mort(F)} \cdot CFish + \left\{-k_{dec(D)}(T) - \frac{velo_D}{H} - Dil\right\} \cdot CDet +$$
$$+ f_{fg} \cdot k_{resu(D)} \cdot \frac{z_s}{H} \cdot CSed \qquad \text{Detritus [mgC/l/d]}$$

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

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

$$\frac{d[CSed]}{dt} = \frac{(1-f_r)\cdot\left(\sum_i[velo_i \cdot CPhyt(i)] + velo_D \cdot CDet\right)}{z_s} + \{-f_{fg}\cdot k_{resu(D)} - k_{dec(Se)}(T)\}\cdot CSed +$$

$$+\frac{\{-CEff_{SeBe}\cdot k_{eat(SeBe)}(T) + k_{mort(Be)}(T)\cdot CBent\}\cdot CBent}{z_s}$$

Upper sediment [mgC/l sed./d]

$$\frac{d[PSed]}{dt} = \frac{(1-f_r)\cdot\left(\sum_i[velo_i \cdot PPhyt(i)] + velo_D \cdot PDet\right)}{z_s} + \{-f_{fg}\cdot k_{resu(D)} - k_{min(Se)}(T)\}\cdot PSed +$$

$$+\frac{\{-PEff_{SeBe}\cdot k_{eat(SeBe)}(T) + k_{mort(Be)}(T)\cdot CBent\}\cdot PBent}{z_s}$$ Upper sediment [mgP/l sed./d]

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

Zoobenthos [gC/m2/d]

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

$$-PCBent\cdot Feed_{BeF}\cdot\frac{CFish}{H}$$ Zoobenthos [gP/m2/d]

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

Interstitial SRP [mgP/l pore water/d]

A.2 Rates and other equations

a) phytoplankton

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

algal P uptake [mgP/mgC/d]

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

P/C ratio of algal species *i* [mgP/mgC]

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

algal growth rate [d^{-1}]

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

extinction coeff. [m^{-1}]

$$f(I_0) = \frac{f_l}{\varepsilon \cdot H} \ln \left(\frac{1 + \frac{I_0}{k_l}}{1 + \frac{I_0}{k_l} \cdot e^{-\varepsilon \cdot H}} \right)$$

light function diatoms and greens [-]

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

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 [W/m^2]

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

chlorophyll-*a* [mg/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 [d^{-1}]

b) zooplankton

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

filtration rate [$(mgC/l)^{-1} \cdot d^{-1}$]

$$PEff_H = \text{MIN}\left[1, \frac{PCHerb_{ref}}{PCFood} \cdot CEff_H \right]$$

P assim. efficiency zoopl. [-]

$$PCFood = \frac{PFood}{CFood} = \frac{\sum_j [\alpha_j \cdot PFood(j)]}{\sum_j [\alpha_j \cdot CFood(j)]}$$

P/C ratio of food consumed by zooplankton [mgP/mgC]

c) fish

$$Pred_{HF} = PrMax_{HF}(T) \cdot \frac{CHerb^2}{k^2_{pred(HF)} + CHerb^2}$$

predation rate of fish on zoopl. [d^{-1}]

$$PEff_{HF} = \text{MIN}\left[1, \frac{PCFish_{ref}}{PCHerb} \cdot CEff_{HF} \right]$$

P ass. eff. of fish for zooplankton food [-]

$$Feed_{BeF} = k_{feed(BeF)}(T) \cdot CBent$$

feeding rate of fish on zoobenthos [d^{-1}]

$$PEff_{BeF} = \mathrm{MIN}\left[1, \frac{PCFish_{ref}}{PCBent} \cdot CEff_{BeF}\right]$$

P ass. eff. of fish for zoobenthal food [-]

If $\cos\left(2 \cdot \pi \cdot \frac{Time}{365}\right) \geq 0$ then:

$$k_{mort(F)} = \mathrm{MAX}\left[k_{mort(F)(\min)}, \frac{k_{mort(F)(\max)}}{2} + \frac{k_{mort(F)(\max)}}{2} \cdot \sin\left(4 \cdot \pi \cdot \frac{Time - 121}{365}\right)\right]$$

If $\cos\left(2 \cdot \pi \cdot \frac{Time}{365}\right) < 0$ then: $k_{mort(F)} = k_{mort(F)(\min)}$

fish mortality rate [d^{-1}]

d) zoobenthos

$$PEff_{SeBe} = \mathrm{MIN}\left[1, \frac{PCBent_{ref}}{PCSed} \cdot CEff_{SeBe}\right]$$

P ass. eff. of zoobenthos [-]

$$k_{eat(SeBe)}(T) = \mathrm{MIN}\left[k_{eat(\max)(SeBe)}(T), k_{eat(low)(SeBe)}(T) \cdot CSed\right]$$

feeding coeff. of zoobenthos [d^{-1}]

e) general

$$k(T) = k(T_{opt}) \cdot \exp\left(\ln(0.5) \cdot \left|\frac{T - T_{opt}}{k_{temp}}\right|\right)$$

temperature function for diatoms [-]

$$k(T) = k(T_{ref}) \cdot \Theta^{T - T_{ref}}$$

temperature function for all other compartments [-]

$$k'_{resp(m)}(T) = \frac{PCAnim(m)_{ref}}{PCAnim(m)} \cdot k_{resp(m)}(T)$$

corrected respiration rate of animal group m [d^{-1}]

$$k_{excr(m)}(T) = \frac{PCAnim(m)}{PCAnim_{ref}} \cdot k_{resp(m)}(T)$$

P excretion rate of animal group m [d^{-1}]

$$Dil = (q_s - q_{evap})/H$$

dilution rate [d^{-1}]

$$f_{det}(\mathrm{in}) = 1 - f_{sol}(\mathrm{in}) - \sum_i [f_{phyt(i)}(\mathrm{in})] - f_{herb}(\mathrm{in})$$

detrital fraction of ext. P loading [-]

$$CSest = CBlue + CGreen + CDiat + CDet$$

C seston < 150 µ [mgC/l]

$$PSest = PBlue + PGreen + PDiat + PDet$$

P seston < 150 µ [mgP/l]

$$PTot = PSest + PHerb + PSol$$

total phosphorus [mgP/l]

$$Secchi = PACoef/\varepsilon$$

transparancy (Secchi depth) [m]

A.3 Symbols and parameter values

$A_{0(i)}$	initial affinity of algal species *i* for external phosphorus	*B*: 20 [l/mgC/d] *Di/G*: 6 [l/mgC/d]
α_j	selection factor of food type *j* for zooplankton grazing	*B*: 0.1 [-] *Di/G*: 1.0 [-] *D*: 0.25 [-]
-B	suffix: denotes blue-green algae	
-Be	suffix: denotes zoobenthos	
CBent	zoobenthos	[gC/m^2]
CBlue	blue-green algae	[mgC/l]
CDet	detritus	[mgC/l]
CDiat	diatoms	[mgC/l]
$CEff_{BeF}$	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 [-]
CFish	fish	[mgC/l]
CFood(j)	food type *j* for zooplankton	[mgC/l]
CGreen	green algae	[mgC/l]
CHerb	zooplankton	[mgC/l]
Chla	chlorophyll-*a*	[mg/m^3]
$ChlC_i$	chlorophyll-*a* content of algal species *i* [mg chlorophyll-*a*/mgC]	*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/l]
CSed	upper sediment	[mgC/l sediment]
CSest	seston < 150 µ	[mgC/l]
-D	suffix: denotes detritus	
-Di	suffix: denotes diatoms	
Dil	dilution rate	[d^{-1}]
$e = \exp(1)$	base of natural logarithm	≈ 2.7
ε	extinction coefficient	[m^{-1}]
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_{det}(in)	detrital fraction of external P loading	[-]
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_l	daylight fraction	[-]
$f_{phyt(i)}$(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 [-]
$Feed_{BeF}$	feeding rate of fish on zoobenthos	[d^{-1}]
Filt	specific filtration rate of zooplankton at 20 °C	[$(mgC/l)^{-1} \cdot d^{-1}$]
$Filt_{con}$	maximum specific filtration rate at 20 °C (reached below *CHold*)	2.9 [$(mgC/l)^{-1} \cdot d^{-1}$]
$Filt_{max}$	theoretical maximum specific filtration rate at 20 °C (reached when *CSest* = 0)	[$(mgC/l)^{-1} \cdot d^{-1}$]
-G	suffix: denotes green algae	
H	water depth	L.Loosdr.: 1.91 [m] L.Vuntus : 1.36 [m] L.Breukl.: 1.45 [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_0	light intensity at depth 0	[W/m^2]
I_{opt}	optimum light intensity	*B*: 100 [W/m^2]
I_{out}	average daily light intensity	[W/m^2]
I(z)	light intensity at depth *z*	[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]
$k_{eat(SeBe)}$	feeding rate of zoobenthos	[d^{-1}]
$k_{eat(low)(SeBe)}$	feeding constant per unit sediment of zoobenthos at 20 °C	$5 \cdot 10^{-4}$ [$(mgC/l\ sed.)^{-1} \cdot d^{-1}$]
$k_{eat(max)(SeBe)}$	(max.) feeding coeff. of zoobenthos at 20 °C	0.21 [d^{-1}]
$k_{\varepsilon(D)}$	specific extinction of detritus	0.25 [m^2/mgC]
$k_{\varepsilon(i)}$	specific extinction of algal species *i*	*B/G*: 0.35 [m^2/mgC] *Di*: 0.25 [m^2/mgC]
$k_{excr(Be)}$	P excretion rate of zoobenthos at 20 °C	[d^{-1}]
$k_{excr(F)}$	P excretion rate of fish at 20 °C	[d^{-1}]
$k_{excr(H)}$	P excretion rate of zooplankton at 20 °C	[d^{-1}]

$k_{excr(i)}$	P excretion rate of algal species *i* at 20 °C	[d^{-1}]
$k_{feed(BeF)}$	feeding coeff. of fish on zoobenthos at 20 °C	0.008 [$(gC/m^2)^{-1} \cdot d^{-1}$]
k_{filt}	half-saturating food concentration for filtration	0.25 [mgC/l]
$k_{harv(F)}$	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
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 [$(gC/m^2)^{-1} \cdot d^{-1}$]
$k_{mort(F)}$	mortality rate of fish	[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]
$k_{resp(Be)}$	respiration constant of zoobenthos at 20 °C	0.02 [d^{-1}]
$k'_{resp(Be)}$	corrected respiration constant of zoobenthos at 20 °C	[d^{-1}]
$k_{resp(F)}$	respiration constant of fish at 20 °C	0.003 [d^{-1}]
$k'_{resp(F)}$	corrected respiration constant of fish at 20 °C	[d^{-1}]
$k_{resp(H)}$	respiration constant of zooplankton at 20 °C	0.10 [d^{-1}]
$k'_{resp(H)}$	corrected respiration constant of zooplankton at 20 °C	[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	L.Loosdr.: 0.05 d^{-1} L.Vuntus : 0.03 d^{-1} L.Breukl.: 0.07 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}]
μ_i	growth rate of algal species *i*	[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 [-]
PBent	zoobenthos	[gP/m^{2}]

PBlue	blue-green algae	[mgP/l]
PCAnim(m)	P/C ratio of animal group *m* (*i.e.*: zooplankton, fish or zoobenthos)	[mgP/mgC]
PCBent	P/C ratio of zoobenthos	[mgP/mgC]
$PCBent_{ref}$	reference P/C ratio of zoobenthos	0.0225 [mgP/mgC]
PCDet	P/C ratio of detritus	[mgP/mgC]
PCDet(in)	average P/C ratio of detritus in inflow	0.01 [mgP/mgC]
PCFish	P/C ratio of fish	[mgP/mgC]
$PCFish_{ref}$	reference P/C ratio of fish	0.057 [mgP/mgC]
PCFood	P/C ratio of food consumed by zooplankton	[mgP/mgC]
PCHerb	P/C ratio of zooplankton	[mgP/mgC]
$PCHerb_{ref}$	reference P/C ratio of zooplankton	0.023 [mgP/mgC]
PCSed	P/C ratio of upper sediment	[mgP/mgC]
PDet	detritus	[mgP/l]
PDiat	diatoms	[mgP/l]
$PEff_{BeF}$	P ass. eff. of fish for zoobenthal food	[-]
$PEff_{H}$	P assimilation efficiency of zooplankton	[-]
$PEff_{HF}$	P ass. eff. of fish for zooplankton food	[-]
$PEff_{SeBe}$	P assimilation efficiency of zoobenthos	[-]
PFish	fish	[mgP/l]
PFood(j)	food type *j* for zooplankton	[mgP/l]
PGreen	green algae	[mgP/l]
PHerb	zooplankton	[mgP/l]
PInts	soluble reactive phosphorus in the interstitial water	[mgP/l pore water]
PLoad	external P loading per m^2 lake area	[$gP/m^2/d$]
Por	porosity of upper sediment	0.91 kg water/l sed
$Pred_{HF}$	predation rate of fish on zooplankton	[d^{-1}]
$PrMax_{HF}$	max. predation coeff. of fish on zoopl.	0.15 [d^{-1}]
PSed	upper sediment	[mgP/l sediment]
PSest	seston < 150 µ	[mgP/l]
PSol	soluble reactive phosphorus in the water	[mgP/l]
PTot	total phosphorus in the water (excl. fish)	[mgP/l]
q_{evap}	areal evaporation from lake surface	[m/d]
Q_i	phosphorus content of algal species *i*	[mgP/mgC]
$Q_{max(i)}$	maximum phosphorus content of algal species *i*	*all*: 0.027 mgP/mgC
$Q_{min(i)}$	minimum phosphorus content of algal species *i*	*all*: 0.0054 mgP/mgC
Q_{phyt}(in)	phosphorus content of algae in inflow	0.0125 [mgP/mgC]
q_s	areal hydraulic loading (= water flow into the lake per m^2 lake area)	[m/d]
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	
Secchi	transparency (Secchi depth)	[m]
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	[d]
Θ_{Be}	temperature constant of zoobenthos	1.07 [$e^{1/°C}$]
Θ_D	temperature constant of detrital mineralisation	1.12 [$e^{1/°C}$]
Θ_F	temperature constant of fish	1.07 [$e^{1/°C}$]
Θ_H	temperature constant of zooplankton	1.10 [$e^{1/°C}$]
Θ_i	temperature constant of phytoplankton species *i*	*B*: 1.07 [$e^{1/°C}$] *G*: 1.05 [$e^{1/°C}$]
Θ_{Se}	temp. constant of mineral. of upper sediment	1.12 [$e^{1/°C}$]
v_i	phosphate uptake rate of algal species *i*	[mgP/mgC/d]
$v_{max(i)}(T)$	max. phosphate uptake rate of algal species *i*	*B*: 1.0 [mgP/mgC/d] *Di/G*: 0.5 mgP/mgC/d
$velo_D$	settling velocity of detritus	0.12 [m/d]
$velo_i$	net settling velocity of algal species *i*	*B*: 0.01 [m/d] *Di/G*: 0.04 [m/d]
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 [-]