Empirical and theoretical models of phosphorus loading, retention and concentration vs. lake trophic state

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Abstract

Models describing the dependence of lake trophic state on external phosphorus loading are of two general types: empirical, steady state models derived from statistical treatment of data from large numbers of lakes, and theoretical, dynamic models based on more or less detailed mathematical descriptions of kinetics of nutrient and population dynamics.

In the former type of models, inlake P concentrations have been found to depend mainly on inflow P concentrations and on water residence time. Efforts to explain the remaining variance by other factors such as iron, calcium, alkalinity, etc. have generally not been successful. Relations between lake P concentrations and chlorophyll may be useful for the prediction of maximum chlorophyll levels with some confidence but large variations in the actual chlorophyll concentrations are caused by, e.g. zooplankton grazing, varying chlorophyll content of the algae and other limiting nutrients.

Dynamic, theoretical models are more suited for the prediction of rates of response to perturbations than the empirical steady state models. Due to the much larger demand for input data and labour investment, these models are generally more suited for the scientist as tools for formalizing and testing hypotheses, than for the water manager. Simple models with flexible structure generally have advantages over complex models.

Both empirical and theoretical models are potentially powerful tools in eutrophication research and management. It is important for both scientists and water managers to select the optimum complexity with regard to the problem to be solved and to the resources available in each case.

Introduction

The concept of nutrient loading as a factor controlling lake productivity or trophic state has been one of the most productive theories in limnology and has stimulated much discussion and research. Originally proposed by Vollenweider (1968) and later refined by him (e.g. 1975, 1976), this concept has had a great impact on all subsequent eutrophi-

cation research and lake management. Many authors have contributed to the verification of Vollenweider's or related loading models by adding new data to the database and by critical discussions and reviews but have also raised doubts about the belief that trophic state can be described solely as a function of nutrient supply. The basic assumption behind the nutrient loading concept is that there is a dependence of lake

trophic state either directly on the nutrient supply rate (loading) or, more commonly, on the nutrient concentration in the water. Models built on this concept often assume steady state conditions and rely on empirical relations between nutrient loading, sediment retention, lake water concentration and phytoplankton biomass and production. The theoretical background is normally the Continuously Stirred Tank Reactor principle adopted from chemical engineering. Another class of models are the theoretical, dynamic models building on a detailed description of the different processes and representing a technique borrowed from engineering and control theory.

There are many good review articles on different types of eutrophication models. The empirical phosphorus loading models were treated, e.g. by Reckhow (1979), phosphorus-chlorophyll models by Nicholls & Dillon (1978), several types of models by Kamp-Nielsen (1985) and Straškraba (1985), dynamic eutrophication models by Scavia & Robertson (1979), Jørgensen (1983) and Straškraba & Gnauck (1985) to mention a few examples. One of the most authoritative treatments of empirical eutrophication models was made by Vollenweider and coworkers in OECD (1982). The benefits of using empirical models in limnology in general was discussed in detail by Peters (1986).

The purpose of this paper is not to give a complete review of the subject but to summarize and discuss some aspects of the present state of the art in modelling lake trophic state as a function of phosphorus loading.

Empirical models

Chapra (1980) proposed an approach to link a number of submodels to predict the trophic characteristics of lakes from their phosphorus loading (Fig. 1). The first submodel, the 'waste source model' will not be treated here. The purpose of the second model the 'phosphorus budget model', is to produce a prediction of the total phosphorus concentration in the lake. It is essentially a model of sediment net retention of phos-
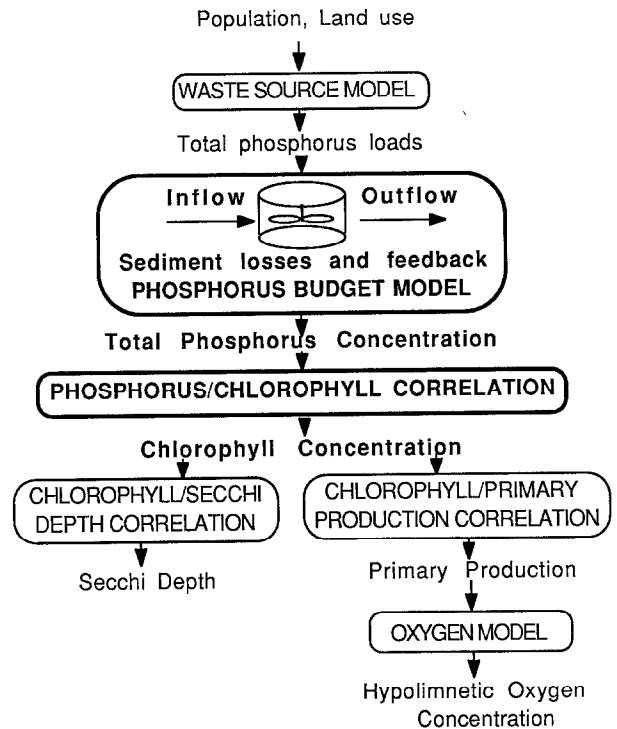

Fig. 1. Schematic of P loading model for lakes (after Chapra, 1980). Only parts printed in bold will be discussed in this paper.

phorus. Subsequent models predict chlorophyll, Secchi disk transparency, primary production, etc. In this chapter we will examine the two first steps, the P budget models and P/chlorophyll models. Symbols and units are summarized in Table 1.

P loading vs. P concentration models
An extensive review of the historic development of this type of models was given by Reckhow (1979).

The basic mass balance model for P can be written as follows:

$$d(PV)/dt = M - PV \cdot Q/V - S \qquad (1)$$

The net retention of phosphorus is the difference between input and output:

$$r = M - PV \cdot Q/V \qquad (2)$$

Table 1. Symbols and units used in this article.

P $\quad$ = TP = inlake total P concentration (mg m^{-3})
P$_i$ $\quad$ = inflow mean total P concentration (mg m^{-3})
a $\quad$ = year
L$_p$ $\quad$ = annual P loading (mg m^{-2} a^{-1})
V $\quad$ = lake volume (m^3)
PV $\quad$ = total mass of phosphorus in lake (mg)
t $\quad$ = time
M $\quad$ = annual input mass of phosphorus (mg a^{-1})
O $\quad$ = annual outflow mass of phosphorus (mg a^{-1})
Q $\quad$ = discharge of the outlet of the lake (m^3 a^{-1})
q$_s$ $\quad$ = water discharge height (m a^{-1})
S $\quad$ = annual net sedimentation of phosphorus (mg a^{-1})
σ $\quad$ = sedimentation coefficient (a^{-1})
v $\quad$ = apparent settling velocity of P (m a^{-1})
z $\quad$ = lake mean depth (m)
ρ_w $\quad$ = Q/V = flushing rate (a^{-1})
τ_w $\quad$ = 1/ρ_w, water residence time (a)
r $\quad$ = annual P retention in lake (mg a^{-1})
R$_p$ $\quad$ = P retention coefficient
chl a = chlorophyll a concentration (mg m^{-3})

and by combination of (1) and (2):

$$r = S + d(PV)/dt \qquad (3)$$

At steady state d(PV)/dt = 0 and thus:

$$r = S \qquad (4)$$

i.e. the retention is equal to net sedimentation.

In mass-balance models steady state is usually assumed and eq. (4) is valid, but distinction should be made between the concepts of retention and net sedimentation. Net sedimentation is defined as the difference between sedimentation (i.e. gross sedimentation) and release from the sediments.

Early attempts were made by Piontelli & Tonolli (1964) to describe net sedimentation as a function of supply rate:

$$d(PV)/dt = (1 - f_s)M - PQ \qquad (5)$$

where f$_s$ = the fraction of incoming P which is retained by the sediment. Later, however, Vollenweider came to the conclusion that reten-

tion is more logically a function of inlake mass or concentration:

$$d(PV)/dt = M - PQ - \sigma PV \qquad (6)$$

where σ is a sedimentation coefficient. This approach may be referred to as the kinetic approach in contrast to the retention coefficient approach which will be discussed later. At steady state (6) gives:

$$PV = M/(Q/V + \sigma) \qquad (7)$$

and substituting ρ_w = flushing rate for Q/V:

$$PV = M/(\rho_w + \sigma) \qquad (8)$$

Division by V to give concentrations gives:

$$P = (M/V)/(\rho_w + \sigma) \qquad (9)$$

M/V is equivalent to L$_p$/z, i.e. surface area loading divided by mean depth and can be designed as 'volumnar loading'. Substitution into (9) gives:

$$P = (L_p/z)/(\rho_w + \sigma) \qquad (10)$$

Equation (10) is the basic equation underlying most P loading models. $1/(\rho_w + \sigma)$ can be seen as a reduction factor (dimension = time) acting on the *volumnar loading rate* (dimension = mass per volume and time). By multiplication of the numerator and denominator by ρ_w equation (7) assumes the form:

$$P = L_p/q_s \cdot \rho_w/(\rho_w + \sigma) \qquad (11)$$

where q$_s$ = water discharge height (m a^{-1}) and the factor $\rho_w/(\rho_w + \sigma)$, which is dimensionless, is a reduction factor (= 1 − R$_p$, where R$_p$ = P retention coefficient) acting on the *mean inflow concentration*.

$$R_p = 1 - \rho_w/(\rho_w + \sigma) = \sigma/(\rho_w + \sigma) \qquad (12)$$

The difficulty in applying this equation is in the

determination of σ. The coefficient σ is not a constant, and the factors controlling its variations are largely unknown. These difficulties were extensively discussed by Vollenweider (1976). He found that σ was inversely related to z and that a good approximation was $\sigma = 10/z$. In this expression, 10 has the dimension m a^{-1} and can be understood as an apparent settling velocity of P which thus would be constant. Multiplication of the numerator and denominator
of equation (12) with mean depth, z, gives:

$$R_p = z\sigma/(z\rho_w + z\sigma) \qquad (13)$$

Substitution of 10/z for σ and q_s for $z\rho_w$ gives:

$$R_p = 10/(q_s + 10) \qquad (14)$$

or more general:

$$R_p = v/(q_s + v) \qquad (15)$$

where v = apparent settling velocity of P (m a^{-1}), and

$$P = L_p/q_s[1 - v/(q_s + v)] \qquad (16)$$

Equations (11) and (16) thus have the same theoretical basis. Chapra (1975) suggested a value for v of 16 m a^{-1} whereas Dillon & Kirchner (1975) found that 13.2 m a^{-1} better described R_p of the lakes included in their database. Although the statistical correlation in their analysis was clearly significant, there still remains a large variance making the application of equation (16) on individual lakes very uncertain. The apparent settling velocities of individual lakes used by Dillon & Kirchner varied between 1.4 and 51.6 m a^{-1}. There is thus strong evidence that neither σ nor v can be treated as constants and, because they are related by $\sigma = v/z$ the same factors are responsible for their variation.

It may be hypothesized that σ is a function of one or several of factors such as ρ_w, L_p, P_j, q_s, alkalinity, pH, Ca^{2+}, iron, aluminum, dissolved humic substances, suspended inorganic solids, algal biomass and species composition, pelagic food-web structure, stratification stability and duration, hypolimnetic anoxia, wind induced turbulence, lake surface area, mean depth, etc. (see e.g. Reckhow, 1979). There are good reasons to believe that each or all of these factors could contribute to the variation of P sedimentation loss rate. Many more or less successful attempts have been made to link σ or R_p to such factors, but the only good relation found so far is with ρ_w. Vollenweider (1976) recognized the difficulties in maintaining dimensional consistency in expressions describing σ. He found a good correlation between σ and $\sqrt{\rho_w}$ which means that dimensional consistency had to be given up: 'we are forced into adopting certain more or less defendable shortcuts' (Vollenweider, 1976, p. 61). Substituting $1/\sqrt{\tau_w}$ ($= \sqrt{\rho_w}$) for σ in equation (11) and rearranging gives

$$P = L_p/q_s \cdot 1/1 + \sqrt{\tau_w}) \qquad (17)$$

Using 10 μg l^{-1} as the 'critical' phosphorus concentration delimiting oligotrophy from mesotrophy, the 'critical' P loading can be expressed as:

$$L_c = 10 \cdot q_s (1 + \sqrt{\tau_w}) \qquad (18)$$

which is the well-known form of Vollenweider's loading model (Vollenweider, 1976). In this expression, P net retention is solely determined by flushing rate (or its inverse, the water residence time). Larsen & Mercier (1976) arrived at the same expression as equation (17) at about the same time as Vollenweider. This model has later been verified by several authors using larger databases (e.g. Chapra & Reckhow, 1979). Welch et al. (1986) found that the relationship $\sigma = \rho_w^{0.78}$ could explain much of the short-term variations in sedimentation loss rates in Lake Sammamish.

In equation (17) $1/(1 + \sqrt{\tau_w}) = 1 - R_p$ and $R_p = 1/(1 + \sqrt{\rho_w})$. The retention coefficient is thus negatively correlated to the flushing rate, whereas σ ($= \sqrt{\rho_w}$) is positively correlated to the flushing rate (Fig. 2b). The consequence is that R_p is negatively correlated to σ (Fig. 2a) which intuitively may be difficult to rationalize but in fact is quite logical (see e.g. Welch, 1980, p. 133).
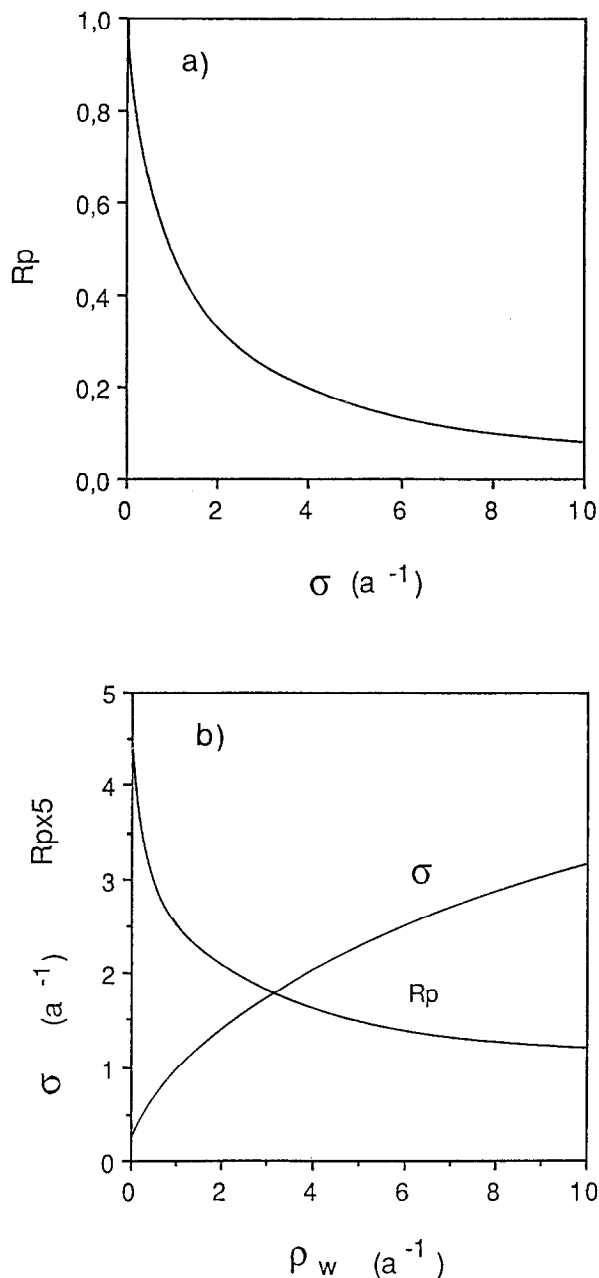
material brought in with the water, rather than the water itself must be responsible for the increased loss rates. They hypothesized that P itself could be that material. Higher P loading rates would promote algal growth and upon sedimentation the algae would remove a larger fraction of phosphorus to the sediments. However, using a large data base of more than 700 cases, they could not find any significant correlations between total P concentrations or chlorophyll concentrations and σ. Neither did they find any correlation with alkalinity, which they thought could be related to calcite precipitation and P removal by coprecipitation and absorption. Therefore they concluded that lake P concentration was not responsible for increased P retention at high flushing rates. However, they found a good correlation between σ and L_p/z (= volumnar loading):

$$\sigma = 0.129(L_p/z)^{0.549} \qquad (19)$$

Considering that $z = q_s/\rho_w$ and substituting into (19) gives:

$$\sigma = 0.129(L_p/q_s \cdot \rho_w)^{0.549} \qquad (20)$$

where L_p/q_s = mean inflow concentration. In their expression, σ is thus a function of mean inflow concentration of P and of flushing rate. A separation of these two variables in the analysis would have been of interest but was not made by Canfield and Bachmann. By combination of eq. (20) with eq. (11):

$$P = L_p/q_s/[1 + 0.129\rho_w^{-0.451}P_i^{0.549}] \qquad (21)$$

and

$$R_p = 0.129\,\tau_w^{0.451}P_i^{0.549}/ \\ (1 + 0.129\,\tau_w^{0.451}P_i^{0.549}) \qquad (22)$$

Fig. 3 shows the relation between predicted and observed concentrations in their analysis. The consequence of Canfield & Bachmann's approach is that P retention increases as P loading increases.
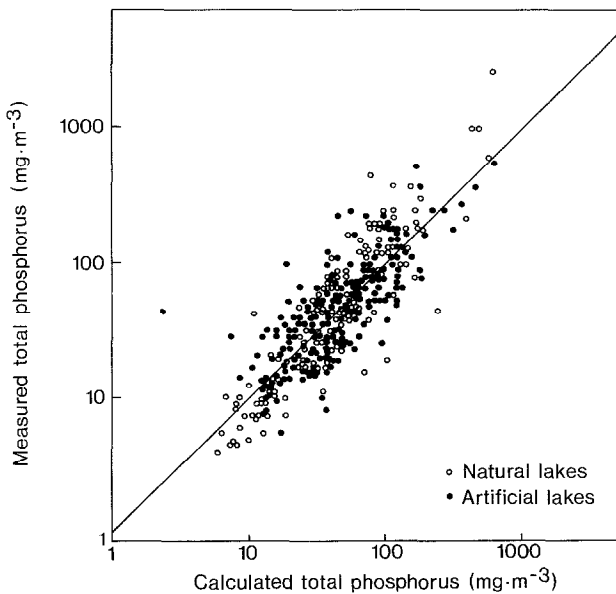
A different approach with a similar result was

Fig. 2. a) Relations between P sedimentation coefficient (σ) and P retention coefficient (R_p), and b) between water flushing rate (ρ_w), P retention coefficient (R_p), and sedimentation coefficient (σ) according to Vollenweider's loading model.

Canfield & Bachmann (1981) found it 'puzzling' that the sedimentation coefficient would be positively correlated to the flushing rate. They concluded that the explanation must be that some

Fig. 3. Relation between predicted and measured lake P concentrations according to eq. (21). (Modified after Canfield & Bachmann, 1981).

Fig. 4. Dependence of R_P on water residence time (τ_w) and inflow P concentration according to equation (23).

presented by Lappalainen (1975). A simplified version of his model was given by Frisk et al. (1981) and by Frisk (1981):

$$R_p = P_i\tau_w/(K_R + P_i\tau_w) \qquad (23)$$

According to this equation, R_p is dependent on mean inflow concentration and on water residence time. Frisk et al. found a value for K_R of $30\ \text{g m}^{-3}$ a and concluded that this model was superior to the first-order kinetic models when applied to several Finnish lakes. Fig. 4 gives a three-dimensional representation of the dependence of R_p on P_i and τ_w.

Equation (17) was applied to predict P concentrations of lakes within the large OECD eutrophication study (OECD, 1982). By regression analysis it was found that the following modification better described the dependence of lake P concentrations on the external P loading:

$$P = 1.55[L_p/q_s/(1 + \sqrt{\tau_w})]^{0.82} \qquad (24)$$

(Fig. 5a) and, since $R_p = 1 - P/P_i$:

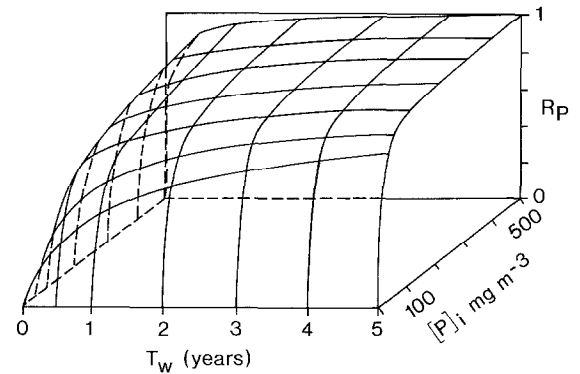$$R_p = 1 - 1.55 \cdot P_i^{-0.18}/(1 + \sqrt{\tau_w})^{0.82} \qquad (25)$$

As was the case in the studies by Canfield & Bachmann and Frisk et al., P retention thus increased with increased inflow P concentration. This does not necessarily mean that P retention is higher in eutrophic lakes than in oligotrophic lakes. Results presented by Janus & Vollenweider (1984) point in the opposite direction. Their study showed that in both oligotrophic and eutrophic lakes P retention increased as P_i increased (P/P_i decreased). However, this trend was more pronounced within the group of oligotrophic lakes. When comparing eutrophic lakes and oligotrophic lakes with the same P_i, P retention therefore was larger (P/P_i smaller) in the oligotrophic lakes (Fig. 6). For individual lakes there is also some evidence that P retention may decrease as eutrophication proceeds and P concentration in the lake increases. One example is the results from Sempachersee by Gächter et al. (1983). Nürnberg (1984) also demonstrated that P retention was smaller in lakes with anoxic hypolimnia. Care should therefore be taken when trying to use empirical models like those of eq. (17), (21), and (24) to predict the response of individual lakes to changed P loading. Although the statistical significance in the OECD study was high, there was still a large variance which becomes more obvious if the correlation and 95% confidence intervals are plotted on linear scales (Fig. 5b).

In contrast to the hypothesis of Canfield & Bachmann (1981), Stauffer (1985) found that calcareous lakes had lower P retention than acidic or softwater lakes. He emphasized that models
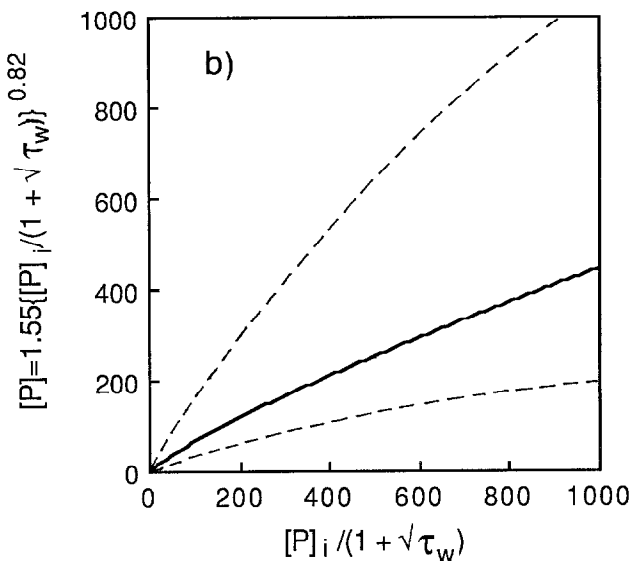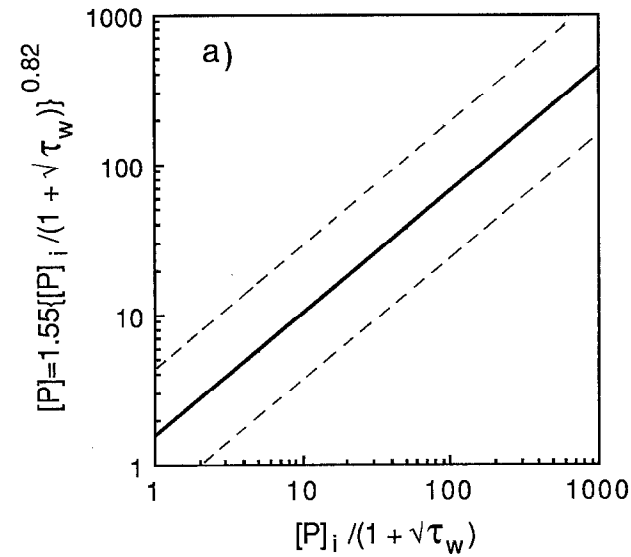
Fig. 5. Relation between predicted and measured lake P concentrations found in the OECD eutrophication study. a) plotted in double logarithmic diagram (from OECD, 1982), b) plotted on linear scales. Broken lines show 95% confidence intervals.

Fig. 6. Quotient between inlake P and mean inflow P concentrations (P/P$_i$) as a function of mean inflow P concentrations in oligotrophic and eutrophic lakes (modified after Janus & Vollenweider, 1984).

Also other studies have shown that the sediments of calcareous lakes have lower P-binding capacity than those of non-calcareous lakes (Ohle, 1964; Williams *et al.*, 1970; Shukla *et al.*, 1971). However, the opposite may be true for lakes with biogenic precipitation of calcite and coprecipitation of P (Lijklema *et al.*, 1983).

In conclusion, the P loading vs. P concentration models developed by statistical analysis of data from many different lakes may give good predictions of the behaviour of large 'populations' of lakes, but their application to individual lakes may result in large errors. It is unlikely that these types of models can be further improved only by inclusion of more data in the databases. Instead, it is more likely that careful analyses of homogenous subsets of data may give models with better predictive value.

Phosphorus vs. chlorophyll models

The chlorophyll to total phosphorus ratio in lakes will vary due to variations in the chlorophyll and phosphorus content of phytoplankton and in the amount of total P which is bound to phytoplankton. The chlorophyll content of phytoplankton varies depending on nutrient status, light and temperature (Ahlgren, 1970, 1977, 1983; Eppley *et al.*, 1973; Heyman, 1986; Heyman & Lundgren, 1988; Smith, 1980). Values within the

developed for heterogeneous groups of lakes will be severely biased when applied to many individual lakes, and 'the loading-response models are so imprecise because we have not sufficiently recognized the factors influencing the results', and further stressed that 'effort will have to be made in relating the efficiency of P recycling in lakes to edaphic, morphometric and hydraulic influences'.
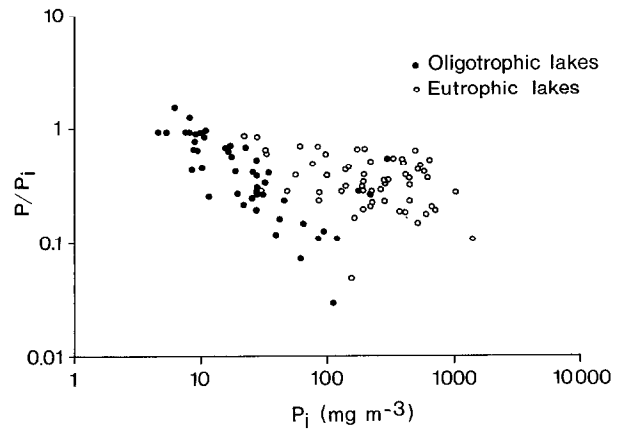
range 0.5–2% of the dry weight can be considered normal. Data on the P content of natural phytoplankton are more sparse in the literature. In eutrophic lakes values normally vary between c. 0.4 and 1% of the dry weight (I. Ahlgren, unpubl.). In cultures and under situations of a P surplus, values as high as 2% or more have been found (G. Ahlgren, pers. comm.). P limitation will cause both chlorophyll and P content to decrease so there is a tendency for covariation which will make the ratio chl/TP less variable. In the eutrophic lakes Norrviken and Vallentunasjön chl/TP ratios of natural phytoplankton during the summer seasons varied between 0.5 and 1 (I. Ahlgren, unpubl.). If lakewater total P during summer were bound entirely to phytoplankton, and cellular chlorophyll a and P contents were constant, then linear correlations with slopes between about 0.5 and 1 could be postulated. However P is also bound to other particulate and dissolved fractions, so lower values are more likely to be found. Especially in oligotrophic lakes and under high grazing pressure the fraction of total P bound to phytoplankton can be quite small (see also Heyman & Lundgren, 1988).

An extensive review of phosphorus-chlorophyll relationships for lakes was given by Nicholls & Dillon (1978). Different expressions for phosphorus-chlorophyll relations may be difficult to compare because authors have used different time periods for their calculations. In most cases summer mean values of chlorophyll have been used. In the OECD eutrophication study, however, annual mean values were used. Smith & Shapiro (1981) treated data for several individual lakes. Data from these two references and elsewhere indicate that there is often a fairly good linear correlation between chlorophyll a and total P concentrations with slopes generally in the range 0.4 to about 1, at least within a limited concentration range (up to about 100 μg P l^{-1}). Some examples are given in Fig. 7 and Table 2. Data from Lake Washington by Edmondson & Lehman (1981) (mean annual total P and July–Aug chl a) give the slope 0.55 and intercept $-4.8\ \mu$g l^{-1}. Megard (1978) found a slope of 0.58 and an intercept of $+4.2$ for Lake Minnetonka summer values.

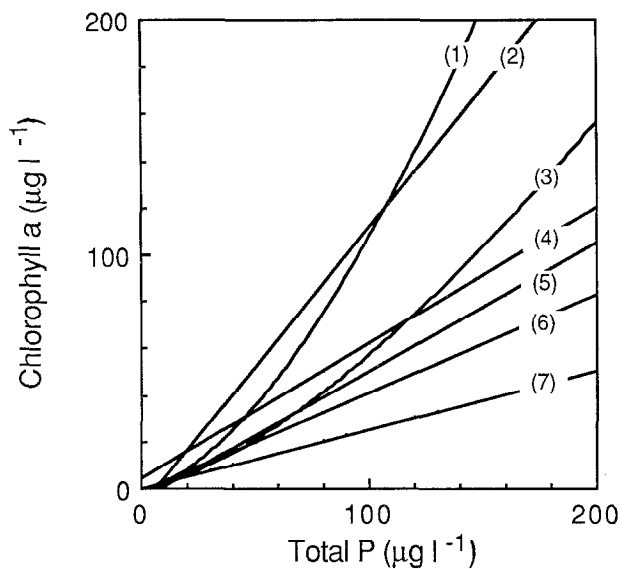Fig. 7. Relationship between chlorophyll a and total phosphorus according to several models: 1) Sakamoto (1966), 2) Schindler et al. (1978), 3) Dillon & Rigler (1974), 4) Megard (1978), 5) Edmondson & Lehman (1981), 6) Berge et al. (1980), 7) OECD (1982).

Schindler, Fee & Ruszczynski (1978) found a slope as high as 1.19 and an intercept of -7.3 for data from ELA lakes during the ice-free season. Data from several oligotrophic Norwegian lakes gave the slope 0.42 and intercept $-0.93\ \mu$g l^{-1} (Berge et al., 1979). The often occurring negative intercepts (i.e. positive intercepts on the P axis) imply that the relation may be curved at low P concentration (less than about 5–10 μg l^{-1}). Apart from that, the slopes are in close agreement with theoretical considerations.

Many authors use logarithmic transforms for their correlations (e.g. Sakamoto, 1966; Dillon & Rigler, 1974). However, on linear scales, these correlations produce curves with varying slopes. Such curves cannot obviously be extrapolated to high total P concentrations since there is an upper limit for chlorophyll concentrations where other factors than P become limiting. This fact has been stressed especially by Straškraba (1980, 1985). Ahl & Wiederholm (1977) considered the upper level for chlorophyll to vary between 50 μg l^{-1} for deep lakes and 150 μg l^{-1} for shallow lakes whereas Straškraba (1978) used maximum

Table 2. Phosphorus-chlorophyll models discussed in this article.

Linear models:	
chl a = 1.19TP − 7.3	Schindler *et al.* (1978)
chl a = 0.58TP + 4.2	Megard (1978)
chl a = 0.55TP − 4.8	Edmondson & Lehman (1981)
chl a = 0.42TP − 0−93	Berge *et al.* (1980)
Logaritmic models:	
chl = 0.0735TP$^{1.583}$	Sakamoto (1966)
chl a = 0.0724TP$^{1.45}$	Dillon & Rigler (1974)
chl a = 0.028TP$^{0.98}$	OECD (1982)
Models with defined maximum levels:	
chl a = 150(1 − e$^{(−0.000867TP−0.0000111TP^2)}$)	Ahl & Wiederholm (1977)[1]
chl a = 50(1 − e$^{(−0.0026TP−0.000102TP^2)}$)	Ahl & Wiederholm (1977)[2]
chl a = 40.1/(1 + 130 e$^{(−0.114TP)}$)	Straskraba (1980)
Model based on total N and total P concentrations:	
log(chl a) = 0.6531 logTP + 0.548 logTN − 1.517	Smith (1982)

[1] for shallow lakes
[2] for deep lakes

values between 30 and 50 μg l^{-1} in his regressions (Fig. 8).

It is still an open question whether the relationship in the lower part of the concentration range is linear or curved. Straškraba (1980) considered the curvature to be adequately demonstrated by the data of Dillon & Rigler, and the negative intercepts mentioned above emphasize the same point. A curvilinear relationship implies an increasing chl a/TP ratio with increasing TP concentrations. It is likely that this is due to the fact that a lower fraction of total P generally is bound to phytoplankton in oligotrophic lakes than in eutrophic lakes (cf. discussion by Heyman & Lundgren, 1988). Fig. 9 compares the chl a/TP ratios as a function of TP concentration of the seven models presented in Fig. 7. Only Megard's model gives a decreasing ratio and the OECD
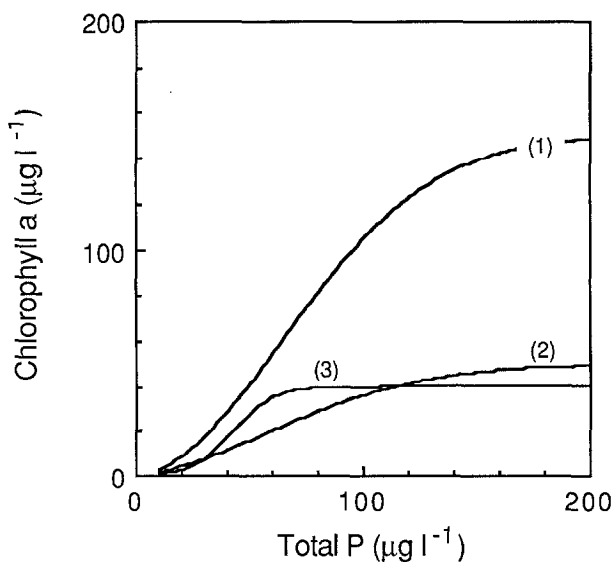

Fig. 8. Relationship between chlorophyll a and total phosphorus according to the models of 1) and 2) Ahl & Wiederholm (1977), 3) Straskraba (1980).
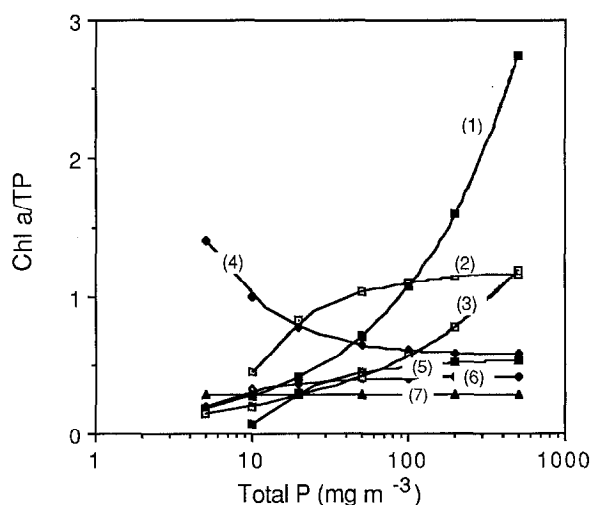
Fig. 9. Variation of the chlorophyll-phosphorus ratio with phosphorus concentration according to the models presented in Fig. 7. Figures at curves refer to references given in Fig. 7.

model a constant ratio. All the others give increasing ratios as TP increases. This implies that as total P in a lake increases, it becomes more efficient at producing a standing crop of algae.

Shapiro (1978) argued convincingly that the chlorophyll-total P regression models can be very misleading when applied to individual lakes. He emphasized the illusion of a good fit between chlorophyll and total P data created by log/log plots. When plotted on linear scales the variance in the chl a/TP relation becomes more obvious (Fig. 10). Shapiro proposed that much of this variance is due to biotic factors such as differences in grazing pressure and species composition between lakes and on other limiting nutrients. Because of such factors, it is not possible to create simple, generally valid regression models of the chl a/TP relation with much better precision than those presented here. Adding more data to the database may even increase the variance.
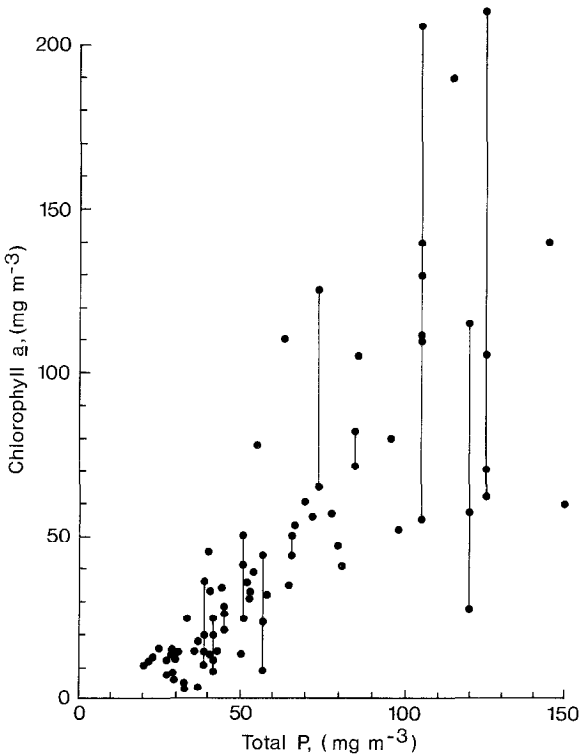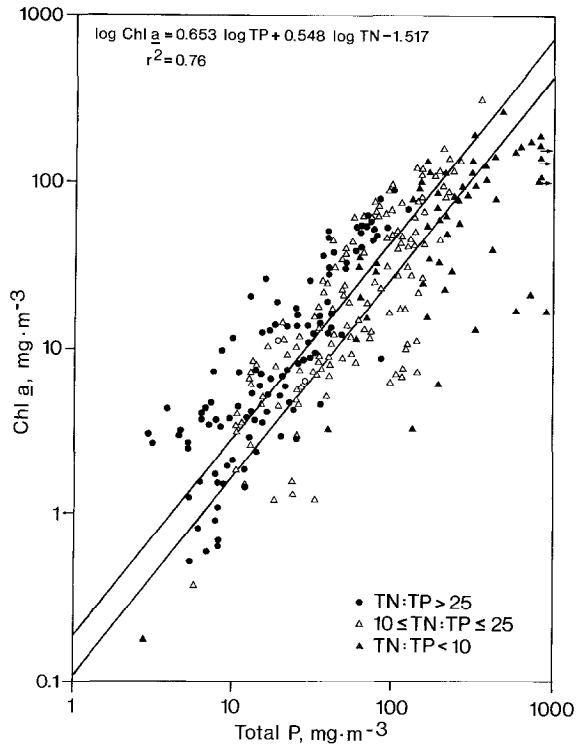
Smith (1982) could explain some of the vari-

Fig. 11. Relation between chlorophyll a and total P at different N:P ratios (after Smith, 1982).

ance in chl a/TP plots by taking into account also lakewater nitrogen concentrations and demonstrated that different regression lines were found for different lake water TN:TP ratios (Fig. 11).

The impression of a comparison of the results of different studies is that the chlorophyll-total phosphorus relationship is very variable. There is certainly a dependence of chlorophyll concentrations on P concentrations, but other factors than P tend to obscure the picture. Phosphorus to chlorophyll relationships may be used to identify the maximum chlorophyll concentrations that are likely to occur. In individual lakes, the variance may be less (Smith & Shapiro, 1981)'but changes in plankton community structure occurring after changes in nutrient loading may change the relation and make predictions less accurate also in such cases.

Fig. 10. Replot of data from Jones & Bachmann (1976) on linear scales (after Shapiro, 1979).

Dynamic phosphorus models

In the search for improving the predictive value of phosphorus models and under the influence of engineering sciences and control theory, the use of theoretical dynamic phosphorus models have been introduced in aquatic ecology and in the management of streams and lakes. Dynamic phosphorus models may be of widely varying complexity, from relatively simple mass balance models such as eq (1) to large 'ecological' models. The latter consist of sets of differential equations describing the behaviour of a number of state variables and the flow of matter between them. The behaviour of the whole system is assumed to be described as a result of the component processes. Many authors have been very optimistic with regard to the possibilities offered by these types of models. Kalčera *et al.* (1982) citing Chen & Orlob (1975), say that: 'Ecosystem models are known to be of much poorer resolution than technical models, owing to the inherent complexity of such systems. Nevertheless, they are now currently used as *the only adequate means for eutrophication management*'. Benndorf & Recknagel (1982) say that: '... given the enormous complexity of lake and reservoir ecosystems, the problem of selecting the optimum measure for control of internal ecological processes can be solved *only by means of dynamic ecological models*'.

The mechanistic way of viewing the ecosystem has been greatly criticized, either because our knowledge of all the component processes is too fragmentary to build working models (Fryer, 1987) or because it is claimed that ecosystem behaviour cannot be described simply as the sum of its parts. Rather, it has emergent properties on higher levels depending on interactions between organisms which cannot be predicted from the properties of the individual species (Harris, 1985). It is sometimes claimed that ecosystem models represent a holistic view of the ecosystem whereas others have considered such models to be examples of extreme reductionism (e.g. Allen & Starr, 1982 as cited by O'Neill *et al.*, 1986). Although there may be many convincing arguments against the idea that the behaviour of ecosystems can be

described with mathematical, dynamic models, such models can certainly be of value in advancing our understanding of more limited aspects of an ecosystem, e.g. the phosphorus dynamics and trophic state of lakes. Fryer (1987), in his severe critique of mathematical modeling of ecosystems, admits that 'One can, in a crude sort of way, model things like the phosphorus cycle in a lake...'. Most models in this category are 'eutrophication models' which aim at describing the trophic level (phytoplankton biomass, chlorophyll, primary production, etc.) of a lake as a function of nutrient supply and physical and chemical environmental factors. Early attempts in this field, however, often lacked realism and insight into the true character of the problems (see e.g. comments by Schindler, 1975) and helped to implant a scepticism in many limnologists against modelling. Normally, eutrophication models are not designed to explain structural properties of the ecosystem (species composition and distribution etc.) and their utility should be judged strictly with respect to their stated purpose.

In this chapter we will concentrate on a discussion of the usefulness of dynamic models for predicting lake P concentrations and trophic state and make some comparisons with empirical models. For details on the techniques used in building and running models the reader is referred to the rich literature on this subject, e.g. Jørgensen (1983) and other references mentioned in the introduction.

Because P is involved in the metabolism of all the organisms in a lake a detailed description of its dynamics would have to include the populations of all possible species and their interaction with each other and the environment. This is of course completely unrealistic. Like all models, lake phosphorus models must be simplifications of reality. Benndorf *et al.* (1985) formulated a number of general principles to be considered before a model can be properly used in either research or decisionmaking: 1) The principle of the maximum possible simplicity, 2) The principle of the maximum necessary complexity, 3) The principle of the maximum possible generalizability and, 4) The principle of the proper validation.

These principles are partly contradictory. For instance, to make a model generally applicable to different types of lakes requires that it can cope with many different situations and therefore has to be very complex. Whereas Benndorf & Recknagel (1982) argued for general models with generally valid parameters that can be used for different lakes without recalibration, Jørgensen et al. (1986) advocated models of medium complexity and flexible structure which can be modified and calibrated for each object of study. Schindler (1975), in his comments on eutrophication modelling, predicted that to succeed, models must be 1) simple, 2) process oriented, and 3) include only experimentally verified relationships.

In the empirical models treated in the first part of this paper, two principle problems were identified 1) the factors responsible for P retention in the sediments, and 2) factors responsible for variations in the relation between P concentration and algal biomass (chlorophyll). These problems have to be dealt with also in a dynamic model and will receive special focus on in the following examination of experiences of using a few models of different degrees of complexity.

Simple hydraulic dilution models

The simplest dynamic models are based on P mass balance equations of the type represented by eq. (6). Among the first attempts in this direction was that made by Rainey (1967) to calculate the rates of displacement of pollutants from the Great Lakes by the water flow through the lakes:

$$C_2 = C_2^0 e^{-\rho w^t/V} + (C_1 + M/\rho_w)(1 - e^{-\rho w^t/V})$$

$$(26)$$

where C_2 is the concentration of the pollutant, C_2^0 is the concentration of the initial time (t = 0), and C_1 is the mean concentration in the streams entering the lake, and M the mass input from point sources. Rainey's equation did not contain any term for the loss to the sediments and thus could only be used to model the fate of a conservative substance. He demonstrated, e.g. that a 90% displacement of such a substance after stopping the effluents would take more than 500 years (2.3 times the water retention time) for Lake Superior but less than 6 years for Lake Erie.

Chapra (1977) used a similar approach to calculate phosphorus concentrations in the Great Lakes but added P retention to the sediments according to the empirical equation (15) using an apparent settling rate of 16 m a^{-1}. The agreement between measured and calculated mean P concentrations were very good (r = 0.94). The largest deviations were found for the central and east basins of Lake Erie where calculated concentrations were about 50% higher than the measured, implying a larger apparent settling rate. According to Chapra this could be due to the fact that a larger fraction of the P loading to this lake was in particulate form. Chapra calculated 90% response times due to reduction of point sources to 1 mg P l^{-1}. For L. Superior the value was 20 years, i.e. considerably less than the value calculated by Rainey thus demonstrating the importance of including internal loss processes.

Ahlgren (1977) showed that the response of total P concentrations in L. Norrviken after the reduction of the external loading by about 90%, could be described as a simple dilution process. Ahlgren (1980) used an approach similar to that of Chapra (1977) to calculate the washout of N and P in a chain of four lakes in the same watershed. In both cases, expressions for the sedimentation coefficient equal to zero gave the best correspondence between simulated and measured values. This showed that due to large 'internal' P loading the annual net P retention was close to zero. Using the Vollenweider model in this case (eq. 17) would have severely underestimated the P concentrations reached after periods corresponding to more than 90% displacement of the water.

Larsen et al. (1979) also used a simple dilution model to advantage in showing that internal loading maintained the high summer P concentrations in Shagawa Lake after reduction of P in sewage entering the lake by about 80%. However, they had to use different values for σ during different time periods to get a good fit of model simulations with observed values. For the period before the treatment, $\sigma = 0.035$ week^{-1} was used

during the ice-covered seasons and 0.072 week^{-1} for the ice-free seasons whereas for post-treatment years, winter values of $\sigma = 0.00$ gave better correspondence between model runs and observations.

EAWAG model

The EAWAG model was developed at the Swiss Federal Institute for Water Resources and Water Pollution Control (EAWAG) in Zürich and has been successively modified (Imboden, 1974; Imboden & Gächter, 1978; Gächter et al., 1983). This model has a very simple biological structure with dissolved orthophosphate (DIP), particulate phosphorus (PP) and oxygen as the only state variables in epilimnion, hypolimnion and sediment. DIP is taken up in PP (assumed to be mainly phytoplankton) by light dependent photosynthesis and recycled to the water by mineralization. The model has a well developed description of thermal stratification and exchange of substance by eddy diffusion between the epi-, meta-, and hypolimnion (Fig. 12) and can be said to fulfill the three criteria suggested by Schindler (1975) quite well. Imboden & Gächter (1978) discussed its use on three lakes, Alpnachersee and Greifensee in Switzerland and Lake Washington in USA. Data from the two first lakes permit a comparison of the results with predictions using empirical models (Table 3). Predictions for Alpnachersee were close to observed values (25 μg/l) whereas the two empirical approaches
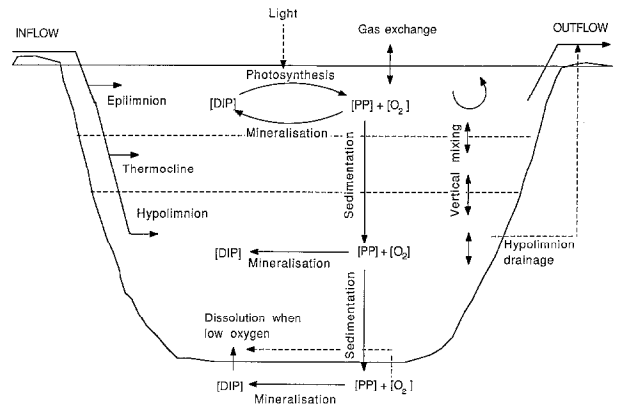

Fig. 12. Schematic diagram of EAWAG model (modified after Gächter et al., 1983).

give somewhat lower P concentrations (18 and 20 μg/l respectively). For Greifensee the P loading data were uncertain but estimated to be c. 5 g P m^{-2}a^{-1}. The OECD model gives a predicted P concentration of 100 μg l^{-1} and the original Vollenweider model 160 μg l^{-1} whereas the EAWAG model gave about 400 μg l^{-1} with P reflux from the sediments and about 180 μg l^{-1} without such reflux. The measured P concentration was about 350 μg l^{-1}. In this case the models gave very different results mainly due to a large P release from the sediments. Without release, the EAWAG model gave a value close to that of the Vollenweider model. Predicted new steady state concentrations after a reduction of the P loading by 90% (to 0.5 g m^{-2} a^{-1}) were

Table 3. Comparison of predictions of P concentrations (μg l^{-1}) in three Swiss lakes made with the EAWAG model and with OECD and Vollenweider models (based on data given by Imboden & Gächter 1978).

	Alpnachersee	Greifensee	Baldeggersee
L$_P$ (g P m^{-2} a^{-1})	2.4	5.0	2.4
Measured P conc.	25	350	500
Predicted P conc.:			
EAWAG model[3]	25	400	500
EAWAG model[4]		180	
OECD model	18	100	67
Vollenweider (1976) model	20	162	98

[3] with sediment reflux
[4] without sediment reflux

about 37 μg l^{-1} with P reflux from the sediments and 10 μg l^{-1} without reflux using the EAWAG model. The authors estimated that oxygen conditions in the hypolimnion would improve so that the P reflux would cease completely and therefore the latter value be more correct. The empirical models gave, respectively, 15 and 16 μg l^{-1} which are similar to predictions with the dynamic model.

Imboden (1985) reported on the use of the EAWAG model as a tool for prediction of the lake's response to different lake restoration strategies in Lake Baldegg. The P concentration in this lake was remarkably high (about 500 μg l^{-1}) considering the estimated loading (13.2 t a^{-1}), corresponding to a mean inflow concentration of 295 μg l^{-1}. The Vollenweider and OECD models predict mean P concentrations of 98 and 67 μg l^{-1} respectively. A reduction of the external P loading to 5 t a^{-1} (1g P m^{-2} a^{-1}) was predicted to give a mean lake concentration of 140 μg l^{-1}. In combination with hypolimnetic aeration, which was supposed to reduce P release from the sediments, the predicted concentration was 110 μg l^{-1}. The Vollenweider and OECD models give only 39 and 31 μg l^{-1}, respectively. The reason for the very large difference between the dynamic and empirical models in this case is not obvious. One possibility is that Imboden, when calibrating his model to the pre-restoration conditions, used too small sedimentation and sediment P release rates. The effect of reducing P release in the subsequent simulations would then result in less P retention than if larger values on both these variables had been used. Both this case, and that of Alpnachersee, clearly demonstrates the difficulties of modelling lakes with large internal nutrient loadings.

Glumsoe model

The Glumsoe model was described by Jørgensen (1976) and results of its application to different lakes have been presented in several papers, e.g. Jørgensen et al. (1978), Jørgensen et al. (1986a). In comparison to the previous examples this model represents a step further in complexity. In its present version the Glumsoe model has 17 state variables of which 8 are related to phos-
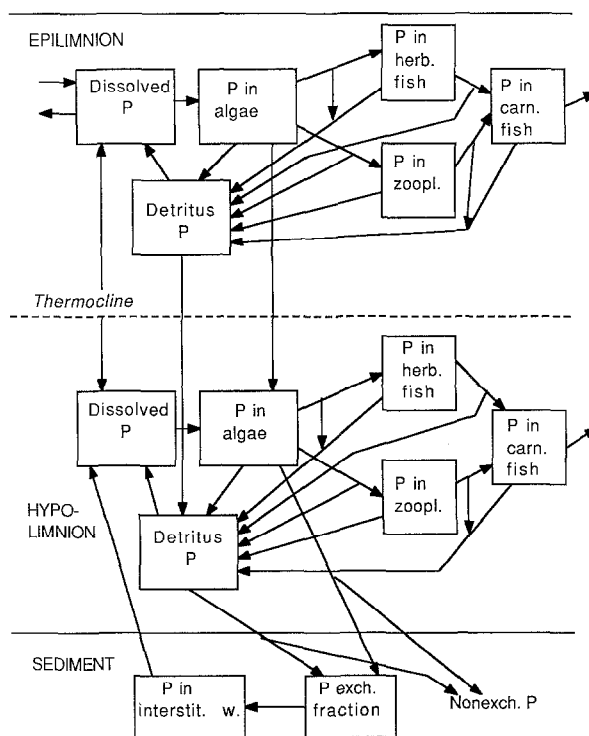

Fig. 13. Schematic diagram of Glumsoe model (modified after Jørgensen *et al.*, 1986b).

phorus dynamics (Fig. 13). In contrast to several other models, the Glumsoe model has a relatively detailed description of sediment-water phosphorus exchange which is based on good experimental work. The performance of this model when applied to 16 cases was reported by Jørgensen et al. (1986b). This study showed that modifications of the model had to be made due to specific characteristics of the individual lakes. The modifications included, e.g. the introduction of a thermocline for deep, stratified lakes, of resuspension of sediment material in some of the shallow lakes, of silica as a limiting factor for phytoplankton in one lake where diatoms dominated, and of nitrogen fixation in two lakes with dominance by nitrogen-fixing blue-green algae. For comparison of the agreement between measured and predicted values they used the 'objective function' or standard deviation

$$Y = \frac{\sqrt{\sum_{i=1}^{i=n} (x_t^i - x_m^i)^2}}{\bar{x}_m n} \qquad (27)$$

where m is the number of time observations, n is the number of state variables, x_t^i is the i'th state variable found by the model at time t and x_m^i is the corresponding observation. Values of Y between 0.07 and 0.36 (7 and 36%) were found for 7 of the cases where enough data were available for a calculation. Regression coefficients for observed vs computed phytoplankton and nutrient data varied between 0.82 and 0.91. The authors consider these results 'acceptable enough to enable the use of the eutrophication models in environmental management'.

In another paper (Jørgensen et al., 1986a) results from a validation of predictions made with the Glumsoe model are presented. Sewage effluents to Lake Glumsoe were cut off in 1981, reducing the P loading by 88%. Previous predictions of the development of nutrient concentrations and phytoplankton were shown to compare favorably with results found during 1981–1983. However, diatoms replaced the previously dominating Scenedesmus in spring, causing an earlier maximum of the bloom to appear. The authors therefore conclude that 'flexible structure models may be more appropriate for prognoses in cases where significant changes in loading take place'. Comparisons with predictions of mean annual total P concentrations using the empirical models of Vollenweider (eq. 17) and OECD (eq. 22) are shown in Table 4 (data from Kamp-Nielsen, 1986). In all cases the empirical models give lower values, which is to be expected due to the very large internal P loading in this lake.

Table 4. Comparison of predictions of total P concentrations in L. Glumsoe before (1975) and after (1985) reduction of external P loading (q_s = 5.4 m and τ_w = 0.37 a were used in the calculation with empirical models). (Data from Christensen & Windolf-Nielsen, 1984 and Kamp-Nielsen, 1986).

	1975	1985
L_p (g m^{-2} a^{-1})	6.0	1.6
Measured P concentration (g m^{-3})	1.4	0.43
Predicted P concentration:		
Glumsoe model	1.38	0.41
Vollweider model (eq. 17)	0.74	0.18
OECD model (eq. 24)	0.33	0.11

Great Lakes models

Many attempts have been made to model the response of the North American Great Lakes to changes in phosphorus loading. One example of a relatively complex model was given by Thoman & Segna (1980) who reported on the application of a dynamic phytoplankton-phosphorus model for Lake Ontario. Their model had six P, four Si and seven N state variables. They calibrated the model against data from one year (1972) and used a 10-year dataset for verification. They found that they had to include two functional phytoplankton groups, diatoms and nondiatoms in the model. Diatoms became silica limited in the spring whereas nondiatom phytoplankton was controlled by phosphorus later in summer. The model also had two functional zooplankton groups, herbivorous and carnivorous. Statistics of the verification gave an overall relative error of about 20%. They found that the model was very sensitive to changes in the net settling rate of particulate phosphorus. Changes on the order of 0.01 m d^{-1} (0.11–0.10) had a profound influence on the result. They used the model to evaluate effects of the implementation of reducing the phosphorus loading to the 1972 Water Quality Agreement target load of 7000 metric tons/year. The long-term simulations (1977–1990) predicted that total phosphorus levels eventually may decline below 10 μg l^{-1}. The Vollenweider model gives a predicted value of about 9 μg l^{-1}, thus in good agreement with the dynamic simulation. The simulations also indicated that the reductions in chlorophyll would not be as marked and even would be difficult to detect. The reason was that the silica-limited diatoms could not be expected to respond to reductions in P concentration. Non-diatom phytoplankton, on the other hand were estimated to be markedly reduced by a reduction in the phosphorus load.

SALMO

The SALMO model developed by Benndorf et al. (1981) was considered by the authors to be a general model which should not need calibration for each individual lake. This model is of about the same complexity as the Glumsoe model but

has two functional groups of phytoplankton: bluegreen algae and green algae including nannoplankton diatoms. It has two physical layers, epilimnion and hypolimnion, and also functions for the description of the exchange of nutrients between sediment and water. Benndorf & Recknagel (1982) applied this model to four very different water bodies in GDR using the same set of parameter values in all cases. Apart from the timing of the spring phytoplankton peak, the model gave a fairly good description of the level of the phytoplankton biomass in all four cases. Data were not presented, however, allowing a comparison of the predictions with empirical models.

Discussion and conclusions

Few comparisons between results achieved with empirical and dynamic models are found in the literature. One exception is the study by Bierman (1980) who compared results from dynamic models and empirical models applied to different parts of the Great Lakes. The results of the comparisons were that all models gave approximately the same predictions of total phosphorus and chlorophyll concentrations. If only annual average values are of interest the logical conclusion would be that the much simpler empirical models were quite adequate for the practical purpose of water management. Similar conclusions can be drawn from many other examples.The good agreement between the different approaches, however, may have added significantly to the credibility of the predictions in the very important case of Great Lakes eutrophication.

Empirical P loading models have been developed for lakes with 'normal' sediment P retention and should not be applied to lakes where 'internal loading' is present (OECD, 1982). It was also demonstrated in the examples given above that the response of such lakes to changes in the external P loading cannot be predicted well with the empirical models. However, also with dynamic models, predictions of sediment P retention and release must be considered an extremely difficult

task, since our knowledge about the processes controlling P release from sediment and the sedimentation of P are inadequate. Predictions of the balance between these two processes over a wide range of P loading therefore cannot be very precise. The strength of the dynamic models probably does not lie in exact predictions of concentration levels but more in the possibilities to evaluate, for example, seasonal differences in processes such as internal loading, seasonal algal maxima, rates of response to changed nutrient loading and the relative benefits of different lake management or lake restoration options and for testing different hypotheses. Good examples of such uses were presented by Benndorf & Recknagel (1982) and by Imboden (1985). Although it may be appealing to the scientist to include as much detail as possible in a model, a general conclusion of the experience so far is that to be of practical value a model should be as simple as possible. A corollary of that is that flexible models, which can be modified according to the objective and problem to be solved, have a distinct advantage, because they can be simplified.

Empirical P loading models have shown that P retention in lakes is controlled mainly by water residence time. Most data also indicate that P retention is positively correlated to mean inflow P concentration at least when comparing lakes of similar trophic level. However, if eutrophic and oligotrophic lakes are treated separately, it is obvious that P retention is smaller in the eutrophic lakes.

Empirical models have without doubt made important contributions to the development of general principles and theories of lake ecosystems, not only within the field of eutrophication. Several examples were given by Peters (1986). They do not necessarily in themselves provide understanding of the underlying processes and of interactions between organisms and their environment in the sense indicated by Lehman (1986), but may help to reveal large-scale properties of lakes and guide limnologists in their search for improved understanding of the functioning of lakes.

Dynamic eutrophication models may be excellent tools for the evaluation of different lake management strategies, but require more data and qualified scientists for their proper use. By necessity, therefore their use will be more limited than that of the empirical models. Theoretical, dynamic eutrophication models are also potentially powerful tools in the process of developing theories about lake ecosystems. An example of such use was given by Jørgensen & Mejer (1977) and other possibilities in this direction were discussed by Straškraba & Gnauck (1985). So far, however, this type of models seem to have played a minor role in this respect than the empirical models.

Acknowledgements

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