Quantitative Understanding and Prediction of Lake Eutrophication

ANDREAS CHRISTOFFER BRYHN
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Abstract

Many lakes around the world have been exposed to increased nutrient input from anthropogenic sources such as sewage discharge and runoff from fertilised agricultural areas. This has led to eutrophication, manifested as intensified algal blooms, murky waters, oxygen depleted lake bottoms, and alterations of considerable parts of the foodweb. However, many of these lakes have also recovered, due to improved nutrient abatement techniques and an improved quantitative scientific understanding of eutrophication and its causes. General, predictive models have played a crucial role in the latter development, as they have made it possible to quantitatively assess expected ecosystem changes from various planned actions against eutrophication.

The present thesis has been aimed at improving the domain of validity and predictive power of a general, dynamic total phosphorus (TP) model (LakeMab) and to provide the basis for constructing a similar model for total nitrogen (TN). Among the findings in the thesis is that dissolved nitrogen gas is probably always available in excess for nitrogen fixation and nitrogen modelling in eutrophication contexts. Two papers have laid the ground for improved nutrient modelling in calcareous lakes, where sedimentation is particularly pronounced. Static models for predicting concentrations of particulate phosphorus, nitrogen, and organic carbon have been presented that may be incorporated into sedimentation algorithms in dynamic nutrient models. Boundary conditions for various flux algorithms have made it possible to greatly expand the domain of LakeMab for TP. The typical uncertainty of TP concentration values is 17% when predicted with LakeMab, whereas the uncertainty in predictions using older, static models is about twice as high.

LakeMab may be very useful for resolving practical issues such as predicting climate-induced eutrophication and drawing up operational guidelines for achieving good water quality as prescribed by, e.g., the European Water Framework Directive.

Andreas Christoffer Bryhn, Department of Earth Sciences, Villav. 16, Uppsala University, SE-75236 Uppsala, Sweden

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Nothing so fair, so pure, and at the same time so large, as a lake, perchance lies on the surface of the earth. Sky water. It needs no fence. Nations come and go without defiling it. It is a mirror which no stone can crack, whose quicksilver will never wear off, whose gilding Nature continually repairs; no storms, no dust, can dim its surface ever fresh; -- a mirror in which impurity presented to it sinks, swept and dusted by the sun's hazy brush -- this the light dust-cloth, -- which retains no breath that is breathed on it, but sends its own to float as clouds high above its surface, and be reflected in its bosom still.

From "Walden; or, Life in the Woods" by Henry David Thoreau
List of Papers Included in the Thesis

This thesis is based on the following papers, which will be referred to in the comprehensive summary by their Roman numerals:


These papers have been reprinted with the kind permission from Elsevier (Paper I) and Springer (Papers II-V).
Description of the Author's Involvement in the Papers

I. Literature study, sampling and analysis of empirical data, model construction and simulations, as well as the major part of the discussion section.

II. Contributions to the discussion section, some treatment of empirical data.

III. Statistical modelling and other statistical treatment, most of the literature study and discussion.

IV. Data mining and treatment, parts of the literature study and discussion.

V. Most of the modelling, comparative testing, error analysis, literature study and discussion section.
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Abbreviations

C  Carbon
Ca  Calcium
Chl Chlorophyll-a
DIN  Dissolved inorganic nitrogen
DIP  Dissolved inorganic phosphorus
N  Nitrogen
N₂  Atmospheric or dissolved gaseous dinitrogen
N-fix  Nitrogen fixation
P  Phosphorus
TN  Total nitrogen
TP  Total phosphorus
1. Introduction

Lake eutrophication is manifested as the appearance of turbid water, the spread of "dead" bottoms with low oxygen concentrations, altered foodwebs, and intensified algal blooms which may look and smell repulsive and in some cases even be poisonous. The large number of eutrophicated lakes around the world has reminded us that human activity can substantially change the structure, function and general appearance of natural aquatic ecosystems (Naumann, 1921; Vollenweider, 1968; Håkanson and Boulion, 2002).

During the last four decades, however, successful reversal of eutrophication in several lakes has called attention to the fact that anthropogenic pollution does not necessarily lead to an irrevocable disaster, but may instead be remediated to a large extent. Eutrophication and its reversal have also provided a true scientific success story in the field of ecology, as our understanding of these processes has increased (Schindler, 1974, 1977; Peters, 1991).

The present understanding of lake eutrophication and its reversal (re-oligotrophication) may not only be expressed in words, but also in numbers, which makes it possible to predict (forecast) the time it takes between abatement and full effect, and to predict the likely ecological changes from a certain extent of remedial action (Peters, 1991; Håkanson, 1999). This thesis will, among other things, show that the certainty in such predictions has increased over the last decades due to improved generalised quantitative descriptions of such lacustrine features and processes which play crucial roles in the causal path between nutrient loading and algal blooms. Increasing prediction certainty with respect to operational ecological target variables is good news to society, and is, in addition, indeed a sign that lake eutrophication studies is a healthy and progressing scientific field.

The works presented in this thesis have been shaped in the tradition of quantitative and predictive limnology, which has been developed by, among others, Richard Vollenweider and Robert H. Peters, as well as my supervisors and other colleagues in the research group that I have had the pleasure to partake in during my postgraduate studies. The papers in this thesis have quantified and increased the predictive power, and expanded the applicability domain, of a general phosphorus (P) model, and also laid the ground for constructing a general, dynamic nitrogen (N) model which takes all major N fluxes into account.
2. The History of Lake Eutrophication and Its Reversal

2.1. Early History and Conceptual Understanding

Human activity has affected lakes and other natural ecosystems ever since humans evolved as an individual species. In early urban settlements, beginning with the Mesopotamian Empire (3500 to 2500 BC; in present-day Iraq), sewage was led away from housing areas and was often discharged into ponds or rivers (Cooper, 2001). However, it was not until the industrial revolution when the structure and function of many natural lakes were fundamentally altered by anthropogenic nutrient inputs as the population increasingly migrated to and concentrated in towns and cities (Naumann, 1924), and as the use of water closets became more widespread (Cooper, 2001).

Problems with excessive algal blooms became apparent in many European and North American lakes towards the end of the 19th and the beginning of the 20th century and were unhesitantly attributed to sewage inputs (Hasler, 1947). For instance, an official Swedish report from 1901 concluded that "Lake Växjö may serve no other purpose than as a large deposit reservoir for the town's wastewater" (Åberg and Rodhe, 1942).

The role of nutrients in promoting algal growth was acknowledged at an early stage. The word "eutrophication" (ευτροφίας means "corpulent" or "well-nourished" in contemporary Greek) was established by the pioneer limnologist Einar Naumann (Parma, 1980) and became synonymous with extensive enrichment of nitrogen (N) and phosphorus (P) (Naumann, 1921, 1931; Åberg and Rodhe, 1942).

Mechanical and chemical sewage treatment were first implemented to prevent the spread of cholera and other diseases (Cooper, 2001), but gradually also became methods for halting eutrophication. For a long time, however, as Hasler (1947) noted, there was no method available which was efficient enough to reverse eutrophication. In the meantime, the use of nutrients as fertilisers in agriculture in industrialised countries dramatically increased in the 1940s and onwards (Griliches, 1958; Chloupek et al., 2004), and the introduction of phosphate in laundry detergents in the 1950s (Kroes, 1980) added even more weight to the eutrophication problem.
2.2. Quantitative, Predictive Understanding and Restoration Success

The first well-documented successful attempt to combat eutrophication was to divert sewage from Lake Monona (USA) to another lake in 1936, which resulted in considerably less intensive algal blooms in Lake Monona beginning in the late 1940s (Edmondson, 1969). However, this method obviously only moved the problem to another natural water body. In the 1960s, nutrient removal in modern treatment plants made it possible to rapidly improve water quality in a few lakes; among them Zellersee (Vollenweider, 1968) and Lake Washington (Edmondson, 1969).

During the following decades, many other lakes were treated in a similar manner, with substantial and positive effects in general, although these effects appeared at various paces (Schindler, 1974; Marsden, 1989; Sas, 1989; Jeppesen et al., 2005). More efficient sewage treatment techniques and improved scientific understanding of eutrophication have both contributed to this ecological success story.

The first scientific turning point came in 1968, when Vollenweider (1968) noted that relatively little scientific work had been aimed at quantitatively and systematically tackling the eutrophication problem. Consequently, he presented simple, practically useful guidelines for "permissible loading levels" of total N (TN) and total P (TP) to lakes in order for them not to be eutrophicated, taking the lake volume into account so that higher loadings were allowed for more voluminous lakes. This work was published as a technical report, but has nevertheless been widely cited ever since and has been very influential on contemporary limnology. Vollenweider (1968) also recognised the importance of the water retention time, the internal P loading from sediments, fixation of gaseous N and denitrification on N and P concentrations.

During the years to come, a large number of simple statistical models based on these insights were constructed by various scientists. Most of these models predict nutrient concentrations from nutrient loading, volume and water residence time, and some of them are reviewed and tested in Paper V of this thesis.

The quantitative link between concentrations of nutrients and chlorophyll-a (Chl; a commonly used proxy of algal biomass) was first established in Japanese lakes by Sakamoto (1966). These data were used together with data from North American lakes by Dillon and Rigler (1974) to construct a statistical model between TP and Chl with a correlation coefficient ($r^2$) of 0.95. These two models have been followed by a large number of similar ones (Peters, 1986; see also Papers II and III). TP concentrations have also been found useful for predicting the Secchi (sight) depth as well as biomasses of secondary producers, such as zooplankton, benthic animals and fish (Peters, 1986).
However, there was still an intensive debate about whether N, P or both should be abated in order to reverse eutrophication. Many scientists even argued that carbon (C) limited primary production (Schindler, 1977). Viewpoints were often backed with results from nutrient enrichment experiments in laboratories, so-called bioassays (see Figure 1; Schindler, 1977; Peters, 1991).

The second scientific turning point in eutrophication research occurred when Schindler (1977) showed that bioassays only indicated instantaneous nutrient limitation, while algal growth on the timescale which is relevant for eutrophication management, the annual or multi-annual scale, may be controlled by P only. By adding various loadings of N and P to three experimental lakes in Canada for several years, he demonstrated that the algal biomass only responded to changes in P loading. All short-term N deficits were counteracted over the year by cyanobacterial fixation of gaseous nitrogen (N₂) of atmospheric origin (Figure 2). This mechanism had first been suggested by Redfield (1958) as the governing principle of marine phytoplanktonic production. Schindler’s (1977) findings conveyed that in order to prevent or reverse eutrophication, no other nutrients than P needed to be removed from water sources which had lakes as a final recipient. This opened the possibility to save plenty of efforts and resources in sewage treatment plants.

![Figure 1](image1.png)

*Figure 1.* Determination of short-term nutrient limitation with bioassays. Dissolved inorganic nitrogen (DIN) and phosphorus (DIP) in different combinations are added in to water samples or microcosms and the subsequent algal growth is measured.

Alongside the development of static, Vollenweider-type load-concentration models, there has also been a surge in the production of dynamic (time-dependent) models which have the advantage that they can quantify fluxes of P and other matter. The first ones were lake-specific and had some shortcomings which are discussed in the following sections. The second generation of general dynamic models is discussed in Papers II, IV and V, and systematically tend to give better predictions than static models (Paper V).
Thus, we have come to the point where we can quantitatively forecast the future impact from nutrient reductions to a very large number of lakes, with quite high precision. This must be regarded as a rather grand achievement, both from a scientific and a management-oriented perspective.

Figure 2. Determination of long-term nutrient limitation. Various combinations of nitrogen (N) and phosphorus (P) are added to lakes during several years and the subsequent algal growth and cyanobacterial nitrogen fixation (N-fix) are measured.
The scientific methodology used in this thesis (and in much research of other disciplines) relies on Popper's (1935; 1972) demarcation criteria for scientific theory, and Peters' (1986; 1991) focus on predictive (forecasting) power, as guiding stars for improved scientific methods and understanding. Dynamic models which are valid for many lakes of different characteristics are well compatible with this methodology, and have been developed along its guidelines. The reason for using quantitative methods is that they leave relatively little room for speculation and personal opinions. Using numbers to quantify concentrations, fluxes, and anthropogenic impacts and effects could therefore be seen as more unbiased than describing these ecosystem features and processes with words only.

3.1. The Role of Prediction

There are two important reasons to spend time and effort at quantifying important limnological features and processes. Formulating quantitative descriptions aims at representing lake ecosystems the way they appear, and as closely to the "truth" as possible. Quantitative prediction is necessary for testing assumed scientific relationships; whether a change in one ecosystem variable may affect another variable. Thus, predictions obviously have great importance for lake management. Lake managers, policymakers, and the general public often have a considerable interest in knowing what the probable environmental effect will be of a certain policy or measure, such as building sewage treatment plants or manure pits. The ability to predict important goal variables, such as the Secchi depth or the algal bloom intensity (as measured by Chl) is thus very useful in practice as a communication tool between natural scientists and the rest of the world (Håkanson and Boullion, 2002).

Furthermore, high predictive power is an important scientific goal in itself. The certainty with which we can predict changes in water quality from changes in external factors, such as nutrient loadings, is a direct, quantitative indicator of how well we understand scientific relationships (Peters, 1991).
Approaches which prioritise conceptual models over predictive power are still attractive among some scientists. Peters (1986) argued that the success record of such approaches has been relatively meagre with respect to lake restoration. Conversely, he continued, quantitative, predictive limnology "has already been instrumental in a massive and successful program of eutrophication control on the Great Lakes and elsewhere and holds promise that more can be done. It has shown what sort of ecology is effective, what sort of information will sway politicians and governments to action, and how scientists can help to improve our world. These are lessons to learn".

3.2. Testable Hypotheses, Theories, and Models

If one agrees that science has a unique and important role in society, and that it is not a complete waste of resources to spend large sums of governmental and private money on scientific research, then this insight should lead one to conclude that the unique status of science requires that it be defined in an unambiguous manner.

There are many variants available in the philosophy of science which in one way or another defines science as "something that scientists do" (Peters, 1991). According to such definitions, we would be able to consider astrology, alchemy and the biblical Book of Revelations as science, since many scientists have been involved in those fields during history. However, if we admit that these fields have generated very limited scientific success and predictive power over the years compared to the primary parts of, e. g., physics, medicine and ecology, then we apparently need a different definition of science.

To this date, Popper's (1935; 1972) demarcation criteria is the only available method which unambiguously separates alchemy and religion from the gravitation theories in physics. These criteria state that (1) the hypothesis or theory has to be supported by some kind of observation and (2) that the hypothesis or theory is refutable (or testable); i. e., that it can be falsified with evidence of the opposite. Using these criteria in the hypothetico-deductive methodology, hypotheses and theories are repeatedly tested, completely or partially refuted, and improved, thus developing our knowledge in various scientific fields and bringing it closer and closer to the unattainable goal; the truth.

Constructs which do not meet Popper's requirements are referred to as metaphysical, or pseudo-scientific (Popper, 1972). Research fields where irrefutable constructs play a central role may produce excellent descriptions of important and relevant features in their area, although the predictive power regarding important goal variables (and thus the quantitative under-
standing of scientific relationships) may nevertheless be very poor (Peters, 1991; Bryhn, 2007).

Yet, even though metaphysical constructs do not have a scientific value of their own, their heuristics and other characteristics may very well promote the development of testable hypotheses, theories and models with high predictive power (Popper, 1972; Peters, 1991). For instance, the widely used concept of steady-state in lakes is unobservable in its direct, literal sense (DeAngelis and Waterhouse, 1987; Peters, 1991). However, if the concept is instead operationally defined as an observable and common phenomenon, such as "stationary conditions; a period of several years with fluctuating short-term conditions but no significant long-term changes with respect to the goal variable", or simply as "long-term mean values", models based on such interpretations of steady-state may indeed be testable and their predictions may be tested against empirical data with good results, as Papers IV and V show.

Another important aspect of refutability concerns the tuning and validation of models. Many dynamic models include several site-specific constants which cannot be measured or determined in a general way but have to be tuned in order to suit empirical data. This circumstance allows for a large number of acceptable combinations of constants (a phenomenon sometimes referred to as equifinality; Beven, 2006). A "valid" solution may then be guaranteed each time, making refutation very difficult (Peters, 1991).

This problem may be avoided by using models which are general (valid for a large number of systems) and do not contain any site-specific constants (see Paper V). If a general model is tested against empirical data and found to provide systematically erroneous predictions, the model should then be considered at least partially falsified and should need to be improved. A second best option could be to limit the model domain of application so that systematic errors do not occur within this domain.

Some successfully tested refutable hypotheses in this thesis are:

- N\textsubscript{2} fixation in lakes cannot be limited by low N\textsubscript{2} concentrations (Paper I).
- Ca concentrations significantly affect Chl and the Secchi depth (Papers II-III).
- A Ca moderator that influences modelled sedimentation will improve the prediction of TP concentrations in calcareous lakes (Paper II).
- Particulate N, P and organic C will be accurately predicted from easily observable data on water chemistry and/or morphometry (Paper III).
- Defining boundary conditions for P flux algorithms will improve a general, dynamic P model (LakeMab), in terms of yielding reliable predictions for lakes of a wider range of geographical, morphometric and chemical characteristics (Paper IV).
- There will be a systematic difference in predictive power and prediction error when comparing LakeMab with static models (Paper V).
4. Nutrient Cycles and Lake Eutrophication

In order to predict lake eutrophication and the recovery from it, it is necessary to possess a quantitative understanding of the cycles of nutrients which regulate primary production. Two operational effect variables that can be used to express the degree of eutrophication and that are commonly used in lake management are Chl and Secchi depth (Håkanson, 1999). They are often strongly correlated to TP and TN (Dillon and Rigler, 1974; Bachmann, 1981; Pienitz et al., 1997; Paper III), but weakly correlated to inorganic nutrient concentrations (Pienitz et al., 1997) whose supply is also poorly reflected by their concentrations (Dodds, 2003). Thus, changes in TP are often used to predict the changes in the trophic status of a lake (see the review in Paper V). However, the TP-Chl relationship is stronger and has a steeper slope for temperate lakes than for tropical and subtropical lakes (Huszar et al., 2006). TN and TP are also rather strongly mutually correlated (Bachmann, 1981; Pienitz et al., 1997; Paper III).

4.1. The Phosphorus Cycle

Since P is the long-term regulating nutrient with respect to primary production in most lakes (Schindler, 1977 and Papers I-V), it is imperative to be able to model the P cycle dynamically in order to quantitatively understand and predict eutrophication and effects from counteracting it. A simplified, schematic overview of the most important fluxes (in mass per time unit) in the P cycle with respect to eutrophication is given in Figure 3.

The dashed line in the figure denotes the average depth that the waves reach. During calm conditions, only shallow bottoms and waters are affected by wave action, but during storms, deeper bottoms and waters are also affected. The average depth of the wave base may be calculated from mean gradients in vertical water temperature or chemistry profiles, or by means of an equation based on the lake area (Håkanson et al., 2004). This depth is called the critical depth or the theoretical wave base and serves as a functional separator between shallow and deep waters and shallow (erosion and transport) and deep (accumulation) sediments (Håkanson et al., 2004; Paper IV). In shallow lakes, the theoretical wave base may be located much lower than in Figure 3, and may even be equal to or below the maximum depth. In this case, the percentual spatial extent of deep waters and accumulation bot-
tom sediments may be quantitatively determined with boundary conditions (Paper IV).

**Figure 3.** Phosphorus fluxes in a lake. Abbreviations are explained in the text.

The tributary and groundwater input of P to the lake ($F_{P1}$) is one of the driving variables in dynamic (Papers IV-V) and static (Vollenweider, 1975; Bachmann, 1984) input-output models for P. Alternatively, $F_{P1}$ may be predicted using the TP concentration in the lake as a driving variable (Bachmann, 1984). Included in $F_{P1}$ is P in the tributaries and in the groundwater inflow. This flux is associated with high uncertainties which may in turn contribute with particularly high uncertainties in model predictions (Håkanson, 2000). Thus, the accuracy in empirical $F_{P1}$ data is of utmost importance for achieving good model predictions (Blenckner, 2008).

The outflow of P ($F_{P2}$) from the lake may be calculated as the TP concentration times the outgoing water flux (in volume per time unit), or the TP concentration times the lake volume divided by the water retention time. $F_{P1} - F_{P2}$ is often referred to the P retention; how much P is retained in the lake over a certain period of time (Vollenweider, 1968; Bachmann, 1984; Håkanson and Boulion, 2002; Papers IV and V).

$F_{P3}$ denotes the vertical sedimentation of particulate P from the water column towards the bottom, another major P flux (Dillon et al., 1990; Paper V). $F_{P3}$ is a function of the TP mass in the water column, the relative influence on the lake from sediment resuspension ($F_{P5}$) and the particulate fraction; i.e., the ratio of particulate to total P (Håkanson and Boulion, 2002; Papers II, III and IV). The particulate fraction shows rather low variability and was determined near 56% by Håkanson and Boulion (2002) and near 60% in Paper III. Papers II and III address the need to improve general, quantitative algorithms to predict $F_{P5}$ in lakes with different calcium (Ca) concentrations, since high Ca concentrations appear to accelerate sedimentation rates. While results in Paper II indicate that the particulate fraction of P is elevated in calcareous lakes, this is not supported by the much larger dataset used in
Paper III, which instead concludes that general sedimentation algorithms need to be adjusted for the Ca concentration in order to improve TP predictions.

The P flux from deep sediments to the water column is referred to as $F_{P4}$ in Figure 3. This flux is driven by animals (bioturbation), or by bacteria and redox conditions (diffusion). When the oxygen concentration exceeds 2 mg/l in waters just above the sediment and in interstitial waters, benthic animals eat and mix the sediment (Matlock et al., 2003; Malmaeus and Håkanson, 2004) while excreting dissolved nutrients which reach the water column (Hansen et al., 1997). However, during anoxic conditions, benthic animals die or leave, while redox conditions and bacterial activity take over as agents in the nutrient release (Hansen et al., 1997; Malmaeus and Håkanson, 2004), which may then in turn vastly increase until the TP concentration in the sediments goes below 0.5 mg/g dry weight (Paper IV). In addition, $F_{P4}$ is positively related to temperature, the TP content in deep sediments (Malmaeus and Håkanson, 2004; Paper IV), as well as sediment pH and iron concentration (Søndergaard et al., 2003).

Resuspension ($F_{P5}$) is the advective flux from shallow sediments and is mainly driven by wind and slope processes (Evans, 1994; Håkanson and Boulion, 2002) but is also affected to various extents by fish, benthic fauna (bioturbation), boat traffic, and river and groundwater intrusion (Weyhenmeyer, 1998). Most quantitative studies on resuspension have concluded that resuspended material constitutes the major part of settling particles in lakes (Weyhenmeyer, 1998). $F_{P5}$ is thus a major contributor to the nutrient cycles (Dillon et al., 1990; Weyhenmeyer, 1998) and may be quantified from morphometrical parameters and TP concentrations in the sediment on erosion- and transport sediments (Paper IV).

Lakes with high depth to area ratios stratify at certain weather conditions; i. e., when the temperature difference between the air and the deep water is greater than about 4°C (see Paper I). In northern temperate lakes, this occurs in the winter when there is an ice cover on the surface, and in the summer, when surface waters (the epilimnion) has been rapidly heated up while bottom waters (the hypolimnion) have gone through a slower temperature increase since they are relatively isolated from the warm air (Wetzel, 2001). Between stratification periods, the water column may mix rather intensively, thus drastically decreasing concentration gradients (Weithoff et al., 2000; Weyhenmeyer, 1998; Paper I). The mixing flux is referred to as $F_{P6}$ in Figure 3.

Nutrients that end up in accumulation bottom sediments and are not released back to the water column are eventually buried by more recently deposited particles and become located sufficiently far from the water column that they may be inaccessible to biota and thus considered part of the geosphere rather than the biosphere. This process which makes lakes a long-
term nutrient sink is commonly called sediment burial ($F_{P7}$; Dillon et al., 1990; Malmaeus and Håkanson, 2004; Brenner et al., 2006).

The final flux in Figure 3, $F_{P7}$, is the atmospheric P deposition. This flux can be a major P source to oligotrophic lakes (Cole et al., 1990) and to lakes located in areas with extensive deforestation and biomass combustion (Tamatamah et al., 2005). Atmospheric P can emanate from distant areas and the annual amount that reaches a lake in the Northern Hemisphere is typically 3-10 kg P per km$^2$ of catchment area and this variability largely depends on catchment area characteristics (Ahl, 1988).

A delicate task for predicting the influence from these fluxes on the TP concentration and trophic state indicators is to quantify them altogether in a general way and model their changes over time. This may be done with the LakeMab model, which will be discussed in 5.4.

4.2. The Nitrogen Cycle

It has already been mentioned in 2.2. that phosphorus is generally regarded as the long-term regulating nutrient in lake eutrophication. Thus, modelling nitrogen concentrations requires a separate motivation. Some important reasons for nitrogen modelling are:

1. Even though Schindler's (1977) successful tests of Redfield's (1958) hypothesis (see 2.2.) have had a great impact on lake management, the generality of the principle has been disputed (Elser et al., 1990). For instance, Bergström et al. (2005) found that primary production in unproductive lakes in Northern Sweden increased with N enrichment and that the correlation between Chl and TP was insignificant for these lakes. A possible explanation to this may be that N$_2$ fixation is inhibited by the low temperature in this boreal region. N$_2$ fixation has also been found to be conspicuously low in shallow, hypertrophic Danish lakes and may in these cases be constrained by, e.g., poor light conditions (Jensen et al., 1994).

2. Smith (1982) suggested that N may explain part of the residual error in the TP-Chl relationship.

3. The ratio of TN to TP may be useful for quantifying nitrogen fixation, and the biomass of cyanobacteria (blue-green algae), some of which form nuisance blooms that may be toxic (Tõnno, 2004).

4. Many scientists argue that although P inputs are more important than N inputs to lakes, the opposite principle may apply to coastal areas and oceans (Boesch et al., 2006; Håkanson and Bryhn, 2008). However, this standpoint is controversial, and general, dynamic TN and TP models could add new dimensions to the debate, since they would greatly increase our ability to quantitatively assess possible
structural differences, with respect to nutrient fluxes, between lakes and other aquatic ecosystems.

The TN cycle in lakes is depicted in Figure 4. Many of the fluxes -- inflow (F_{N1}; Vollenweider, 1968), outflow (F_{N2}; Vollenweider, 1968), release from deep sediments (F_{N4}; Hansen et al., 1997; Wang et al., 2008), resuspension (F_{N5}; Weyhenmeyer, 1998), mixing (F_{N6}; Weyhenmeyer, 1998), and burial (F_{N7}; Dillon et al., 1990; Saunders and Kalff, 2001) -- are governed by similar mechanisms as the corresponding P fluxes (see 4.1.).

Figure 4. Nitrogen fluxes in a lake. Abbreviations are explained in the text.

Sedimentation of particulate N (F_{N3}; Dillon et al., 1990) also shows many similarities with the corresponding P flux in 4.1.; it depends on the TN mass in the water column (Saunders and Kalff, 2001) and a considerable part of the particulate N comes from resuspended matter (Weyhenmeyer, 1998). The particulate fraction of N is difficult to predict and much more variable than the particulate fraction of P. However, particulate N may be rather accurately predicted from TP, although the slope of the regression line between TP and particulate N is not constant but lower at higher TP concentrations (Paper III).

Atmospheric deposition of bioavailable N (F_{N8}) may serve as a large N source to aquatic ecosystems (Holland et al., 2005). Data are often very variable (Weyhenmeyer et al., 2007) but there are extensive online databases available for, e. g., Europe (EMEP, 2008) and North America (United States EPA, 2008; NADP, 2008). The variation of F_{N8} can have a substantial impact on short-term nitrogen limitation of primary production (Weyhenmeyer et al., 2007).

The most abundant form of N in lakes is dissolved N\textsubscript{2}, although it cannot be metabolised by most primary producers except cyanobacteria and some other microorganisms (Paper I). Their uptake of N\textsubscript{2} is known as N\textsubscript{2} fixation (F_{N9}) and may be a dominant N flux to lakes (Schindler, 1977; Patoine et al., 2006) Fixation may be spurred by high temperature, good light conditions,
high TP concentrations and low TN:TP ratios (Tõnno, 2004). However, many eutrophication models which include N do not take this mechanism into account (see Paper I and references therein). The main conclusion from Paper I is that N$_2$ is probably always available in excess for F$_{N9}$.

Autochthonous N$_2$ production (F$_{N10}$) primarily consists of denitrification, the bacterial transformation of nitrate to N$_2$ and occurs in oxygen depleted bottom waters and anoxic sediment. Denitrification is influenced by many factors such as nitrogen supply, concentration of dissolved oxygen, water residence time, temperature, and presence of aquatic plants (Piña-Ochoa and Álvarez-Cobelas, 2006; Paper I). Bacterial N$_2$ production has recently been discovered to include anammox (anoxic ammonium oxidation), which occurs in the same parts of the lake as denitrification. This discovery has not provided a reason to revise previous estimates of N$_2$ production or N retention, but has instead provided increased understanding of the causal path for the transformation from bioavailable nitrogen to dissolved N$_2$, which may eventually leave the lake as gaseous bubbles (see Paper I and references therein). F$_{N10}$ may be predicted from the N loading per area unit (Saunders and Kalff, 2001).

At present, there are, to the best of the author's knowledge, no validated general, dynamic TN models available for any types of aquatic systems which account for all internal and external fluxes that are needed to correctly predict changes in TN concentrations. The most successful attempt hitherto may be the model PCLake, which has been validated for a large number of shallow European lakes, but lacks a general algorithm for F$_{N9}$ in Figure 4 (N$_2$ fixation; Janse, 2005), which may dominate all other external N inputs to lakes (Schindler, 1977). Papers I and III in this thesis are partially intended to provide more solid and quantitative ground for future dynamic predictions of N concentrations in lakes.

General, static TN models have been available for several decades. Bachmann (1981) presented static TN models whose average predictions had an error of 44% which is higher the static TP models reviewed in Paper V (typical error = 37%) and much higher than dynamic TP models (typical error = 17%).
5. Modelling Approaches

As explained in the previous sections, nutrient models have played and will continue to play a central role in the quantitative understanding and prediction of lake eutrophication. Predicting nutrient concentrations and the trophic state in lakes by means of modelling is presently done in a considerable number of different ways. This multitude may indeed benefit eutrophication management, as different models can have different advantages; even though it may also be the case that one model or a few models outperform the rest. The Intergovernmental Panel of Climate Change states regarding climate models (IPCC, 2007):

"It continues to be the case that multi-model ensemble simulations generally provide more robust information than runs of any single model".

Nevertheless, models and approaches may improve greatly by means of comparative evaluations (IPCC, 2007; Blenckner, 2008). The quality of modelling approaches should not merely be seen as the extent to which each approach pleases the eyes of the beholder, but evaluation should instead be quantified in terms of user-friendliness (Paper V), applicability (Håkanson, 1999; Paper V), testability (Popper, 1968; Peters, 1991; Paper V), and predictive power (Peters, 1991; Aldenberg et al., 1995; Paper V). Thus, the modelling approach used in the papers of this thesis merits a motivation.

5.1. Comparative Studies and Modelling

One aim with nutrient modelling is to evaluate the ecosystem effects from the nutrient load to it as well as its sensitivity compared to other ecosystems. The sensitivity differs between systems and it is important to study the reasons thereof to understand why lakes respond differently to nutrient inputs. Models based on such comparative studies may be used for a large variety of ecosystem states that fall within the defined range of each model (Blenckner, 2008). If a model is developed for one ecosystem only, which is very common, the range will be substantially smaller and it will be very hard to predict what would happen to the ecosystem if, e.g., the nutrient concentration would change to a completely different level than what has been observed before in the system in question. This is illustrated in Figure 5.
Figure 5. Lake-specific versus general models. If a model is based on one ecosystem, its data range (within which it can be used) will be rather narrow. If the model is instead developed for several systems simultaneously, the range widens.

Moreover, dynamic models contain several calibration constants that need to be estimated in order to match empirical data. For a model that is based on comparative studies, the calibration may be less arbitrary, since it has to fit conditions from several different lakes at the same time. A model that is developed for one lake only may follow empirical data rather closely during a variety of different sets of calibration constant values -- although when applied to a large number of lakes, the number of calibration constant sets may decrease drastically (see Aldenberg et al., 1995; Janse, 2005; Papers IV and V).

5.2. Static Vollenweider-Type Models

As discussed in 2.2., many of the first nutrient load-concentration models were based on comparative studies. They were also static, in the sense that they were based on a statistical regression which calculated typical nutrient concentrations from data on nutrient input, lake hydrology and morphometry (see Bachmann, 1981 for N models and Paper V and references therein for P models). More specifically, apart from nutrient input, they often require the water retention time, which is calculated as lake volume divided by water inflow (in volume per time unit), and the mean depth of the lake. Some models are based on loading per meter of mean depth, and some account for the water retention rate (flushing rate), which is the inverse of the water retention time (Paper V).
An advantage with static models is that they are easy to use for non-specialists and that they give a rough estimation of what the expected nutrient concentration may be after a change in nutrient loading. However, all of the models reviewed in Paper V gave systematically erroneous predictions and their prediction error leaves much to desire. Possibly, if a large number of static models are used, the average prediction may be more certain than the average model. Nevertheless, they predict the eutrophic process and its recovery rather poorly, to some extent because they cannot account for internal nutrient fluxes (fluxes F_P3-F_P6 in Figure 3 and F_N3-F_N6 in Figure 4; see Paper V).

5.3. Dynamic Models

Dynamic nutrient and eutrophication models differ from static models in the sense that the former describe changes over time while the latter expresses a snapshot of generalised conditions within a certain time-span. Thus, the two approaches suit different purposes to some extent. Which type of model should be preferred is a question of predictive power (Peters, 1991; Aldenberg et al., 1995). If the predictive power is equal, dynamic modelling should be used since it gives a deeper insight into processes which substantially affect the modelled goal variable (Håkanson, 1999).

A dynamic nutrient model basically describes the dynamic mass-balance of one or several nutrients. The concept of mass-balance in aquatic ecosystems is that the change of the mass of a substance in a water body over time is the sum of all substance fluxes to and from the water body. If the volume of the water body is known, it is also possible to calculate changes in substance concentrations (see Figure 6). Since most nutrient fluxes are not constant but vary over time, simulating the mass balance dynamically may predict changes in nutrient concentrations more accurately.

![Figure 6. A dynamic mass-balance for an aquatic ecosystem.](image-url)
5.4. The LakeMab Model

The LakeMab model for TP was first presented and motivated in Håkanson and Boulion (2002) as a TP sub-model in the foodweb model LakeWeb, and as a somewhat simplified variant of the LEEDS model (Håkanson, 1999; Malmaeus and Håkanson, 2004). Both LakeMab and LEEDS were developed along the principles from a lake radiocesium model (Håkanson, 1999), whose generalised flux algorithms could be quantitatively determined as a consequence of the disastrous Chernobyl accident in 1986 which, rather ironically, also made it possible to trace the detailed flux pattern of dissolved and particulate radioactive matter in lakes. A comprehensive description of LakeMab is provided in Håkanson and Boulion (2002) and in Paper IV.

5.4.1. Model Domain and Input Variables

The model domain (conditions for which it has been tested) of LakeMab stretches rather widely (see Paper IV) with respect to latitude (28.6-68.5°N), lake area (0.014-3,555 km²), maximum depth (4.5-449 m), mean depth (1.2-177 m), annual precipitation (600-1,900 mm/year), drainage area (0.11-44,200 km²), altitude (11-850 m.a.s.l.), and empirical TP-concentrations in the water column (4-1,100 µg/l).

Table 1 in Paper IV gives all the necessary driving variables for LakeMab. Some nutrient models (Romero et al., 2004; Pers, 2005; Hu et al., 2006 and references therein) are partly driven by weather data such as wind speed, wind direction, or cloud coverage, which cannot be predicted for longer periods in advance than a few days (Barbounis et al., 2006). However, eutrophication management requires predictive power that covers an annual or multi-annual time-frame (Håkanson, 1999). Therefore, none of the driving variables for LakeMab include weather data. Instead, driving variables that can change over time (the monthly TP input and the monthly water flux) can be predicted from changes in climate, waste treatment and land use. Similarly, daily riverine nutrient loading data that were required for running two reviewed models by Dahl and Pers (2004) were found to be inaccessible. Driving variables for LakeMab are instead readily available from lake monitoring programs and standard maps (Papers IV-V).

5.4.2. Output Variables and Scales

Table 5 in Paper IV lists all output variables, some of which may be used to predict Chl and Secchi depth, while others may be used to determine which TP fluxes dominate in the lake and how a decrease in one or several of the fluxes can affect the water quality. There are four state variables in LakeMab; TP in surface waters, TP in bottom waters, TP in erosion and transport bottom sediments and TP in accumulation bottom sediments. Wa-
ters and sediments are functionally separated by the theoretical wave base (Håkanson et al., 2004; see also 4.1.), which also expresses the average vertical position of the thermocline (the boundary layer between warm and cold water) during thermal stratification. All fluxes in Figure 3 are represented in the model. $F_{P1}$ is an obligatory driving variable, $F_{P8}$ is given as an average default value while the rest of the fluxes are dynamically modelled and produced as output data (see Table 5 in Paper IV).

LakeMab is normally run on a monthly time-scale, and on a lake-wide spatial scale with one surface water and one bottom water compartment, which provides predictions that can be compared with reliable empirical mean values (Papers IV and V). If necessary, the time-step in LakeMab can be decreased to weeks (Paper II) or less. Likewise, large lakes may be represented by an increased number of state variable compartments in LakeMab if there is a strong areal TP concentration gradient.

A delicate problem concerning scales and output variables is that the latter should be possible to compare with reliable empirical data, in line with Popper's first scientific criterion as listed in 3.2. Since empirical data are highly variable in nature (Blenckner, 2008) and since the sampling and measurements add even more uncertainty to the data, mean or median values are associated with much lower uncertainties (Håkanson and Peters, 1995).

According to Håkanson and Peters (1995), the coefficient of variation of TP is about 0.35 on both an annual and a monthly scale, which means that about 50 samples are necessary to calculate a mean value with an error of 10%. This implies that it must be feasible to analyse a number of samples that are in the magnitude of 50 for each of the predicted variables for each time-step.

Collecting and analysing 50 samples of dissolved, particulate and total P per month is indeed possible (Paper III), although 50 samples per week is much more tedious. The same line of reasoning could apply to the relative distribution of erosion, transport and accumulation bottoms, and to sedimentation, resuspension and other internal TP fluxes (Håkanson and Jansson, 1983).

However, aiming at much smaller time steps than one month and a higher spatial resolution, such as in the modelling works by Pers (2005) or Hu et al. (2006), may not be feasible with respect to collecting empirical data for comparison with model predictions. Thus, the time step in LakeMab should preferably remain at more than one week in future modelling studies.

5.4.3. Calibration Strategy

Instead of having parameters that have to be calibrated to lake-specific values which may make the model structure irrefutable (see 3.2), LakeMab has a set of model constants which have been calibrated to suit a large number of lakes. These constants must not be changed when applying the model to a
new lake within the model domain. The only parameters which may be changed are the obligatory driving variables (see 5.4.1.). A similar approach is promoted and used for the model PCLake by Janse (2005; see also Paper V). The gas model in Paper I was not calibrated at all, but instead, equations and empirical values for gas fluxes from the literature were introduced to a model structure that was based on LakeMab (see Paper I for a full description).

Statistical optimisation of model constants or other calibration parameters is also used by some modellers, by means of, e.g., Bayesian methods (Janse, 2005) or GLUE (Arhonditsis et al., 2008). If general dynamic models based on statistical optimisation should in the future prove to yield systematically superior cross-systems predictions, such optimisation may also have to be applied to LakeMab.
6. Main findings

The main findings in this thesis are as follows:

- \( \text{N}_2 \) in Lake Erken and in other eutrophicated lakes appears to be available in great excess of what is needed for \( \text{N}_2 \) fixation (Paper I).
- Eutrophication models which simulate the \( \text{N} \) cycle in lakes do probably not need to take the \( \text{N}_2 \) concentration into account. More research on \( \text{N}_2 \) concentrations is not urgently needed for improving our quantitative understanding of lake eutrophication (Paper I).
- \( \text{Ca} \) increases the sedimentation of particulate nutrients and therefore affects the TP-Chl and the TP-Sec relationships (Paper II). However, \( \text{Ca} \) did not affect the ratio of particulate to total nutrient concentrations when a large set of lakes was studied. The impact of \( \text{Ca} \) on sedimentation is probably best described by a moderator on the sedimentation algorithm than on the ratio of particulate to total nutrient concentrations (Paper III).
- Particulate concentrations of \( \text{N} \) and organic \( \text{C} \) can be predicted from TP concentrations with high certainty. Particulate \( \text{P} \) generally constitutes 60\% of TP. These findings may be used to improve sedimentation algorithms in dynamic models (Paper III).
- By clearly defining boundary conditions within algorithms for calculating mixing, burial, diffusion, resuspension and sedimentation of \( \text{P} \) in lakes, the general, dynamic load-concentration TP model LakeMab has been improved to better describe conditions in a set of lakes with a wide range of geographical, morphometric and chemical characteristics (Paper IV).
- General dynamic \( \text{P} \) models may be run using data from more or less the same types of empirical field studies compared to what is needed to run static \( \text{P} \) models. Dynamic models are comparatively complex, but can deliver predictions of important internal fluxes, of nutrient fractions, and of nutrient concentrations in sediments and in various parts of the water column. Moreover, they can simulate the eutrophication process and its reversal by means of quantifying changes in internal and external loading, whereas static models require stationary conditions (Papers IV-V).
- LakeMab has a typical prediction error of 17\%, which is much lower than the prediction error of static \( \text{P} \) models whose errors cannot be expected to be below 30\% (Paper V).
7. Concluding Remarks

The successful recovery from eutrophication that many lakes have gone through during recent decades can partly be attributed to predictive nutrient models and to regressions between nutrient concentrations and trophic state indicators such as Chl and Secchi depth. Predictive models have become very useful in lake management because they are the only means by which expected effects from restoration action can be quantitatively assessed.

The latest generation of predictive eutrophication models can answer questions like: (1) what will the trophic state (as measured by, e.g., algal bloom intensity) be like if we decrease the nutrient loading with X kilograms per year, (2) what effects can be expected from alternative strategies such as sediment removal, sediment covering, liming, aeration of bottom waters, or manipulation of the foodweb, (3) what actions are required to reach a significantly different, or a pre-industrial, environmental state, (4) to which extent can different lakes respond differently to the same type of action, (5) what are the most important nutrient fluxes regulating algal productivity in a certain lake (6) how long will it take before the new conditions will occur after nutrient abatement and (7) what is the uncertainty in these predictions (Håkanson and Boulion, 2002).

The approach used in the general, dynamic mass-balance model LakeMab has been discussed in this thesis, and it is probably necessary to continue to use easily accessible driving variables that are also reliable for predicting future nutrient concentrations and trophic states. Furthermore, an ecosystem-wide spatial scale and a time scale of more than a week should also be preferable, since that allows for comparing predictions of nutrient fluxes and concentrations with empirical data that have a reasonably low uncertainty.

TP is of great concern in eutrophication modelling, since P is generally regarded as the key regulating nutrient for algal production in most lakes. This thesis has demonstrated that LakeMab for TP can be applied to lakes of very different types without any tuning procedures but instead using relatively easily accessible driving variables. A clear decrease in prediction error has been demonstrated as compared to older, static P models (an error decrease from >30% to about 17%). The future development of the TP model largely depends on access to reliable, regularly measured data from long time series. Expanding the model domain to tropic climates could be seen as top priority in future model development works, whereas the second priority
may be put on testing the model against additional lake data from the present model domain.

TN models may also be useful since N may control algal production in cold, remote lakes and shallow, hypertrophic lakes, and since low N concentrations in relation to P can give a competitive advantage over other algae to cyanobacteria which often form nuisance blooms that may be toxic. Some of the preparation work for constructing a LakeMab model for TN is also included in this thesis. It would be desirable to fully develop and test such a model in the future.

However, the best potential for using the work presented in this thesis in future studies is probably to apply the TP model when resolving current and urgent issues related to lake eutrophication. How lakes will respond to climate change has been investigated with models similar to LakeMab, and the need for such research may remain or increase in the future (Blenckner, 2008). LakeMab may also be very useful for determining which TP loading reductions to various lakes are needed for achieving the intended water quality prescribed by legal documents such as the European Water Framework Directive (Blenckner, 2008). Thus, the future seems to shine bright for general, dynamic nutrient models and for those people who are able to use such models properly to quantify possible causes of lake eutrophication and to predict its extent and effects.
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A final source of inspiration has been the relentless but cheerful motto of my late grandmother, the adventurous writer Christina Söderling-Brydolf:

"Allt går, och det som inte går, det går det också".

A rough translation from Swedish is "Everything works out, and what does not work out will still work out".
Många av världens sjöar har utsatts för ökad närsaltsbelastning från mänskliga källor såsom avloppsutsläpp och avrinning från gödslade jordbruksområden. Detta har lett till övergödning, som yttrar sig i intensifierade algbloominator, grumligt vatten, sjöbottnar med syrebrist, samt förändringar i betydande delar av näringsväven. Många av dessa sjöar har dock återhämtat sig, på grund av förbättrad reningsteknik och förbättrad kvantitativ vetenskaplig förståelse av övergödningen och dess orsaker. Generella, prediktiva (prognosticerande, förutsägande) modeller har spelat en avgörande roll i den senare utvecklingen, eftersom de har gjort det möjligt att kvantitativt uppskatta förväntade förändringar i ekosystemet från olika planerade åtgärder mot övergödning.

Denna avhandling har författats med målsättningen att förbättra giltighetsintervall och prediktionskraften hos en generell, dynamisk (tidsberoende) totalfosförmodell (LakeMab) och att skapa förutsättningar för att konstruera en liknande modell för totalkväve. Bland avhandlingens slutsatser återfinns att vattenupplöst kvävgas förmodligen alltid finns i överskott för kvävexifering och för kvävemodellering i övergödningssammanhang. Två artiklar har berett väg för att förbättra närsaltsmodellering i kalkrika sjöar där partikelsedimenteringen är särskilt intensiv. Statiska modeller för att förutsäga halten av partikelbundet fosfor, kväve och organiskt kol har tagits fram och kan infogas i sedimentationsalgoritmer till dynamiska närsaltsmodeller. Randvillkor för olika flödesalgoritmer har gjort det möjligt att utöka giltighetsintervallet betydligt för LakeMab med avseende på totalfosfor. Den typiska osäkerheten i värden på totalfosforkoncentration är 17% när de förutsägs med LakeMab, medan motsvarande osäkerhet i prognoser från äldre, statiska modeller är omkring dubbelt så hög.

LakeMab kan användas till att hantera praktiska problem, som att förutsäga klimatdriven övergödning, samt att dra upp operationella riktlinjer för att uppnå god vattenkvalitet, exempelvis enligt föreskrifterna i den europeiska unionens vattendirektiv.
References

Åberg, B., and Rodhe, W., 1942. On the environmental factors in some Southern Swedish lakes. Almqvists & Wiksells, Uppsala, 256 p (in German).


Neményi, P. F., 1975. The main concepts and ideas of fluid dynamics in their historical development. Archive for History of Exact Sciences, 2: 52-86.


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