

waterloopkundig laboratorium  
delft hydraulics laboratory

BEGEHANDELT

mathematical simulation of algae blooms  
by the model BLOOM II

report on investigations

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R 1310-7

July 1982

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## GENERAL REMARKS

This report describes the phytoplankton model BLOOM II, which is an extended and modified freshwater version of the Algae Bloom Model developed by the Rand Corporation for the Oosterschelde sea estuary. The model computes the maximum potential biomass consistent with a number of environmental conditions.

This research is part of a multidisciplinary project called Water BASIn Models (WABASIM), which is joint research project of the Environmental Division of the Delta Department and the Environmental Hydraulics Branch of the Delft Hydraulics Laboratory. Several members of the Rand Corporation, in particular J. H. Bigelow, have also contributed to this project. Other mathematical models developed for WABASIM concern water chemistry (CHARON) and bottom biochemistry (SEDMOD).

The measurements, which are necessary to develop these models, have been collected in four separate bodies of water in the drinking water reservoir 'Grote Rug' by the National Institute for Drinking water supply (RID) and the Environmental Division.

The present report differs considerably from the draft which was published in January 1981. In particular Chapters 4 and 5 have been completely rewritten in reaction to the comments we received. Also the number of illustrations is extended. Finally some new developments are briefly included, notably on the coupling between the models CHARON and BLOOM II, which was established after publication of the draft report.

Outside the WABASIM (R1310) project, the model BLOOM II was also applied in several other projects: the Policy Analysis for the Water Management of the Netherlands (PAWN; R1230); a study on the impacts of management measures in Lake IJssel (R1552); a study on the impacts of management measures in a Dutch polder area called Rijnland (R1651).

BLOOM II was developed by F. J. Los of the Delft Hydraulic Laboratory, who has also written this report.

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## SUMMARY

### S.1 PROBLEM DESCRIPTION

Man's activities have for a long time affected the environmental conditions on earth but never on such a global scale as witnessed during the last one or two centuries. Since then the amounts of various substances, which are released into the environment, have increased dramatically. This is partly because the human population has grown more or less exponentially, but also because industrial and agricultural production per capita grew to unprecedented levels.

Many of these substances are seriously toxic. But other chemicals, which are on the contrary beneficial to certain organisms, are also released in enormous quantities. Among these are several compounds of the elements nitrogen and phosphorus which are required by species of phytoplankton, among others. As a result the concentrations of these plants have increased up to a level where they are considered a nuisance. This process, which is called eutrophication, is accompanied by several objectionable symptoms: it gives the water a green, turbid appearance; it can cause bad odours; it may harm other organisms because the minimum daily oxygen level can become extremely low during the night due to phytoplankton respiration; it can even cause the water to become completely deprived of oxygen (anaerobic) when a bloom declines rapidly, since the biological degradation processes consume large amounts of oxygen; it may cause clogging of filters in water transportation systems.

In the Netherlands the situation is worse than in many other countries because (1) it is densely populated, (2) it receives a major part of its water from the polluted and nutrient loaded river Rhine and (3) most of its lakes are shallow. Hence it was decided that eutrophication would be the first major topic of the Water BASIn Models (WABASIM) joint research project of the Environmental Division of the Delta Department and the Environmental Hydraulics Branch of the Delft Hydraulics Laboratory. This report describes one of the results of this study: the phytoplankton model BLOOM II. Other models concern water chemistry (CHARON) and bottom biochemistry (SEDMOD).

The measurements, which are necessary to develop these models, have been collected in four separate bodies of water in the drinking water reservoir 'Grote Rug' by the National Institute for Drinking water supply (RID) and the Environmental Division.

### S.2 PURPOSE AND APPROACH

Biologically speaking, phytoplankters are relatively primitive plantlike organisms. They require considerable amounts of nitrogen, phosphorus, solar energy and sometimes silicon to become a nuisance. In theory each of these factors could become limiting, but the question is where and when. Also the physiological data indicate that species of phytoplankton differ greatly in nutrient requirements, efficiency of solar energy fixation (photosynthesis) and (potential) net growth rates.

To understand this complexity and predict the impacts of changing circumstances, a modified and extended version (BLOOM II) was developed from Rand's Algae Bloom Model, which was applied to the Oosterschelde sea estuary by Bigelow et al [1977]. Its purpose is to compute the maximum total biomass concentration of several phytoplankton species at equilibrium in a certain time-period under a given set of environmental conditions. The maximum biomass, species composition, and limiting factors are computed by an optimization technique called Linear Programming (LP). BLOOM II calculates maximum rather than actual biomasses for the following reasons:

1. The largest blooms are a manager's main interest.
2. Otherwise more physiological knowledge would be required.
3. It is assumed that those species, which can produce most offspring under the prevailing conditions will ultimately outcompete the others.

To compute values for the environmental constraints, the model needs information on the concentrations of total available nutrients, temperature, the influx of solar radiation and certain lake-specific characteristics (depth and turbidity). These conditions can all be determined directly or indirectly from measurements and are sufficient for the model's calibration and validation.

Under many conditions, phytoplankton species can achieve high net growth rates enabling them to double their biomass several times a week, sometimes even a day. Thus the model assumes steady states for both phytoplankton biomass and nutrient recycling with a nominal time-step of one week. In BLOOM II, therefore, succeeding time-steps are completely independent, although slowly changing environmental conditions tend to give the model's output a smooth appearance. Besides these nominal options, BLOOM II has additional options to:

1. Increase its nominal time-step during the entire year or some parts of it.
2. Solve the equations for nutrient recycling dynamically, maintaining the steady state for phytoplankton [Sec. 3.6].
3. Constrain species, which were not present at the previous time-step by a larger extinction value than species, which were already in the bloom [Sec. 6.2.3].
4. Include constraints for the maximum growth rates of individual species during one time-step [Sec. 6.2.4].

In addition to the abiotic conditions, zooplankton biomasses may be provided to the model to compute losses due to grazing. No attempt was made, however, to actually compute zooplankton concentrations with the model because 80 percent of the computed blooms in the Grote Rug cases were dominated by presumably unedible species such as blue-green algae. In terms of biomass the dominance of these unedible species is even more overwhelming. Modelling zooplankton might be reconsidered if edible species increased significantly under new, simulated conditions.

## S.3 STRUCTURE OF BLOOM II

### S.3.1 Requirement for solar energy

All plants require raw materials (nutrients) and energy in order to grow. The sun provides the energy, at a rate per square meter of surface area that depends upon latitude, cloud cover, time of day, and season of year. The energy must be shared among all the phytoplankton cells floating in the water column below that square meter of surface area, with an allowance set aside for reflection from the water surface and absorption by the bulk water and its contents other than phytoplankton (the background extinction). The more phytoplankton there is, the less solar energy is available for each, until the energy per phytoplankton cell is too small to sustain growth. At that point, solar energy becomes limiting to the phytoplankton biomass.

### S.3.2 Nutrient requirements

Plants also require about a dozen chemical elements for a normal development, among which are nitrogen, phosphorus, sulphur, calcium, potassium, magnesium, and iron. The requirements for each element vary widely and, particularly in terrestrial ecosystems, elements which are only required in small amounts (trace elements) are frequently limiting. Because aquatic systems are much more homogeneous, and usually receive water from sources which are heavily loaded with many chemical elements, it is rather unlikely that trace elements will limit phytoplankton in eutrophic waters, although the possibility cannot be ruled out completely. Thus we have not included trace elements as potential phytoplankton biomass limiting factors.

Four macronutrients are often reported as limiting factors: carbon, nitrogen, phosphorus, and silicon, of which the latter is essential to only one phytoplankton group, diatoms. These species use silicon to build strong skeletons surrounding the cell walls. As calculation with the nutrient model CHARON has shown that depletion of carbon is rather unlikely under typical Dutch conditions, it is not included as a limiting factor in BLOOM II. This leaves the three major nutrients, nitrogen, phosphorus, and silicon, which along with solar energy are considered in the model to be potential biomass limiting factors for phytoplankton.

Nitrogen and phosphorus are vital to all phytoplankton species. Nitrogen is an essential component of cell proteins such as enzymes, for genetic material, and of light-sensitive pigments like chlorophyll-a, which are used for fixation of solar energy. Because of its importance to many vital physiological processes, nitrogen deficiencies cannot be tolerated for long.

Phosphorus is an important component of proteins, nucleic acids, and lipids (e.g., in the cell walls). Coupling and uncoupling of ortho-phosphate groups to certain sugars are the main reactions by which energy is stored or released in the cell. Phytoplankton cells are usually less sensitive to phosphorus than to nitrogen deficien-

cies, hence survival at extremely low internal phosphorus concentrations is often possible for some time.

Nutrients appear in many forms in a phytoplankter's environment, of which usually only a fraction can be assimilated. An even smaller number of forms may be used directly in metabolic processes. But this does not imply that any nutrient is limiting as soon as the metabolically preferred forms are depleted. Chemical and bacterial processes in the water may convert one form of a nutrient into another, phytoplankton species may sometimes shift their uptake preference between different forms, and phytoplankton cells can often internally convert one form of a nutrient into another by enzyme-catalyzed reactions. For example  $\text{NH}_4^+$  is often preferred as nitrogen source, but many species can internally convert  $\text{NO}_3^-$ ,  $\text{NO}_2^-$ , or various organic nitrogen compounds to  $\text{NH}_4^+$ , and some species of blue-green algae can even use atmospheric  $\text{N}_2$ . Those fractions of a nutrient which may be used directly or after some rapid conversion process will be called available, in contrast to the unavailable fractions, which either cannot be used or can only be used after some slow conversion process.

### 5.3.3 Using the model for predictions

To estimate the impacts of various management measures on the potential bloom maxima, we should be able to predict effects on the available nutrients and solar energy. This is not so difficult for solar energy as temperature, influx of solar radiation and depth are all well known. Only the prediction of the future turbidity provides some difficulties.

Calculating future nutrient concentrations requires in fact a transportation model to relate the inflows of a lake to discharges in rivers and canals. Chemical and biological processes strongly interact in the lake, determining the fate of the inflowing nutrients. How much becomes available to phytoplankton? What happens with the rest? How much nutrients are transported to the bottom? How much nutrients are released by the bottom? Answering all of these questions in detail is too great a task for the phytoplankton model BLOOM II. For this we need the integrated version of the the current models CHARON and BLOOM II, which is now available at the Delft Hydraulics Laboratory.

## 5.4 RESULTS OF THE MODEL

BLOOM II has been calibrated for one of the Grote Rug basins (Ring 2, 1977). Data of other cases (Ring 2, 1976; Ring 3, 1976) have, however, been used to some extent to establish coefficient values e.g. by linear regression between two sets of measured variables. All other results in this report, both for Grote Rug and natural lakes, can be considered as validations of the model.

Fourteen out of a total of about twenty validation cases in different projects are included in this report (nine for Grote Rug and five for natural lakes). The occurrence and magnitude of observed blooms is well reproduced by the model, although it has a clear tendency to compute higher than observed levels particularly in those periods when the observed biomass levels are below the standard of

an objectionable bloom. This, however, has little practical significance from a manager's point of view.

Because factors not included in the model may sometimes be limiting, or because the growth history of the phytoplankton has resulted in another combination of species being present than that computed by the model, the computations will tend to overstate the risk of large blooms. Also notice that the agreement between observed and computed biomasses is consistently better in the natural lakes than in Grote Rug. This may be due to the irregular water intake and dosing with iron and aluminum salts to remove phosphates in the latter. Besides overprediction, underprediction is also possible due to uncertainties in some model parameters, notably the mortality rate of phytoplankton.

Limiting factors to the blooms are highly site and time specific. For instance phosphorus is the main limiting factor in many Grote Rug cases due to the addition of iron and aluminum salts. But nitrogen is most important in Lake Veluwe and energy is the sole important limiting factor in Lake IJssel. These results indicate that indeed several factors are involved in eutrophication and not just phosphorus as suggested in some publications. Hence studies on the impacts of management tactics looking at only one factor are prone to give erroneous results. Many computed blooms are limited by several factors at the same time. As a consequence of the mathematical structure of BLOOM II, these blooms consist of as many species as there are limiting constraints.

The time and site specific differences in limiting factors also result in substantially different species compositions of computed blooms for various cases. Both in Grote Rug, where detailed observations are available from the RID, and in the natural lakes species dominance is often computed in remarkable agreement with the observations. Usually the dominant group of species is depicted correctly, often computations are correct at the species level. These results are the more impressive since they were obtained with a fixed set of coefficients which

1. Represents only a subset of all important factors.
2. Is not changed seasonally or regionally.

As for the nominal results, those obtained by a systematic sensitivity analysis of lake-specific and some universal inputs, vary regionally and seasonally. For example perturbations of the nitrogen concentrations have almost no effect in any of the Grote Rug cases, but in Lake Veluwe they change the computed blooms, including the year maximum, more than any other factor.

BLOOM II is rather unique in its ability to consider more than one potential limitation and a relatively large number of species. The impact of perturbing one factor is determined by the entire set of potential limitations and species, and is usually non-linear. In many cases the observed change in total biomass following a perturbation is smaller than perhaps expected, because a shift in limiting factor and/or bloom composition partly compensates the impact of the perturbation.

The model proves to be relatively insensitive to many of its universal inputs. For instance, a 50 percent change in the nominal values of the remineralization rates of the nutrients affects the model's results in a similar way as a 20 percent change in nutrient concentrations, which is small relative to possible measurement errors.

BLOOM II is sensitive, however, to the natural mortality rate constant for which a minimum estimate is normally used. With a 50

percent increase, the computed total biomasses are significantly lowered. This improves the model's results when nominally they were too high, but at the same time many computed peak levels are reduced below the observations. Unlike most other factors, perturbations of the mortality rates produce essentially similar results in all cases.

The species and group specific coefficients of the calibrated model were not varied, because (1) the number of combinations is too large (there are about one hundred coefficients), and (2) the total biomass is little affected. The reason is that the existing variations in the nominal set of coefficients already covers most of the values found in the literature. However, the bloom compositions are strongly determined by the values of these coefficients.

## S.5 RECOMMENDATIONS FOR FURTHER RESEARCH

The development of BLOOM II was favored by the availability of an exceptionally large, high quality database from Grote Rug. Nevertheless the model could be further improved if we had more, better or new data on:

- Mortality rate constants.
- Buoyancy control.
- Biomass to chlorophyll<sup>1</sup> ratios.
- The relations between several factors determining the net growth rates<sup>2</sup> (the maximum gross production, and respiration rate constants; the production efficiency as a function of the light intensity; temperature; day length).
- The attenuation of light in the water by other than dead or live phytoplankton particles (the background extinction).

Integration of BLOOM II with the nutrient model CHARON, which has now been accomplished, improves the applicability of both models. The present version of BLOOM II is restricted to homogeneous bodies of water. However, one may want to apply the model to hydraulically complex systems with for example differences in depth or a residence time of only a few weeks.

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<sup>1</sup> The only commonly measured phytoplankton indicator.

<sup>2</sup> Currently investigated at the Microbiological Department of the Amsterdam University.

## PREFACE

### P.1 EUTROPHICATION PROCESS

Eutrophication is generally recognized as one of the world's major pollution problems, influencing ecosystems in many places. Its importance is well illustrated by Lund [1972], quoting Ridley, who estimated the number of publications on the subject over 2000. No doubt, this number has increased markedly since 1972. Recent publications on eutrophication for example are by Reynolds [1979] and Barica and Mur [1980].

It may be surprising though, that few definitions on eutrophication cover all aspects. Often they are limited to:

- Phytoplankton only, not to weeds and other plants.
- One or two major nutrients, neglecting others and energy requirements.
- Alterations of the ecosystems, directly related to human activities.

A more detailed description is given by Parma [1980], who's broad definition we will follow here:

'Eutrophication is the process in water, at which those factors become optimal, that promote autotrophic growth.'

Although the modeling activities reported here are limited to phytoplankton, they do consider constraining influences of nutrients and energy, without distinguishing between human and natural causes of eutrophication:

Because of its complexity, the symptoms of eutrophication vary between places and in time. Also, the severity of the problems depends on the function of a particular body of water: drinking water reservoirs, fish ponds, recreational lakes, or lakes in nature reserves have such different functions, that what is acceptable or even desirable in one type of lake, is objectionable in another.

Some rather common symptoms of eutrophication are:

1. Bad appearance of the water (color: green 'soup', visibility: reduced to a few decimeters).
2. Bad odours of for instance sulphides, if a bloom dies off suddenly (a collapse).
3. Large variations in the diurnal concentration of dissolved oxygen because during a bloom, oxygen consumption by respiration of phytoplankton continues during the night, while oxygen production by primary production is confined to the day time.
4. A major risk of anaerobic conditions following a collapse, possibly for several days, leading to massive killings of organisms in the upper levels of the foodchain such as fishes.
5. A low diversity of the ecosystem (regardless which definition of diversity is applied).
6. Clogging of filters at the intakes of water for industrial or drinking water purposes.

7. Toxic effects on other organism, although literature information on this subject is rather scarce.

These and other symptoms are considered objectionable for many reasons, although by itself eutrophication is no direct threat to public health as pollution of waters with pesticides, PCB's, or heavy metals. Nevertheless, major alterations of the world's ecosystems usually have serious consequences for any kind of life on earth and in this sense concern about eutrophication is fully justified.

## P.2 DUTCH SITUATION

Eutrophication problems in the Netherlands are much more serious than in many other countries for several reasons:

- The country is (and in recent times has always been) densely populated; man's influence is extremely large.
- A relatively large part of the country is covered by water (rivers, canals, natural- and man-made lakes, ditches, pits).
- Most of these waters are very shallow (in the order of 1 to a few meters) and not stratified in summer. Thus no nutrients are removed to the hypolimnion, where they become temporarily unavailable for growth of primary producers. Quite the opposite, Dutch bottoms may well serve as an excellent source for nutrients.
- Concentrations of nutrients in many waters are to a large extent determined by the loadings from rivers, of which the most important (the river Rhine) happens to be heavily loaded with nutrients.
- Pollution of the Rhine is an international problem, because it is a border crossing river. Hence there is a limit to the attainable reductions of nutrients that may be achieved by management tactics in the Netherlands. Further reductions are only possible in cooperation with other countries.

## P.3 THE GROTE RUG PROJECT

One of the most important investigations into the causes of eutrophication and possible measures to reverse the process, is the so-called 'Grote Rug' project, in which the Delta Department of the Rijkswaterstaat (ministry of Public Works) and the National Institute for Drinking water supply (RID) cooperate.

Grote Rug is a storage drinking water reservoir near the city of Dordrecht fed by water from the Wantij (in fact the river Rhine). There are three large enclosures in the basin (called Rings) of butyl rubber, with a diameter of 46 m and the same water regime as the main basin. Since their installation in 1975, extensive measurements are made weekly or even daily of biological and chemical variables in bulk water and bottom including concentrations of nutrients, chlorophyll, wet weights of phyto- and zooplankton, solar intensities, extinction coefficients, primary production by the  $^{14}\text{C}$  method.

The project was initiated to compare the results of two in-water treatments of one nutrient, namely phosphorus; Ring 1 (and the main basin) are dosed with  $Fe^{2+}$ , Ring 2 with  $Al^{3+}$  salts and Ring 3 is a control, receiving Rhine water without any treatment. It was expected that phosphorus concentrations and hence phytoplankton levels would be lowest in Ring 2, because of the low equilibrium constant of  $AlPO_4$ ; phosphorus concentrations would be low in Ring 1 too, and Ring 3 of course was likely to suffer heavily from phytoplankton blooms.

The part of the prediction concerning the phosphate concentrations was confirmed: generally, Ring 2 has the lowest concentrations of both ortho- and total P, followed by Ring 1, while the average concentrations in Ring 3 are much higher than in the other two Rings. Unfortunately, the implied one to one relationship between phosphorus and phytoplankton biomass was incorrect, as Ring 2 has had by far the largest phytoplankton blooms over the period 1975 through 1978, followed at a long distance by Ring 3 (only a major bloom in 1976) and Ring 1, with comparatively low phytoplankton concentrations for all years of observations.

In spite of these results, perhaps even thanks to these results, the measurement program was improved and extended over the years in order to obtain enough field data to generate and test hypotheses about the main processes in the rings. As a result, the present databank for Grote Rug is among the best existing in the world [Di Toro; pers. comm.]; hence it is very well suited for developing mathematical models.

Most results of the studies have only been published in annual reports, but some are more generally available; see for example [Bannink et al., 1980].

#### P.4 THE WABASIM PROJECT

In February 1953 extensive territories in the South-Western part of the Netherlands were inundated, when an exceptionally high tide coincided with a severe North-Western storm, lasting for several days. Especially the province of Zeeland suffered heavily and the number of casualties rose to over 1800. To improve the security of the country and prevent a repetition of the 1953 events, the Delta act was passed through Parliament: dikes would be rebuilt at a higher level than before the disaster and most of the present estuaries would be closed off from the sea by large dikes, connecting the former islands.

Thus the ecological conditions in many of the Delta waters have changed or will change dramatically in the years to come. To optimize the functions of the individual basins, the Environmental Division of the Delta Department initiated the Water BASIn Models (WABASIM) project. The word 'model' already indicates, that mathematical models are regarded as an important tool to accomplish this general optimization purpose.

The project is intended to cover several years, but first because many important results are expected before its completion and second to have a project with a well defined objective as a sort of training project, the purpose was divided into a long- and a short term objective:

'The long term objective of the project is to produce the necessary understanding of aquatic ecosystems for the derivation of adequate

guidelines for environmental management, in order to realize optimally the functions assigned to each water basin.'

'The short term objective is to develop a semi-stagnant fresh water model of the model reservoirs in the 'Grote Rug' and of this storage reservoir itself.'

WABASIM is organized as a multidisciplinary co-project of the Environmental Division of the Delta Department and the Environmental Hydraulics Branch of the Delft Hydraulics Laboratory, with technical assistance of the Rand Corporation in the U.S.A., responsible for the POLicy ANalysis of the Qosterschelde (POLANO), of which WABASIM is a partial follow up.

Because chemical and biological phenomena are involved in eutrophication and both are difficult to model, two different models have been developed to accomplish the short term objective. Chemical data, either from measurements or the chemical model CHARON have been used as boundary conditions, designing and calibrating the phytoplankton model. For CHARON a similar approach was adopted, by which observed phytoplankton levels have been used in the model. To make optimal use of the predictive capabilities of both models, an integrated version has been developed and applied during several projects. This report, however, presents the results on only one of the two: the phytoplankton model BLOOM II, although some remarks on the integrated model will be made.

## 1. THE PHYTOPLANKTON MODEL BLOOM II

### 1.1 INTRODUCTION

One of the models developed during POLANO is the Algae Bloom Model, reported in volume IV [Bigelow et al., 1977]. This model was applied to a salt water basin (the Oosterschelde), not some eutrophic fresh water lake. Data from the basin were in short supply and moreover the available time for literature studies was limited.

The WABASIM model BLOOM II has kept part of the structure of its predecessor such as the objective and some of the basic assumptions, but many modifications and extensions are discussed in this report. To understand the BLOOM II model, it is not strictly necessary to know the POLANO report, because the complete model formulation will be presented here.

### 1.2 APPROACH: A MANAGEMENT MODEL

The general purpose of the WABASIM project, as pointed out in Sec. P.4, is to help managing aquatic ecosystems. Various types of models could be constructed for such a general purpose: scientific or applied, deterministic or stochastic (empirical) models etc. It was, however, early decided during the project that the best way to predict future situations would be by deterministic models. Thus the WABASIM models such as BLOOM II can be described as applied, deterministic, management oriented models, that is they should inform a manager, what kind of system responses he might expect under specific conditions.

Many processes involved in eutrophication proceed slowly: it takes many years before a large body of water becomes eutrophic and it will also take many years to stop and possibly reverse this process. On the other hand, phytoplankton species are usually rapidly growing: one or two divisions per day are no exception. Thus BLOOM II has a relatively short computational time-step of one week [Sec. 5.2], but since changes in the eutrophic state of waters occur over much longer periods, the model will not be applied to predict the impact of a change in conditions say next week, but rather what will be the long term effect of these changes over several years.

The performance of a management model should not simply be judged by looking at a prediction vs. observation course of some variables for each time-period, because it depends on its purpose, when a model should be correct anyhow and when this is less important. Thus what may seem to be a large disagreement, could be unimportant to the overall policy conclusion, for instance if the computations indicate that probably no eutrophication problems will occur in a particular water body. However, if the model predicts severe problems during at least a certain period, then any major difference between observations and predictions becomes critical.

Designing management models always involves an estimation of the penalties for making incorrect decisions, for which there are three possibilities:

1. Taking incorrect measures when measures are necessary (false reaction).

2. Taking measures, when they are not necessary (false alarm).
3. Taking no measures when they should have been taken (overlooking an alarm).

Estimating the penalties for these three error types is difficult, because economic, ecological as well as social aspects are involved, which cannot be expressed in comparable units (for instance money). The ultimate decision which errors should be minimized is therefore political.

Models may help the manager to minimize type 1 errors, because the impacts of many combinations of management measures may be analysed. In an ideal case, both type 2 and type 3 errors should be minimal at the same time but generally minimizing type 2 errors, increases the probability of type 3 errors and visa versa. In the case of BLOOM II, it was decided to minimize the number of type 3 errors, i.e. it is better to have some false alarms, than to overlook any true alarms. The model therefore is conservative rather than (over?)optimistic: if it predicts no problems, a major bloom is unlikely, but if it predicts a large bloom, it may not occur in reality.

### 1.3 PURPOSE OF BLOOM II

The phytoplankton model BLOOM II has been designed according to the following objective:

**BLOOM II maximizes the total biomass concentration of several phytoplankton species at equilibrium in a certain time-period given a set of environmental conditions.**

What are the implications of this objective for the model?

1. The method of calculation is linear programming, an optimization technique. Until recently mathematical optimization methods were infrequently used in biological models. A proposal by Patten [1968] was one of the first in the ecological and limnological literature. Recently there is an increasing interest in these methods, however, [Jameson, 1979]. The principle of linear programming (L.P.) is easy to understand and computationally it is much more inexpensive than a comparable differential equation model with a similar number of equations.
2. The model computes the maximum rather than the actual biomass concentrations, because:
  - The largest blooms are a manager's main interest.
  - Otherwise more physiological knowledge would be required.
  - It is assumed that those species, which can produce most offspring under the prevailing conditions will ultimately outcompete the others.

Remember, that like any other equilibrium model, BLOOM II gives no information on the kind of transitions between different periods, thus the way towards equilibrium could well be infeasible.

3. Blooms can be constrained by two kinds of environmental conditions:
  - Nutrients (nitrogen, phosphorus and silicon) for cell structure and metabolism.
  - Energy (complex of interactions between primary production, respiration and various causes of mortality) for maintenance and reproduction.
4. All environmental conditions are specified externally to the model for each time-period. These include meteorological and physical variables, such as the temperature, the influx of solar radiation and the mixing depth. As the model is described here, the concentrations of the total available nutrients are prespecified as well, which is the main difference between BLOOM II and the now existing integrated version of BLOOM II and CHARON.
5. Environmental conditions are specified to the model based upon:
  - Observations (for calibration).
  - Other models (CHARON).
  - Tactics (to investigate impacts of management scenarios).

This report is mainly restricted to the first: observations.

6. Under many conditions, phytoplankton species can achieve high net growth rates enabling them to double their biomass several times a week, sometimes even a day. Thus the model assumes steady states for both phytoplankton biomass and nutrient recycling with a nominal time-step of one week. Normally succeeding time-steps are completely independent, but slowly changing environmental conditions tend to give the model's output a smooth appearance. Besides these nominal options, BLOOM II has additional options to:
  - a. Increase its nominal time-step during the entire year or some parts of it.
  - b. Solve the equations for nutrient recycling dynamically, maintaining the steady state for phytoplankton [Sec. 3.6].
  - c. Constrain species, which were not present at the previous time-step by a larger extinction value than species, which were already in the bloom [Sec. 6.2.3].
  - d. Include constraints for the maximum growth rates of individual species during one time-step [Sec. 6.2.4].
7. Zooplankton concentrations cannot be calculated in the present version of BLOOM II, but may alternatively be specified as an input to the model. This approach has been adopted for two reasons:
  - a. It has not been proved unequivocally that mortality due to grazing by zooplankton is an important source of mortality for phytoplankton species in eutrophic lakes. According to many authors, the most frequently dominating species: the blue-greens, are not grazed at all [Chap. 7].

- b. Modelling zooplankton proves to be difficult; therefore it seems much more appropriate first to calibrate the phytoplankton Sec. of the model with known (observed) zooplankton densities and then decide whether a separate zooplankton module has to be included or not.

#### 1.4 SPECIES IN THE MODEL

Natural blooms often consist of assemblages of different phytoplankton species, sometimes of rather distinct groups of species such as diatoms, green or blue-green algae. However, groups or even species within a group, often have rather distinct characteristics. Therefore many of the adverse impacts of eutrophication depend on the dominant (group of) species. For example a bloom of blue-green algae is usually considered far worse than one which is dominated by for example diatoms or green algae. Thus it makes sense to distinguish between groups.

But particularly within the group of blue-green algae still more details are required, because the impacts of a bloom of, for example, Oscillatoria agardhii are quite distinct from a bloom of Microcystis aeruginosa. If there is a bloom of the latter, the probability of a sudden collapse, hence of anaerobic conditions, seems much greater. Microcystis is also the most important blue-green algal species for which toxic effects have been reported by Gorham [1964] and others. Thus it is a major advantage if a management model includes a moderately large number of species with distinct ecological characteristics.

Many phytoplankton models do consider some 'species', but it should be noted, that these are not really species according to the standards of biological taxonomy. Usually these model units are genera (groups of related species), or worse: major taxonomical divisions. These models therefore do not contain the details, which are vitally important for a eutrophication model.

Many of the species considered in BLOOM II are taxonomical species. Others are more closely related to genera, because (1) some taxonomical species of the same genus are rather homogeneous in their ecological characteristics, (2) available data on species identifications sometimes do not consider smaller units than genera.

Its structure -a steady state model- and its method of calculation -linear programming- enable BLOOM II to handle a relatively large number of ecologically realistic species. Thus the present version of the model runs with ten species, which were selected from an original list of fifteen. These fifteen species seemed most important according to the Dutch literature and the species identifications in Grote Rug by the RID Five species are not included in the model, because (1) either available data demonstrated that some species was inferior to at least one other in all aspects considered by the model, or (2) there were simply not enough reliable input data. As might have been expected, however, lack of data was worse for species of relatively minor importance, which they did not bloom frequently.

All assumptions of Sections 1.3 and 1.4 will be reexamined in later chapters to present details why they were adopted and to evaluate the consequences for the model if they are violated.

## 1.5 BEHAVIOR AND PERFORMANCE

In accordance to its purpose BLOOM II has been set up in a way, that makes overpredictions more likely than underpredictions: it computes maximum equilibria rather than actual biomasses. Thus it is important (1) how often the model overpredicts and (2) by what magnitude. A simple approach would be to compare the outputs of the model to the observed biomass and record how often the former exceeds the latter. However, a 10 percent overprediction has a different significance than a 500 percent overprediction, both of which can occur. Thus recording the frequency of overpredictions, without the magnitude is obviously too simple. In addition, however, an overprediction by no matter how many percent is of no significance to a manager, if the predicted biomass is nonetheless very small.

Therefore the degree of overprediction should always be considered in relation to a biomass standard. If carefully selected, bloom levels are acceptable as long as they remain below the standard. If on the other hand the standard is exceeded, phytoplankton becomes a serious nuisance.

Unfortunately biomass standards are usually expressed in units chlorophyll per volume rather than in dry weight per volume, which is a more reliable indicator for the phytoplankton biomass. The provisional (marginally acceptable) Dutch standard, according to the 'Indikatief Meerjaren Plan' (IMP 80-84), is 100 mg chlorophyll per m<sup>3</sup>. Considering the usual range of conversion factors between chlorophyll and dry weight in Dutch lakes [Sec. 8.1.3], this roughly corresponds to a concentration of 7.5 to 16.5 mg dry weight per l. This is somewhat higher than the value proposed by Morton and Lee [1974]: 6-12 mg dry weight per l. We will, however, accept the IMP chlorophyll standard, but not as a summer average but as a marginally permissible peak value.

Therefore we will use the following definition. Any predicted bloom, which (1) exceeds the provisional chlorophyll standard and (2) exceeds the observed concentration by more than 50% will be considered an overprediction. A 50% difference is still regarded acceptable, because the uncertainty of the dry weight to chlorophyll ratio is at least a factor two. Hence even at a 50% deviation between predicted and observed chlorophyll, the dry weight prediction of the model could still be correct.

As up till now the calibrated BLOOM II model has been verified for over 20 cases, we may reasonably judge how often and by how much it overpredicts:

1. Of all the blooms predicted for a one year calculation, at least one was indeed observed in about two of every three cases.
2. Usually the observed bloom size is more than 50% of the value predicted by the model, hence BLOOM II does not overpredict the size of these blooms.
3. But observed phytoplankton concentrations are often less than 50% of the computed biomass, if in reality no bloom was observed.

Because in addition the species composition calculated by the model is very reasonable so long as it does not overpredict, we concluded that BLOOM II is an important tool to simulate the impacts of management measures on eutrophic ecosystems.

## 2. STRUCTURE OF THE MODEL

### 2.1 LIMITING FACTORS SELECTED FOR THE MODEL

Many factors influence the growth of plants, but according to the classical theory of von Liebig: 'Growth of a plant is dependent on the minimum of foodstuff presented'. At the beginning of the century, Blackman generalized Liebig's idea to include the light intensity and temperature in addition to nutrients. Thus according to these classical theories, the yield of each species will be limited by only one factor at a time.

According to what has become known as the Gaussian principle of competitive exclusion, of all species competing for the same limiting factor, the most efficient should outcompete all the others in well mixed systems such as eutrophic lakes. Thus the number of (dominant) species in the bloom should be equal to the number of limiting factors. It was pointed out by Bigelow et al. [1977], that this one to one correspondence between limiting factors and the number of species also exists in BLOOM II as a consequence of the linear programming technique.

Of course, it is impossible to include all (potential) limiting factors in the model, but those which are infrequently limiting, can be ignored. We must therefore select which factors are most likely to become limiting to phytoplankton blooms. Furthermore we must decide how to incorporate each selected factor into the model.

Text books on aquatic ecology usually consider many factors (Parsons and Takahashi, 1973; Bougis, 1974; Wetzel, 1975), some of which will be briefly discussed in the next sections. We will consider three general categories: physical (including meteorological), chemical and biological factors.

#### 2.1.1 Physical factors

**Geography:** our main concern are lakes and reservoirs in the temperate zones with distinct seasons; probably the same methodology could be used to develop a model version for other geographic regions, but the limiting factors and species included in the model could be quite different.

**Salinity:** eutrophication is most severe in the fresh water environment, but there is no fundamental difference to salt waters. In fact as pointed out in Sec. 1.1, the POLANO algae bloom model was developed for a sea estuary and still many of the inputs to BLOOM II are from a mix of fresh and salt water observations. The two types of environments are clearly distinct in dominating species, however, which is most obvious in the case of blue-green algae, being of little importance in salt waters, but frequently predominating in fresh waters up to the level of mono-cultures.

**Climate:** during the seasons many physical factors change but some of them are particularly important to phytoplankton:

- Temperature generally varies between 0° and 20° to 25° centigrade and as the rates of many biochemical processes

approximately double every 10°, these temperature differences are significant.

- The influx of solar radiation varies by more than a factor 15 between summer and winter and as phytoplankton depends almost completely on sun light for energy supply, these large differences are quite significant.
- The length of the light period (in this report called 'day length') varies by approximately a factor 2 between winter and summer from about 8 hours in winter to over 16 hours in summer. Hence in winter respiration exceeds production for two third of the day.

**Mixing depth:** an exponential decrease of light intensity with depth is usually assumed [Sec. 5.1] and thus any increase or decrease in mixing depth has a profound effect on the available solar energy.

**Background extinction:** each body of water has its own optical properties and the attenuation of light over a certain water column may therefore differ considerably between lakes.

**Buoyancy:** some species, particularly blue-green algae and dinoflagellates have floating devices that may prevent their homogeneous mixing through the water column. Thus they attempt to use the available solar energy more efficiently.

**Thermal stratification:** very important in many of the world's lakes, but practically absent in the eutrophic Dutch lakes to which BLOOM II was applied, because they are too shallow (generally 5 meters or less). As the mixing depth is an input to the model, it can be applied quite easily to different layers of water, given that the usual inputs are provided and assuming no exchange between the layers; however, BLOOM II has not been tested for stratified lakes.

**Residence time:** flushing rates have a profound impact on the biology of reservoirs in terms of available nutrients, turbidity etc. As formulated in the short term objective of WABASIM, BLOOM II has been designed for semi-stagnant reservoirs (residence times in the order of months or more).

### 2.1.2 Chemical factors

**Nutrients:** plants need about a dozen chemical elements for a normal development, among which: nitrogen, phosphorus, sulphur, calcium, potassium, magnesium and iron. Some nutrients which are required in small quantities only, frequently limit plant growth at least in terrestrial ecosystems. There is a vast amount of literature on the subject of these trace elements especially regarding agricultural systems.

A comparison of requirements by phytoplankton and concentrations of trace elements in eutrophic waters, makes it very unlikely for them to be limiting. Typical requirements reported by Gerloff and Fishbeck [1969] are: < 0.06% for calcium, 0.15-0.30% for magnesium and 0.8-2.4% for potassium, all as percentage of dry weight. Typical concentrations in Dutch waters are: 60, 10 and 4.5 mg/l for respectively calcium, magnesium and potassium. As the requirement for potassium is the highest and its typical concentration the low-

est, this is the best candidate to be limiting, but the amount of potassium required by a very large bloom of 40 mg dry weight per litre is still only about 1 mg potassium per litre, taking the highest reported requirement. Compared to an available amount of 4.5 mg/l, there is still an excess of potassium.

There are less data on some of the other trace elements, but as most lakes have residence times shorter than a year and are connected by rivers and canals, overloaded with all kinds of elements as a result of human activities, even a local exhaustion of some element would probably be replenished rather quickly.

Four macro nutrients are often reported as limiting factors: carbon, nitrogen, phosphorus and silicon, of which the latter is a special case, as it is only required by diatoms in a substantial amount. Recently there has been some debate on C as a potential limitation, but we have not incorporated a C limitation in BLOOM II, because calculations with CHARON seem to rule out the possibility of a C limitation in the lakes we have studied. The main reason is that carbon supply from the air to the water is relatively high in Dutch lakes, because as a consequence of their shallowness, they have a relatively high surface to volume ratio. However, deNoyelles et al. [1978] point out that changes in C availability might affect the species composition.

Thus the two nutrients with the greatest overall importance for eutrophic systems are N and P and these two with Si were selected for modeling in BLOOM II.

**Chemical environment:** uptake of nutrients and biochemical processes within the cells are certainly influenced by chemical factors such as pH, but it is difficult to separate direct effects on phytoplankton from indirect effects, although all phytoplankters die at extreme pH values [Moss, 1973].

The influence of pH on the P-cycle may serve as an example. While producing, a phytoplankter withdraws CO<sub>2</sub> from the water, and pH goes up. But a rise in pH usually correlates with an increase of available phosphate and if this nutrient is limiting, growth may continue up to a higher biomass level than without pH increase. Without detailed observations, it is virtually impossible to find out, whether the growth rate remains high because the pH rises to a more favorable level (direct effect), or because more phosphate becomes available (indirect effect).

Little is known about possible toxic effects of certain chemical substances such as heavy metals, herbicides or pesticides on algae, but as the highest concentrations of these substances are observed in those lakes, which also have the highest phytoplankton blooms, we may probably ignore these effects for the time being.

Effects of pH and other chemical factors are not incorporated in BLOOM II, but they are modeled in CHARON in as far as they have an (in)direct effect on the nutrient cycles.

### 2.1.3 Biological factors

**Other primary producers:** rooted waterplants have some advantages over floating phytoplankters: they have access to nutrients stored in the bottom, they have a more advanced level of internal structure and organization, hence better facilities for biochemical reactions and transport both within the plant as between plants and surrounding environment. Thus these plants seem to be

strong potential competitors for nutrients and particularly sun light.

It is intriguing though that so many waters which were formerly dominated by rooted macrophytes, are presently dominated by phytoplankton (for instance Lake Veluwe). We shall not try to give an explanation in this report, since there are hardly any rooted macrophytes in any of the eutrophic lakes we have studied, thus they have not been incorporated into BLOOM II. Notice, however, that it is by no means impossible that these higher plants once again will gain importance if these lakes become less eutrophic in the future.

Predators seem a direct threat to phytoplankton cells because they increase mortality. Predators include zooplankton, Daphnia in particular, fish and shell-fish e.g. mussels, but to study the influence on phytoplankton is complicated for several reasons:

1. Experimental data are in short supply because it is extremely difficult to obtain a reliable estimate of
  - The predator concentrations (patchy distribution; variations in the volume of individuals).
  - The rate at which phytoplankton is actually consumed by the predator.
2. It is not quite obvious which particles are consumed and digested by the predators (Is detritus used? Are blue-green algae consumed or rejected because their size is too big, their taste not well enough, perhaps even toxic [Lampart, 1981]? Do many ingested cells like *Jona* return alive from the intestines of the grazers [Porter, 1975]?)
3. Predators have a highly efficient digestive system and may speed up the overall rate of remineralization because they ingest large dead phytoplankton particles and large organic macro molecules and excrete nutrients in a directly available form. In other words, their net effect may even be beneficial to phytoplankton [Hargrave et al., 1968; Larow et al., 1978].

The number of references could have been extended easily. All these problems make it difficult to include grazing in a model. The role of one kind of predator, namely zooplankton will be discussed later [Chap. 7].

## 2.2 THE LINEAR PROGRAMMING MODEL

In the following two sections we shall first consider the mathematical formulation of the linear programming model, illustrated by some examples. This section is based upon the pioneering work by Danzig [1963].

In Sec. 2.2.2 we shall outline how the phytoplankton bloom problem is converted into a standard linear program.

### 2.2.1 General formulation

Compared to most other mathematical techniques, linear programming is a relatively new invention. Most work was done shortly before and during World War II. The real breakthrough, however, was the development of the simplex solution algorithm in the late 1940s. Still solving linear programs was rather expensive, because the numerous matrix inversions either had to be computed by hand, or on the first existing computers. With the tremendous drop in the cost of computer time in the 1970s, the cost of solving a linear program has become marginal in comparison to the cost of the expert, who formulates the model.

Linear programming is applied when an optimization problem can be represented by a set of linear equations. For example consider a mother of four kids, who wants to feed her children well, but unfortunately has a very limited budget. To keep her children healthy each should eat a minimum daily amount of essential foodstuffs such as calories, minerals, vitamins.

She could, however, satisfy the daily needs in an infinite number of ways because so many food items (bread, vegetables, meat etc.) are on the market. But she has no (completely) free choice to combine all of these food items, because for example eating more than 100 grams of fat per day can be considered unhealthy, eating sugar is bad for teeth, etc. To make life even more complicated, she has to minimize the total cost of food, because otherwise no money is left for the cost of living, heating etc.

Linear programming provides a simple solution to this problem because it could tell her exactly what the cheapest combination of food items is that still satisfies all formulated constraints: the menu will contain at least a certain amount of calories, not more than a certain amount of fat and sugar, but a minimum amount of protein, vitamins, etc.).

It is easy to find numerous other examples of similar problems: a farmer, who feeds cattle on various wheats and wants to minimize the cost of buying food; a manufacturer, who produces components for house construction with known characteristics of for example strength, and thermal and noise isolation, at a minimum cost. These kinds of problems are known as 'blending problems'.

Another general applications of linear programming is the transportation problem (find the shortest route to supply a number of factories with materials, given certain constraints; develop timetables for railroad or airline companies).

We shall now consider the mathematical formulation of a linear program. Define the following symbols:

- $x_j$  is activity (variable)  $j$ ,
- $c_j$  is the cost of activity  $j$ ,
- $a_{i,j}$  is the proportionality constant,
- $e_i$  is the slack variable  $i$ ,
- $b_i$  is the value of constraint  $i$ .

In the standard linear program we must

$$\begin{aligned}
\text{Find} & \quad : \quad x_j \geq 0 \quad \text{and} \quad e_i \geq 0, \\
\text{Minimizing:} & \quad \sum_j c_j \cdot x_j, \\
\text{Subject to:} & \quad \sum_j a_{i,j} \cdot x_j + e_i = b_i \quad (2.1)
\end{aligned}$$

The 'slack variables' are introduced, because as we have previously seen most constraints are formulated as minimum or maximum conditions which results in inequalities rather than equations. By adding the non-zero slacks the ' $\leq$ ' and ' $\geq$ ' signs can be replaced by '=',

Linear programming can be used not only to minimize some objective function, but also to maximize one, for instance to maximize the yield of a plot of land. It has been shown, that each maximization problem can be converted into a minimization problem or visa versa.

### 2.2.2 Mathematical formulation of the bloom problem

Many physical, chemical and biological factors are considered as important potential limitations to phytoplankton blooms. Although the influence on phytoplankton is not always straightforward, each factor ultimately influences one of the model's linear constraints. These state that the minimum requirement of factor  $i$  per unit of phytoplankton species  $j$  is less or equal to the total available amount of  $i$ . Nutrients easily fit into this scheme; thus the three nutrients in the model are each represented by a single constraint (see below).

All other factors such as temperature, solar intensity, mixing depth and grazing influence the energy budget of the phytoplankton species one way or another. Unlike nutrient limitations, however, energy limitations cannot be described by a single linear equation: (1) the response of phytoplankters to a change in the availability of energy, i.e. photons, is non-linear, and (2) photons are not homogeneously available in a column of water. In this case the non-linearity can be described by two linear constraints [Sec. 6.1]: the energy constraints.

Thus, originally five mathematical constraints were included in BLOOM II of which the two energy constraints represent many different factors. In the present BLOOM II model optionally we include one additional growth-constraint for each species which limits its rate of increase in a time-step [Sec. 6.2.4].

Each of the constraints has the same formulation; for each resource at each time-step we consider:

- $x_j$  is the amount of phytoplankton species  $j$ ,
- $a_{i,j}$  is the amount of resource  $i$  per unit of species  $j$ ,
- $v_i$  is the amount of resource  $i$  which is temporarily unavailable for growth,
- $e_i$  is the surplus amount of resource  $i$ ; it is directly available,
- $b_i$  is the total amount of resource  $i$  in the water.

If a resource is limiting to the bloom, the surplus equals zero, thus a higher biomass yield is impossible, unless the available

amount of the limiting factor is increased. This concept is represented in the model by the following set of equations:

$$\sum_j a_{i,j} \cdot x_j + v_i + e_i = b_i \quad (2.2)$$

Eqs. (2.2) conserve mass within a time-step of the model and are identical to a standard linear program, except for the amount in detritus ( $v_i$ ). When  $v_i$  can be removed, Eq. (2.2) becomes identical to (2.1). In the model we use two different methods to eliminate  $v_i$ . It is considered constant on one occasion, in which case we substitute

$$b_i^* = b_i - v_i$$

for  $b_i$ . In another case  $v_i$  is expressed as a function of the form:

$$\sum_j f_{i,j} \cdot x_j$$

thus we may substitute  $a_{i,j}^*$  for  $a_{i,j}$ .

Maintaining the original symbols for simplicity, we subtract  $v_i$  from the total available amount in the first case, but in the second the necessary amount per unit of phytoplankton is increased. Thus the new coefficients  $a_{i,j}^*$  are corrected for the amounts of  $i$  that will become unavailable to phytoplankton as a bloom is developing.

The first method is applied in BLOOM II to correct the total available concentration of nutrients for the amounts incorporated in zooplankton. The amounts of nutrients in detritus are eliminated by the second method. Assuming that the rate of change of the detritus pools is a first order differential equation achieving equilibrium within the time-step of BLOOM II,  $v_i$  may be eliminated from (2.2). These assumptions will be explained in the sections on nutrient and energy constraints in more detail and discussed in Sections [3.6.2 and 5.8].

The LP solution of BLOOM II is illustrated by Fig. 2.1. Consider two species with concentrations denoted by  $x_1$  and  $x_2$ , which can be limited by two nutrients (N1 and N2) and energy. Each constraint is represented by a straight line in the  $(x_1, x_2)$  plane resulting in eight intersection points (A through H). Each point in this plane in which no constraint is violated, is called a valid solution. Consider the three points on the  $x_2$  axis. Points D and E have a larger distance from the origin than point A, but in these points obviously the constraint of nutrient N2 is violated, hence A is the only valid solution point on the  $x_2$  axis. Similarly C is the only valid solution point on the  $x_1$  axis. Of the remaining two points, B is a valid solution because two constraints intersect but they are not violated, but in point F constraint N1 is violated.

So there are three valid solutions (A, B and C), but it can be shown that only one of these three points is the optimal solution, because here the objective function (the total biomass) is maximal. From Fig. 2.1 it is immediately clear that in this case point B is the optimal solution because it has a larger distance from the ori-

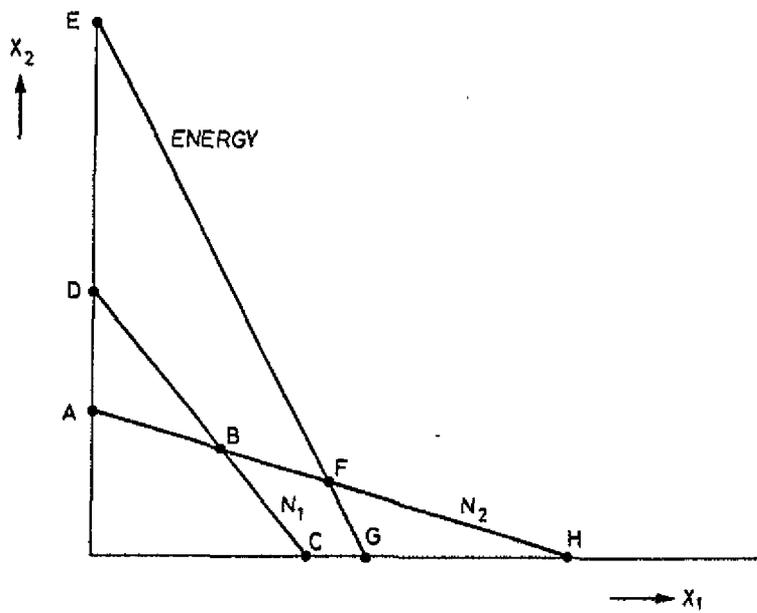


Figure 2.1 Graphical illustration of the linear programming solution of BLOOM II.

gin than points A and C. In this point both  $x_1$  and  $x_2$  are non-zero and two constraints (nutrients  $N_1$  and  $N_2$ ) are limiting to the bloom.

### 3. NUTRIENT REQUIREMENTS OF PHYTOPLANKTON SPECIES

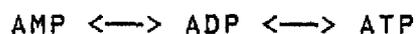
#### 3.1 INTRODUCTION

Of the three nutrients included in BLOOM II, nitrogen and phosphorus are essential to the physiology of all phytoplankton species. Diatoms in addition require a third nutrient, silicon, in fairly large quantities. In the following we shall briefly discuss the role of each nutrient in the physiology of phytoplankton species [Sec. 3.1 and 3.2]. Next we shall discuss the nutrient cycle of an aquatic ecosystem and how it is modelled in BLOOM II [Sec. 3.3 through 3.8]. Finally in Sec. 3.9 we shall give an overview of this chapter.

Nitrogen is particularly important as a component of the proteins in the cell, including the enzymes, because with oxygen it forms the so-called amino-bridge which connects aminoacids in polypeptides. It is an important constituent of the genetic material of the cells and also of light sensitive pigments such as chlorophyll a.

Because it is involved in many vital physiological processes, nitrogen deficiencies cannot be tolerated for a long time: if the internal concentration drops below a certain level, phytoplankton cells die rather quickly.

Phosphorus is an important component of proteins, nucleic acids and lipids for instance in the cellwalls. Particularly its role in the reactions of energy-rich sugars should be noted:



By these reactions chemical energy is either stored or released in the cell; AMP, ADP and ATP are abbreviations of respectively: adenosine mono-, di- and tri-phosphate. From the left to the right, two ortho-phosphate groups are bound, thus increasing the Gibbs free energy. This will be the main direction when energy production starts to exceed the use of energy by the cell, but after some time an equilibrium will be achieved, since ATP is an intermediate rather than a storage product of chemical energy. Thus there is less variation in the ATP contents of a cell than might have been expected by just looking at the variation in primary production during a day.

Most phytoplankters seem to tolerate much larger variations in their internal phosphorus concentrations than in their nitrogen contents. Extremely low internal phosphorus levels occur occasionally without fatal consequences. This is partly because phosphorus is less directly involved in (re)production processes than nitrogen, but also because phosphorus reserves can be stored when external concentrations are relatively high.

Diatoms require silicon as a building component to strengthen the cellwalls. In contrast to nitrogen and phosphorus it is recycled at an extremely low rate which implies that the total silicon concentration is mainly determined by two processes: external loading and mortality and subsequently sinking of diatoms. In many waters dia-

toms take up all available silicon during the spring bloom and when most of them have died, the few survivors have to await a rise in concentration due to external loading. Considering that in summer (1) most Dutch lakes have long residence times and (2) large quantities of silicon have been used upstream in rivers such as the Rhine, a significant rise in silicon concentration in the lakes is usually not observed until the late fall or even winter. As diatoms grow relatively fast when there is ample silicon, the characteristic silicon cycle has important consequences for the species dominance in many lakes.

### 3.2 NUTRIENT AVAILABILITY

Nutrients appear in many forms in a phytoplankton's environment, but not all of these can be assimilated. Those fractions of a nutrient which may be used directly or after some rapid<sup>1</sup> conversion process will be called available, in contrast to the unavailable fractions, which either cannot be used or only after some slow conversion process.

The first fraction of nutrients we consider to be available are those incorporated in living phytoplankton cells. Obviously, since phytoplankton reproduces by means of cell divisions, each new cell automatically receives one half of the nutrients of the old cell. Thus the pool of nutrients in living phytoplankton is perpetually redistributed among all living individuals.

The second available fraction are a number of inorganic, dissolved chemical species. Many phytoplankton species can use different sources of inorganic nitrogen such as  $\text{NO}_3^-$ ,  $\text{NO}_2^-$  and  $\text{NH}_4^+$ , although only the latter may be used directly. Other nitrogen components first have to be reduced to  $\text{NH}_4^+$ , a reaction catalysed by the enzyme nitrate reductase which is either available or readily synthesized by the cell. Several species of phytoplankton can also utilize organic sources of nitrogen [Eppley et al., 1971; McCarthy, 1972]. Moreover, bacteria can very rapidly convert organic into inorganic nitrogen; Satoh et al. [1976] report a conversion rate constant of 0.73 per day.

In addition several species of blue-green algae can convert molecular nitrogen ( $\text{N}_2$ ) into  $\text{NH}_4^+$  using the multi-enzyme complex nitrogenase [Painter, 1970; Steward, 1974; Horne, 1978; Carpenter et al., 1978; Pearl and Kellar, 1979]. Nitrogen fixation, however, seems rare in highly eutrophic lakes which according to Horne et al. [1979] and Zevenboom et al. [1980] must be due to the large energy requirement of this process. For the PAWN project we made several computations with BLOOM II in which a nitrogen-fixing strain was added to the nominal set of species in the model. We concluded, that indeed nitrogen-fixation was relatively unimportant in the twelve lakes studied [Los et al., 1982].

Phosphorus is generally taken up in just one inorganic form: ortho-P but as with nitrogen, many phytoplankton species can use organic phosphates [e.g. Fogg, 1973]. Silicon is always taken up as  $\text{Si}(\text{OH})_4$ .

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<sup>1</sup> 'Rapid' conversion means that a substantial part of an unavailable form can become available during one time-step.

The most important unavailable nutrient fractions are zooplankton and detritus. Phytoplankton does not eat zooplankton and detritus fragments mainly consist of large, organic macro molecules, which cannot be taken up by living phytoplankton cells.

### 3.3 NUTRIENT CYCLES IN THE MODEL

There is a continuing turnover of nutrients in the aquatic system: they usually enter the system in dissolved form, and can become incorporated into living phytoplankters. When they die, part of the nutrients in their bodies dissolves, but another fraction consists of more resistant material: detritus. Eventually most of the detritus is remineralized, but another part sinks to the bottom. However, not all of this material is permanently lost to the water system, since degradation processes in the bottom also release dissolved nutrients which can return to the overlying water.

Apart from these biochemical processes, several inorganic processes are important at least to the phosphorus cycle. Computations with CHARON for both Grote Rug and natural waters such as Lake IJssel indicate, that a substantial amount of phosphorus is removed from the water by inorganic processes.

In this complicated system both the concentrations of the various forms and their turnover rates may vary considerably with the kind of lake, temperature, dominant phytoplankton species and many other variables. A schematic representation of these processes is given in Fig. 3.1.

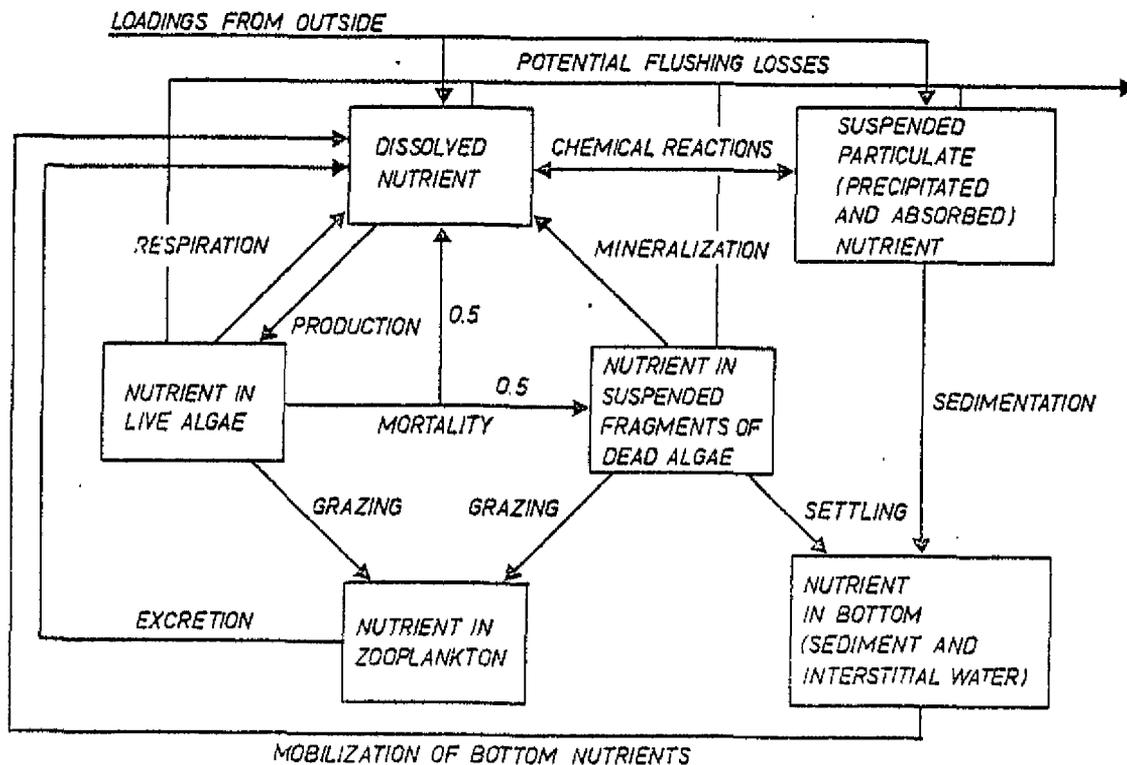


Figure 3.1 Basic nutrient cycle for BLOOM II. The model computes dissolved nutrients and those in live and dead phytoplankton and in zooplankton.

Notice that zooplankton is the highest trophic level included in the nutrient cycles. Occasionally other organisms might be important, not because they ever contain a significant amount of nutrients but because they may increase some of the turnover rates. Generally, however, the influence of these organisms on the nutrient cycles of eutrophic lakes seems negligible.

Many modellers attempt to describe nutrient cycles by first order differential equations, which are solved analytically or more often numerically, depending on the form of the equations. This approach has indeed been used so often, that it could be called classical. Some of numerous examples may be found in: Di Toro et al., [1977]; Nyholm [1978]; Jorgensen [1978]; and Bierman [1981].

Many of these models were, however, developed for lakes with a depth of more than 10 m, which become stratified in summer and show little or no significant exchange between the hypolimnion and overlying water during the growing season. In such systems the most important transport is sedimentation of organic material to the hypolimnion. The rate of change of the total amount of nutrients in the productive part of the water, is small relative to the changes in phytoplankton kinetics. A simple approach, using first order equations has often been applied successfully, for instance in modeling phytoplankton populations of the Great Lakes in the United States.

By contrast, many Dutch lakes are shallow. The average depth in some of the most eutrophic lakes is less than 2 m. Their nutrient concentrations are often ten times higher than those in lakes to which the classical models were applied and vary sometimes greatly even within short time intervals such as one week. Several Scandinavian authors [Nyholm, 1978; Jorgensen, 1978] have used the classical approach to model similar lakes by empirically determined rate constants for the exchange transports between water and bottom, but the predictive value of this approach is questionable, since the parameters of the models seem specific to a particular lake and to a specific interval of time.

During the WABASIM project, it soon became obvious that a small number of equations with a single set of rate coefficients was insufficient to reproduce the observed nutrient concentrations in several Dutch lakes in various years. Thus CHARON was developed, which considers many inorganic reactions, and biochemical processes in the water. Processes in the bottom are not yet modelled elaborately, but they can be established by calibration. A so-called 'explosive' bottom flux [de Rooij, 1980], however, cannot be modelled. Information on phytoplankton kinetics can be obtained from observations, or computations by BLOOM II in the coupled version of the two models.

In the stand-alone version of BLOOM II we have not attempted to approach the complexity of the nutrient cycles as they are modelled in CHARON by some simple equations as was the case in the classical models described previously. We have decided to use measured nutrient concentrations directly or after some simple conversion as the right-hand sides of the nutrient constraints. This means that (1) the model does not consider inorganic processes and (2) the water in the lake is considered a closed system: there are no transports by water-ways, or to and from the bottom.

Occasionally these simplifications may be too rough, for instance when a bloom suddenly dies off and a substantial amount of nutrients is removed to the sediment within a short time period. In those cases the model will not be using correct values for the available nutrient concentrations, but as it receives a new concen-

tration value after a one-week time-step, this error will not be carried over to the next time-step in the steady state version of BLOOM II.

In BLOOM II the nutrient cycle is solved under certain simplifying assumptions such as a steady state for the detritus pool, although a quasi dynamic solution is optionally available [Sec. 3.6.2]. The nutrients are partitioned over the various compartments in accordance to the objective of the model: the calculation of the maximum feasible phytoplankton biomass. Thus the model does not claim to calculate the actual concentrations of the nutrient pools nor the flows between them, but rather one special way to partition the available nutrients: if circumstances were favorable to phytoplankton and the maximum equilibrium were achieved, how would the concentration be for each pool of each nutrient?

### 3.4 NUTRIENT MASS BALANCES

To calculate how much phytoplankton biomass can be sustained, it is necessary to determine (1) the total amount of each nutrient in the water and (2) the available and unavailable fractions as defined in Sec. 3.2. As indicated in Fig. 3.1, the total nutrient amounts in the water change by means of two processes: water transport (inflow and outflow) and exchange with the bottom. Both are modelled in CHARON, but not in BLOOM II, as stated previously.

Define the following symbols:

#### For zooplankton:

- $z$  is the total amount of zooplankton,
- $h_i$  is the amount of nutrient  $i$  per zooplankton biomass unit.

#### For each phytoplankton species $j$ :

- $x_j$  is the amount of phytoplankton species  $j$ ,
- $a_{i,j}$  is the amount of nutrient  $i$  per unit of species  $j$ : the minimum stoichiometric constant,
- $M_j$  is the natural mortality rate constant per day of species  $j$ , which includes all death processes except grazing.

#### For each nutrient $i$ :

- $y_i$  is the amount which is temporarily unavailable because it is incorporated in dead phytoplankton (detritus),
- $e_i$  is the surplus amount which is directly available,
- $b_i$  is the total readily available amount,
- $u_i$  is the mineralization rate constant of detritus per day,
- $s_i$  is the sedimentation rate constant of detritus per day,
- $q_i$  is the nutrient fraction which becomes detritus when a phytoplankton dies, since it is not immediately released to the dissolved nutrient pool after cell lysis.

For the total amount of nutrient  $i$  in the water, the following mass balance equation should hold:

$$b_i = \sum_j a_{i,j} \cdot x_j + y_i + h_i \cdot z + e_i \quad (3.1)$$

Thus, the total amount of nutrient  $i$  in the water-phase equals the amounts contained in phytoplankton, zooplankton, detritus and the amounts which are dissolved. Eq. (3.1) is the same as Eq. (2.1), except that there is extra term for nutrients in zooplankton.

Taking the derivative to  $t$ , the rate of change of  $b_i$ , the total amount of nutrient  $i$ , per unit of time of course equals:

$$\frac{d b_i}{d t} = \frac{d (\sum_j a_{i,j} \cdot x_j) + d y_i + d h_i \cdot z + d e_i}{d t} \quad (3.2)$$

As we have explained previously, the water in the lake is assumed to be a closed system, hence

The total amounts of the available nutrients ( $b_i$ ) is constant for a time-step of the model (usually one week).

This assumption generally holds better for nitrogen and silicon (in case there is no diatom bloom) than for phosphorus. Also there tend to be more violations in summer than winter, when the total amounts of the nutrients vary less, but given the complicated chemical processes involved, there is no way to predict changes in  $b$ -values in the framework of BLOOM II.

As we have already mentioned in Sec. 3.3 some of the nutrient fractions shown in Fig. 3.1 are directly available to phytoplankton, but not all. Dissolved nutrients and those in phytoplankton are available, nutrients in detritus and zooplankton are unavailable. However, we use the total measured amount of each nutrient in BLOOM II, which includes detritus and zooplankton. Therefore the model must allocate a certain fraction of the total amounts of nutrients to the unavailable fractions and prevent phytoplankton from taking it all up. The way this is determined by the model will be the subject of the next Sections.

### 3.5 NUTRIENT EXCHANGE WITH THE BOTTOM

In many lakes the annual concentration pattern of the nutrients is more or less the same in each year. However, the annual nutrient amounts entering the water by external loading strongly exceed the nutrient amounts that are flushed out. Hence on a yearly basis there must be a net transport to the bottom: averaged over a year the bottom is a sink. Still it is possible that a net flow of nutrients, particularly of phosphorus, occurs from the bottom to the water during part of the year, as was shown by de Rooij [1980] for Grote Rug and other lakes in the Netherlands such as Lake IJssel.

First the 'normal' flux from the bottom may exceed precipitation and sedimentation for instance during a bloom, when most of the nutrients are incorporated in live phytoplankton. Second an 'explosive' bottom flux may occur, a process by which large amounts of nutrients are released from the bottom at an unusual rate. Moreover this process is favored by conditions resulting from phytoplankton growth, i.e. there is a positive feedback mechanism that tends to

increase the total nutrient amounts when there is a phytoplankton bloom. However, when the bloom declines the reverse happens and nutrient concentrations in the water decrease unusually fast.

These processes are too complicated to be considered by BLOOM II only, which is the main reason why the coupled model was developed. Without CHARON we can only assume that the values of  $b_i$  are constant [Sec. 3.4]: there is no net transport between the bottom and water during a time-step. But this assumption still makes it possible that the partitioning of nutrients among the various compartments in the water is modified because for example unavailable nutrients of the detritus pool might sediment at the same rate at which available nutrients are released by the bottom.

Therefore in BLOOM II we make the following additional assumption:

**The sedimentation rate of (unavailable) nutrients in detritus and the release rate of dissolved (available) nutrients from the bottom are equal.**

Hence if we assume a non-zero sedimentation rate  $s_i$ , the effect in the model is exactly the same as if we had increased the mineralization rate by  $s_i$ . In other words, to keep  $b_i$  constant during a time-step we assume that 1 gram of dissolved nutrient  $i$  enters the water for each gram of nutrient  $i$  in detritus that goes to the sediment.

With few exceptions, however, we have assumed  $s_i = 0$  in the computations with the model. Thus there is no exchange of nutrients at all between the water and the bottom. These assumptions will be reviewed at the end of this chapter.

## 3.6 NUTRIENTS IN DETRITUS

### 3.6.1 Introduction

Frequently a substantial amount of nutrients is tied up in dead phytoplankton cells (detritus) and is thus temporarily unavailable to living cells. In BLOOM II this amount is denoted by  $y_i$ . Modelling detritus is difficult for two reasons: (1) there is no way to separate detritus from other fractions in a sample, and hence the computed number cannot be compared to an observation and (2) there is considerable uncertainty about the rates at which detritus is generated and removed.

To simplify the discussion, we shall usually refer to a single detritus pool, but actually the model distinguishes four detritus pools: one for each of the nutrients and one for chlorophyll [Sec. 5.7].

A certain fraction of each species  $j$  dies during each time-step, withdrawing its nutrient content from the live phytoplankton pool. Only a fraction of this material becomes a part of the detritus pool, however. The rest becomes directly available to growth of new individuals, because the dead cells break apart (a process called autolysis), spilling a substantial part of their contents into the water in dissolved form. Detritus may be removed to the bottom or to the dissolved nutrient pool at rates in proportion to its concentration. We can express this mathematically by the following equation:

$$\frac{d y_i}{dt} = \sum_j (q_i \cdot a_{i,j} \cdot M_j \cdot x_j) - u_i \cdot y_i - s_i \cdot y_i \quad (3.3)$$

There is evidence in the literature that a large fraction of the nutrients of a dying phytoplankton cell becomes 'immediately' available, which in practice means rapid relative to the model's time-step of one (optionally several) week(s). Harrision [1978] reports that more than 50 percent of the nitrogen contents can become available within a day. Bougis [1974] quotes several authors who have found similar numbers for phosphorus. Wetzel [1975] quotes results of Krause, who showed that 15 percent of a the nutrients of a dead diatom became available within 24 hours after death. For a green alga this fraction was larger: 33 percent and even 45 percent after 5 days.

In BLOOM II we assume that  $q_i = 0.5$ . Thus for each nutrient 50 percent of the amount in living cells becomes immediately available upon dying and the remaining 50 percent becomes detritus. The validity of this assumption can of course be questioned. For example the conditions before a cell dies are probably important. A phytoplankter with an ample supply of phosphorus may have stored a great reserve, which is released soon after its death, whereas the phosphorus contents of a cell grown under phosphorus limiting conditions may be much more resistant. It is also possible that dead diatom cells release a smaller part of their nutrient contents into the environment.

We have adopted a value of  $q_i$  in agreement to the lowest numbers reported in the literature for several reasons:

1. It is consistent to the objective of the model. A higher value of  $q_i$  would make a larger fraction of nutrients unavailable.
2. Most experiments consider the rate at which dissolved nutrients are generated. However, as we have already stated in Sec. 3.2, many phytoplankton species can also use (some) organic substrates for nitrogen and phosphorus. This implies that more nutrients are actually available than indicated by the reported numbers.
3. Most experiments have been performed with (healthy) laboratory cultures, which are deliberately killed. It is not unlikely that a dying cell in a natural system is in bad shape and will release a greater part of its contents immediately.

Computations with BLOOM II and the coupled version of this model and CHARON indicate that a completely different value of  $q_i$  leads to deviations between computed and observed variables, unless the mineralization rates are changed to compensate the change of  $q_i$ . Something similar was observed by other modellers such as Di Toro (pers. comm.) and Nyholm [1978] who have used a value of 0.5 or even 0.4 for  $q_i$ .

The remineralization rate constants of phosphor, nitrogen and silicon are computed in BLOOM II as:

$$u_i = 0.006 * T \quad (P \text{ and } N)$$

$$u_i = 0.025 \quad (Si)$$

where  $T$  is temperature in degrees centigrade. These number are based upon experimental results by many authors (see for example the literature research by Smits [1981]).

### 3.6.2 Two solutions for the detritus equation

A steady state solution for Eq. (3.3) is easily obtained, since putting the derivative to zero, gives:

$$y_i = \frac{q_i - \sum_j (a_{i,j} \cdot M_j \cdot x_j)}{u_i + s_i} \quad (3.4)$$

Without an additional assumption, Eq. (3.3) cannot be solved analytically since  $x_j$  is among others a function of  $y_i$ . Because usually both the observed and the predicted changes in the net total biomass are relatively small during a week, there is a reasonably constant input of nutrients into the detritus pool. Thus we could consider  $x_j$  to be approximately constant during a time-step and solve Eq. (3.3) analytically as an ordinary first order, inhomogeneous differential equation. Using the time-scale of the model (one or more weeks), Eq. (3.3) is solved with constant coefficients, among which  $x_j$ . Thus there is a discontinuity of  $y_i$  at the end of each time step, which is often small, however, because the changes in the coefficients are small. Leaving out the subscript  $i$ , the following solution for  $y_i$  is obtained:

$$y = (y_p - y_e) \text{EXP}[(-u - s)\Delta t] + y_e \quad (3.5)$$

where:

- $y$  is the value of  $y_i$  at time  $t$ ,
- $y_p$  is the initial value of  $y_i$  at the beginning of a time-step,
- $y_e$  is the equilibrium value of  $y_i$ , calculated according to Eq. (3.4),
- $\Delta t$  is the time-step of the model.

### 3.6.3 Steady state or dynamic solution?

If the amount of detritus were always small compared to nutrients in living phytoplankton, we could simply use the steady state solution under all conditions, but this is not the case. Usually the size of both nutrient pools are of the same order of magnitude. Therefore it is necessary to discuss how closely  $y_i$  approaches equilibrium. According to Eq. (3.5), this depends on (1) the rate of approach ( $u_i + s_i$ ), multiplied by the time-step  $\Delta t$ , and (2) the difference between equilibrium and initial value of the detritus concentration ( $y_p - y_e$ ).

The characteristic time-scale of Eq. (3.3) equals the reciprocal value of  $s_i + u_i$ . The sedimentation rate depends on many factors such as the weather conditions (wind) and is highly uncertain. Typical numbers found in the literature cover a wide range of about 0.01 per day up to 0.10 or even 0.20 per day [e.g. reviews by Smayda, 1970; Lingeman-Kosmerchok, 1978]. But as we have stated in Sec. 3.5, we have usually assumed a value of 0.0.

According to Sec. 3.6.1 the mineralization rates of N and P can become as low as 0.03 per day when temperatures are less than 5° centigrade and as high as 0.12 per day when temperatures exceed 20°.

Thus the characteristic time of Eq. (3.3) is in the order of a week in summer and in the order of a month in winter. This means that the nominal one-week time-step of the model is rather short, at least in winter. Fortunately the difference between the initial and the equilibrium values of the detritus pools ( $y_s - y_e$ ) tends to be rather small because all the important processes such as phytoplankton mortality, mineralization and changes in the total amounts of nutrients are rather smooth functions of time (actually of temperature in most cases). Thus errors from these steady state assumptions seem to be tolerable under ordinary conditions.

Considering our conclusion that the characteristic time-scale of the detritus equation is one week or even longer, we may wonder why normally we still assume a steady state for detritus. The main reason is a practical one: the computed biomasses based upon Eq. (3.4) agree equally well, sometimes better to the observations than those based upon Eq. (3.5). This is particularly true for Grote Rug [Sec. 8.6.1].

How can we explain this counter-intuitive result? In the present BLOOM II model, the total amount of nutrients is a forcing function, which means that there is no structural linkage between the values at different time-steps. The same holds for one of the most important nutrient pools: nutrients in live phytoplankton. If we make a dynamic computation for detritus, its rate of change is, however, solely determined by the rates of various processes in the model. Hence the derivatives of  $b_i$  and  $y_i$  are not necessarily of the same order of magnitude, they can even disagree quite strongly.

For example after the spring-bloom a rather strong increase in the sedimentation rate of detritus has often been observed, which results in a strong decrease in the total amounts of nutrients in the water. The net effect is taken into account by the model at the next time-step, when it receives new values for  $b_i$ .

If we make a dynamic computation with the usual assumption that there is no sedimentation [Sec. 3.5], the model will allocate too much nutrients to the detritus pool. Hence the same fraction of nutrients is made unavailable twice: (1) it has disappeared from the water, hence  $b_i$  will be lower than at the previous time-step, but (2) part of it is allocated to detritus by the model nevertheless. Thus we have observed that the detritus pool size of silicon computed according to (3.5) sometimes becomes larger than the total available amount, which obviously is incorrect.

These effects are probably more obvious in Grote Rug than in natural lakes, because of the irregular intake regime and the unnatural perturbation of the nutrient cycles (dosing of P-precipitates).

Thus the steady state assumption for detritus seems most satisfying with the present nutrient cycles. In the coupled version of BLOOM II and CHARON, however, where a much larger part of the nutri-

ent cycle is modelled, this steady state assumption is no longer necessary.

Notice, however, that both the steady state solution or any kind of dynamic solutions depends on the ratio  $q_i M_j / (u_i + s_i)$ . At low temperatures both the numerator and the denominator become rather small, hence the detritus pool size is very sensitive to the values of these coefficients; errors in any of these might well have a larger impact on the final result than the type of solution in the model.

### 3.7 NUTRIENTS IN ZOOPLANKTON

Presently the amount of zooplankton is an input to the model with a constant value for each time-step. A zooplankter has a very high energy requirement and eats about its own body weight a day. But it does not require all the nutrients its food sources contain. Therefore it will rather easily maintain a constant internal level and excrete the nutrient surplus. In the model both the amount of nutrient per unit of zooplankton ( $h_i$ ) and the amount of zooplankton ( $z$ ) are constant and hence  $h_i \cdot z$ . As the derivative of a constant is zero, the zooplankton term vanishes from Eq. (3.2): zooplankton has no influence on the rate of change of  $b_i$ .

Because the zooplankton concentration is usually small relative to the phytoplankton concentration (in the order of 10 percent or less) it seems that zooplankton is unimportant to the nutrient cycles. However, because of its high energy requirement the amount of nutrients passing the digestive system of a zooplankter can be considerable in a week. Thus it might influence the partitioning of nutrients among the available and unavailable fraction.

Depending on what is eaten and how nutrients are released, the net effect on the available fraction could be positive, zero or negative. Example of a positive effect: eating detritus and releasing dissolved nutrients. No effect occurs when nutrients are ingested from living phytoplankton cells and released as dissolved nutrients. A negative effect would occur when nutrients of living phytoplankton cells are taken up, but released as fecal pellets, which sink to the bottom.

The importance of these processes is rather widely discussed. For instance Hargrave et al. [1968] and Smith [1973] claim, that uptake of detritus and release of dissolved nutrients is occasionally of great importance, particularly in marine systems. Not all data are, however, consistent. Thus we feel that we cannot predict the impact of zooplankton on the nutrient partitioning accurately enough to be used in the model and we have therefore assumed that zooplankton does not alter the partitioning of nutrients at all.

Under this assumption, the amounts of nutrients in zooplankton are constant, unavailable fractions ( $h_i \cdot z$ ) which can simply be subtracted from  $b_i$  in the mass balance Eq. (3.1).

One final remark: because (1) there is usually little nutrient in zooplankton and (2) we have ignored any possible effect on the partitioning of nutrients, the importance of the zooplankton term is small in comparison to those for live and dead phytoplankton:  $h_i \cdot z$  was never larger than 10 percent of  $b_i$  in all years we considered in Grote Rug.

### 3.8 FORMULATION OF NUTRIENT CONSTRAINTS

The final equations used by the model are easily derived after the previous Sections. From the set of mass balance equations (3.1), the unavailable terms for zooplankton and detritus should be eliminated to obtain an equation with only one set of variables:  $x_j$ . First the constant zooplankton term will be put to the right hand side and subtracted from the b-values. Next the amount of nutrients in detritus  $y_i$  may be eliminated from (3.1) by either using (3.4) or (3.5) depending whether or not a steady state is assumed. Using (3.4) as steady state solution for  $y_i$ , we find the following set of nutrient constraints:

$$\sum_j \left[ \frac{(u_i + s_i + q_i \cdot M_j)}{u_i + s_i} a_{i,j} \cdot x_j \right] + e_i = b_i - h_i \cdot z \quad (3.6)$$

The expression using the dynamic detritus pool, is more complicated, but substituting (3.4) into (3.5) for the equilibrium value  $y_{e_i}$ ,  $V_i$  for  $u_i + s_i$  and leaving out the subscript  $i$  we may obtain:

$$\sum_j \frac{V + (q \cdot M_j)[1 - \text{EXP}(-V \cdot \Delta t)]}{V} a_{i,j} \cdot x_j + e = b - h \cdot z - y_p \text{EXP}(-V \cdot \Delta t) \quad (3.7)$$

In both cases  $x_j$  are the only unknown variables in the resulting system, which can be solved by a Linear Program (see also Eq. 2.1).

### 3.9 NUTRIENT CYCLES: RETROSPECTIVE

Of crucial importance to our discussion on the nutrient cycles in the previous Sections, are:

- The interdependence of chemical and biological processes.
- The uncertainties in the values of several parameters, particularly of the mortality rate ( $M_j$ ) and the fraction of dead algal cells that immediately releases its nutrient contents ( $1 - q_i$ ).

We have set up a rather simple nutrient cycle for BLOOM II because there are too many complications to describe the crucial chemical reactions by some simple equations. Unless these equations are solved simultaneously with the phytoplankton equations as in the coupled version of BLOOM II and CHARON, we use weekly measurements of the total amount of nutrients.

An important problem for which measurements give no direct answer, however, is the fraction of each nutrient to be allocated to the detritus pools. Usually we assume these pools to be at steady state which perhaps is not always justified, but there is presently little alternative [Sec. 3.6.2]. As, however, a dynamic solution is

optionally available in the model, it is possible to determine when the two solutions differ significantly and to analyse the causes and the consequences.

The mortality rate constant is one of the most important parameters determining the size of the detritus compartment, regardless of the computational method. Mainly because there is no estimate for the actual value of  $M$ , a method of partitioning the nutrients over all compartment was adopted according to the objective of the model: maximizing total biomass. Using a minimum estimate for mortality, the fraction of nutrients allocated to detritus by this procedure tends to be lower than it is based upon observed mortality rates.

Moreover we haven chosen a rather low value of 0.5 for  $q_1$ , which means that 50 percent of the nutrients in dead phytoplankton become immediately available. As with the mortality rate we have adopted a value for  $q_1$ , that tends to give an over-estimation of available nutrients.

On the other hand we do not take several other processes into account that might increase the amount of available nutrients. We usually neglect the loading with dissolved nutrients from the bottom. We do not consider positive effects of zooplankton on the overall turnover rates of nutrients.

Thus it was remarked already at the beginning in Sec. 3.3, that the model does not claim to calculate the actual sizes of the nutrient pools or the flows between them.

What are the implications for the predictive value of BLOOM II? Observed nutrient cycles result from complicated interactions of biological and chemical processes. Thus, there is no doubt, that the coupled model based upon the basic equations and structures of CHARON and BLOOM II, solving the complete system simultaneously for both fast (=equilibrium) and slow processes, improves the predictive capabilities of the individual models considerably.

But we can make many useful computations with BLOOM II alone. First of all the model is of great help to gain understanding of a particular body of water. Second it can answer certain questions adequately, depending on the specific conditions in a lake and the specific results produced by the model. How well certain questions can be answered by BLOOM II alone depends on several factors:

1. What is presently the main limitation, some nutrient or energy?
2. Is a drastic change in this situation expected?
3. If we expect a change, can we tell something about its direction? Will there be an increase, or decrease, compared to the present situation?
4. How high are the blooms predicted by the model, are they far above some biomass standard?
5. What species dominance is predicted by the model? Is there a strong dominance of blue-greens?
6. Is there presently a strong interaction between nutrients in water and bottom and do we, based upon previous experiences and the results of CHARON, expect an in- or decrease of the intensity of these interactions?

These questions can be illustrated by some examples, mainly based upon results of the PAWN study in which BLOOM II was applied to a dozen Dutch lakes. Suppose energy is the main limitation in a lake, but phosphate removal is considered as a sanitation measure. With

BLOOM II we can compute by how much the phosphorus concentration in the lake should be lowered before it becomes limiting. If the answer is by more than 50 percent as we have found for several Dutch lakes [Los et al., 1982] we should not expect miracles following phosphorus removal in that particular lake.

The storage reservoirs in the Biesbosch present an extreme example of this situation. Phytoplankton biomasses are relatively low because of a consistent energy limitation in these 15 m deep, artificially mixed basins. Even a reduction by a factor 5 would not make phosphorus limiting, hence it seems unlikely that a phosphate removal strategy would be successful here.

Lake IJssel is another example of an energy limited lake [Los et al., 1982], but here phosphorus concentrations in summer are low enough to be nearly limiting. In this case a relatively small reduction of phosphorus could have a positive effect, even though we cannot predict the future phosphorus concentrations exactly. However, a concentration drop of at least 50 percent seemed necessary to reduce phytoplankton biomasses far enough to meet the official Dutch standard.

From these and similar computations with BLOOM II we could also conclude, that the official standards for phosphorus and biomass were not consistent: if we reduced the phosphorus concentrations far enough to meet their official standard, the model computed biomass levels still in excess of the phytoplankton standard.

## 4. ENERGY CONSTRAINTS

### 4.1 INTRODUCTION

The division into autotrophic and heterotrophic organisms is one of the most important ways to classify living creatures into functional units. Photoautotrophic organisms such as all the well known terrestrial plants, phytoplankton and many bacteria are essentially independent of other creatures for survival, because sunlight is their main source of energy. There is no doubt that life on earth depends almost completely on the photosynthetic products of the plants (energy rich compounds and oxygen), because these are required by all other organisms whether directly or indirectly, (e.g. as fossil fuels).

Plant cells contain a number of light-sensitive pigments, such as chlorophyll-a and -b, which can absorb light quanta (photons). In a complicated sequence of photochemical reactions, the energy from the photons is transferred to and stored as readily available chemical energy (mainly in the form of carbohydrates). Notice that other important products of photosynthesis such as proteins are not considered in the model.

Photosynthesis, which is one of the most complicated physiological processes, varies with circumstances and between species. There are great differences in the preferred light intensities (Fig. 4.3) and in the ability of species to adapt to new light or temperature conditions. As shown by Jorgensen [1969], van Liere [1979] and others, many adaptations involve a change in internal chlorophyll levels, which is one of the main reasons why chlorophyll can only be an approximate indicator of phytoplankton biomass, as will be discussed in Sec. 8.1.3.

It is difficult to compute the carbon fixation rate of phytoplankton because the light intensity varies with (1) the seasonal rhythm, (2) the daily rhythm, and (3) the water depth. The last factor is particularly important since light attenuates exponentially with depth, and because many Dutch waters have a high turbidity. Thus, the lowest light intensity at which photosynthesis is still possible (the euphotic depth) is usually found far above the bottom. Meanwhile the light intensities in the surface layers are supersaturating to photosynthesis. An additional complication is the ability in some groups of species (blue-green algae, dinoflagellates) to avoid homogeneous mixing [Sec. 5.7]. Superimposed on all variations are weather-induced light fluctuations (clouding).

Considering these and other complications reported in the physiological and ecological literature [see for instance the review by Harris, 1978], one starts seriously doubting whether any sensible mathematical model could ever be constructed for such a complicated and variable process as primary production. There is only one reasonable explanation, why not all modeling attempts are failures and why production rates may even be predicted with a rather good accuracy: plants do not immediately respond to rapid environmental changes but do adjust to overall trends in conditions in order to keep the photosynthetic machinery going as well and as regularly as possible. Therefore much of the variations occurring between short time intervals, between individuals of the same species and between

species average out over longer time-steps and larger groups of organisms [see also Chap. 5].

For simplicity most coefficients in this chapter are written without a subscript  $j$ , but actually they depend on the species and are treated as such by the model.

## 4.2 THE RELATION BETWEEN PHOTOSYNTHESIS AND GROWTH

Before discussing the energy budget in more detail, we must consider some aspects of the relation between growth and photosynthesis and indicate some methodological problems. Strictly speaking photosynthesis, which may be defined as photochemical carbon fixation, is of no concern to BLOOM II, because carbon may be the most important element on a dry weight basis, but just an increase in carbon is of no use to a cell. Growth, which may be defined as increase in biomass (dry weight), requires a balanced uptake of other essential elements in addition to carbon and is usually followed by a cell division. Thus the growth rate determines the ultimate biomass concentration.

Obviously, photosynthesis is a prerequisite to growth because without photosynthesis the amounts of all cell substances after a cell division would be halved. On the other hand, photosynthesis without growth is not unlikely, if part of the incorporated material is not used for growth, but released by the cell (extra cellular release). There is some debate in the literature, however, whether this process is so important to healthy phytoplankters [Sharp, 1977] as reported elsewhere [Fogg, 1971 and 1977] and even among those considering it a natural process, [Mague et al. 1980] say that its quantitative importance is small relative to photosynthesis. Thus it seems quite logical, that usually the rates of photosynthesis and growth are closely connected and show a very high correlation [Harris, 1978] on a daily basis.

There is an additional complication which prevents a simple conversion between the rates of photosynthesis and growth: they are measured in different units. The instantaneous growth rate ( $P$ ) is usually expressed per unit of time, alternatively as number of divisions per day ( $U$ ) or as its reciprocal: the generation time ( $T$ ). Because growth rates may be related to a first order differential equation [Sec. 4.3] and division is a process by which one cell gives two<sup>1</sup> new ones, the first process is related to a natural logarithm, but the latter to a logarithm to the basis of 2. Therefore the following relation holds:

$$P = \log_2 U = \log_2 / T \quad (4.1)$$

Photosynthetic rates on the other hand are usually measured as carbon incorporated or oxygen produced, depending on the measuring technique, per unit of time and per unit of biomass. However,

1. The unit of biomass is usually the chlorophyll concentration which is an indirect indicator of phytoplankton

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<sup>1</sup> The number of new cells is not always 2. In some species such as Scenedesmus 2 to the power  $n$  cells are produced, where  $n > 1$ .

biomass. It depends on many environmental conditions [Sec. 8.1.3] and varies during the year.

2. Photosynthesis is measured per hour, growth is measured per day. But a computation of the daily rate of photosynthesis is not straightforward because photosynthetic rates (1) vary strongly during the day and (2) are usually a non-linear function of the number of daylight hours [Sec. 5.2].

In the remainder of this report we shall use the term production for the rate of photosynthesis and growth for the in- or decrease of a population on a per unit weight basis.

#### 4.3 THE ENERGY BUDGET OF PHYTOPLANKTON

Phytoplankton blooms develop when, during a substantial period, the environmental conditions enable the population to fix more energy than required to compensate for all current losses. Energy gains are determined by the rate of production, which is a function of the solar intensity, the surface reflection, the attenuation in the water (mixing depth, background extinction, contribution of live and dead phytoplankton to extinction), the day length, the water temperature, perhaps the spectral distribution, or the variations in light intensity<sup>2</sup>

Energy is lost by several processes: respiration (to some extent the opposite of primary production), mainly for maintenance; mortality (old or unhealthy cells die); grazing by zooplankton or fish; sedimentation (most phytoplankton species have a positive sinking rate).

Define the following symbols:

- $P_g$  is the depth and time averaged gross production rate constant per day,
- $R$  is the respiration rate constant per day,
- $M$  is the natural mortality rate constant per day, including all death processes except grazing,
- $G$  is the mortality rate constant per day due to grazing by zooplankton.

The net effect of these processes may be summarized in the well-known differential equation:

$$\frac{dx}{dt} = (P_g - M - R - G) x \quad (4.2)$$

Notice that no functional relations are indicated, which could suggest there are no feedback mechanisms to prevent unlimited growth. Actually the gross production rate  $P_g$  depends on the light

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<sup>2</sup> Short periods with high intensities and long periods of moderate intensities might have a different impact even if the total number of quanta received is the same.

intensity and therefore on the attenuation caused by the phytoplankton cells themselves. Thus as the number of cells grows, the light intensity (and hence the energy available) at any depth is reduced, a phenomenon called self-shading.  $P_g$  also depends upon the nutrient availability and declines when nutrients are scarce. However, when the light intensity is optimal, nutrients are abundant and all other conditions are favorable, phytoplankton will achieve a maximum gross production rate ( $P_{gmax}$ ), which we can think of as an innate characteristic of each species of phytoplankton.

In the next sections we shall discuss (maximum) production, respiration and natural mortality. Of these primary production is certainly the best known. It, however, also one of the most complicated processes which influences the phytoplankton energy budget. There are thousands of publications on photosynthesis and the problem here is to select, rather than to find them because there is much confusion about methodology, which makes it hard to compare the results by different authors.

Less is known about respiration, maybe because its importance has long been under-estimated. Quantitatively it is, however, very important. Its rate may look small compared to the maximum rate of production, but respiration continues for 24 hours a day, while primary production is confined to only those periods of the day, when a phytoplankton cell receives light quanta. This period can be much shorter than 24 hours depending on the day length and the circulation pattern.

Natural mortality is often completely neglected, but two common observations suggest, that mortality could be very important: (1) the amounts of detritus and of live phytoplankton are often of the same order of magnitude [our own calculations for several Dutch lakes, Chap. 3, in addition to Banse, 1977; Knoechel and Kalff, 1978; Rich and Wetzel, 1978], and (2) the amounts of detritus and of live phytoplankton are often strongly correlated. Thus there is usually a considerable amount of detritus which moreover changes in a way that seems somehow related to the net growth rate of phytoplankton. The most simple assumption is that the rate of change of detritus is mainly governed by mortality of phytoplankton.

When we constructed the model we have attempted to describe each process separately in agreement to observations. This was, however, not always possible because (1) there are many species in the model and (2) authors infrequently report the rates of all energy related processes.

#### 4.4 MEASURING TECHNIQUES

Photosynthesis can be measured in several ways, but we only need to consider two of them which either measure oxygen production or carbon uptake of phytoplankton. The experimental conditions to which phytoplankton cells are exposed before and during the measurements vary to a large extent. In some experiments they are kept in bottles at different water depths (hence light intensities) for several hours. In other cases a recently collected sample is incubated in a special apparatus with an artificial light source. The experimental difficulties are numerous [Strickland, 1960; Harris, 1978] and make it hard to compare the results obtained by different methods directly, although an excellent agreement between different techniques has sometimes been observed [Jewson, 1977].

Extrapolation of production measurements to actual growth rates of in situ populations is always difficult.

It is usually assumed that net<sup>3</sup> production is measured by the oxygen method. Because part of the phytoplankton cells are kept in the dark, the oxygen consumption (respiration) can also be measured. Adding the two numbers yields the gross production rate. Values measured by the <sup>14</sup>C method are closest to net production although influenced by respiration to some extent, as was already recognized by some of the earliest workers with <sup>14</sup>C techniques [Strickland, 1960]. But a direct estimate of respiration (hence gross production) is impossible by this method.

There are no practical methods to measure natural mortality rates because dead phytoplankton cells do not contain some tracer by which they can be distinguished from other organic particles. A direct estimate through microscopic counting of dead phytoplankton cells has sometimes been obtained for diatoms [Knoechel and Kalff, 1978]. This method is, however, extremely cumbersome and furthermore non-applicable to dead particles of blue-green algae because these cannot be distinguished well enough from living particles under a microscope.

Consequently natural mortality rates must usually be estimated indirectly, for instance by subtraction of the observed (net) rate of change of a phytoplankton population from the measured production rate [Sec. 4.9]. Considering the importance of natural mortality rates to the performance of our model, this has always been a major problem [Sec. 9.2].

Since March 1977 the Delta Department has determined the photosynthetic rate of phytoplankton samples taken from the Grote Rug and the three enclosures weekly (two-weekly in 1977). Samples were placed in an incubator and primary production was measured by the <sup>14</sup>C method. These data are of great value for calibration of the production estimates of the model and show some very intriguing differences between the three enclosures.

Because <sup>14</sup>C methods do not measure the rate of respiration, this had to be estimated from literature data. Indirect estimates of the natural mortality rates have been used to some extent [Sec. 8.4.1].

#### 4.5 PRIMARY PRODUCTION

The rate of primary production is determined by many environmental conditions, which moreover have a different impact on different species. Therefore each mathematical equation will always be a (rather simple) abstraction of reality. As in many dynamic models [Bierman, 1974; Nyholm, 1978; Scavia 1980], in the following the gross production rate constant  $P_g$  will be written as the product of various terms, which presumably act independently.

Given sufficient nutrients,  $P_g$  can be described as a function of temperature and light, which achieves a single maximum for any given temperature  $T$ , called  $P_{gmax}(T)$  at a particular light intensity that we call  $I_{opt}$ . If only a small portion ( $e_i$ ) of nutrient  $i$  is

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<sup>3</sup> By convention net production equals gross production minus respiration. Hence mortality or grazing are not yet accounted for. To compute the net rate of increase of the population, these and perhaps other loss processes must also be included.

left available,  $P_g$  could decrease by a factor  $g(e_i)$ , which is equal to or less than one, according as  $e_i$  is large or small. Similarly if light energy is scarce,  $P_g$  will decrease by a factor of  $E(I,T)$ , which depends on both temperature  $T$  and light intensity  $I$ :

- $I$  is the total radiation in Joules /  $m^2$  / hr of the photosynthetically active part of the spectrum.

$P_g$  may be calculated according to:

$$P_g(I,T,e_i) = E(I,T) * P_{gmax}(T) * g(e_i) \quad (4.3)$$

For the nutrient function  $g(e_i)$ , often the so-called Michaelis-Menten or Monod expression is used:

$$g(e_i) = \frac{e_i}{K_{e_i} + e_i} \quad (4.4)$$

in which  $e_i$  is the available external concentration and  $K_{e_i}$  the half saturation constant for nutrient  $i$ . An alternative approach using internal nutrient concentrations was proposed by Droop [1973], but Di Toro [1980] has demonstrated, that usually these two approaches give essentially indistinguishable results.

Eq. (4.4), or a similar function with a comparable effect, is usually included in dynamic models for technical reasons. These functions take care that the growth rate smoothly approaches to zero when a nutrient becomes depleted, thus preventing (1) phytoplankton growth at negative nutrient concentrations and (2) numerical integration problems.

In contrast there is no technical reason to include an equation for  $g(e_i)$  in BLOOM II. Because the nutrient mass-balance equations (3.6) are used as constraints in the linear program, negative dissolved nutrient concentrations ( $e_i$ ) are impossible. Furthermore, because it is a steady state model, there are of course no numerical integration problems.

We have decided not to incorporate a Monod or some other explicit equation for  $g(e_i)$  into BLOOM II for several reasons. First there is an additional complication, which may not be very important to models with one or a few species, but which is paramount to the performance of multi-species models. Unfortunately as it turns out species dominance in these models strongly depends on the values of the half-saturation constants  $K_{e_i}$ . Values for  $K_{e_i}$  are, however, certainly not available for many important phytoplankton species, several of which are included in BLOOM II. Moreover, as the experimental techniques improve, the established values for  $K_{e_i}$  seem to decline according to the literature. Thus it seems that the time when a species was last investigated strongly affects its ability to become dominant in model computations.

To illustrate how small values for  $K_{e_i}$  can be notice that the population of Aphanizomenon flos aquae in Ring 2 increased from less than 30 to over 340 mg chlorophyll/ $m^3$  within a few weeks in the spring of 1977, although the ortho-P concentrations were less or equal to 0.003 mg/l during this entire period.

Second dynamic models usually consider two or three nutrients, hence several functions  $g(e_i)$ . The question arises how these different functions interfere. In many models they are multiplied, but since  $g(e_i)$  is less or equal to one for each factor  $i$ , the growth rate tends to decrease as  $i$  becomes larger. Moreover it is unknown, whether indeed growth limiting terms of light and one or more nutrients should be multiplied. We could well argue, that phytoplankters will tend to maximize their growth rate under all conditions [Harris, 1978; Shuter, 1979], thus compensating for a nutrient or any other limitation by physiological adjustments. In that case the final growth rate would be higher than expected following a simple multiplication of all limitation terms.

Rather than using an explicit functional form for  $g(e_i)$ , we have assumed:

$$g(e_i) = 1 \quad \text{for any species limited by energy} \quad (4.5a)$$

$$g(e_i) < 1 \quad \text{for any species limited by a nutrient} \quad (4.5b)$$

Hence in the case of an energy limitation, nutrients do not affect the growth rates; in the case of a nutrient limitation, the bloom will be calculated according to Eq. (3.6) as if the growth rate were to remain sufficiently high for phytoplankton to achieve the nutrient-limited bloom level within a single time-step. This approach, of course, is consistent with the purpose of the model: maximizing the total biomass concentration.

We must add one final remark. If more and better data were available for  $Ke_i$  and if it could be shown, that these constants indeed determine species dominance in natural waters we could replace (4.5) by an equations such as (4.4). Thus we would include an additional term in the computation of the depth and time averaged rate of production. This would have an effect on the energy constraints [Chap. 5] and the (optional) growth rate constraints [Sec. 6.2.3]. Aldenberg [1981], however, shows that the linear program with a function  $g(e_i)$  and a dynamic model with the same function do not have to give the same answer.

#### 4.6 MAXIMUM PRODUCTION AND TEMPERATURE

It is generally believed that primary production is a two-step process: light absorption by pigments and transfer of electrons through a series of biochemical reactions [Parsons and Takahashi, 1973; Harris, 1978; and many others]. Absorption of light of course depends on the light intensity and will be discussed in Sec. 4.7. The rate of biochemical reactions is usually assumed to be temperature dependent. Indeed an overwhelming majority of investigations has indicated, that the maximum rate of production  $P_{gmax}(T)$  can be described as an exponential function (van 't Hoff type) of temperature, at least over the entire range of temperatures observed in lakes in the temperate climatic zones.

The maximum rate of primary production of many phytoplankton species is frequently measured, both in situ and in laboratories. Despite the large physiological differences between (groups of)

species, the interspecific variations are rather small, often less than a factor of two. Nevertheless, these differences have a significant impact on the results of the model and are therefore incorporated in BLOOM II. In the original bloom model [Bigelow et al., 1977]  $P_{gmax}(T)$  was equal for each species.

In the following we shall first review some of the relations published in the literature, which we shall later compare to Grote Rug observations. Following the practice of the original papers, we shall not always write the maximum production rate as a function of temperature.

As we have already pointed out in Sec. 4.4, many investigators measure the (maximum) net production (photosynthetic) rate  $P_{nmax}(T)$  rather than the (maximum) gross production (photosynthetic) rate  $P_{gmax}(T)$ . Since we are interested in the latter, we shall use the following relation:

$$P_{gmax}(T) = P_{nmax}(T) + R(T) \quad (4.6)$$

To enable a comparison between the equations discussed in the following sections these and the relation used by Di Toro et al. [1980], are plotted in Fig. 4.2.

#### 4.6.1 Literature data and observations

In a classical paper on the relation between temperature and growth of phytoplankton species in the sea, Eppley [1972] plotted more than a hundred observations on the maximum number of doublings per day ( $U_{max}$ ) from continuous cultures against  $T$  and drew an envelope curve through the highest points at each temperature. This curve, which can be regarded as an upperbound for all species, was described by the following equation:

$$U_{max}(T) = 0.851 * 1.066^T \quad [\text{doublings/day}] \quad (4.7a)$$

which is equivalent to:

$$U_{max}(T) = \text{EXP}(0.0639T - 0.16) \quad [\text{doublings/day}] \quad (4.7b)$$

from which, according to Eq. (4.1), the maximum net growth rate can be computed as:

$$P_{nmax}(T) = \log 2 * \text{EXP}(0.0639T - 0.16) \quad [1/\text{day}] \quad (4.7c)$$

Eppley's  $U_{max}$  curve was applied in the salt water bloom model, although erroneously (4.7b) was used in stead of (4.7c) [Bigelow et al., 1977, page 30].

Several comments can be made about Eppley's relation:

- It represents net production, thus respiration, natural mortality and grazing should all be accounted for separately.
- Most observations were on single-celled marine species of phytoplankton.
- Little observations were included for temperatures below 10° centigrade.
- In all cases species were grown under laboratory conditions with continuous illumination.

The restriction to marine organisms is no problem, since there are no fundamental differences between photosynthesis in fresh and in salt waters. Thus similar growth rates have been measured for many phytoplankton groups with representatives in both types of environment [Goldmann and Carpenter 1974; Harris, 1978].

Many eutrophic lakes are, however, dominated by blue-green algae with a completely different cell structure than any other group of phytoplankton species. In addition many blue-greens form large colonies. Hence we cannot simply assume that  $P_{nmax}(T)$  of blue-greens can be computed according to Eq. (4.7).

In contrast to (4.7) all the following relations are based upon a least squares fit through sets of data points. Thus in general they should yield lower values for the maximum production rate. This fit procedure seems, however, more appropriate for a limited number of data points than drawing an envelope curve. This is true in particular for data obtained from field populations under uncontrolled conditions.

Laws [1975] was impressed by the importance of the size on the maximum net growth rate of a phytoplankton cell, as observed for instance by Eppley and Sloan [1966] for diatoms and flagellates. Defining

—  $V_j$  is average volume of species  $j$  in cubic microns,

he proposed to describe  $P_{nmax}$  as a function of a species' volume:

$$P_{nmax}(V) = 4.27 * V^{-0.1075} \quad [1/day] \quad (4.8)$$

In contrast to Eppley's equation, Laws' includes multi-cellular species with great differences in average size, but no indication was given how to apply it at other temperatures than 20° centigrade. The constant 4.27 includes a correction for day lengths of 12 in stead of 24 hours. As may be seen, (4.8) and (4.7c) yield essentially the same values for small species (about 500 cubic micron) at a temperature of 20° centigrade. The maximum net growth rate of a species with a volume of 80000 cubic micron, which is a typical value for a blue-green algal colony, however, is only 0.58 times the value of a species of 500 cubic micron according to Eq. (4.8).

Among the few who have performed growth rate experiments with blue-greens, Foy, Gibson and Smith [1976] presented the following least squares equation based upon data of several species isolated from the highly eutrophic Lough Neagh in Northern Ireland:

$$P_{nmax}(T) = \log 2 * 0.1571 * 1.1126^T \quad [1/day] \quad (4.9a)$$

Their equation yields much lower values for  $P_{nmax}(T)$  than (4.7c) over the entire range of temperatures observed in natural lakes. However, Foy et al. discovered a great discrepancy between their equation and observed growth rates in Lough Neagh, which they largely contributed to a non-linear response of  $P_{nmax}(T)$  to changes in day length. In a second series of experiments under alternating day lengths, they obtained much higher  $P_{nmax}(T)$  values on a hourly basis. We have calculated an alternative equation from these data to arrive at:

$$P_{nmax}(T) = \log 2 * 0.5342 * 1.0621^T \quad [1/day] \quad (4.9b)$$

$P_{nmax}(T)$  values calculated according to Eq. (4.9b) are much higher than according to (4.9a), particularly at low temperatures. It is interesting that the temperature coefficient of (4.9b) is almost the same as Eppley's, but the difference in multiplication constant is still quite significant, indicating lower values of  $P_{nmax}(T)$  compared to other species.

Other authors have presented similar data, but more interesting than summarizing all of these is a comparison to observed production rates under natural conditions. There are many published data on observed photosynthetic rates of natural populations, although only some of these are useful to the model. Frequently results are expressed in incomparable units, or the dominant species are not reported. We shall therefore present only one literature example of a eutrophic lake and then discuss the results for Grote Rug.

Jones [1977a, 1977b, 1977c] has plotted  $P_{nmax}$  data for Kinnego Bay (a part of Lough Neagh). From his graph we have estimated that the regression equation is approximately:

$$P_{gmax} = 4.356 * 1.048^T \quad [mg O_2/mg Chl.hr] \quad (4.10a)$$

His equation was established for the two major groups in the bay: diatoms and blue-greens, using the in-situ light and dark bottle method. To compare (4.10a) to data obtained by the  $^{14}C$  method, it should be converted to milligram carbon per mg chlorophyll per hour by multiplication with the respiratory quotient (RQ), which is approximately 1.0 under normal circumstances [Strickland, 1960; Jewson, 1977] and the ratio of the molecular weights of carbon and oxygen (12/32). Hence (4.10a) is approximately equivalent to:

$$P_{gmax} = 1.634 * 1.048^T \quad [mg C/mg Chl.hr] \quad (4.10b)$$

In 1977 the Delta Department started its regular measurements of production rates in Grote Rug. For the entire data set the relation

between the maximum net production rate and the temperature is highly scattered. However, using the RID data on the presence of various phytoplankton groups, we were able to split the data set in two parts: one containing all data for periods, when blue-green algae were dominant, and one containing the rest of the data. The latter mainly consists of data on diatoms and flagellates. In addition we have excluded measurements for periods when the total chlorophyll concentration was less or equal to  $5 \text{ mg/m}^3$ . Results are shown in Fig. 4.1. For blue-greens, using all but two observations for 1977, we obtained:

$$P_{n\max}(T) = 0.756 * 1.081^T \quad [\text{mg C/mg Chl.hr}] \quad (4.11)$$

And for diatoms and flagellates:

$$P_{n\max}(T) = 1.178 * 1.045^T \quad [\text{mg C/mg Chl.hr}] \quad (4.12)$$

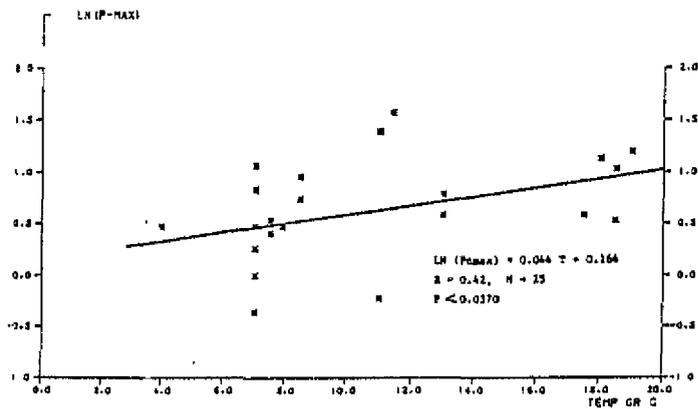


Figure 4.1a

Linear regression of logarithm  $P_{n\max}$  and temperature for diatoms and flagellates.

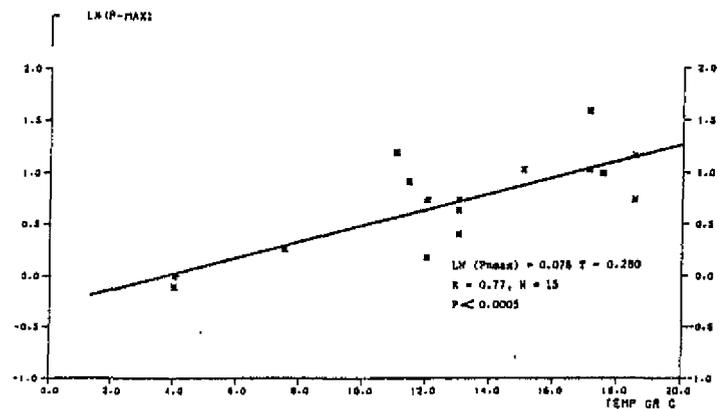


Figure 4.1b

Linear regression of logarithm  $P_{n\max}$  and temperature for blue-green algae.

Compared to (4.10b), both (4.11) and (4.12) yield much lower values over the entire temperature range, which is an illustration of the kind of problems encountered interpreting in situ production rates. It could be that production rates are higher in Kinnego Bay, but because carbon to chlorophyll ratios may vary by a factor of three, it could well be that actually growth rates per unit of time are higher in Grote Rug.

For a comparison between photosynthetic rates (in milligram carbon or oxygen per milligram chlorophyll per hour) and growth rates (in unit per day) either one of them has to be converted. The relation between oxygen and carbon measurements has been shown

before, hence we shall only give the conversion from milligram carbon per mg milligram chlorophyll per hour to daily growth rates.

To estimate the growth rate under continuous illumination, we propose a multiplication by 16 rather than 24 hours [Sec. 5.2], which is of course only an approximation. Furthermore we must divide the photosynthetic rates by the carbon to chlorophyll ratio, which has an approximate value of 30 for all species in Grote Rug upon which the Eqs. (4.11) and (4.12) are based. Hence to compare these equations to (4.7) and (4.9) they should be multiplied by 16/30 or 0.53. But we might well find another conversion more appropriate under different conditions. Because a higher carbon to chlorophyll ratio than 30 is more often observed than a lower value, this conversion tends to over-estimate growth rates calculated from photosynthetic rates.

As was mentioned earlier a plot of the various equations is given in Fig 4.2.

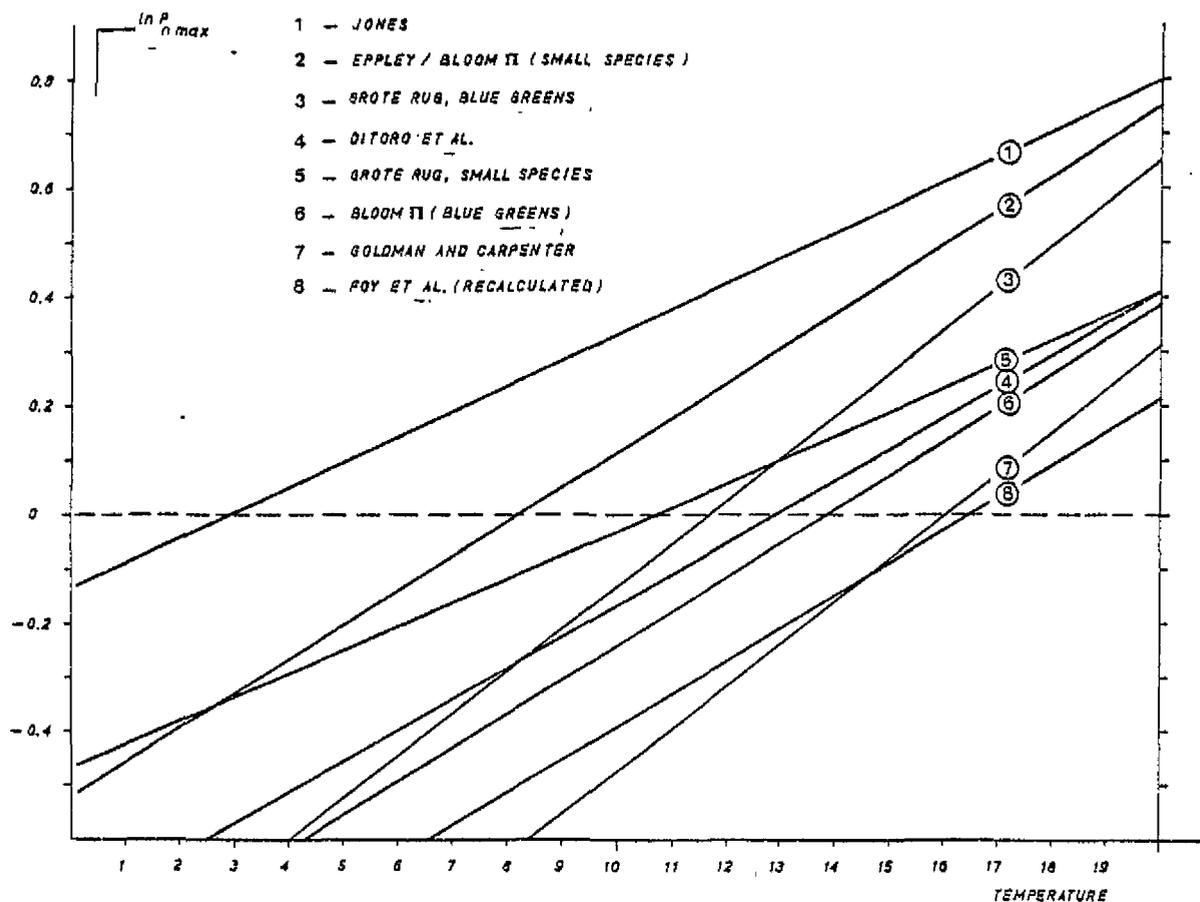


Figure 4.2 Equations to relate logarithm  $P_{n \max}$  per day to temperature in ° C. References are in the text.

#### 4.6.2 Calculation of maximum production in BLOOM II

Most equations given in the foregoing section have very similar temperature dependences. Values of the  $Q_{10}$  under laboratory condi-

tions are 1.89 [Eppley] and 1.83 [Foy et al.]. For natural populations the Q10 shows a broader range from 1.55 to 2.19. A survey of literature data indicates that these results are in agreement to what has been observed by almost anyone else, see for instance Goldman and Carpenter [1974], or Sakshaug [1977] in addition to references in Harris [1978], who reports values for the Q10 between 1.8 and 2.3. Since both Eppley and Foy et al. have reported almost identical values for the Q10 of the main groups of species in the model when they were grown under similar conditions, we have adopted the same temperature coefficient (Eppley's) for each species in BLOOM II.

We have some doubt about a Q10 value of 1.89 for dinoflagellates. Relatively low growth rates have been reported frequently for temperatures between 10° and 20° centigrade [Bruno and McLaughlin, 1977; Harris et al., 1979; references in Laws, 1980]. We have determined a Q10 value of 3.57 for the period when the dinoflagellate Ceratium hirundinella was dominant in Ring 2 in 1978 using the production measurements of the Delta Department. But the temperature range was too short (only about 5°) and moreover all low values of P<sub>nmax</sub>(T) were observed when the bloom was already declining. Hence the high value of the Q10 may have been caused by changes in the general health of the population rather than by changes in temperature. We concluded that there is presently insufficient information on controlled experiments at different temperatures to assume a higher Q10 value for dinoflagellates than for other groups of species.

Unfortunately a comparison of the constants in the various equations shows that there is less agreement on the absolute value of P<sub>nmax</sub>(T) than on the temperature dependence (Fig. 4.2). We must therefore make some assumptions. For small single-celled species we have adopted Eppley's equation, because it is based on so many data and is able to represent a large variety of observations reasonably well. For instance our Grote Rug Eq. (4.12) multiplied by 0.53 yields practically the same values at low temperatures as (4.7c), but starts to deviate from it at higher temperatures (Fig. 4.2). However, small species usually bloom at low temperatures in eutrophic lakes and moreover using a relatively high value of P<sub>nmax</sub>(T) at high temperatures is consistent to the objective of the model. Thus we are confident that (4.7c) is a reasonable estimate for P<sub>nmax</sub>(T) of small species under natural conditions.

There is reasonable agreement that blue-green algae have comparatively low maximum production rates [Harris, 1978]. According to Eq. (4.9b) of Foy et al. their P<sub>nmax</sub>(T) value is only 0.63 times the value of small species computed by Eppley's equation. As shown earlier, the ratio between the maximum production rate of blue-greens and of small species according to Laws' Eq. (4.8) is even smaller: 0.58.

Jones in contrast found no different value for the maximum photosynthetic rate of various species, and we have found a ratio of 0.64 at 0° but only 0.90 at 10° centigrade. Why the ratio between the production rates of large blue-greens and small species seems smaller under natural conditions than in the lab, is not obvious. A simple explanation would be if small species had lower carbon to chlorophyll ratios than blue-green algae because computed growth rates depend on these ratios [Sec. 4.6.1]. But based upon measurements by the Delta Department for several years we have established the same value of about 30 both for diatoms, and flagellates as for Aphanizomenon which provided most of the data points for Eq. (4.11).

As a compromise, we have assumed that  $P_{nmax}(T)$  of blue-greens is 0.7 times  $P_{nmax}(T)$  of small species. To obtain this difference a lower dependence on volume was assumed than suggested by Laws, namely a power of  $-0.07028$  instead of  $-0.1075$  (80000 divided by 500 to the power of  $-0.07028$  equals 0.70). Thus the final equation for the maximum growth rate in BLOOM II becomes:

$$P_{nmax}(T,V) = \log 2 * 1.3171 * V^{-.07028} * 1.066^T \quad [1/day] \quad (4.13a)$$

which is equivalent to:

$$P_{nmax}(T,V) = 0.9129 * V^{-.07028} * 1.066^T \quad [1/day] \quad (4.13b)$$

and:

$$P_{nmax}(T,V) = 1.0729 * \text{EXP}(0.0639T - 0.16) * V^{-.07028} \quad [1/day] \quad (4.13c)$$

Eqs. (4.13a,b,c) are completely equivalent to Eq. (4.7c) for a species with a volume of 500 cubic micron (an average value for a small, single-celled species). Because Foy et al. did not find an obvious difference between the maximum growth rates of various species of blue-green algae related to their volume, we have used the same volume of 80000 cubic micron for all blue-greens in the model.

As will be shown later, BLOOM II is not very sensitive to the exact ratio between  $P_{nmax}(T,V)$  of large and small species. The reason is that we have scaled the respiration rates to represent a specific fraction of  $P_{nmax}(T,V)$  at some given temperature, hence differences in  $P_{nmax}(T,V)$  are (partly) compensated by equivalent adjustments of the respiration rates.

$V_j$  is a species dependent constant, but as we have left out all subscripts  $j$  in this chapter, we shall maintain our original notations of  $P_{nmax}(T)$  and  $P_{gmax}(T)$ . In the model, however,  $P_{nmax}(T,V_j)$  and  $P_{gmax}(T,V_j)$  are used.

## 4.7 PHOTOSYNTHESIS, LIGHT AND TEMPERATURE

### 4.7.1 Photosynthetic efficiency and light

Since the mid 1950s, when techniques to measure photosynthetic rates were greatly improved, many results have been obtained relating production to light intensity. Some of these earlier results, especially those of Rhyther [1956], have become classical and are reproduced by Parsons and Takahashi [1973] and Bougis [1974] in their books on aquatic ecology. Usually production is an optimum-type function of light. The production rate increases with

increasing intensity  $I$ , as long as  $I$  is below  $I_{opt}$ . For intensities above  $I_{opt}$ , the production rate decreases as intensities increase.

To compare the curves of different species, we standardize them (i.e. divide by  $P_{max}(T)$ ). The standardized curves, which we call efficiency curves, range from 0.0 to 1.0. It is obvious from Eq. (4.3) that without nutrient limitation this scaling procedure exactly gives us the function  $E(I,T)$  for BLOOM II at a particular temperature.

Because several groups of species are included in BLOOM II, an efficiency curve should be specified for each. Unfortunately published production (or efficiency) curves of different authors show great variations [Lingeman-Kosmerchok, 1979a] even for a single species, mainly because generally accepted methodologies are lacking. Comparable results can only be obtained if all phytoplankters are cultivated at the same temperature, nutrient levels, light intensity, light regime, light spectrum etc. Moreover, the experimental conditions should be the same when production is measured. This, however, is usually not the case and as will be shown later [Chap. 5], differences between the initial slopes (hence  $I_{opt}$ ) in particular have large implications.

To obtain a consistent data set for the species in the model, a large experimental research project was initiated for WABASIM at the Microbiological Laboratory of the University of Amsterdam. The results were, however, not yet available for the model computations included in this report. For these we have used production curves which were measured by the Delta Department using samples from Grote Rug. There are some obvious disadvantages in comparison to laboratory measurements:

- Several species are present in each sample.
- The conditions previous to the measurements (light regime, nutrients, temperature) are by definition unique for each sample.

Still we think that the efficiency curves of the Delta Department are much more useful than similar results obtained by others because:

1. The number and frequency of measurements is unusually high (weekly data in four basins provide over 200 measurements a year).
2. Each of the four basins is sampled weekly, giving us the opportunity to compare each individual result to three others, which were measured under partly similar conditions of for instance temperature and surface light intensity.

Unfortunately the first year of primary production measurements (1977) only provided efficiency curves for a limited number of species. Phytoplankton concentrations were low and populations consisted of several species in all but one enclosure (Ring 2), which was dominated by a single species Aphanizomenon almost all year. Except for diatoms and flagellates, data for other (groups of) species were scarce or completely absent.

In 1978 there was a succession of diatoms and flagellates followed by Aphanizomenon flos aqua, then by Ceratium hirundinella and finally by Oscillatoria rubescens in the same enclosure according to the data of the RID

After two years altogether five to twenty curves were available for each group of species in the model, except green algae. We have

carefully selected those in which the environmental conditions before and during the measurements were very similar; for instance the temperature was always about 15° centigrade. Because usually different efficiency curves gathered for one group are almost identical so long as the temperature is the same, we are confident that the differences between photosynthetic efficiency curves of the species have a real ecological significance.

For green algae we use the same curve as for flagellates, since the small number of curves for this group resembled those of flagellates closely. A plot of the efficiency curves of the model is shown in Fig. 4.3.

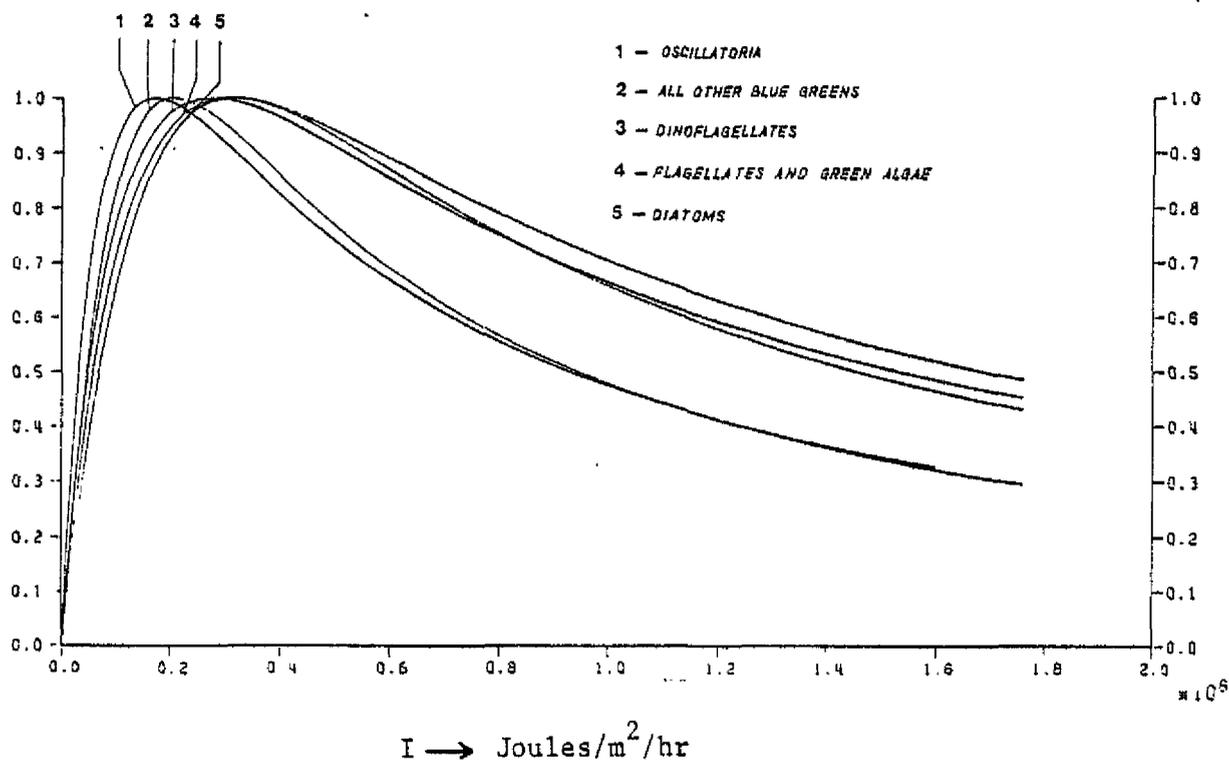


Figure 4.3 Photosynthetic efficiency curves of phytoplankton species in the model. Data derived from measurements by the Delta Department.

In the foregoing we have consistently used the term 'efficiency curve', as if it would be obvious how to fit a curve through the discrete points of measurements in a plot of production (efficiency) data against the light intensity. Actually this is not the case and many different equations for production curves have been proposed for instance by Smith [1936], Talling [1957], Steele [1958] and Murphy [1962]; see also the review by Patten [1968]. Recently an alternative equation was proposed by Eilers and Peeters of the Delta Department [unpublished]. Usually these equations have to satisfy two criteria: of course they should fit well, but moreover they should be integratable over depth and time to account for variations in light intensity under natural conditions. The last condition has sometimes led to a substantial simplification of

<sup>4</sup> Spline functions can be regarded as the mathematical analogue of 'fitting by eye'.

the equations with negative consequences for their ability to fit the observations.

As an alternative to each of these equations, several authors have used more empirical fit procedures. Among these are, of course 'fitting by eye', but also more sophisticated methods such as using 'splines'<sup>4</sup>. We will not, however, discuss any of these methods in detail.

In BLOOM II an empirical method is used. For each species the input of the model contains an efficiency value for a great number of light intensities (usually 34). Values at intermediate intensities are obtained by interpolation. These tabulated efficiency data sets are integrated numerically to account for variations in light intensity over depth and time [Chap. 5]. Notice that this procedure still enables us to use one of the earlier mentioned equations, because we can first fit some curve through the measurements and then feed the efficiency values of the equation rather than the measurements into the model. This procedure was usually employed with the production data of the Delta Department which were fitted by the Eilers - Peeters equation.

#### 4.7.2 Photosynthetic efficiency and temperature

So far we have only discussed the production efficiencies at a constant temperature, but we shall now investigate the effect of temperature. Given sufficient nutrients,  $g(e_i) = 1.0$  for each nutrient  $i$  in Eq. (4.3). Hence it follows from Eqs. (4.3) and (4.5a) that:

$$P_g(I,T) = E(I,T) * P_{gmax}(T)$$

and

$$E(I,T) = P_g(I,T) / P_{gmax}(T) \quad (4.14)$$

To compute the average efficiency in the model,  $E(I,T)$  must be integrated over  $I$ , as will be shown in Chap. 5. As, however,  $P_{gmax}(T)$  is an exponential function of temperature,  $E(I,T)$  is a function of temperature as well. Thus we shall find a different value for the average efficiency for each temperature, even if  $I$  is constant. This is a great computational disadvantage, which could force us to reintegrate  $E(I,T)$  for each temperature. In the following we shall demonstrate, that this reintegration can be circumvented by an appropriate transformation of the variable  $I$ .

The relation between the rate of production and the light intensity is basically a photochemical reaction. Thus we should not expect any effect of temperature so long as the light intensity is below  $I_{opt}$ , that is the initial part of the production curve should remain the same. When, however, the light intensity equals  $I_{opt}$ , temperature rather than light is limiting to the rate of production. Any further increase in light intensity has no effect (we will ignore the effect of photoinhibition for the moment).

If the temperature is changed, the initial part of the production curve remains the same, but the light intensity at which temperature becomes limiting ( $I_{opt}$ ), now has a different value because  $P_{gmax}(T)$  has changed. If the slope of the production curve is fairly linear until  $I$  approaches  $I_{opt}$ , we may even go one step further and suggest that the coefficient which describes the dependence of  $I_{opt}$  on temperature must be the same as for  $P_{gmax}(T)$ .

Harris [1978] gives some more physiological details and summarizes results for various phytoplankton groups. Indeed in the case of green and blue-greens algae,  $I_{opt}$  is a function of temperature, but he also gives an example of the diatom Asterionella formosa, in which the initial slope does change with temperature.

When a phytoplankton cell is exposed to a light intensity above  $I_{opt}$ , it may be damaged and the production rate goes down. This process is called **photoinhibition**. Repair of the damage is usually possible following certain chemical reactions which are exponential functions of temperature. Thus the rate of photoinhibition is also an exponential function of the temperature. Because the  $Q_{10}$  of most biochemical reactions is approximately 2.0, we can reasonably assume that the  $Q_{10}$  of photoinhibition and of  $P_{gmax}(T)$  are approximately the same.

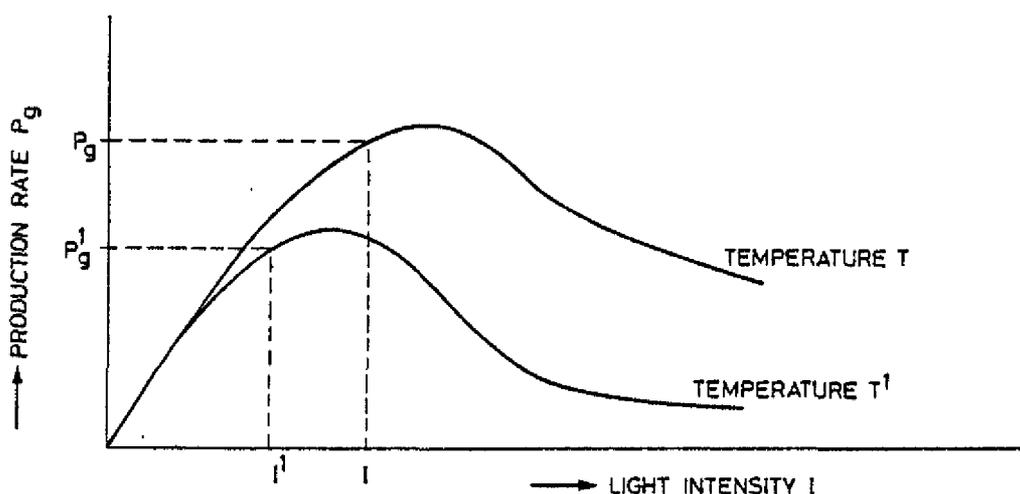


Figure 4.4 The gross production rate constant as a function of the light intensity  $I$  at two different temperatures  $T$  and  $T'$ .

The overall effect of temperature on the production curve is therefore as shown in Fig. 4.4. Notice that the initial slope remains the same and that the shape of the curves at two different temperatures are equal. Thus it follows that

$$\frac{I'}{I} = \frac{P_{g'}}{P_g}$$

or:

$$I' = I * \frac{Pg'}{Pg} \quad (4.15)$$

Since temperature only affects the gross production rate constant via  $Pg_{max}(T)$ , the ratio of  $Pg'$  at temperature  $T'$  and  $Pg$  at temperature  $T$  is according to Eq. (4.13c)

$$\frac{\text{EXP}[0.0639*T'-0.16]}{\text{EXP}[0.0639*T -0.16]} = \text{EXP}[-0.0639*(T-T')]$$

Hence

$$I' = I * \text{EXP}[-0.0639*(T-T')] \quad (4.16)$$

Thus we can transform  $E(I,T)$  to a function of a single variable  $I'$ , where

$$E(I') = E(I,T)$$

Because the efficiency curves used by the model are measured at a temperature of  $15^\circ$ ,

$$T' = 0.0639*15 = 0.96$$

hence Eq. (4.16) can be replaced by

$$I' = I * \text{EXP}(-0.0639*T-0.96) \quad (4.17)$$

Notice that  $I' = I$  at  $T = 15^\circ$ . We might call  $I'$  an equivalent intensity.

Before we continue we must add some comments on the temperature dependence of the net and gross maximum production rate constants. As we have shown earlier in Eq. (4.6)  $Pg_{max}(T)$  is computed adding  $R(T)$  to  $Pn_{max}(T)$ . Because respiration has a higher temperature dependence than  $Pn_{max}(T)$ ,  $Pg_{max}(T)$  and  $Pn_{max}(T)$  are different functions of temperature. However,  $R(T)$  is so small in comparison to both  $Pn_{max}(T)$  and  $Pg_{max}(T)$  [Sec. 4.8], that the difference in temperature coefficient of  $Pn_{max}(T)$  and  $Pg_{max}(T)$  created by Eq. (4.6) can be ignored for all practical purposes. According to Eq. (4.7a) the temperature constant of  $Pn_{max}(T)$  equals 1.066, adding  $R(T)$  we find a range of 1.066 to 1.069 for  $Pg_{max}(T)$ , depending on the specific respiration rates of different species in the model. Thus a relation between  $I_{opt}$  and temperature which is determined from measurements of the net rate of primary production, is also valid for the gross rate of primary production and can be used in the model.

So far out analysis has been theoretical. We shall now investigate if there is any evidence in the data of the Delta Department that Eq. (4.17) is indeed valid. For simplicity we shall consider one special light intensity namely  $I_{opt}$ , because it is much easier to compare the values of  $I_{opt}$  at different temperatures than of the entire efficiency curve.

As for  $P_{max}(T)$  the Delta Department has only correlated  $I_{opt}$  and temperature for a whole year data set of each separate basin and since none of them has a constant species composition, the correlations are obscured by species dependent differences in  $I_{opt}(T)$ . Nevertheless, a significant correlation was observed for each basin in 1977 with a temperature coefficient of 1.05 in one of them and 1.06 in the three others. These values are rather close to what we expected to find 1.066, the temperature constant of  $P_{max}(T)$  in BLOOM II.

As in the case of  $P_{max}(T)$  we have regrouped all measured values of  $I_{opt}$ . Each group consists of only those values when according to the RID one or several closely related species were clearly dominant. Next we have performed a linear regression of the logarithm of  $I_{opt}$  against temperature:

$$\text{Log}(I_{opt}(T)) = a \cdot T + b \quad (4.18)$$

The correlation was significant for each (group of) species (Fig. 4.5) with temperature coefficients close to 1.066 (Table 4.1).

Table 4.1

Linear regression of  $\text{Log}(I_{opt})$  and temperature for four (groups of) species in Grote Rug and the three enclosures in 1977 and 1978. Coefficient  $b$  is in  $\text{Joules}/\text{m}^2/\text{h}$  and  $P$  is the significance level.

Group/Species	a	b	P	Temperature range
diatoms	1.078	1.03 D05	0.0246	5.0 - 14.5
flagellates	1.081	7.93 D04	0.0005	7.0 - 18.5
Aphanizomenon	1.077	6.48 D04	0.0008	3.5 - 15.5
Oscillatoria <sup>1</sup>	1.058	5.91 D04	0.0002	1.5 - 14.0

<sup>1</sup> One exceptional measurement was excluded.

Although there are insufficient data for other species in Grote Rug, these results clearly demonstrate that  $I_{opt}(T)$  and  $P_{max}(T)$  have a very similar temperature dependence. Hence  $I_{opt}$  at a temperature of  $T$  degrees can indeed be calculated from  $I_{opt}$  at  $15^\circ$  according to:

$$I_{opt}(T) = I_{opt}(15) \times \text{EXP}(-0.0639 \cdot T + 0.96) \quad (4.19)$$

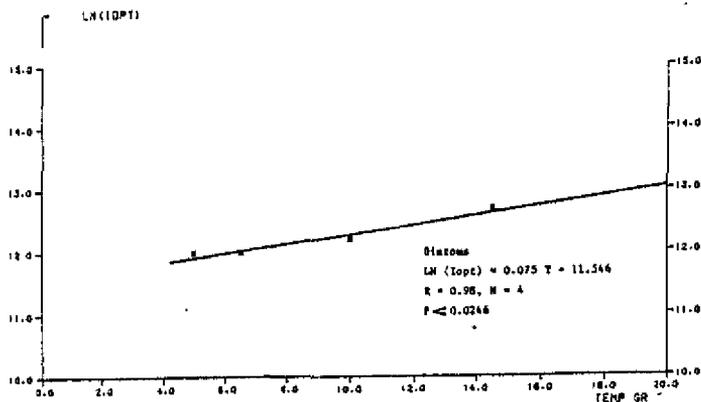


Figure 4.5a

Linear regression of logarithm Iopt and temperature for diatoms.

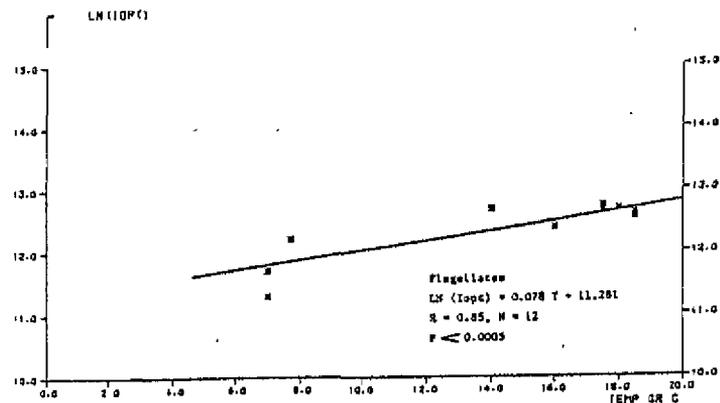


Figure 4.5b

Linear regression of logarithm Iopt and temperature for flagellates.

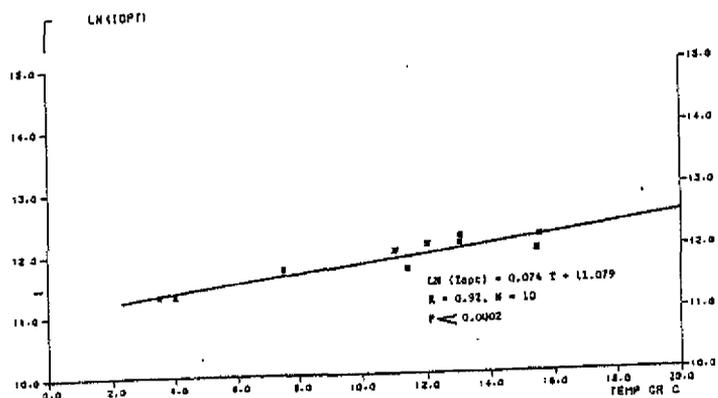


Figure 4.5c

Linear regression of logarithm Iopt and temperature for Aphanizomenon.

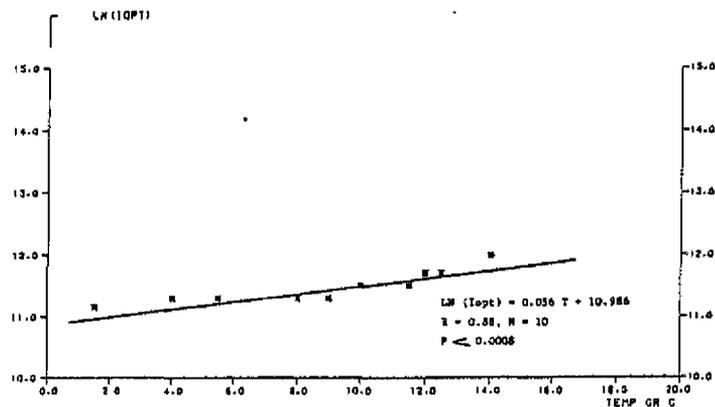


Figure 4.5d

Linear regression of logarithm Iopt and temperature for Oscillatoria.

### 4.7.3 Retrospective and additional remarks

At the beginning of Sec. 4.7 we have said that two distinct processes determine the rate of photosynthesis, one depending on the light intensity and one on the temperature. We have investigated both processes in detail and shown that for physiological reasons, both  $P_{gmax}(T)$  and  $I_{opt}(T)$  must not only depend on temperature, but also in strictly the same way. This prediction was confirmed by literature data and results of the Grote Rug production measurements.

The light intensity is highly variable in a natural environment, but temperature may well be considered constant during a week. Thus to calculate the average production rate during a time-step, we must integrate over I, but not over T: temperature effects appear as multiplication constants in the equations. Because E(I,T) is a function of temperature, it seemed as if we would have to integrate E(I,T) for each temperature which would be computationally unacceptable. This serious problem was completely overlooked by Bigelow et al. [1977], who had considered E(I,T) as a function of I only. However, we have showed that a simple transformation of I lets us compute an efficiency value for each temperature T given the standard efficiency curve at 15° C.

Summarizing: to compute the average efficiency at a given temperature T and light intensity I, the model (1) integrates the standard, 15° C efficiency curves and puts the results in a table, (2) transforms the light intensity I to the corresponding 15° value I', and (3) looks up the average efficiency at this transformed intensity level I' (and not I).

We have discussed one mechanism by which Iopt(T) could vary with season, but it may be argued that other factors, correlated with temperature, actually cause the variation in Iopt(T). We could assume for instance that Iopt(T) is a function of the light regime to which each phytoplankter adapts. If the average light intensity (Iav) would become low for example we might speculate that Iopt would decrease. Jorgensen [1969] has demonstrated adaptation to the average light intensity for several species, who either change (1) the amount of chlorophyll per unit of biomass, or (2) the rate of certain biochemical processes.

Integrating the Lambert-Beer equation (5.1), which computes the light intensity at each depth, it may be shown that approximately:

$$I_{av} = \frac{I_s}{K * Z_{max}}$$

where:

- Iav is the depth averaged light intensity,
- Is is the surface light intensity,
- K is the total extinction per m,
- Zmax is the maximum depth in m.

In most cases the surface light intensity (Is) and temperature are highly correlated, because they follow more or less the same annual pattern. However, as the extinction (K) is among others determined by the concentration of phytoplankton, the average light intensity is not necessarily correlated to temperature. Moreover the relation between the surface light intensity and temperature will be similar for many Dutch lakes in a particular year, because they are shallow and heat up or cool off rapidly in response to changes in surface light intensities. But as the extinction and the depth vary per lake, so does the relation between the average light intensity and temperature.

To investigate the relation between Iav and Iopt, we have performed linear regressions between:

1. The average light intensity (Iav) and the water temperature (T).
2. Iopt and temperature.
3. Iopt and the average light intensity Iav.
4. Iopt and temperature and the average light intensity Iav (multiple regression).

As for the regression between Iopt and temperature [Sec. 4.7.2] we have sorted the measurements according to species dominance during the observations. The significance levels are shown in Table 4.2.

Table 4.2

Significance level of linear regressions between Iopt, temperature, and Iav for periods when one (group of) species was dominant. Data from primary production measurements in Grote Rug in 1977 and 1978.

Group or Species	Iav to T	Iopt to T	Iopt to Iav	Iopt to T and Iav
diatoms	0.24	0.025	0.11	0.14
flagellates	0.01	0.0005	0.02	0.0029
Aphanizomenon	0.13	0.0002	0.002	0.0007
Oscillatoria <sup>1</sup>	0.01	0.0008	0.0001	0.0002

<sup>1</sup> One exceptional measurement was excluded.

From Table 4.2 we concluded that treating Iopt(T) as a function of temperature and not of the average light intensity or both temperature and the average light intensity is justified in the case of Grote Rug. For three out of four cases Iopt(T) is more strongly correlated to T than to Iav or Iav and T. Only for Oscillatoria both temperature and the average light intensity seem important. Notice that also in the case of Aphanizomenon, when Iav and T were not significantly correlated, the correlation between Iopt(T) and T was higher than between Iopt(T) and Iav.

One final remark: preliminary results of the incubator research project at the University of Amsterdam suggest that Iopt of several species grown at a constant temperature do change as a function of the average light intensity. Hence it may be necessary to include light adaptation in the model at a later stage.

#### 4.8 RESPIRATION

It takes a long sequence of biochemical reactions before the photochemical energy which was trapped by the pigments of a cell, has been transformed into chemical energy. There are often several different pathways and many intermediate products. Actual energy gains take only place at few of these reactions, when a molecule ADP and an ortho-P group form one molecule ATP.

If for some reason part of the sequence is blocked, intermediates may be excreted [Harris, 1978], or oxydized, thereby seriously reducing the number of ATP molecules that is formed. Glycolate for instance may be released but it may also react with O<sub>2</sub>, producing CO<sub>2</sub>, among others. This reaction, known as photorespiration, is favored by high light intensities and high internal concentrations of O<sub>2</sub> and seems important in many terrestrial plants. Green algae, however, are the only phytoplankters with the necessary enzyme system [Harris, 1978] and as the rate of photorespiration is presumably small, it seems unimportant in the present context.

Another process by which O<sub>2</sub> is taken up and CO<sub>2</sub> released, is known as dark respiration. Using substrates of the previous light period, it serves two functions: (1) formation of ATP plus reductants, and (2) formation of carbon skeletons. Raven [1976] makes a distinction between 'growth' and 'maintenance' respiration. 'Growth' respiration produces the ATP and carbon for new cell material and its specific rate is proportional to the specific growth rate of a species. 'Maintenance' respiration produces the ATP for the basal metabolism of the cells and its specific rate is independent of the specific growth rate.

Unlike suggested by its name, dark respiration usually continues in the light at approximately the same rate in many species. In species of blue-green algae, however, 'growth' respiration can decrease considerably at low light intensities, thereby reducing total respiration to 'maintenance' respiration only [Harris, 1978].

Strickland [1960], Harris [1978] and many others have shown that instantaneous dark respiration rates are difficult to measure. Moreover, as we already mentioned in Sec. 4.4, the usually employed <sup>14</sup>C method to estimate primary production does not allow respiration to be measured as well. As this method is also used in Grote Rug, our estimates of the respiration rates must be based on literature data.

Similar to P<sub>nmax</sub>(T), R(T) is usually described as an exponential function of temperature:

$$R(T) = \text{EXP}(A * T - B) \quad (4.20)$$

According to Harris [1978] R(T) usually varies between 0.05 and 0.20 times P<sub>nmax</sub>(T) at 20° centigrade. He also points out, however, that R(T) is a stronger function of temperature than P<sub>nmax</sub>(T) with a Q<sub>10</sub> between 2.3 and 2.9. Thus respiration becomes relatively less important as temperatures decrease. Dinoflagellates are the only phytoplankton group in which a higher ratio of R(T) to P<sub>nmax</sub>(T) has frequently been observed, as we shall later discuss in some detail.

The coefficients A and B for various (groups of) species (Table 4.3) have been established using results by: Mur et al. [1978] on blue-greens; Jones [1977a,b,c] on blue-greens and diatoms; Humphrey [1975] on diatoms and dinoflagellates; Falkowski and Owens [1978], Prezelin and Sweeney [1978] on dinoflagellates; Burris [1977] on dinoflagellates and various others; Raven [1976] on various species; the reviews by Strickland [1960], Parsons and Takahashi [1973], Harris [1978] and Lingeman-Kosmerchock [1979b] on various species.

Table 4.3.

Ratio of  $R(T)$  to  $P_{\max}(T)$  at  $20^{\circ}$  centigrade and  $Q_{10}$  values of  $R(T)$  for several groups of species. Coefficients A and B of Eq. (4.20) may be calculated using Eq. (4.13c) for  $P_{\max}(T)$ .

Group of Species	$R(20) / P_{\max}(20)$	$Q_{10}$
blue-greens	0.05	2.5
diatoms	0.125	2.5
flagellates	0.125	2.5
greens	0.125	2.5
dinoflagellates	0.20	1.89

The assumptions for dinoflagellates require some explanation. Originally we had assumed a ratio between  $R(T)$  and  $P_{\max}(T)$  of 0.30, which was already a low estimate considering that most literature values are between 0.30 and 0.50. But if such a large fraction of the maximum production would be required for respiration, the model could never compute a significant dinoflagellate bloom, because the sum of the loss terms would simply be too high. The high ratios reported in the literature can only be explained if respiration is considered as the **only** loss term. However, in BLOOM II we consider natural mortality and respiration [Sec. 4.3].

Our mortality estimate is based on the assumption that net photosynthesis is measured by the  $^{14}\text{C}$  method and that all calculated losses are uninfluenced by respiration [Sec. 4.9]. When we calibrated the model with this assumption, we found that a  $R(T)$  to  $P_{\max}(T)$  ratio of 0.20 for dinoflagellates resulted in a total loss rate in the model that was sufficiently low to reproduce observed bloom levels [Chap. 8].

With this new ratio of  $R(T)$  over  $P_{\max}(T)$  and a  $Q_{10}$  of 2.5, however, the only dinoflagellate species in the model, Ceratium frequently dominated computed winter blooms, which has never been observed in reality. One possible explanation has been given earlier in Sec. 4.6.2, where it was pointed out that the maximum rate of primary production could be a stronger function of temperature for dinoflagellates than for other species.

As another explanation consider the following. At  $20^{\circ}$  the respiration rates of dinoflagellates are about twice as high as those of other, physiologically similar species, because dinoflagellates need additional energy for buoyancy control [Sec. 5.7]. To regulate their position in a water column, dinoflagellates make active swimming movements. Assuming that they do so regardless of temperature, the extra energy required by these species should hardly be a function of temperature. Thus total respiration should be less temperature dependent than in other species such as flagellates: dinoflagellates have a lower  $Q_{10}$  for respiration. We have therefore assumed a  $Q_{10}$  value of 1.89 for respiration, the same  $Q_{10}$  value which is used for  $P_{\max}(T)$ .

We can illustrate this reasoning by the following example:

At 20°:

R(T) dinoflagellates = 0.40  
R(T) flagellates = 0.25  
Required for buoyancy control = 0.15 (0.40 - 0.25)

At 10°:

R(T) flagellates = 0.10 (0.25 / 2.5)  
R(T) dinoflagellates = 0.15 + 0.10 = 0.25

Hence the effective Q10 for respiration of dinoflagellates in this example equals 0.40 divided by 0.25 which is 1.6.

Notice that in contrast to Laws [1975] or Steele and Frost [1977], we have not assumed a dependence between R(T) and a species' volume. It seems that metabolic and ecological differences are much more important than differences in size. According to our present assumptions, the highest respiration rates are computed for species with intermediate sizes (dinoflagellates), which could never be explained if R(T) was a monotonously decreasing function of size.

#### 4.9 NATURAL MORTALITY

Although respiration and natural mortality are both loss terms, they are physiologically quite distinct. Respiration is mainly (though not entirely) a loss of carbonic substances (energy). But a healthy cell will avoid respiring proteins for example, unless conditions become extremely unfavorable. Thus respiration will not affect any of the nutrient cycles in the model.

After a number of divisions, particularly under unfavorable conditions, any phytoplankter will stop producing new cells and will eventually die. Afterward it disintegrates and releases its cell contents to the surrounding water. A certain fraction will be released in a form, that is available to living cells (our present estimate is 50 percent, Sec. 3.6.1), but the rest will be lost temporarily to the detritus pool and has to be remineralized. Thus mortality has two effects on a phytoplankton population: like respiration, it is a loss of energy, but because the whole cell disintegrates, it is also a loss of cell material (available nutrients).

As we have said previously [Sec. 4.4], there are no direct ways to measure the natural mortality rate constant because there is no selective distinction between dead cell materials and other organic substances. The only way to estimate M(T) is to subtract observed net changes in biomass from measured rates of production. Assuming that grazing can be ignored and defining

- Pn is the depth and time averaged net production rate constant per day, which is equal to the gross production rate constant Pg minus respiration,
- xav is the average phytoplankton concentration during interval Δt,

Eq. (4.2) may be rewritten as

$$M = P_n - \frac{1}{x} \frac{dx}{dt} \quad (4.21a)$$

which, for small values of  $dx/dt$ , can be approximated by:

$$M = P_n - \frac{\Delta x}{x_{av} \Delta t} \quad (4.21b)$$

Employing this indirect method to Grote Rug data for 1977, we concluded that

1. Both production and mortality rates are often large (up to 1.0 per day) compared to the observed net rates of change in phytoplankton populations (usually less than 0.1 per day). Hence net production and mortality are closely balanced.
2.  $M(T)$  is exponentially correlated to the water temperature,
3. But  $M(T)$  can become exceptionally low at any temperature. (A values of  $M = 0.0$  has been observed at  $15^\circ$  centigrade in Grote Rug).

Annual time series of  $M$  could not be related to any variable in a way that enables mortality rates to be computed in agreement with observed numbers. This has been recognized as one of the most serious problems in our model since the very beginning of the WABASIM project. Like most other phytoplankton models, BLOOM II is rather sensitive to the value of specific mortality rate constant [Chap. 9]. An extensive literature research provided little help, first because few people measure mortality, but second because other results [Jassby and Goldman, 1974; Megard and Smith, 1974], are equally unpredictable as those in Grote Rug.

In some dynamic models [see for example Nyholm, 1978] it is assumed that there is a negative feedback between  $M$  and  $x$  (steadily increasing mortality rates as a bloom rises). However, the theoretical background of this assumption is meagre. For example in Grote Rug we have observed quite the opposite: mortality rates achieved a minimum during a bloom and were relatively high when there was little phytoplankton.

Thus we had to conclude that we cannot compute mortality rates accurately with our present knowledge. Only the correlation with temperature seems reasonably well established. Therefore we have adopted an alternative approach in agreement with the model's purpose to estimate the highest feasible phytoplankton biomass concentrations. Obviously these are obtained if the mortality is set to the minimum value that might 'reasonably' be expected. Since mortality rates can become practically zero at any temperature, we could of course ignore mortality altogether. But with this assumption the model computes bloom levels which are unrealistically high in all but a few cases.

We have therefore set  $M(T)$  equal to a higher, temperature dependent value that we will call  $M_{min}(T)$ . Since we cannot measure mortality rates directly, we shall first consider an estimate of the minimum production rate  $P_{min}(T)$  rather than  $M_{min}(T)$ . Remembering how Eppley obtained his equation for  $P_{max}(T)$ , we have plotted all

observations of the net production rate per day in Grote Rug against temperature (Fig. 4.6). Next we have fitted an envelop curve by eye through the lower data-points at each temperature. We have followed this procedure not only for the entire data set, but also for the three enclosures and the main Grote Rug reservoir separately. Fortunately three out of four curves were rather similar. Only the minimum production rates in Ring 1 were considerably higher than in the other basins. The overall curve for the entire data set could be described as:

$$P_{min}(T) = 0.04 * 1.103^T \quad (4.22a)$$

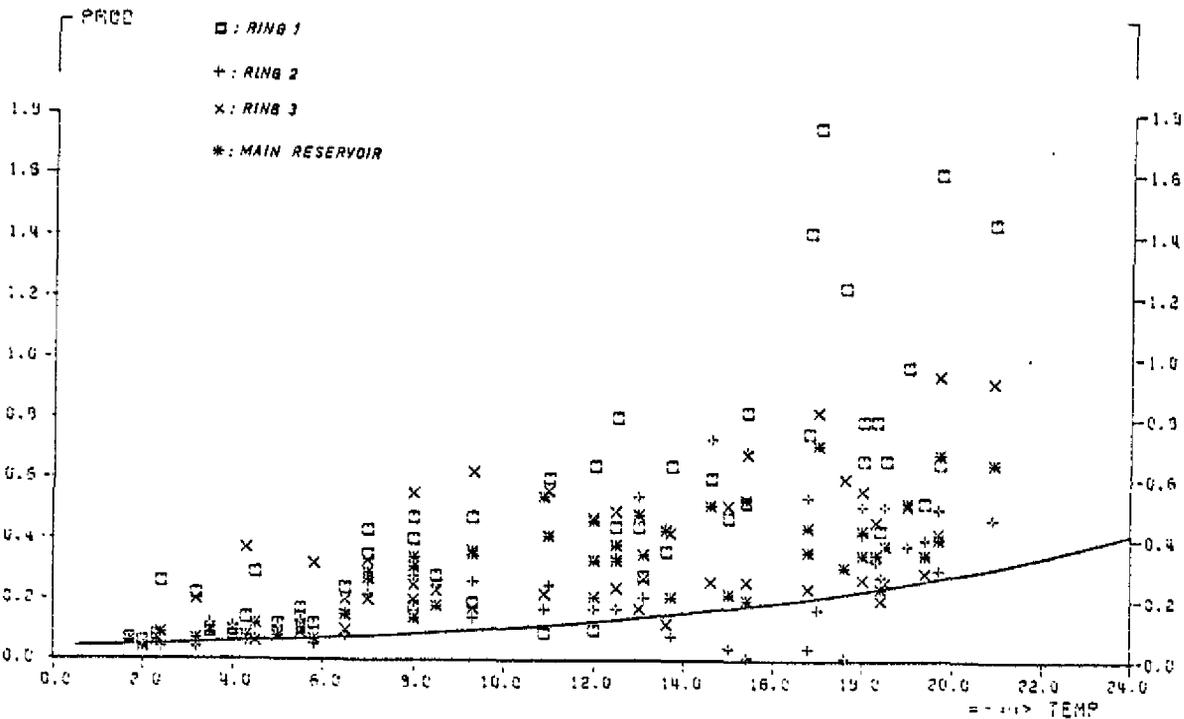


Figure 4.6 Production rate constant per day at different temperatures in Grote Rug 1977. The drawn curve represents the minimum estimate for mortality used by the model. Data from the Delta Department.

Of 204 data-points only 12 (6 percent) fell below this curve, most of them during the early summer bloom of Aphanizomenon in Ring 2, when Pn was close to zero for several weeks.

As previously remarked, there is often only a small difference in value between Pn and M, particularly during blooms and at low temperatures, when the model is most sensitive to variations in mortality. Thus we may also regard (4.22a) as an estimator for Mmin(T). Rewritten in its exponential form we obtain:

$$M_{min}(T) = EXP(0.098T - 3.219) \quad (4.22b)$$

Considering our present knowledge and the similarity in estimates of  $M_{min}(T)$  for blooms of different species, we currently use the same overall estimate for each species. Notice that this assumption does not imply that the actual mortality rates of different species should always be the same, but rather that all could have the same low mortality rate under favorable circumstances.

For the nutrient cycles of BLOOM II this means that the ratios between the amounts of nutrients in detritus and living phytoplankton are the same, regardless of the species in the bloom. Thus only the differences in stoichiometric constants  $a_{i,j}$  of the species determine which will dominate under nutrient limited conditions Eq. (3.7).

Whether or not our assumptions to estimate  $M_{min}(T)$  are reasonable, can only be verified comparing the performance of BLOOM II with observations. We should expect an over-prediction on most occasions, but an occasional under-prediction is not impossible. For example actual mortality rates in Ring 2 in 1977 were lower than computed by Eq. (4.22b) for  $M_{min}(T)$ . Hence BLOOM II under-predicts the peak of this bloom by almost a factor of two.

The sensitivity of the model for different values of  $M_{min}(T)$  is discussed later [Sec. 9.2].

## 5. AVERAGING THE PRODUCTION

### 5.1 INTRODUCTION

The light intensity encountered by, and hence the efficiency  $E(I,T)$  of, a phytoplankton cell, is not constant but varies with the water depth, turbulence and time. To account for these variations, the model must compute the average efficiency  $E_{AVG}$  in a certain period. Several biological and mathematical complications are involved in this computation which will be the subject of the next sections.

The mathematical procedures used in BLOOM II to calculate the average efficiency during a time-interval do not differ strongly from those developed by Bigelow et al. [1977] for the Oosterschelde bloom model. Modifications in the calculation of  $P_{gmax}(T)$ ,  $M_{min}(T)$ , and  $R(T)$  and even the temperature correction of  $E(I,T)$ , which were discussed in Chap. 4, change the values going into the integration routines rather than these routines themselves. The same holds for some additional modifications which are to be discussed in this chapter.

To calculate the average production during a time-step, it must be integrated over  $I$ :

$$\int P_{gmax}(T) * E(I,T)$$

and since  $P_{gmax}(T)$  is independent of the light intensity, we can write

$$P_{gmax}(T) \int E(I,T)$$

In other words our purpose is to find the integrated value of the production efficiency  $E(I,T)$ . To calculate this integral, we should average over the light intensity, thus we should account for:

1. Variations in time (day length, surface intensity, intensity pattern).
2. Variations over the depth.

Averaging over time presents some interesting biological problems. Averaging over depth is both mathematically and biologically interesting, because there is a positive and negative feedback between the total phytoplankton biomass and the depth averaged production rate  $P_g$ . With increasing phytoplankton biomasses the extinction becomes larger, hence the average light intensity and  $P_g$  decrease (self-shading). Theoretically,  $P_g$  could also become smaller as the average light intensity increases (photoinhibition). If the total extinction is low (little phytoplankton, a low background extinction), a decrease in biomass results in a higher average light intensity. Hence the time spend by phytoplankton at super-optimal light intensities is increased and  $P_g$  becomes lower. However, the average light intensities in eutrophic waters are usu-

ally very low. Thus self-shading is a much more common phenomenon than photoinhibition.

As we have shown in Sec. 4.7.2, we can transform  $E(I,T)$  to  $E(I')$  where  $I'$  is an exponential function of the temperature. Thus to simplify the notations we shall write  $E(I)$  for  $E(I,T)$  in several sections of this chapter.

## 5.2 AVERAGING OVER TIME: BASIC ASSUMPTIONS

Define:

- DL is the number of hours between sunrise and sunset, in this report called the 'day length'.

According to Bigelow et al., averaging over time is straightforward. They had made two implicit assumptions:

1. The production efficiency is a linear function of the day length; thus the integrated production for a day with DL hours of light, equals  $DL/24$  times  $P_g$  under continuous illumination.
2. The phytoplankton cells are well mixed through a column of water, and each cell spends an equal amount of time at each depth. Hence the frequency at which the light intensity varies is unimportant.

Many laboratory results on phytoplankton growth rates such as those reviewed by Eppley [1972] have been performed with a constant illumination during 24 hours a day. The light intensity under natural conditions, however, shows more variations than any other environmental factor. Thus we should be very careful in extrapolating results of laboratory experiments.

Experiments with alternating light and dark periods are a first step towards more realism, although usually the light intensity during the day period is still kept constant. The results for different species seem to fall into three general categories:

1. Growth rates saturate, sometimes even decrease, at moderate day lengths (between 12 and 16 hours). This has been observed for some diatoms [Castenholz, 1964; Paasche, 1968; Admiraal, 1977; Humphrey, 1979] and for some flagellates [Humphrey, 1979]
2. Growth rates saturate at approximately 16 hours and are more or less proportional to  $DL/16$  for shorter day lengths. This has been observed for some diatoms [Castenholz, 1964; Paasche, 1967; Humphrey, 1979], some flagellates [Paasche, 1967], Greens [Eppley and Coatsworth, 1966; Humphrey, 1979; Loogman, 1980] and for some blue-greens [Foy et al., 1976; Loogman, 1980].
3. Growth rates saturate at a day length of 24 hours. This has been observed for some green algae [Paasche, 1967].

It seems well established that at a day length of DL hours, most species acquire higher growth rates than expected according to a simple proportionality factor  $DL/24$ . In most cases a factor of  $DL/16$  seems more appropriate. Because there is insufficient infor-

mation on the individual species in the model, we have for each of them assumed that the growth rates for the natural day lengths (8 to 16 hours in the Netherlands) are equal to DL/16 times those observed under constant illumination during 24 hours a day.

In some recent experiments there is not only a light and a dark period, but also a variable light intensity during the period of day light to simulate the daily rhythm. Some investigators even attempt to simulate variations in light intensity due to mixing: superimposed on the daily cycle are variations in intensity between zero and the maximum light intensity at the current part of the cycle. Marra [1978], who has published results on a number of marine species, remarked that fluctuations in irradiance enable a phytoplankter (1) to avoid photoinhibition and (2) to benefit several times from the high initial rate of photosynthesis, which is often observed after a relatively dark period ('flashing light effect').

Comparing growth rates of Oscillatoria agardhii to those of Scenedesmus protuberans under different light regimes Loogman [pers. comm.] observed an interesting difference. The blue-green alga, which has a greater production efficiency at relatively low light intensities than the green alga, was much better able to maintain a constant daily growth rate at different ratios between light and dark periods. These and similar results could be of great importance to our understanding and modelling of phytoplankton. Unfortunately, they are far too scarce up to this moment to be useful to the model.

### 5.3 AN APPROXIMATE SOLUTION FOR THE AVERAGE EFFICIENCY

Before we discuss how the average efficiency of each phytoplankton species is computed in BLOOM II, we shall first consider a simplified solution, in which the relations between various parameters are more transparent than in the more sophisticated solution of the model. Furthermore we can easily use the simplified solution for a discussion of the time-scales of phytoplankton populations [Sec. 5.5].

To integrate  $E(I,T)$  analytically over  $I$ , we must describe it by one or several functions. Considering the purpose of our solution, we have simply approximated  $E(I,T)$  by two straight lines: one for the initial part of the efficiency curve (from  $I=0$  to  $I=I_{opt}$ ) and one for the descending part of  $E(I,T)$  ( $I > I_{opt}$ ). These two lines are shown in Fig.5.1.

Define the following symbols in addition to those previously defined:

- $I_{max}$  is the highest light intensity considered for  $E(I,T)$  which is set to  $1.75 \cdot 10^6$  Joule/m<sup>2</sup>/hr,
- $E_{inb}$  is 1.0 minus the efficiency at  $I=I_{max}$ .  $E_{inb}$  is in the order of 0.75 in winter and 0.50 in summer for most species according to the efficiency data of the Delta Department,
- $K_b$  is the background extinction per m,
- $K_l$  is the total extinction due to live phytoplankton per m ( $\sum_j K_j x_j$ ), where:
- $K_j$  is the specific extinction in m<sup>2</sup> per mg dry weight of living cells of species  $j$ .

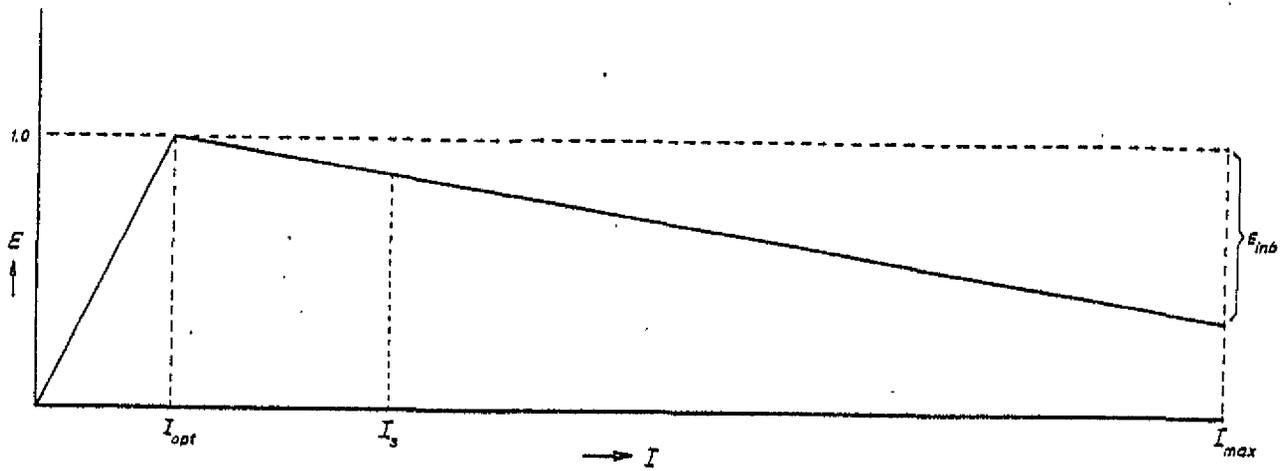


Figure 5.1 Simplified photosynthetic efficiency curve of a phytoplankton species.

Step 1: is to integrate  $E(I,T)$  over the maximum mixing depth  $Z_{max}$ . If light absorbing particles are homogeneously distributed, the light intensity  $I_z$  at a depth of  $z$  meters is, according to the Lambert-Beer equation, equal to:

$$I_z = I_s * \text{EXP}(-K.z) \quad (5.1)$$

In which

$$K = K_b + K_l + K_d \quad (5.2)$$

To average the efficiency over depth, we must calculate:

$$\frac{1}{Z_{max}} \int_0^{Z_{max}} E(I_s * \text{EXP}(-K.z)) dz \quad (5.3)$$

Using Eq. (5.1) we find that

$$\frac{dI}{dz} = -K * I_s * \text{EXP}(-K.z) = -K * I$$

Hence

$$dz = \frac{-1}{K * I} dI$$

Thus with the appropriate transformation of the integration limits, and defining

-  $I_{Zmax}$  as the light intensity at the bottom ( $z=Z_{max}$ ),

we can rewrite Eq. (5.3) to

$$\frac{1}{K \cdot Z_{max}} \int_{I_{Zmax}}^{I_s} E(I) \frac{1}{I} dI \quad (5.4)$$

From Fig. 5.1 obviously

$$E(I) = C_1 \cdot I \quad (I < I_{opt})$$

$$E(I) = C_2 - C_3 \cdot I \quad (I_{opt} \leq I \leq I_{max})$$

From Fig 5.1 it is easily verified, that:

$$C_1 = 1/I_{opt}, \quad C_2 = 1 + \frac{E_{inb} \cdot I_{opt}}{I_{max} - I_{opt}} \quad \text{and} \quad C_3 = \frac{E_{inb}}{I_{max} - I_{opt}}$$

Thus to integrate  $E(I)$  over  $I$ , we must find:

$$\int_{I_{Zmax}}^{I_{opt}} C_1 dI - \int_{I_{opt}}^{I_s} C_3 dI + \int_{I_{opt}}^{I_s} C_2/I dI$$

which yields for the depth averaged efficiency EDEP:

$$EDEP = \frac{1}{K \cdot Z_{max}} \left[ \left( 1 - \frac{I_{Zmax}}{I_{opt}} \right) - \left( \frac{E_{inb} (I_s - I_{opt})}{I_{max} - I_{opt}} \right) + \left( 1 + \frac{E_{inb} \cdot I_{opt}}{I_{max} - I_{opt}} \right) \log \frac{I_s}{I_{opt}} \right] \quad (5.5)$$

**Step 2:** averaging over time is trivial as at any instant most phytoplankton is found in regions where  $I < I_{opt}$ , because usually the depth averaged light intensity  $I_{av} < I_{opt}$ . Then assuming there are no 'flashing light effects' on  $E(I)$ , the time and depth averaged efficiency EAVG is:

$$EAVG = \frac{DL}{16} EDEP \quad (5.6)$$

The term between the first pair of brackets in Eq. (5.5) is the efficiency for light intensities below  $I_{opt}$ . As usually  $I_{Zmax} \ll I_{opt}$ , this first term in the expression for EDEP is always close to 1. The term between the second pair of brackets indicates the effect of photoinhibition. This term is in the order of 0.00 to 0.05 in winter when:

$$I_{opt}, I_s \ll I_{max}$$

and in the order of 0.1 to 0.2 in summer when  $I_{opt}$  has increased by a factor of 3 [Sec. 4.7.2] and  $I_s$  by a factor of 10.

The remaining part of the expression represents the effect of saturation. The expression in front of the logarithm is in the order of 1.00 to 1.05 in winter and 1.05 to 1.10 in summer and the log term is in the order of  $\log 1$  to  $\log 2$  in winter and  $\log 2$  to  $\log 4$  in summer. Thus for a typical winter situation with a day length of 8 hours, approximately:

$$E_{AVG} = \frac{8/16}{K \cdot Z_{max}} (1 - 0.03 + 1.03 \cdot \log 1.5) = \frac{0.7}{K \cdot Z_{max}}$$

and for a typical summer situation with a day length 14 hours, we may obtain:

$$E_{AVG} = \frac{14/16}{K \cdot Z_{max}} (1 - 0.15 + 1.08 \cdot \log 3) = \frac{1.8}{K \cdot Z_{max}}$$

Notice that the increased efficiency in summer is mainly due to a greater number of day light hours and not to a larger efficiency per hour.

Photoinhibition is always small under typical eutrophic conditions: in winter, the second term of Eq. (5.5) decreases EDEP by only  $0.03/1.4$  which is about 2 percent, and in summer this ratio has only increased to  $0.15/2$  or about 7.5 percent.

In Sec. 4.7.2 we have shown that  $E(I,T)$  must be corrected for temperatures other than  $15^\circ$  centigrade. But instead of changing  $E(I,T)$ , we said that a transformation of the surface intensity ( $I_s$ ) would yield the same result. It is easily verified that indeed this is the case in our simplified solution. Multiplying  $E(I,T)$  by a constant  $w$  means writing  $w \cdot I_{opt}$  for  $I_{opt}$  and  $w \cdot I_{max}$  for  $I_{max}$  in Eq. (5.5). Rescaling  $I$  means writing  $I_s/w$  in stead of  $I_s$  in Eq. (5.5). Both transformations yield exactly the same value for EDEP.

$E_{AVG}$  is inversely proportional to the product of the extinction ( $K$ ) and the depth ( $Z_{max}$ ), hence extinction and depth are reciprocal terms. Suppose light is limiting to the bloom, the depth is  $Z_1$  meters and the total extinction is  $K_1$ . If the depth increases from  $Z_1$  to  $Z_2$ , than in order to maintain the same efficiency

$$K2 = \frac{Z1}{Z2} K1$$

or using Eq. (5.2):

$$K12 + Kd2 = \frac{Z1}{Z2} (K11 + Kd1) + \left( \frac{Z1}{Z2} - 1 \right) Kb \quad (5.7)$$

This expression shows, that under light limited conditions mixing depth and extinction (i.e. biomass) are strongly related. Often the background extinction is smaller than the sum of the extinctions by live and dead phytoplankton particles. Therefore phytoplankton biomass tends to become inversely proportional to depth. Thus an increase in depth will cause a large decline of the maximum potential biomass. On the other hand, a decrease in effective mixing depth due to buoyancy regulation by blue-green algae and dinoflagellates leads to a considerable increase in potential biomass, as we shall later discuss in more detail.

These conclusions also hold for the more sophisticated solution used by BLOOM II, thus they are no artefacts of our simplistic approach.

#### 5.4 SOLUTION OF BLOOM II FOR THE AVERAGE EFFICIENCY

We shall now consider how the average efficiency is computed in BLOOM II. This part of the model is basically similar to Sec. 5.4 of Bigelow et al. [1977]. The depth averaged efficiency EDEP is according to Eq. (5.3):

$$EDEP = \frac{1}{Z_{max}} \int_0^{Z_{max}} E[I_s * EXP(-K.z)] dz$$

Introduce a new variable s:

$$s = K.z - \log I_s, \text{ hence: } z = \frac{s + \log I_s}{K}$$

Also:	$dz = ds/K$	
and:	$s = K*Z_{max} - \log I_s$	(z=Z <sub>max</sub> )
	$s = -\log I_s$	(z=0)

Thus Eq. (5.3) is transformed to:

$$EDEP = \frac{1}{K*Z_{max}} \int_{-\log I_s}^{K*Z_{max} - \log I_s} E [ \text{EXP}(-s) ] ds$$

Next define:

$$F(v) = \int_0^v E [ \text{EXP}(-s) ] ds$$

Then obviously:

$$EDEP = \frac{F(K*Z_{max} - \log I_s) - F(-\log I_s)}{K*Z_{max}} \quad (5.8)$$

This equation only holds for a constant light intensity  $I_s$ ; therefore the next step is to account for variations in light intensity with time. Writing  $I_s(t)$  as a function of time, define:

$$G(v) = \frac{1}{24} \int_0^{24} F[ v - \log I_s(t) ] dt \quad (5.9)$$

Then the time and depth averaged efficiency EAVG is:

$$EAVG = \frac{G(K*Z_{max}) - G(0)}{K*Z_{max}} \quad (5.10)$$

Eq. (5.10) only holds for one specific function  $I_s(t)$  in other words: only for the intensity pattern of one particular day. So theoretically, we must recalculate Eq. (5.10) for each day. However, Bigelow et al. have shown that two important changes of  $I_s(t)$  are possible without recalculation of Eq. (5.10):

1. A change in the number of day light hours, but with the same intensity pattern  $I_s(t)$ .
2. A change in intensity at each instant by a constant fraction  $w$ .

Any combination of the two can also be accommodated for. Strictly speaking the average intensity pattern is a function of season, and moreover the actual intensity at any instant depends on stochastic events such as cloud cover. There is no practical way to deal with these factors, however, and there is no reason to expect a major impact on the average efficiency, because phytoplankton cells spend most of the time at light intensities below  $I_{opt}$ , where the response of  $E(I,T)$  to changes in irradiance is fairly linear.

Finally define:

$$H(v) = \frac{1}{DL} \int_0^{DL} F[v - \log I_s(t)] dt \quad (5.11)$$

hence:

$$EDEP = \frac{DL}{24} \frac{H(K*Z_{max} - \log w) - H(-\log w)}{K*Z_{max}} \quad (5.12a)$$

Eq. (5.12a) is replaced by Eq. (5.12b) in BLOOM II, because we assume the efficiency to be proportional to DL/16:

$$EAVG = \frac{DL}{16} \frac{H(K*Z_{max} - \log w) - H(-\log w)}{K*Z_{max}} \quad (5.12b)$$

As in the simplified solution (Eqs. (5.5) and (5.6)) EAVG is strongly determined by the term DL/(16\*K\*Z<sub>max</sub>) in Eq. (5.12b).

## 5.5 TIMESCALE OF PHYTOPLANKTON GROWTH

### 5.5.1 Introduction

Rapid variations in phytoplankton populations have been observed frequently, both under laboratory and under natural conditions. Usually, however, concentrations change more gradually, which could be caused by a slow approach to some steady state, but also by slowly altering environmental conditions.

To investigate, how rapidly phytoplankton populations can approach equilibrium under various environmental conditions, we shall use a numerical solution for the basic set of differential equations of the model:

$$\frac{dx_j}{dt} = [Pg_{max}(T)_j \cdot EAVG_j - M_{min}(T) - R(T)_j - G_j] x_j \quad (5.13)$$

EAVG<sub>j</sub> in Eq. (5.13) is computed according to the simplified solution (Eq. 5.5 and 5.6)).

Whether a species can achieve equilibrium within a particular time-interval is determined by:

- The difference between the equilibrium and initial biomass. (How far is it from equilibrium?).
- Its rate of change. (How quickly does it approach equilibrium?).

Our calculations are for three typical situations in different parts of the year, using the coefficients of a characteristic species. We shall investigate how rapidly a species can approach equilibrium beginning at various initial conditions with 'zero', here defined as 10 percent of the equilibrium value, as the most extreme value.

Notice that the results of the next section only give an order of magnitude: they are based upon an approximate solution for a single species under average conditions etc. Deviations from average conditions in particular may have a large impact. For instance the intensity of solar radiation can easily vary by a factor of five under winter and spring conditions.

Our analysis focuses on energy as the ultimate limiting factor. If a bloom were nutrient limited equilibrium would always be approached more quickly in the model because:

1. By definition the equilibrium value is lower (otherwise it would not be nutrient limited).
2. The average efficiency (hence the net growth rate) is always larger, since we have assumed that growth rates are independent of the nutrient concentrations [Sec. 4.5].

The value of EAVG computed by the approximate solution agrees reasonably well to the value calculated by BLOOM II. Typically there is less than  $\pm 20$  percent difference between the steady states calculated by BLOOM II and those calculated by the simplified solution.

The program for the time-scale calculations was written on a TI 59 pocket calculator, using Runge-Kutta methods with a fixed time-step.

### 5.5.2 Steady state assumption

The most characteristic winter species of the model is Oscillatoria because its efficiency curve has the steepest initial slope. We have calculated its potential growth rate under extremely unfavorable conditions such as infrequently occur for more than about a month in a normal Dutch winter. From the results (Fig. 5.2) we concluded that

1. Biomass can only change by about 10 to 20 percent per week, regardless whether energy is limiting or some nutrient. Thus the species can only maintain a steady state if the environmental conditions change slowly.
2. The efficiency is too low to enable a rapid increase of the population, even if self-shading is insignificant. On the other hand the specific mortality and respiration rate constants are too low to enable a rapid decline of a dominant species. Hence a (complete) shift in species dominance will require many weeks.

Spring blooms, which are typically dominated by diatoms and flagellates, often develop remarkably fast. As in winter temperatures are low ( $5^{\circ}$  or less), but the day length and solar intensity are significantly higher. From the results (Fig. 5.3) we concluded that

1. Biomass concentrations can change by a factor of 2 to 4 per week as long as the population size is smaller than

half its energy limited equilibrium value. Hence, moderately large changes in phytoplankton concentrations are possible within a week, particularly if a nutrient (silicon) would be exhausted before energy.

2. The minimum amount of time required to build up an equilibrium population starting at concentration 'zero' is still several weeks. If the limiting factors persist, however, and particularly after one or two bright weeks, a species should be able to approach equilibrium within 2 to 4 weeks.

In summer (here defined as May through September) blue-greens are frequently dominant. Our calculations are for one of the slowest growing species in the model, Aphanizomenon with a higher specific extinction than Microcystis or Oscillatoria. Thus it suffers more from the adverse effects of self-shading. From Fig 5.4 we concluded that

1. A population could easily change in abundance by a factor of 5 or more during one week if the initial concentration were low. Hence it can maintain a steady state, even if the environmental conditions change rather drastically during a short time-interval.
2. When the initial concentration is 'zero' there is no self-shading ( $K=K_b$ ) and the population can achieve a net growth rate of no less than 2 per day. After about two weeks the concentration will be within 20 percent of the steady state value. Therefore, rapid changes in species dominance seem possible, not in the least considering that Aphanizomenon populations change slowly compared to those of other species.

With respect to the time-scale of phytoplankton we can draw the following conclusions:

1. In summer, when in nature many of the worst blooms occur, large variations in the steady states of succeeding time-periods may be followed rather easily by a phytoplankton population. Although the moment when a shift in composition of the bloom occurs, may not always be predicted exactly, the difference should only be one or two weeks.
2. In spring, between 1 and 3 weeks seem sufficient to achieve equilibrium. Complete changes in species composition, however, require a longer period of time.
3. In winter, all phytoplankton species can only grow or decrease slowly. Hence they are unable to follow large variations in environmental conditions, particularly if these would ultimately lead to a shift in species composition.

Considering that BLOOM II is a management model to predict size and composition of objectionable blooms, we concluded that it would be reasonable to assume a steady state for phytoplankton with a one-week time-step, because the worst blooms usually occur in summer. But there are obviously periods, when this time-scale is too short, at least if the model predicts a shift in the composition of the bloom. How this affects the performance of the model depends, however, not only on the growth rate but also on the initial biomass. If the steady states of succeeding periods have about the same value and composition, the model's result may still be

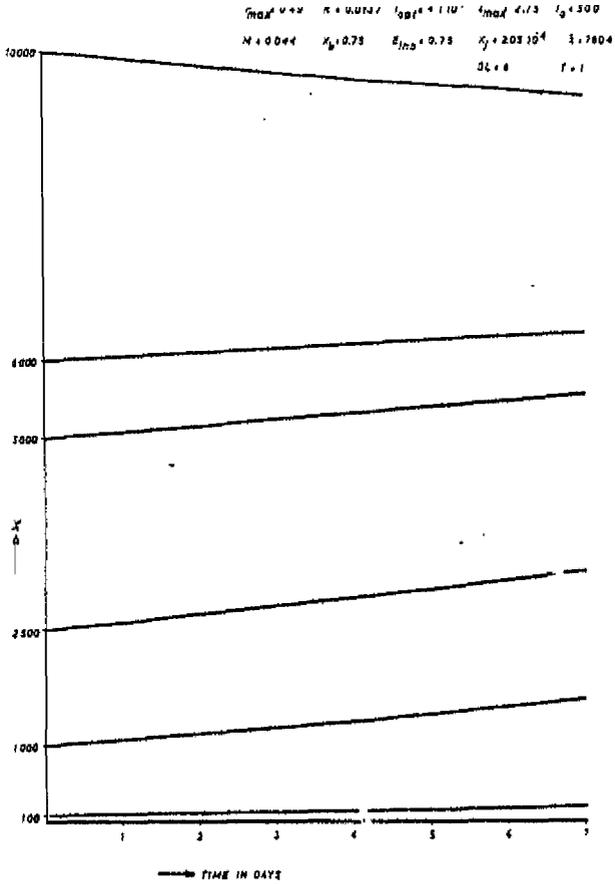


Figure 5.2

Approach to steady state ( $\bar{x}$ ) under severe winter conditions of a species according to the simplified solution of the growth equation. Symbols are defined in the text.

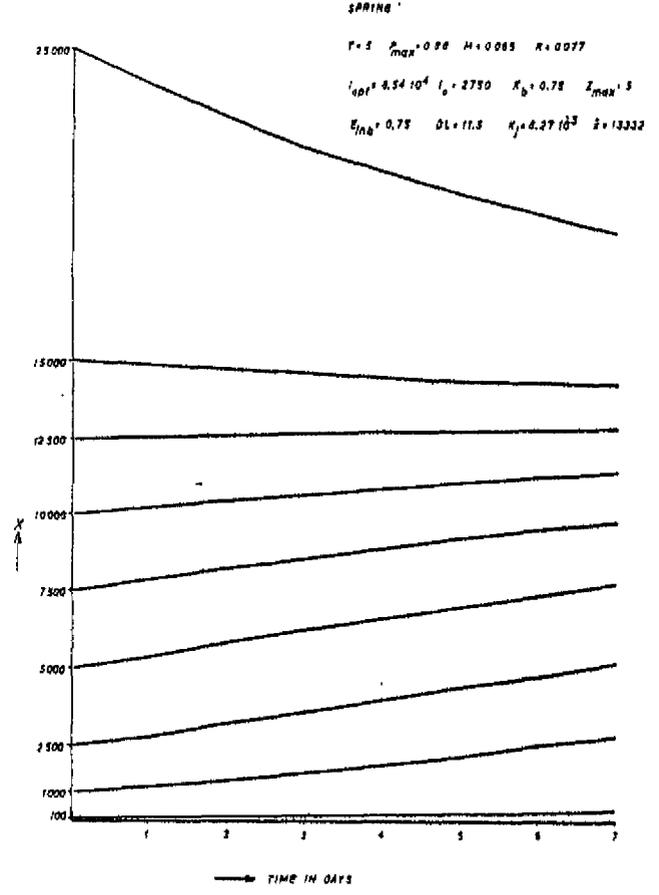


Figure 5.3

Approach to steady state ( $\bar{x}$ ) under average spring conditions of a species according to the simplified solution of the growth equation. Symbols are defined in the text.

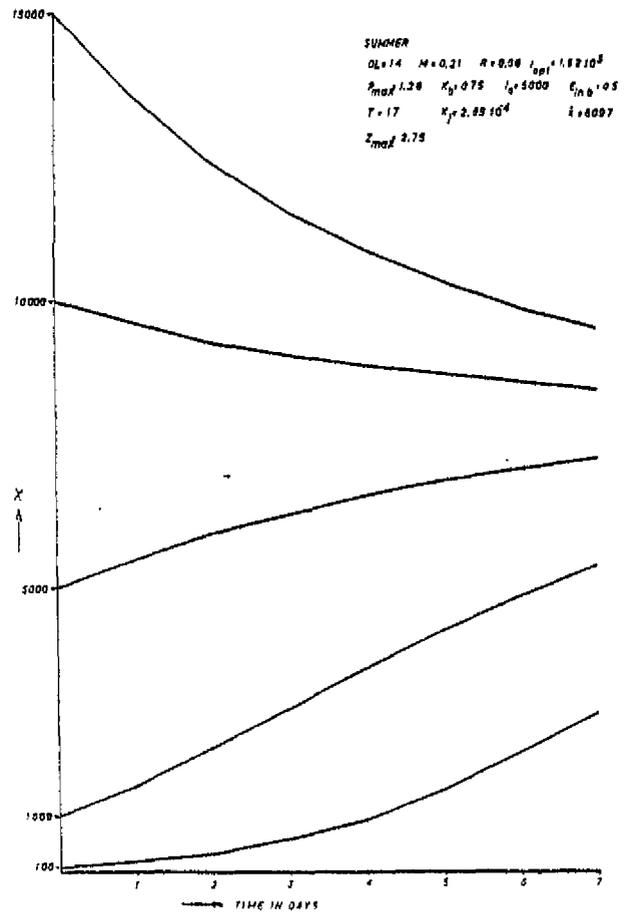


Figure 5.4

Approach to steady state ( $\bar{x}$ ) under average summer conditions of a species with a low production rate constant according to the simplified solution of the growth equation. Symbols are defined in the text.

correct. So there is no general answer. To investigate the impact on the model predictions in each particular case, BLOOM II was extended with three alternative options which are discussed in Sec. 6.2.

Notice that in the foregoing we have mainly considered one species. If several species are present, it is much more difficult to determine the net rate of change of each species, because this depends on the population dynamics of the other phytoplankton species, among others. For example consider two species A and B of which A is dominant at time  $t$ . If at time  $t+1$  the environmental conditions are more favorable to species B, it might rapidly obtain dominance if A declines quickly. If, however, species A decreases slowly, it will postpone the shift in dominance, because it contains nutrients, which must be remineralized and because it contributes to the extinction, which decreases the net growth rate of species B. If the situation in which species B can outcompete species A does not persist for a sufficiently long period, perhaps species dominance will not change at all.

As a consequence BLOOM's species composition could be incorrect during transient periods. Fortunately, the impact on total biomass will be much smaller, because the basic requirements of the species in the model are not extremely different. It has been our experience with the model that often several solutions exist with a completely species composition but a total biomass of 70 to 99 percent of the optimum solution.

Notice that the ability to switch the composition of the bloom is one of the most important differences between BLOOM II and a dynamic model. If we run BLOOM II without additional growth constraints, its species composition can switch completely in one time-step, which means that the previously dominant species effectively have an infinite mortality rate constant.

In a dynamic model the rate at which the biomass of previously dominant species disappears is determined by their mortality rate constants  $M(T)$  among others. Unfortunately, we cannot predict  $M(T)$  accurately [Sec. 4.9]. We could of course use the same minimum value  $M_{min}(T)$  as in BLOOM II, but considering how this was derived, it is probably too low for a declining population.

Therefore we think that both a dynamic model and BLOOM II could easily mispredict the species composition at transient conditions; BLOOM II is perhaps too radical, but a dynamic model is perhaps too conservative in its removal of the species who dominated in earlier periods.

## 5.6 MINIMUM EFFICIENCY REQUIREMENT

To proceed the result of Eq. (5.12b) could be substituted into the differential equation (5.13) for each species  $j$ . Using the appropriate expressions for  $P_{gmax}(T)$ ,  $EAVG$ ,  $M_{min}(T)$ ,  $R(T)$  and  $G$ , it is now possible to solve Eq. (5.13) numerically. There is no analytical solution, however, because  $EAVG$  is a function of  $K$  and hence a (complicated) function of  $x$ .

Rather than solving Eq. (5.13), BLOOM II assumes a steady state with a nominal time-step of one week [Sec. 5.5]. Under this assumption obviously

$$\frac{dx}{dt} = 0$$

which can only be true if either:

$$Pg - M - R - G = 0 \quad (5.14)$$

or:

$$x = 0 \quad (5.15)$$

For each species  $j$  either (5.14) or (5.15) should hold. Substituting Eq. (4.5a) and (4.5b) for the nutrient function  $g(e_i)$  into Eq. (4.3), we obtain:

$$Pg \leq E(I,T) Pg_{\max}(T) \quad (5.16a)$$

Notice the difference between Eq. (4.14) and Eq. (5.16a); in the first it was assumed that nutrients were abundant hence  $g(e_i) = 1.0$ , but in the latter we make no assumptions about the amount of nutrients hence  $g(e_i) \leq 1.0$ . Substitution of Eq. (5.16a) into Eq. (4.2) gives:

$$E(I,T) \geq \frac{M + R + G}{Pg_{\max}(T)} \quad (5.16b)$$

Any species for which (5.16b) does not hold, has a negative net growth rate and is unable to sustain itself; thus it is excluded from the bloom. The value of  $E(I,T)$ , for which (5.16b) is an equality is called the minimum efficiency requirement,  $E_{\min}(T)$ . This is the lowest possible value of  $E(I,T)$  at which gains and losses are balanced.

Next EAVG is set equal to  $E_{\min}(T)$ , and then Eq. (5.12b) is solved for  $K$ . Because of the shape of the efficiency curves, there are usually two roots, one called  $U_{k\min}$ , the other  $U_{k\max}$ ; the first is the limit where the light intensity becomes too high (photoinhibition), the second where it becomes too low (energy limitation). Since these two roots include only the physiological responses of the model's species to the light regime as if there were no background extinction, the latter must be subtracted from both roots, hence:

$$\left. \begin{aligned} K_{\min} &= U_{k\min} - K_b \\ K_{\max} &= U_{k\max} - K_b \end{aligned} \right\} \quad (5.17a)$$

A species can only sustain a positive net growth rate if the total extinction is between its  $K_{\min}$  and  $K_{\max}$  value:

In most eutrophic waters,  $K_{min}$  of any species is smaller than the background extinction; hence the average light intensity is too low for photoinhibition to be of major importance. Under unfavorable conditions, there may be no root for  $K$ , implying that the average light intensity is too low (or, conceivably, too high) for production to compensate total losses. The degenerate solution of two coinciding roots ( $K_{min} = K_{max}$ ) will infrequently occur, if ever.

## 5.7 BUOYANCY REGULATION

So far in our discussion how to average production we have not specified a value for the depth ( $Z_{max}$ ). Of course  $Z_{max}$  cannot be larger than the physical depth of the lake, but conceivably a smaller value should be used. Also we may wonder whether the same value should be used for all species.

Presumably most groups of species are homogeneously distributed over the entire water column in an unstratified lake. Among these are all the diatom, flagellate and green algal species of BLOOM II. An exceptional stratification of these species has been reported [References in Harris, 1978], but we may well ignore this in the model.

Members of two groups of species: dinoflagellates [Heaney, 1976; Blasco, 1978; Harris et al., 1979; Lannergren, 1979] and blue-green algae [Reynolds, 1971, 1972, 1973; Okino, 1973; Whitton and Sinclair, 1975; Clark and Walsby, 1978; Konopka et al., 1978; Walsby, 1980; Walsby et al., 1982] are often inhomogeneously distributed. Through this behavior these species can increase their net production rate improving their ability to utilize resources (nutrients and particularly solar energy) efficiently.

Buoyancy regulation in these two groups is achieved by two completely different physiological mechanisms. Dinoflagellates, as indicated by their name, are flagellated organisms, who can actively swim. They can travel a distance of several meters per day, which is quite substantial considering the depth of many eutrophic lakes and it is well known that they change their position during a day. The only disadvantage of their method of buoyancy regulation is its large energy consumption. Thus as we have pointed out in Sec. 4.8, observed respiration rates of dinoflagellates are higher than of any other phytoplankton group in the model.

As explained by several of the above mentioned authors, the physiological mechanism for buoyancy control in blue-green algae is completely different. Blue-green algae control their specific gravity by adjusting the size of so-called gas-vacuoles ('air-bubbles'). When the average light intensity is low, the gas-vacuoles increase in size giving the cells an upward velocity. After some time the cells reach the euphotic zone and start photosynthesising. Then after a period of carbon fixation, the gas-vacuoles become smaller, the specific gravity of the cells increase and they sink out of the euphotic zone again.

Considering the importance of buoyancy regulation it is curious how little information is available from Dutch authors in comparison to foreign authors, British in particular. In 1976 the Delta Department gathered a number of depth profiles of chlorophyll and particulate nutrients in Grote Rug. When diatoms and flagellates were dominant, chlorophyll was evenly distributed between the sur-

face and the bottom as was to be expected. When, however, dinoflagellates or blue-green algae were dominant they were inhomogeneously distributed. Moreover they showed a clear tendency to move further upward during the day. Of the dominant species (the blue-greens Microcystis and Aphanizomenon and the dinoflagellates Ceratium and Eudorina, (not represented in BLOOM II) typically 55 to 60 percent of all chlorophyll was found in the upper half of the lake in the morning, which rose to 65 or even 80 percent in the afternoon. In each observation the fraction in the upper half increased during the day. Usually, the highest concentration was found in the first meter of water.

For other years only measurements of particulate nutrients at three depths are available, which underestimate live biomass in the upper layers, because they include other fractions such as detritus, which presumably are homogeneously distributed. Still often 55 to 60 percent of particulate material was found in the upper half during blooms of blue-greens and dinoflagellates, but not during blooms dominated by other species.

Undoubtedly some species in Grote Rug show buoyancy regulation, hence the question arises how beneficial that is to them. If the rate of primary production is significantly increased, we must also consider the consequences for the model.

Consider a homogeneously distributed, energy limited species  $j$ , who has an ample supply of nutrients. Its minimum efficiency requirement equals  $E_{min}(T)$ , its mixing depth is equal to the depth of the water ( $Z_{max}$ ) and it can only sustain a non-negative growth rate if the total extinction is less or equal to its value of  $K_{max}$  (situation 1).

Next consider a species with exactly the same characteristics, but in addition the ability to regulate its vertical position in the water. Because it is energy limited each individual of this species tends to move upwards, hence a depth profile will emerge. For simplicity we shall approach this situation by assuming a depth  $Z_{mix} < Z_{max}$ , above which all individuals are homogeneously distributed. No cells are present between  $Z_{mix}$  and the bottom (situation 2).

Define the following symbols:

- $K_{l1}$  is the extinction per m by living cells of species  $j$  when it is mixed over the entire depth ( $Z_{max}$ ),
- $K_l$  is the total extinction per m when species  $j$  is mixed over the entire depth ( $Z_{max}$ ),
- $K_{l2}$  is the depth averaged extinction per m by living cells of species  $j$  when it is mixed over the smaller depth ( $Z_{mix}$ ),
- $K_2$  is the extinction per m between the surface and  $Z_{mix}$  when species  $j$  is mixed over  $Z_{mix}$  meters. (In this situation the extinction between  $Z_{mix}$  and  $Z_{max}$  has a different value).
- $K_b'$  is the total extinction per m of all homogeneously distributed particles (the background extinction plus the extinction of dead phytoplankton plus the extinction of phytoplankton species without buoyancy control).

Because by definition our hypothetical species  $j$  has the same maximum production, mortality and respiration rate constant as its homogeneously distributed twin brother, both have the same minimum efficiency requirement  $E_{min}(T) < Sec. 5.6 >$ . As both species are

mixed over a different depth, they can according to Eq. (5.12b) only have the same integrated efficiency if there is a compensating difference in the value of the extinction:

$$K_2 * Z_{mix} = K_1 * Z_{max} \quad (0 \leq z \leq Z_{mix})$$

By definition

$$K_1 = K_{11} + K_{b'1} \quad (0 \leq z \leq Z_{max})$$

$$K_2 = K_{12} + K_{b'2} \quad (0 \leq z \leq Z_{mix})$$

$$K_2 = K_{b'2} \quad (Z_{mix} \leq z \leq Z_{max})$$

hence

$$K_{12} + K_{b'2} = \frac{Z_{max}}{Z_{mix}} (K_{11} + K_{b'1}) \quad (0 \leq z \leq Z_{mix})$$

or

$$K_{12} = \frac{Z_{max}}{Z_{mix}} K_{11} + \left( \frac{Z_{max}}{Z_{mix}} - 1 \right) * K_{b'1} \quad (0 \leq z \leq Z_{mix}) \quad (5.18a)$$

Finally

$$K_{12} = 0 \quad (Z_{mix} \leq z \leq Z_{max}) \quad (5.18b)$$

Obviously the average value of  $K_{12}$  over the entire depth  $Z_{max}$  equals the expression at Eq. (5.18a) times  $Z_{mix}/Z_{max}$ :

$$K_{12} = K_{11} + \left( 1 - \frac{Z_{mix}}{Z_{max}} \right) * K_{b'1} \quad (0 \leq z \leq Z_{max}) \quad (5.18c)$$

Eq. (5.18c) is fundamental to our understanding of the possible impacts of buoyancy control:

1. The most favorable situation for the species with buoyancy control arises when the ratio of  $Z_{mix}$  to  $Z_{max}$  is extremely small. In the limit ( $Z_{mix} \ll Z_{max}$ ) all photons, which would otherwise be absorbed by homogeneously distributed particles, are now absorbed by living cells of the species with buoyancy control, hence:

$$K_{12} = K_{11} + K_{b'1}$$

2. The impact of buoyancy control is, however, small or negligible when
  - a. The ratio of  $Z_{mix}$  to  $Z_{max}$  is close to one (the distribution over depth is close to homogeneous).
  - b.  $K_b'$  is small relative to  $K_{ll}$ . In other words: when the depth averaged extinction of phytoplankton species with the potential to regulate their vertical position is large compared with the extinction of homogeneously distributed particles (dead phytoplankton, species without buoyancy control, background material).

Because extinction and biomass are linearly proportional, similar conclusions hold for the biomass of a species with buoyancy control.

Buoyancy control is an important mechanism to absorb photons which would otherwise be absorbed by homogeneously distributed particles whether living or dead. Clearly it can be a strong competitive advantage. Notice, however, that there is no reduction in self-shading because there is no term in front of  $K_{ll}$  in Eq. (5.18c).

To take the effects of buoyancy control into account in the model we use the following procedure. Define

- $K_{lh}$  is the total extinction per m by living cells of all homogeneously distributed species,
- $K_{dh}$  is the total extinction per m by dead particles of all homogeneously distributed species,
- $K_{db}$  is the total extinction per m by dead particles of all species with buoyancy control.

Obviously the total extinction of all homogeneously distributed particles ( $K_b'$ ) equals:

$$K_b' = K_b + K_{lh} + K_{dh} + K_{db}$$

First we compute a value for the maximum extinction of species  $j$  ( $K_{max,j}$ ), as if it were homogeneously distributed. Next we specify a value for the ratio  $Z_{mix}/Z_{max}$  (to be discussed later) and we correct  $K_{max,j}$  according to Eq. (5.18c) assuming that  $K_{lh}$  and  $K_{dh}$  are both zero ( $K_b' = K_b + K_{db}$ ). This assumption is necessary because the model does not know the values of  $K_{lh}$  and  $K_{dh}$  before the end of the computations for a period. For purely numerical reasons, however, this is no serious drawback. Due to their relatively high efficiency at low light intensities (Fig. 4.3) and their low respiration rate constants, blue-green algae always achieve their energy limited biomass peak at an extinction level which is far above the  $K_{max}$  of any homogeneously distributed species. Hence computing the  $K_{max}$  of blue-green algae we can indeed ignore the extinction by homogeneously distributed species. How the effect of dead phytoplankton is modelled is shown in Sect. 5.8.

The ratio of  $Z_{mix}/Z_{max}$ , which we call  $R_{mix_j}$  (the relative mixing depth of species  $j$ ), has been established by calibration. First we have made a computation with the model assuming a homogeneous distribution of all species. We have compared the results of BLOOM II to observations in terms of biomass, limiting factors and species composition. As might have been expected, the computed biomass was sometimes considerably lower than observed when species with buoyancy control were dominant. Second we have parametrically decreased  $R_{mix_j}$  and made new computations with the model until the blooms of species with buoyancy control could be reproduced fairly by the model.

Using data for three Grote Rug cases with blooms dominated by dinoflagellates and blue-greens algae: the 1976 blooms in the Rings 2 and 3 and the 1977 autumn bloom in Ring 2, we found that a reasonable overall estimate would be to take  $R_{mix_j} = 0.275$  for all species with buoyancy control ( $R_{mix_j} = 1.0$  for all other species). In other words the model can reproduce observed biomass concentrations of species with buoyancy control if we assume that they can reduce the effects of the background extinction and the extinction of dead phytoplankton cells by approximately a factor 3.5.

We have assumed the same value of  $R_{mix_j}$  for each species with buoyancy regulation at every place and at each period and ran BLOOM II for all available cases to test the validity of our assumptions. So far they seem very reasonable; for instance the calculations for the mainly energy limited Lake IJssel show an excellent agreement with observed bloom levels in 1976 (Fig. A-14.1).

Our assumption that  $R_{mix_j}$  is constant per lake and species implies, that we increase  $K_{max_j}$  by the same amount for different species with buoyancy control. As they have different specific extinctions, the corresponding change in biomass is species dependent. Thus buoyancy control is more favorable to species such as Microcystis and Ceratium than to Aphanizomenon, or Oscillatoria, because the latter have a much higher specific extinction.

The reader should realize that buoyancy control by phytoplankton species can have several additional impacts which are not explicitly incorporated into the model. These species achieve relatively high vertical velocities enabling them to travel rather easily to and from the euphotic zone. This strongly improves their ability to optimize their physiological performance and to maximize their growth rate. They can avoid unfavorable conditions and actively search for favorable circumstances: they can be 'at the right place at the right time'.

For example they could reduce the damage due to photoinhibition at high light intensities simply by moving downwards. Also most, if not all, individuals could benefit from the exceptionally high initial rate of photosynthesis in the first half hour after a period of darkness [Harris, 1978], because they could move to the euphotic zone at least once a day. In contrast, cells of homogeneously distributed species are much more static and can enter the euphotic zone less often. But buoyancy control also permits a cell to leave the euphotic zone and hence to avoid the reduction in the photosynthetic rate after a long period in the light during long sunny days which is known as the 'afternoon depression'.

Species with buoyancy control can much better balance different synthetic processes, because an actively moving individual could leave the euphotic zone once it becomes growth saturated. For

instance if protein- rather than photosynthesis is growth rate limiting, any quantum which is absorbed in addition to the required amount to maintain the present rate of protein synthesis, is wasted and the incorporated carbon must be released or photorespired. In addition it becomes easier to adjust processes which proceed at a higher rate in the dark (protein synthesis) to those preceding more rapidly in the light.

Finally an actively moving cell can better counterbalance the negative effects of nutrient gradients, (1) on a local scale since they do not have to wait until substances are transported to and from the cell by diffusion, and (2) on a global scale in periods when there are nutrient profiles in the water.

Additional remarks:

- The established value of  $R_{mix}$  depends on  $E_{min}(T)$  and thus on the uncertain estimate of the minimum mortality rate constant. Therefore a different estimate of  $M_{min}(T)$  (but also of  $R(T)$  or  $P_{gmax}(T)$ ) could make it necessary to use a different value of  $R_{mix}$ , as well.
- The sensitivity to the exact value of  $R_{mix}$  is less than perhaps expected; in many cases  $R_{mix}$  increases the available amount of light to such an extent that blue-greens become nutrient rather than energy limited. Thus with a moderate change in the value of  $R_{mix}$ , the model would still compute exactly the same solution. Of course the total biomass prediction of the model is (much) more sensitive to  $R_{mix}$  when blue-greens are (nearly) energy limited. This will be true in particular when the potential bloom levels of other species are considerably lower or even zero.

### 5.8 EXTINCTION OF DEAD PHYTOPLANKTON

Before we can derive the energy constraints of the model, we must determine the extinction due to dead phytoplankton particles. Analogue to the detritus equations for nutrients [Sec. 3.3], we may write:

$$\frac{d K_d}{dt} = \sum_j (q \cdot M_j \cdot L_j \cdot x_j) - v \cdot K_d - s \cdot K_d \quad (5.19)$$

where:

- $K_d$  is the total extinction of all dead phytoplankton particles per m,
- $q$  is the fraction of a phytoplankton cell which becomes detritus when it dies,
- $M_j$  is the natural mortality rate constant per day of species  $j$ ,
- $L_j$  is the specific extinction in  $m^2$  per mg dry weight of dead fragments of species  $j$ ,
- $v$  is the rate constant by which the effect of dead phytoplankton material on the extinction diminishes,

- s is the sedimentation rate constant of detritus per day.

Calculating the extinction of dead phytoplankton is rather difficult, because it depends on the amount of detritus, its extinction and the rate, at which extinction disappears ('mineralizes'). To solve Eq. (5.19), we shall make four assumptions.

**Assumption 1:**  $q = 0.5$ , which means that the light absorption by phytoplankton cells in the euphotic zone is immediately reduced by 50 percent upon dying. What happens to detritus below this depth is unimportant, because production is limited to the euphotic zone. There are two reasons for assuming such rapid disappearance of light absorbing capacity: first when a cell dies 50 percent of all particles immediately dissolve, as we have previously assumed [Sect. 3.6], hence less particles contribute to the extinction. Second, most pigments degrade very rapidly in the light once they are no longer protected by the structures of the healthy phytoplankton cell [Wetzel, 1975]; and moreover, according to Moss [1968] the first intermediate breakdown products of chlorophylls have already lost 39 percent of their light absorbing capacity. Thus a 50 percent reduction in total absorption seems a reasonable estimate.

**Assumption 2:**  $L_j = K_j$ , which means that the extinction per unit of detritus remaining after the initial removal of 50 percent, has the same values as the specific extinction of the phytoplankton species, from which it originated. Probably this assumption overestimates the value of  $L_j$ , but we have no information for any other assumption.

**Assumption 3:** the disappearance rate constant is an exponential function of temperature, described by the following equation:

$$v = \text{EXP}(0.0296 * T - 1.897) \quad (5.20)$$

This equation yields values between 0.15 and 0.30 for the normal temperature range and was based upon the observation by Fallon and Brock [1979], that dead chlorophyll mineralizes about 2.5 times as fast as nitrogen<sup>1</sup>. At low temperatures we have assumed a larger factor, however, when we calibrated the model. Whether indeed this rate is representative for the disappearance of light absorption by dead phytoplankton fragments, is unknown.

**Assumption 4:** Eq. (5.19) achieves a steady state within a time-step of the model. Because  $v$  is considerably larger than the remineralization rate of nutrients, this steady state assumption is less critical than the one for nutrients. Depending on temperature, the characteristic time equals 3 to 10 days, even if we assume no sedimentation. Putting  $dK_d/dt$  to 0, we obtain:

$$K_d = \frac{\sum_j (q \cdot M \cdot K_j \cdot x_j)}{v + s} \quad (5.21a)$$

Using the temperature dependences for  $M$  and  $v$  and a value of 0.5 for  $q$ , it is easily verified that  $K_d$  is in the order of 0.20 to 0.40 times  $K_l$ : the extinction of live phytoplankton. Thus our computa-

<sup>1</sup> The mineralization rate constant of nitrogen is 0.12 per day at 20° C [Sec. 3.6.1].

tions are less sensitive to errors in  $K_d$ , than they are to errors in the steady state detritus pools of the nutrients.

There is one final complication for species with buoyancy control, because living and dead phytoplankton do not have the same depth profile. Assuming a homogeneous distribution for dead phytoplankton [Sec. 5.7], we must according to Eq. (5.18c) multiply  $K_d$  by the relative mixing depth factor  $R_{mix_j}$ , hence

$$K_d = \frac{\sum_j (q.M.R_{mix_j}.K_j.x_j)}{v + s} \quad (5.21b)$$

## 5.9 FORMULATION OF ENERGY CONSTRAINTS

Modelling nutrients by linear constraints, was relatively straightforward, since the mass-balance equations were almost formulated as linear constraints. The only major step was expressing nutrients in detritus as a function of living phytoplankton, although this was more a biochemical than a mathematical problem.

Conceptually it is much more difficult to describe the energy budget by linear constraints for essentially three reasons:

1. There is no mass-balance for light.
2. The available amount of light varies non-linearly in time and with depth: there may be too little or too much within the same 24 hour period.
3. Several complicated, non-linear biological processes are involved which among others have the effect, that the efficiency of light utilization varies with time, depth, location, season and per species.

Bigelow et al. [1977] solved these problems elegantly. When light is transformed into extinction, energy and nutrient equations have a similar mathematical formulation. The energy constraints for species  $j$  follow logically from condition (5.13b), substituting the appropriate expressions for living and dead phytoplankton for  $K$ :

$$K_{min_j} \leq \sum_j K_j.x_j + K_d \leq K_{max_j} \quad (5.22)$$

Substitution of Eq. (5.21b) yields the final energy constraints:

$$K_{min_j} \leq \sum_j \left[ \frac{(v + s + q.R_{mix_j}.M)}{v + s} K_j.x_j \right] \leq K_{max_j} \quad (5.23)$$

The solution algorithm for the entire set of equations of BLOOM II will be explained in Chap. 6.

## 6. SOLUTION ALGORITHM

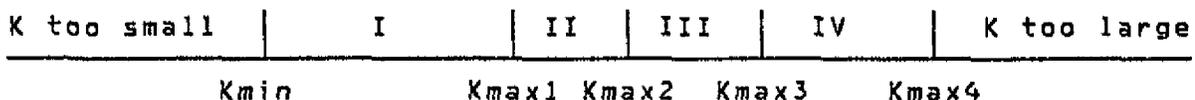
### 6.1 CONSTRUCTION OF EXTINCTION INTERVALS

The energy constraints which we have set up in Sec. 5.9, permit each species to grow within certain limits of the total extinction coefficient of the water. Usually each species has a negative value of  $K_{min}$ , in the eutrophic lakes to which BLOOM II has been applied [Sec. 5.6] but  $K_{max}$ , is often positive for one or several species. Thus there exists an overlapping range of possible extinction limits for these species.

To set up the linear program of BLOOM II one could think of adding two energy constraints for each individual species to the 3 nutrient constraints of Sec. 3.8. Thus we would solve a linear program of  $3 + 2N$  equations and  $N$  variables, where  $N$  is the number of species. This set of equations, however, is inconsistent because it could permit the model to compute a solution with more than one value for the total extinction coefficient. For instance it could find a bloom of two species, both limited by energy, but with two different extinction roots.

This problem was already solved by Bigelow et al. [1977] in the following way. For  $N$  species there are  $2N$  (or less) different extinction roots  $K_{min}$ , and  $K_{max}$ . These roots are sorted in ascending order, resulting in  $2N-1$  (or less) extinction intervals. No species is able to grow if the extinction is outside the range depicted by the smallest  $K_{min}$  and the largest  $K_{max}$  value. In each interval, however, a subset of species can sustain a positive net growth rate.

This is illustrated below for four species with an equal  $K_{min}$  root, but a different value of  $K_{max}$ . Blooms are impossible if the extinction is smaller than  $K_{min}$  or larger than  $K_{max4}$ . In interval I all four species can exist, but in interval II growth of species 1 is impossible etc. Finally in interval IV only species 4 can still maintain a positive net growth rate.



Rather than solving one (large) LP at each time-step, we set up a number of small LPs, one for each extinction interval  $l$  with an associated subset of species  $S_l$ . In each of these intervals we use the same three nutrient constraints because these should hold regardless of the extinction value. Also the (optional) growth constraints of the species, which put an upperbound ( $x_{limj}$ ) to the biomass concentration that can be attained in a time-step [Sec. 6.2], are kept constant in each interval. Finally the coefficients of the extinction rows are the same in each interval, because the light absorption per unit of living and dead phytoplankton does not vary between intervals. Thus for each interval we solve the following LP:

Find :  $x_j \geq 0$  and  $e_i \geq 0$ , (for subset  $S_i$ )

Maximizing:  $\sum_j x_j$ ,

Subject to:

$$\sum_j \left[ \frac{(u_i + s + q_i \cdot M_j)}{u_i + s} a_{i,j} \cdot x_j \right] + e_i = b_i - c_i \cdot z \quad (1)$$

$$x_j \leq x_{lim_j} \quad (2)$$

$$Kmin_i \leq \sum_j \left[ \frac{(v + s + q \cdot Rmix_j \cdot M)}{v + s} K_j \cdot x_j \right] \leq Kmax_i \quad (3)$$

We then find the maximum total biomass  $Bmax_i$ , the species composition and limiting factors. After each LP for a time-step has been solved, we compare their  $Bmax_i$  values; the interval with the highest  $Bmax_i$  value contains the ultimate solution of BLOOM II, the others can be considered as local maximums.

## 6.2 TIME ASPECTS

When we discussed the steady state assumptions of the model for nutrient recycling [Sec. 3.6] and phytoplankton growth [Sec. 5.5], we concluded that deviations from steady state could sometimes influence the behavior of the model significantly. To investigate how often and to what extent, BLOOM II was extended with several new options which were not included in its predecessor.

It is, however, strongly recommended to start each series of computations with the steady state assumptions to see how the results of the model agree to the observations. Some differences between computed and observed data may be due to the model using incorrect values for certain parameters such as mortality, stoichiometric constants etc. Other disagreements might indicate that some steady state assumption is violated. For example strong fluctuations in the total biomass or radical changes in the species composition within one week are unlikely in many parts of the winter [Sec. 5.5]. In these cases we may turn to one or several of the options discussed in the next section.

### 6.2.1 Variable time-steps

Changing the time-step of the model is of course a straightforward and logical way to reduce errors due to the steady state assumptions of the model. BLOOM II was therefore extended with an option to use any multiple number of the nominal one week time-step. All inputs are averaged and the model computes the steady state solution at the end of the period. The time-step can be varied in the course of a model run, thus we can use for instance a

time-step of four weeks in January and December, two weeks in spring and one week during the rest of the year.

### 6.2.2 Dynamic recycling of detritus

In Chap. 3 we have discussed whether or not we should use a steady state solution for nutrient recycling in the model. Notwithstanding our conclusion that the steady state solution often yields better results in the present framework of the model where total nutrients are a forcing function, it is at least a valuable exercise to make a computation using the dynamic solution for the detritus equations. For that purpose BLOOM II allows us to replace the nutrient constraints in the linear programs by Eq. (3.7). In Sec. 8.6.1 we shall give some results and compare them with the nominal results.

### 6.2.3 Memory on total extinction

To compute the extinction limits  $K_{min,j}$  and  $K_{max,j}$  of each species we subtract the background extinction ( $K_b$ ) from the physiologically permissible extinction roots  $UK_{min,j}$  and  $UK_{max,j}$  [Sec. 5.6]. Hence the model has the possibility to switch between a solution composed of species with a high specific extinction (high total extinction) at time  $t$  and a solution composed of species with a low specific extinction (low total extinction) at time  $t+1$ . In reality such a succession is often impossible because the high total extinction might not even permit any other species to grow, but the ones already present at time  $t$ .

Therefore BLOOM II was extended with an option to remember the total extinction of the bloom at time  $t$  and use this value<sup>1</sup> rather than  $K_b$  as energy limiting term in Eq. (5.17a) only for those species, who were not present at time  $t$ . Obviously this option can prevent changes in composition when the extinction is high. If for example there is a shift in limiting factor from phosphorus to nitrogen, the species which requires the least amount of nitrogen could be suppressed.

This option increases the performance of BLOOM II considerably for some, certainly not all cases. The reason is it favors species which can grow at relatively high extinctions, but once these are present, it is hard to have any change in species composition. Thus in lakes with a continuous bloom problem such as the Lakes Veluwe and Wolderwijd, the results of the model improve in terms of biomass and species composition. But if the model over-predicts in a certain period (early summer in most Grote Rug cases), it may select a particular species which then remains dominant even at times when a real bloom was observed, which may or may not have been dominated by this particular species.

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<sup>1</sup> In the current version of the model the total extinction of the previous time-step is no longer used, but rather some smaller value that takes the mortality of existing cells into account.

#### 6.2.4 Additional growth constraints

When the external conditions remain constant during a sufficiently long period of time, each phytoplankton species  $j$  will achieve an equilibrium value. Provided that there is an ample supply of nutrients, this means that Eq. (5.13) equals zero: the losses compensate the total production. This equilibrium is achieved at a certain extinction level: the total attenuation of light, including the contribution due to phytoplankton, results in a value for the average production efficiency  $EAVG_j$ , which, multiplied by  $P_{gmax}(T)_j$ , just compensates the sum of all loss terms. Hence we can compute the maximum permissible value of the extinction  $K_{max}_j$  of each species and its energy limited biomass maximum, as we have explained in the previous chapter.

When, however, the average light intensity is low it may be impossible to achieve this energy limited maximum within a one-week time-step. The average efficiency under those conditions will be so low, that the phytoplankton species can only increase their biomass a few times a week or even worse, not at all. A species with a low initial biomass, therefore, cannot possibly reach its energy limited biomass maximum in a period of one week. Conditions with so little available energy occur in many lakes when the solar radiation is low during winter. In some lakes, however, energy poor condition prevail more or less permanently, because phytoplankton and background extinction in combination with the depth, result in a consistently low average light intensity.

For these conditions the model was extended with an option to include additional constraints in the LPs to take the growth conditions into account. At the beginning of a time-step we know the values of the total extinction (the level of the previous period), the depth and the surface light intensity  $I_s$ . From Eq. (5.12b) we can now compute the initial efficiency  $EAVG(0)_j$  of each species. Solving the differential equation (5.13) and putting this value  $EAVG(0)_j$  for  $EAVG_j$ , we can compute the growth limited biomass level  $x_{lim}_j$  by the end of the time-step:

$$x_{lim}_j = x_j(0) * \text{EXP}(\Delta t * [P_{gmax}(T)_j * EAVG(0)_j - M_{min}(T) - R(T)_j - G_j]) \quad (6.1)$$

As we have already mentioned in Sec. 6.1, we add one growth constraint for each species to the normal set of equations for the LP:

$$x_j \leq x_{lim}_j \quad (6.2)$$

Notice that we have kept  $EAVG_j$  constant (equal to  $EAVG(0)_j$ ) during the entire time-step. This is obviously incorrect since  $EAVG_j$  decreases when the extinction  $K$  rises and  $K$  increases with biomass, hence  $EAVG_j$  will become smaller as a bloom develops. This is not considered a serious error, however, as

1. Computations have shown that the difference between the initial and final value of  $EAVG_j$  is usually rather small, particularly when the growth constraints are most important:

- The initial growth rate is small (Fig. 5.2).
- The initial biomass is equal to the base level.

2. This procedure is consistent to the objective of the model because it leads to an overestimation of  $x_{lim,j}$ .

If the initial growth rate is high, for instance in summer, or if the initial biomass  $x_j(0)$  is large,  $x_{lim,j}$  is usually (much) higher than the energy limited steady state biomass, hence the normal energy constraint (or some nutrient constraint) will limit the bloom, regardless of the value of  $x_{lim,j}$ .

For the initial biomass value  $x_j(0)$  we either use the concentration calculated in the preceding period if species  $j$  was present, or some base level if it was absent. Our normal base level is 100 mg dry weight per  $m^3$ , or approximately 1 mg chlorophyll per  $m^3$ . This initial value has mainly been determined by trial and error. With a considerably smaller value, the model becomes so rigid that it can hardly switch its bloom composition. With larger initial values the growth constraints hardly affect the species composition of the model. Rather than using a fixed value we could have taken a certain fraction of the steady state value, for example 10 percent, but we have not tried this out.

Since the number of species in the bloom equals the number of limiting constraints [Sec. 2.1], the nominal version of BLOOM II can never compute a bloom consisting of more than four species at the same time (three limited by a nutrient and one by energy). When, however, we add a new constraint for each species, blooms are no longer confined to only four species and could theoretically even be composed of all species in the model, most of which would then be growth limited.

Adding growth constraints to the model is one of the most important extensions and improvements of BLOOM II compared with the POLANO algae bloom model. This option prevents dynamically infeasible changes in species biomasses, without being as rigorous as the extinction memory option [Sec. 6.2.3] or a dynamic model: as in the case of the purely steady state version, former errors may still be 'forgotten'.

One disadvantage is an increase in the average computation time by about a factor of 3. This can probably be reduced to a factor of 1.5 to 2, however, if a subroutine is implemented in the program to solve the 'dual' rather than the normal ('primal') LP of BLOOM II [Dantzig, 1963; also Sec. 2.2]. The 'dual' problem can be solved more efficiently than the 'primal', if the number of equations exceeds the number of variables, which is usually the case when growth constraints are included. Using this option in addition to the nominal steady state mode is recommended for the most important cases for which the model is run, particularly if the species composition should be computed accurately.

## 7. ZOOPLANKTON

### 7.1 INTRODUCTION

There is an old, unsettled controversy among limnologists about the importance of zooplankton in regulating phytoplankton populations. For example, whenever someone reported unexpectedly low phytoplankton concentrations at the 'Workshop on Hypertrophic Ecosystems' in Vaxjo, 1979, J. Shapiro would ask: 'Are there any Daphnias'? Others can discuss what limits phytoplankton biomasses extensively without even mentioning zooplankton.

According to our interpretation of the literature both extreme points of view are correct in some situations. Oligotrophic lakes are often characterized by a classical foodweb, in which the primary producers such as phytoplankton are eaten by herbivores such as zooplankton. The herbivores get eaten by omnivores and carnivores etc. In these systems zooplankton seems to contribute significantly to the mortality rate of phytoplankton.

In many eutrophic lakes nutrients are so abundant that the phytoplankton species can achieve extremely high biomass levels. Once a bloom is present there is not enough zooplankton to have a major impact on phytoplankton and moreover the specific rate of increase of zooplankton is usually too low to become a main source of phytoplankton mortality. Perhaps even more important: blooms in eutrophic lakes are usually dominated by large-sized species such as blue-green algal colonies or Ceratium. There is no agreement in opinion whether these groups are eaten at all, but many zooplankton species either prefer smaller preys, or cannot even handle large-sized preys [Lingeman-Kosmerschock, 1979c].

These controversies also persist because it is difficult to obtain quantitative information on zooplankton grazing. There is considerable uncertainty how to estimate the biomasses, filtration rates, preference rates for different species of live and dead phytoplankton, ingestion rates, digestion efficiency, mortality rates etc. of various species of zooplankton. Because several of these terms operate in a multiplicative way, some of these uncertainties are multiplied as well.

Unfortunately, a zooplankton model will be characterized by huge uncertainties about its structure and parameter values. It will probably have many degrees of freedom which makes it relatively easy to fit, but difficult to use for predictions.

Hence it was decided for the WABASIM project to start with a simple, pragmatic approach which would only be abandoned, if we were to find that zooplankton is crucial to BLOOM II's performance. In this initial approach we would not try to model the zooplankton biomass, but use it as input to the model, trying to estimate its effect on the computed phytoplankton levels.

### 7.2 INCORPORATION INTO BLOOM II

Before we explain how we compute the grazing rate constant in the model, we must first consider some indirect effects of zooplankton. In their bodies zooplankters contain nutrients which are not directly available to phytoplankton cells. It was demonstrated

earlier [Sec. 3.7], however, that the effect on the nutrient constraints could simply be taken into account by subtracting the amount of each nutrient in zooplankton from the total available amount (Eqs. 3.6, 3.7). Also, like every other particle, zooplankton cells might contribute to the extinction of the water. As (1) the number of zooplankton cells is usually small in comparison with the total number of particles and (2) these cells do not contain large amounts of pigments, the effect of zooplankton on the extinction can be neglected.

To calculate the specific grazing rate constant  $G_j$ , we shall use an equation similar to Scavia and Eadie's [1976]:

$$G_j = \frac{PR_j \cdot ZG \cdot z (x_j - x_{min_j})}{[ZK + \sum_j (PR_j \cdot x_j - x_{min_j})] x_j} \quad (7.1)$$

in which:

- $z$  is the total amount of zooplankton in mg dry weight of zooplankton per  $m^3$ ,
- $x_j$  is the amount of phytoplankton species  $j$  in mg dry weight per  $m^3$ ,
- $PR_j$  is the relative preference of  $z$  for species  $j$  (from 0.0 to 1.0),
- $ZG$  is the filtration rate constant of  $z$  in mg dry weight of phytoplankton per mg dry weight of zooplankton per day,
- $x_{min_j}$  is the amount of species  $j$  in mg dry weight per  $m^3$  which escapes grazing,
- $ZK$  is a zooplankton constant, closely related to a half saturation constant in mg dry weight of phytoplankton per  $m^3$ .

It may be verified that  $G_j$  has unit per day, which is also the unit of the other energy related rate constants of the model.

Eq. (7.1) states that the amount of phytoplankton ( $G_j \cdot x_j$ ) which is eaten by a given amount of zooplankton  $z$ , saturates as  $x_j$  increases, and becomes zero, when phytoplankton becomes too scarce to be found ( $x_j < x_{min_j}$ ). The grazing equation is illustrated in Fig. 7.1 for two sets of coefficient values.

To compute  $G_j$  from Eq. (7.1) we must know  $x_j$ : the amount of species  $j$  during a time-step. Obviously, this number is known only at the end of each time-step but  $G_j$  should be known in advance. Therefore, we have developed an iteration scheme:

1. Make a computation with  $G_j=0.0$  for each species, hence assume no grazing.
2. Calculate  $G_j$  for each species, recalculate its minimum efficiency requirement  $E_{min}(T)_j$ , recompute its extinction limits  $K_{min_j}$  and  $K_{max_j}$ , set up a new LP and recompute the bloom.
3. Compare this result to the result of the previous iteration and exit, if:
  - a. The two solutions are identical.
  - b. The newly computed bloom consists completely of species which are not grazed ( $PR_j=0.0$ ).

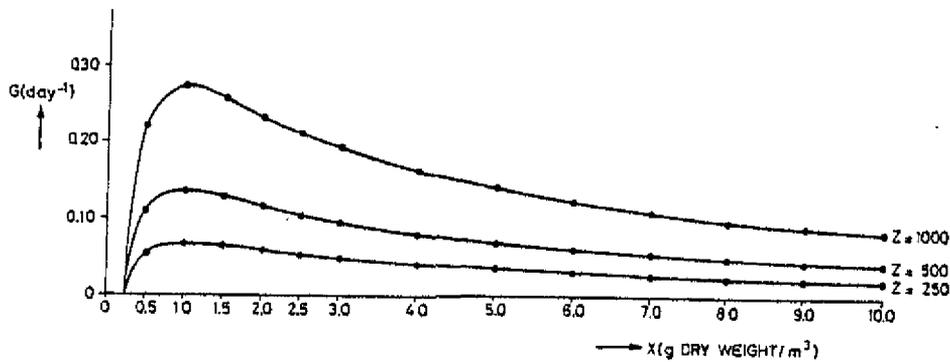


Figure 7.1a Grazing rate constant as a function of the edible biomass at different zooplankton concentrations. Nominal parameter values:  $Z_g = 1.0$ ,  $X_{min} = 250$ ,  $ZK = 2000$ .

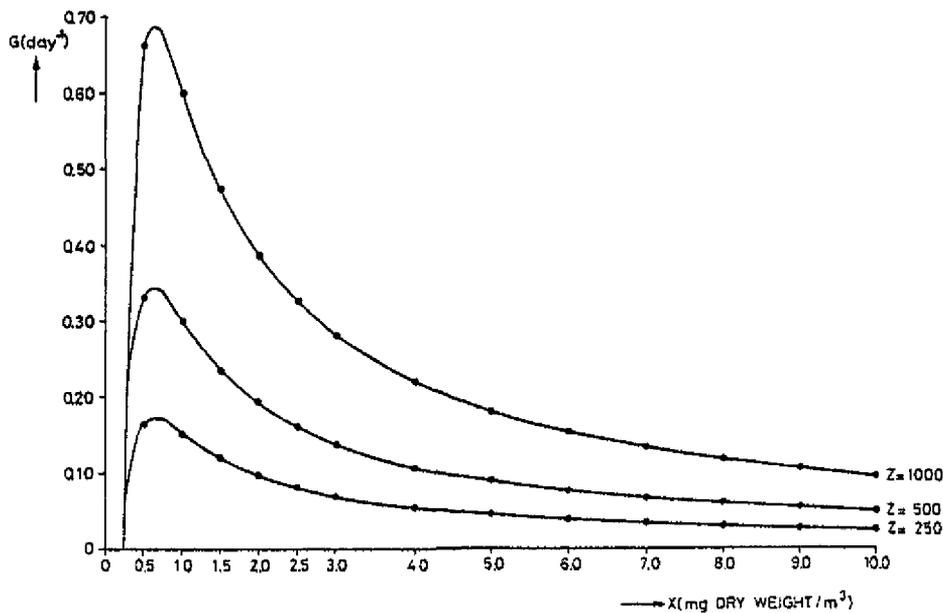


Figure 7.1b Grazing rate constant as a function of the edible biomass at different zooplankton concentrations. Nominal parameter values for  $Z_g = 1.0$ , and  $X_{min} = 250$ ;  $ZK$  reduced to 500.

c. The maximum number of iterations is reached, provided there is little additional change.

4. Otherwise, make a new iteration.

In most cases this algorithm converges rapidly (within two or three iterations), because even if the results of two iteration steps are not identical, the difference diminishes rapidly (the usual pattern are damped oscillations). We only had to make one modification since application of Eq. (7.1) to each individual species  $j$  may lead to cycling. Suppose the model computes a bloom in

which one species  $x_1 = 1000$  and a second species  $x_2 = 0$  in the first iteration. Next it computes the specific grazing rates which may be for instance  $G_1 = 0.1$  and of course  $G_2 = 0.0$ . When the model recalculates the bloom with these values for  $G_1$  and  $G_2$ , it might obtain a solution in which  $x_1 = 0$  and  $x_2 = 800$ . When it recomputes the specific grazing rates, it will now find  $G_1 = 0.0$  and  $G_2 > 0.0$ . However, with these grazing rate constants the model will find the initial solution again:  $x_1 = 1000$  and  $x_2 = 0$  etc.

To solve this problem we apply Eq. (7.1) to the total biomass of all species which are potentially grazed rather than to an individual species  $j$ . Hence we use an overall grazing rate constant. Our main justification is that all other mortality processes are also represented by a single, species independent constant ( $M_{min}(T)$ ) which is usually even larger than  $G$ . Putting:

$$X_{ed} = \sum_j PR_j \cdot x_j$$

$$X_{min} = \sum_j x_{min,j}$$

we find:

$$G = \frac{ZG \cdot z (X_{ed} - X_{min})}{(ZK + X_{ed} - X_{min}) X_{ed}} \quad (7.2)$$

Hence:

- $X_{ed}$  is the total biomass of all species which are potentially grazed: edible species,
- $X_{min}$  is the total biomass of all species which escape grazing,
- $G$  is the overall mortality rate constant due to grazing by zooplankton.

We have never used other preference factors but 0.0 or 1.0, hence each species in the model is either edible, or unedible without any further distinction.

### 7.3 RESULTS

With the exception of Grote Rug, BLOOM II has never been applied to a lake for which an adequate set of zooplankton data was available. This, of course, makes it difficult to calibrate or validate its grazing computation. Also it proved to be extremely difficult, to find reliable values for the various zooplankton parameters. As nominal values we have taken:

$$ZK = 2000 \text{ mg dry weight / m}^3$$

$$X_{min} = 250 \text{ mg dry weight / m}^3$$

$$ZG = 1.0 \text{ / day}$$

based upon Scavia and Eadie [1976] and the literature review by Lingeman-Kosmerchok [1979c], but values an order of magnitude different are reported for ZK and Xmin as well. For simplicity we have assumed that ZG is constant at each temperature, using a value which is typical for a temperature of about 10° centigrade. The reason is that up till now grazing has never been important in summer, because in this period the computed blooms usually consist of unedible species for which  $PR_j = 0.0$ . Of course it would be rather simple to calculate ZG as function of temperature if it were decided necessary in the future.

We have furthermore assumed that blue-greens and dinoflagellates are not eaten at all, hence for these  $PR_j = 0.0$ ; if we had assumed a small positive value of for instance 0.1 or 0.2 [Scavia, 1979], we would have obtained essentially the same results.

The possible impacts of grazing are illustrated in Fig. 7.2. Here  $x_1$  is the biomass of an unedible, and  $x_2$  of an edible species;  $N_1$  and  $N_2$  are two nutrient constraints. If  $x_2 \neq 0.0$  in the initial solution, zooplankton iterations are necessary, which will lower the value of  $K_{max2}$ . Of course the value of  $K_{max1}$  is not affected by zooplankton, hence due to grazing the energy constraint  $k$  will be rotated around the point where it intersects with the  $x_1$  axis. The initial solution of the LP is called P, the final solution following the grazing iterations is called Q. The results fall into three basic categories:

1. Grazing has no effect (P and Q coincide) because either:
  - a. The initial solution completely consists of unedible species ( $x_2 = 0.0$  in the example;  $X_{ed} = 0.0$ , and  $G = 0.0$  in general).
  - b. The initial and final solution are both nutrient limited. Grazing does not decrease the  $K_{max}$  of edible species to such an extent that energy becomes limiting: the gross production is sufficient to replace eaten individuals ( $G$  is relatively low).
2. The composition of the bloom shifts to unedible species due to grazing (point Q on  $x_1$  axis). Edible species are completely removed.
3. Grazing changes the composition of the bloom, but edible species remain present in every iteration (P and Q do not coincide; Q not on  $x_1$  axis).
  - a. Edible species increase their biomass due to grazing on the expense of unedible species who decrease. This may happen when edible species are nutrient limited and unedible species are energy limited. In the example this means that the nutrient constraint ( $N_1$ ) intersects with the  $x_2$  axis at a point closer to the origin than the energy constraint ( $k$ ), but  $N_1$  intersects with the  $x_1$  axis at a point farther from the origin than the energy constraint.
  - b. Edible species decrease in biomass due to grazing; unedible species increase. This case is the reverse of the previous one.
  - c. Edible species decrease in biomass due to grazing; unedible species, which were not present initially, enter the bloom. This case is more or less similar to the previous one.

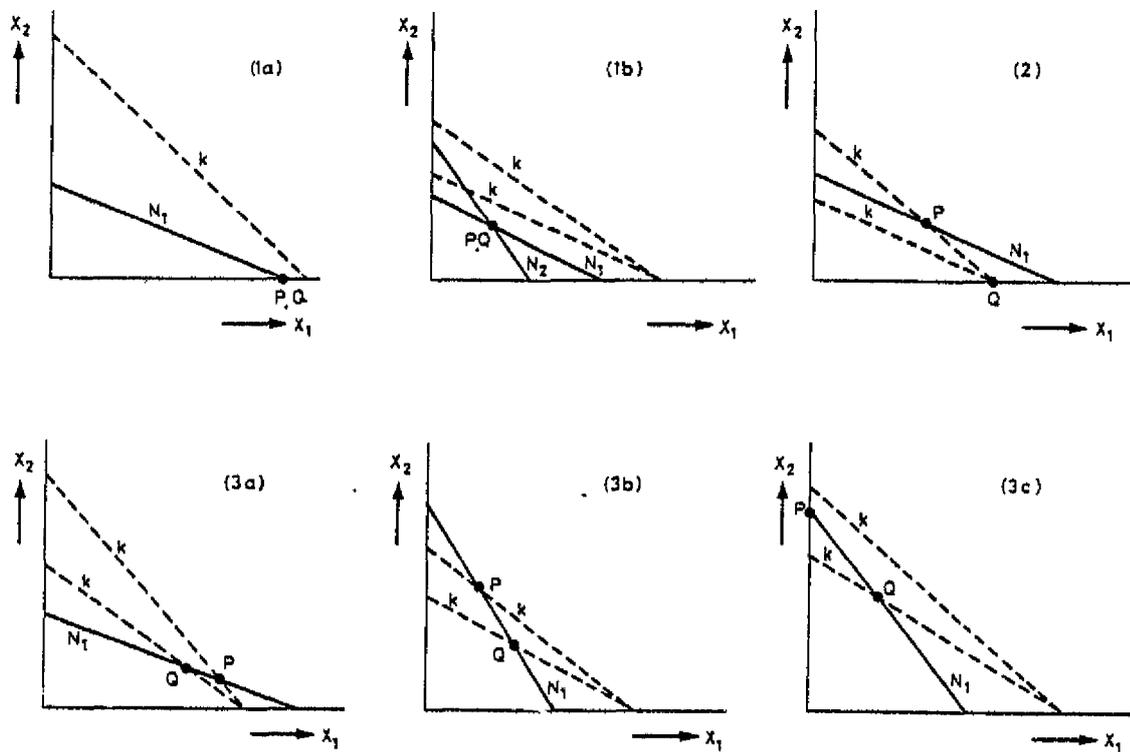


Figure 7.2 Possible effects of grazing on the LP solution of BLOOM II at several parameter and coefficients values.

Table 7.1

Impact of zooplankton grazing on the computations of BLOOM II for the available Grote Rug cases of 1975, 1976 and 1977.

- A: number of weeks with edible species in iteration 1.
- B: number of weeks with edible species in final solution.
- C: number of weeks without edible species in final solution.
- D: number of weeks when edible species increase due to grazing.
- E: number of weeks when grazing does not affect edible species.

Case	Year	A	B	C	D	E
Ring 2	1975	19	13	6	8	5
Ring 3	1975	4	2	2	2	0
Ring 1	1976	10	8	2	3	5
Ring 2	1976	17	11	6	8	3
Ring 3	1976	11	7	4	4	3
Ring 2	1977	12	3	9	3	0
Ring 3	1977	1	0	1	0	0
Grote Rug	1977	7	6	1	6	0
Total		81	50	31	34	16

From the results of Table 7.2 we may conclude, that the overall importance of zooplankton to the performance of the model is limited. In over 80 percent of all time-periods (335 out of 416 weekly

results) BLOOM II starts with a solution of unedible species. When edible species are initially present (20 percent of all periods), they usually remain in the bloom (12 percent of all periods) and often even increase (8 percent of all periods). Grazing is responsible for a switch in dominance from edible to unedible species in only 7 percent of all periods, but usually in terms of total biomass, the difference is small.

Notice that we cannot conclude from these results that the observed amounts of zooplankton cannot contribute significantly to the mortality of the actual phytoplankton populations in Grote Rug. When we would feed the observed rather than computed phytoplankton levels into Eq. (7.2), we would find a higher grazing rate constant  $G$  in periods when the model over-predicts.

## 7.4 DISCUSSION

### 7.4.1 Sensitivity and predictions

We have little or no zooplankton data for other lakes but Grote Rug, hence a similar analysis is impossible. The main conclusion is, however, the same for each eutrophic lake which has been modelled: in by far the most cases the initial biomass is dominated by unedible species. However, if due to restoration programs lakes would become more or less oligotrophic in the future, the role of zooplankton would probably become (much) more important.

Of course, the present version of the model cannot be used to predict the importance of zooplankton in future situations, but we may investigate its potential role by running the model for different scenarios. For instance, in spite of its inability to regulate phytoplankton, the zooplankton concentrations of many eutrophic lakes are relatively high. We may therefore probably consider the present zooplankton levels as an upperbound for the future. We might also adopt other approaches, but as long as the initial solution is mostly dominated by unedible species, zooplankton will remain relatively unimportant to phytoplankton.

To investigate the sensitivity to other values for the zooplankton parameters, we have varied  $ZK$ ,  $X_{min}$  and  $ZG$  over a considerable range. Our main conclusions remain unaltered, however, unless we increase  $ZG$  considerably: when zooplankton becomes a better hunter, significantly more blooms switch to unedible species, but the importance in terms of total biomass is still limited.

### 7.4.2 The algorithm and multiple steady states

As we have shown that the present grazing pressure is rather insignificant, we may wonder by how much it should be increased to become important. We have therefore included an option ('MAXGRA') in the program of BLOOM II to calculate the maximum potential grazing rate constant of species  $j$  ( $G_{max_j}$ ). When  $G = G_{max_j}$ , species  $j$  has a  $K_{max_j} = 0.0$ , thus its net growth rate is zero and its steady state biomass is zero as well. If we rewrite Eq. (7.1) to solve  $z$

and put  $G_{max}$ , for  $G$ , into the right hand side, we can also compute the corresponding zooplankton concentration. It comes out that on many occasions  $z$  has to be considerably larger than the maximum values presently observed in order to decrease the biomass of edible phytoplankton species to zero.

Option 'MAXGRA' has also been applied to show that taking  $G = 0.0$  in the first iteration is a valid assumption, which moreover results in a rapid convergence of the solution algorithm. For the moment assume that each species is edible with the same preference factor  $PR_j = 1.0$ . Computations with the model have clearly shown, that as long as the initial grazing rate ( $G_{in}$ ) is smaller than  $G_{max_k}$  of at least one species  $k$ , the model will always converge to the same solution. This is even true if in the first iteration  $G_{in}$  is so high that  $k$  is the only species with a positive net grow rate, regardless whether  $k$  appears in the final solution. In other words, if there is some feasible initial solution, the algorithm will always find the same ultimate solution.

However, convergence slows down when the initial and final value of  $G$  differ much, and as typically  $G$  is rather small after the final iteration,  $G = 0.0$  is an efficient initial condition. Another reasonable assumption would have been to start with the value of  $G$  of the previous time-step, but in this case convergence proved to be a little less efficient, although the final solution of the model is the same.

Normally we consider both edible and unedible species in the model and therefore the value of  $G_{in}$  can influence the results of the model. This was first demonstrated by T. Aldenberg when he was a member of the WABASIM team for the Delta Department, although his analytical results were derived for a much more simple system. In the following we shall discuss an example in which there are two different steady state solutions in BLOOM II. Denote the total biomass of edible species by  $X_{ed}$  and of unedible species by  $X_{ned}$ . Consider the following three cases:

Case 1:  $X_{ed} = A_1$ ,  $X_{ned} = B_1$ ,  $A_1 + B_1 = C_1$ ,  $G = 0.0$

Case 2:  $X_{ed} = A_2$ ,  $X_{ned} = B_2$ ,  $A_2 + B_2 = C_2$ ,  $G = G(t)$

Case 3:  $X_{ed} = 0$ ,  $X_{ned} = B_3$ ,  $0 + B_3 = C_3$ ,  $G > G_{lim}$

Assume :  $C_1 > C_2 > C_3$

Define:

-  $G_{lim}$  is the smallest value of  $G$  for which  $X_{ed} = 0.0$ ,

Obviously Case 3 is the highest possible bloom which consists exclusively of unedible species.  $G(t)$  is the actual value of  $G$  at time  $t$  which we may find putting the appropriate zooplankton coefficients and  $X_{ed} = A_2$  into Eq. (7.2).

If we use the normal iteration scheme, BLOOM II starts with the solution indicated as Case 1 ( $G = 0.0$ ) and it converges to the solution indicated as Case 2, because  $C_2 \geq C_3$ . Suppose on the other hand that we take  $G_{in} \geq G_{lim}$ . Now of course BLOOM II finds the solution indicated by Case 3 in the first iteration step and as the concentration of edible species is zero, it will not make any fur-

ther iterations but rather consider Case 3 as the optimal solution. Obviously, whether we find the solution of Case 2 or Case 3 depends on the value of  $G_{in}$ .

How important is this phenomenon to the performance of BLOOM II in those 20 percent of all cases, when edible species are present in the initial iteration step? An analytical analysis is extremely difficult because (1) Eq. (7.2) is quadratic in the denominator, which makes  $G$  an optimum-type function of  $X_{ed}$  and because (2) grazing affects the minimum efficiency requirement  $E_{min}(T)$  and thus extinction root  $K_{max}$ . This, as we have previously seen [Chap. 5] is a complicated function of several abiotic and biotic conditions. Since even the less dimensional cases are complicated we were only able to perform some sort of sensitivity analysis of the model to investigate these problems.

We have maintained the present algorithm of BLOOM II with  $G_{in} = 0.0$  for several reasons:

- The exact value of  $G_{lim}$  depends on the uncertain coefficient  $z$ ,  $ZG$  and  $X_{min}$ , hence even if we had an equation to compute  $G_{lim}$ , it would still be difficult to determine how it relates to a particular value of  $G_{in}$ .
- But our present coefficient values strongly suggest that  $G_{lim}$  is usually large relative to the actual grazing rate constant  $G$  of any bloom with edible species. This means that the necessary grazing pressure to make  $G_{in}$  about as large as  $G_{lim}$  is usually so high, that the model will switch to a bloom of unedible species anyhow.
- Our assumption to take  $G_{in} = 0.0$  implies that the model tends to minimize the impact of zooplankton on the phytoplankton biomasses and considers the highest possible bloom in which edible species are present among all possible steady state solutions. This procedure is consistent to the model's objective.

## 8. CALIBRATION AND VALIDATION

### 8.1 INPUTS TO THE MODEL

Mathematical models such as BLOOM II require many data which differ in importance, origin, quality ('softness') etc. a considerable portion of the available time to develop the model, therefore, had to be devoted to data research and data handling. These efforts will only be discussed rather briefly here (1) to keep the report readable, but (2) because it would be difficult to reproduce the history of each number. Thus we shall only mention the required inputs of BLOOM II and give some general indication how each coefficient was derived (Table 8.2). Some additional information is provided in the Addendum volume to this report. We shall also mention which outputs are produced by the model and discuss the results of several calibration and validation runs.

There are two kinds of inputs to the model: universal and lake-specific inputs. In most cases the initial values for universal inputs were determined from (many) literature sources and Grote Rug observations. In some cases these values were modified when the model was calibrated. The lake-specific inputs were directly or sometimes indirectly determined from measurements.

#### 8.1.1 Lake specific inputs

Contrary to the universal inputs, lake-specific inputs vary between lakes and years. These inputs are:

1. The average weekly water temperature.
2. Weekly concentrations of total available N, P and Si.
3. Weekly solar intensities.
4. The background extinction  $K_b$  of the water.
5. The mixing depth  $Z_{max}$ .
6. The flushing rate constant or residence time.
7. Weekly zooplankton concentrations.
8. An adjustment in the specific ratio of carbon to chlorophyll (only in a few lakes).

Already at a brief examination the reader will notice, that frequently data for some of these variables will be missing for either some time-periods, or entirely. How significant that is to the model's performance, depends on which data are missing and how frequently. Obviously, we have to supply the model with reasonable values for the nutrient concentrations. But as we have shown in Sec. 7.4.1, a run for a eutrophic lake without zooplankton data is still valuable.

For Grote Rug almost all lake-specific inputs were weekly available. In all other cases, however, data were measured two-weekly or even monthly. Missing values for these were generated by linear interpolation.

### 8.1.2 Universal inputs

Because most inputs have already been discussed, we shall confine ourselves to a brief summary. As universal inputs BLOOM II requires:

1. The remineralization rates ( $u_i$ ) of the nutrients as a function of temperature.
2. The fraction of dead phytoplankton ( $q_i$ ), which has to be remineralized.
3. Minimum stoichiometric coefficients ( $a_{i,j}$ ) for the nutrients.
4. The ratio of carbon to chlorophyll ( $C/Chl_j$ ) of each species  $j$ .
5. The disappearance rate of dead chlorophyll ( $v$ ) as a function of temperature.
6. The specific extinction coefficients ( $K_j$ ) for each species  $j$ .
7. The average cell volume  $V_j$  of an individual or colony of species  $j$ .
8. The ratio of respiration to maximum gross production and the temperature dependence of respiration.
9. The production curve  $E(I,T)$  of each species  $j$ .
10. The relative mixing depth  $R_{mix,j}$  of each species  $j$  to compute the impact of buoyancy regulation.
11. The average day length.
12. Several grazing coefficients ( $ZG, ZK, X_{min}$  and  $PR_j$ ).
13. The nutrient contents of zooplankton ( $h_i$ ).

### 8.1.3 Chlorophyll to biomass ratio

The carbon to chlorophyll ratio ( $C/Chl_j$ ) of a species is not used in the actual computations of the model, but is necessary to convert its dry weight output to chlorophyll, the only commonly measured biomass indicator. Because chlorophyll to biomass ratios may vary considerably, we would prefer not to make any conversion at all, but rather compare BLOOM II's output directly to some observed number such as planktonic dry weight. Unfortunately, it is impossible in routine measurement programs to separate C or dry weight in live phytoplankton from all other fractions.

The  $C/Chl_j$  ratio is not only a function of the species, but also of several abiotic conditions such as: temperature, (average) light intensity and variations in light intensity. For example a species is more likely to contain a high amount of light-absorbing chlorophyll when it is energy limited than under nutrient-limited conditions. Thus a species dependent variation in time and place may be expected, and the question arises whether it is at all possible to say anything about  $C/Chl_j$  ratios, other than that they vary over a wide range. Indeed literature values from 20 to 90, sometimes even much higher, have been reported frequently, for example by Strickland [1960], Eppley and Sharp [1976], and Banse [1977].

Initial estimates for the  $C/Chl_j$  ratios were obtained from linear regressions between chlorophyll and several phytoplankton-related

variables<sup>1</sup> measured in Grote Rug such as total dry weight, ash free dry weight, particulate organic carbon and particulate nitrogen and phosphorus. The reader should consult the previous references for a discussion of the methodological problems involved in these estimates. Approximate values for three relatively constant internal ratios are presented in the Table 8.1.

Table 8.1

Expected ratios of biomass indicators relative to dry weight according to literature data.

Group	Carbon	Ash free dry weight	Dry weight
diatoms	0.2-0.3	0.4-0.5	1.0
all others	0.4-0.5	0.8-0.9	1.0

Apart from the difference between diatoms and all other groups, which is explained by the high silicon contents of the former (10 to 30 percent of dry weight), the results for various groups are fairly constant.

Using data for periods, when only one species was dominant (RID data), we obtained very reasonable results for Grote Rug (Table A.3) because (1) most of the correlations are highly significant, (2) the differences between the various ratios are within the range of expected values, and (3) they are consistent through the years.

In many other lakes the average C/Chl ratios agreed well with the Grote Rug estimates. The differences between individual lakes could usually be related to observed differences in species dominance. Hence in the most recent version of the model the same specific conversions of dry weight to chlorophyll are used in all but a few cases such as the lake Wolderwijd. Previously, we made an adjustment in some other (PAWN) lakes as well, but after recent improvements in the computed composition of species, an adjustment was no longer necessary. The average C/Chl ratio of 65 in lake Wolderwijd is beyond the nominal range of any of BLOOM II's species, however, and thus a lake-specific adjustment for this case is inevitable.

The model's dry weight computation will always be converted to chlorophyll. However, in comparing blooms under alternative conditions, one should use dry weight rather than chlorophyll, because:

- The conversion depends on the dominant species, thus any change, or the absence of any change in chlorophyll levels, may be due to a change in composition, rather than a change in dry weight.
- If the average light conditions change drastically, some or all species may adjust their chlorophyll to biomass ratios; thus it is uncertain whether the present conversion coefficients still hold in future situations.

<sup>1</sup> The background extinction  $K_b$  was estimated from the intercept of the dependent variable. More details are reported by Los et al. [1982].

## 8.2 Model outputs

Because BLOOM II is a multispecies model with several potential limiting factors, a great deal of output (up to 5000 lines of detailed information) is potentially available, although the output may be limited to only two summary tables if desired. The following outputs are always or optionally produced by the model for each time-step and sometimes for each extinction interval and each zooplankton iteration:

1. Concentration of each species in mg dry weight per  $m^3$ .
2. Total concentration of all species in mg dry weight per  $m^3$ .
3. Total concentration of all species in mg chlorophyll per  $m^3$ .
4. Concentration of 'planktonic' and 'rest' nutrients in mg per  $m^3$  [Sec. A.2].
5. The total extinction per m.
6. Production, mortality grazing, respiration and flushing rates of each species in mg C and mg O<sub>2</sub> per  $m^3$  per day.
7. Diurnal distribution of the total production and respiration rates in mg O<sub>2</sub> per  $m^3$  per hour.

## 8.3 CALIBRATION PROCEDURE

The universal inputs, which are necessary for calibration and validation of the model, have all been established by the following procedure:

1. Literature research.
2. Analysis of Grote Rug data.
3. A comparison between the results of step 1 and 2, if necessary followed by a repetition of one or both steps.
4. A comparison between the model outputs and the observations for selected calibration cases. If the disagreements are considered too large, step 1 or step 2 (or both) are repeated.
5. Validation of the model for those Grote Rug cases, which were not used for calibration.
6. Validation of the model for the PAWN lakes.

Although the required number of (species dependent) data is large, we were able to obtain sufficient information from the literature to establish an almost complete initial set of universal inputs (model parameters). For this we have used many papers which are included in the list of references, including the WABASIM reviews by Lingeman-Kosmerchock [1978; 1979a; 1979b; 1979c]. We shall, however, not attempt to include all references for each individual model parameter. The extent to which these initial estimates are important to the present version of BLOOM II is indicated in Table 8.2.

The accuracy, completeness and frequency of the Grote Rug measurements have been of great help developing a model which requires many, some rather unconventional, data. Fortunately, data were available for four basins in three separate years, during which

many important species have dominated the phytoplankton population at least once.

The primary production measurements by the Delta Department since 1977 made it possible to verify the temperature constant of  $P_{nmax}(T)$  [Sec. 4.6] and to adjust the original volume coefficient for blue-greens in Eq. (4.13c). The calculation of the minimum mortality rate constant Eq. (4.22b) and the photosynthetic efficiency curves  $E(I,T)$ , are completely based upon these measurements. Also, the expected temperature dependence of  $E(I,T)$  according to the literature, could indeed explain the seasonal variation of  $E(I,T)$  in Grote Rug. We have used both 1977 and 1978 data of all four reservoirs and included those in the model, which were measured at approximately 15° centigrade [Sec. 4.7].

Linear regression of two, sometimes three, related variables was applied to obtain estimates for the stoichiometric constants ( $a_{i,j}$ ), the chlorophyll to biomass ratios, and for the specific extinction coefficients ( $K_j$ ). Usually only data were included for periods when one species was clearly dominant according to the RID species identifications. Compared with regressions for periods of a whole year, the significance of many correlation coefficients increased and data for several species became available, for which there were no literature data. In general the values for  $K_j$  and  $C/Chl_j$  from Grote Rug agreed well to the literature, but the nutrient coefficients  $a_{i,j}$  of some species were rather different.

Table 8.2

Origin and modifications of BLOOM II's universal input coefficients. The symbols indicate the significance of literature (Lit), Grote Rug (GR) and calibration (Cal) to the current value:

++ very large, + large, o moderately large, - small, -- absent.

Coefficients	Lit	GR	CAL	Remarks
Pgmax	++	+	--	GR only for blue-greens
Mmin	--	++	-	
Resp	++	--	o	Cal only for dinoflagellates
G	++	--	--	
$K_j$	++	+	--	GR for two blue-greens
$v$	++	--	o	Cal for low temperatures
$R_{mix,j}$	--	--	++	No quantitative data
$E(I,T)$	--	++	--	
SRFL	++	--	--	Surface reflection of I
CPAR	++	--	--	Conversion total to active I
$a_{i,j}$	+	++	-	
$u_i$	++	+	--	
$q_i$	++	--	--	
$C/Chl_j$	++	++	--	C to chlorophyll ratio of j
ZG	++	--	--	
ZK	++	--	--	
Xmin	++	--	--	
$PR_j$	++	--	--	
$h_i$	++	--	--	Nutrient contents zooplankton

Table 8.2 shows that most of BLOOM II's coefficients were established from the literature and Grote Rug rather than by

calibration, although a clear distinction is not always possible. For instance we had made many runs with the model, before we obtained all the current efficiency curves. Hence we knew that some of the previous ones could be improved, but when new data became available, we have simply used them without further changes.

Unlike the ++ and + signs could suggest, literature was not the most important source for the universal inputs as some of the coefficients, to which BLOOM II is most sensitive such as  $M_{min}(T)$  and  $a_{1,j}$ , were mainly estimated from Grote Rug data. Actual calibration was in fact limited to coefficients such as  $R_{mix,j}$  for which there were little or no data in either the literature or the Grote Rug observations.

## 8.4 CALIBRATION RESULTS

Measurements of several Grote Rug cases have been used to some extent to calibrate the model. This is true in particular for the primary production measurements from which we have determined the production efficiency, the maximum rate of primary production and the minimum mortality rate constant. Three cases, however, had a major impact on the calibration result of the model: Ring 2 and Ring 3 in 1976, and Ring 2 in 1977. All three of them were used to adjust some stoichiometric coefficients, and the buoyancy factor ( $R_{mix,j}$ ). The respiration rate constant of Ceratium was lowered based upon the run for Ring 2 in 1976.

For one case (Ring 2 in 1977) we have also used a forcing function for the mortality rate constant which was derived from observations. This case, therefore, can be considered as the only complete calibration of the model. The cases of Ring 2 and Ring 3 in 1976 are partial validations (mortality rate;  $P_{max}(T)$ ). All other cases from Grote Rug and the five PAWN cases are considered as complete validations of BLOOM II.

### 8.4.1 Grote Rug, Ring 2, 1977

Ring 2 in 1977 contributed more to the calibration of the model than any other case. Here we have not only changed some universal inputs after running the model, but moreover we have not used Eq. (4.22b) to calculate the minimum mortality rate constant. Instead Eq. (4.21b) was employed to obtain a time-series of  $M$  from observed changes in chlorophyll and the measured production rates. These values of  $M$  were fed into the model as a forcing function. This approach was adopted because we wanted to eliminate the effect of one of the most uncertain coefficients ( $M$ ) during calibration.

With these mortality estimates BLOOM II computes total biomass extremely well. Moreover it computes the dominant species remarkably well (Fig. A-1.1). Phosphorus is by far the most important limiting factor in the computations, which is no surprise considering that the concentrations of total phosphorus are extremely low in this case (a peak as low as 0.103 mg/l, at the peak of the phytoplankton bloom). During the early summer bloom the observed ratio between total phosphorus and chlorophyll is exceptionally low. This suggests that the mortality rate constant should also be very low, because almost all phosphorus must have been incorporated by live phytoplankton rather than detritus. Indeed the computed mortality rates for

this bloom are even lower than BLOOM II's minimum estimate. With its minimum mortality estimate  $M_{min}(T)$ , BLOOM II can only compute a peak which is about half the observed level (153.5 mg chlorophyll per  $m^3$ ).

In this case where we provided the model with a good estimator for the mortality, BLOOM II behaved better than we might have expected from its objective. It is not just capable of reproducing the highest phytoplankton levels but it also computes fairly reasonable values in periods between blooms.

Although we have assumed a small value for the relative mixing depth ( $R_{mix} = 0.275$ ), the model is unable to achieve equally high bloom levels as have been observed during the last months of the year. As the dominant species, Aphanizomenon, is energy limited in the model, perhaps we have still underestimated the impact of buoyancy control.

#### 8.4.2 Grote Rug, Ring 2 and Ring 3, 1976

With the exception of the previous case, the weekly mortality rates have always been computed by BLOOM II according to Eq. (4.22b)<sup>2</sup>. As there are no production measurements for Grote Rug in 1976, the following cases can be considered as partial validations of the model particularly for the energy constraints. However,

1. The respiration rate constant of Ceratium was reduced to 20 percent of  $P_{max}(T)$  at 20° [Sec. 4.9], because otherwise BLOOM II could not achieve the observed concentrations in Ring 2 when this species was dominant.
2. The summer blooms in both cases have been used in addition to Ring 2, 1977 to determine  $R_{mix}$ , [Sec. 5.7].

None of BLOOM II's stoichiometric constants was modified after we ran the model for these two cases. But measurements of particulate nutrients and biomass have been used, in addition to other data in the regressions to determine these constants.

The results for both cases (Fig. A-2.1 through A-3.3) are very similar. An observed spring bloom of diatoms and flagellates is reasonably well reproduced by the model, although computed bloom levels are somewhat high at the start. Also the computed species composition in Ring 2 agrees better to the observations than in Ring 3, which has a higher background extinction. This is a considerable disadvantage to diatoms and flagellates when the light intensities are low, because they have a relatively high energy requirement and low production efficiency [Sec. 4.6.1; Fig. 4.3].

In the first half of the summer the computed biomass levels are higher than observed in both rings, but they are still lower than the biomass standard (10 g dry weight per  $m^3$ , approximately 65 to 135 mg chlorophyll per  $m^3$ ) of an objectionable bloom [Sec. 1.5].

In the second half of the summer, however, the model computes blooms in both cases of the same order of magnitude and at about the same time as was actually measured. The observed difference in species composition between the two rings: a mixture of blue-greens and Ceratium in Ring 2 and a complete dominance of Microcystis in

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<sup>2</sup> Other equations have been used recently, but none are included in this report.

Ring 3 after week 29, is remarkably well reproduced by BLOOM II. This according to the computations is caused by a different combination of limiting factors. In Ring 2 phosphor and energy are the main limitations, in Ring 3 Microcystis is initially limited by nitrogen (an exception in Grote Rug) and after week 34 by energy until the end of the year. Computed potential bloom levels in the last two months of the year are achieved in neither of the two Rings.

## 8.5 NOMINAL VALIDATION RESULTS

### 8.5.1 Grote Rug cases

If it were BLOOM II's purpose to make an accurate prediction of the weekly phytoplankton concentrations, the validation results for Grote Rug (Fig. A-4.1 through A-9.3) would not seem impressive, since usually computed biomasses are higher than observed. However, in Secs. 1.2 and 1.3 we have explained that before anything else, BLOOM II should be able to compute time, size and composition of objectionable blooms. A close examination of the results indicates that the model rarely computes violations of the biomass standard. The maximum levels in some cases (Ring 3, 1975; Ring 1, 1976) are more or less at the standard, but in other case (for example Ring 2, 1975; Grote Rug, 1977), computed concentrations infrequently approach the standard. This is one of the reasons, why the Grote Rug cases are not very attractive for validation purposes and why the results on some of the PAWN lakes are included in this report.

There are two exceptions to this general picture. The model results for Ring 3 in 1977 are worse, those for Ring 2 in 1978 better than average. Nutrient concentrations in Ring 3 remained extremely high for almost a year after the enormous Microcystis bloom of 1976 [Sec. 8.4.2]. At first this has a limited impact on the results of the model because energy is limiting in winter. But during the spring of 1977, when the amount of solar energy is steadily increasing, the model continues to maximize biomass until it becomes phosphor and energy limited at a much higher biomass level than was observed.

So far the most plausible explanation is that BLOOM II largely overestimates the available amount of phosphor. Computations with the WABASIM chemical model CHARON suggest that phosphor was mainly present in particulate inorganic (=unavailable) form. Details on these results will be published by Nico de Rooij in his report(s) on CHARON's results.

In contrast to the previous case, the results for Ring 2 in 1978 are much better than average. Both total biomass and the species composition agree fairly well to the observations, which is remarkable considering the rather unusual observed succession of species.

The most interesting disagreement occurs in summer, when the computed chlorophyll concentrations are lower than observed. A thorough analysis of all available data on (1) the observed phytoplankton biomass (in chlorophyll, as well as in total- and total ash free dry weight units), (2) the C/Chl ratios, (3) the phosphor to biomass ratios and (4) the mortality rates, suggests

that probably more phosphor was available than according to the measurements of total phosphor. If we subtract the estimated amount of phosphor in detritus (based upon the 'observed' mortality rates) from the total measured amount, there is already too little phosphor left to support the observed phytoplankton population.

The measurements themselves contain information to support this hypothesis. We have compared the total phosphor concentrations of two independent, differently collected samples of this ring. It turns out that there is a difference of about a factor two and that the lowest levels were used as input to the model. Hence we may conclude that the phosphor measurements are at least suspect in this case.

### 8.5.2 PAWN lakes

There are two major reasons to include some results of the PAWN project (R1230) which have been reported by Los et al. [1982] here:

1. The observed phytoplankton levels exceed the standards much more frequently in several PAWN lakes than in any of the Grote Rug reservoirs.
2. Grote Rug is a man-made lake, which may not be representative for any natural lake.

The latter is true in particular for the rings upon which the model is mainly based. Moreover intake and withdrawal of water is highly irregular and management measures for phosphor removal in the reservoir and two of the rings result in much lower average phosphor concentrations than commonly observed in Dutch lakes (compare for example Table A.7 to A.16). Hence phosphor is much more important as a limiting factor in Grote Rug than in most natural lakes in the Netherlands.

In this report we have included those five cases for which the best lake-specific data are available: Lake Veluwe (1975 and 1976), which is one of the most eutrophic lakes in the Netherlands, Lake Wolderwijd (1975 and 1976) and Lake IJssel (1976), the largest lake in the country. The lake-specific inputs (Tables A.16 through A.20) are from the Rijkswaterstaat's WAKWAL data base.

The observations indicate that these natural lakes differ considerably from Grote Rug:

- The average and maximum phytoplankton concentrations are (much) higher.
- These concentrations vary comparatively little during a year. Low minimum values in summer, which are typically observed in Grote Rug, are lacking.
- There is not a single dominant limiting factor (phosphor), but a seasonal and regional variation.

Because information on observed species compositions is qualitative rather than quantitative, species dominance is not included in the figures. Instead, computed yearly averaged compositions are shown in Table 8.3.

Lake Veluwe is obviously the most eutrophic of the lakes considered in this report: chlorophyll concentrations in the order of 500 mg/m<sup>3</sup> are not only computed, but also observed in 1975. BLOOM II tends to compute concentrations about 100 mg/m<sup>3</sup> too high in some

parts of the year (the third quarter), but considering the magnitude of the blooms and the uncertainty in several coefficients such as the dry weight to chlorophyll conversion, we may conclude that the computed total biomass is very reasonable for this lake in both years.

In both years, the limiting factors vary in a complex way: energy, phosphor and silicon are the main limiting factors in the first quarter, nitrogen (sometimes with phosphor) in the second and third, and energy, phosphor and nitrogen limit the blooms in the fourth quarter. Sometimes only one factor is limiting, but more often two, or even more than two factors are limiting at the same time.

The phytoplankton population in Lake Veluwe is dominated by Oscillatoria agardhii most of the time (pers. comm. S.H. Hosper), although other blue-greens are occasionally present in large quantities as well. Also the steep decrease in dissolved silicon after the spring bloom strongly suggests, that a considerable amount of diatoms must have been present.

BLOOM II indicates Microcystis as most important species with Oscillatoria coming in second place both in 1975 and 1976. In spring a temporary dominance of diatoms, flagellates, sometimes green algae is computed (Table 8.3). Oscillatoria is less dominant in the computations than in the observations because it has a higher stoichiometric constant for nitrogen than Microcystis and when the highest biomasses are observed (in summer), nitrogen is the main limiting factor.

Lake Wolderwijd is similar to Lake Veluwe in many respects (depth for example). But there are also some important differences: (1) the background extinction is considerably lower (Table A.5) and (2) the nutrient concentrations do not achieve such extreme values as in Lake Veluwe, although they are still high enough to enable massive phytoplankton blooms. Because both the background extinction and the extinction due to live phytoplankton are lower, the average light intensity is higher. This is the most likely explanation for the exceptional biomass to chlorophyll ratio in Lake Wolderwijd, which according to linear regressions of several measured variables, must be approximately 1.5 times higher than the nominal dry weight to chlorophyll ratio for all species in the model [Sec. 8.1.3.]. This exceptional ratio was used to compute chlorophyll from dry weight for this lake (Fig. A-12.1, A-13.1).

The overall agreement between computed and observed total chlorophyll is excellent in both 1975 and 1976. The extremely high computed values after week 40 in 1975 and in the middle of 1976 are not due to a large increase in dry weight, but to a temporary (and erroneous) change in species dominance. The reader may furthermore note that BLOOM II computes total chlorophyll equally well in both years, although the observed concentrations in 1976 are considerably lower than in the previous year.

As in Lake Veluwe the limiting factors vary with season, but in Lake Wolderwijd phosphor is at least equally important as nitrogen, which is also illustrated by the results of the sensitivity analysis [Sec. 9.2]. Only in the third quarter of both years nitrogen becomes the main limitation.

In spite of the differences in ecological conditions, the observed species dominance is more or less the same as in Lake Veluwe: Oscillatoria agardhii is the most important species. BLOOM II computes a complicated seasonal succession of many different species, some of which coexisting when more than one factor is limiting to the bloom. The most important species, however, are the blue-greens Microcystis, Oscillatoria and Aphanizomenon (in this

order), hence as in the Lake Veluwe cases, BLOOM II reproduces the phytoplankton group correctly, but it fails to reproduce the strong dominance of one single species (Table 8.3).

Lake IJssel is the largest lake in the Netherlands, but like so many others it is rather shallow (its average depth is 4.5 m, Table A.5). The current results for this lake are based upon averaged lake-specific inputs, but considering its size, there may be regional variations which could not be taken into account.

Predicted total chlorophyll levels match the observations well, although the model has some difficulties to achieve observed levels in the second part of the year. Why this occurs, is hard to say because energy is the main limiting factor this entire period: it could be anything from the production or mortality rate, the effect of buoyancy control or the background extinction, to the C/Chl ratios.

Except during the second quarter, when both phosphor and energy are limiting, energy is the only limiting factor in the 1976 computations, which clearly distinguishes this case from any of those previously discussed.

The observed species dominance in various years is less constant in Lake IJssel than in for instance Lake Veluwe or Lake Wolderwijd. In some years (e.g. 1977) there is a dominance of green algae (including various Scenedesmus species but also others), in other years blue-greens such as Oscillatoria and Microcystis dominate. In 1976, the blue-greens were dominant (data of RIZA and the Rijksdienst for the IJsselmeer Polders: RIJP).

BLOOM II computes a complete dominance of two species of blue-green algae: Microcystis and Oscillatoria but unlike most other cases, small changes in coefficient values, may have rather dramatic impacts on the computed species composition in Lake IJssel [Sec. 8.6].

## 8.6 OTHER VALIDATION RESULTS

### 8.6.1 Dynamic nutrient recycling

For each case we ran BLOOM II with the dynamic computation scheme [Sec. 3.6; 6.2.2] in addition to the nominal steady state nutrient recycling. As the results are rather consistent, we have only included three typical examples in this report: Ring 1, 1976; Ring 2, 1978; and Lake Wolderwijd, 1975 (Fig. A-15.1 through A-17.3).

In the Grote Rug cases, the effect on total biomass is small, though the fluctuations increase, particularly in spring (Fig. A-15.1). Moreover the computed spring blooms may be more out of phase than nominally, appearing too early since at the start of a bloom the dynamically computed detritus pools lag behind their steady state values. On the other hand at the collapse of these spring bloom the model allocates a considerable amount of nutrients to detritus, more than in the nominal steady state case and sometimes even more than the total available amount (a few weeks in both examples). This, as we have previously explained [Sec. 3.6.2], is due to our using measured nutrient concentrations as forcing functions.

Species compositions are rather similar compared with the nominal runs although not completely in Ring 2, 1978, where the annual species succession is rather complicated in this particular year.

For the considered PAWN lakes, there is little difference to the nominal cases (compare Fig. A-17.1 with Fig. A-12.1). In the example of Lake Wolderwijd in 1975, the computed spring bloom agrees somewhat better to the observations than in the nominal case, but the improvement is by no means spectacular. Species composition (Table 8.3) limiting factors, and average biomass are essentially similar in both cases.

### 8.6.2 Additional growth constraints

The option to put a limit on the growth rate of each species mainly affects the computed species composition, since unrealistic switches are prevented. It is easily verified that with this option the total biomass is always smaller or equal to the nominal result, since constraints are added to the original system. Therefore this option might reduce total biomass considerably, at least in some periods of the year.

So far it has been our experience with all considered Grote Rug and PAWN cases, however, that the addition of growth constraints reduces the yearly averaged total biomass only by 0 to 10 percent, which is little compared with potential errors in the model. This is because (1) the solutions are identical to the nominal results in most periods in the majority of cases and because (2) the nutrient and energy requirements of the individual species cover a rather continuous range of values. Thus if the optimal set of species at the prevailing conditions becomes infeasible, another set cannot have an equally high total biomass, but it is only under rare conditions significantly smaller than the original steady state solution.

Often the computed species compositions improve: abrupt switches are prevented if they are caused by a temporary change in limiting conditions. If these conditions persist, the model usually converges to the nominal species composition in a few weeks, but not always. Occasionally dominance of blue-greens in the first weeks of a year prevents that diatoms and flagellates become dominant during the spring bloom, because week after week the set of species in which the latter appear (growth limited) is sub-optimal to a solution in which only blue-greens persist (Ring 2, 1976; Lake Veluwe, 1975, Table 8.3).

Table 8.3

Predicted relative species composition (as percentage of total dry weight) in the lakes Veluwe and Wolderwijd for various cases (explained in main text). Four (groups) of species are distinguished:

B2: Aphanizomenon

B3: Microcystis

B4: Oscillatoria

AO: All other species

LAKE	YEAR	NOMINAL				DYN.RECYCL.				GROWTH CON.			
		AO	B2	B3	B4	AO	B2	B3	B4	AO	B2	B3	B4
Veluwe	1975	11	0	71	18	7	2	73	19	0	2	74	24
Veluwe	1976	5	8	64	23	7	7	61	26	3	10	59	28
Wolderwijd	1975	15	22	37	26	14	24	38	24	6	21	37	35
Wolderwijd	1976	23	17	32	28	26	18	30	27	16	23	35	26

The addition of growth constraints affects the species composition much more strongly in Lake IJssel than in any other case. Using the nominal base level of 100 mg dry weight per m<sup>3</sup>, the order of importance of the two dominant blue-green algal species is completely reversed. No species can increase its biomass strongly enough in one week to beat the total biomass of a bloom of only Oscillatoria (Table 8.4). An increase in the base level to 250 mg dry weight per m<sup>3</sup> suffices to change dominance by the middle of the year and with a base level of 500, the yearly averaged composition approaches the nominal one.

In contrast to all other cases, there is only one important limiting factor (energy) in this case. As the number of species in the bloom is equal to the number of limiting constraints [Sec. 2.1], the bloom composition of the model will be much more static compared with a case where various limiting factors alternate during a year.

Thus sometimes the initial conditions determine species dominance for a considerable period. This is a rather common phenomenon in models with some kind of memory: often they converge to a particular solution under a broad range of initial conditions, but occasionally small variations have long lasting effects. The sensitivity of the species composition to the initial conditions is one possible explanation for the observed differences in dominance in this lake in different years [Sec. 8.5].

Table 8.4

Predicted relative species composition (as percentage of total dry weight) in Lake IJssel, 1976 in the nominal case and in three cases with additional growth constraints but different biomass base levels (mg dry weight per m<sup>3</sup>). Species abbreviations are the same as in Table 8.3.

Case	Baselevel	A0	B3	B4
Nominal		7	73	20
Growth Con.	500	0	55	45
Growth Con.	250	0	43	57
Growth Con.	100	0	0	100

## 9. SENSITIVITY ANALYSIS

### 9.1 INTRODUCTION

The number of universal and lake-specific inputs to BLOOM II is so large that a complete sensitivity analysis of each individual factor is impossible, not to mention combinations of several factors. However, during the development of the model more than just a vague idea has emerged how it would react to certain changes. With these experiences in mind, we have set up a limited, yet representative series of runs to investigate the sensitivity of the model.

We have not included any results on perturbations of the species or group dependent coefficients such as the stoichiometric constants, the efficiency curves, or the specific extinctions, for essentially three reasons:

1. The number of possible combinations is too large.
2. The results strongly depend on the selected cases.
3. The impacts on total biomass are moderate or even small. Although the value of each individual coefficient may be uncertain, the entire set of BLOOM's ten species cover a broad range of values [Sec. 8.6.2; Table A.3; A.4].

We have selected the most important lake-specific inputs such as the nutrient concentrations, solar radiation and the depth, and some universal inputs for example the remineralization and mortality rate constants. Except in the case of mortality, where a minimum estimate is used by the model, we have made one run with a higher than nominal and one with a smaller than nominal value. We have usually perturbed a factor to such extent that the results of the model differ significantly from the nominal results. But we have tried to keep each factor within reasonable limits. Only for the depth and background extinction we have deliberately used more extreme perturbations to indicate the regional and seasonal variations in sensitivity.

The nominal nutrient concentrations were only varied over a moderately wide range because it is not the intention of this report to investigate the possible impacts of specific sanitation strategies. For instance in a nutrient removal study we would have extended this range considerably and made more runs.

We have selected five representative cases (two from Grote Rug and three from the PAWN lakes), which strongly differ in total biomass, species composition and limiting factors. The results for each case are illustrated for three or four typical weeks in different periods of the year. Weeks were selected when (1) the nominal results of BLOOM II agreed well to the observations and (2) bloom levels were high, although not at the peak for this period.

### 9.2 RESULTS

Although many of BLOOM's basic equations are relatively simple (e.g. the nutrient equations are linear), its reaction to a perturbation even of a single factor is usually non-linear. To understand why we shall start with a brief summary of some of its basic characteristics.

BLOOM II selects among (normally) ten species that particular combination of species which has the highest total biomass at the prevailing conditions. Linear programming (LP) is used to find this optimal solution which consists of as many species as there are limiting constraints. The potential limiting factors (constraints) are three nutrients, solar energy and (optionally) the growth rates. Each species which is not selected by the model requires a larger amount of at least one constraining factor than at least one species in the bloom. How much more and of what, is not determined by BLOOM II. Except in degenerate cases, there is only a single optimum but the total biomass of the second best solution could just as well be 0 or 99.9 percent of the optimum solution. It could be limited by the same constraints, or (partly) by others and its species composition could be similar to the nominal composition, but also completely different.

When the value of one coefficient is modified, one, sometimes several constraints are changed. For example a change in the mortality rate constant affects the partitioning of nutrients between live and dead phytoplankton, but also the level of the energy constraints. Some perturbations affect the available amount of a constraint (nutrient concentrations), others affect the required amounts per unit of phytoplankton biomass (stoichiometric constants).

Let us for example consider what may happen if we change the available amount of a constraint C. From Fig. 2.1 it is immediately obvious that there are three possible situations:

1. C is the only limiting constraint.
2. C and at least one other factor are simultaneously limiting.
3. C is not limiting but one or several other constraints.

A change in the available amount of C can cause a transition from one situation into another, which will often be accompanied by a partial or complete shift in species composition. However, this is not always the case. For example in the computations for Lake Veluwe and Lake Wolderwijd, Oscillatoria is dominant in the autumn and winter, although three different constraints (nitrogen, phosphor, and energy) are limiting in turn. On the other hand, changes in species composition can occur without a change in limiting constraint(s).

Because there are many constraints and many species in the model, we cannot nearly always predict what its response will be to a change in one constraint. Therefore we shall only consider three typical examples: one with a linear, one with a non-linear and without any response. Suppose we decrease the available amount of C by n percent. This may be the case in a nutrient removal study.

First the total biomass will also decrease by n percent if and only if

1. C is the only limiting factor.
2. One and the same species remains dominant.

Second the total biomass will not change if

1. C is not limiting initially.
2. C does not become limiting when the available amount is reduced.

This may happen for example when the removal of phosphor in a presently energy or nitrogen limited lake is insufficient to make phosphor limiting.

Third the total biomass will change by less than n percent if a bloom consists of two species limited by C and some other constraint. In the following example a 30 percent reduction in the available amount of nitrogen results in a reduction by less than 15 percent in total biomass because the relative composition of the bloom is adjusted.

Case 1.							
Species	Stochiom. coefficient		Available nutrient		Nutrient limited maximum		Maximum of one species
	N	P	N	P	N	P	
1	0.1	0.005	100	6	1000	1200	1000
2	0.05	0.0075	100	6	2000	800	800
<p>Optimum LP solution: <math>x_1 = 900</math>  <math>x_2 = 200</math>                      Total biomass = 1100</p>							

Case 2: N reduced by 30%.							
Species	Stochiom. coefficient		Available nutrient		Nutrient limited maximum		Maximum of one species
	N	P	N	P	N	P	
1	0.1	0.005	70	6	700	1200	700
2	0.05	0.0075	70	6	1400	800	800
<p>Optimum LP solution: <math>x_1 = 450</math>  <math>x_2 = 500</math>                      Total biomass = 950</p>							

Comparing the results (Fig. A.18 through A.23), it is obvious that the impact of many perturbation differ

1. **Regionally:** e.g. Grote Rug and Lake Wolderwijd are relatively sensitive to phosphor; the Lakes Veluwe and Wolderwijd to nitrogen; Lake IJssel to energy.
2. **Seasonally:** e.g. in autumn the computations for each lake are relatively sensitive to changes in the energy constraints, and in spring to changes in the silicon con-

straint. The results for Ring 3 in 1976 are only sensitive to nitrogen in a short period around week 32.

The regional variations are easily explained by local differences in environmental conditions. Some of the seasonal variations may be explained by rather common trends in nutrient concentrations. For example in many lakes available silicon is relatively high in autumn and winter, but extremely low near the end of spring. Phosphor concentrations are often high in summer (normal and explosive bottom fluxes), but nitrogen levels are relatively low in summer.

The large sensitivity of all cases to perturbation which affect the availability of light energy (solar radiation; depth; background extinction) requires an additional explanation. The level of solar radiation is a symmetrical function of season, but water temperature lags one or two months behind with a peak in July and August rather than June and with its yearly minimum in February or March. Hence temperature is high relative to solar radiation in autumn, which is unadvantageous to phytoplankton cells as respiration and mortality depend more strongly on temperature than primary production [Chap. 4]. Therefore at high temperatures but low solar radiation levels, losses are high relative to growth.

For POLANO Bigelow et al. [1977] essentially reached the opposite conclusion: high temperatures favored phytoplankton growth. This difference is easily explained, however, since their mortality rates were specified externally as a forcing function, but primary production rates depended on temperature. Hence gross production rates increased relative to the (constant) mortality rates with rising temperatures. Therefore the net production rate also increased with temperature.

Notice that in many cases blooms are sensitive to more than one factor, even if they are nominally limited by a single factor. Some examples:

Lake	Year	Week	Sensitive to:
Ring 3	1976	32	N, P
Veluwe	1976	22	N, P
Wolderwijd	1975	44	P, N, I
IJssel	1976	26	P, I, N

Of the universal coefficients which were varied, the sensitivity to the remineralization rate constants ( $u_i$ ) proved to be moderately small. The impact of a 50 percent change in  $u_i$  value of the limiting nutrient is similar to a 20 percent change in its concentration, which is small relative to measurement errors.

We have increased the weekly mortality rate constant by 50 percent to study the sensitivity of the model to this important parameter. Notice that the increased mortality rates are not exceptionally high, because many values computed from production measurements in Grote Rug are still higher (Fig. 4.6). Actually the curve for the 50 percent increased mortality rates looks like a least squares fit through the observed rates.

The sensitivity to this perturbation is large. Computed total biomasses agree better to the measurements when the nominal results of BLOOM II were too high, but now the computed peak levels are

(sometimes considerably) below the observations. There is hardly any time or site specific variation, because M affects the detritus pool sizes of all nutrients in a similar way regardless which of them is limiting. Only in autumn there is a significantly larger reduction in total biomass than in other parts of the year, because besides the (unsignificant) increase in the amount of dead chlorophyll, the energy limited steady state biomasses are reduced considerably more than in other parts of the year. This is for the same reason as previously explained for the depth and background extinction.

## 10. CONCLUSIONS

### 10.1 OVERVIEW OF BLOOM II

Many different phytoplankton models existed when the WABASIM project started in April 1977. Most of them seem to fall into two categories:

1. Empirical relations of the Vollenweider type. These models try to relate the average chlorophyll (not biomass) concentration over a long period of time to a limited number of abiotic conditions (mainly phosphorus and the residence time).
2. Dynamic (differential equation) models. These models relate the total biomass of phytoplankton (or a few groups of phytoplankton species) to some abiotic conditions (always phosphorus, usually also nitrogen and energy, sometimes silicon).

Both types of models have certain disadvantages, which limit their applicability at least under the conditions which typify Dutch eutrophic lakes. The empirical models are black boxes which, as far as we know, have always failed to compute the chlorophyll levels in Dutch lakes reasonably well. Usually the bloom sizes are strongly under-predicted.

The results of dynamic models are rather mixed. In some cases the computed chlorophyll levels agree well to the measurements, in other cases a fair agreement is only possible when important model coefficients are adjusted during calibration. For management purposes there seem to be two structural problems:

1. The time-dependence of these models makes predictions of objectionable blooms (sometimes extremely) sensitive to the results in earlier periods when the bloom-sizes were of no concern to a manager.
2. One of the essential characteristics of a bloom: its species composition, cannot be computed because there are not enough data to include realistic species (half-saturation constants; Chap. 4).

It was therefore decided in the WABASIM project to adopt a completely different approach. We would construct a management model to compute size, species composition and limiting factors of objectionable blooms. This model would be based upon the POLANO Algae Bloom Model which was developed by the Rand Corporation for the Oosterschelde sea estuary [Bigelow et al., 1977]. This model (called BLOOM II) computes the maximum bloom-size consistent to the prevailing biotic and abiotic conditions. The potential limiting factors include the concentrations of essential nutrients, the temperature, the solar intensity, the light climate in the water etc. According to its objective the model may often compute phytoplankton levels which are higher than observed. However, the model should be most accurate when it computes a bloom with an objectionable size or species composition according to certain standards.

BLOOM II is rather unique among biological models in its using Linear Programming as solution technique. Theoretically the results of the model could be rather discontinuous because it is an

equilibrium model. Usually, however, its results have a rather smooth appearance because the external conditions, which are forcing functions to the model, tend to change slowly during a year.

Essentially there are two steady state assumptions: one for phytoplankton growth and one for nutrient recycling. The first may be reasonably justified by the potential net growth rates under various conditions, but the latter is questionable, at least in relatively cold parts of the year. With nutrients as forcing functions, however, there is little alternative for this assumption.

To evaluate its equilibrium assumptions, BLOOM II was equipped with new options to use (1) a dynamic nutrient recycling scheme, (2) a variable time-step, and (3) to add growth limiting constraints to the nominal set of equations. The results with the dynamic nutrient recycling are essentially similar to the nominal results in natural lakes, indicating that deviations from equilibrium do not invalidate the overall performance of the model. Significant deviations sometimes occur in the Grote Rug cases, particularly at low temperatures in spring, which are contributed to irregularities in nutrient concentrations caused by management measures in this storage reservoir.

The agreement between observations and computations in terms of biomass, limitations and composition tends to be better in natural lakes than in Grote Rug, although (large) over-predictions have been obtained for some natural lakes [Los et al., 1982]. Probably some or all of the management measures (dosing with iron or aluminum, irregular intake and withdrawal of water) affect phytoplankton growth. The consistently great difference in biomass concentrations between the Fe-dosed Ring 1 (never a significant bloom in four years) and the Al-dosed Ring 2 (some blooms every year, some extremely high) indicates that indeed management measures are important.

Operation of BLOOM II is straightforward and relatively simple. After its calibration, further adjustments of its universal inputs can usually be avoided as the model tends to give good or even excellent results in many new cases. Its structure makes it particularly well suited (1) for a sensitivity analysis and (2) to compute the impacts of management scenarios.

It has the advantage over most other (dynamic) phytoplankton model that it may change its species composition under alternative conditions. Thus the existing variations in phytoplankton coefficient values is implicitly reflected in the results of BLOOM II. This can only be the case in models with one or a few species if they can vary the rates of internal processes or the values of internal coefficients.

The computer program of the model allows both 'batch' and 'interactive' processing. In the first case the user has no control over the model once a computer run has begun. In an interactive run he can turn each option of the model 'off' or 'on', and change the value of practically each coefficient. After the results have been displayed on a terminal, the user may reformulate the problem and continue with a new computation. This mode of operation is particularly useful for calibration and sensitivity analysis of the model, to test (alternative) hypothesis, and to evaluate management scenarios.

The program is efficient and inexpensive. A normal run requires between 30 and 50 seconds of CPU on the IBM 4331 model 2 of the Delft Hydraulic Laboratory, which roughly corresponds to 2.5 to 4 seconds

of CPU on an IBM 370/168. This range exists because (1) the number of extinction intervals to be solved in a particular run depends on the abiotic conditions (light regime) and (2) zooplankton data are not always available.

## 10.2 RECOMMENDATIONS FOR FURTHER RESEARCH

The current version of the model has been rather successfully applied to more than twenty different cases. It is obvious that many difficult problems have been solved adequately which makes the model an important tool to help managing eutrophic lakes. However, several serious problems have not yet been (completely) solved. Also various coefficient values might be improved as new and better data become available.

Perhaps the most important extension of the phytoplankton model is the development of an integrated version of the nutrient model CHARON and BLOOM II. This 'coupled model' is now operative at the Delft Hydraulics Laboratory, but no results could be included in this report. Unlike the stand-alone models, the coupled model can directly relate nutrient and phytoplankton concentrations in a lake to the nutrient loadings.

Many high quality data both from the literature and especially from Grote Rug were available when BLOOM II was developed. No doubt, however, the model could still be improved if more data became available. A laboratory investigation at the Microbiological Department of the Amsterdam University to relate net primary production ( $P_{gmax}(T)$ ,  $R(T)$ ,  $E(I,T)$ ) of six important species to several abiotic conditions (average light intensity; temperature; day length) is in its reporting stage. The results of this study may contribute strongly to the ability of the model to compute the total biomass concentrations and particularly the competition between different species of phytoplankton.

Bigelow et al. [1977] already stressed the importance to estimate the natural mortality rate constants. It would definitely improve the model if we knew how to compute these for individual species and if they could be related to more (a)biotic conditions than just temperature.

There is considerable uncertainty about the impacts of buoyancy control in several phytoplankton species. We do not know exactly how much the net growth rates (or in the terms of our model: the permissible extinction  $K_{max}$ ) is increased relative to a situation without buoyancy control. In the present model this increase was established by calibration. Also it is uncertain why some species for example Microcystis with the ability to regulate their vertical position in a column of water only seem to become dominant in some lakes in some parts of the year. The importance of environmental conditions e.g. wind is not very well known.

The present version of the model is restricted to homogeneous bodies of water. However, one may want to apply the model to hydraulically complex systems with for example differences in depth or a residence time of only a few weeks.

The necessity to convert the primary output of the model in mg dry weight of phytoplankton into chlorophyll adds a serious uncertainty to the model's results. It would be of great help if techniques were developed (1) to measure biomass directly, or (2) to compute chlorophyll as a function of the physiological state of a phytoplankton cell.

In Grote Rug the annual course of the background extinction ( $K_b$ ) shows little variations. Moreover approximately the same value is established for each year. Usually, however, the extinction is not measured in Dutch lakes, but the available estimates based upon the Secchi disc visibility suggest that  $K_b$  could vary significantly in the course of a year. Thus the performance of BLOOM II could be improved if we had some technique to compute the background extinction as a function of the (a)biotic conditions, particularly in lakes where energy and the growth rates are important limiting factors.

Presently zooplankton seems of little importance in eutrophic Dutch lakes, because most of them are dominated by phytoplankton species which do not belong to the preferred diet of zooplankton. Moreover the observed concentrations in the only case where we have detailed data (Grote Rug) seem too low compared with computed phytoplankton levels to be a major regulating factor. However, zooplankton could become much more important in the future if phytoplankton levels begin to drop and particularly if blue-green algae lose their position as the only quantitatively important phytoplankton group. Thus it could become necessary to extend BLOOM II with a set of equations to compute zooplankton levels and the resulting grazing pressure.

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