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the influence of nutrient availability on the ecosystem behaviour of Lake Grevelingen

report on investigations

R 1310-11

August 1984

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CONTENTS

PREFACE

The research described in this report is carried out within the framework of WAter BASIn Model (WABASIM). WABASIM is organized as a multidisciplinary coproject of the Environmental Division of the Delta Department (DDMI) and the Environmental Hydraulics Branch of the Delft Hydraulics Laboratory (DHL), and is financed by the Delta Department.

The project aims at the development of aquatic ecological and water quality models, which can serve as tools in providing adequate guidelines for environmental management in the (future) water basins in the Delta area.

This report deals with the influence of nutrient availability on the ecosystem behaviour of Lake Grevelingen. Data analysis and model formulation with respect to relations between nutrient availability and the primary producers in Lake Grevelingen are reported.

The research and reporting are carried out by:

Drs. I. de Vries, drs C.F. Hopstaken and drs. M. Veul.

The research activities are executed in cooperation with the WABASIM-salt project group, in which next to members of DDMI and DHL, also members of the Delta Institute for Hydrobiological Research (DIHO) participate. The WABASIM-salt project group consists of the following members:

Ir. S. van de Kamer (DDMI), chairman

Drs. I. de Vries (DHL), secretary

Drs. C. Bakker (DIHO)

Dr. B. van Eck (DDMI)

Drs. C.F. Hopstaken (DHL), from October 1983

Drs. P. Kelderman (DIHO), till September 1983

Ir. R. Klomp (DHL)

Dr. H.J. Laanbroek (DIHO), from May 1984

Drs. R.H.D. Lambeck (DIHO)

Dr. H.J. Lindeboom (DIHO), till May 1984

Ing. J.H.M. van der Meulen (DDMI)

Dr. P. Nienhuis (DIHO)

Drs. A.C. Smaal (DDMI)

Ir. J.H.G. Verhagen (DHL)

Drs. M. Veul (DHL), till June 1983

Drs. L.P.M.J. Wetsteyn (DDMI), from November 1983

1. INTRODUCTION

Lake Grevelingen is a stagnant salt water lake in the Delta region, situated in the south western part of the Netherlands. It was created by the construction of two dams; the Grevelingen dam on the east side (closed in 1964), and the Brouwers dam on the west side (closed in 1971).
The average depth of the lake is 5.3 m. The geomorphology of the lake still reflects its estuarine origin. It is characterized by gullies (up to a depth of more than 40 m.) and shallow areas. Since 1978 a sluice in the Brouwers dam for flushing with sea water has been put in operation, because the salinity of the lake steadily decreased since the closure in 1971. Flushing has increased the salinity within the lake to about North Sea level. Differences in salinity between the brackish lake water and the North Sea water caused salt stratification during the summers of 1978 and 1979. This salt stratification enforced the regular occurring thermal stratification, especially in the deeper parts of the lake. Therefore flushing with seawater is at the moment limited to the winter periods.

Several models and submodels related to the aquatic ecosystem of Lake Grevelingen have been constructed or are under construction. An overview of the most important components and their interrelations of the Grevelingen ecosystem is given in **Fig. 1.1.** An annual carbon budget model (CABAMOD) has been developed to identify the importance of the various components in the Grevelingen foodweb (de Vries, 1984). CABAMOD gives a description of the annual fluxes in the organic carbon cycle. It provides an overall picture of the distribution of carbon on a high aggregation level of the various ecosystem components. This model is used as a framework for the development of submodels on the component level.
The submodels developed within the WABASIM-salt program are also outlined in the figure. The broken lines enclose the components and relations that are taken into account in the balance calculations presented in this report. Other components for which mathematical models are being developed up till now are eelgrass (Verhagen and Nienhuis, 1983) and macrozoobenthos (Verhagen, 1983). These two submodels are also represented by broken lines in fig. 1.1.

The following objectives for development of a model of nutrients and primary producers can be formulated.

1. Conceptualization and formulation of the principal processes related to nutrient- and algal dynamics.
2. Presentation of existing knowledge in a model.
3. Description of the behaviour of the system under changing conditions.

Besides data from DDMI the modelling activities are based on data resulting from biological investigations carried out in Lake Grevelingen by DIHO. Also the joint research program 'ZOWEC' of DDMI and DIHO has to be mentioned because this salt water ecological research program was especially directed towards experimental investigation in Lake Grevelingen.
Available biological data, relevant for modelling activities with respect to nutrient availability and primary producers, only concern the period 1977-1980. Therefore the reported balance calculations are restricted to this period.

2. DATA BASE GREVELINGEN

From 1972 on monitoring programs have been set up by DDMI for Lake Grevelingen. The DDMI program consists of several sampling stations which are spread over the entire lake. An extensive evaluation of the DDMI data is given by van der Meulen (1980) over the period 1972-1977. Water quality characteristics in the Grevelingen are described and process knowledge of the ecosystem is described by means of mass balances of the lake.
The biological data monitored by DIHO, in combination with routine water quality variables, are available for the period 1977-1980.

2.1 DATA ACQUISITION

An attempt has been made to collect data, relevant for ecological studies concerning the Grevelingen, that cover the period 1971-1980. The data are stored in a computerized data base enabling easy retrieval of information. In the Grevelingen data base, water quality data, biological data, mass balance data and meteorological data are available. The data are provided by DDMI, DIHO, KNMI and DIV (see *footnote*).
A summary of the data available in the GREVELINGEN DATABASE is given in **table 2.1.** The sequence of activities concerning the data acquisition is shown in **Fig. 2.1.** The locations of water quality monitoring stations in the Lake Grevelingen are presented in **Fig. 2.2.**

Water quality Data.

As shown in **table 2.1.** water quality data are provided by DDMI and DIHO for the years 1972 - 1980 (DDMI) and 1976 - 1980 (DIHO). The water quality data of DDMI are data from the WAKWAL DATABASE and are stored on magnetic tape by DIV at Rijswijk. The WAKWAL DATABASE contains the water quality data of the routine sampling network of state waters in the Netherlands. *These data were read from tape* at DHL and processed to the GREVELINGEN DATABASE by SAS conversion routines. **Tables 2.2 - 2.8** show for each DDMI sampling station a summary of all the DDMI water quality data in the GREVELINGEN DATABASE. Measurements at 3 depths are available, which are joined in the frequency tables. Each value presents the frequency of sampling for each depth per year.
DIHO water quality data are provided on laboratory output sheets. **Tables 2.9 and 2.10** show for each DIHO sampling station a summary of all the DIHO water quality data in the GREVELINGEN DATABASE. There are measurements at

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DDMI:	Environmental Division of the Delta Department of the Ministery of Public Works at Middelburg.
DHL:	Delft Hydraulics Laboratory
DIHO:	Delta Institute for Hydrobiological Research at Yerseke.
DIV:	Department for information processing of the Ministery of the Public Works.
KNMI:	Royal Dutch Meteorological Institute at de Bilt.
SAS:	*Statistical Analysis System*
WAKWAL:	Waterquality data of the Ministery of Public Works.

more than 3 depths, which are joined in the frequency tables. Each value presents the frequency of sampling for each depth per year.

Biological Data.

As shown in **table 2.1**, biological data are provided by DDMI and DIHO for the years 1972 - 1980 (DDMI) and 1976 - 1980 (DIHO). DDMI data are retrieved from the WAKWAL data base (DIV).
DIHO data are provided on data sheets and stored in the GREVELINGEN DATABASE by means of hand typing. Most of the biological DIHO data are directly stored. An exception is made for the Bottom-POC and the Bottom-pigment measurements. These observations are averaged to values (per station) for an upper sediment layer (0-2 cm) and a deeper sediment layer (3-5 cm).
Tables 2.11-2.15 show a summary of all biological data in the GREVELINGEN DATABASE for each sampling station. The values are the sampling frequencies per year.

Loadings and withdrawals.

Mass balances for the Grevelingen on the basis of data concerning loadings and withdrawals for the period 1977-1980 are also stored in the data base. These data are provided by DDMI.
On a monthly basis the following sources of loadings and withdrawals are incorporated in the mass balances.

- Polderwater discharges.
- Gross precipitation.
- Surface run off from the areas outside the dikes.
- Waste water discharges.
- Seepage via the Grevelingen dam and the Brouwers dam from the North Sea Eastern Scheldt.
- Leakage from the lake through the dikes to the neighboring polders.
- Intake of water via the sluice in the Grevelingen dam necessary for regulation of the water level of the lake and lock operation.
- Intake and outlet of water through the sluice in the Brouwers dam (since 1978).

Nutrient fluxes related to the water balance of Lake Grevelingen are calculated for the variables: dissolved inorganic silicon, dissolved inorganic and total nitrogen and dissolved orthophosphate.

Meteorological Data.

The data are provided on tape for the period 1971-1980 by the KNMI. The global radiation data are from the KNMI stations Naaldwijk and Oostvoorne and the wind velocity data are from the KNMI stations Hellevoetsluis and Zierikzee (**Fig. 2.3**). The original data have been converted to time series representative for the whole lake (weekly totals for total radiation and daily averages for wind velocity).

2.2 DATA MANIPULATION

Interpolation

Interpolation is the generation of function values at stations and/or at times where no observations are available. The method used for interpolation is strongly dependent on the use that will be made of the generated function values. If for physical or computational reasons a smooth curve is needed (e.g. for the computation of derivatives), high order polynomial approximations, Fourier series or similar smooth functions will be chosen to compute missing values. The interpolating function will be fitted exactly through the available observations if the observations are obscured only by a negligible amount of noise. If however the observations contain a large amount of noise it is better to choose an interpolating function which does not pass through the observations exactly but instead fits the observations as good as possible in some sense. Often least squares criteria are used for this purpose.

A special class of interpolating polynomials is formed by the so called smoothing spline functions, where piecewise third order polynomials are used. At the base points the first and second derivatives of the polynomials are the same. By that no discontinuities occur at the base points when these polynomials are linked together. Furthermore the total curvature in the interpolating function is made as small as possible. The result is an interpolating function with a very satisfactory smooth behaviour.

If it is not necessary to generate smooth curves, a much simpler way of interpolation can be used. Computationally the simplest form is the so called piecewise linear interpolation. In that case missing values are replaced by linear interpolation between two adjacent base points where observations are available. The interpolating function is formed by piecewise linear functions between the base points with generally more or less sharp transitions at the base points. In case of the water quality variables investigated in this report, this method is reasonably well balanced between the given accuracy of the observations at one hand and the amount of programming and computational effort on the other hand.

Missing data of variables which are used as model input have been generated by application of linear interpolation.

Moving Average

Time series of chemical and biological variables can show strong variations within short periods. These variations are due to the variations in time and space. In order to analyse the influence of chemical and biological processes, it is necessary to average over the spatial variation with little influence on the time series. This can partly be realized by means of a **moving average** procedure. This procedure calculates mean values for subsequent partly overlapping periods. By this, rapid fluctuations are filtered out. The procedure is frequently used for presentation of measured data. Moving averages are calculated over 3-week periods. A weighting factor of two is assigned to the intermediate observation.

3. HORIZONTAL HOMOGENITY AND COMPARISON OF DIHO AND DDMI DATA SETS

The modelling activities are primarily based on the DIHO data set. From this data set, which consists of 'routine' water quality monitoring observations and data of biological variables, primary production and algal biomass are the most important for the balance calculations reported here. The data set of DDMI is used for comparison with the DIHO data set and as option for modelling 1979-1980 with DDMI primary production data. Both data sets are used for calibration of the balance calculations.
In this chapter the following items are discussed.

- Presentation of the DIHO data set, that provided most of the input data for the model, and the DDMI data set.
- Horizontal homogenity of water quality variables in the upper water layer of the lake.
- Comparison of the DIHO and DDMI data.

Aspects of vertical (in)homogenity are described in the next chapter.

3.1 PRESENTATION OF DIHO-DATA

The DIHO data set combines measurements of water quality variables with biological measurements such as primary production and biomass of phytoplankton.
From 1976 till 1980 a monitoring program has been in operation at sampling location G11. Sampling station G11 consists of two sites situated close to each other, one in a gully (depth 22 m.) and the other above a shallow area **(Fig. 2.2)**. The sampling frequency was about once a week during the summer and biweekly in the winter. The gully is sampled at 6 or 7 depth levels and the shallow area at 2 or 3 depths.
To get an overview of the available data, variables are plotted as function of time and water depth. The plots are constructed by means of a moving average procedure with a 3 week interval.
The water column of sampling site G11 is divided by depth in 3 layers to visualize depth dependency.

The variables temperature, chloride, pH, suspended solids, oxygen, ortho- and total phosphate, ammonium, nitrite, nitrate, total inorganic nitrogen, silicon, chlorophyll, POC, phytoplankton-C and phytoplankton net primary production are presented **(Fig. 3.1-3.15, 3.18)**.
The water quality variables measured at the shallow area are not included in the figures, because the observations in the shallow area overlap with the data of the upper water layer (0-5 m.) in the gully. (see also memo ML-58).

The general annual patterns of the nutrients silicon, nitrogen and phosphorus will be described in the introduction of the nutrient balances (see chapter 5). Some remarks however can be made concerning the water quality tendencies in Lake Grevelingen.
Apart from the increase of salinity since 1978, an obvious trend in the whole period is the yearly occurrence of stratification during the summer, outlined by most variables. In 1977 stratification is not observed, but measurements beneath 12 meter are missing. The DDMI data of a neighboring sampling station however show a pronounced stratification in this year.

A factor analysis, applied to the DIHO data set, outlined 3 factors which suggest the following trends (see memo ML-58):

1. A coupling of biological variables such as chlorophyll, POC and phytoplankton cell counts with the variables nitrate and ammonium.
2. Phosphorus dynamics behave independent from other nutrient and biological variables.
3. Yearly occurrence of stratification in the deeper parts of the lake.

3.2 PRESENTATION OF DDMI-DATA

The DDMI monitoring network comprises 7 stations **(Fig. 2.2)**, which were sampled weekly or biweekly in the period of 1972-1976. From 1977 the sampling frequency is reduced to once a month. Sampling occurs at 3 depths (surface, half water depth and bottom).
As an addition on the DIHO data, suspended particulate nitrogen and total manganese of the DDMI data are presented **(Fig. 3.16-3.17)**. Alike the DIHO measurements these DDMI measurements are split up by depth, in most cases causing averages of less than 7 stations.

In order to get an impression of the variation of the observations in the upper water layer, the measurements of the 7 (or less) DDMI-stations are averaged by week and confidence limits are calculated.
The distribution of all the measured values of nutrient concentrations can be described as lognormal (memo ML-58). A similar distribution is assumed for the variation between the 7 DDMI stations at one time. For these variables mean and confidence limits are calculated for the log-transformed variables, resulting in a geometric instead of an arithmetic mean, and an asymmetrical confidence interval. The asymmetry is however hardly visible, because the interval in most cases is very small.
For the variation of other variables, in most cases not influenced by biological mechanisms, a normal distribution is assumed.
The 95% confidence intervals are constructed by means of the critical values of the Student's t-distribution.

The results for the variables temperature, chloride, acidity, oxygen, orthophosphate, total phosphate, inorganic nitrogen, silicon, chlorophyll, particulate organic-C and primary production are presented in the **figures 3.19-3.29.**
The presentation is limited to the period 1976-1980 to enable comparison with the DIHO-data. For 1979 and 1980 no surface observations are available from station G11. In this period sampling of the water column started at 2.5 meter water depth.

3.3 HOMOGENITY OF THE UPPER WATER LAYER

The description of the morphology of the lake by the mean depth obscures its estuarine origin. The morphology is characterized by large shallow areas cut by deep gullies which are remnants of the former tidal motions. The surface-depth ratio (van der Meulen, 1980) indicates that approximately 65% of the lake area has a depth of less than 5 meter. About 10% of the lake area is deeper than 15 meter.
Stratification is known to occur in the gullies. The question of horizontal homogenity in the lake is therefore only relevant for the upper water layer of the lake.

From the DDMI data presented, can be concluded that variation in the observations of the upper water layer at the 7 stations is rather small. This is especially the case for the variables temperature, chloride, ortho-phosphate and total phosphate, which are not or only slightly influenced by biological processes (see chapter 5).
The oxygen measurements vary considerably between the 7 stations. This variation however is probably not due to horizontal inhomogenity of oxygen (i.e. variation in space) but may be attributed to rapid diurnal fluctuations (i.e. variation in time) of oxygen, reflecting the sampling schedule during a monitoring cruise.
The variation in the POC and chlorophyll measurements is considerable. The variability is probably due to geographical variation.
Based on the DDMI data the conclusion can be drawn that the upper water layer (above the gullies) is rather homogeneous over the entire Lake Grevelingen.

3.4 COMPARISON OF DDMI- AND DIHO-DATA, 1976-1980

Comparison of the nutrient balance calculations with DIHO data, is based on the assumption that DIHO sampling station G11 is representative for at least the central part of the Grevelingen basin. Therefore the assumed representativity of G11 is evaluated by means of a comparison with the DDMI data set.
As to this comparison the following remarks can be made.

- The comparison of the two data sets is limited to the upper water layer.
- The input for the nutrient balances is based on the DIHO data set. Biomass and primary production data are available for the period 1977-1980. Therefore the investigation of horizontal homogenity and comparison of both data sets is specially aimed onto this period. Where possible the period 1976-1980 is presented.
- The DDMI data set of the period 1972-1977 is already extensively elaborated (van der Meulen, 1980).

The DIHO data set contains one station, namely G11, divided in two substations: one in a gully with a water depth of 22 meter and another in the neighboring shallow area with a water depth of a few meters. No differences for the upper water layer between these two substations are noticed. For comparison the original measurements in the upper water layer at G11 for the period 1976-1980 are included in the **figures 3.19-3.29.** These data originate from weekly or biweekly measurements at the surface of the gully. In contrast to the presentation in the figures 3.1-3.15 and 3.18 no moving average procedure is applied. The following remarks concerning the comparison can be made.

- Comparison of DIHO and DDMI data-sets is difficult.
  - Sampling takes place in a highly active medium. Concentration measurements represent only an instantaneous observation of a dynamic system resulting from chemical, physical and biological processes. This implies differences in observations as a function of time and space. So differences in measurements may arise from sampling different waterparcels at different times (patchiness and daily variation). For these systematic differences no correction procedure is applied.
  - The generation of data concerning the same object by two different institutes provides two different data sets which ideally should be equal. Explanations for differences are multiple. Apart from

  differences in analytical methods other sources of error may arise from sampling methods and sample handling.
  - The comparison involves data sets based on approximately the same measuring frequencies in 1976-1977 (weekly to biweekly). From 1977 the measurements were reduced to once a month by DDMI, whereas DIHO maintained a weekly measuring frequency for sampling site G11.

- The **temperature** shows a convincing agreement of both data sets, relative to variation in time.
- The **chlorida** measurements show a systematic looking difference for 1978-1980. This can partly be due to different units; permil for DIHO and g/l for DDMI.

  DDMI averages of 1977 are most times based on less than 3 measurements, or only 1 measurement.
- **Acidity** measurements show a reasonable agreement, though DDMI data sometimes have a too large interval of measurement.
- The comparison of **oxygen** concentration measurements is probably hampered by the effects of the diurnal variation of the oxygen concentration. In the first place a relatively large spreading in data can be remarked, illustrated by the broad range between the 95% confidence limits. Secondly the DIHO oxygen measurements seem to be systematically lower in 1977 and higher in 1978 compared to the DDMI-data. Reasons for these deviations are unknown.
- The **phosphorus** data of DDMI and DIHO correspond well in absolute levels especially in 1978-1980. In 1976-1977 the phosphorus measurements of both data sets diverge to some extent.
- **Inorganic nitrogen** is presented because nitrogen is used only in this manner in the nutrient balances. Specified in nitrate, nitrite and ammonium some differences between the data-sets are observed.

  The DIHO-measurements of ammonium and nitrite are higher than those of DDMI-data, whereas the nitrate measurements are lower.

  As to total inorganic dissolved nitrogen the summer levels agree quite well, whereas the winter levels of the DDMI-data are higher in 1977 and 1979.
- The **dissolved silicon** measurements by DIHO and DDMI are similar.
- **Chlorophyll** DDMI data have, like POC, a wide confidence interval, but nevertheless most DIHO measurements don't fall in this interval.

  Also the annual path of the DDMI curves differs from the DIHO data points. Especially in 1979, where DDMI data show low summer concentrations and DIHO data show high summer concentrations.

  The comparison of the two data sets is hampered by the high frequency of variations in the chlorophyll concentration as shown by the DIHO data set. The frequency of the DDMI measurements is too low to represent these variations.
- **POC** measurements of DIHO mostly fall in the broad DDMI interval. DIHO measurements don't show large concentration differences during the years. DDMI data show a spring peak in 1979, that coincides with the chlorophyll peak in the same data set.
- **Primary production** measurements are not similar. Although the range of primary production between summer and winter is about equal, large differences in time between production peaks are visible. These differences return in the model calculations with DDMI 1979-1980 production measurements.

  An eye striking production peak is the spring (week 15) peak of 1980 in the DIHO data set, that is not remarked by DDMI.

4. VERTICAL GRADIENTS IN THE WATER COLUMN

The exchange between the water and bottom compartments, causing the observed variation in the water quality variables along the vertical in periods with stratification, seems to be one of the driving and less understood processes in the ecosystem-dynamics of Lake Grevelingen. An important and interesting question is the uniformity of the bottom-water exchange over the entire lake bottom.
Into this respect the following questions concerning the available data are evaluated:

1. Can the lake be considered as a homogeneously mixed watermass in vertical direction, with exception of the deep gullies where thermal stratification is a common phenomenon during the summer period?
2. Are the observed features of the bottom-water exchange limited to the stratified deep gullies?
3. What kind of additional information can be obtained by combination of DDMI and DIHO data sets?

4.1 STRATIFICATION

The occurrence of thermal stratification in Lake Grevelingen during the period 1972-1977 and the implications concerning nutrient availability are described by van der Meulen (1982). Thermal stratification is observed every year in the deeper parts of the gullies (G2, GB7, G3, GB6). The observations at the shallow stations (with a water depth of 15 m. or less), do not show evidence of the occurrence of stratification. However the observations in the upper water layer and the layer near the bottom diverge to some extent.
Stratification is also observed at the G11 sampling site (DIHO) during each summer in the period 1976-1980 except 1977. In that year observations beneath 12.5 meter are lacking. G11 is situated close to DDMI station G2 which has a similar water depth (22 and 24 m.). The observations in 1977 at station G2 show clearly stratified conditions during the summer.

During the years 1978 and 1979 stratification became pronounced by chloride gradients, as a result of flushing with North Sea water. The chloride increase near the bottom of G11 during the summer of 1978 **(Fig. 3.2)** might be attributed to irregular opening of the sluice in the Brouwers dam during the months May and June (Stokman 1978). In 1979 the sluice has been open during the whole year. As a consequence the salinity in the lake increased to North Sea level, accompanied with steep chloride gradients.
At station G11 effects of chloride stratification are also manifest in the water layer between 5 and 15 m **(Fig. 3.2)**. To prevent salt stratification flushing with sea water after 1979 is limited to the winter periods.

4.2 VERTICAL GRADIENTS BETWEEN BOTTOM- AND UPPER-WATER LAYER

Vertical gradients are obvious for the DDMI stations with a water depth of more than 20 meter. However also at the shallow stations the observations

in the upper water layer and the layer near the bottom seem to diverge during the summer period. In contrast to the gullies a stable stratification is not developed during the summer at the shallow stations.
The DDMI data set provides an opportunity to investigate the differences in water quality variables of the upper and deeper water layers.

The DDMI data set in Lake Grevelingen data base covers the period 1972-1980. It consists of 7 stations which are sampled at 3 depths (upper-water layer, half water depth and 1m above the bottom). Sampling frequency was (bi)weekly till 1976. Then the sampling frequency is reduced to once a month. **Table 4.1** below gives the water depth of the sampling stations.

Table 4.1 DDMI sampling stations

station	depth (meter)
G1	8.2
G2	24
G3	42
GB4	12.2
GB5	13.5
GB6	29
GB7	38

For an evaluation of the effects of the bottom-water exchange on the nutrient concentrations in the overlaying water it is important to know whether or not the bottom-water exchange may be considered homogeneous over the entire bottom area of the lake.
The evaluation of bottom-water exchange in this section is restricted to bottoms deeper than 8 meter, because no continuous data sets are available for shallow stations. Specific information on bottom-water exchange at shallow stations can be obtained from Holland and Al (1980). Also the possible influence of sediment composition and eelgrass are not discussed in this report.
The effects of release of nutrients from the bottom into the overlaying water become evident in case of stratification. Density differences, resulting from vertical temperature or salinity gradients, cause a stratified water body where exchange between the deeper and upper water layer is limited. In such a situation the deeper water layer becomes an isolated system enabling quantification of the effects of bottom-water exchange.
Extrapolation of this exchange to a shallow, not stratified situation is questionable. The exchange may be influenced by processes prevailing in the water layer near the bottom. Anaerobic conditions in this water layer occur regularly in the deeper parts of Lake Grevelingen, whereas in the more shallow parts only low but hardly ever zero oxygen concentrations near the bottom are observed.

Insight in the differences between the observations in the upper water layer and near the bottom at stations of different depth, may provide an opportunity to test the hypothesis of an uniform exchange over the bottom-water interface for the entire lake.
Therefore the variation along the vertical, of water quality variables of 5 stations (G1, G2, G3, GB4 and GB5), is investigated. Differences between measurements at different depths are calculated for each station. The differences are averaged by week over a range of 6 years (1972-1977). The differences for 1979 and 1980 are presented separately, because of the changed hydrodynamical situation.

All differences are converted to concentration gradients per meter, by dividing by the water depth, to facilitate the comparison between stations with different water depths.

The results are presented in the **figures 4.1-4.10.**
Positive values indicate higher concentrations in the upper water layer compared to the layer near the bottom (temperature, acidity and oxygen). Negative gradients result from higher concentrations near the bottom (chloride, nutrients, manganese and iron). The following remarks can be made.

- These figures give no information on absolute concentrations, they only reflect gradients, averaged over the total depth interval.
- The DIHO data set is not included because the maximal sampling depth is mostly 17.5 m. on a total water depth of 22 m. In contrast the DDMI sampling takes place close to the bottom. For this reason also comparison between DIHO and DDMI has been omitted.
- The 5 stations are selected in such a way that observations over several depth intervals are present. The figures sometimes look a bit confusing because most gradients are about equal. This only accentuates the most deviating peaks, that are numbered according to the station number in the legend.

4.2.1 Evaluation of the figures 4.1 - 4.10

Temperature (fig. 4.1) illustrates occurrence of thermal stratification each year at each station. Striking is the pronounced gradient in 1979, caused by the chloride stratification. The sequence of the gradients for each station in this year is exactly reflected in the chloride figure, with the steepest gradients for the shallow stations. In all other years, gradients are about equal (0.1-0.2 degr.C/m) in the summer period, with an exception for the deepest gully station 5 (G3) in late summer (0.2-0.3 degr.C/m).

Chloride (fig. 4.2) normally shows no gradients, except the, rain induced, occasional gradients at the shallow stations.
1979 shows complete chloride stratification, with the steepest gradients for the shallow stations. In fact there has been a boundary layer at about 4-5 meters; this depth can be calculated based on the gradients in the figure. Also the DIHO measurements show a gradient (fig. 3.2), but from this figure the existence of a boundary layer is less obvious. Beneath the boundary layer there is still a density gradient, instead of homogeneously mixed salt water.
In 1980 the situation has returned to the situation of 1972-1977. Only early spring, the stations 4 (GB3) and 1 (G1) show some stratification; which is also observed at G11 (fig 3.2), a nearby station. These gradients may be due to rain. The three stations are situated in the south-east part of the lake.
The deep gully station 5 (G3) shows a chloride gradient throughout 1980, probably causing the more pronounced temperature gradient.
Noticable is the strohg reverse chloride gradient in week 10 (1980) at station 3 (GB5). This gradient and the pronounced temperature gradient at the same station 6 weeks later, are probably due to fresh water seepage in this part of the lake (area between 'Veermansplaat' and 'Slikken van Flakkee'). This is confirmed by the chloride gradient at this station in summer 1979; the chloride concentration below the supposed 5 m. boundary is 0.6 g Cl/l lower than at all other studied DDMI stations, while the temperature gradient is 'normal' for 1979.

Concentration gradients in pore water also deviate in this area. Kelderman (1983) reports a reverse pore water ammonium profile at a station (21) nearby GB5. Finally salt balances of the lake indicate the occurrence of runoff or seepage of fresh water from the isles and marshes, as 'Veermansplaat' and 'Slikken van Flakkee' (Van Der Meulen 1980).

Acidity (figure 4.3) gradients are more or less comparable for the 5 stations. Only station 3 (GB5) deviates by steeper gradients, probably due to seepage of water with a different chemical composition and/or lower pH.
Acidity gradients originate from uptake of CO2 in the upper water layer by primary producers (pH increase), and the release of CO2 by mineralization of organic matter near the bottom (pH decrease).

Oxygen (figure 4.4) gradients are caused by the same processes as acidity gradients: release of oxygen by photosynthesis and uptake by mineralization. Oxygen gradients are steeper at shallow stations, because averaged by depth photosynthesis and mineralization are more intensive here.
Steeper gradients at station 3 (GB5) may be due to oxygen-poor seepage water.
Oxygen gradients can induce vertical inhomogenities of other variables (manganese, iron, orthophosphate, ammonium etc.), especially at the deeper stations. There even a moderate oxygen gradient can result in low oxygen concentrations near the bottom and anoxic bottom surfaces, promoting release of reduced substances from pore water.

Orthophosphate (figure 4.5) gradients before and after 1979 are moderate and comparable for the five stations. The picture for 1979 is erratic, caused by the flushing with North Sea water during the whole year. North Sea water accumulates in the deeper water layer as a result of the higher salt content. This has a diluting effect on orthophosphate, because of the low phosphate concentration in sea water compared with Lake Grevelingen before the opening of the Brouwers sluice.
Station 5 (G3) shows a steeper gradient in 1972-1977, caused by anoxic bottom surfaces in the deep gullies, promoting phosphate release. In 1979-1980 no steep gradient at this station is observed; an indication of the flushing with North Sea water.
Station 3 (GB5) again deviates from all other stations. The occasional highly negative orthophosphate gradients may be caused by advective transport of phosphate rich pore water in upward direction due to seepage.

Ammonium (figure 4.6) gradients are comparable with those of orthophosphate. Strong release of ammonium from deep anoxic bottoms (1972-1977) and seepage of ammonium rich pore water at station 3 (GB5), also observed by Kelderman (1983) as reversed ammonium gradients in the pore water profile of his station 21.
Apparently the bottom-flux of ammonium at station 4 (G2) in 1979 is larger than the dilution effect of the sea water.

Nitrate (figure 4.7) gradients are almost absent in the period before salt stratification (1972-1977), in spite of the sharp decrease in spring and increase in autumn of the nitrate concentration itself (see fig. 3.1).
The small but consistent negative gradient in week 14 must be due to uptake of nitrate during the spring bloom of phytoplankton. The effect of the spring bloom is also visible in the 1972-1977 figures of silicon (fig 4.8), acidity (fig. 4.3) and oxygen (fig. 4.4). The negative nitrate gradient in week 25 of 1980 at station 5 (G3), and the absence of an ammonium gradient at that time, indicate flushing with North Sea water.

Silicon (figure 4.8) gradients resemble those of orthophosphate and ammonia, but without the steep gradients at deep stations. Apparently silicon release from the bottom does not increase (to the same extent) when the

bottom surface becomes anoxic. However, in 1980 gradients of silicon were comparable with those of ammonium and not with those of orthophosphate.
The absent or sometimes slightly positive silicon gradients at the shallow station 1 (G1), indicate exchange with silicon rich Volkerak water through the shipping sluice at Bruinisse.

Total manganese (figure 4.9) gradients clearly reflect the oxygen dependency of the bottom release of manganese. Especially at deep gully station 5 in 1972-1977 and 1980, due to temperature stratification, the build up of high total manganese concentrations in the hypolimnion is perfectly illustrated in fig. 4.9.
In 1979 the dilution of the deeper water layer with sea water must be responsible for the absence of a manganese gradient at station 5. The gradients in week 25 (1979) at the shallow stations 1 and 2 indicate the expansion in 1979 of the area with an anoxic bottom surface to the shallow parts of the lake.

Total iron (figure 4.10) gradients are less pronounced than those of manganese (one order of magnitude smaller). The oxygen dependency is less clear. Apparently other factors, that are still unknown, than oxygen depletion in the bottom are more important for the bottom lease of iron, especially in spring at station 5 (G3).
The effects of chloride stratification in 1979 on the iron release at the shallow stations is comparable with manganese. Finally seepage of pore water can explain the occasional negative gradients at station 3 (GB5).

4.2.2 Uniformity of the bottom-water exchange of nutrients

From the presented figures can be concluded that oxygen depletion near the bottom increases the release of **phosphorus and ammonium**, and only to a lesser extent the release of silicon.
The bottom-water exchange of phosphorus and ammonium is thus not uniform, and a distinction has to be made between oxic and anoxic bottom surfaces. Under normal circumstances, without salt stratification, anoxic bottom surfaces are restricted to bottoms deeper than 20-30 m. (less than approximately 5% of the lake area). Observations since 1980, however, also indicate the occasional occurrence of anoxic bottom surfaces in shallow parts of the lake.
In years without salt stratification, the increased release of phosphorus and ammonium from bottoms with anoxic surfaces can thus probably be neglected for the lake averaged nutrient balances.
In 1978 and especially in 1979, higher manganese concentrations are also observed above shallow bottoms (fig. 3.17 and 4.9), indicating anoxic surfaces below a depth of circa 10 m. or even less (more than 20% of the lake area).
In these years increased phosphorus and ammonium fluxes during a short period may have been significant. In 1979 this increased release is however counterbalanced by export of these nutrients from the deeper water layers to the North Sea.

Seepage probably induces the second kind of non-uniformity. Station GB5 shows that advective transport of pore water in upward direction by means of seepage, probably leads to increased release of orthophosphate, ammonium and/or nitrate and silicon into the overlaying water. The significance of this seepage for lake averaged nutrient balances is unknown untill an estimation is made of the percentage bottom area where seepage occurs.

From the figures 4.1-4.10 the overall conclusion can be drawn that the bottom release of nutrients is uniform over the entire lake bottom area with exception of:

- bottoms with **anoxic surfaces** (normally less than 5% of the bottom area), especially for orthophosphate and ammonium,
- bottom areas where **seepage** occurs, for all three nutrients to the same extent.

These conclusions are only valid for bottoms deeper than 8 meter. Differences between these bottoms and more shallow bottoms are not evaluated in this section.

4.3 QUANTIFICATION OF THE BOTTOM-WATER EXCHANGE OF NUTRIENTS

A continuous interaction exists between bottom and overlaying water. Neither the water phase nor the bottom phase can be interpreted as a closed system. Both compartments act as an interactive system. Concentration gradients between pore water and overlaying water, bioturbation, water turbulence and advective pore water transport by seepage provide mechanisms for a bottom-water exchange. Fluxes over this boundary are rather dynamic and difficult to quantify.

Only in case the water near the bottom is completely isolated from the overlaying water, the concentration increase in the water layer near the bottom may be used as an estimate for the amount of bottom-water exchange. This is only the case in the deep parts of the gullies, for instance at station G3.
The bottom-water exchange at this station however deviates from less deep parts of the lake, because of the anoxic hypolimnion and the anoxic bottomsurface. The bottomfluxes estimated for this station can thus not be extrapolated to the entire bottom area of the lake.

During the onset of stratification, accumulation of silicon and nitrogen is also obvious at less deep stations, as G11. The DIHO data set of this station provides an opportunity to estimate bottom fluxes, that are presumably representative for large parts of the bottom of Lake Grevelingen.
The data set for this station is also more appropriate to calculate bottom fluxes, because of the higher sampling frequencies compared to DDMI stations.
The best year for an estimation is 1978 (week 20-32), because then the bottomflux of nutrients is captured in a little volume. This volume is assumed to be 7 m3 per square meter bottom area (according to the water layer at 15-22 m. depth), because little or no concentration increase is observed in the 5-15 m. water layer (see **fig. 3.11 and 3.12**).
The results are given in **Table 4.2**, and compared with fluxes calculated by Kelderman (1983), from concentration gradients in the pore water of the upper bottom layer.
The range of the G11 calculations for silicon and nitrogen agrees with the fluxes calculated by Kelderman for shallow bottoms. But both calculations are probably underestimations. G11 values because of diffusion/entrainment through the halocline, and the shallow bottom values because of uptake by benthic diatoms.
When this is true, the data from Kelderman for deep bottoms are the best estimations for the bottomfluxes of ammonium and silicon in Lake Grevelingen, exclusive the influence of benthic diatoms.

Table 4.2 **Nutrient bottom fluxes**

	calculated from G11	calculated by Kelderman March 1982		July 1982	
	1978	Sh.(<7m)	De.(>7m)	Shallow	Deep(>7m)
silicon mg Si/m^2.day	85	85	110	95	210
ammonium mg N/m^2.day	25	35	25	75	105

The differences between bottomfluxes for shallow and deep stations as observed by Kelderman, should then indicate the influence of benthic diatoms.

Phosphorus behaviour is different compared to the other nutrients. In the first place an increase of the maximal phosphorus concentrations in the water phase is observed since the creation of Lake Grevelingen. This increase ended with the opening of the sluice in the Brouwers dam. Explanations for the longterm accumulation of phosphorus in Lake Grevelingen are given by Van Der Meulen (1980), Kelderman (1983) and Verhagen (Memo ML-45, 1980).
In the second place the following differences in the seasonal pattern, compared with the other nutrients, are observed.

- Increase and decline of the phosphorus concentration is not synchronous with the other nutrients.
- In 1978 and 1979 even a reverse gradient of phosphorus is present at the beginning of stratification. In 1979 such a gradient is observed during the entire period of stratification. This phenomenon is already explained by the sea water flushing.

The behaviour of phosphorus in Lake Grevelingen is analysed by Kelderman (1983). He describes the seasonal behaviour with two processes.

- Mobilization, induced by microbial mineralization and therefore temperature dependent. P-mobilization occurs from May to August with a rate of 12.5 mg P/m^2*day.
- Sorption, depending on the phosphorus content of the overlaying water and depending on the area of sediment available for adsorption. P-accumulation takes place in the remaining part of the year with a rate of 5.5 mg P/m^2*day.

The assumption of mineralization as the driving mechanism for mobilization can be tested by comparing the nutrient concentrations that result from bottom release to stoichiometric relations. To confirm this assumption the ratios between the nutrient concentrations must reflect the stoichiometry of the organic matter being mineralized.

For the deeper water layer during stratified conditions in the 'Veerse meer', Van Der Meulen (1982) obtained the following concentration ratios: P : N : Si = 1 : 2.78 : 3.47.
For nitrogen and silicon these ratios are within the range of algal stoichiometry as given in tabel 5.1. The value for P is higher than the general range given in this table.

For Lake Grevelingen linear regression plots are made, using DDMI data from the deep water layers for 1972-1977. Only the period of 1972-1977 is taken into account to avoid the period of flushing with sea water. From these years the weeks 20-28 are selected as the main period of linear increase of nutrient concentrations near the bottom.

The results are presented in **figure 4.11** for the stations G2 and GB6 (23 and 28 m. deep), and in **figure 4.12** for the stations G3 and GB7 (41 and 37 m. deep).

The regression plots of **figure 4.12** (deep bottoms) are very scattered, especially for N/Si and P/N. This is perhaps due to the fact that during the onset of stratification at the deep stations, the bottom surface becomes anoxic (in some of the 6 years), promoting the release of phosphorus and ammonium (figure 4.5-4.6, station 5 (G3)). In this way data from two bottom types, oxic and anoxic, are combined in one regression plot, giving scattered results.

The overall concentration ratios for **figure 4.11** are: P/N = 0.71, P/Si = 0.28 and N/Si = 0.27.

As for the 'Veerse meer', the value for P is very high, especially in relation to nitrogen, and compared with algal stoichiometry as presented in table 5.1.

It is therefore unlikely that phosphorus fluxes from moderately deep bottoms are directly driven by mineralization of organic matter. This direct dependency of the phosphorus flux on mineralization was concluded by Kelderman in his analysis of the seasonal behaviour of the phosphorus concentration.

In **figure 4.13** linear regression plots of dissolved nutrients are presented for the anoxic hypolimnion of Lake Grevelingen (unpublished data from Van Der Meulen).

The overall concentration ratios for these figures are: P : N : Si = 1 : 3.70 : 1.11. These ratios reflect the fact that especially the release of phosphorus and ammonium is promoted by an anoxic bottomsurface. The release of silicon is not promoted to the same extent, causing the deviations of P/Si and N/Si ratios from algal stoichiometry (see also figures 4.5 - 4.8).

5. CARBON AND NUTRIENT CYCLING

5.1 INTRODUCTION

Concentrations of dissolved nutrients in Lake Grevelingen show pronounced fluctuations. The inorganic dissolved fractions of nitrogen (N) and silicon (Si) behave more or less similar. Winter concentrations of these nutrients are rather high, and during summer the inorganic dissolved fractions are almost zero in the upper water layer (see **Fig. 3.11 and 3.12**).
Inorganic dissolved phosphorus (orthophosphate) behaves different. The concentration decrease of orthophosphate starts during winter, instead of during spring at the beginning of the growing season (see **Fig. 3.6**). The subsequent concentration increase starts already early summer, whereas the other two nutrients remain at low levels for still some months. So nitrogen and silicon seem to be limiting for primary production in the water phase during summer, in contrast to orthophosphate.
The amount of nutrients in suspended particulate material during summer is far less than the quantity that disappears out of the dissolved pools. The difference between winter and summer concentration of inorganic dissolved nitrogen is 0.6 g N/m^3 or more (see **Fig. 3.11**). The increase of the particulate nitrogen concentration is 0.15 g N/m^3 or less (see **Fig. 3.16**), which is only 25% of the quantity that disappears out of the dissolved pool.
Comparison is also possible with the potential algal biomass, that can be formed from the available nutrients (according to the stoichiometry for silicon and nitrogen as given in **Table 5.2**
From the dissolved silicon, available during winter, more than 50 mg chlorophyll/m^3 of diatoms can be formed. As well an algal biomass of more than 100 mg chlorophyll/m^3 can be produced from available dissolved inorganic nitrogen. However measured phytoplankton concentrations are lower than 10 mg chlorophyll/m^3 (see **Fig. 3.13**) which is less than 10% of the maximal possible amount.
Moreover, the net annual nitrogen load to the lake, mainly due to rainfall and polder water discharges, equals the amount of dissolved inorganic nitrogen present in the water phase during winter. The net annual load of silicon, mainly from polder water discharges, is approximately 50% of the amount present in the water phase during winter.

Thus, large amounts of nitrogen and silicon disappear from the water phase during spring, and appear again during late summer and autumn. Especially the spring decrease of silicon is remarkable, since the phytoplankton spring bloom mainly consists of small flagellates, and hardly any planktonic diatoms are observed at that time (Bakker and de Vries 1984).

Long term changes of some characteristics of the lake indicate a slow eutrophication process. One, the gradual increase of planktonic primary production, from 60-80 gC/m^2.year in 1976-1977 up to 225 gC/m^2.year in 1981 (Vegter and de Visscher 1984). Two, the increasing winter concentration of dissolved inorganic nitrogen with approximately 0.4 gN/m^2.year, which is 10-15% of the net load. Three, the gradual rise of the redox discontinuity layer in shallow bottoms from more than 20 cm depth until December 1977 to less than 5 cm depth from June 1979 onwards, accompanied by a distinct concentration of the nematode fauna in the upper sediment layer (Willems et al 1984).

To explain the disappearance of nutrients from the water phase during spring, and to evaluate the possible causes for the above mentioned tendencies, nutrient balance calculations are carried out.

5.2 NUTRIENT BALANCE MODEL

A nutrient balance model is constructed to evaluate the behaviour of the nutrient concentrations in relation to primary producers and detritus. The model has only descriptive value. It is based on a four year dataset (1977-1980) of biological measurements (biomass and production of primary producers), and chemical variables that represent external influences (net load of dissolved nutrients and particulate organic matter). Purpose is the integral analysis of the relations between primary producers, detritus and nutrient dynamics. Two specific questions are analyzed.

1. Is it possible to explain the behaviour of the concentrations of dissolved inorganic phosphorus, nitrogen and silicon by **uptake by primary producers** (phytoplankton and benthic diatoms) and **release by mineralization**?
2. For those nutrients that are controlled by these biological processes: how are these nutrients distributed, in the course of time, over the inorganic and organic pools that form part of the nutrient cycle?

The following processes, schematically presented in **Fig. 5.1** are incorporated in the model.

- **Primary production.** Synthesis of living organic matter is incorporated in the calculations by the use of primary production measurements of microphytobenthos and phytoplankton.
  As illustrated by Fig. 1.1 these components are the most important primary producers in the lake.
- **Load** represents the net result of loadings and withdrawals on the nutrient budgets of the lake. The net load of nutrients determines the external influences on the nutrient cycles in Lake Grevelingen. The reliability of the net load data depends on the accuracy with which the water balance of the lake is known and the availability of data concerning the composition of the various incoming and outgoing water volumes.
- The calculation of **mortality** and **mineralization** forms an essential part of the model because it provides the base for the calculation of detritus. In contrast to the other components, measurements of detritus derived from primary production of phytoplankton and microphytobenthos, are not available.
  Mortality is defined as the difference between measured production of phytoplankton and microphytobenthos and the measured change in algal biomass. The production of dead organic material by mortality of algae provides detritus which is distributed over the bottom and water compartments by means of sedimentation and resuspension.
  Mineralization is the process in the nutrient cycling that determines the availability of dissolved inorganic nutrients for primary production. Mineralization is formulated as a function of temperature and substrate concentration. Substrate is present in the bottom resulting from dead microphytobenthos and settled phytoplankton detritus. Also suspended detritus consisting of dead phytoplankton, resuspended bottom detritus and imported POC is subject to mineralization.
- **Sedimentation/resuspension.** In shallow lakes a considerable amount of the particulate organic matter which is produced is decomposed at and in the bottom as a result of the rapid removal from the water phase by processes as sedimentation and grazing by filter feeding bottom fauna.
  For sake of simplicity the distribution of detritus over a suspended- and a bottom pool by resuspension and sedimentation is simulated by

means of net sedimentation only. If the calculated amount of suspended detritus (derived from phytoplankton and POC-import, after mineralization) is larger than the measured concentration of suspended detritus, the surplus is sent to the bottom detritus pool. Occasionally a negative sedimentation (net resuspension) is calculated.
The overall result is a suspended detritus pool (almost) entirely derived from phytoplankton, and a bottom detritus pool derived from microphytobenthos as well as settled phytoplankton and imported POC.

- **Mobilization.** The nutrient exchange to and from the bottom and water compartment is a mixture of biological and physico-chemical processes. For instance effects of bioturbation and the uptake and release of nutrients by microphytobenthos from either the bottom- or the water compartment are difficult to describe in quantitative terms. Mobilization of nutrients which is determined by physical (resuspension) and chemical processes is beyond the scope of the current calculations. Hence the exchange of dissolved inorganic nutrients over the bottom-water interface is excluded. Instead the existence of pools of dissolved nutrients in the bottom is ignored.
  This means that the following assumptions are made in the calculations of the dissolved nutrient pools in the overlaying water.
  1. The measured dissolved inorganic nutrient concentration in the overlaying water at the beginning of 1977 is imposed as initial value representing the total available amount for the biological processes.
  2. The mineralization products from bottom detritus are directly released into the overlaying water.
  3. Both phytoplankton and benthic diatoms depend on the nutrient pools in the overlaying water. Thus benthic diatoms are assumed not to use nutrients from the bottom (pore water).
     This assumption seems unrealistic, especially for the summer periods, when hardly any nutrients are available in the water phase. However the combination of the assumptions 2 and 3 means in practice that during summer benthic diatoms (and phytoplankton) are provided with nutrients, mainly by mineralization of bottom detritus. This is in accordance with observations of for instance Kelderman (1983) (see chapter 4).
- **Denitrification**, ammonification and nitrification, are processes distinguishing nitrogen from carbon and other nutrients. Especially denitrification is of interest, because it provides a pathway for nitrogen to leave the system. By denitrification nitrate is transformed to elemental nitrogen, which enables exchange with the atmosphere.
  Denitrification is formulated as a function of temperature, according to Stanford (1975) and substrate concentration, according to Van Kessel (1978). In the calculation no distinction is made between the constituents of dissolved inorganic nitrogen (ammonia, nitrite and nitrate). So the total (calculated) amount of dissolved inorganic nitrogen is regarded as substrate for denitrification.
  To simulate the (possible) limitation of denitrification by inhibition of nitrification (due to low oxygen concentrations) also an oxygen dependency is incorporated in the denitrification function.
- **Refractory silicon:** comparison of the loading of dissolved silicon on the lake (see **Table 5.4**) and the dissolved silicon concentration during the subsequent winters (see **Fig. 3.12**) shows that the loading does not result in an increase of the concentration to the same extent. Apparently some silicon is irreversibly removed from the dissolved pool every year. In the silicon cycle no release mechanism, like denitrification in the nitrogen cycle, can serve as a removal process. Therefore it is assumed that every time a diatom cell is formed, a certain amount of silicon is irreversibly fixed in the cell wall. When

a diatom cell dies, this fraction will not enter the silicon cycle again, but will 'disappear' in a refractory pool.
Such a mechanism leads to enrichment of silicon in detritus, as is observed in fresh water lakes (De Pinto, 1979).

5.2.1 Model formulation

The program listing is presented in the addendum of the report.

Components and processes (see **Fig. 5.1**), for which no measurements are available, concern bottom detritus (formation of detritus by mortality, decay by mineralization, the refractory silicon fraction), denitrification and uptake of nutrients by primary producers.

The formation of detritus is deduced from the mortality of phytoplankton and bottom detritus (**equation 5.1**).
Detritus is redistributed over the water and the bottom pool by means of net sedimentation. The amount of suspended detritus is set equal to the measured suspended detritus concentration and the surplus is sent to the bottom pool (**equation 5.2**).
Decay of detritus is simulated by calculation of the mineralization of carbon, nitrogen and phosphorus and dissolution of silicon. The mineralization and dissolution rates are formulated as a function of temperature.
Mortality and mineralization are incorporated in the detritus equations for suspended (incorporated in the sedimentation) as well as bottom detritus (**equations 5.2 and 5.3**). Optionally the import of particulate organic matter can be taken into account.
The amount of inorganic dissolved nutrients is calculated as a function of uptake of nutrients by primary producers and release of nutrients from detritus by mineralization and dissolution. Also the net load to or net export from the lake is taken into account (**equation 5.4**).
Denitrification is incorporated in the nitrogen balance by means of a temperature- (and optionally oxygen-) dependent formulation (**equation 5.5**).
From the mortality of planktonic and benthic diatoms a fraction of silicon disappears in a refractory pool and does not enter the silicon cycle again (**equation 5.6**).
The timestep (Δt) is chosen in such a way that the model output is independent of Δt.

Equations

Mortality

$$M(t) = P(t) - \Delta X/\Delta t \;,\; \Delta X = X(t+\Delta t) - X(t) \qquad (5.1)$$

Sedimentation

$$\begin{aligned}\Delta SED = {} & (1 - mins*\Delta t)*DETs(t) + Mp(t)*\Delta t - DETs(t+\Delta t)\\ & (+\ QP(t)*\Delta t)\end{aligned} \qquad (5.2)$$

Bottom detritus

$$DETb(t+\Delta t) = (1 - minb*\Delta t)*DETb(t) + Mb(t)*\Delta t + \Delta SED \qquad (5.3)$$

Inorganic dissolved nutrients

$$\begin{aligned}NUT(t+\Delta t) = {} & NUT(t) + mins*\Delta t*a*DETs(t) + minb*\Delta t*a*DETb(t)\\ & - P(t)*\Delta t*a + Q(t)*\Delta t\end{aligned} \qquad (5.4)$$

Denitrification

$$\Delta DEN = cden*\Delta t*NUT\ (*\ ffox)\ ,\ (ffox=OX/10) \qquad (5.5)$$

Refractory silicon

$$\Delta SR = ksr*a*(M + QP) * \Delta t \qquad (5.6)$$

M = mortality of phytoplankton and benthic diatoms ($gC/m^2.day$)
P = net primary production of phytoplankton and benthic diatoms ($gC/m^2.day$)
X = biomass of phytoplankton and benthic diatoms (gC/m^2)

DETs = suspended detritus, measured (gC/m^2)
DETb = bottom detritus (gC/m^2)
Mp = mortality of phytoplankton (gC/m^2)
Mb = mortality of benthic diatoms (gC/m^2)
SED = net sedimentation of detritus (gC/m^2)

NUT = dissolved inorganic nutrient concentration (g/m^2)
Q = net load of dissolved nutrients ($g/m^2.day$)
QP = net load of particulate organic matter ($g/m^2.day$)
DEN = denitrification (gN/m^2)
OX = measured oxygen concentration at G11, 5-15 m depth ($gO2/m^3$)
SR = refractory silicon (gSi/m^2)

a = stoichiometric coefficient (g/gC)
mins = mineralization rate, suspended detritus (/day)
minb = mineralization rate, bottom detritus (/day)
cden = denitrification rate (/day)
ffox = oxygen dependent coefficient (-)
ksr = coefficient refractory silicon (-)

Δt = timestep (day)

Remarks

- the equations for mortality, sedimentation and bottom detritus are only given for **carbon**. The same equations are used for the nutrients, by multiplication with stoichiometric factors (see **Table 5.2**).
- In the **silicon**- equations for sedimentation and bottom detritus not the total mortality of respectively phytoplankton and bottom detritus is incorporated, but mortality minus the refractory fraction (SR).
- In the **nitrogen**- equation for inorganic dissolved nutrients also denitrification is subtracted.

5.2.2 Input-data and coefficients

Input-data

The balances related to the carbon and nutrient cycles are mainly based on the measurements of the organic carbon cycle in the lake. These measurements concern:

- Biomass of phytoplankton in wet weight (cell volume) units (data from Bakker, DIHO, see Bakker and de Vries 1984). These measurements are converted to g C/m^3 by using the regression equations of Strathmann (Parsons and Takahashi, 1973).
- Biomass of microphytobenthos in mg chlorophyll/m^2 in the upper 2 cm sediment layer (see Nienhuis and de Bree 1984). These measurements are converted to g C/m^2 by using a chlorophyll to carbon conversion of 40.
- The concentration of suspended dead organic carbon (suspended detritus). These data are obtained by correcting measurements of suspended particulate organic carbon (POC) for the carbon contribution of living phytoplankton.
- Production by phytoplankton (see Vegter and de Visscher 1984). The measured ^{14}C-data are interpreted as net production data. For 1977 the original production data are used, i.e. not yet corrected for the too high excretion values which have been measured in that year (annual report DIHO-1977). This means that the total range of lake-averaged net production data, which have been used in the balance calculations vary from approximately 70 g C/m^2/year in 1977 to 200 g C/m^2/year in 1980 (see table 5.4).
- Production by microphytobenthos (benthic diatoms). These input data form the weakest part of the balance calculations. Production by microphytobenthos is only measured in 1980 by means of a net oxygen production technique (unpublished data from Lindeboom, DIHO) and in 1979 and 1980 by means of the 14C method (see Nienhuis and de Bree 1984).

  These measurements are combined to a 'standard bottom diatom net production curve' (see **Fig. 5.2**). The shape of this standard curve is obtained from the 14C-data, the magnitude (approximately 90 g C/m.yr) from the oxygen production measurements.

Coefficients

The measurements on the organic carbon cycle are converted to nutrients according to the average stoichiometry of marine algae, obtained from several literature references.
The stoichiometric data from literature are arranged in three groups:

- planktonic non diatoms
- planktonic 'spring' diatoms
- planktonic 'summer' diatoms.

The data from different literature sources are averaged for every species (or genus) within these three groups, and presented in **Table 5.1. a,b,c.** The mean stoichiometric values (and standard deviations) for each of the three groups are summarized in **Table 5.1.d.**

By means of calibration (within the range given by the standard deviations in table 5.1.d) the stoichiometric values that are used in the balance calculations are obtained. These values are given in **Table 5.2.**
In the literature no stoichiometric data are found for marine benthic (pennate) diatoms. Therefore the same stoichiometric values are used for planktonic and benthic diatoms.

The coefficients that are used for mineralization, denitrification and formation of refractory silicon are given in **Table 5.3.**

No specific literature references can be mentioned for the values that are chosen by calibration. Therefore the sensitivity of the balance calculations to variations in the coefficients is examined (see section 5.4).

5.3 RESULTS

The balance calculations are carried out for a period of four years, 1977-1980. The model is applied sequentially for the whole period.
The initial values for dissolved nutrient concentrations, suspended detritus, and biomass and production of phytoplankton and bottom diatoms are obtained from the first data for 1977. The initial value for the amount of bottom detritus is set equal to the calculated amount at the end of that year (by means of an iteration procedure).
For the calibration of the model the whole period of 4 years is considered.
The aim of the calibration was the best possible resemblance between calculated and measured concentrations of the dissolved inorganic nutrients.

The effect of the **timestep** on the calculated dissolved inorganic concentration of nitrogen and silicon is illustrated in **fig. 5.8.** The differences between the results for timesteps of 1 week or less are minimal. A timestep of 1 day is used for all the calculations.

calibration run
The main results of the **calibration run** are presented in the **figures 5.3 - 5.7.**

- For the figures 5.3 - 5.5 the phytoplankton production data of DIHO are used.
- For the figures 5.6 - 5.7 production data of DDMI are used for the last two years.

In the balance figures the distribution of nutrients over the components or pools that are incorporated in the calculations is presented. Pool sizes are expressed in g/m² (= concentration * 5.3 m for the pools ir the water phase). Starting from the base line, the following pools are plotted on top of each other.

1. Phytoplankton, measured concentration * nutrient stoichiometry.
2. Suspended detritus, measured concentration * nutrient stoichiometry.
3. Benthic diatoms, measured concentration * nutrient stoichiometry.
4. The amount of nutrient stored in bottom detritus, calculated.
5. Dissolved inorganic pool, calculated.

The calculated dissolved inorganic pool sizes are also presented below the corresponding nutrient balances, in combination with the measured concentration (* 5,3 m) according to DIHO- and DDMI-data. For this comparison the original datasets are used, no interpolation nor moving average procedure is applied.
For the calibration run also additional information is presented in the **figures 5.14 and 5.15**: the calculated nutrient fluxes from mineralization of bottom detritus and the calculated carbon fluxes from mineralization in water and bottom, in combination with measured ecosystem respiration in water and bottom in 1980-1981.
Finally the annual values of some measured and calculated fluxes and turnover rates for the calibration run are summarized in **Table 5.4 and 5.5.**

sensitivity analysis
Besides calibration an analysis is carried out to investigate the **sensitivity** of the model to optional functions and to variations in the coefficients. The results of the sensitivity analysis are presented by means of comparison of the calculated dissolved inorganic pool sizes with the calibration run. The following variations are examined.

- The possible influence of the import of suspended organic matter (fig. 5.9).
- Variation of stoichiometric coefficients (fig. 5.10).
- Variation of mineralization rates (fig. 5.11).
- The influence of disappearance of silicon to a refractory pool (fig. 5.12).
- The influence of denitrification (fig. 5.13)

The results of the calibration run and the sensitivity analysis are presented in some more detail in the next three sections.

5.3.1 Nutrient balances

Silicon

The silicon balance and the comparison between calculated and measured dissolved silicon concentration (see **fig. 5.3**), shows that the dynamics of this nutrient can quite well be described in terms of the biological processes that are taken into account. Apparently about 75% or more of the silicon that is present in a dissolved form during winter, is stored during summer in the bottom detritus pool. During summer nearly all available silicon is allocated in living or dead organic matter. At the end of the year nearly all the silicon is dissolved again.
Fig. 5.3 and 5.6 differ in that the model input for fig. 5.3 is entirely derived from DIHO-data, while fig. 5.6 is partly (1979, 1980) based on phytoplankton production data from DDMI. The differences between the calculated dissolved concentrations in these figures for the last two years is of the same order of magnitude as the differences between calculations and measurements. This means that the resemblance between calculated and measured concentrations is as good as possible for the given accuracy of the input data.

Figure 5.10.a shows the large sensitivity of the silicon calculations to variations of the stoichiometry, within the ranges given in table 5.1. For the calibration run a variable stoichiometry is used, varying between a spring-value (0.45 g Si/g C) and a summer-value (0.20 g Si/g C) as a function of the calculated dissolved concentration. This is illustrated by **fig. 5.10.d.**
Only with this relatively low summer stoichiometry for planktonic and benthic diatoms a good fit with the measured silicon dynamics can be obtained.
Low silicon content of diatom cells can result from limiting circumstances, as illustrated in table 5.1.c. For planktonic diatoms also the ability to form thin cell walls, resulting in increased buoyancy as an adaptation in non-turbulent waters, may play a role (Bakker and de Vries 1984).

The calculations for silicon are not very sensitive to variation of the dissolution rates, as far as the dissolved concentration is concerned. This is shown in **fig. 5.11.a.**

The influence of the assumption on refractory silicon is shown in **fig. 5.12**. Without this assumption the external loading leads to a continuously increasing dissolved concentration, which is not in accordance with the measurements. The effects of loading are however reflected by the measured concentration in another way. The lower concentration during the winter 78-79 compared to the preceding winter 77-78 coincides with a small net load in 1978 (see **Table 5.4**). This means that the process that removes silicon out of the cycle, is indeed of the same order of magnitude as the loading, but does not directly depend on the loading itself. This is true for the way refractory silicon is incorporated in the model, as a fraction (3%) of the mortality of diatoms.

Finally the calculated bottom flux of dissolved silicon, resulting from dissolution of silicon from bottom detritus, is presented in **fig. 5.14.a**. For this flux estimation an instantaneous release to the water phase is assumed, without retention in pore water. Retention leads to a lower release during summer and higher release during winter. Taking this into account the calculated flux (solid line in the figure) agrees very well with the fluxes from table 4.3 for deep bottoms as given by Kelderman (1983).
The broken line in figure 5.14.a represents the bottom flux corrected for uptake by benthic diatoms (see model scheme in fig. 5.1), assuming that

- benthic diatoms only use the flux from the bottom for their nutrient requirements
- benthic diatom production is restricted to 60% of the bottom area of the lake (depth of 4m or less, Nienhuis and de Bree 1984).

The first assumption is not valid, and leads to negative bottom fluxes during spring. These negative values are in fact indications for the period in which benthic diatoms depend on nutrients from the overlaying water, and for the amount of this dependency. The residual positive flux agrees quite well with the fluxes for shallow bottoms in table 4.3, as given by Kelderman (1983).

Nitrogen

Like silicon, the dynamics of nitrogen can quite well be described in terms of biological processes, as is shown by **fig. 5.4**. Storage in bottom detritus during summer is also important for nitrogen.
Comparison of **fig. 5.4 and 5.7** is very illustrative as to the dependency of the calculations on input data for phytoplankton primary production.

- The production peak in spring 1979 according to DIHO-data causes a good fit with the measurements (week 127). This production peak is almost absent in the DDMI-dataset, leading to a bad fit in the same period.
- The situation is reverse in late summer 1979 (week 140), a good fit based on DDMI-data, and not for DIHO-data.
- The spring peak in 1980 seems to be overestimated by DIHO, and not by DDMI.
- And the equilizer: the late summer production peak in 1980 according to DIHO-data, that is almost absent in the DDMI-dataset.

Given these deviations, that entirely depend on the input data used, it is probable that also a production peak of non-diatoms in late summer 1978 is missing in the DIHO-dataset, leading to the bad fit with the measurements in this period.

The sensitivity of the nitrogen calculations to variations of the stoichiometry is much less than in case of silicon (see **fig. 5.10.b**). Also the range of different stoichiometric coefficients that is applied (as obtained from table 5.1) is much smaller. The variable stoichiometry between a spring value of 0.17 g N/g C and a summer value of 0.14 g N/g C that is used for the calibration run is shown in **fig. 5.10.d.**

The calculations for nitrogen are not very sensitive to variation of the mineralization rate, as far as the dissolved concentration is concerned. This is shown in **fig. 5.11.b.**

Denitrification is a key process in the nitrogen cycle. Without a removal mechanism like denitrification the dissolved concentration should exhibit a five-fold increase within four years as a consequence of loading, as illustrated in **fig. 5.13.** The same figure shows the large sensitivity of the nitrogen calculations to variation of the denitrification rate.
The annual values for denitrification in the calibration run are, averaged over the four years, 0.5 g N/m^2 lower than the net loading (see table 5.4). This difference is almost equal to the increase of the dissolved inorganic concentration, as can be seen in fig. 5.4.
In the calibration run the denitrification is calculated **without oxygen dependency** of this process. This means that the calculated increase of the dissolved concentration in the winter of '79-'80 compared to the winter '78-'79 (see fig. 5.4), is caused by the relative high load in 1979, and not by inhibition of denitrification.
In **figure 5.13.c** the possible influence of low oxygen concentrations on denitrification is illustrated. According to the formulation that is chosen in the model for this dependency, the influence is not that large. However, especially in the winter '79-'80, the effect of the low oxygen concentrations, due to salt stratification in the preceding year, is visible. The inhibition of denitrification in 1979 and thus the increase of the subsequent winter concentration is estimated at 0.3 g N/m^2 (see **Table 5.4**), a decrease of 10%.

In **fig. 5.14.b** the bottom flux of dissolved nitrogen is given, resulting from mineralization of bottom detritus. The flux of gaseous nitrogen, resulting from denitrification, is not incorporated in this figure (see for the denitrification flux fig. 5.13.b).
As for silicon, the solid line in fig. 5.14.b represents the flux from deep bottoms (> 4 m, 40% of the bottom area), the broken line represents the flux from shallow bottoms (< 4 m, 60% of the bottom area), corrected for uptake by bottom diatoms. Again the agreement with the values in table 4.3 for deep and shallow bottoms is quite good.

Phosphorus

The phosphorus balance **(fig. 5.5)** confirms the fact that phosphorus is not limiting for primary production in Lake Grevelingen. The dynamics of orthophosphate depend only to a minor extent on the uptake of primary producers and subsequent release resulting from mineralization.
The calculated orthophosphate concentration illustrates the export of orthophosphate to the North Sea, in the few months after the opening of the Brouwers sluice. (3.5 g P/m^2 in winter and spring 1979, see table 5.4). The measured concentration in the subsequent winter is however only 1.5 g P/m^2 lower. Also the overall seasonal pattern of concentration increase during week 20-40 (May-August) and decrease in the rest of the year remained the same.
Both phenomena, the buffering of the orthophosphate concentration against net export to the North Sea, and the distinct seasonal pattern, cannot be described at all in terms of the biological processes that are taken into account in the balance calculations.
Also doubling of the stoichiometric coefficients for phosphorus does not alter this conclusion (see **fig. 5.10.c**).

The calculated bottom fluxes, averaged for shallow and deep bottoms (**see fig. 5.14.c**) agree more or less with the mobilization from and accumulation in the bottom according to the model of Kelderman (see section 4.3). When however also uptake by phytoplankton is taken into account, and subsequent settling of phytoplankton detritus, these bottom fluxes are far too low to explain the observed increase of the orthophosphate concentration during May-August, as is shown in fig. 5.5.
The balance calculations confirm the conclusion drawn from the analysis of the nutrient concentration ratios in the water layer near moderately deep bottoms (see section 4.3): the bottom flux of phosphorus is not directly driven by mineralization of organic material. Other, merely physical and chemical processes must be responsible for the observed seasonal behaviour of the phosphorus concentration in the water column.

5.3.2 The influence of import of suspended organic matter

In the calibration run the import of suspended organic matter from the North Sea is not taken into account, because no information is available on the degradability and the nutrient content of this material. At least part of the material is probably more or less refractory with a low nutrient content.
To investigate anyhow the possible influence of POC-import on the nutrient balances, a 'worst case' calculation is made. Therefore it is assumed that nutrient content and degradability of imported POC is comparable with recently died phytoplankton (at the same time) within the lake. So 'worst case' means the maximal possible influence of POC-import on the nutrient balances.
The results are presented in **fig. 5.9.** Only the last two years are of interest. Before the opening of the Brouwers sluice in December 1978, there was no POC-import from the North Sea.
The maximal influence (winter '79-'80) on the dissolved silicon concentration is approximately 25%, on the dissolved nitrogen concentration less than 10%. Because these values are overestimations (see above), the influence of POC-import from the North Sea after opening of the Brouwers sluice has probably little or no influence on the nutrient dynamics in Lake Grevelingen.

5.3.3 Carbon mineralization

Since mineralization is separately calculated for suspended and bottom detritus, comparison between the calculated mineralization rates in water and bottom and measured oxygen consumption rates is possible. Comparing these rates for both compartments is also the only possible control for this moment, because for instance the exchange with the atmosphere with respect to oxygen and carbon dioxide is not incorporated in the calculations. This means that comparison between measured and observed state variables (oxygen and alkalinity) is not yet possible.
The calculated mineralization fluxes of suspended detritus from phytoplankton and the measured oxygen consumption rate in water (see **fig. 5.15.a**). are converted to the same carbon units.
These data are derived from the tables given by Goossens et all (1983). For the conversion of oxygen to carbon a factor 0.29 is used. The data (g C/m^3/week) are multiplied with the average depth of Lake Grevelingen (5.3 m) to present the data in units (g C/m^2/week) that are comparable with the calculations.

Fig. 5.15.b shows the calculated mineralization fluxes of bottom detritus from settled phytoplankton and microphytobenthos and the measured oxygen consumption rate in the bottom, converted to the same units.
These data are derived from figures given by Lindeboom et al (1983). In these figures the data are already presented in carbon units. They are read from the figures and mean values for the stations Hals, Herkingen and Archipel are calculated. The data from station Monument are not used because this station is considered representative for only a small part of Lake Grevelingen.

The shape of the calculated and measured curves is in general more or less the same, taking into consideration the fact that calculations and measurements concern only partly overlapping periods.
There are however strong differences between the absolute magnitude of calculated and measured values. These differences can easily be seen by comparing the total annual fluxes, which are given in **Table 5.4**.
The differences are further discussed in section 6.5.

5.3.4 Turnover rates of phytoplankton and nutrients

In **Table 5.5** turnover rates of phytoplankton biomass and nutrient pools are given. The turnover rate of phytoplankton biomass is calculated as

$$\frac{\text{net annual production}}{\text{mean biomass}}$$

The turnover rates of the dissolved inorganic silicon and nitrogen pools as

$$\frac{\text{sum of the fluxes from mineralization in water and bottom}}{\text{max. winter conc.} + (\text{net load} - \text{denitr. or refr. Si})/2}$$

The turnover rate of phytoplankton increases with a factor 2 during the period of 4 years. Also the turnover rates of the dissolved silicon and nitrogen pools increase continuously during the four years studied, although to a lesser extent.
In other words, phytoplankton primary production increases more than proportionally compared with phytoplankton biomass, but also compared with the size of the dissolved silicon and nitrogen pool, causing faster turnover of these nutrients.

6. DISCUSSION

6.1 DECREASE OF THE SILICON CONCENTRATION IN SPRING

For the calculations of the available dissolved inorganic nutrient pool, the assumption is made that the nutrient concentrations in the overlaying water during winter provide an estimate of the total amount of nutrients available for the biological nutrient cycling. According to this assumption, the decrease of dissolved inorganic nitrogen and silicon at the beginning of each year is mainly caused by uptake by microphytobenthos, in stead of uptake by planktonic algae. This feature is repeated each year during the period 1977-1980.
Since hardly any planktonic diatoms are observed in Lake Grevelingen during spring in 1977-1979, the uptake of nutrients from the overlaying water by microphytobenthos provides an answer for the decrease of silicon in the waterphase. It makes also probable that nitrogen as well is taken up during spring from the overlaying water by benthic diatoms.
The rapid decrease of nitrogen and silicon in the waterphase during spring and the zero levels during summer, indicate that the primary production and biomass of phytoplankton depends on a balance between accumulation of detritus in the bottom and release of nutrients due to mineralization.
The difference of one order of magnitude between the decrease of dissolved nutrients and the increase of phytoplankton biomass during spring, can be explained by storage of nutrients in the bottom detritus pool.

6.2 POSSIBLE CAUSES OF INCREASED PHYTOPLANKTON PRODUCTION

The phytoplankton production has increased with a factor 3 in the period 1976-1981, according to measurements of DIHO (Vegter and de Visscher, 1984) (see **Table 5.5**). What may be the reason of this observed production increase?

The major change within this period is the connection with the North Sea via a sluice in the Brouwers dam, that has been put in operation at the end of 1978. The influence of flushing with North Sea water on the nutrient cycles of nitrogen and silicon is, however, limited. Exchange via the sluice in the Brouwers dam increases the gross nutrient fluxes, but not the net import of dissolved inorganic silicon and nitrogen (see **Table 5.5**). Thus, the direct influence of flushing with North Sea water on the nutrient availability cannot be responsible for the increased primary production.

Three other possible causes for this example of marine eutrophication are

1. the continuous concentration increase of nitrogen, due to loadings from other sources than the North Sea
2. anoxic surfaces of shallow bottoms, causing a shift from benthic primary production to planktonic primary production
3. increasing activity of filter feeding bottom fauna.

The net import of nitrogen from rainfall and polder water discharges, causes an average increase in the maximum winter concentration of 0.4 g N/m^2.year. The larger availability of nitrogen is probably partly responsible for the observed production increase. Nutrient availability as such, however, cannot explain the higher turnover rate of phytoplankton biomass. The relative production increase with a factor 3 is also much larger than the relative concentration increase of nitrogen (40% over 4 years), reflected by the higher turnover of the nitrogen pool itself.

The absence of tidal water movements in Lake Grevelingen has increased net settling of suspended sediments and organic particles. Especially in the gullies, the mud contents and the organic carbon contents of the upper sediment layer became significantly larger since the closure of the former estuary in 1971 (Kelderman et al 1984). The reduction of the current velocity probably also promoted the net settling of organic matter on shallow bottoms. The deposition of organically rich faeces and pseudofaeces by filtering bottom fauna may be important for the organic enrichment of shallow bottoms too (see section 6.6). The resulting higher oxygen demand in the bottom may have caused the gradual rise of the redox discontinuity layer, as reported by Willems et al (1984). As a consequence, anoxic bottom surfaces, a common phenomenon in the deep gullies (less than 5% of the bottom area), are also to be expected in the shallow parts. Observations since 1980 indeed indicate the occasional occurrence of anaerobic bottom surfaces in shallow parts of the lake.
This leads to the second possible explanation of the increased phytoplankton production. The existing community of benthic diatoms may have shown decreased survival abilities on an anoxic bottom surface (Admiraal and Peletier 1979). When this is true, the assumed constant production level of benthic diatoms, based on measurements in 1980 only, is wrong. In stead, the benthic production may have been higher in the first years after closure of the Grevelingen estuary, and decreased from 1976-1977 onwards. Reduced benthic production means less influence on the nutrient flux from shallow bottoms during summer, and thus increased nutrient availability for phytoplankton.
According to this second explanation, the turnover rates of the nutrient pools did not change during the period 1977-1980, because the total primary production of small benthic and planktonic algae should have remained the same. Only a shift should have occurred from benthic to planktonic production.
Unfortunately, this explanation cannot be tested because data of benthic production are only available for 1980. However, as was the case for the increased nitrogen availability, the shift from benthic to planktonic production can only explain a production increase, and not the increased turnover rate of planktonic algae.

High turnover rates implies a combination of high production, mortality and mineralization rates. Because primary production during summer is apparently limited by the release of nutrients resulting from mineralization, the increase of phytoplankton production at a relatively constant biomass level must be caused by some factor promoting algal mortality as well as mineralization of detritus.
This factor may be found in the increase of biomass and/or activity of bottom fauna since 1977. The filter feeding bottom fauna is (directly or indirectly) an important mortality factor for phytoplankton in Lake Grevelingen. Bottom fauna probably also promotes the release of dissolved nutrients from organic particles by their metabolic activity. Positive effects on nutrient mobilization by mussels are reported by Kuenzler (1961) and Jordan and Valiela (1982). Pomroy et al (1983) demonstrated that the ammonia flux from the sediment of Bristol Channel was significantly related to biomass of polychaetes, molluscs and other macrofauna, either by ammonium excretion, or, in addition, by increasing the exchange of nutrients by bioturbation. Blackburn and Henriksen (1983) estimated that benthic infauna increased the ammonium flux from the sediment in Danish coastal waters by 50%.
Only increasing bottom fauna activity from 1977 onwards can fully explain the increasing phytoplankton production, combined with relatively con-

stant low phytoplankton concentrations, and acceleration of silicon and nitrogen turnover.
No data on the amount of macrozoobenthos in Lake Grevelingen have as yet been published. Verhagen (1983) estimated the biomass of the mussel Mytilus edulis (the main filter feeder in the lake in 1977) from biomass measurements in natural mussel beds (236.4 gram dry weight per m², unpublished results from Lambeck, Delta Institute for Hydrobiological Research) and the percentage of the lake bottom covered with dense mussel beds (estimated as 6%, based on measurements of the Institute for Fishery Research). An estimate of the biomass density of mussels, averaged over the whole lake area, is therefore about 14 gram dry weight per m².
Based on this biomass estimate, Verhagen (1983) concludes that the main part of the primary production goes into the food chain, and that the filtering bottom fauna is food limited. An additional indication is the location of mussel beds at those places, where the advective transport of food particles to the bottom is maximal. In such a situation, increased phytoplankton production will induce a higher consumption rate, leading to a faster turnover of phytoplankton biomass and nutrients.

The different influences of the bottom fauna on phytoplankton and nutrient cycling are further discussed in section 6.6.

6.3 DENITRIFICATION

Denitrification rates are reported to be temperature dependent, and vary in salt water ecosystems from 3 to 130 mg N/m².day (Billen, 1978; Valiela, 1979; Smits, 1980). For North Sea coastal sediments denitrification amounts to 25 mg N/m².day (Billen, 1978).
According to the calculations 3-4 g N/m².year is yearly removed from Lake Grevelingen by denitrification. The calculated denitrification rate is 10-20 mg N/m².day during summer, with maximal values up to 25 mg N/m².day, the same as reported for the North Sea coastal zone.

Combining the results for the three nutrients, nitrogen seems to be the key factor controlling the behaviour of the ecosystem components that are incorporated in the balance calculations. Especially because of (1) the nitrogen limitation of primary production, (2) the nitrogen load to the system which is annually as large as the total amount of nitrogen incorporated in the biological cycling and (3) the importance of redox processes as a removal mechanism of nitrogen out of the system, which can compensate the net load.
Net loading of nitrogen on the lake is the result of polderwater discharges and rainfall. Flushing of the lake with North Sea water since 1978 causes a considerable import of nitrogen at high tides, but also an export of the same order of magnitude at low tides. So the net nitrogen load is not influenced by flushing.
Net loadings from polder discharges and rainfall will not change or may even increase to a certain extent in the future. Therefore the environmental factors enabling denitrification are important for the consolidation of the process capable to compensate the nitrogen load to the lake.

A denitrification rate of 3-4 g N/m².year is low compared with the range given in literature, as indicated above. So the available substrate, i.e. the availability of nitrogen in an oxidized form (nitrate) near and in the bottom probably limits the denitrification rate (Nedwell, 1982; Derks, 1981; Van Kessel, in Smits, 1980).

Since nitrogen resulting from mineralization is released in a reduced form (ammonium), the presence of an aerobic upper sediment layer and aerobic water near the the bottom is necessary for the nitrification of ammonium.
The activity of nitrifying bacteria in coastal marine sediments diminishes by decreased oxygen availability, by competition for ammonium, and by the poisoning effect of hydrogen sulfide (Hansen et al 1981). As a consequence, planktonic *nitrification is far more important* to the nitrogen budget in waters with anoxic sediments than the nitrate flux from the sediment (Somville 1984). Denitrification, on the other hand, is restricted to anaerobic or nearly anaerobic conditions. Therefore, this process is only investigated for sediments (Billen 1978, Nishio et al 1982, Blackburn and Henriksen 1983, Kaspar 1983).
By the extension of anaerobic conditions in the sediment, denitrification becomes exclusively dependent on the diffusion of nitrate from the overlaying water into the sediment. This nitrogen source (nitrate as well as ammonium), however, is also available for benthic and planktonic primary producers. This will initially result in a reduction of the nitrate availability in the bottom and by that of the denitrification rate. As a consequence the nitrogen concentration in the overlaying water will increase which promotes primary production.

Stratification can cause anaerobic circumstances near the bottom because of the isolation of oxygen consumption in the deeper water layers from the upper water layer, where oxygen production by primary producers and exchange with the atmosphere takes place.
The area with an anoxic bottom surface extended in summer 1979 to 20% or more of the bottom area of the lake, instead of less than 5% in other years (see section 4.2.2). At the end of 1979 the ammonium concentration doubled, compared with the preceding winter, an increase of more than 1 g $NH4-N/m^2$, according to DIHO-data.
It seems logical to explain this increase as being caused by *inhibition of* nitrification under anaerobic circumstances. The DDMI-data however show a less dramatic increase. Also the results of the balance calculations suggest that (see table 5.4 and fig. 5.4 and 5.13.c):

- the relative high load (4.1 $g.N/m^2$.year) in 1979 causes an increase of the dissolved nitrogen concentration of approximately 1 g N/m^2
- the indirect inhibition of denitrification by anaerobic circumstances may have caused an extra increase of approximately 0.3 g N/m^2 (a reduction of 10% of the 'normal' denitrification rate)
- the lower denitrification rate in 1979 may have been compensated immediately by a higher rate in the next year, 1980, due to increased substrate availability, and recovery of the oxygen concentration near the bottom.

The calculated inhibition of denitrification in 1979 by approximately 10%, combined with the observation that 20% or more of the bottom surface area of the lake became anoxic during late summer, indicates a direct relation between the percentage anaerobic bottom surface and the percentage decrease of denitrification.
Another strong indication of the coupling between nitrification and denitrification is given by the preliminary results of the nutrient addition experiments in the MERL mesocosms (Nixon et al 1984). They found that ammonia remained more abundant at the higher rates of nutrient input, whereas at the lower input rates over 75 % of the inorganic nitrogen was transformed to nitrite and nitrate. This suggests that nitrification could not match the higher loading rates. They also found that denitrification, *although enhanced by nitrogen addition, could eliminate* in the most enriched mesocosm only 20% of the nitrogen addition, while at low addition levels 100% could be eliminated.

In nitrate enrichment experiments in enclosures in Lake Grevelingen high ammonium concentrations were also found in the enclosures in which the water column was not isolated from the sediment (Derks 1981).

These results and references indicate that, in case of a continuous presence of anoxic sediments and anaerobic conditions near the bottom, the denitrification rate will be reduced for a certain period, and the nitrogen concentration and primary production will increase. A higher overall nitrogen concentration will be needed to reach again the same denitrification rate. Defining the equilibrium concentration of dissolved inorganic nitrogen as the concentration at which the denitrification rate equals the net load of nitrogen on the system, a higher equilibrium concentration will evolve.
In other words, the steady state concentration of dissolved inorganic nitrogen is positively related to the extension of the area with anaerobic conditions in and near the bottom. Therefore, management directed to the avoidance of anaerobic conditions, is crucial for the maintenance of oligotrophic properties of the lake.

6.4 EFFECT OF INCREASING TURNOVER RATES ON THE SILICON CONCENTRATION

According to the model formulation, refractory silicon is formed by means of irreversible fixation of a certain amount of silicon, every time a diatom cell is formed. By this formulation a good fit is obtained between calculated and measured silicon concentrations, for a continuous period of four years. This formulation is also in accordance with observed enrichment of silicon in detritus in fresh water lake bottoms (DePinto 1979).
An implication of such a mechanism is an increasing formation of refractory silicon at a higher turnover rate of the dissolved silicon pool. This can even result in a decrease of the dissolved silicon concentration, when refractory silicon formation exceeds the loading. Another consequence can be a decrease of the portion diatoms in the total phytoplankton assemblage, induced by stronger silicon limitation.
Both phenomena may alternate each other. Periods with a large portion diatoms in phytoplankton, exhibiting long term decrease of the silicon concentration, followed by a period in which diatoms are less important, and the silicon concentration increases again.
Perhaps examination of the importance of diatoms in time series of plankton records, in combination with the winter concentrations of dissolved silicon, can give insight in the existence of such a cyclic successional behaviour.
Both phenomena, mentioned above, are indeed observed (see **Table 5.5**).

- Decreasing silicon winter concentration from 1978 onwards, while in the same period the nitrogen winter concentration increases.
- Decreasing importance of diatoms in the phytoplankton assemblage, in spite of the import of new species from the North Sea and the increase of the chloride concentration.

The same phenomena, on a shorter time scale, i.e. the seasonal succession within a year, are discussed by Officer and Ryther (1980). They present arguments that the introduction of nutrients to (marine) aquatic ecosystems leads to the dominance of flagellates in the summer bloom, after a diatom dominated spring bloom. They suggest that this sequence from one population to the other is controlled by the silicon regeneration cycle. The time constant of the recycling of silica by re-solution of diatom tests should be high (45-190 days), compared with the time constants of the recycling of phosphorus and nitrogen from decomposition (8.3-13.3 days) and zooplankton grazing (1.0-2.0 days). The high time constants for silicon regeneration causes depletion in silicon of the nutrient pool for the summer bloom and a flagellate bloom could be anticipated.

More recent references than used by Officer and Ryther, however, indicate that silica re-solution might be directly related to biological processes involved in nitrate and phosphate regeneration (Grill and Richards 1964). Kamatani (1969) simultaneously studied the regeneration of silicon, nitrogen and phosphorus from the marine diatoms Skeletonema costatum, Thalassiosira decipiens and Chaetoceros gracilis. The first two species occur in Lake Grevelingen. At 30 degrees Celsius, about 70% of all three nutrients and carbon was mineralized in the first 10 days. The time constant at 20 degrees Celsius for mineralization of both nitrogen and silicon was 14.4 days, i.e. a coefficient of 0.07/day, the same as used in this study for mineralization of bottom detritus. At the early stage of the mineralization, the diatom tests began to dissolve silicate into the medium, even before the liberation of ammonia and phosphate started. Only about 20-30% of the silica remained refractory after 25 days. The dissolution rate of diatom frustules in sea water was faster than in distilled water, explained by the catalizing effect of salts. DePinto (1979) explains the quick mineralization found by Kamatani by the presence of normal seawater bacterial populations in his cultures.

Also Nixon et al (1984) conclude from their nutrient addition experiments that silica is cycled more rapidly than commonly supposed.

Based on these references, in the model formulation a distinction is made between labile and refractory silicon in diatom tests with a high re-solution rate for the labile part. The very small refractory part (3%, obtained by calibration) still leads to a significant disappearence of silicon into a refractory pool, on average 22% of the sum of the winter concentration and net loading, due to the fast turnover of phytoplankton biomass.

In this way the same phenomena as studied by Officer and Ryther (1980) could be explained. Not as a seasonal succession of a diatom dominated spring bloom to a flagellate dominated summer bloom, but as a trend over several years towards a lower silicon concentration and/or a reduction of diatoms in the phytoplankton assemblage. Not caused by the slow regeneration of silicon from diatom frustules, but on the contrary by high turnover rates of phytoplankton biomass and both nitrogen and silicon, in combination with a small percentage of refractory silicon in diatom tests.

6.5 CARBON MINERALIZATION

The calculated carbon mineralization rates in water and bottom, as given in **Figure 5.15.a,b and Table 5.4** are smaller than the measured mineralization rates as reported by Goossens et al (1983) and Lindeboom et al (1983). These differences may to some extent be caused by the difference in periods of calculation and measurement and by the conversion from oxygen to carbon units. Far more important, however, is the fact that several other processes than mineralization of dead organic material contribute to the measured oxygen consumption, on which the overall mineralization rates of Goossens and Lindeboom are based.

In the production - mineralization carbon balances presented by Lindeboom et al (1983) the following processes are mentioned in this respect (the estimated magnitude of the different processes for 1980/1981 in g C/m^2.year from Lindeboom are also given)

bacterial mineralization in water	160

respiration by phytoplankton	135
respiration by zooplankton	10
total mineralization in water column	**305**

bacterial mineralization in bottom	135
respiration by eelgrass and macro-algae	70
respiration by benthic diatoms	70
respiration by benthic meiofauna	20
respiration by benthic macrofauna	95
total mineralization in bottom	**390**

The calculated mineralization rates in this report are based on:

- carbon mineralization coefficients which are assumed equal to the regeneration (mineralization and dissolution) coefficients for N, P and Si (see table 5.3).
- calibration of these coefficients on the behaviour of the dissolved concentrations of N and Si as a function of the biological processes that are incorporated in the balance calculations.

This implies that the calibrated values of the carbon mineralization coefficients are based on the combination of processes that regenerate nutrients from organic material. These processes are:

In water: bacterial mineralization
respiration by zooplankton
In bottom: bacterial mineralization
respiration by benthic meiofauna
respiration by benthic macrofauna

For the bottom, the estimated magnitude of these processes in 1980/1981 according to Lindeboom (250 g C/m^2.year) agrees very well with the calculated mineralization rate for 1980 in this report (255 g C/m^2.year). This estimation of the intensity of these processes in the bottom is thus consistent with measured oxygen consumption rates in the bottom and the behaviour of the dissolved silicon and nitrogen concentration.

For the water column, the estimated magnitude of the nutrient regenerating processes according to Lindeboom (170 g C/m^2.year) does not agree at all with the calculated mineralization rate for 1980 in this report (45 g C/m^2.year). Two possible explanations of this difference are:

- Other processes, contributing to the total mineralization rate in the water column, are not accurately estimated in the carbon balances of Lindeboom. For instance the assumption that the **phytoplankton respiration** is only 50% of the net phytoplankton production may be wrong. Assuming a higher phytoplankton respiration rate automatically reduces the estimated contribution of other processes in these carbon balances, because the overall mineralization rate (305 g C/m^2.year) is the fixed number, based on measurements.
- there are other processes, contributing to the overall mineralization (oxygen consumption) in the water column, which are not incorporated in the carbon balances of Lindeboom. One process in particular, **nitrification**, can be mentioned in this respect. The nitrogen flux from the bottom at least partly consists of ammonium in stead of nitrate. The bottom flux of nitrogen in 1980 is estimated at 38.2 g N/m^2.year (table 5.4). When 50-100% of this bottom flux is oxidized to nitrate in the water column, the oxygen consumption by nitrification (converted to carbon units) should be 23-46 g C/m^2.year (1.83 moles oxygen per mole ammonium, Smits 1980). Although this is probably an overestimation, because of uptake of ammonium by benthic diatoms and phyto-

plankton before it is oxidized, nitrification may be a significant oxygen consuming process in the water column.

Further analysis of the overall carbon balances and overall mineralization rates fall beyond the scope of the nutrient balance calculations as reported here. For the time being the following conclusions can be formulated.

- The mineralization of suspended organic material forms a minor contribution to the oxygen consumption in the water column. (estimation: 15%). Respiration by phytoplankton is probably the most important contribution to the oxygen consumption in the water column. Oxygen consumption by nitrification may be important too.
- Mineralization of detritus derived from benthic diatoms, but also from phytoplankton, mainly takes place on and in the bottom. This mineralization process (bacterial mineralization and respiration by benthic fauna) forms an important contribution to the oxygen consumption in the bottom (estimation: 65%).

6.6 THE ROLE OF BOTTOM FAUNA IN NUTRIENT CYCLING AND PHYTOPLANKTON CONTROL

Three, direct or indirect influences of bottom fauna on nutrient cycling are already mentioned in the preceding sections.

1. Acceleration of the flux of particles from the water column to the sediment by suspension feeding and deposition of faeces and pseudofaeces. This directly affects the nutrient balances by decreasing the amount of nutrients in living biomass (of phytoplankton) and increasing the storage of organically bound nutrients in the bottom.
2. Accelerated regeneration of nutrients from organic material in the bottom, either by direct excretion, or by increasing the exchange of nutrients by bioturbation, or by increased bacterial mineralization due to extra substrate availability.
3. Increased oxygen consumption in and near the bottom. This promotes the extension of anoxic conditions, directly by bottom fauna respiration and indirectly by increased bacterial mineralization. This influence the nutrient cycling, especially nitrogen, by the coupling of nitrification and denitrification. As explained in section 6.3, anoxic conditions in the bottom inhibit nitrification, by which substrate limitation for the denitrification process is enforced, and the natural removal of nitrogen out of the system will be reduced.

The possible influence of benthic filter feeding on phytoplankton is discussed for South San Fransisco Bay by Cloern (1982) and Officer et al (1982). They conclude that a benthic filter feeding community is important as a natural control on eutrophication by reducing phytoplankton biomass, especially in shallow waters with long residence times, when the water recycling time for the benthic community is equal to the time constant of phytoplankton growth.
In Lake Grevelingen these criteria are fulfilled; the average water depth is slightly more than 5 m, the residence time is approximately 0.5 year or longer, the year averaged time constant (= 1/turnover rate) for phytoplankton net production is 1.4-4.6 days (see table 5.5) and it can be estimated that the benthic suspension feeders filter the whole volume of the lake in several days (based on the filtering rate equation given by Verhagen, 1983).

Also the preliminary results of the nutrient addition experiments in the MERL mesocosms indicate a controlling role of bottom fauna on phytoplankton biomass (Nixon et al 1984). They observed that phytoplankton biomass as well as the diurnal net oxygen production did not increase in proportion to the nutrient loadings, but to a lesser extent. Only the biomass of benthic macrofauna showed a linear response compared with the loadings, especially polychaetes and the fast reproducing bivalve *Mulinea lateralis*.

It can thus be concluded that benthic fauna may control phytoplankton biomass, at least in the short term, by their grazing pressure (**influence no 1**). Officer et al (1982) explicitly exclude the recycling of nutrients by benthic excretion from their analysis. But even when nutrients are regenerated more quickly (**influence no 2**), the control of phytoplankton biomass still holds. This is indicated by the fact that the turnover rate of phytoplankton biomass increases in response to increased nutrient availability, i.e. net production increases more than proportionally to the biomass increase. The only criterion is food limitation for the benthic fauna (see section 6.2).

The influence of bottom fauna on the oxygen situation in the sediment (**influence no 3**) is not taken into account by Cloern (1982) and Officer et al (1982). This influence may counteract the phytoplankton control, or may even enhance phytoplankton biomass in the long run by the heightening effect on the equilibrium concentration of dissolved inorganic nitrogen, as explained in section 6.3.

There are several indications that benthic fauna, at least some species, adversely affects the oxygen concentration in the bottom. Nixon et all (1984) mention a large enrichment of the top 1 cm of the sediment with organic carbon in the nutrient enriched mesocosms, up to an excess of 112 g C/m^2.year after the winter/spring bloom in the most enriched mesocosm compared with the controls. Willems et al (1984) mention the biomass increase of the cockle *Cerastoderma edule* from 1977 onwards as a possible cause of the observed rise of the redox discontinuity layer in parts of Lake Grevelingen.

To evaluate in greater detail the influence of bottom fauna on the oxygen situation in the sediment, a distinction between functional groups has to be made.

All species increase the oxygen consumption in or near the sediment by their own respiration. Only suspension feeders increase the oxygen consumption in the sediment by bacterial mineralization due to transport of suspended organic material to the bottom. On the other hand, some species promote oxygen transport to the sediment by bioturbation, especially polychaetes which pump overlaying water downwards, and burrowed bivalves like *Macoma balthica*. The exhalent siphon of *Macoma* does not extend to the sediment surface and thus discharges oxyginated water and nutrients into the sediment (Reise 1983). By this, *Macoma* promotes meiofaunal abundance and stimulates growth of benthic diatoms, its own food source, a so-called 'gardening' effect. The siphon aperture of other burrowed bivalves like the cockle *Cerastoderma edule*, extend to the sediment surface. These species discharge water and nutrients directly into the overlaying water and do not produce oxidized and nutrient enriched zones in the sediment like *Macoma* , and also show no gardening effects (Reise 1983). The same probably holds for non-burrowing species, like the mussel *Mytilus edulis* and tunicates.

So, especially suspension feeding bottom fauna species that do not enrich the sediment with oxygen and nutrients by bioturbation are important with respect to **influence no 3**. There are indications that species from this functional group increase in biomass in response to higher phytoplankton production: *Mulinea lateralis* in the nutrient enriched MERL mesocosms (Nixon et al 1984), *Cerastoderma edule* in Lake Grevelingen, and tunicates in both the mesocosms (pers. comm. Donaghay) and Lake Grevelingen. These species may have a competitive advantage in situations with an excess of suspended food (phytoplankton) available, compared with gardening species promoting the growth of their own food source.

It can be concluded that on the short term grazing by suspension feeding bottom fauna may prevent eutrophication effects like high phytoplankton concentrations, especially in shallow waters with a long residence time. Acceleration of nutrient regeneration promotes the turnover of phytoplankton biomass, but the phytoplankton control still holds at least when the bottom fauna is food limited.

On the other hand, deterioration of the oxygen situation in the sediment by bottom fauna respiration and enhancement of bacterial mineralization by organic enrichment of the sediment, may affect the coupling between nitrification and denitrification. This may gradually heighten the equilibrium concentration of dissolved inorganic nitrogen and by that counteract the phytoplankton control in the long run. Especially opportunistic species that do not enrich the sediment with oxygen by bioturbation are important in this respect. Examples in Lake Grevelingen are the cockle Cerastoderma edule and tunicates.

7. CONCLUSIONS AND RECOMMENDATIONS

7.1 CONCLUSIONS

Conclusions chapter 3

- The upper water layer of Lake Grevelingen can be interpreted as well-mixed, considering the small differences between the data of the 7 DDMI-stations, which are spread over the lake.

- Comparison of the DDMI data set and the DIHO data set does not suggest important differences in measurements of most water quality variables.
  Biological variables show considerable differences.

- The measurements of most variables in the upper water layer of G11 can be interpreted as representative for the upper water layer in Lake Grevelingen.

Conclusions chapter 4

- The bottom release of nutrients is uniform over the entire lake bottom area with exception of:
  - bottoms with **anoxic surfaces** (normally less than 5% of the bottom area), for ammonium and orthophosphate
  - shallow bottoms **covered with diatoms** (depth 7 m. or less), for silicon
  - bottom areas where **seepage** occurs, for all nutrients.

- The ratios between nutrient concentrations near moderately deep bottoms (23-28 m.) and especially the **high values for phosphorus** in these ratios, indicate that phosphorus release from the bottom depends on other sources than mineralization of recently formed detritus.

Conclusions chapter 5

- The seasonal pattern of the dissolved inorganic silicon- and nitrogen concentration in Lake Grevelingen is to a large extent determined by uptake by primary producers, and mineralization. More than 75% of both nutrients present in an inorganic dissolved form during winter, is stored as detritus in the bottom during the growing season.

- According to the model formulation, on average 1.7 g Si/m^2.year is removed from the silicon cycle as refractory silicon; the measured average net loading of silicon was 2 g Si/m^2.year during 1977-1980.

- The calculated denitrification amounted to 13 g N/m^2 over four years, the net loading to approximately 15 g N/m^2. The difference of 0.5 g N/m^2.year corresponds with the measured average winter concentration increase of 0.4 g N/m^2.year.

- The negative influence of salt stratification in 1979 on the denitrification rate, caused by inhibition of nitrification under anoxic circumstances, is estimated at 10%. According to the calculations, this is almost entirely compensated in the next year, 1980, a year without salt stratification.

- In contrast to the other two nutrients, phosphorus cycling is only to a minor extent influenced by the biological processes incorporated in the balance calculations.

- The calculated fluxes of silicon and nitrogen from shallow and deep bottoms agree quite well with estimates by Kelderman (1983).
  The phosphorus flux, calculated in the same way as a result of mineralization, also agrees with calculations by Kelderman. These flux estimations are, however, far too low to èxplain the observed increase of the orthophosphate concentration during May-August.
  This again indicated the importance of physical and chemical processes in the phosphorus cycling.

- The influence of POC-import from the North Sea after opening of the Brouwers sluice has probably little or no influence on the nutrient dynamics in Lake Grevelingen.

Conclusions chapter 6

- The decrease of dissolved silicon in the water column during spring in 1977-1980, while hardly any planktonic diatoms are present, can be explained by uptake of silicon by benthic diatoms.

- The observed increase in phytoplankton primary production with a factor 3 in the period 1976-1981 cannot be explained by the influence of flushing with North Sea water and only partly by:
  - the continuous net import and concentration increase of nitrogen,.
  - anoxic surfaces of shallow bottoms, causing a shift from benthic primary production to planktonic primary production.

  Only increasing bottom fauna activity from 1977 onwards can fully explain the increasing production, combined with relatively constant low phytoplankton concentrations, and acceleration of silicon and nitrogen turnover.

- The calculated denitrification rate of 10-20 mg N/m^2.day during summer with maximum values up to 25 mg N/m^2.day, agrees very well with denitrification rates reported for the North Sea coastal zone.

- The reduction in denitrification in 1979, caused by anoxic circumstances under stratified conditions, is estimated at 10% of the 'normal' rate. In this year 20% or more of the bottom surface of the lake became anoxic during late summer, instead of less than 5% in other years. This indicates a direct relation between the percentage anoxic bottom surface and the reduction of denitrification.

- The calculated denitrification rate is on the average 0.5 g N/m^2.year lower than the net load of nitrogen to Lake Grevelingen.
  10-15% of the annual net load is not removed from the lake by denitrification, leading to a continuous concentration increase of dissolved inorganic nitrogen during the period studied.

- The equilibrium concentration of dissolved inorganic nitrogen can be defined as the concentration at which the denitrification rate equals the net load of nitrogen to the system. The equilibrium concentration is positively related to the extension of the area with anaerobic conditions in and near the bottom, due to the competition for nitrate between nitrifying bacteria and primary producers.
  Therefore, management directed to the avoidance of anaerobic conditions, is crucial for maintening the oligotrophic properties of the lake.

- According to the model formulation a higher turnover rate of silicon causes an increased formation of refractory silicon. This may lead to:
  - a decreasing silicon concentration,
  - a decreasing importance of diatoms in the phytoplankton assemblage.

  Both phenomena are observed in Lake Grevelingen during 1977-1980.

- The mineralization of suspended organic material forms a minor contribution to the oxygen consumption in the water column. (estimation: 15%). Respiration by phytoplankton is probably the most important contribution to the oxygen consumption in the water column. Oxygen consumption by nitrification may be important too.
  Mineralization of detritus derived from microphytobenthos, but also from phytoplankton mainly takes place on and in the bottom. This mineralization process forms an important contribution to the oxygen consumption in the bottom (estimation: 65%).

- Grazing by suspension feeding bottom fauna may control eutrophication effects like high phytoplankton concentrations in Lake Grevelingen on the short term. Acceleration of nutrient regeneration promotes the turnover of nutrients and phytoplankton biomass but the eutrophication control still holds when at least the bottom fauna is food limited.
  On the other hand, deterioration of the oxygen situation in the sediment by bottom fauna respiration and enhancement of bacterial mineralization by organic enrichment of the sediment, may affect the coupling between nitrification and denitrification. This may gradually heighten the equilibrium concentration of dissolved inorganic nitrogen and by that counteract the eutrophication control in the long run. Especially opportunistic species that do not enrich the sediment with oxygen by bioturbation are important in this respect. Examples in Lake Grevelingen are the cockle Cerastoderma edule and tunicates.

7.2 RECOMMENDATIONS

- Formulation of temperature-, oxygen- and substrate dependent ad- and desorption processes is recommended to enlarge the process knowledge with respect to the phosphorus dynamics and especially the interaction between bottom and water.

- Apart from the nutrients silicon, nitrogen and phosphorus also an oxygen balance should be set up as an overall control on the ecosytem description because the oxygen cycle is involved in nearly all important ecological processes.

- For the moment measurements of primary production of phytoplankton and microphytobenthos are used as model input. However measurements are scarce and interpretable in different ways (gross-net). Modelling of salt water algae including competition between benthic and planktonic algae is recommended.

- Verification by means of field and experimental work of the hypotheses formulated in this report with respect to the nitrogen cycling and the influence of the bottom fauna, is recommended. This concerns especially the inhibition of nitrification under anoxic conditions in the bottom and the subsequent reduction of denitrification caused by substrate limitation.

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