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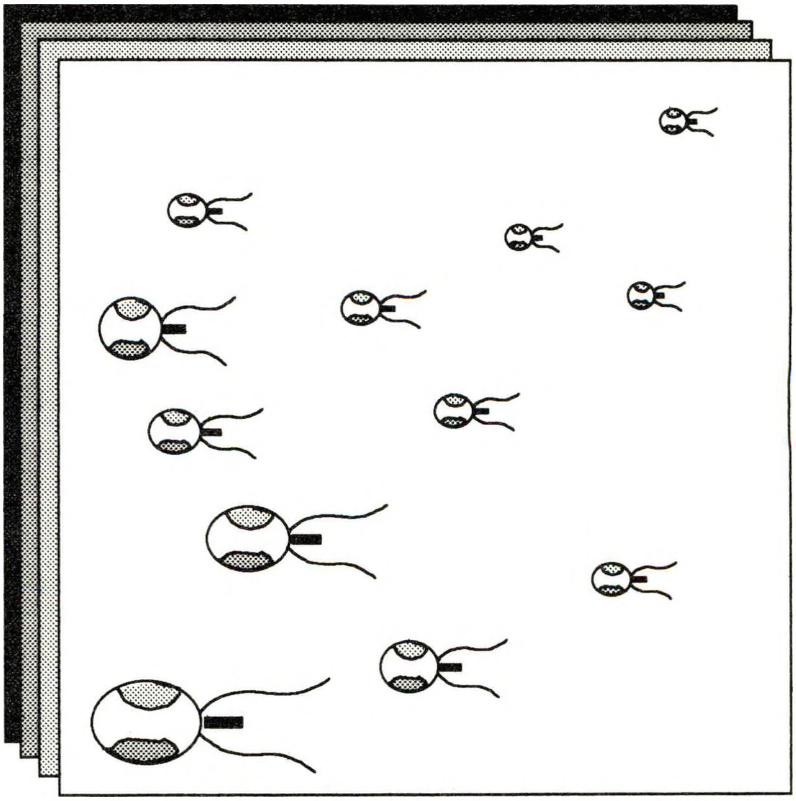
R. Riegman



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of the Ministry of Transport and Public Works

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1. Preface

The main purpose of this report is to present the ideas and results that have been elaborated from research that has been performed by the BEWON-working group (Applied and Fundamental Research NIOZ). The scientific research of the BEWON is focussed on the fundamental mechanisms and principles that are present in natural ecosystems. The generation of more insight in basic aspects is first of all needed when the possibilities for waterquality management in marine ecosystems are explored. This urgent need is illustrated by experiences in the management of terrestic and freshwater ecosystems. Examples like aldrins and dieldrins in terrestic environments and the recent experiences with biological management attempts in freshwater systems share the basic assumption that natural systems could be manipulated in an easy way. Also it was expected that the results of manipulation were highly predictable. One of the lessons we should learn from these experiments with nature is that our insight in the structure and functioning of natural ecosystems is far from what it should be before one starts to manipulate with measures that affect the symptoms rather than the causes of unwanted phenomena. To my opinion this conclusion implies that applied research should be devoted to the most fundamental principles in ecology. In todays science an increasing trend is observed where research is fragmentated into a variety of topics, all of them covering only a small fraction of the entire system. It is easier to raise fundings for environmental research when it is narrowed down to a single, and easy recognizable topic. Consequently, these clear-cut questions usually lead to clear answers to solve the particular problem. One should be aware that the very same clear solution to an environmental problem may introduce a whole series of unwanted negative effects in the same system or elsewhere. Apart from pollution the most serious treat of natural systems will be the opinion that mankind is able to manage natural systems. With the present fragmentated knowledge measures may lead to catastrophs just as easily as to improvement. It is obvious that pollution can not be banished but reduction will give us time to improve our knowledge on the basic principles in nature, enabling us to develop strategies that garantee a durable existence of the biosphere.

This report is only a small contribution to the research on algal blooms and the impact of eutrophication on natural ecosystems. It is neither giving a complete overview from the information available in the literature. Nor it is ment to give a complete compilation of all mechanisms that might be involved in the triggering of new (nuisance) algal blooms in a certain area. On the other hand it is focused on the two possible mechanisms that at present are considered as the most crucial ones in eutrophicated natural systems.

The first mechanism is the alternation of nutrient ratios. This shift in nutrient regime is frequently observed during eutrophication and due to the fact that the nutrient composition of discharges is not equal to the nutrient composition in the disposed area. A clear example, based on observations in the Marsdiep area (The Netherlands), is discussed in Chapter 3.

The second mechanism is the selective grazing by zooplankton that will favor the dominance of less edible species. The principle of this mechanism, and the impact of eutrophication on this selection mechanism, is discussed on the basis of a theoretical study (Chapter 4).

Concluding remarks are given in the summary.

The author, may 1991.

2. Introduction

Usually these type of reports begin with a compilation of all negative effects that can be attributed to eutrophication. One should not forget that a general nutrient enrichment may have some possitive effects. Especially in those cases where economical activities like fisheries are involved the productivity of a system usually will increase after eutrophication.

Climatological, meteorological and intrinsic biological factors create fluctuations in biomass of all kind of species within the ecosystem. In eutrophicated systems the amplitude of these natural variations will be enlarged. Those negative effects that are associated with the amplitude of varying biomasses (oxygen deficiency, foam formation on beaches) will become more obvious. Negative effects that are associated with a specific species composition of phytoplankton may be caused for various reasons. The amplitude effect on zooplankton is expected to create more periods with a great selective grazing pressure, selecting for the poorly edible (and sometimes toxic) algae in the system.

The question is whether this selection mechanism plays a significant role in natural systems and if so, at what eutrophication levels should this be the case?

It is interesting to remark that those (incidentally occurring) toxic algal blooms that are suspected to be selected by this mechanism clearly are depending on meteorological conditions.

The general increase in average nutrient levels (median effect) is expected to cause mainly positive effects like enhanced biomasses and a higher productivity of the system. The median effect is reflected in the frequent (year after year) appearance of the same type of algal blooms in a certain region, relatively independent on meteorological conditions. It is very likely however that in those cases where extreme eutrophication has caused a shift towards light controll (hypertrophic systems) the median effect can be held responsible for a negative effect: a major shift in the phytoplankton species composition and consequently, alternation of the foodweb structure.

The most direct impact of nutrient enrichment on algal species composition is based on induced changes in the nutrient regime. Marine aquatic ecosystems usually consist of various geographical areas that differ in their nutrient composition. When more than one of these areas will be affected by one and the same nutrient source (river discharge, or atmospheric input) by definition the discharge will cause a change in the nutrient composition in at least one of the regions. This means that phytoplankton species will become selected for other properties than before eutrophication took place. This is the stimulus for new (nuisance) algal blooms in that particular area.

One of the major difficulties in explaining the appearance of novel algal blooms is the fact that usually more than one reason can be held responsable. Within the complexity of the ecosystem various factors will be affected by eutrophication and this will encourage biologists to focus on a wide range of possible forcing factors. It is a misunderstanding that a broad inventarisation of possible forcing factors automatically leads to more insight in the natural system. More important is the answer to the following question:

Which selective environmental factors are affected by eutrophication and what algal properties are selected for by these factors?

In general, algal blooms have a low species diversity. This indicates that the dominating species are selected by a whole series of environmental factors of which the combination enables only a select number of species to become dominant. If we were able to explain the dominance of a particular species in an eutrophicated area waterquality measures could be taken by changing the identified scope of selecting factors to reduce the abundancy of this particular species. These type of measures are a garantee for the creation of novel algal blooms. In the worst case these novel algal blooms are nuisance. This emphasises the urgent need for fundamental knowledge about the mechanisms involved in phytoplankton selection.

Some factors are more crucial than others. A species has the potential to become dominant when it is able to compete succesfully for the available growth rate limiting nutrient. Therefor it is not surprising that resource competition is generally accepted as the major selective mechanism. In Chapter 3 a clear example will be given were eutrophication induced a shift in the type of growth rate limiting factor. Consequently, the species composition in the particular area changed.

Whether a good competitor actually becomes dominant depends on the balance between its growth rate and its specific loss rates. In Chapter 4 it will be shown that losses due to grazing as selection mechanism increase in importance with eutrophication.

3. Nutrient ratios

3.1. Nutrient ratios and harmfull species

Man-induced eutrophication usually involves an increase in nitrogen (N) and/or phosphorus (P) rather than silicate (Si). The consequent increase in N/Si ratio and/or P/Si ratio favors the blooming of flagellates since the maximum biomass of diatoms remains limited by the availability of silicate (van Bennekom, Gieskes & Tijssen, 1975; Smayda, 1990). There is a large variety of toxic and non-toxic flagellates. In contrast, most diatoms are non-toxic. The type of flagellate that will profit from eutrophication is less easy to predict. In some areas the dominant species is harmfull to other organisms in the ecosystem whereas in other areas unharmfull algal species have become dominant. Illustrative are the eutrophicated waters along the European continental coast. Along the Belgian coast *Phaeocystis* single cell flagellates increased (Lancelot et al., 1987) whereas along the Dutch coast colonial *Phaeocystis* appeared during the nutrient controlled period (Cadée, 1986). In the German Bight especially dinoflagellates have increased (Radach, Berg & Hagmeier, 1990) whereas in 1988 the scandinavian countries were surprised by impressive blooming of the toxic *Chrysochromulina* (Haumann, 1989). Until now, no clear relationship between nutrient ratios and the presence of nuisance blooms has been identified. It is obvious that besides region specific knowledge about nutrient regimes also information on the ecophysiology of the involved algal species is needed to explain the various responses to eutrophication. This brings us to the following question:

What type of ecophysiological properties of a species should be studied in order to explain its natural distribution in relation to eutrophication?

The following section of this chapter describes the increased blooming of *Phaeocystis* in eutrophicated Dutch coastal waters. In this case study a succesfull attempt was made to explain the spatial and temporal distribution of *Phaeocystis* on the basis of its ability to compete for nutrients and the low edibility of the colonies.

3.2. *Phaeocystis* blooms and eutrophication

Phaeocystis blooms are regarded a nuisance because of the intensive foam production during the wane of the bloom making the beaches less attractive for tourists. This haptophycean has a life cycle in which flagellate single cells can transform into a non-motile cell type which after division remain embedded in a muco-polysaccharide matrix. Such colonies (up to 1cm in diameter), comprising of more than 10,000 cells, are less edible to different grazers (Weisse & Scheffel- Möser, 1990) compared to the flagellate stage. Under light limitation, protein synthesis by the colonial cells continues in the dark at the expense of the extracellular muco-polysaccharides synthesized in the light (Lancelot & Mathot, 1985). This feature gives *Phaeocystis* a selective advantage over other phytoplankton in light controlled environments. Especially in coastal waters, where vertical mixing along a turbidity induced light gradient creates a highly fluctuating light regime, *Phaeocystis* will benefit from continued protein synthesis in the dark. Therefore, it is not surprising that spring blooms of *Phaeocystis* have been already reported in coastal waters long before eutrophication took place (Cadée & Hegeman, 1991). Hence, it is not the presence of *Phaeocystis* that is affected by eutrophication, but its maximum biomass. In Dutch coastal waters maximum *Phaeocystis* cell numbers showed a tenfold increase (up to 10^8 cells . L^{-1}; Cadée & Hegeman, 1986) at the end of the spring bloom, emphasizing that during the past decades an increasing amount of N and P remains after the diatom spring bloom becomes Si limited (van Bennekom et al., 1975). As to be expected, also the length of the spring bloom increased (**Fig. 1**).

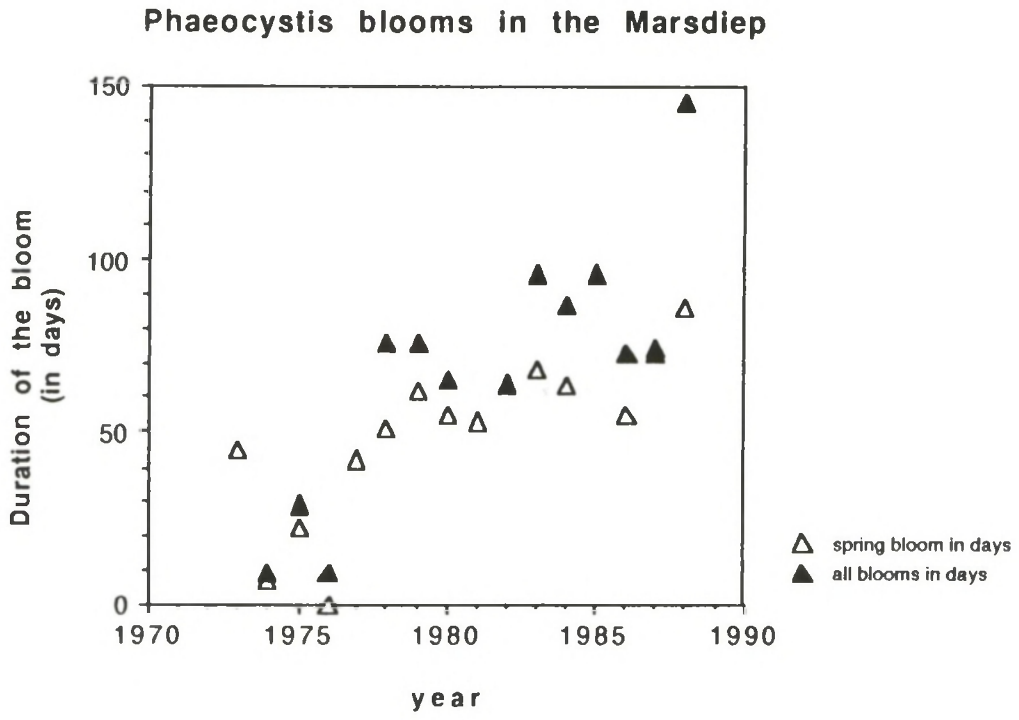

Fig. 1. **Duration of *Phaeocystis* blooms (periods with more than 1000 cells ml^{-1}) during spring (open symbols) and during each year (closed symbols). Data from Cadée, 1990.**

In addition, the yearly total blooming period increased even stronger which illustrates that *Phaeocystis* blooms also started to appear during the nutrient-controlled summer period.

Apparently, eutrophication had created conditions in the dutch coastal waters (Marsdiep area) that are specifically favourable to *Phaeocystis*. The discharge of the river Rhine reaches this area in two different ways (**Fig. 2**). The nutrient discharges from the Rhine (measured at Lobith; Fig. **2(1)**, and measured at Kampen; Fig. **2(2)**) increased gradually from the early sixties.

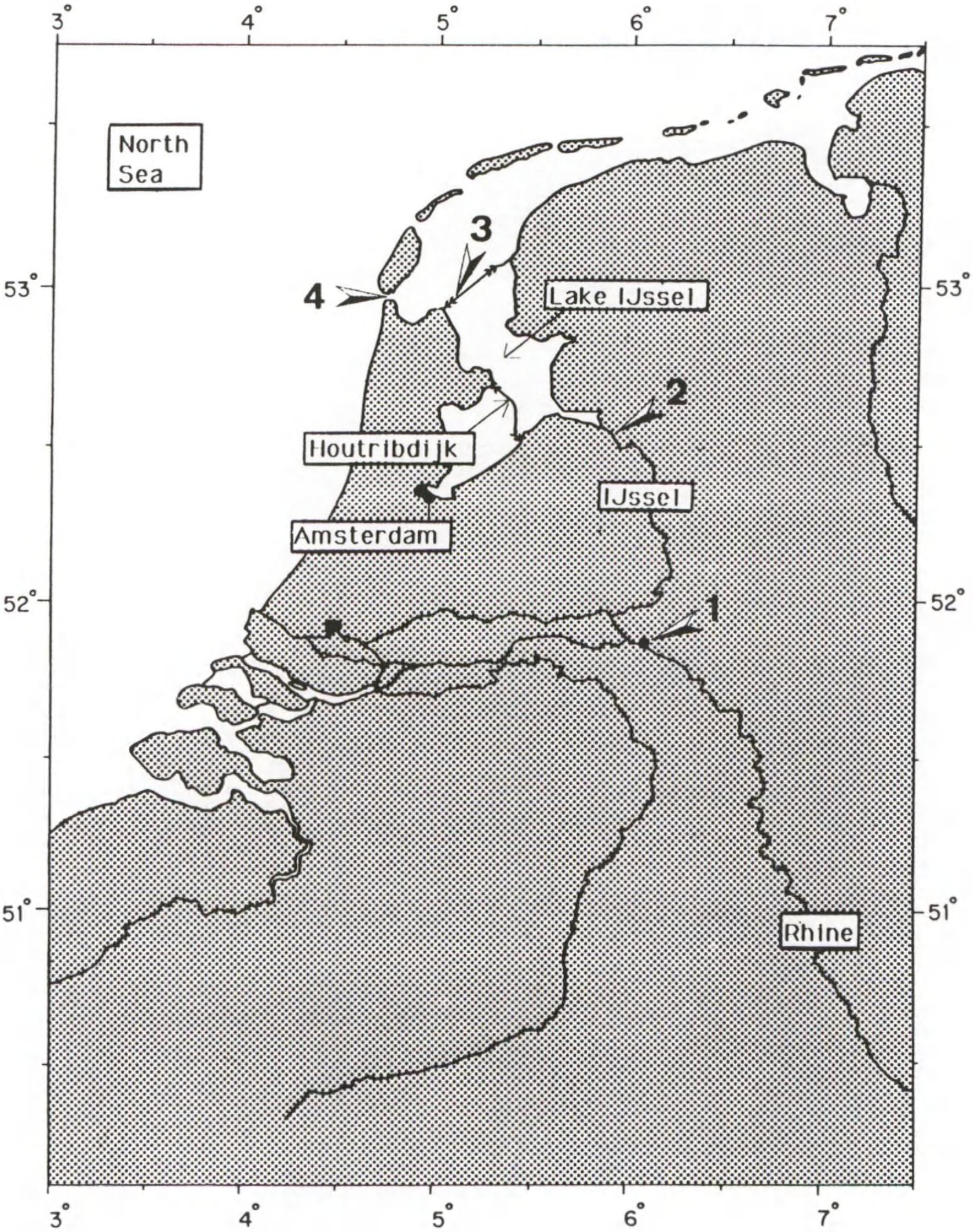

Fig. 2. Geographical locations of Lobith (1), Kampen (2), the sluices of Lake IJssel (3), and the Marsdiep area (4) in the Netherlands.

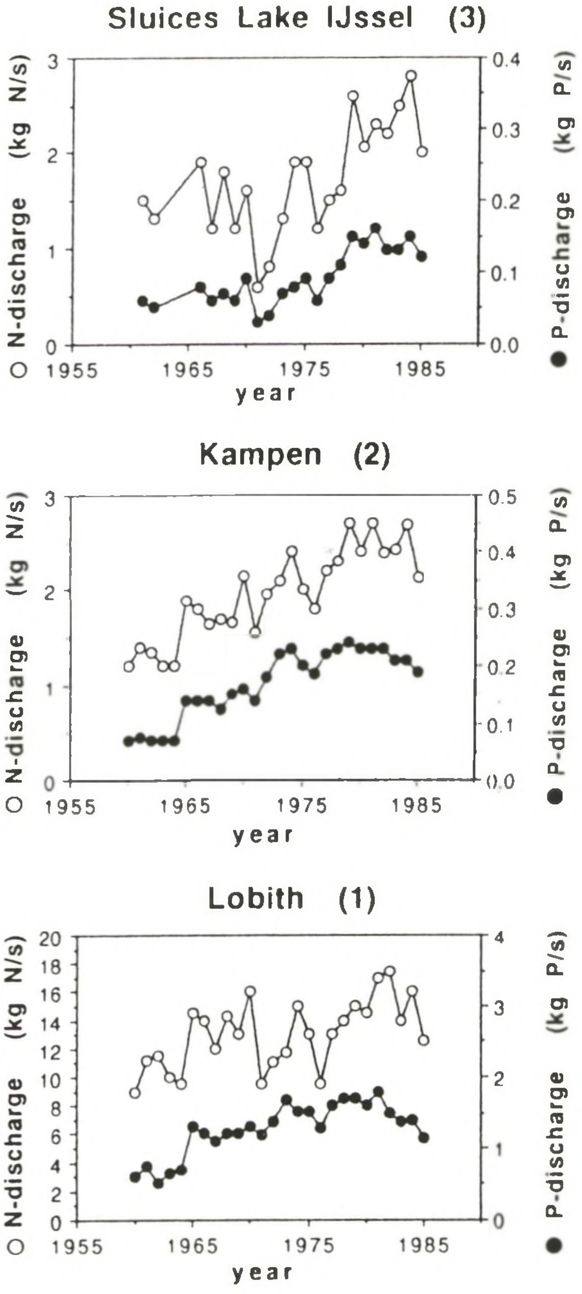

Fig. 2 (continued). Longterm changes in annual averaged nutrient discharges at Lobith (1), Kampen (2), and the sluices of Lake IJssel (3). (Data from RIZA, previously published by v.d. Veer et al., 1989).

About 50% of the freshwater in the Marsdiep originates from Rhine water discharged directly into the North Sea at Hoek van Holland. The other 50% is water from Lake IJssel, the basin into which the river IJssel, a side river of the Rhine, discharges. The southern half of the lake, having sediments rich in clay and organic matter which are regarded as having the highest phosphate binding capacity, was disconnected by the construction of a dam ("Houtribdijk") in 1975. This caused a subsequent decrease in the flushing time of the northern half which in contrast has sandy sediments. Consequently, the P-discharge into the Wadden Sea and the Marsdiep area doubled (**Fig. 2(3)**) and the N-discharge increased by 50% in the following four years (data from **Fig. 2(1,2,3)** were originally published by van der Veer et al., 1989 and based on measurements performed by the RIZA, The Netherlands). Within three years the molar total N/ total P ratio during the nutrient controlled period (summer) shifted from 38 down to 13 (**Fig. 3**) in the Marsdiep area.

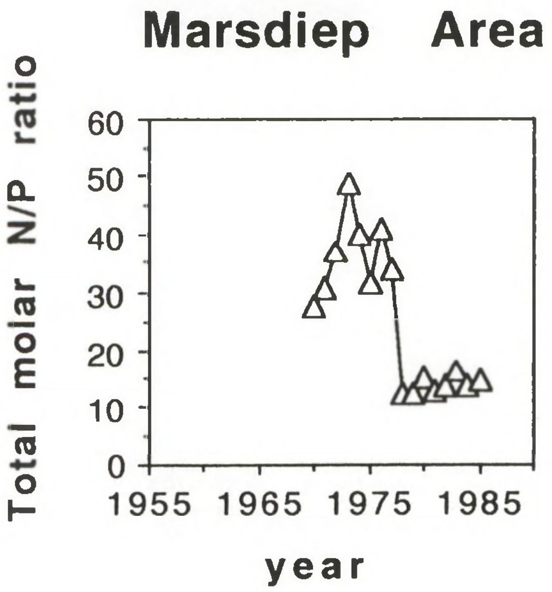

Fig. 3. Longterm changes in N/P ratio in the Marsdiep area calculated for april-september periods.

Regarding the Redfield ratio (N/P=16) as critical, it could be concluded that the presence of N-controll during summer months had increased whereas the probability of P-controlled periods was diminished.

From these results it was concluded that the inland hydraulic development had inconceivably induced eutrophication in a natural system: a doubling of P-input into an originally P-controlled area made the total annual average chlorophyll-a increase from 5 (1972-1976) to 8 ug. L^{-1} (1982-1990; **Fig. 4**).

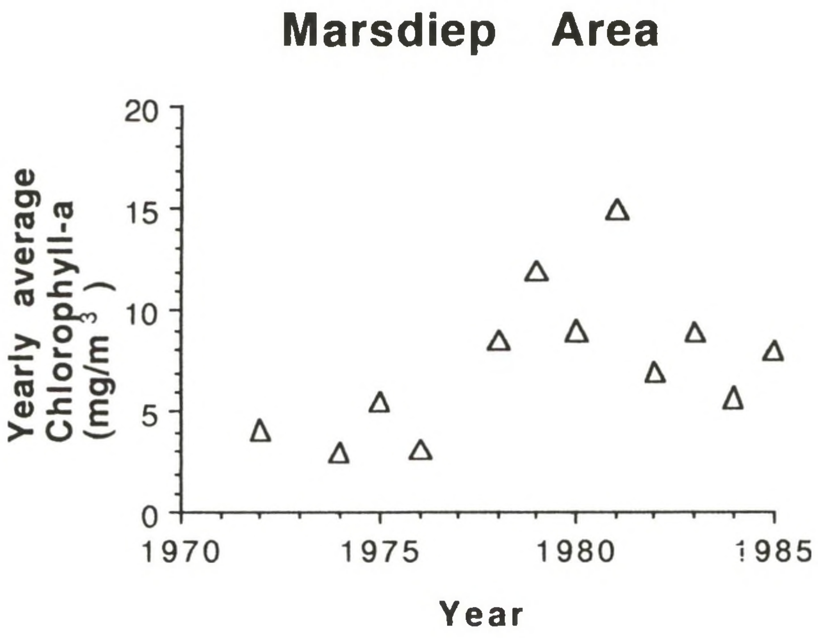

Fig. 4. **Yearly average chlorophyll-a in the Mardiep area. (after Riegman et al., subm.).**

Also, 1978 was the first year in which *Phaeocystis* started to extent for longer periods.

Unfortunately, no specific data on the dominance of *Phaeocystis* (relative to other species) have been published. However analysis of the data on an annual base (**Fig. 5**) shows that *Phaeocystis* became more abundant at summer N/P ratios below 16.

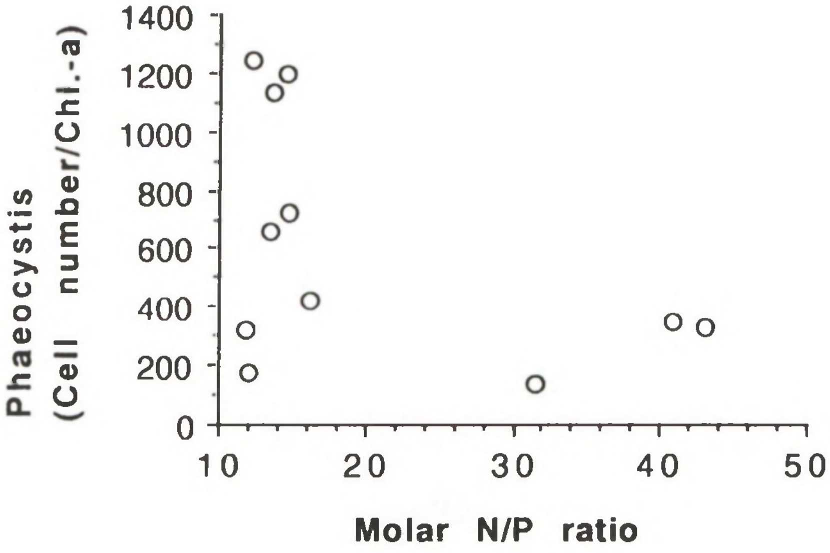

Fig. 5. **Annual average *Phaeocystis* dominance related to N/P ratio during its growth season (april-september) for 1974-1985 (except for 1977 because of insufficient data; after Riegman et al., subm.).**

This correlation led to the working hypothesis that *Phaeocystis* is a poor competitor under P-limitation and a good competitor under a N-limitation. This hypothesis was tested in the laboratory by the performance of competition experiments with ten different algal species (flagellates and diatoms). After one month of competition in continuous cultures the species composition was determined. *Phaeocystis* lost the competition for the growth rate limiting nutrient (P) at N/P ratios above 16 (**Fig. 6**).

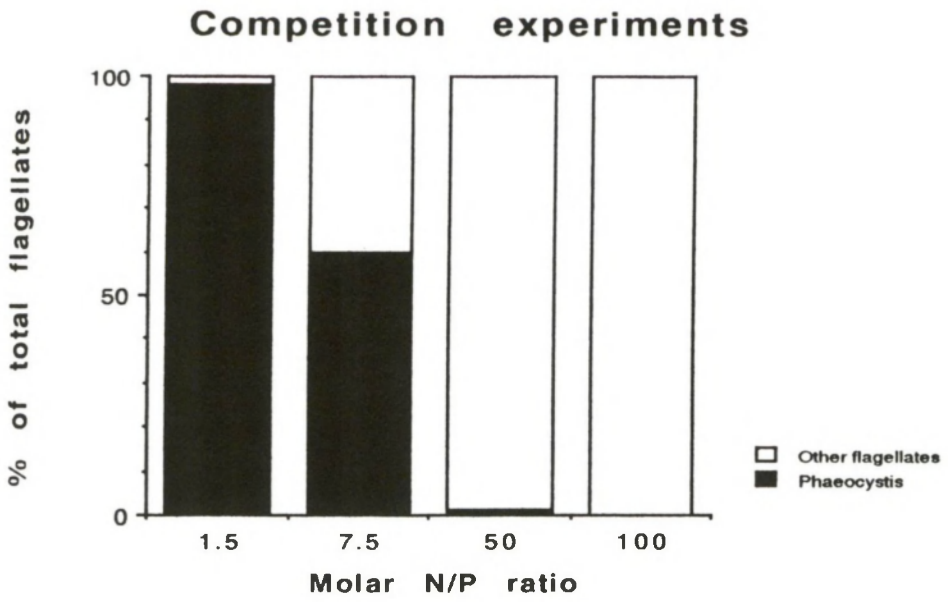

Fig. 6. Abundancy of *Phaeocystis* (in black) relative to other flagellates (white) after four weeks of competition in continuous cultures at various N/P ratios.

Under nitrogen limiting conditions (N/P<16) *Phaeocystis* was able to outcompete the other flagellate species. From these experiments it was conluded that *Phaeocystis* is a poor competitor under a P-limitation. The observation that *Phaeocystis* was able to outcompete other flagellates under a N-limitation does not allow the conclusion that *Phaeocystis* always will dominate in N-controlled environments. Firstly, other species, not involved in the experiment, may be bether competitors. Secondly, the dominance of a species in the natural environment is, apart from its competitive ability, also determined by mortality losses, for example due to grazing. In contrast with the flagellate stage (Weisse & Scheffel-Möser, 1990), colonies escape grazing by microzooplankton and some mesozooplankton species (Verity and Smayda, 1989). This implies that also factors that affect colony formation will determine the natural distribution of *Phaeocystis*.

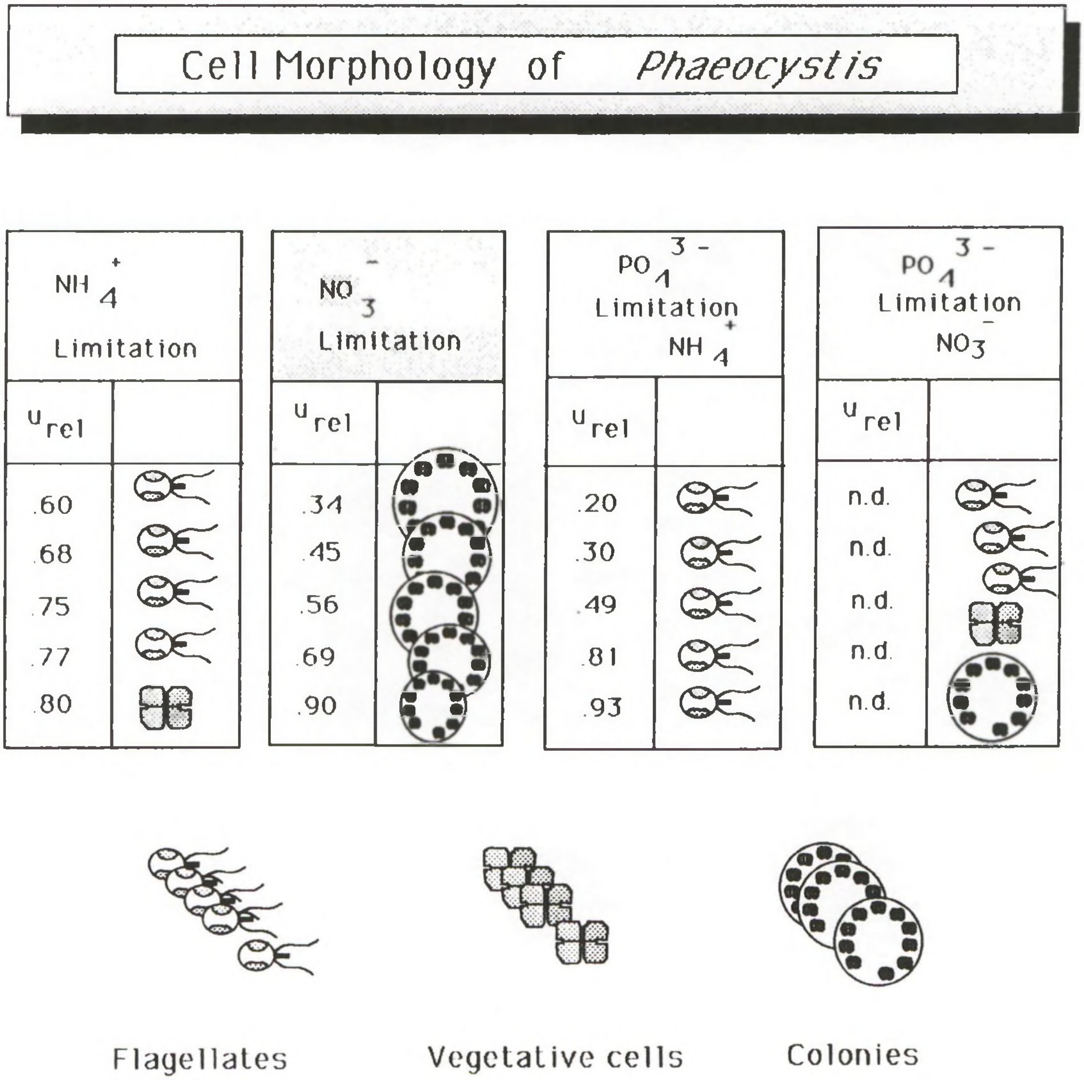

Table 1. ***Phaeocystis*** **morphology under various nutrient controlled steady state conditions. Phosphate limitation was tested with either ammonium or nitrate as sole nitrogen source. Relative growth rate (u_{rel}) was calculated as the ratio between the actual specific growth rate and the maximum specific growth rate (u_{max}= .8 d^{-1}).**

Colony formation was studied in discontinuously diluted axenic batch cultures under nutrient- controlled conditions. Under N-limitation colonies were only present when nitrate was the sole nitrogen source (**Table 1**).

Under a P-limitation no colonies were formed except at near maximum growth rates with again nitrate as sole N-source. In addition, *Phaeocystis* formed colonies when nutrients were not limiting (data not shown), i.e. at its maximum growth rate or under light limiting conditions with nitrate and/or ammonium as N-source.

Summer colony forming *Phaeocystis* blooms in the Marsdiep area were absent before 1978 (Cadée, 1986) because *Phaeocystis* is a poor competitor under P-limitation. After 1977 N-controll and high nitrate inputs relative to ammonium, favoured *Phaeocystis* dominance. Between 1972 and 1986 nitrate discharge from the Rhine increased from 5 to 10 kg N s^{-1} whereas the ammonium discharge decreased from 4 to 1 kg N s^{-1} (v.d. Veer et al., 1989). A similar trend was observed in the river IJssel (**Fig. 7**; measured at Kampen; after v.d. Veer et al.,1989).

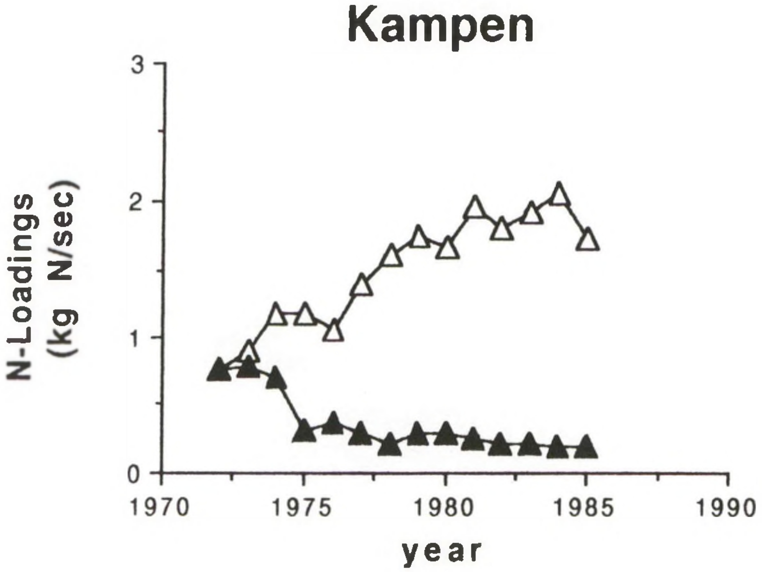

Fig. 7. **Annual river IJssel discharge of ammonium (closed symbols) and nitrate (open symbols) during the period 1972-1985. After v.d. Veer et al., 1989.**

These shifts may be the result of the increased number of water treatment installations along the Rhine. In addition, Admiraal et al. (1991) suggest that lower concentrations of toxic substances in the Rhine may have favoured microbial activity and thus the rate of nitrification. Both explanations relate the shift from ammonium towards nitrate to increasing water quality improvement efforts. In combination with the hydraulic engineering in Lake IJssel inland water quality measures have created conditions for increased nuisance *Phaeocystis* blooms in the Dutch coastal waters.

These results strongly emphasize the importance of **integrated waterquality management**, that is with emphasis **on both freshwater and marine ecosystems** within the same catchment and discharge area.

The conclusions on competitive ability and colony formation enables an additional evaluation of the temporal and spatial distribution of *Phaeocystis* in the European continental coastal waters (for a summary, see **Fig. 8**). Along the Belgian coast *Phaeocystis* is only present in the flagellate stage during the summer (Lancelot, pers. commun.). The absence of colonies in this N-controlled environment (Lancelot et. al., 1986) can be explained by the low availability of nitrate. This particular area is mainly influenced by the Scheldt estuary where denitrification acts as a sink for nitrate (Billen et. al., 1985) leaving ammonium transported to the sea.

During May-august the N/P ratio (>16) and phosphate concentrations (<.25 uM) indicate P as the controlling factor (Radach et. al., 1990) at Helgoland Reede (outher part of the German Bight) (**Fig. 8**). Colony forming *Phaeocystis* blooms are absent because under a P-limitation no colonies are formed and the flagellate stage has shown to be a poor competitor. In the central North Sea ammonium is regarded to be the major nitrogen source during the summer which explains the rarity of colony forming blooms during the summer months in this area.

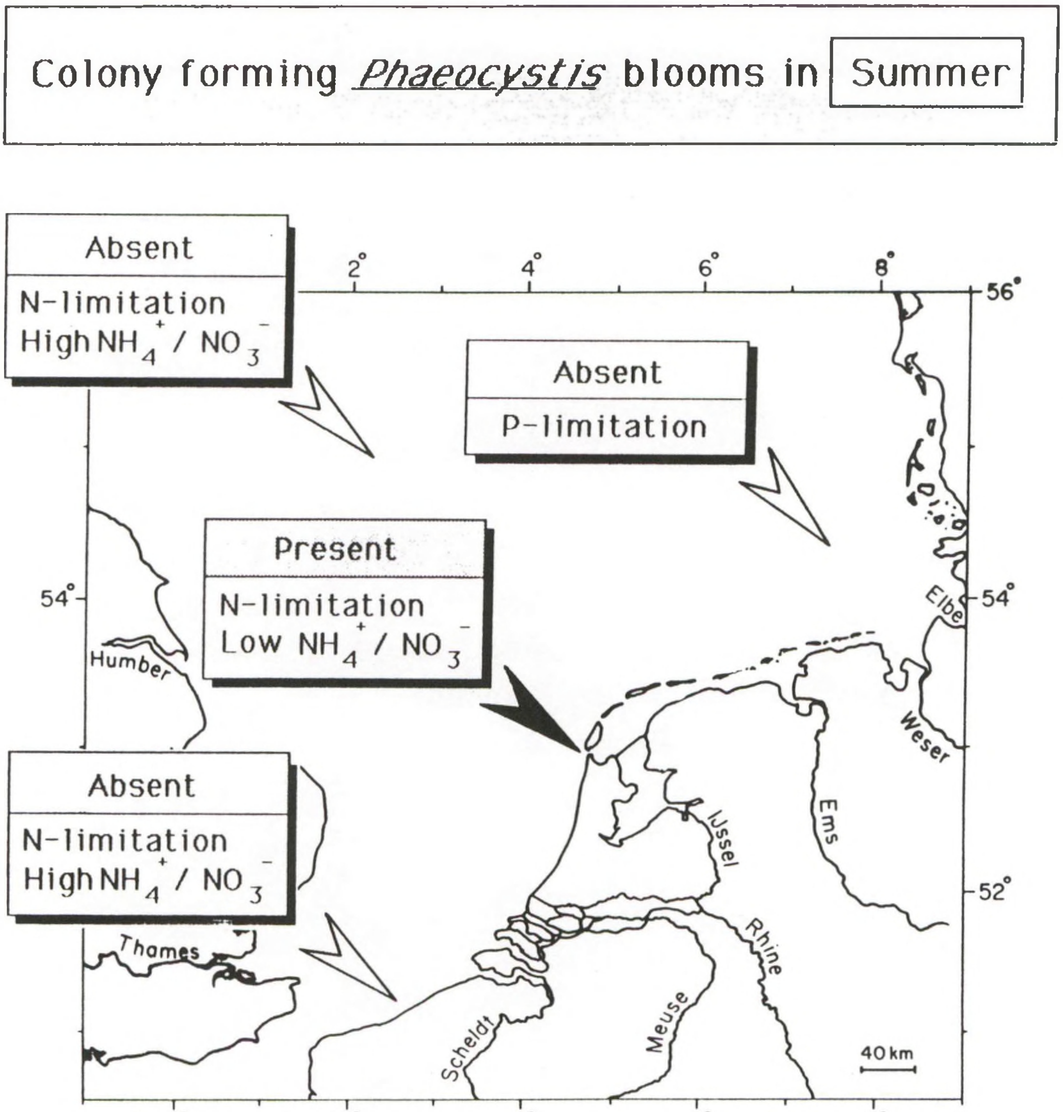

Fig. 8. Expected selection mechanisms that determine the temporal and spatial distribution of *Phaeocystis* in European continental coastal waters.

The presented approach enabled the identification of the mechanisms underlying the distribution of summer *Phaeocystis* blooms in different eutrophicated regions along the European continental coast. With respect to the Marsdiep area, *Phaeocystis* blooming is expected to decrease if the N+P discharge from Lake IJssel is manipulated in such a way that P returns as the controlling factor. At present it is not clear which species will become dominant when *Phaeocystis* is eliminated by such a manipulation. If the major selecting factor is selective grazing by zooplankton it is to be expected that poorly edible dinoflagellates will take over. In some cases these blooms are even more harmfull than *Phaeocystis* blooms. At present efforts are made to construct an eutrophication model for the Dutch coastal area in order to kwantify the effects of different discharge scenarios on summer *Phaeocystis* blooms in the Marsdiep area.

3.3. Concluding remarks on eutrophication and nutrient ratios

The major conclusion of the presented results is that novel nuisance algal blooms can be the result of major shifts in N/P and NH_4^+/NO_3^- ratios rather than a general N+P enrichment effect. This implies that measures taken to improve the waterquality of the North Sea should be evaluated in advance on their region specific effects on algal composition and foodweb structure and functioning. A non-specific measure like a 50% reduction of the present discharge of all nutrients is expected to give equivocal results in that in some areas these measures may even lead to the appearance of new nuisance algal blooms.

4. Selective grazing

4.1. Conceptual models

Relative simple conceptual models are being used to study the effects of nutrient enrichment on food webs (for example: Smith, 1969; Thingstad & Sakshaug, 1990). Differences in conclusions derived from these idealized models, are either due to differences in the incorporated basic principles or to more or less subjective choices which are made implicitely during the ecosystem compartimentalisation. Nevertheless, concepts of this kind have inspired a large body of investigations in oceanography and limnology. Illustrative of this are for example the series of food chain analyses (Riley, 1963; Smith, 1969; Lane & Levins, 1977) that have encouraged biomanipulation of various lakes in order to reduce phytoplankton biomass by the enhancement of herbivoruous zooplankton via stimulated top-down control. Equivocal results of biomanipulation programmes (Sterner, 1989) indicate that at least one essential basic principle seems to be missing in the previous models.

Essentially, conceptual models are not constructed to simulate natural systems but to analyse the impact of certain biological principles on the structure and functioning of a simplified, but still complex, biological system. In the present study, a basic pelagic foodweb nutrient recycling model was constructed to study the determinable impact of selective grazing on communities structure and functioning of the foodweb.

The model was equipped with three principles and/or mechanisms.

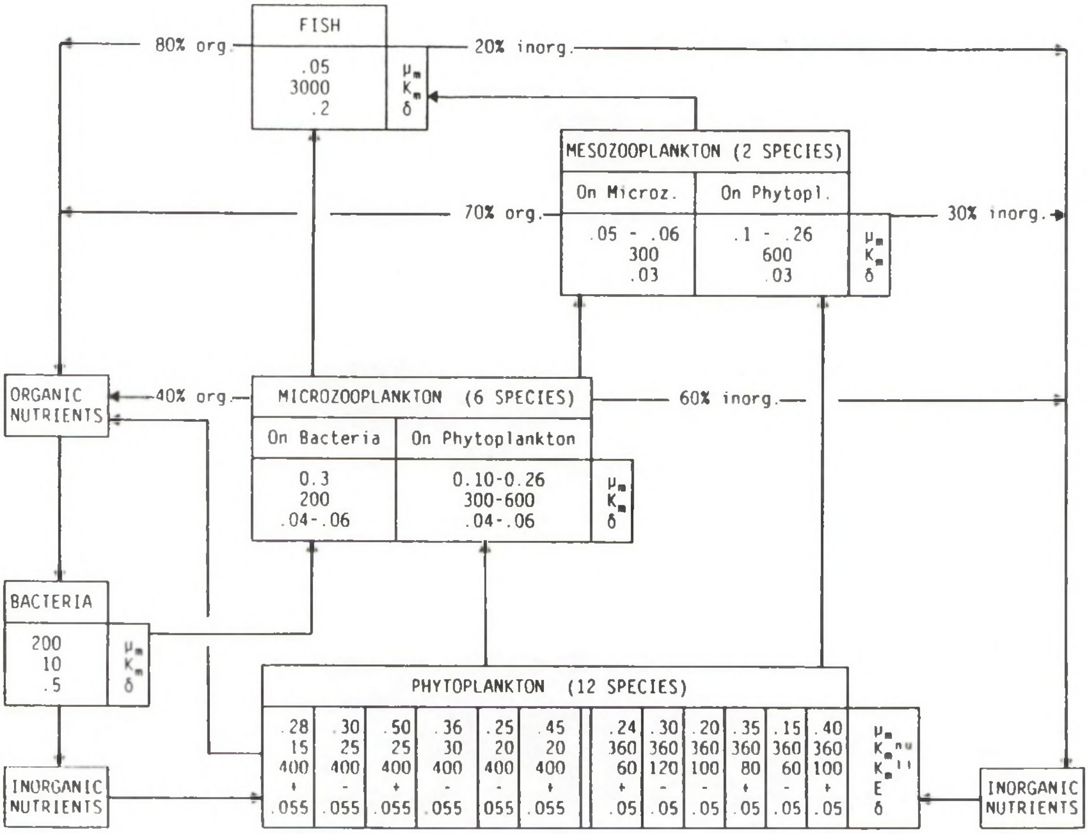

Fig. 9. Nutrient flow diagram of the pelagic foodweb model. Specific maximum growth rate (u_m) and mortality rate (∂) in units t^{-1}; Half saturation constant K_m in dimensionless units. E stands for edibility (+, predator has high affinity for the particular phytoplankton species; -, predator has low affinity). For the sake of clarity, the inorganic nutrients pool is twice presented in this diagram.

4.2. The selective grazing model

Firstly, I used multiple species per trophic level (algae 12, microzooplankton 6, mesozooplankton 2; see **Fig.9**) which made these trophic levels variable in functioning, depending on species composition. The toppredator (fish) and bacteria consisted of single species.

Secondly, the mechanism of selective grazing was implemented, i.e. each consumer was assumed to exert a preference among its prey, whereever in the foodweb.

Thirdly, species were defined according to the following superiority principle: a single species can not be superior to all the others in more than one property, otherwise evolution would have generated new species.

(See diagram **Fig. 9**).

The model describtion was based on the mineral nutrient sequestered by each population in a foodweb. The first subgroup of phytoplankton (6 species) with a high affinity for nutrients and a low affinity for light is preferably eaten by microzooplankton. The second subgroup (of six species) has a lower affinity for nutrients and a higher affinity for light and is preferably eaten by mesozooplankton. In fact these two groups represent "large" and "small" phytoplankton. The general conclusion of various studies (see Raven, 1988) seems to be that small species have a lower half saturation constant for nutrients compared to larger species. If two species have the same maximum growth rate (u_{max}), the smaller will dominate under nutrient limiting conditions. This principle is extended in the model by using lower halfsaturation constants for light for larger phytoplankton. Microzooplankton graze on bacteria, small phytoplankton species and are grazed by mesozooplankton. Fish was given a low growth efficiency to prevent the occurance of large fish biomass during a simulation period. Within each functional group species vary in edibility which is reflected in the half saturation constant for uptake of their predator. Organic nutrients are mineralised by bacteria. Growth rate of a population is assumed to be equivalent to nutrient/prey uptake in a non-linear, Michaelis-Menten type of equation and comparable to Monod (Monod, 1942). More detailed information on the model will be published elsewhere (Riegman, submitted).

4.3. Modelling results

To study the intrinsic behaviour of this system the model was run as a closed system and numerical analysis were performed at various light irradiances and total nutrient levels as external forcing functions. The results were analysed for system behaviour with respect to stability, foodweb structure and species selection. The presented results reflect the average biomass for each functional group, calculated between time (t)=100 and 150. One time step is approximately equivalent to .5 day. The results are discussed in relation to the total amount of light (I_0) and nutrients (N_0). These are referred to as Absolute Boundary Conditions (ABCs) because they determine the maximum biomass that potentially can be formed by the community. Although natural communities usually develop in an open system, I_0 can be compared with the daily photosynthetically active radiation (PAR) divided by the depth of the watermass in which a community develops. According to Liebig`s Law of the minimum, the conceptual base of N_0 is the total amount of that particular nutrient per litre that persists the lowest maximum community biomass attainable. In practice, this will be nitrogen for marine ecosystems and phosphate for fresh water systems (Hecky & Kilham, 1988).

The equilibrium structure of the 21 element food web is shown in **Fig. 10**. The total biomass of the foodweb increased in a somewhat irregular way with the ABCs (**Fig. 10a**). About 5% of the total biomass constituted of bacteria (data not shown). Their biomass was relatively independent of ABCs but depended on the affinity of their predators. Due to their high mortality rate fish never exceeded 3% of the total biomass. At low ABCs, the foodweb mainly consisted of phytoplankton (**Fig. 10b**). Its biomass was not sufficiently high to maintain grazers above their treshold level. At moderate L_0 (90-200) mesozooplankton (feeding herbivore) appeared (**Fig. 10c**), whereas at moderate N_0 (200-1000) micro-zooplankton (feeding on small phytoplankton and bacteria) dominated the grazing population (**Fig. 10d**). This separate occurance is of course due to the basic assumption that small algae have a higher affinity for nutrients whereas large algae (preferably eaten by mesozooplankton) have a higher affinity for light. At higher N_0 levels (1000-5000) the third trophic level, mesozooplankton (feeding carnivorously on microzooplankton) was established. At high ABCs, the absolute grazer concentrations no longer increased whereas the phytoplankton biomass did, resulting in a food web structure that was highly dominated by phytoplankton. Their growth rate was related to the relative abundance of zooplankton (data not shown).

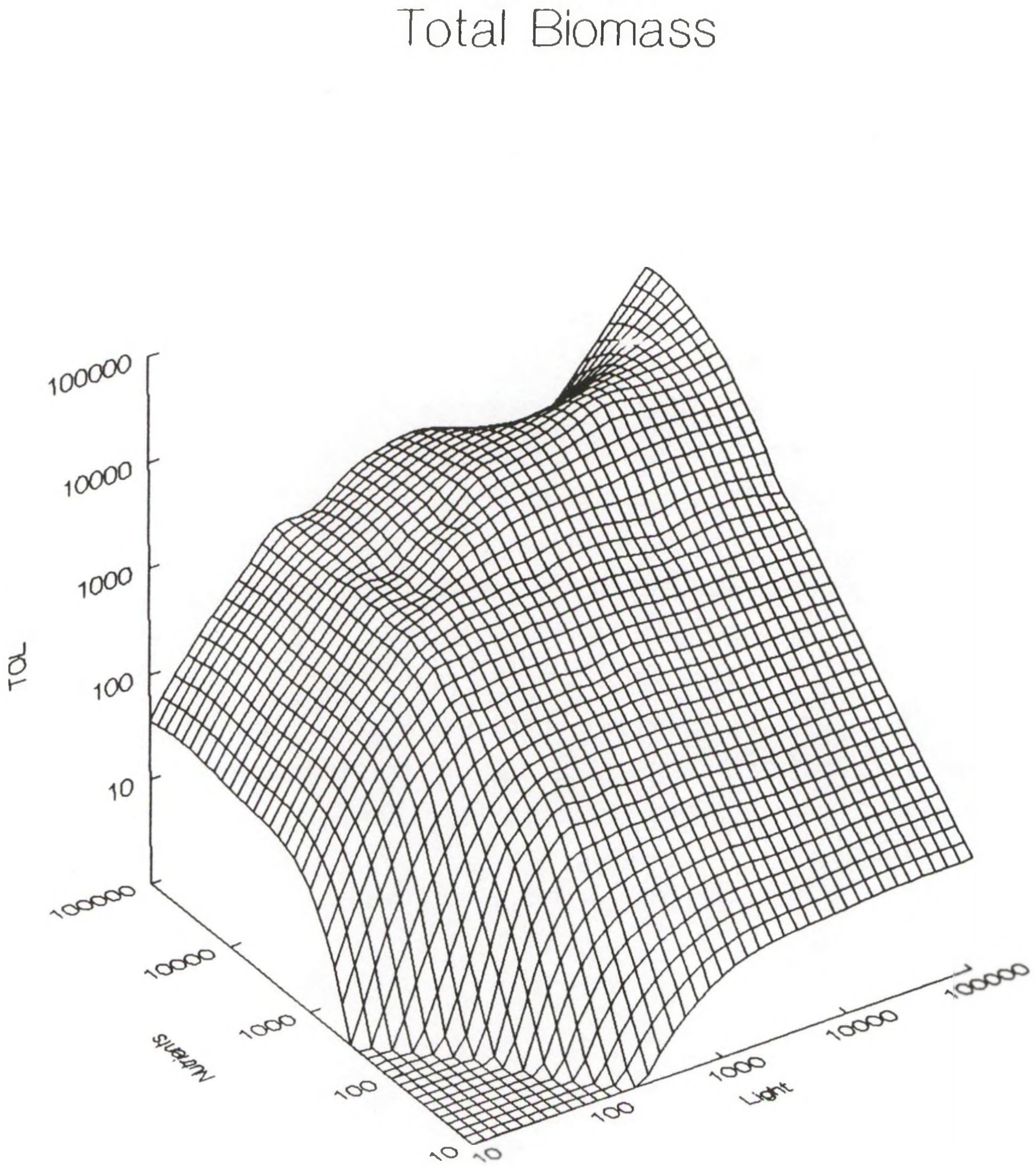

Fig. 10. Steady state analyses of community structure in relation to absolute boundary conditions, that is the total amount of light and nutrients available for the system.

10A: Total biomass of the community in dimensionless nutrient equivalents.

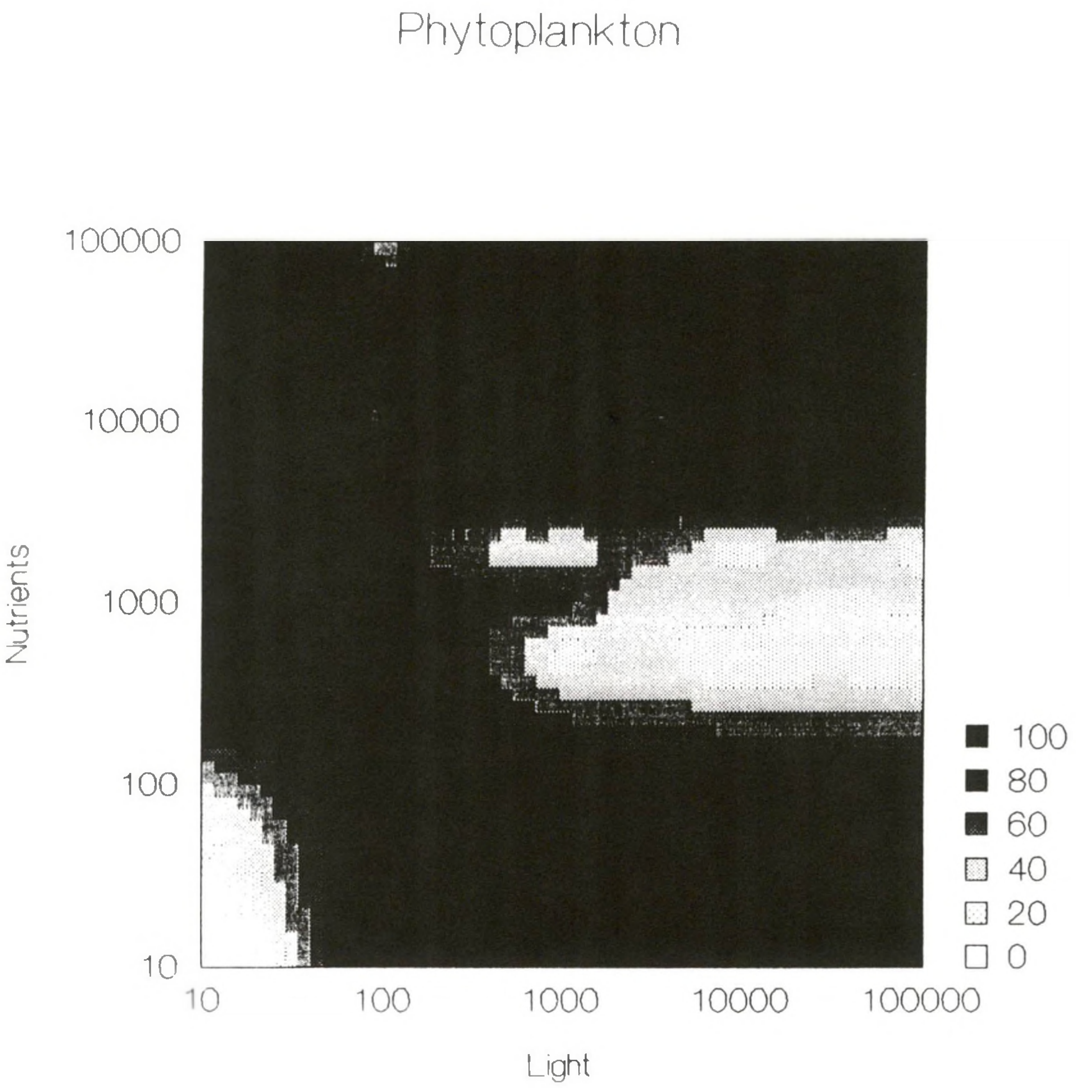

Fig. 10. **(continued) Steady state analyses of community structure in relation to absolute boundary conditions, that is the total amount of light and nutrients available for the system.**

10b. Phytoplankton biomass, relative to total biomass of all trophic levels.

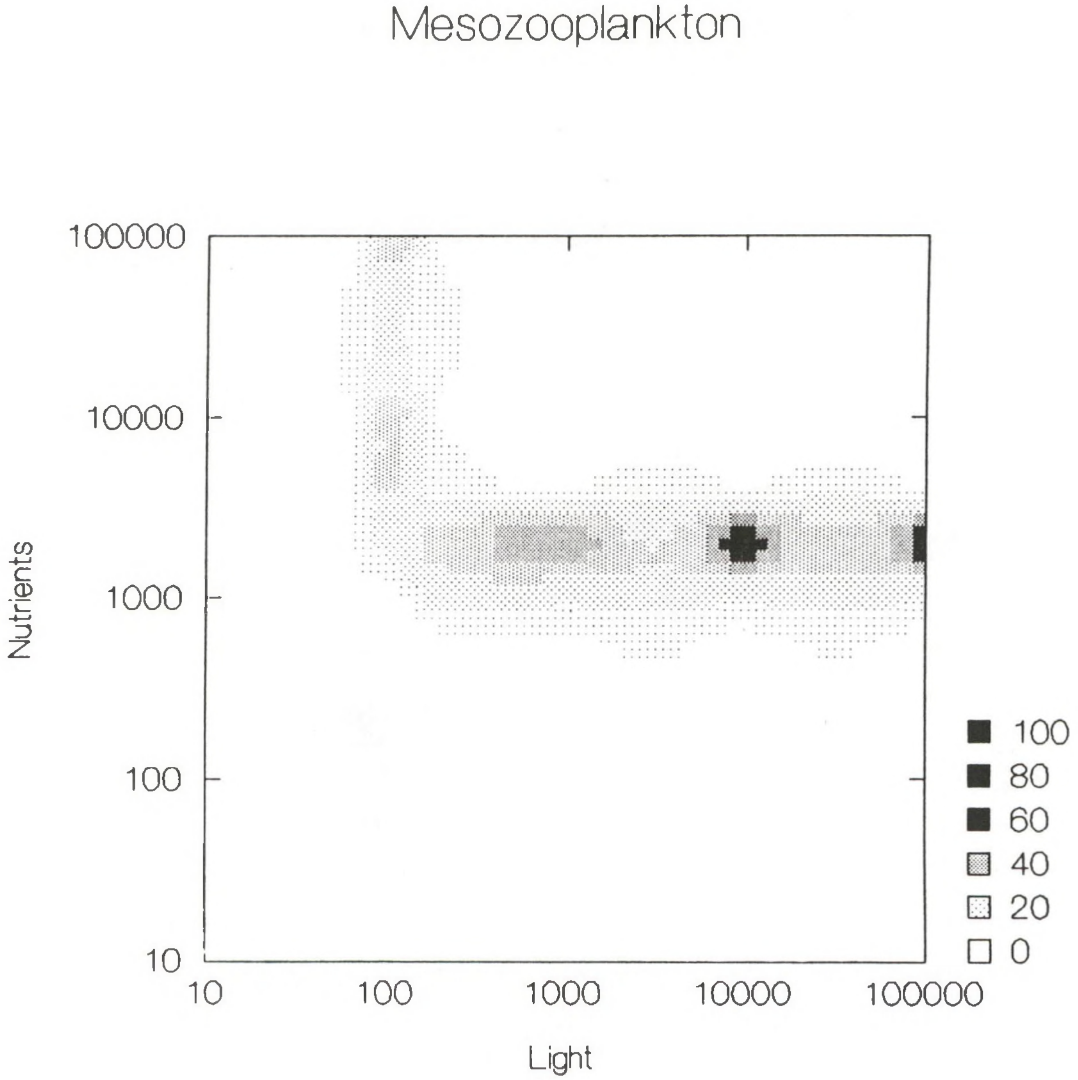

Fig. 10. (continued) Steady state analyses of community structure in relation to absolute boundary conditions, that is the total amount of light and nutrients available for the system.

10c. Mesozooplankton biomass, relative to total biomass of all trophic levels.

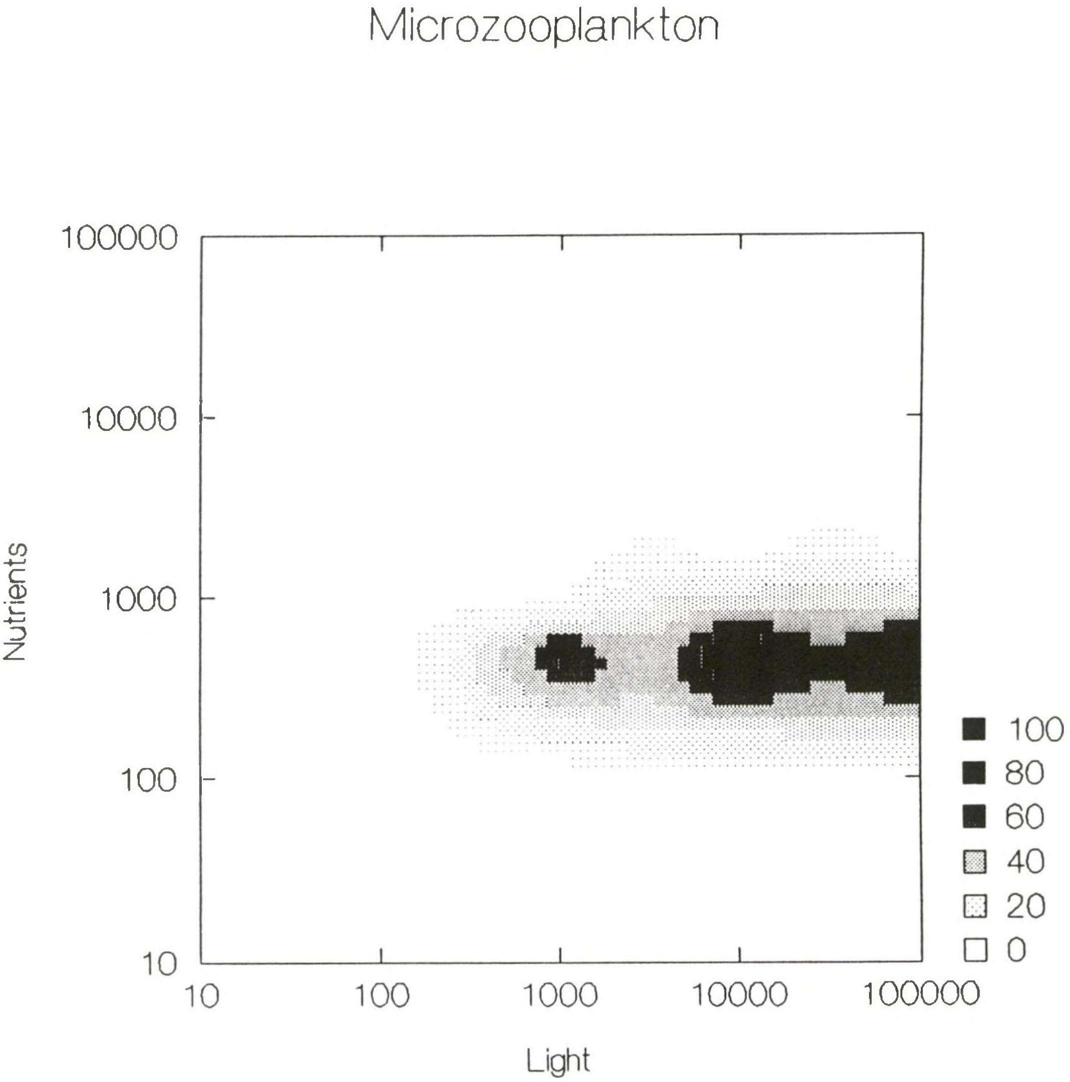

Fig. 10. (continued) Steady state analyses of community structure in relation to absolute boundary conditions, that is the total amount of light and nutrients available for the system.

10d. Microzooplankton biomass, relative to total biomass of all trophic levels.

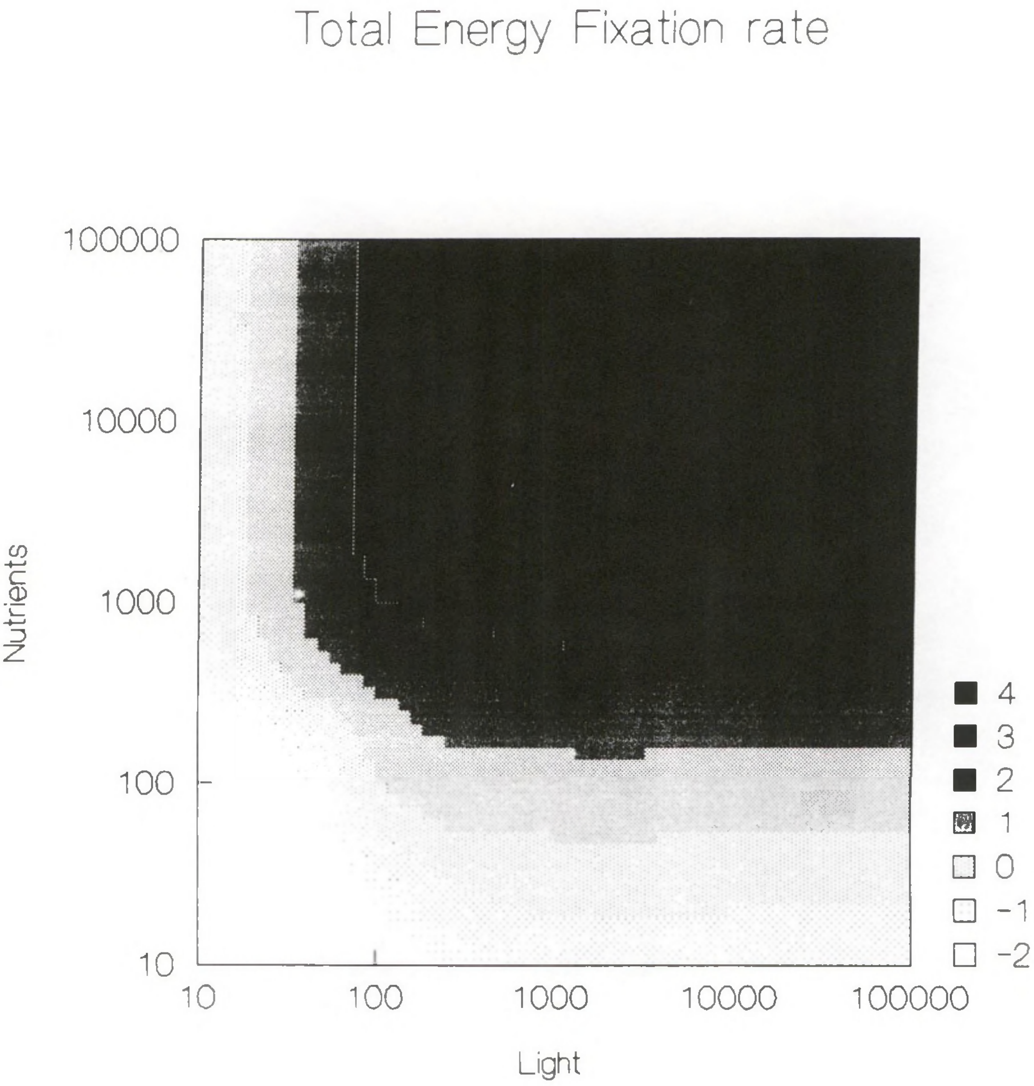

Fig. 11A. Average energy fixation rate of the community. Dimensionless units on a log scale in nutrient equivalents per unit of time.

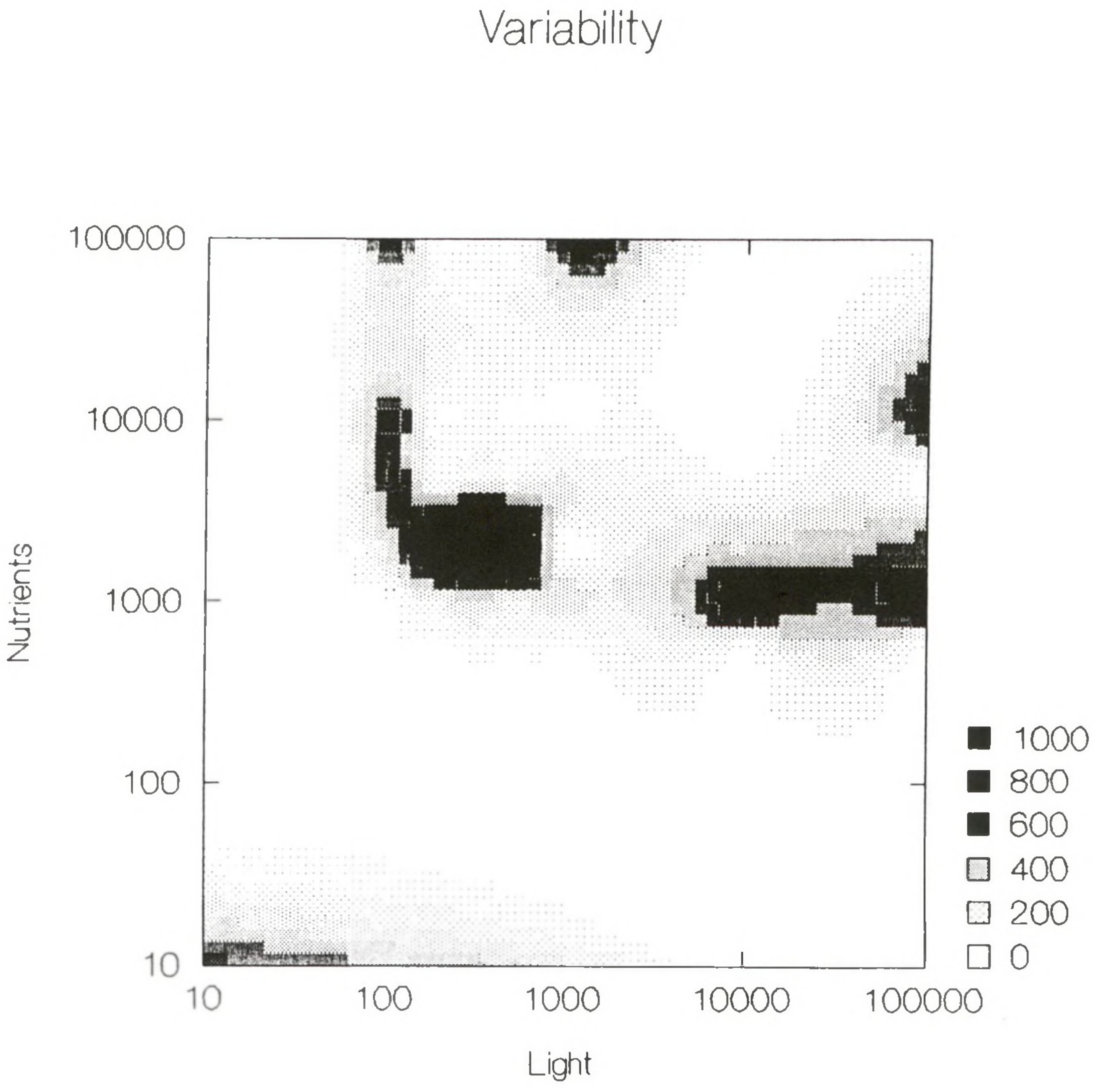

Fig. 11B. **Variability of phytoplankton biomass during t=100-150 Calculated as the difference between maximum minus minimum biomass as a percentage of the average biomass.**

The different types of foodweb structure were not recognized in the foodweb functioning. The total average energy fixation rate (the product of phytoplankton biomass and growth rate) increased gradually with L_0 and N_0 (**Fig. 11a**). It is remarkable that neither the presence or absence of fluctuations in phytoplankton biomass (**Fig. 11b**) nor the differences in foodweb structure (**Fig. 10**) affect the average energy fixation rate of the system. The stability of the equilibria is reflected in the variations in phytoplankton biomass (**Fig. 11b**). At the regions with a high abundance of zooplankton (relative to the total community biomass) and coincidently high specific growth rate of the phytoplankton, instability was enhanced. Extending the duration of the runs resulted in an increase of the stability (data not shown).

At the transition zone, between light- and nutrient limited growth, three phytoplankton species dominated. In the zooplankton dominated regions (N_0=200-5000 and L_0>100; L_0=90-200 and N_0>100) only one species dominated. On the basis of species distribution at different ABCs the major selective factors for the phytoplankton could be identified (**Fig.12**). In watermasses with a low light energetic input, species are selected for their affinity for light. In a comparable way, at low N_0 algae are selected for their affinity for nutrients. At moderate ABCs the establishment of herbivores becomes possible, resulting in an additional selection towards algal species with a high maximum growth rate. At high ABCs top-down control dominated the entire foodweb. Under these conditions phytoplankton species are selected completely for being poorly edible to the herbivores present.

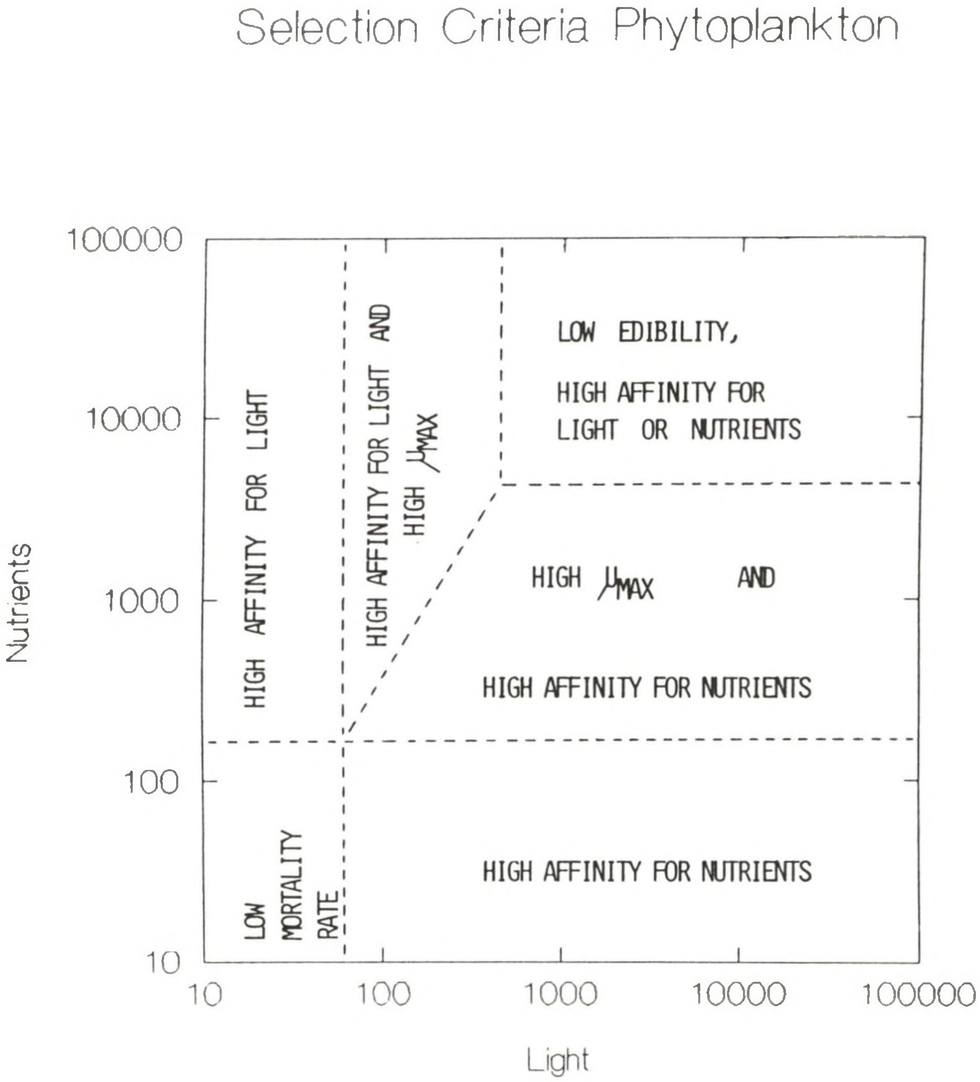

Fig. 12. The structure of the phytoplankton community in terms of species characteristics as it was established at various ABC's.

Eutrophication of a closed system with a linear food chain will increase either phytoplankton biomass or growth rate, depending on the number of trophic levels in the chain (Thingstad & Sakshaug, 1990). A closed system with a multi-species, non-linear foodweb behaves differently **(Fig. 13)**.

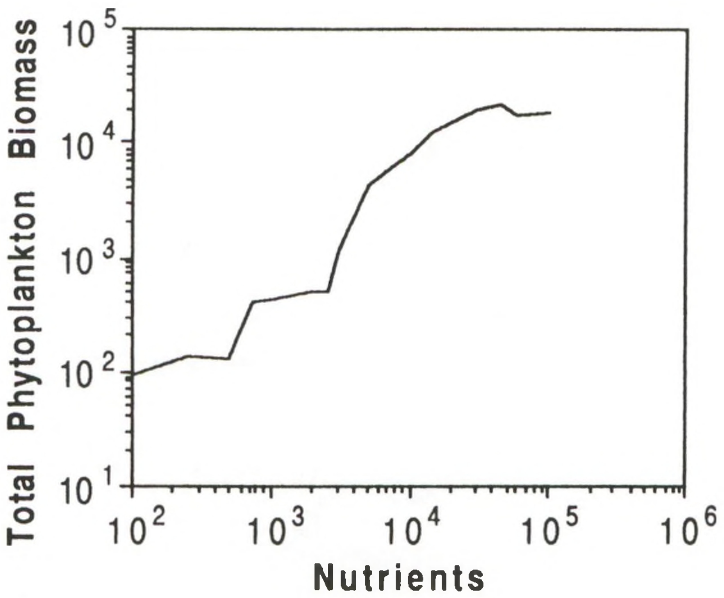

Fig. 13. **Impact of eutrophication (calculated at I_0=100000) on the average phytoplankton biomass. Dimensionless units in nutrient equivalents.**

The irregular increase of phytoplankton biomass with eutrophication did not correlate with the number of trophic levels. It is clear that if there is more than one food chain present, the transition point between the enhancement of biomass or productivity due to eutrophication, will become less visible when their position in the eutrophication scale differs for each food chain. In fact, species succession during eutrophication will make the existence of discrete transition points with respect to biomass increase of a trophic level very unlikely.

4.4. Eutrophication and selective grazing

The model generated three different types of communities which were fluently connected with each other. In severe oligotrophic waters, the highly stable phytoplankton community will be dominated by specialists, in competition for the limiting nutrient. In mesotrophic and moderate eutrophic waters, intrinsic fluctuations will occur due to predator-prey interactions and phytoplankton is mainly selected for its numerical reactivity, i.e. maximum specific growth rate. Severe eutrophic and hypertrophic waters will harbor a more stable community with low turn-over rates and which is mainly dominated by poorly edible phytoplankton. This type of communities is observed in both fresh water and marine ecosystems. Red tides (e.g. Smayda, 1990) and hypertrophic shallow lakes (e.g. Sommer et al.,1986) are dominated by populations of dinoflagellates and cyanobacteria respectively. Ecological studies show that these species have a low maximum specific growth rate (van Liere & Mur, 1979; Falkowski et al., 1985; Langdon, 1987) and are relative to other species poorly eaten by zooplankton (Nizan et al., 1986; Huntley et al., 1987; Lampert, 1987). In fact, *Phaeocystis* colonies fall in the same category of poorly edible species.

In marine ecosystems an increasing number of toxic algal blooms have been reported (Smayda, 1990). Usually these toxic algal blooms seem to occur in watermasses with high nutrient and high irradiance levels. Several authors (e.g. Carlsson et al., 1990; Smayda, 1990) have questioned the possible role of eutrophication and speculate about the mechanisms involved. The present results indicate that selective grazing by zooplankton populations, being enhanced indirectly by eutrophication, will be the driving force in cases where the toxicity of a species makes it poorly edible.

(Although it is beyond the scope of this study, it is interesting to notice that shifts in communities will occur with temperature when the different trophic levels differ in their temperature optimum. In moderate climate zones zooplankton reaches its highest abundance during the summer because of its higher temperature optimum in comparison to phytoplankton. This means that the zooplankton zones move towards the axis in **fig. 10** at increasing temperatures and vice versa at decreasing temperatures. An increase in water temperature as a consequence of the greenhouse effect may lead to the presence of dense and more stable algal biomasses in systems with a lower degree of eutrophication then they occur nowadays. Especially with grazing as selective factor toxic algal blooms will become more abundant. In oligotrophic oceans more carbon will be stored in zooplankton rather than phytoplankton. This mechanism affects the light attenuation of the photic zone and, as a consequence, will also affect the vertical heat distribution in the various oceans. The suggestion to fertilize oceans with iron (Martin et al., 1990) in order to decrease CO_2 levels in the atmosphere should be motivated by a conceptual model comprehending all trophic levels in the ecosystem before one even starts a discussion about the technical aspects).

One of the arguments to regard eutrophication as a positive development is the expected increase in productivity of the higher trophic levels. This assumption is based on the following view on the functioning of aquatic ecosystems: more nutrients will give more algae, more zooplankton and consequently more fish, shrimps, mussels, id.. In highly eutrophicated areas this "principle" clearly is not expected to hold true. According to the model, a reduction of the nutrient load will not necessarely lead to a reduction in fish production since the reduction in phytoplankton biomass will be compensated by the increase in its edibility for zooplankton. Filter feeders like the mussel are more directly dependent on algal biomass and will be affected. In less eutrophicated areas, which are dominated by rapidly growing phytoplankton species, a reduction in nutrients is likely to reduce fish productivity. From these arguments its becomes clear that the impact of waterquality measures on the productivity of a systems will vary for different areas. Also the effects will vary for the different types of economically interesting species. However, conclusions on productivity are still highly speculative. The present model has a low degree of reality because of the absence of aspects like reactivity of the organisms to changing environmental conditions, import and export as a consequence of mixing or migration, and the exclusive dependence of diatoms on silicate. At the moment, attempts are made to validate the model using field data on foodweb structure and ABCs.

4.5. Concluding remarks on selective grazing

According to the present concept, increasing eutrophication will replace phytoplankton specialists in competition by generalists and finally by poorly edible primary producers. The underlying assumption is that species that invest part of their energy in being poorly edible can not use the same energy to optimize their growth response. Therefore poorly edible species are poor competitors.

The present multi-species model behaves different from (ecosystem) models inwhich trophic levels consist of only one species. This observation questions the predictive value of those ecosystem models inwhich trophic levels have no variable set of properties (single species approach).

5. Summary

In this report it is shown that **novel algal blooms in eutrophicated areas can be the result of major shifts in N/P or ammonium/nitrate ratios rather than a general nutrient enrichment.** This statement is based on the results of a study on the impact of eutrophication on *phaeocystis* blooms in dutch coastal waters. Inland hydraulic engineering (the "Houtribdijk" in lake IJssel) caused a shift from P-controll (before 1975-77) towards N-controll in the Marsdiep area (Dutch coastal waters). After this shift the colonial flagellate *Phaeocystis sp.* became more abundant and started to bloom also during the nutrient controlled period (late spring- autumn). Competition experiments showed that *Phaeocystis* is indeed a poor competitor under a P-limitation and a good competitor under a N-limitation. Colony formation was absent under P- and ammonium- limitation. Colonies were formed during N-limited growth with nitrate as nitrogen source which indicates that colony forming *Phaeocystis* blooms are (besides light controlled environments) to be expected in N-controlled environments with a high new production relative to regenerative production.

As a consequence of increased waste water treatment along the Rhine a significant shift from ammonium towards nitrate occurred during the past ten years. **These efforts to improve the waterquality of the Rhine have favoured the blooming of *Phaeocystis* in dutch coastal waters.** Since the major mechanisms are now identified, it would be possible to reduce the *Phaeocystis* summer blooming but at present it is unclear which species will take over.

Comparison of the distribution of *Phaeocystis* along various eutrophicated areas in the North Sea shows that eutrophication itself not necessarely leads to dominancy of *Phaeocystis*.

Measures to reduce the blooming of a harmfull algal species should be geographical region specific and based on those local circumstances that stimulate the development of nuisance blooms.

An idealized, mathematical multispecies model of the pelagic foodweb was used to explore the impact of resource competition, selective grazing and species composition within a functional group of a foodweb at a variety of light and nutrient levels.

The presented ecosystem concept shows that with increasing degree of eutrophication specialists in resource competition will be replaced by phytoplankton generalists and subsequently by poorly edible primary producers. Red tides, dense algal blooms in shallow lakes, and the varying results of biomanipulation in different lakes can be explained with the present concept. Apart from changing nutrient ratios, also a reduction of the load of all nutrients is expected to lead to a shift in algal species composition in eutrophicated areas. Especially for highly eutrophicated regions it is expected that fish productivity will not decrease because the reduction in algal biomass will be compensated by its specific productivity. Filter feeders like mussels will be affected more rapidly because of their dependence on total algal biomass (including poorly edible (for zooplankton) species).

6. Samenvatting (*in dutch*)

In dit rapport wordt aangetoond dat **nieuwe algenbloeien in geëutrofieerde gebieden ondermeer het gevolg kunnen zijn van verschuivingen in N/P en/of ammonium/nitraat verhoudingen.**

Als specifiek voorbeeld wordt de toegenomen *Phaeocystis* bloeien voor de Nederlandse kust besproken. De aanleg van de Houtribdam (Enkhuizen-Lelystad) in het IJsselmeer heeft geleid tot een veranderde nutriëntenbelasting van het Marsdiep. Vooral de fosfaatbelasting uit het IJsselmeer nam sterk toe. In het Marsdiep heeft in de periode 1975-77 een verschuiving plaats gevonden van een fosfaat- gecontroleerd - naar een stikstof- gecontroleerd systeem. Na deze verandering werd de schuimvormende alg *Phaeocystis* dominanter en behalve in het voorjaar ontstonden er ook gedurende de (nutriënt gecontroleerde) zomer bloeien van deze alg. Uit competitie-experimenten bleek dat *Phaeocystis* inderdaad dominant kan worden in stikstof- gecontroleerde systemen en dat dit niet gebeurt in fosfaat-gecontroleerde systemen. Bovendien bleek dat de vorming van grote slijmerige kolonies niet plaats vindt onder een fosfaat-limitatie of een ammonium-limitatie. Wel worden deze kolonies gevormd onder licht-limiterende omstandigheden of wanneer nitraat limiterend is voor de groeisnelheid van de alg.

Als gevolg van een verbeterde afvalwater-zuivering langs de Rijn is de verhouding tussen ammonium en nitraat gedurende het laatste decenium sterk verschoven in de richting van nitraat. **De waterkwaliteitsverbetering van de Rijn heeft als onbedoeld neveneffect het bloeien van Phaeocystis kolonies voor de Nederlandse kust gestimuleerd.** In principe is het met behulp van de verkregen kennis nu mogelijk om gericht maatregelen te nemen tegen *Phaeocystis* bloeien. Het is op dit moment echter onvoorspelbaar welke algensoorten we daarvoor in de plaats zullen krijgen.

Een vergelijking van de verspreiding van *Phaeocystis* langs de geëutrofiëerde continentale kust laat zien dat eutrofiëring op zich niet in alle gevallen leidt tot *Phaeocystis* bloeien. In sommige gebieden komen geen schuimvormende maar giftige algenbloeien voor. Een belangrijke conclusie n.a.v. de huidige studie is dat **schadelijke algenbloeien regionaal bestreden kunnen worden wanneer de specifieke locatie-gebonden aanleidingen tot deze bloeien bekend zijn.**

Een andere, niet geographisch gebonden, factor die invloed heeft op de soortsamenstelling van algenbloeien is de selectieve begrazing van algen door zooplankton. Bij dit proces worden goed eetbare algen geconsumeerd en leidt begrazing door het zooplankton tot een verschuiving naar minder eetbare soorten. Deze slecht eetbare soorten zijn in sommige gevallen toxisch voor verschillende groepen van organismen. In mariene milieus zijn dinoflagellaten de meest beruchte groep. Door middel van een wiskundig multi-species model van een voedselweb werd aangetoond dat een **toename van eutrofiëring leidt tot een verschuiving van specialisten in competitie om voedingsstoffen naar snelgroeiende soorten en uiteindelijk tot het optreden van stabiele bloeien van slecht eetbare algen.** Het verantwoordelijke mechanisme is de in sterk eutrofe wateren periodiek voorkomende hogere biomassa's van zooplankton waardoor selectieve begrazing een belangrijke rol gaat spelen. De "verbraseming" in zoetwatersystemen, het optreden van sterfte van broed van schelpdieren, en het optreden van "red tides" zijn terug te voeren op dit mechanisme. **In eutrofiërings- modellen dient het mechanisme van selectieve begrazing aanwezig te zijn.**

Een reductie van de systeem-controllerende nutriënt-belasting zal kunnen leiden tot een verschuiving in de algen-soortsamenstelling. Vooral in sterk geëutrofiëerde gebieden zal de visproductie niet per definitie afnemen en misschien zelfs wel toenemen omdat de afname in algenbiomassa wordt gecompenseerd door een toename in activiteit en/of eetbaarheid van de algen. Filter feeders zoals mosselen zijn meer afhankelijk van de algenbiomassa en zullen mogelijk sterker beïnvloed worden.

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