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The Bounds and Potential Effects of NH_4^+ (Loading) on the Pelagic System of a Baltic Estuary

With 14 Figures and 5 Tables

Abstract

Complex experimental studies regarding effects of different NH_4^+ loadings were performed on enclosed samples of the Zingster Strom, a highly eutrophic estuary of the Baltic Sea. The load capacity of the pelagic enclosures is not exceeded in summer by the addition of 50 µmol · l^{-1} NH_4^+. In contrast the addition of 270 µmol · l^{-1} NH_4^+ induces obvious disturbances in the system: toxic effects on the zooplankton and temporal reduction of the rate of bacterial activity. Under P-limiting conditions, surplus NH_4^+ is stored in algal cells and is liberated rhythmically. This NH_4^+ rhythm is restricted mainly to the blue-green algae.

During the 8 days of investigation the most striking changes take place in the structures of phytoplankton and zooplankton. The relative slight variation in the bacterial counts and biomasses is remarkable.

In regard of performance parameters the tendency to stabilize productivity is typical of phytoplankton and zooplankton. Bacterial activity is characterized by distinct and sometimes also very rapid fluctuation. The principal factor that governed the development of the phytoplankton succession during the experiment was the temperature. The loading with N and P simultaneously permitted the development of green algae.

Contents

1. Introduction

The shallow inland waters called boddens south of the Darß-Zingst Peninsula (Fig. 1a) form an estuary with a slightly fluctuating salinity that is typical of Baltic conditions. Despite the high phosphorus loading, intensive interactions between the sediment and the substances dissolved in the water lead to a relatively stable concentration of 0.35—0.40 µmol · l^{-1} PO_4^{3-} in the free water (SCHLUNGBAUM 1979). Since this concentration scarcely varies during the vegetation period, it seems unlikely that the development of the phytoplankton is limited by phosphorus. Free water concentrations of the nitrogen components NH_4^+, NO_2^- and NO_3^-, in contrast, show distinct seasonal variations. Substantial daily and, when the measuring intervals are short enough, even hourly variation can be recorded (cf. BLOSS 1981). Increasing NH_4^+ concentrations since 1975 have led to a relative stabilization of the NO_3^- concentration during the summer (SCHLUNGBAUM 1979) and to a reduction in N_2 fixation (HÜBEL 1980). Field phytoplankton studies and laboratory investigations with a test alga have experimentally confirmed the logical conclusion that phytoplankton development is N-limited (SCHIEWER 1982, 1984, SCHWARZ 1976). In view of the mean annual biomass of 13.9—23.9 $mm^3 \cdot l^{-1}$

(with peaks of 100—200 $mm^3 \cdot l^{-1}$ during the bloom of the blue-greens in summer), the water must be considered to be at least eutrophic. At present there are no generally accepted guidelines for classifying the trophic states of brackish waters (SCHLUNGBAUM & NAUSCH 1982). During the main vegetation period phytoplankton growth can be expected to be limited increasingly by light. Major daily fluctuations in the values for in situ primary production support this speculation (BÖRNER 1980). But neither the biomass development nor the in situ primary production values for the period 1969 to 1979 show a distinct trend in the development of the bodden waters (PANKOW & KELL 1980).

Investigation of microbial activity in the waters has confirmed their eutrophic character. Despite fluctuations of considerable amplitude, the bacterial cell counts and biomass values obtained during the summer consistently yield the same plateau values (JOST & BALLIN 1984). Due to the shallowness of the waters and their degree of eutrophication, the detritus plays an important role in this respect, whereas the effect of the dissolved organic matter is obviously of only minor importance (VIETINGHOFF 1982).

The importance of the zooplankton in terms of biological production has clearly declined. Productivity curves with a single peak (75% of the annual biomass in April/May; 5 $mm^3 \cdot l^{-1}$) and a high mean annual primary production lead to ratios of 6...7.4:1 (eastern, more saline parts of the boddens) to 12:1 (western, more limnic parts of the boddens) between gross primary production and the rate of grazing by zooplankton. The dominance of the copepods (represented by only a few species) in the eastern parts and the increasing dominance of the rotifers towards the western end of the boddens is striking (SCHNESE 1980b).

The results obtained hitherto permit no estimation of the limits to which the boddens can be loaded, nor can they be used to predict how the boddens will develop if nutrient inputs continue to increase. Moreover, the complexity of the interactions between the free water and the sediment make it very difficult to interpret the results in ecological terms. It is therefore necessary to consider the pelagic zone and the sediment separately for experimental purposes in order to distinguish between causes and their effects.

Basing our approach on the experience gained by other authors (BARICA et al. 1980, KOMÁRKOVÁ 1979, WALL & BRIAND 1979, ZEITZSCHEL 1978) and our own experimental investigations performed in 1980, we turned our attention in 1981 to a short-term structural and functional analysis of a compartmentalized model of the pelagic system (PEKOM). By restricting our attention to the ecosystem components bacterioplankton, phytoplankton and herbivorous zooplankton we were able to use relatively uncomplicated enclosures. Laboratory studies performed in parallel were used to ensure that the in situ experiment and the laboratory experiment were as closely related as possible. The aim of the experiment was to answer the following questions:

- How would the biocoenosis respond to a change from nitrogen limitation to phosphorus limitation?
- To what extent is the system at present N-limited?
- Are diurnal rhythms changed or induced as a result of the NH_4^+ import?
- How much NH_4^+ can still be imported without affecting the stability of the biocoenosis?
- In which direction can the development of the structure and capacity of the biocoenosis be directed by management?

Attention was concentrated not only on obtaining theoretical knowledge regarding the adaptation of eutrophic pelagic biocoenoses but also on aspects that permit or assist in the practical utilization of the waters.

2. The summer situation in the Zingster Strom

During the summer the biocoenosis is as a rule dominated by the blue-greens, which can account for up to 90% of the biomass. The principal species are *Oscillatoria limnetica*, *Merismopedia punctata*, *Aphanizomenon flos-aquae*, *Nodularia harveyana*, *Anabaena* spec. and *Gomphosphaeria lacustris*. These are accompanied mainly by the green algae *Monoraphidium contortum* and *Scenedesmus quadricauda*, whereas the diatoms *(Stephanodiscus hantzschii)* are present only in low abundances.

The water body of the Zingster Strom (Fig. 1a) is 6 m deep (maximum depth: 10 m) and is generally well mixed due to the constant alternation of inflow and

Fig. 1a Map of the Darß-Zingst estuary system.
● = Location of the investigation area.

outflow. Due to this additional energy input the potential primary production of the Zingster Strom is ca. 1/3 higher than in the Kirr Bucht, a region of shallow water immediately adjacent to it (SCHIEWER 1984). The water temperatures during the summer are about 20 °C. CO_2 limitation has never recorded. Extremes in the oxygen situation are restricted to densely vegetated shallow water regions. As can be expected of a highly eutrophic brackish water, the pH values of 8.2—9.0 are relatively high.

The experimental studies started on 10 July 1981 at the end of a period of good weather (5—11 July 1981). Global irradiations over 2,000 $J \cdot cm^{-2} \cdot d^{-1}$ were measured during this period. Thereafter (12—17 July 1981) global irradiation was about 1,250 $J \cdot cm^{-2} \cdot d^{-1}$. In view of these conditions, the carbohydrate reserves in the phytoplankton in the evening of 9 July 1981 must have been high, but those of N and P were probably low. The decline of an *Oscillatoria limnetica* bloom in the Zingster Strom and the four enclosures coincided with the period of investigation.

3. Material and methods

3.1. Enclosures and experimental measures

The four enclosures consisted of plastic compartments with a volume of 1 m^3 each with open surfaces of 1 m^2. All four enclosures were filled during the late afternoon on 9 July 1981 with thoroughly mixed water taken from the Zingster Strom at a depth of 1.5 m. Checks showed that in terms of salinity, nutrient and chlorophyll-a concentrations, bacterial biomass and bacterial cell count the initial conditions were identical in all enclosures. The fraction of the biomass accounted for by herbivorous zooplankton, in contrast, differed greatly from one enclosure to the another. The experiment began at 0430 hrs on 10 July 1981 when the baseline values were recorded and NH_4^+ and a $NH_4^+ + PO_4^{3-}$ mixture was added to the different compartments. The amounts added and other details are given in Fig. 1b. Since the salinity of the surrounding water fluctuated constantly (sinking to $2.6^0/_{00}$ on occasion), the stability of the original salinity ($4^0/_{00}$) was used to check the integrity of the enclosures during the experiment. Inspection upon conclusion of the experiment confirmed that the plastic enclosures were still completely intact.

The experiment involved not only the investigation of samples from the four compartments and the Zingster Strom but also of samples from subenclosures with incubation times of 12—24 h. Standard methods, modified in some cases, were used to record environmental parameters, the structural elements of the biocoenosis and capacity.

3.2. Sample collection and analysis

Samples were collected with a sampler daily at 0500 hrs, 1330 hrs and 2100 hrs. Additional samples were taken at 0700, 0900, 1100 and 1700 hrs on the first two days and the last day of the experiment. The contents of all enclosures were thoroughly mixed manually by paddles before each sampling. This ensured uniform sample quality but did not prevent the formation of an oxygen gradient (particularly in enclosure C) between samplings. The following physical, chemical and biological parameters were recorded:

a) daily global irradiation (Marines Observatorium Zingst) and photosynthetically active radiation at wave lengths of 425 nm (blue), 545 nm (green), 660 nm (red) and as white light measured with the LM 2 radiation meter (WALTER 1981)
b) temperature, wind direction and velocity, direction of the current in the Zingster Strom
c) nutrients (phosphate, nitrate, nitrite, ammonium and iron). The samples were analyzed for nutrients immediately after they had been taken. Analysis was done by standard methods (ROHDE & NEHRING 1979) using flow-through analyzers (VEB MLW Medingen, Freital)

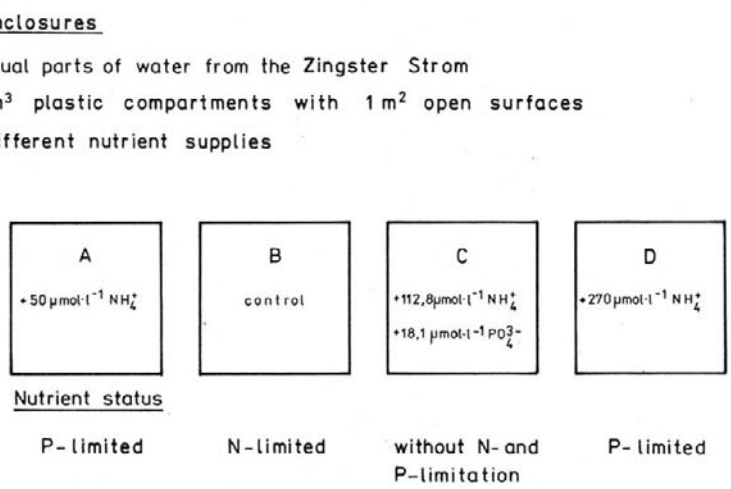

Fig. 1 b. Scheme of the complex investigations of the effects of NH_4^+ on enclosed pelagic plankton populations from the Zingster Strom.

Investigations: environmental factors (including temperature, light, pH, salinity, nutrients); bacteria, phytoplankton, herbivorous zooplankton; productivity a) in situ, b) in vitro (light incubator), c) in sub-enclosures; comparison with field populations in the Zingster Strom.

d) total carbon concentration of the water by means of the Warburg apparatus (HÜBEL 1966) and the oxygen concentration using O_2 electrodes and an automatic recorder (WALTER 1981)

e) chlorophyll-a after methanol extraction (RIEMANN 1978) as total chlorophyll, active chlorophyll and phaeophytin. The figures show only the active chlorophyll concentration. The factor 75 was used for conversion to carbon

f) in situ primary production by the ^{14}C technique in light and dark bottles after SCHINDLER et al. (1972) expressed as total ^{14}C fixation and by in situ O_2 electrodes. The excreted fraction of the ^{14}C was also recorded. The radioactivity was measured in a scintillation counter[1])

g) the heterotrophic potential means of ^{14}C glucose net uptake at 7 concentrations (from $0.32 \cdot 33.4\ \mu g \cdot l^{-1}$ C) after 1 h incubation, fixation with formalin and filtration. The values were analyzed by means of the EADIE transformation of the MICHAELIS-MENTEN equation

h) bacterial production by the dark fixation of $NaH^{14}CO_3$ using the ROMANENKO method (ROMANENKO 1964)

i) zooplankton biomass and grazing rate by the methods described by SCHNESE & HEERKLOSS (1978)

j) bacterial count and bacterial biomass estimation by a modification of the method described by ZIMMERMANN & MEYER-REIL (1974) as modified by JOST & BALLIN (1980)

k) saprophyte count and groups by means of the standard method (NEUBERT 1978)

l) phytoplankton count, volume and species by UTERMÖHL's (1958) method after fixation of the samples with Lugol's solution

m) detritus after GEORGI et al. (1980).

The following aspects were investigated by laboratory experiments and in the subenclosures:

- daily respiration variation (O_2 electrodes), changes in light saturation and the compensation point of the phytoplankton (O_2 electrode)
- dependence of the ^{14}C fixation rate on light intensity at the natural water temperature in a light incubator
- determination of nutrient limitation during a short term test in the light incubator by means of the dark fixation rate and the effect of NH_4Cl and NaH_2PO_4 addition on nutrient limitation
- effect of 12 h preincubation with NH_4Cl, NaH_2PO_4 and a combination of both substances on the light and dark fixation rates in a light incubator in subenclosures with a volume of 5 l
- the NH_4^+ rhythm in subenclosures made of Jenaer glass and under laboratory conditions.

The values were converted into C-equivalents by means of the plankton equivalents elaborated for the boddens south of Darss-Zingst by HEERKLOSS & VIETINGHOFF (1981). All measured values were statistically analyzed: standard deviation, confidence interval, correlation coefficient, rank correlation coefficient after SPEARMAN and STUDENT's *t*-test.

1 We wish to thank Dr. SCHULZE of the Physiochemical Institute at the Medical Faculty of the Wilhelm-Pieck-University Rostock for performing the numerous measurements.

4. Results and discussion

4.1. NH_4^+ rhythm and chemistry of the water

The results from enclosure A (Fig. 2) show that after irregular fluctuations on 11 and 12 July 1981 an ammonium rhythm coupled with the day/night rhythm set in on the third day (13 July 1981, 0500 hrs): ammonium liberation during the night and ammonium uptake during the day. This rhythm is significant at the $\alpha < 0.01$ level from 13—16 July 1981 (STUDENT's t-test).

Comparable results were obtained from enclosure D (Fig. 3), where due to the higher ammonium concentration used, the fluctuations were more striking. No stable rhythm appeared in enclosure D until the fourth day after the ammonium had been added, but thereafter it also remained significant at the $\alpha < 0.05$ level from 14—16 July 1981. In this enclosure the mean minimal value of the free ammonium N of ca. 60 µmol NH_4^+ was distinctly higher than in enclosure A (ca. 5 µmol). By the end of the investigation period the majority of the ammonium N added was again present in free form in enclosure D (Fig. 3). Comparison of the absolute NH_4^+ uptakes by the plankton in these two compartments shows that considerable proportions of additional NH_4^+ can be taken up when surplus NH_4^+ is available. Investigations by MURPHY & BROWNLEE (1981) into populations of blue-greens in hypertrophic lakes yielded the same result. This behaviour obviously gives the blue-greens some sort of advantage in competition with other algae.

Both enclosures, with active chlorophyll-a concentrations of 70 and 68.3 µg $\cdot l^{-1}$ respectively (cf. Figs. 2 and 3), had identical initial photosynthetically active biomasses. Their relatively small increases to 91.3 and 100.3 µg $\cdot l^{-1}$ chl-a respectively show once again that nitrogen limitation in the Zingster Strom is only slight (SCHIEWER 1984). The drop in chlorophyll concentration up to 16 July 1981 correlated with the appearance of a larger proportion of free ammonium.

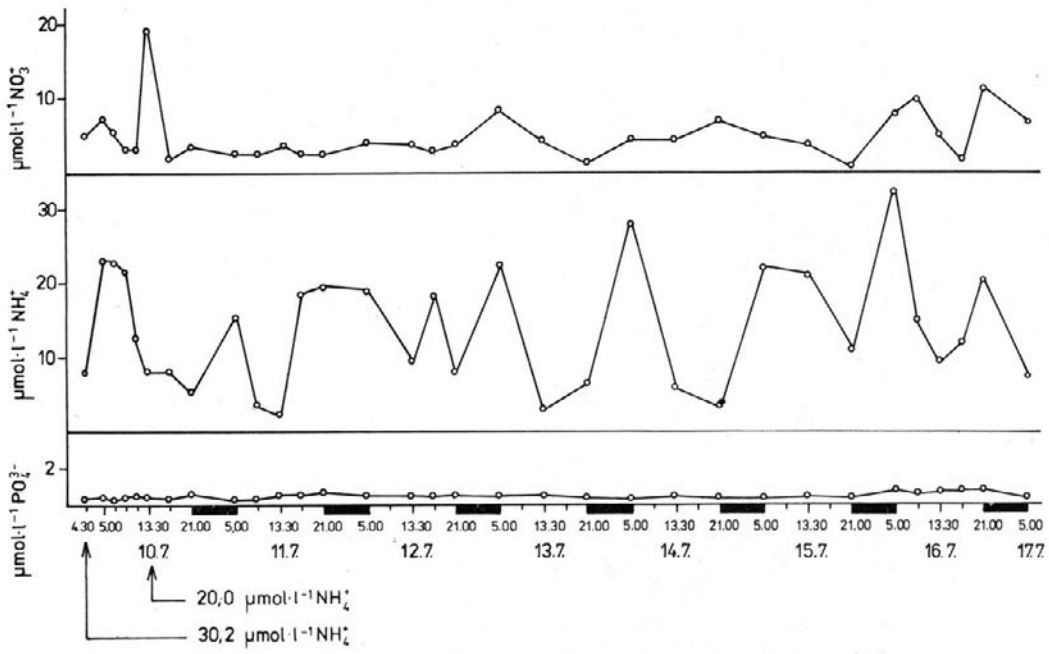

Fig. 2. Dissolved PO_4^{3-}, NH_4^+ and NO_3^- in enclosure A (µmol $\cdot l^{-1}$).

0430 hrs on 10 July: control values without addition of nutrients. Arrows and figures: time and amount of NH_4^+ added. Samples collected at 0500, 0700, 0900, 1100, 1330, 1700 and 2100 hrs. Dark parts of the abscissa: periods from sunset to sunrise. The diurnal NH_4^+ rhythm is significant at the $\alpha < 0.01$ level from 12 July—17 July 1981.

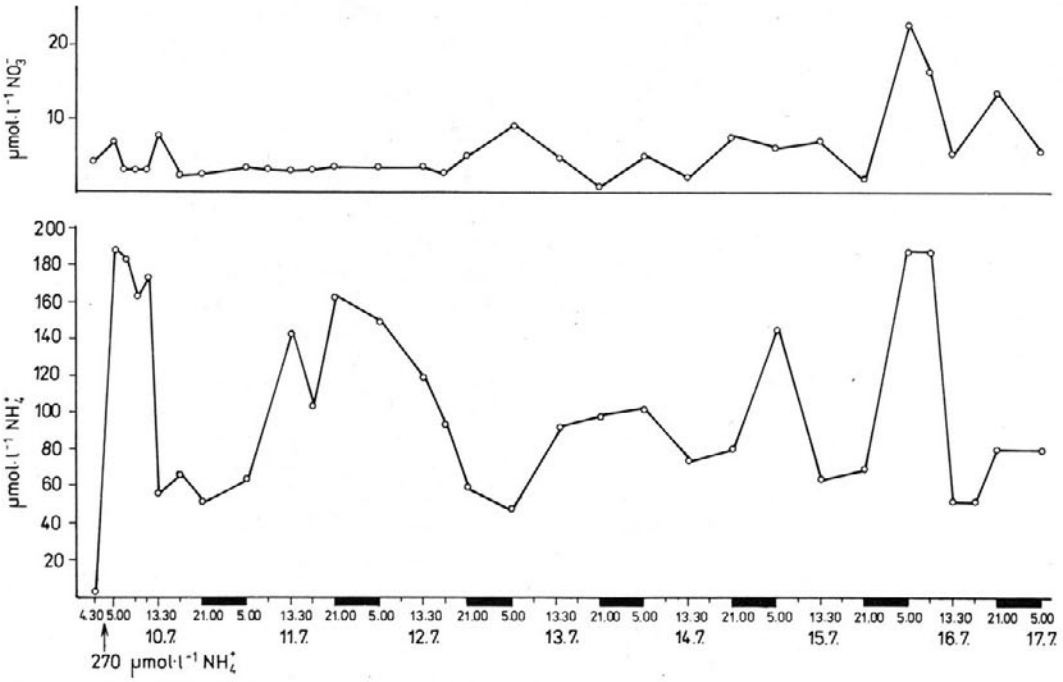

Fig. 3. Dissolved NH_4^+ and NO_3^- in enclosure D (µmol · l^{-1}).
Further particulars as for Fig. 2. The diurnal NH_4^+ rhythm is significant at the $\alpha < 0.05$ level from 13 July—17 July 1981.

As far as we are aware from the literature at our disposal, these results show for the first time that NH_4^+ storage in phytoplankton populations under conditions of limited growth cannot be maintained but breaks down rhythmically. The mechanism assumed to underly this process is dealt with in SCHIEWER & BAADER (1982).

The NO_3^- and NO_2^- concentrations, which were determined parallel to the NH_4^+ levels changed only slightly in the course of the investigations (Figs. 2 and 3). A trend towards higher NO_3^- concentrations is apparent in enclosure D only. The PO_4^{3-} concentration (Figs. 2, 3, 5) remained constant between 0.2 and 0.4 µmol · l^{-1} PO_4^{3-}.

The similarity between the changes in concentration and between the concentrations of free PO_4^{3-}, NO_3^- and NH_4^+ in enclosure B and the Zingster Strom is striking (Fig. 5). This also shows that in the boddens there is no correlation between the free P or N concentrations and the photosynthetic performance of the plankton population (Figs. 3, 4).

In enclosure C, which received additional PO_4^{3-} and NH_4^+ (Fig. 5), there are signs of NH_4^+ oscillations (temporary NH_4^+ surplus) on 14 and 15 July 1981. In this compartment the NH_4^+ concentration of 112.8 µmol · l^{-1} after NH_4^+ addition was reduced to the initial concentration of 5 ... 10 µmol · l^{-1} within 7 days. The NH_4^+ concentrations in neither the other three enclosures nor in the free water did not drop substantially below this figure. Under eutrophic conditions with a high nitrogen input the algal populations obviously have high K_m values which, together with an appropriate nitrogen turnover rate, lead to a relatively high free NH_4^+ concentration. From results obtained with *Microcystis firma* in a hypertrophic lake, KAPPERS (1980) concludes that there is a connection between the half-saturation value for uptake and the free NH_4^+ concentration. The fact that a *Nodularia* bloom, which fixes N_2, nevertheless took place in enclosure B is remarkable.

The absolute phosphate uptake capacity of the biocoenosis in enclosure C was about 12 µmol · l^{-1}. Related to the initial concentrations, four times more P than N

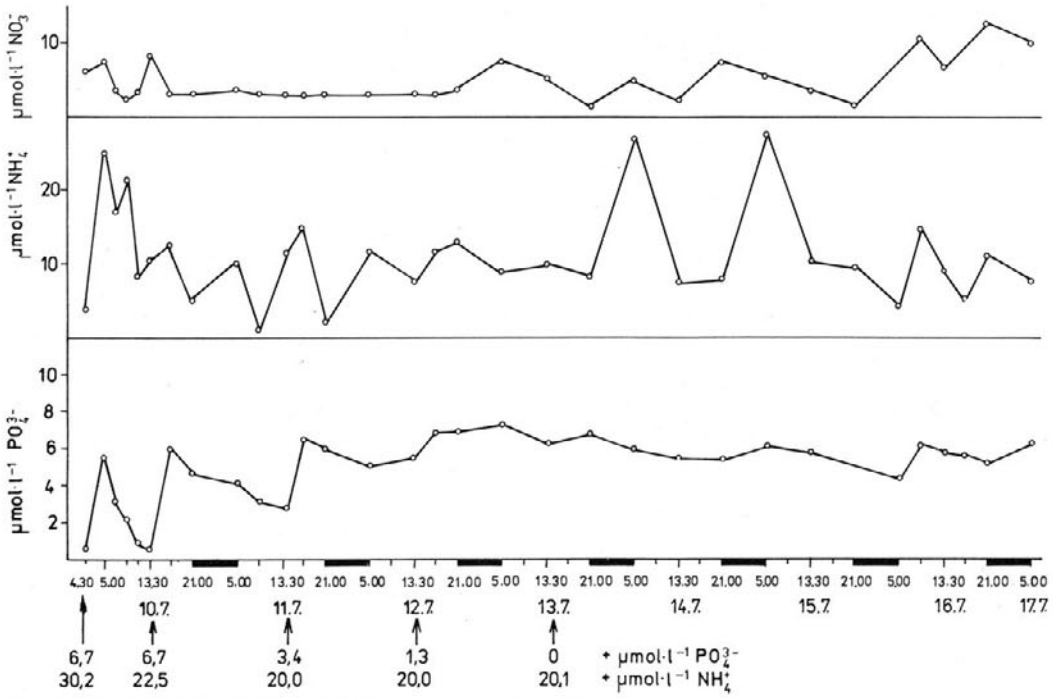

Fig. 4. Dissolved PO_4^{3-}, NH_4^+ and NO_3^- in enclosure C ($\mu mol \cdot l^{-1}$).
Further particulars as for Fig. 2.

was taken up. Like in compartment D, NO_3^- concentrations were above normal in compartment C on the 6th day.

4.2. Biomass and detritus

4.2.1. Phytoplankton

The phytoplankton biomass values calculated from the active chlorophyll-a concentration and the biovolume are in good agreement. Substantial discrepancies appeared only in enclosure D on the 6th and 7th day when, due to the *Nodularia* bloom, the biovolume increased very rapidly. Figs. 6—9 give only the values for active chlorophyll-a. The phaeophytin content of the total chlorophyll-a was 35—40% virtually throughout the experiment.

Enclosures A, B and D, with an initial biomass of 68—70 $\mu g \cdot l^{-1}$ chl-a, achieved biomasses of 88 (enclosure B) — 97 $\mu g \cdot l^{-1}$ (enclosure D) on the 7th day. The differences are significant at the $\alpha < 0.05$ level. The curves showing the biomass development plotted against the time differ (Figs. 6, 7, 9): in enclosures A and D the biomass had reached its maximum on the 12 July, but in enclosure B the biomass first passed through a minimum before reaching its maximum on 16 July.

Biomass development in all three of these enclosures was finally restricted by phosphate, because even in enclosure B N-limitation was overcome by N-fixation. The phosphorus surplus in the algae at the beginning of the experiment was, even if accelerated turnover is assumed, not high and permitted the phytoplankton biomass to increase only by a factor of 1.3.

During the experiment, the phytoplankton biomass in the Zingster Strom rose on occasion to 130.5 $\mu g \cdot l^{-1}$ (15 July 1983). This was less the result of P-remineralization from the sediment than the outflow of water which transported denser phytoplankton populations into the Zingster Strom from the inner boddens.

The simultaneous addition of P and N in enclosure C (Fig. 8) permitted the biomass to

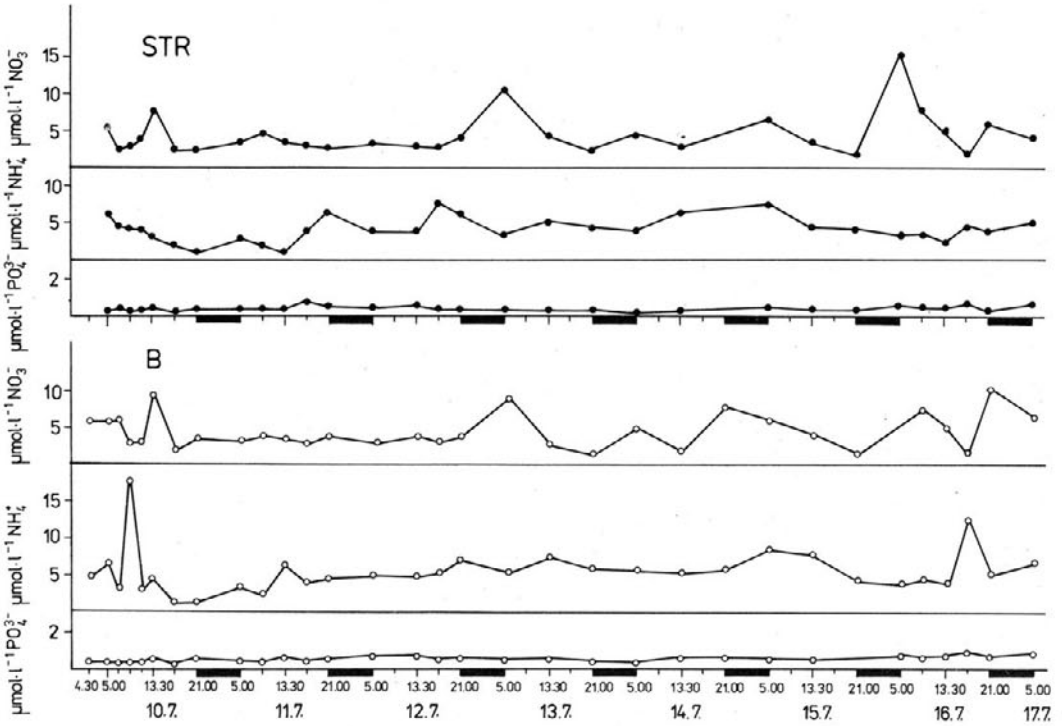

Fig. 5. Dissolved PO_4^{3-}, NH_4^+ and NO_3^- in enclosure B (B) and in the Zingster Strom (STR; µmol · l^{-1}).
Further particulars as for Fig. 2.

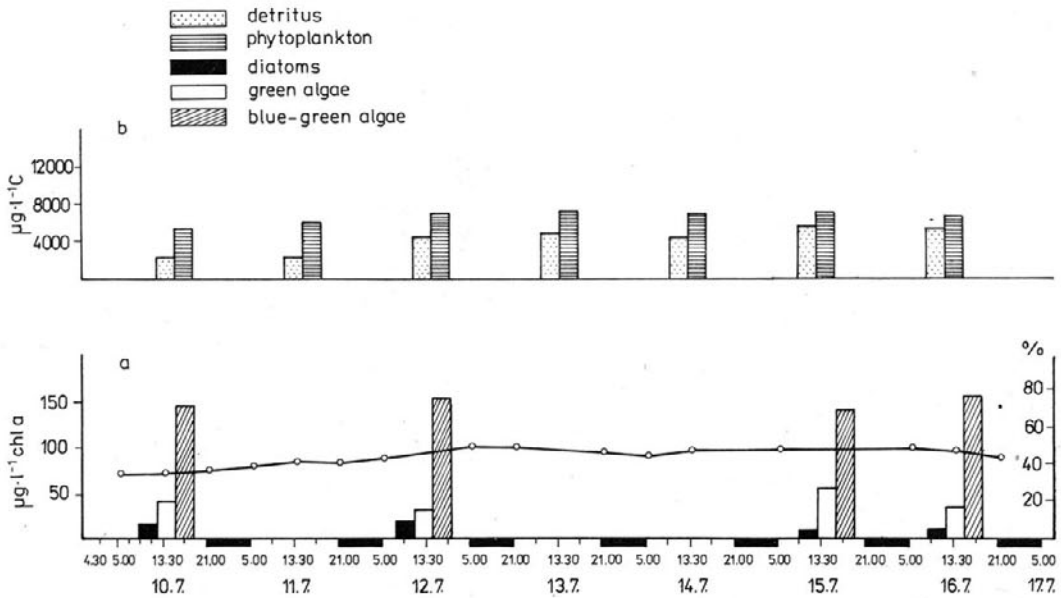

Fig. 6. a: Active chlorophyll-a concentration (µg · l^{-1}) and relative percentages of blue-green algae (B), green algae (G) and diatoms (D) in the total phytoplankton volume in enclosure A.
b: Relative amounts of detritus and biomass (measured as chl-a concentration) in enclosure A.

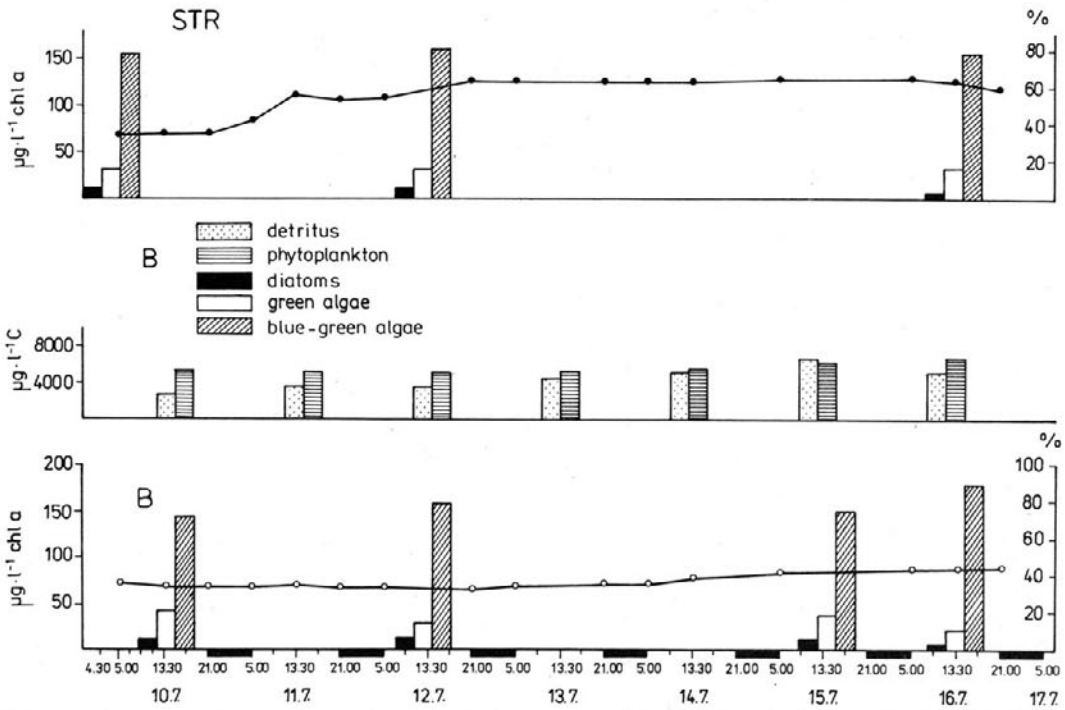

Fig. 7. Active chlorophyll-a concentration and relative amounts of the different algal groups in the total phytoplankton volume in the Zingster Strom (STR). Active chlorophyll-a concentration, relative amounts of the algal groups, detritus and biomass in enclosure B (B).
(Cf. Fig. 6 for details).

increase to 223 $\mu g \cdot l^{-1}$ chl-a in the course of the experiment. The plateau reached on the 6th and 7th days is mainly a result of the onset of light limitation. According to results obtained during the IPB (Le Cren & Lowe-McConnel 1980), biomass values of 150—620 $\mu g \cdot m^{-2}$ chl-a represent the threshold at which light limitation starts in limnetic waters.

The development of detritus took place as expected (Figs. 6b—9b). It is striking that on the 6th and 7th days the values for enclosures C and D are significantly ($\alpha < 0.10$) higher than in enclosures A and B. The physiological status of the algal populations changes with the onset of light limitation, and this is probably associated with a drop in the C:Chl-a ratio to values <75. Due to the absence of proof, however, this was not taken into account when converting the biomass into µg C for Fig. 8.

The changes in the biomass and detritus are associated with significant changes in the species composition of the phytoplankton population, particularly in regard of the relative percentages of the blue-greens, the greens and the diatoms (Figs. 6a—9a). The occurrence of the *Nodularia harveyana* bloom in enclosure B from 15—16 July 1981 (N_2 fixer), the great increase in the numbers of the flagellate *Mallomonas* spec. in compartment D and the proliferation of the green algae *Monoraphidium contortum* and *Scenedesmus quadricauda* (by a factor of 5) in enclosure C are particularly striking. The situation in enclosure A, in contrast, remained almost unchanged.

Barica et al. (1980) reported on shifts in favour of the green algae and cryptomonads in algal populations when nutrient supplies increase. The multiplication of *Mallomonas* in enclosure D indicates a development rather towards a more heterotrophic system.

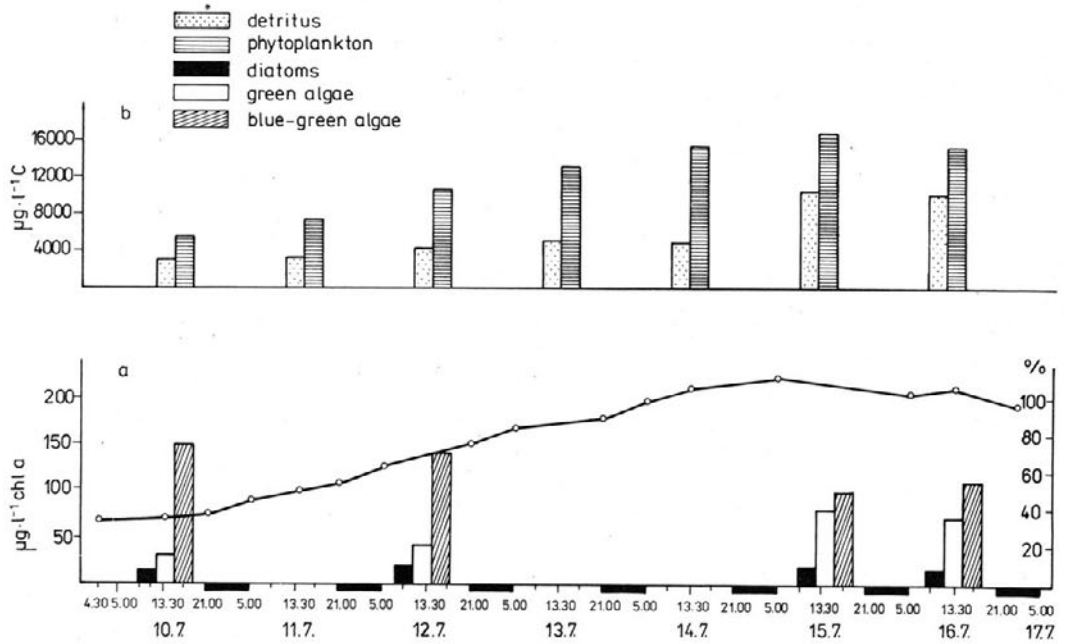

Fig. 8. a: Active chlorophyll-a concentration and relative amounts of the algal groups in the total phytoplankton volume in enclosure C. .
b: Amounts of detritus and biomasses in enclosure C.
(Cf. Fig. 6 for details).

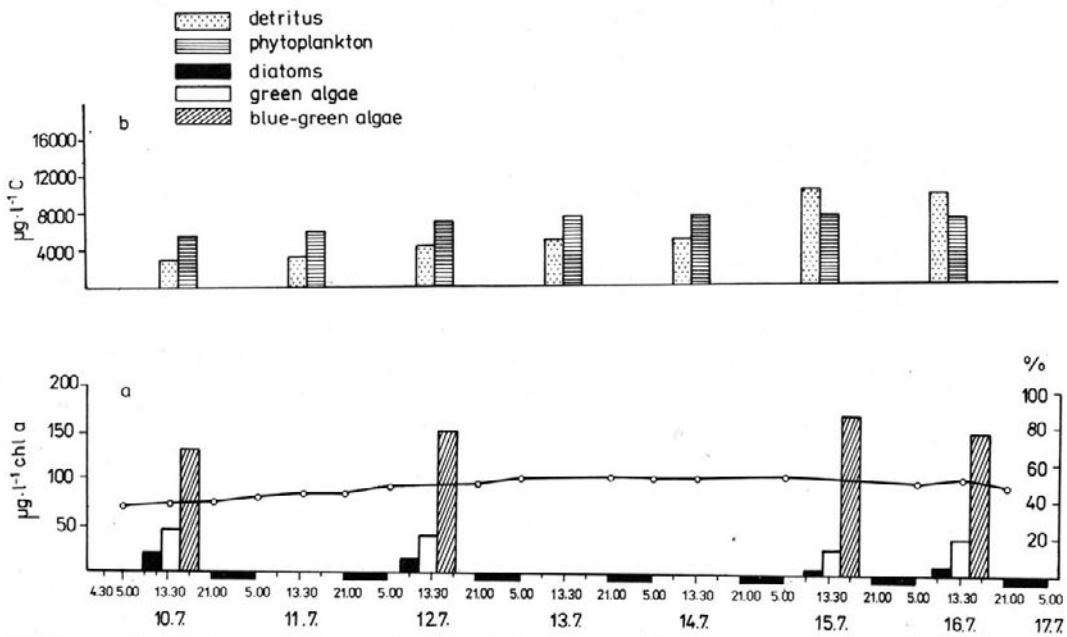

Fig. 9. a: Active chlorophyll-a concentration and relative amounts of the algal groups in the total phytoplankton volume in enclosure D.
b: Detritus and biomasses in enclosure D.
(Cf. Fig. 6 for details).

4.2.2. Bacteria

Unlike the phytoplankton, the bacteria showed no statistically significant changes in cell number or biomass except in enclosure *C* ($\alpha < 0.05$) (Table 1).

The lack of variability shown by the total bacterial count is in good agreement with the results obtained in the far less eutrophic Kieler Förde (RHEINHEIMER 1978). It is surprising, however, that neither the increased NH_4^+ input (enclosure D) nor the above normal phytoplankton biomass in enclosure C had any appreciable effect on the bacterial biomass. LARSSEN & HAGSTRÖM (1979) reported a rapid increase in bacterial biomass and bacterial counts in connection with a spring bloom of diatoms.

Since the ratio between pigmented and non-pigmented saprophytic bacteria was found to vary in rhythm with the day/night cycle, we suspect that, under the prevailing conditions, fluctuations in bacterial activity were sufficient to compensate for phytoplankton-induced changes in the pelagic zone. This is supported by the substantial diurnal variations in bacterial performance (see below). According to BELL (1980), a fourfold increase in bacterial activity is sufficient to prevent the accumulation of organic substance when the blue-greens bloom.

Our results also show that major short term fluctuations in bacterial counts and bacterial biomass in the boddens south of Darss-Zingst (JOST & BALLIN 1980) are as a rule caused by sediment turbulence.

4.2.3. Herbivorous zooplankton

Patchiness and flight ability are obviously the cause of the differences between the enclosures in regard of the initial situation.

It was therefore rather difficult to calculate statistically significant differences.

In enclosures A, B and C the zooplankton biomass had proliferated to about the same extent (2.9 to 4-fold) within 7 days (Table 2). This increase was due mainly to the development of the naupliae of the dominant calanoid copepod, *Eurytemora affinis*, to the copepodid stage. In enclosure D, in contrast, the mortality rate for this species was about 95%, possibly as a result of the high concentration of toxic NH_3. Mortality of the copepod *Acartia tonsa*, which is obviously even more sensitive, was 100% in both enclosures C and D. The cladocer *Podon polysphaericus*, which was able to maintain its biomass only on enclosure B, showed a similarly sensitive response. In contrast, the cladocer *Chydorus sphaericus*, which is typical of eutrophic waters, increased its biomass in all four enclosures. The large numbers of eggs show that all enclosures provided good conditions for the development of this eury-ecological microfilterer.

At the beginning of the experiment, the plankton was dominated by the three rotifers *Brachionus quadridentatus*, *Filinia longiseta* and *Keratella cochlearis*. Mortality of *K. cochlearis*, which lives almost exclusively as a planktic form, was almost 100% in all enclosures, possibly due to lack of turbulence, but the two other species proved able to maintain

Table 1. Comparison of bacterial counts and biomasses in the enclosures at 0500 hrs on 10 July and 2100 hrs on 16 July 1981.

A factor of 0.1 was used to convert mg wet weight into mg C. cou. = counted; cal. = calculated by linear regression between duration of experiment and bacterial counts.

Enclosures	0500 hrs, 10 July 1981				2100 hrs, 16 July 1981			
	Bacterial count $10^6 \cdot ml^{-1}$		Biomass $\mu g \cdot l^{-1}$ C		Bacterial count $10^6 \cdot ml^{-1}$		Biomass $\mu g \cdot l^{-1}$ C	
	cou.	cal.	cou.	cal.	cou.	cal.	cou.	cal.
A	7.09	7.67	2360	2220	9.21	8.85	2420	2270
B	8.97	7.42	2530	2100	8.46	8.70	2400	2400
C	7.45	7.63	2160	2140	8.84	9.54	2560	2440
D	8.00	7.98	2160	2320	9.06	9.92	2630	2760

Table 2. Initial biomass, final biomass and proliferation factors for the herbivorous zooplankton in the enclosures in $\mu g \cdot l^{-1}$ C on 10 July and 16 July 1981

Enclosures	Biomass		Proliferation rate
	10 July	16 July	
A	554	1611	2.9
B	338	1152	3.4
C	234	945	4.0
D	522	86	0.2

their populations, although with lower numbers of individuals. The great increase in the biomass of the green algae in enclosure C may have been the cause of the signs of exponential development of the *B. quadridentatus* population in that enclosure.

Long-term experiments must be performed to permit analysis of the distinct changes observed in the structure of the zooplankton populations.

4.3. Metabolic performance

4.3.1. Primary producers

The in situ results obtained by the ^{14}C method and by O_2 measurement using electrodes were in good agreement with each other (Figs. 10, 11). Production rates were about the same in enclosures A, B and D, but production rate in enclosure C was considerably higher from 13—16 July 1982 ($\alpha < 0.05$). As expected, significant correlations ($\alpha < 0.05$) were found only with the daily global irradiation (A, B: $r = 0.82$; D: $r = 0.73$). No such correlation was found for enclosure C due to the constantly growing biomass and the resultant changes in light absorption capacity.

Measurements show that respiration in enclosures A and B decreased significantly ($\alpha < 0.10$) as a result of the decrease in global irradiation. This reduction is only slight in enclosure D, and in enclosure C respiration remained roughly constant throughout the

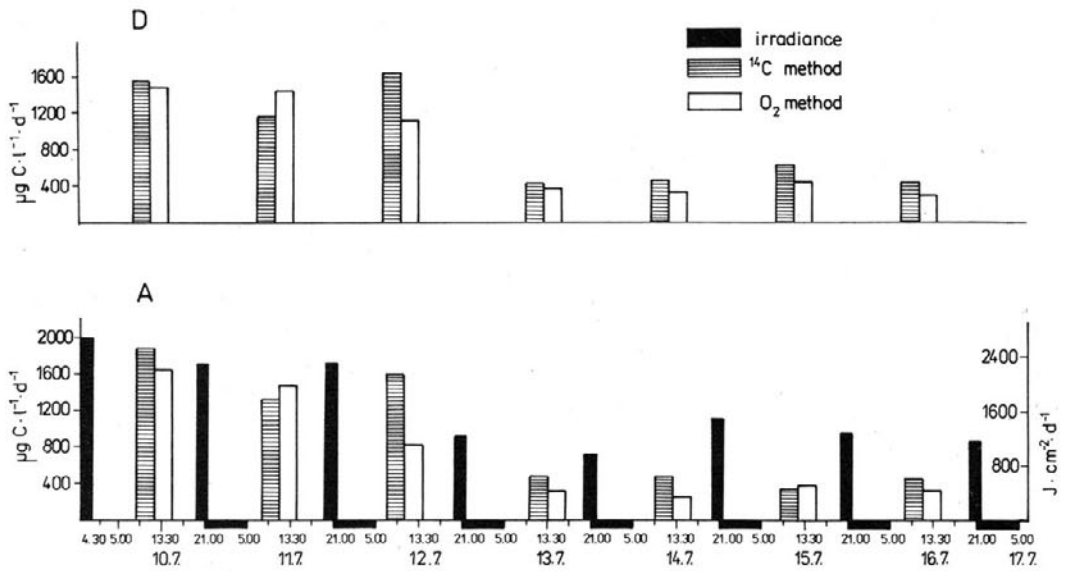

Fig. 10. Daily production values in enclosures A (A) and D (D) ($\mu g \cdot l^{-1}$ C $\cdot d^{-1}$) and daily global irradiation sums ($J \cdot cm^{-2} \cdot d^{-1}$). Production measured as total ^{14}C fixation and O_2 measurement in situ with O_2 electrodes.

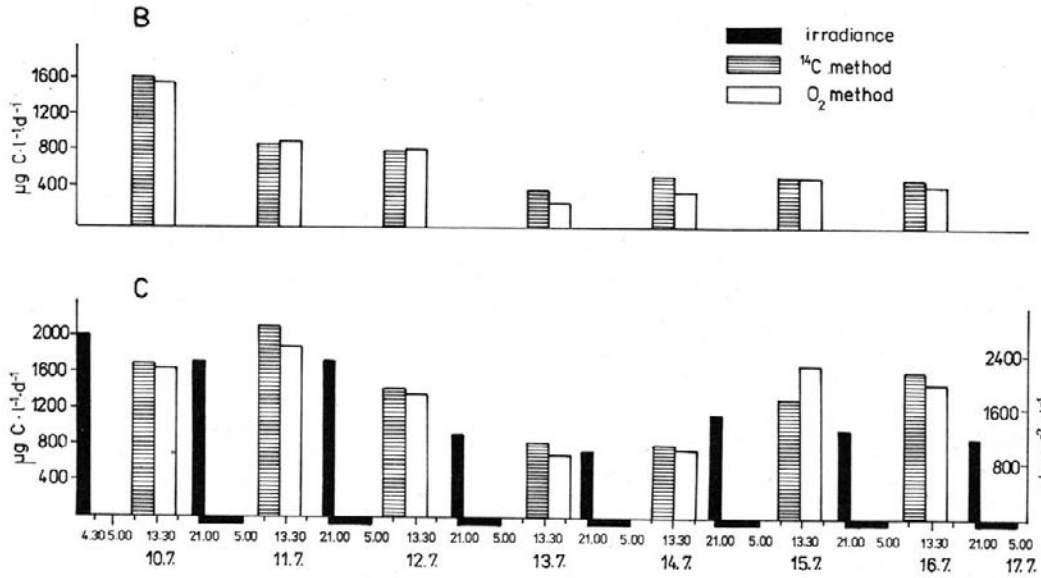

Fig. 11. Daily production values in enclosures C (C) and B (B) ($\mu g \cdot l^{-1}$ C $\cdot d^{-1}$) and daily global irradiation sums ($J \cdot cm^{-1} \cdot d^{-1}$).
(Cf. Fig. 10 for further particulars).

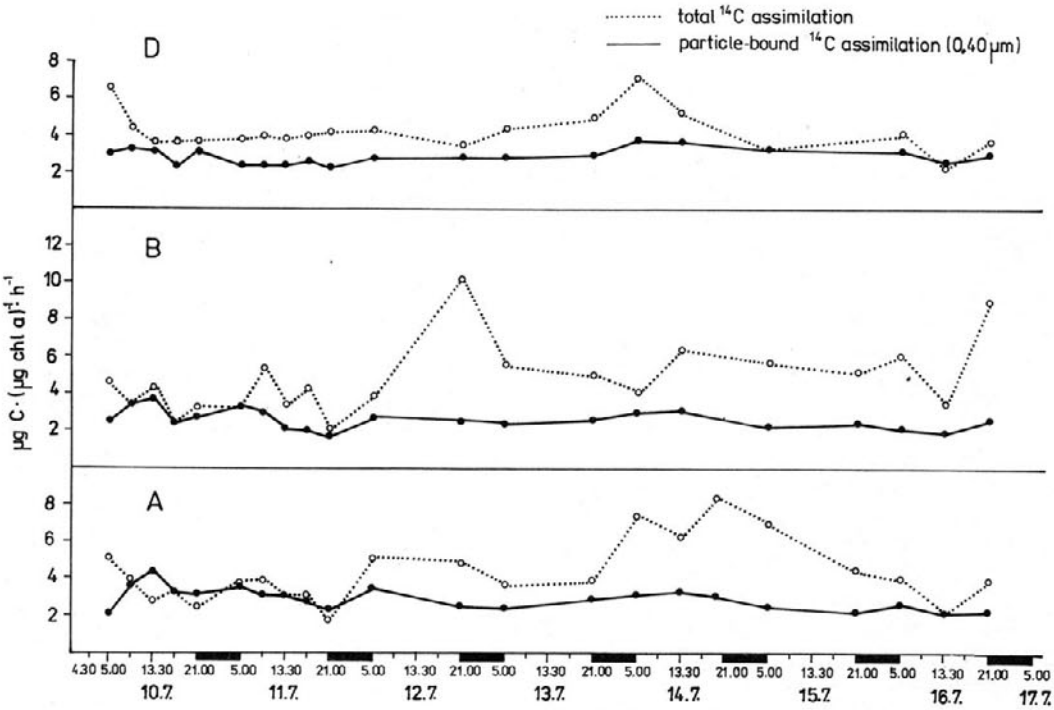

Fig. 12. Assimilation numbers of the phytoplankton in enclosures A, B and D (μg C $\cdot$ (μg chl-a)$^{-1} \cdot h^{-1}$).
Measured by incubation for 90 min in light incubator at temperature of natural water. - - - - = total ^{14}C fixation, ——— = particulate ^{14}C fixation (Synpore filter, 0.40 µm pore size).

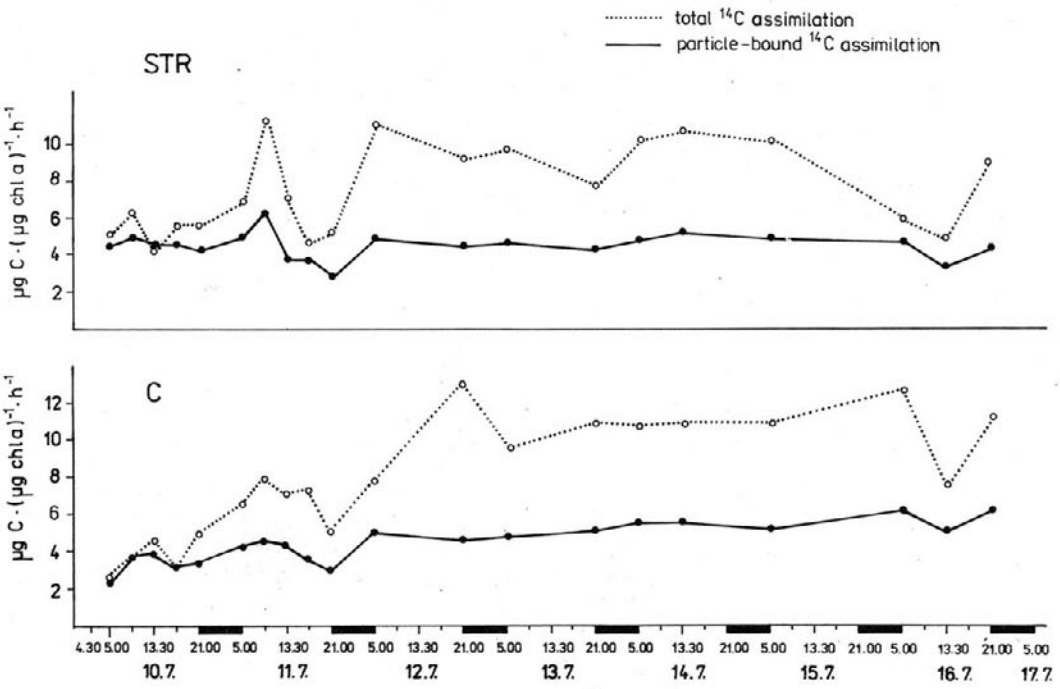

Fig. 13. Assimilation numbers of the phytoplankton in enclosure C and in the Zingster Strom (µg C · (µg chl-a)$^{-1}$ · h^{-1}). (Cf. Fig. 12 for other particulars).

experiment. In enclosure D the ratio between gross photosynthesis and respiration changed clearly in favour of respiration (from 3:1 to 1.6:1).

The phytoplankton excretion values measured in situ amounted to ca. 20% of the total ^{14}C assimilation. Major fluctuations are particularly typical of enclosure D, whereas in enclosure C the values were always below 10% from 14 July on.

The in vitro experiments (light incubator), by eliminating light and biomass as variables (inclusion of the chlorophyll-a concentration), permitted genuine comparison between the enclosures and the Zingster Strom. In other words, they allowed the influence of the nutrient situation to be investigated (Figs. 12, 13). The assimilation numbers found in this way were of the same order as those obtained for phytoplankton from shallow Danish Fjords (GARGAS 1980) and from Lake Trummen in Sweden (GELIN & RIPL 1978).

The constancy and the considerable adaptability of the phytoplankton to the changed conditions is astonishing. Although in enclosures A and D N-limitation was changed to P-limitation, NH_4^+ loading reached its limits in enclosure D, and a bloom of nitrogen-fixing blue-green algae set in in enclosure B, the photosynthesis rates per unit chlorophyll-a were almost identical in all three enclosures. The total ^{14}C fixation rate fluctuated more than the particle-bound ^{14}C fixation rate. On the 7th day, for instance, significant differences were observed between enclosure B and enclosures A and D: the N_2 fixing phytoplankton population excreted large amounts of fixed ^{14}C.

The rate of photosynthesis per unit chlorophyll only increased significantly (particulate ^{14}C fixation rate increased from 3.3—6 and from 3.8—10.7 respectively) when the phosphorus and nitrogen imports were increased simultaneously. Under these conditions, it even significantly exceeded the photosynthesis rate of the phytoplankton in the Zingster Strom on the 7th day. The increased performance

Table 3. Heterotrophic activity; V_{max} fluctuations for glucose uptake in the different enclosures. Maxima and minima in $\mu g \cdot l^{-1} \cdot h^{-1}$

Enclosures	Minima	Maxima
A	1.9 (2100 hrs, 10 July)	24.7 (1300 hrs, 16 July)
B	1.9 (1700 hrs, 10 July)	21.6 (0900 hrs, 16 July)
C	2.7 (1300 hrs, 11 July)	47.1 (1300 hrs, 16 July)
D	2.0 (2100 hrs, 16 July)	14.7 (0500 hrs, 16 July)

capacity of the phytoplankton community per unit biomass and its stabilization in enclosure C as a result of nutrient import are the main causes of the increase in biomass.

According to SENFT (1978) the dependence of photosynthesis by algae on nutrient supply can be described by a saturation function. This certainly also applies to the different species in our pelagic community. Quantitative and qualitative variations in the composition of species will be superimposed upon this function because different species will find the conditions particularly good. If the nutrient import can maintain high rates of photosynthesis for a certain time, the result can be a highly productive plankton community with one or more dominant species.

4.3.2. Bacteria

Turnover times of 1 ... 2 hours in the heterotrophic potentials of all enclosures show that the pelagic zone is definitely eutrophic (cf. HAUBOLD 1981). This conclusion is corroborated by glucose uptake as V_{max} rates of 1.9 to 47.1 $\mu g \cdot l^{-1} \cdot h^{-1}$ (Table 3). The large short-term fluctuations in the maximum glucose uptake rates are particularly striking. On 16 July 1981, for instance, the V_{max} rate fluctuated between 2 and 15 in enclosure D, between 3.2 and 21.6 in enclosure B and between 4 and 25 $\mu g \cdot l^{-1} \cdot h^{-1}$ in enclosure A. These results clearly show that fluctuations in activity can compensate for changes in the enclosure.

Despite the considerable amplitude in the fluctuations of the V_{max} values, the highest values were as a rule obtained at 0900 hrs. This is possibly related to the cell division of the bacteria which, in North German lakes, reach its maximum in the early morning (KRAMBECK 1978).

Comparison of the V_{max} values for 16 July shows that in terms of glucose uptake the differentiation between the enclosures probably follows the trend C > A > B > D. The reduction in the glucose uptake rate in D is associated with a change in the bacterial species composition: the peptide consuming species proliferated at the expense of the carbohydrate consumers.

In enclosures A, C and D bacterial production was increased considerably by the import of NH_4^+ on 10 July. This cannot be considered an expression of a general increase in metabolic activity, however, but a consequence of the previous nitrogen deficiency. Bacterial production at first declined rapidly in enclosure D (Table 4), but on 16 July enclosures A, B and D scarcely differed, whereas the production rates

Table 4. Bacterial production (carbon in $\mu g \cdot l^{-1} \cdot d^{-1}$) and bacterial generation times (h) in the different enclosures. Changes during the experiment

Date	A		B		C		D	
	prod.	gen.	prod.	gen.	prod.	gen.	prod.	gen.
10 July	490	14.8	160	34.4	790	10.8	810	10.7
11 July	150	35.7	190	20.6	370	15.6	170	27.3
12 July	210	24.1	220	24.1	360	16.4	130	45.7
13 July	230	26.5	250	24.6	340	19.0	130	53.8
14 July	290	18.1	300	19.0	270	22.9	170	24.3
16 July	230	23.3	210	25.7	330	17.7	230	27.8

in enclosure C were about one third higher than in the others.

The mean bacterial generation times were between 23 and 27 hours. They were slightly shorter (18 h) in enclosure C and distincly longer (53.8 h) in enclosure D. The greater mean generation time in enclosure D can be considered an expression of the loading of the pelagic system due to the high NH_4^+ import.

4.3.3. Herbivorous zooplankton

At the end of the experiment the specific filtration rates ($\mu l \cdot ind.^{-1} \cdot h^{-1}$) of the two dominant species, *Eurytemora affinis* and *Chydorus sphaericus*, in all enclosures and in the Zingster Strom were measured. The filtering rates in enclosure A proved to be closest to those obtained for the Zingster Strom. The specific filtering rates of both species correlated positively with their production rates in the different enclosures.

Table 5. Feeding rates of the herbivorous zooplankton ($C_{phytopl.}$ in $\mu g \cdot l^{-1} d^{-1}$).
Comparison of initial and final values together with value of their quotients (1 µg $DW_{phytopl.}$ = 0.45 µg C).

Enclosures	Feeding rate		Quotient 16/10 July
	10 July	16 July	
A	415	810	1.9
B	252	560	2.2
C	174	470	2.7
D	391	40	0.1

Table 5 shows how the absolute feeding rates changed in the different enclosures. They increased in enclosures A, B and C and decreased in enclosure D.

Due to the small number of herbivorous zooplankton species, stress situations under these conditions have a more persistent effect on the zooplankton than on the phytoplankton or bacteria. However, despite the disappearance of species, relatively stable performances were in some cases retained for restricted periods of the experiment.

The feeding activity of the zooplankton followed a diurnal rhythm (Fig. 14). This, however, is of only minor importance in connection with the NH_4^+ rhythm that was observed because, for instance in enclosure D, there was scarcely any grazing activity at all.

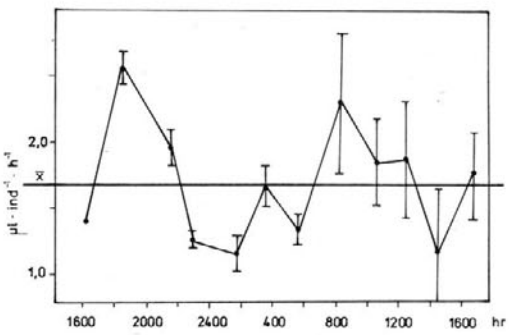

Fig. 14. Diurnal rhythm in food uptake by *Eurytemora affinis*. ^{14}C method; measured from 10—11 July 1981

5. Conclusions

5.1. Load capacity and rhythm

The performance potential and load capacity of the pelagic zone of the boddens are not yet being fully utilized during the summer, particularly in the permanently well mixed regions such as the Zingster Strom. At the phytoplankton level, this is due to the diversity of species. The total number of algal species hitherto found in the boddens is 375 (SCHNESE 1980a). Six genuinely planktic species (*Scenedesmus quadricauda*, *Lyngbya contorta*, *Stephanodiscus hantzschii*, *Oocystis* spec., *Monoraphidium contortum*, *Gomphosphaeria pusilla* and Cryptomonads as the principal species and another 20 accompanying species are present almost throughout the year. Changes in the relative dominances of the species ensure sufficient plasticity of the overal performance.

The higher assimilation numbers ($\mu g \cdot h^{-1}$ carbon per µg chlorophyll) found in the Zingster Strom in comparison with the Kirr Bucht (35% difference) (SCHIEWER 1984) are a result of the constant mixing in the former due to the alternation of inflow and outflow (additional energy input into the system as current energy) and can be verified experimentally by comparing enclosures A, B and D with the Zingster Strom. They can thus be considered typical of the whole chain of boddens.

The unilateral input of NH_4^+ at concentrations up to 50 µmol · l^{-1} has scarcely any effect on the pelagic system in the course of eight days. Any oscillations in the free NH_4^+ concentration become synchronized to a diurnal NH_4^+ rhythm as a result of the day/night alternation.

This rhythm correlates ($\alpha < 0.10$, SPEARMAN's rank correlation coefficient) with an opposing rhythm in the assimilation number (total ^{14}C fixation). The situation following an NH_4^+ input of 270 µmol · l^{-1} is similar ($\alpha < 0.15$, SPEARMAN's rank correlation coefficient). This high concentration, however, not only delays synchronization but also has a negative effect on the bacterial population and the herbivorous zooplankton, probably as a result of the temporarily high NH_3 concentrations.[2]

According to HELMER & SEKOULOV (1977), at a pH of 10 and a water temperature of 20 °C some 75 % of the ammonium is present as NH_3.

When NH_4^+ (113 µmol · l^{-1}) and PO_4^{3-} (18 µmol · l^{-1}) were added together, their concentrations were reduced to 5 ... 6 and 10 µmol × l^{-1} respectively within 8 days. The mean concentrations in the Zingster Strom during the experiments were 4 ... 5 µmol · l^{-1} NH_4^+ and 0.2 ... 0.4 µmol · l^{-1} PO_4^{3-}. This nutrient uptake in enclosure C was accompanied by a 2.8-fold increase in phytoplankton biomass (measured on the basis of the chlorophyll-a concentration). This means that light became the factor limiting further development in this enclosure.

The results presented here show that in summer the eutrophic pelagic zone is, because its NH_4^+ import is about 10 times as high as that of the free water, near the limit of its load capacity. This is signified by the occurrence of dangerous oscillations and a gradual transition to light limitation associated with a threefold increase in biomass. In the pelagic community, the NH_4^+ rhythm we have described and the correlated fluctuation in the assimilation number were accompanied by diel rhythms of ^{14}C dark fixation (by algae at suitable N concentrations) by rhythms in the saprobic population and in the filtering and feeding activities of the herbivorous zooplankton. In other words, disturbances in the system lead first to oscillations on the functional plane. The amplitude of the oscillations increases with the load until, if the disturbance is great enough, changes appear in the structures of the phytoplankton and zooplankton populations.

Metabolic performance per unit biomass remains relatively constant over a large range of variation in the level of the disturbance. This does not apply in regard of the bacteria, however, which compensate for any external influences acting upon the system by short-term fluctuations in activity without appreciable changes in biomass or bacterial counts.

A rather close interaction between the bacteria and the protozoans seems probable in view of the high degree of eutrophication. A closed cycle in the pelagic zone (phytoplankton — dissolved organic matter — bacteria — protozoans — phytoplankton) would yield plausible answers to many of the questions remaining open in regard of the material and energy flux. Such a closed cycle might in particular be based on the assimilation efficiency (50 % for bacteria, not more than 30 % for the protozoans) and the relatively high mortality of the protozoans. Appropriate investigations have already been planned for the coming years.

5.2. Successions

Although the experiment lasted only eight days, the following conclusions may be drawn regarding the trends followed by the pelagic community in summer:

Enclosure A: The phytoplankton and bacteria compensate more or less completely for the NH_4^+ import by means of their diurnal rhythms. The biomass increases, but there is no major change in species composition compared to the Zingster Strom. The net rate of increase in biomass (measured as the chlorophyll-a concentration) is 0.050 · d^{-1} on average, with maximum values up to 0.12 · d^{-1}.

Enclosure B: Changes in biomass are accompanied by changes in species composition of

2 Displacement of the dissociation balance $NH_4^+ + OH^- \rightleftharpoons NH_4OH$ in favour of NH_4OH. NH_4OH is written as NH_3 for the sake of simplicity.

the phytoplankton. Mass development of *Nodularia harveyana* fixes N_2 and thus leads to a steady state due to P-limitation. The mean net rate of increase in biomass is 0.045 $\times d^{-1}$, with maximum values up to $0.11 \cdot d^{-1}$.

Enclosure C: Development of a highly productive system accompanied by a major increase in biomass and a shift in favour of the green algae in the species composition. The onset of light limitation signifies that the steady state has been reached. The mean net rate of increase in biomass is $0.21 \cdot d^{-1}$ with maximum values up to $0.47 \cdot d^{-1}$.

Enclosure D: The diurnal rhythms of the community can only compensate for the high NH_4^+ import. Toxic effects appear due to the occasional presence of large concentrations of free NH_3. These slow down the bacterial activity and, depending on the NH_3 concentration, more or less eliminate the herbivorous zooplankton. The biomass increases, but the species composition remains the same as in the Zingster Strom except that the abundance of *Mallomonas* spec. increases. There are also clear changes in bacterial activity patterns. Organic substances accumulate because, at first, phytoplankton production remains constant. Declining NH_4^+ storage capacity of the system and an increase in pH during the daytime probably lead to an occasional "overturn" of the system into a more heterotrophic state. The mean net rate of increase in biomass reaches $0.063 \cdot d^{-1}$, with maximum values of 0.11 $\times d^{-1}$.

The changes in the species composition of the phytoplankton are reactions to the changes in the nutrient situation in the enclosures. The fact that the grazing rates in enclosures A, B and C were roughly identical shows that in a period of 8 days the feeding activities of the herbivorous zooplankton are insignificant in our context.

The main factor governing the development of the succession is the temperature. Due to the period of fine weather, the temperature rose from 16.5 °C on 4 July to 23.5 °C on 12 July 1981. This led to the collapse of the *Oscillatoria limnetica* bloom and encouraged the development of *Nodularia harveyana* and *Nodularia spumigena*, as is shown by the fact that the response to the increased temperature was similar in the Zingster Strom and all enclosures. The fact that the *Nodularia* species developed more vigorously in enclosure B than in the others is a sign of the fact that this development is encouraged by a relative nitrogen deficiency.

It is striking that the proportion of heterocysts on the *Nodularia* filaments in enclosure B was greater than in the Zingster Strom although the free NH_4^+ and NO_3^- concentrations were virtually the same in both environments.

Neither 50 nor 270 $\mu mol \cdot l^{-1}$ NH_4^+ led to appreciable changes in the phytoplankton succession in the course of seven days. The only hint of any such change was the more intensive development of *Mallomonas* spec. in enclosure D.

The decline of *Oscillatoria* can be accelerated by the simultaneous addition of NH_4^+ and PO_4^{3-}. But the most striking effect is that it counteracts the effect of the temperature: despite the high temperature, this double addition encouraged the development of the green algae (*Monoraphidium contortum*, *Scenedesmus* species) and, to a lesser degree, the diatom *Stephanodiscus hantzschii*. Had the nutrients not been added, these species would, due to their lower temperature optima, have been able to resist the competitive pressure of the *Nodularia* species.

6. Summary

1. Complex experimental studies (PEKOM) regarding effects of different NH_4^+ inputs on the pelagic system in the Zingster Strom were performed on enclosed samples from 9 July—17 July 1981. The short sampling intervals permitted a detailed analysis of the whole system.

The Zingster Strom is highly eutrophic in summer, and its phytoplankton community is N-limited.

2. Under P-limiting conditions (and possibly under other growth limiting conditions), surplus NH_4^+ is stored in organic form in the cells and is liberated rhythmically. The synchronization of this rhythm by the alternation of day and night leads to a diurnal variation in the pelagic NH_4^+ concentration. This NH_4^+ rhythm, which was described for the first time by SCHIEWER & BAADER (1982), is restricted mainly to the blue-greens. It is an important key to the process of eutrophication and the role played by the blue-green algae in eutrophic waters.

The NH_4^+ rhythm correlates with the total ^{14}C fixation

rate of the phytoplankton and with the day/night alternation of the saprophytic population.

3. The load capacity of the pelagic enclosures is not exceeded in summer by the addition of 50 µmol · l^{-1} NH_4^+ alone. The addition of 270 µmol · l^{-1}, in contrast, induces obvious disturbances in the system: toxic effects on the zooplankton and temporary reduction in the rate of bacterial activity.

4. The simultaneous addition of 113 µmol · l^{-1} NH_4^+ and 18 µmol · l^{-1} PO_4^{3-} leads to a 2.8-fold increase in biomass (measured in terms of chlorophyll-a concentration). The biomass of 223 µg · l^{-1} chl-a indicates that under these conditions light becomes the limiting factor.

In the course of 8 days the free NH_4^+ concentration was reduced to 10 ... 6 µmol · l^{-1} NH_4^+ (normal concentration in the Zingster Strom: 4 ... 5 µmol · l^{-1}) and the PO_4^{3-} concentration was reduced to 6 µmol × l^{-1} (normal concentration in the Zingster Strom: 0.2 ... 0.4 µmol · l^{-1}).

5. The most striking changes take place in the structures of the phytoplankton and zooplankton populations. The zooplankton changes are hardest hit on account of the small number of species present. The relatively slight variation in the bacterial counts and biomasses is remarkable. The existence of a closed cycle (phytoplankton — bacteria — protozoans — phytoplankton) appears probably.

6. In regard of performance parameters, the assimilation number (µg · h^{-1} carbon per µg chlorophyll-a) of the phytoplankton is fairly stable. It does not increase significantly until both nitrogen and phosphorus are added. The tendency to stabilize productivity is also typical of the zooplankton. Bacterial activity, in contrast, is characterized by distinct, and sometimes also very rapid fluctuations.

7. Although the pelagic system in summer was studied for only 8 days, the following trends in development were apparent: Enclosure A: NH_4^+ input is largely compensated for by oscillations that become diurnal rhythms.

Enclosure B: development of a *Nodularia harveyana* bloom which, by N_2 fixation, leads to a new steady state due to P-limitation.

Enclosure C: development of a highly productive phytoplankton system with distinct changes in the assimilation number and the structure of the phytoplankton population: green algae proliferate at the expense of the blue-greens.

Enclosure D: trend to establishment of a more heterotrophic system due to the development of flagellates and the increased appearance of proteolytic bacteria. Occasional elevated NH_3 concentrations lead to toxic effects particularly for the herbivorous zooplankton.

8. The principal factor that governed the development of the succession during the experiment was the temperature. It was the rising temperature that led to the collapse of the *Oscillatoria limnetica* bloom and the development of *Nodularia* species. This situation was encouraged by increasing N limitation (enclosure B). When NH_4^+ and PO_4^{3-} were added simultaneously, the *Oscillatoria* disappeared rapidly. However, it simultaneously permitted the development of green algae and, to a smaller degree, the diatom *Stephanodiscus hantzschii* although the temperature would have been too high for these species under normal circumstances.

9. The enclosure approach described here has proved to be a good way of analyzing the pelagic system of the shallow boddens south of the Darss-Zingst Peninsula and has the additional advantage of being economical. The results obtained have permitted a substantial reduction of research effort. Further improvement to the enclosure system will permit even better simulation of the situation in the boddens.

Zusammenfassung

1. Vom 9. 7. bis zum 17. 7. 1981 wurden am kompartimentierten Pelagialsystem (PEKOM) des Zingster Stromes komplexe Untersuchungen zum Einfluß von NH_4^+-Einträgen auf dessen Struktur und Funktion durchgeführt. Der enge Probennahmeabstand ermöglichte eine detaillierte Analyse des Gesamtsystems.

Der Zingster Strom ist im Sommer hoch eutroph. Blaualgen sind die dominierende Phytoplanktongruppe. Die Phytoplanktongemeinschaft ist N-limitiert.

2. Unter den Bedingungen einer P-Limitation (wahrscheinlich generell bei Wachstumslimitierung) werden überschüssige NH_4^+-Mengen vom Phytoplankton zellintern gespeichert und oszillierend freigesetzt. Die Synchronisation dieser Oszillationen durch den Tag/Nacht-Wechsel führt zur Ausprägung einer NH_4^+-Rhythmik im Pelagial.

Die von Schiewer & Baader (1982) erstmals beschriebene NH_4^+-Rhythmik ist vorwiegend an Blaualgen gebunden. Ihr kommt als wichtiger Schlüssel zum Verständnis des Eutrophierungsprozesses und der Rolle der Blaualgen in eutrophen Gewässern ökologische Bedeutung zu.

Die NH_4^+-Rhythmik ist mit der Rhythmik der Gesamt-^{14}C-Fixierungsrate des Phytoplanktons und dem Tag/Nacht-Wechsel der saprophytischen Population korreliert.

3. Die Belastungskapazität des kompartimentierten Pelagials wird im Sommer durch den einseitigen Zusatz von 50 µmol · l^{-1} NH_4^+ noch nicht überschritten. Der Zusatz von 270 µmol · l^{-1} NH_4^+ führt dagegen bereits zu deutlichen Störungen im System: toxische Wirkungen auf das Zooplankton, zeitweise Verlangsamung der bakteriellen Aktivität.

4. Durch den gleichzeitigen Zusatz von 113 µmol × l^{-1} NH_4^+ und 18 µmol · l^{-1} PO_4^{3-} wird die Biomasse um das 2,8fache erhöht (Chlorophyll-a-Basis). Sie er-

reicht mit 223 µg · l^{-1} Chl. a einen Wert, bei dem das submerse Licht zum begrenzenden Faktor wird.

Innerhalb von 8 Tagen werden die freien NH_4^+-Konzentrationen auf 10—6 µmol · l^{-1} NH_4^+ (Normalkonzentration im Zingster Strom 4—5 µmol · l^{-1}) bzw. 6 µmol · l^{-1} PO_4^{3-} (Normalkonzentration im Zingster Strom 0,2—0,4 µmol · l^{-1}) verringert.

5. Die auffälligsten Strukturveränderungen vollziehen sich beim Phyto- und Zooplankton. Auf Grund der geringen Artenzahl des Zooplanktons wirken sie sich hier am stärksten aus. Bemerkenswert ist die Konstanz der Bakterienzahl und -biomasse. Ein kurzgeschlossener Kreislauf Phytoplankton—Bakterien—Protozoen—Phytoplankton erscheint wahrscheinlich.

6. Innerhalb der Leistungsparameter ist die Assimilationszahl des Phytoplanktons (µg · h^{-1} Kohlenstoff pro µg Chl. a) eine recht stabile Größe. Erst unter dem Einfluß des gemeinsamen Zusatzes von N und P wird sie signifikant erhöht. Auch im Bereich des Zooplanktons ist die Tendenz zur Leistungsstabilisierung charakteristisch. Demgegenüber sind die bakteriellen Leistungen durch deutliche, zum Teil sehr schnelle Fluktuationen gekennzeichnet.

7. Trotz der nur 8tägigen Analyse des sommerlichen Pelagialsystems lassen sich Entwicklungstrends fassen:

Kompartiment A: Weitgehende Kompensation des NH_4^+-Eintrages über Oszillationen, die in diurnale Rhythmen übergehen.

Kompartiment B: Entwicklung einer *Nodularia harveyana*-Blüte, die über die N_2-Fixierung ein durch P-Limitation bedingtes neues Steady State erreicht.

Kompartiment C: Ausprägung eines hochproduktiven Phytoplanktonsystems mit deutlichen Veränderungen in der Assimilationszahl und in der Phytoplanktonstruktur (Förderung von Grünalgen und in geringem Maße von Diatomeen).

Kompartiment D: Tendenz zum Aufbau eines mehr heterotrophen Systems: Entwicklung von Flagellaten, verstärktes Auftreten proteolytischer Bakterien. Toxische Effekte, vor allem auf das herbivore Zooplankton, durch zeitweise höhere NH_3-Konzentrationen.

8. Der steuernde Umweltfaktor für die Sukzessionsentwicklung während des Untersuchungszeitraumes ist die ansteigende Temperatur. Sie verursacht den Zusammenbruch der *Oscillatoria-limnetica*-Blüte und das Aufkommen von *Nodularia*-Arten. Diese Entwicklung wird durch eine zunehmende N-Limitation begünstigt (Kompartiment B). Bei gleichzeitigem N- und P-Zusatz vollzieht sich das Absterben von *Oscillatoria* schneller. Gleichzeitig können sich vor allem Grünalgen, aber auch die Diatomee *Stephanodiscus hantzschii* trotz der für sie zu hohen Temperaturen erfolgreich durchsetzen.

9. Die vorgestellte Kompartimentierungsmethode ist für die Pelagialanalyse der Darß-Zingster-Boddenkette gut geeignet und besitzt ein günstiges Aufwand/Nutzen-Verhältnis. Die Ergebnisse gestatten eine erhebliche Verringerung des Untersuchungsprogramms. Durch zielgerichtete Verbesserungen am Kompartimentsystem kann es den Boddenbedingungen weitgehend angepaßt werden.

Резюме

Результаты комплексных восьмидневных экспериментальных исследований в эвтрофной солоноватоводной пелагической системе показывают, что добавление 50 мкмоль × $л^{-1}$ NH_4^+ или 113 мкмоль × $л^{-1}$ NH_4^+ и 18 мкмоль × $л^{-1}$ PO_4^{3-} хорошо переносится. Но прибавление 270 мкмоль × $л^{-1}$ NH_4^+ проявляет, напротив, токсическое действие на зоопланктон и вначале воздействует и на бактерии.

Одностороннее смещение содержания питательных веществ в пользу NH_4^+ приводит к появлению NH_4^+-ритмичности. При одновременном добавлении NH_4^+ и PO_4^{3-} биомасса фитопланктона в период исследований увеличивается в 2,8 раза. При этом свободная концентрация NH_4^+ снижается до 10 — 6 мкмоль × $л^{-1}$.

В пелагическом сообществе изменения в отношении фито- и зоопланктона являются наиболее заметными. Биомасса бактерий почти не изменяется.

Усилением N-ограничения фитопланктонная популяция смещается в пользу N_2-фиксирующих *Nodularia harveyana*. Избыток питательных веществ приводит к выраженному преобладанию зеленых водорослей.

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