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Abstract

In spring, summer and autumn enclosure experiments were performed in the central part of the Arkona Sea. The natural water with the plankton community was enriched by nutrients to about winter levels, and to the double of these concentrations.

In spring and summer, the phytoplankton responded with rapid uptake of nutrients and an increase in primary production and biomass. In autumn, the uptake of nutrients was also fast, whereas productivity did not increase, and biomass only in diatoms.

Not only did the production increase with higher nutrient supply, but also the productive season was prolonged. This fact is of importance for the function of the pelagic system in the Baltic, because the biomass and nutrients remaining after the spring bloom determine to a great extent the productivity of the whole year.

Introduction

Eutrophication is in nearly all natural ecosystems, and so in the Baltic Sea, a feature of increasing concern. It has now been proved to occur in most compartments of the Baltic ecosystem (ELMGREN 1984, LARSSON et al. 1985). Differences in the degree of eutrophication exist, dependent on the area under consideration. Generally, the coastal areas and the entrances to the Baltic are more menaced.

The effects of eutrophication, and also the sources are known in principle, but the pathways of the nutrients into the compartments, the transfer and the response to the impact are in most cases a matter of speculation.

This paper deals with some of the results of mesocosm experiments (ÖKEX, ecological experiments) carried out under *in situ* conditions in the Arkona Sea. By nutrient additions, natural (upwelling events) or artificial (man-made inputs) impacts on the pelagic system were simulated, and the response of the phytoplankton was studied. An attempt is made to apply some findings of the experiments on the pelagic system and to describe possible consequences.

Material and methods

The experiments were carried out at GDR-station 113 (also a site in the frame of the Baltic Monotoring Programme of the HELCOM), located at 54°55.5' N, 13°30.0' E. Cylindrical enclosures with a volume of 25.4 I floated in 2.5 m depth, fastened to a 200 m long rope between two moored marker buoys. The enclosures had a top and bottom side made of plexiglass, and a wall of 2 mm "gölzathen" foil. Further details on the containers and on the performance of the experiments are described in detail by SCHULZ et al. (1985).

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The experiments were carried out during the following periods:

ÖKEX '81	April 8 – 28, 1981
ÖKEX '78	July 7 – 27, 1978
ÖKEX '83	September 13 - 30, 1983

The chemical and biological methods used followed the standard procedures accepted for the Baltic Sea (ROHDE and NEHRING 1979, DYBERN et al. 1976). The doubling times of the phytoplankton (cell number) were calculated according to KNOECHEL and KALFF (1978), using the initial and the final values.

Results

Spring

The experiments started just before the onset of the spring bloom. Therefore, in the first experiment (Fig. 1), the nitrate concentration showed the high winter level. Also in the second experiment, this high concentration remained. After about one week, the surface water was depleted of nitrogenous nutrients, and the experiments with additions of



Figure 1

Nitrate concentration (μ mol dm⁻³) in experiments in spring 1981. OW - surface water

OW + N - surface water plus nutrients

OW + 2N - surface water with doubled nutrient concentration



Figure 2

Phytoplankton biomass (mg C m $^{-3}$) during experiments I – IV in spring 1981. Carbon is depicted on a logarithmic scale. Further details cf. Fig. 1 nutrients were started (experiments III + IV). Nitrate was taken up very rapidly. Differences between the four experiments did not occur.

The rapid development of the phytoplankton biomass and the partitioning between the different groups are shown in Fig. 2.

The phytoplankton was dominated by diatoms like *Thalassiosira rotula, Achnanthes taeniata, Skeletonema costatum* and *Chaetoceros* spp. The proportion of microalgae was relatively small, although they also increased during the experiments. Dinoflagellates appeared only in the last two experiments.

Summer

The surface water was completely depleted of nitrogenous nutrients, as is typical for this season (Fig. 3 and 4). In this experiment, deep water from the station (sampling depth 43 m) was added to the surface water in relation 2: 1, to simulate high ammonia input compared to nitrate. This comes closer to the natural conditions during this season in the sea area under consideration.

The phytoplankton consisted mainly of cyanobacteria and microalgae. Dinoflagellates and diatoms became more numerous during the experiments (Fig. 5). In all experiments with deep water additions, the microalgae responded fast at the beginning of the experiments. Similarly, the diatoms reacted with an increase in biomass. After a few days, however, the increase in biomass was only produced by the cyanobacteria, among other effects (e.g. recycling), an indication of their ability to fix molecular nitrogen (HÜBEL and HÜBEL 1980). In contrast to the spring experiments, in this period an increase of biomass was also observed in the control bags.

Autumn

Although the phosphate concentrations in the surface water showed a slight increase, the limiting nitrogenous compounds were still nearly depleted in this layer. After additions of nutrients to about winter concentrations (Fig. 6 and 7), only in the third experiment were both ammonia and nitrate taken up, whereas in the second experiment only ammonia was used up, because of the high nitrate concentration.

The phytoplankton was dominated by *Rhodomonas minuta*, diatoms and dinoflagellates played a minor role, whereas the cyanobacteria were completely absent during this season. Nutrient addition had nearly no effect on the total phytoplankton biomass (Fig. 8). This is caused mainly by the inactivity of the dominating microalgae. On the other hand, diatoms and dinoflagellates showed a remarkable increase in cell numbers. Diatoms like *Rhizosolenia fragilissima, Coscinodiscus radiatus*, and later *Skeletonema costatum*, as well as small dinoflagellates, became more abundant.

Discussion

Experiments with enclosed plankton communities ought to be considered only as approximations of natural conditions for several reasons (BOYD 1981). They can only in certain limits describe the processes which govern natural ecosystems. On the other hand, they are the only possibility to study these processes under conditions as close to the environment as possible. In addition to the enclosure experiments (with all their advantages and restrictions) described here, short-term experiments (hours to days) were used to explain the reactions of the plankton community in the long-term process of eutrophication (years to decades).

The results obtained confirmed findings from time series investigations and long-term studies in the pelagic system (NEHRING et al. 1984) (see discussion of increased



OW

- surface water OW + TW - surface water plus deep water



Nitrate concentration (µmol dm⁻³) during experiments I - IV in summer 1978. Further details cf. Fig. 3

phytoplankton productivity and biomass after nutrient addition and reaction of phytoplankton species composition).

In the experiments, of course, the nutrient concentrations used were much higher than the natural annual increase obtained from linear regression. NEHRING (1981) calculated a value of 0.05 µmol dm⁻³ a⁻¹ for phosphate and of 0.19 µmol dm⁻³ a⁻¹ for nitrate for the Arkona Sea. These concentrations were not used in the experiments, because the response of the plankton community would have ranged within the margin of error of the methods. Therefore, concentrations in the dimension of the winter surface values were used, also from the viewpoint that they might be the maximum inputs after upwelling events lift up nutrient rich deep water from below the halocline.



Figure 5

Phytoplankton biomass (mg C m⁻³) during experiments I – IV in summer 1978. The scales for carbon overlap; and carbon is depicted on a logarithmic scale. Further details cf. Fig. 3



Concentration of ammonia (µmol dm⁻³) during experiments I – III in autumn 1983. Further details cf. Fig. 1



Further details cf. Fig. 1

Response of phytoplankton to nutrient additons

The nitrogen compounds were taken up by the phytoplankton in the order ammonia – nitrate (SCHULZ et al. 1985). This has been stated by DUGDAL and GOERING (1967), and also proven for the Baltic Sea by GRANÉLI (1981) in her experiments. Both ammonia and nitrate were taken up after four days in the experiments with simulation of the winter concentrations. A doubled amount of nitrogen resulted in an uptake prolonged by about one day. This fact is especially important if we consider the proven nutrient increase in the winter surface water in the last years (NEHRING 1981), and its possible consequences will be discussed later in detail.



Figure 8

Phytoplankton biomass (mg C m^{-3}) during the experiments I – IV in autumn 1983. Carbon is depicted on a logarithmic scale. Further details cf. Fig. 1

The relative uptake of nutrients (except for nitrate in autumn) was surprisingly similar in all three seasons investigated (Tab. 1), although important factors for this process (phytoplankton composition, and physiological stage, light) were different. At least for phosphate, the dependence of the absolute uptake rates on the initial concentrations was obvious (KETCHUM 1939). In the case of ammonia and nitrate, this relation is not clear, probably due to the changing relation between the two nitrogen compounds in the experiments.

Table 1

Initial concentrations I (μ mol dm⁻³), mean daily uptake rates U (μ mol dm⁻³ d⁻¹) and relative uptake of phosphate, nitrate and ammonia in the experiments with single nutrient addition (n = number of values)

	PO ₄ ³⁻			NO ₃				NH ₄ +				
	I	U	<u>U</u> · 100	n	1	U	$\frac{U}{I} \cdot 100$	n	I	U	<u>U</u> · 100	n
spring '81 summer '78 autumn '83	0.92 0.54 0.93	0.16 0.08 0.13	17.4 14.8 14.0	20 20 15	3.20 1.01 4.32	0.65 0.23 0.42	20.3 22.8 9.7	20 20 15	2.98 3.09 2.66	0.65 0.55 0.51	21.8 18.1 19.2	20 20 15

Phytoplankton biomass and species composition

For the discussion of the changes in the phytoplankton after nutrient additions, doubling times were used, because they give more detailed information on alterations at the level of species or groups of phytoplankton, in comparison to the values for chlorophyll or primary production, which were also available.

As could be seen from Tab. 2, which shows two consecutive periods from experiment I (compare Fig. 2), the doubling activity of the diatoms and microalgae decreased with the depletion of the nutrient stock. The response of the various species, however, was different. Tab. 3 shows a phase where the nutrients were exhausted and additions performed in two different concentrations. An effect of nutrient addition and the dependence from the concentration were visible at these levels. Striking differences also existed between the species considered.

Table 2

Doubling time ($t_{\rm D}$ [h]) of phytoplankton groups (cell number) during experiment I in spring 1981 (TCN – total cell number, SW – surface water)

	SW (April 8–13, 1981)	SW (April 14–20,1981)
TCN	34.4	80,8
Microalgae	35.7	81.6
Thalassiosira spp.	28.0	268.5
Skeletonema costatum	34.0	91.3
Chaetoceros spp.	23.4	79.6

Tab. 4 exemplifies the situation during the summer experiment. An effect on the phytoplankton activity was shown in all groups, but the different groups exhibit remarkable differences in their response. Slow reactions of microalgae and dinoflagellates stand against high activity in diatoms and in cyanobacteria.

Table 3

Doubling time (t_D [h]) of phytoplankton groups (cell numbers) during experiment II (April 15–21) in spring 1981

(SW + N - surface water plus nutrients

SW + 2N - surface water plus doubled amount of nutrients)

	SW	SW + N	SW + 2 N
TCN	102.1	49.7	42.1
Microalgae	111.1	65.5	57.6
Thalassiosira spp.	82.1	74.6	61.3
Skeletonema costatum	59.1	46.3	39.2
Chaetoceros spp.	126.4	33.9	28.5

Table 4

Doubling time ($t_{\rm D}$ [h]) of phytoplankton groups (cell numbers) during experiment III (July 17–25) in summer 1978

(SW + DW - surface water plus deep water)

	SW	SW + DW
TCN	- 226.5	140.6
Microalgae	- 186.0	158.0
Cyanobacteria	82.8	68.3
Dinoflagellates	- 53.8	534.3
Diatoms	50.1	32.5

The autumn conditions reflected the low activity of the dominating flagellate stock and therefore the unimportant changes in biomass as a whole. Diatoms and dinoflagellates, on the other hand, responded quickly, and their doubling times clearly decreased (Tab. 5).

Table 5

Doubling time (t_{D} [h]) of phytoplankton groups (cell number) during experiment III (September 21–27) in autumn 1983

	SW	SW + N
TCN	- 165.4	2613.7
Microalgae	- 164.8	2126.6
Dinoflagellates	64.0	48.7
Diatoms	228.6	83.1

Alterations in the species composition of the dominating forms did not occur in any of the three seasons of the experiment, because of the differing response of the considered groups to nutrient additions. Changes in the dominance relation appeared, however.

The clearest response of the phytoplankton to nutrient addition in the three seasons considered, was noticed in spring. In summer as well as in autumn only a part of the phytoplankton community answered the impact. Because it was the dominating part in summer (cyanobacteria and microalgae) also the biomass as well as the primary production and the chlorophyll content showed an increase. In autumn, however, the

dominating microalgae did not respond, and only a small part of the diatoms and dinoflagellates answered. Therefore no reaction in total biomass, primary production or chlorophyll was observed.

The phytoplankton, however, took up the nutrients at nearly the same rate and dimension as in the spring and summer experiments. The high amount of nutrients added was possibly a physiological stress for the low-nutrient-adapted microalgae (PARSONS et al. 1977). Another explanation could be that starving phytoplankton has anomalous C : N and C : P ratios with a surplus of carbohydrates and lipids (HEALEY 1979). After nutrient addition, uptaken nutrients will be used for the synthesis of stored carbon to protein. There is no need for photosynthesis in this phase. LEAN and PICK (1981) arrived at similar results and concluded that in the case of a very low internal nutrient pool, primary productivity measurements are sufficient as a measure of activity.

Possible consequences of nutrient additions for the pelagic ecosystem of the Baltic Sea

As the experiments have shown, the input of nutrients leads not only to higher phytoplankton activity (primary production), but also to a prolongation of the productive period (SCHULZ et al. 1985). This seems to be especially important under spring conditions, because the gap in the time scales of phyto- and zooplankton development becomes smaller. This means that a bigger proportion of the spring phytoplankton biomass may be utilized by the developing zooplankton, which increases its biomass and thus retains a larger part of potential chemical energy in the pelagic system. In this way, summer production might be influenced positively.

From the experiments, however, it also turned out that the input of nutrients in the different seasons does not lead to changes in the species composition. Only the dominance relations change as a response. This is also the actual result of most of the phytoplankton studies until now, which conclude that although winter nutrient levels increased significantly, changes in species composition could not be proved (WULFF et al. 1986).

Nutrient inputs to the pelagic system in different seasons have a different meaning for the ecosystem. In spring, the phytoplankton production responds fastest to the impact, and because of the early stage of zooplankton development, the largest part of the addition is sedimented and acts as an oxygen sink in deep water. Only a small share increases the productivity over the whole year, as was mentioned above.

The summer situation in the Baltic is characterized by a well-balanced pelagic community (SCHULZ and BREUEL 1984), a grazed down phytoplankton stock and a highly developed zooplankton community. This system also reacts very rapidly to an input of nutrients. In contrast to the spring conditions, however, the additional energy leads to an enhancement of the productivity of all compartments of the pelagic system. The organic substance is retained in the euphotic layer and recirculated several times, and sedimentation is negligible during this time (PRANDKE 1980, PEINERT et al. 1982).

If the addition is not completely transferred to fish biomass or higher predatores, it threatens the oxygen in deep water later on.

The autumn situation equals the spring conditions again, because the decrease of the zooplankton stock tends to misbalance the pelagic system, leading to a higher sedimentation of newly produced algal biomass.

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