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The Effect of Sediment Flushing by Density Displacement of Interstitial Water on Pelagic Primary Production and Microbial Activity*)

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Summary: Nutrient and oxygen levels and ratios, primary production and data on bacterial activity recorded during an enclosure experiment carried out in July/August 1974 in Kiel Bight are presented and discussed. Considerable amounts of nutrients were released from the sediments due to density displacement of interstitial water and this was found to have a direct effect on phytoplankton production. Ammonia levels outside the enclosure were low and, in contrast to other nutrients and oxygen which were highly correlated with each other, ammonia showed no correlation with any other parameter. Presumably, ammonia released from the sediments escaped detection due to rapid uptake by phytoplankton. Reactive nitrogen, specifically ammonia thus seemed to be the limiting factor for primary production during the experiment. Sediment flushing also led to increased bacterial numbers and activity in the water column, however, this effect could only be measured inside the enclosure.

These aspects of sediment/water interaction and their effect on the dynamics of shallow coastal ecosystems are discussed.

Der Effekt von Sedimentdurchspülung durch Dichteverdrängung des interstitiellen Wassers auf die pelagische Primärproduktion und mikrobielle Aktivität (Zusammenfassung): Nährsalz- und Sauerstoffgehalt, Nährsalzverhältnisse, Primärproduktion sowie Daten über Bakterienaktivität, die während eines Plastikschlauchexperiments in der Kieler Bucht im Juli/August 1974 gesammelt wurden, werden beschrieben und diskutiert. Hohe Nährsalzfreisetzung aus dem Sediment, hervorgerufen durch Dichteverdrängung des interstitiellen Wassers, hatte einen direkten Einfluß auf die Phytoplanktonproduktion. Alle Nährsalze korrelierten hochsignifikant untereinander und mit Sauerstoff, nur Ammoniak außerhalb des Schlauches zeigte keine Korrelation mit den anderen Parametern. Außerhalb wurden nur sehr niedrige Ammoniakkonzentrationen gemessen, da wahrscheinlich durch die sofortige Aufnahme durch das Phytoplankton das aus dem Sediment freigesetzte Ammoniak nicht erfaßt werden konnte. Reaktiver Stickstoff, in diesem Fall Ammoniak, schien der limitierende Faktor für die Primärproduktion während dieses Experiments zu sein. Die Ausspülung des Sediments führte ebenfalls zu einer Erhöhung der Bakterienzahl und -aktivität, dieser Effekt war jedoch nur innerhalb des Schlauches meßbar.

Diese Aspekte der Wechselwirkung Meer — Meeresboden und ihre Auswirkung auf die Dynamik von Flachwasserökosystemen werden behandelt.

Introduction

The plankton tower is a 16.5 m steel structure used both as a sampling platform and as a support for suspending cylindrical plastic enclosures of 2 m diameter and 11 m length. These enclosures isolate a column of water from the surface to the bottom, including the sediment. These experiments are used to study the interaction between a given water column and the patch of sediment underlying it.

In this paper, further results of an experiment conducted within the plankton tower from 26. 7.—27. 8. 1974 are presented and discussed. Salinity data from within the

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enclosure and the outside water showed that leakage of enclosure water took place through the sediments and through holes in the enclosure fabric close to the surface. This water exchange was driven by density changes in the surrounding water, and resulted in the displacement of interstitial water leading to rapid increase in nutrient content of the bottom water. Sediment flushing took place both inside the enclosure and in the outside waters but due to lesser dilution of interstitial water within the enclosure, the effects of flushing were accordingly more pronounced here. This mechanism of sediment flushing has been described elsewhere in detail (SMETACEK et al. 1976), the effect of flushing on nutrient relationships, primary production and bacterial activity will be discussed here.

Sampling and Methods

The sampling site had a depth of about 10 m. Only one enclosure was used during the experiment. This was a bottle-shaped structure 12 m long, open at both ends. The lower end (diameter 2 m) was attached to the sediment which consisted of coarse sand overlying hard glacial marl. The neck of the enclosure was 0.8 m in diameter and protruded out of the water. A detailed description of the experimental set up has been given by v. BODUNGEN et al. (1976).

Temperature and salinity were measured at 1 m intervals with a T/S sensor (Electronic Switchgear, London, accuracy $\pm$ 0.1 C° and $\pm$ 0.1‰ S). Discrete samples were taken with a 5 l water bottle from inside and outside the enclosure at depths of 0, 3, 6 and 9 m. Nutrients were determined by the following methods: phosphate (MURPHY and RILEY 1962 modified by KOROLEFF 1964[1]), dissolved silicate (GRASSHOFF 1964a), ammonia (GRASSHOFF and JOHANNSEN 1972), nitrate (GRASSHOFF 1964b), nitrite (BENDSCHNEIDER and ROBINSON 1952). Oxygen (Winkler method) and pH were also determined.

Samples for chlorophyll *a*, phytoplankton counts, dissolved organic carbon (DOC) and primary production measurements were also taken from the same bottles. DOC was determined according to EHRHARDT (1969). The ^{14}C-method was used for primary production (STEEMANN-NIELSEN 1952). The bottles were incubated in-situ from 1200 to 1600 hrs.

Microbiological samples were taken every second day with sterile 2 l glass bottles from surface, 6 m and 9 m depths inside and outside the enclosure. They were worked up within 2 hours after sampling and kept at "in-situ" temperatures during the intervening period.

Counts of viable bacteria were carried out using the KOCH plating method with ZOBELL's medium 2216 E of a salinity of 8‰.

Maximum uptake velocity of glucose (V_{max}) was determined according to WRIGHT and HOBBIE (1966) as described by GOCKE (1975). The consumption in per cent per hour of the pool of free dissolved amino acids by heterotrophic bacteria was determined by the method of WILLIAMS and ASKEW (1968), modified by GOCKE (1976).

Incident radiation was measured with a solarigraph (KIPP and ZONEN, Holland) according to MOLL-GORCZYNSKI. This instrument measures solar radiation between 350—1500 nm in cal cm^{-2} sec^{-1}.

[1]) Personal communication by Graßhoff.

Results

Nutrients

Nutrient distribution within the enclosure shows four distinct phases where concentrations at the bottom rose abruptly and dropped again. These four periods, accompanied by corresponding depressions in O_2 and pH values, always coincided with an increase in salinity within and outside the enclosure. In a previous paper (SMETACEK et al. 1976) this phenomenon has been attributed to higher density water entering the enclosure from outside, thus flushing in sediment pore water with its high nutrient and CO_2 load. This density displacement was also observed outside the enclosure, although nutrient levels here were lower than levels within the enclosure. In fig. 1, salinity, O_2, PO_4—P, NH_4—N, SiO_4—Si values measured at the 9 m depth both outside the enclosure and within it have been depicted. The 4 periods of sediment flushing have been indicated by roman numerals. The close correspondence between all parameters measured inside the enclosure, is clearly evident. Outside the enclosure, a similar correspondence is to be seen, inspite of the lower nutrient and higher O_2 values recorded here. The NH_4—N curve, however, does not follow this pattern as closely as the other nutrients, the ammonia values measured outside were also much lower, by a factor of about 10, than inside the enclosure. Nitrate and nitrite levels both inside and outside the enclosure were consistently very low throughout the experiment, remaining at the level of detection of the method employed. These values have therefore not been taken into account here.

Correlations carried out between oxygen (μgat l^{-1}) and individual nutrients (μgat l^{-1}) for 9 m values outside and inside the enclosure were highly significant ($p < 0.1\%$) with the exception of ammonia outside the enclosure where no significant correlation was present.

Correlations in table form:

	Outside			Inside	
	ratio	n	r	ratio	n	r
O : P	— 243 : 1	22	— 0.68***	— 184 : 1	22	— 0.91***
O : N	no correlation			— 17 : 1	22	— 0.84***
O : Si	— 14 : 1	21	— 0.68***	— 11 : 1	21	— 0.81***
Si : P	14 : 1	21	0.77***	11 : 1	21	0.82***
N : P	no correlation			8 : 1	22	0.80***

Correlations between the nutrients were also highly significant with the exception of ammonia outside the enclosure. The Si : P ratio inside and outside the enclosure was 11 : 1 and 14 : 1 respectively. The lower ratio recorded from within the enclosure was partly caused by the steady accumulation of phosphate which took place after the III flushing event within the enclosure. Ammonia and silicate values decreased after the higher density water left the enclosure although phosphate values remained at about the same high level (2 μgat l^{-1}). Simultaneously, phosphate levels at the 6 m and 3 m depths also increased steadily, the highest phosphate value recorded during the experiment was 3.3 μgat l^{-1} and was measured at 6 m at the end of the experiment (day 33). No similar accumulation was observed between III and IV flushing events in the case of the other nutrients, except for O_2 and pH values which followed phosphate inversely. The high phosphate levels were certainly not due to leaching from the enclosure walls.

Nutrient levels in the upper 6 m were generally low throughout the experiment, although the increased nutrient input from the sediments due to flushing was occasionally

noticeable in the entire water column both inside and outside the enclosure. On the whole, nutrient levels in the upper 6 m were higher within the enclosure than outside, O_2 and pH values accordingly were also generally lower here.

Primary Production

In Kiel Bight, the euphotic zone generally extends to about 15 m depth during the summer months (v. BODUNGEN 1975). During the experiment, maximum production values in outside water were generally recorded at the 3 m depth, and production at 9 m was comparatively low. The dominant phytoplankter was *Ceratium tripos*, an organism known to carry out vertical migration (HASLE 1950). It seems likely that this dinoflagellate actively maintained the depth best suited to it, which seemed to be at 3 m in the outside water and at the surface within the enclosure as shown by plankton counts. Thus, almost all primary production within the enclosure took place at the surface and the values recorded here tended to be higher than those recorded from outside for any one depth. The highest value for the 9 m water column recorded for any one day inside the enclosure was 0.3 g C m^{-2} d^{-1} for day 29. Outside the enclosure, values close to 0.5 g C m^{-2} d^{-1} were measured on 4 occasions (days 17, 21, 27, 31).

In fig. 2, integrated values for primary production (g C m^{-2} I^{-1}) for the 9 m water column outside the enclosure have been compared with total irradiation (cal cm^{-2} I^{-1}) recorded during the incubation period of 4 hours (I = 1200—1600 hrs) and with one nutrient (mgat SiO_4—Si m^{-2}). The primary production curve is evidently linked to nutrient concentration and not to radiant energy, although variation in both is by a factor of about 8. Correlations between the nutrients phosphate and silicate with primary production outside the enclosure were highly significant ($p < 0.1\%$), whereas neither total irradiation, phytoplankton biomass nor chlorophyll *a* correlated with the primary production.

Photosynthetic rates per unit of population, expressed as chlorophyll *a*, in the 9 m water column (mg C / mg chl *a* / h) showed little variation apart from three values recorded during the III flushing event. In the period preceding the III flushing (up to day 15) values ranged between 1.3 and 1.9 mg C / mg chl *a* / h. No apparent effect of either irradiation or flushing was observed. From day 17 to day 21, corresponding to the III flushing event, values increased to 6.3, 2.6 and 3.7; these higher values were accompanied by an increase in both radiant energy and nutrients. Thereafter, the photosynthetic rate declined and remained steady at 2.2 mg C / mg chl *a* / h during the last week of the experiment.

Inside the enclosure, primary production was uniformly low and hence did not correlate with any other parameter. This is not surprising, as within the enclosure nutrient concentrations were relatively high and poor light conditions evidently limited production. However, light measurements at the surface inside the enclosure showed that variation here was much less than outside. This was due to the bottle-shaped enclosure with its long narrow neck, which allowed only light from directly above to enter the enclosed water column. Incident radiation at the surface inside the enclosure therefore, did not differ as much from day to day depending on cloud cover, as was the case outside.

In a subsequent experiment carried out in 1975, the shape of the enclosure was changed, the neck was made conical with a wider opening. Primary production inside the enclosure was higher than in the outside water here.

Tafel 1 (zu B. v. Bodungen et al.)

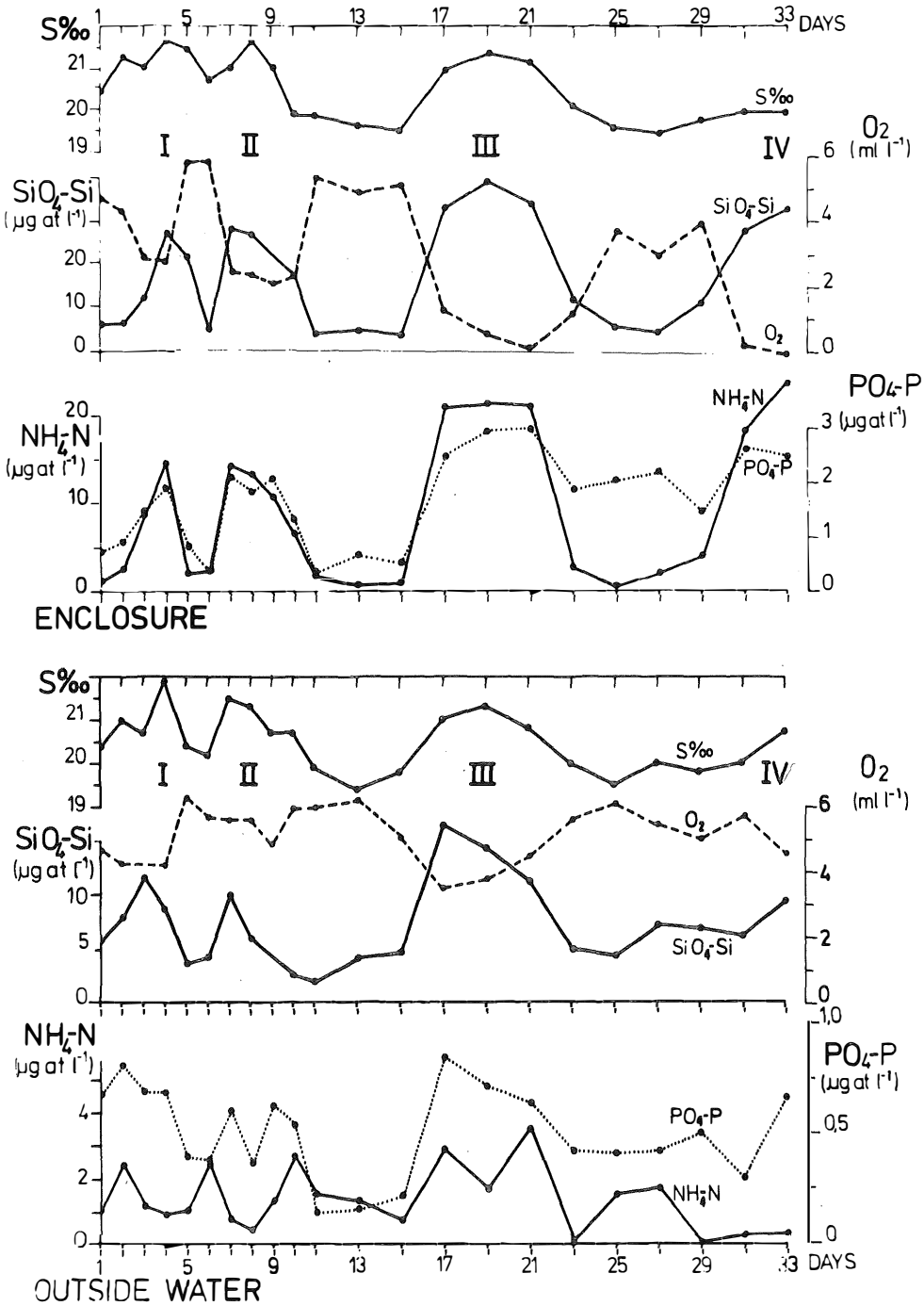

Fig. 1: Salinity, oxygen, silicate, phosphate and ammonia values from the 9 m depth of the enclosure and outside water (note different scales used for nutrients in enclosure and outside water).

Tafel 2 (zu B. v. BODUNGEN et al.)

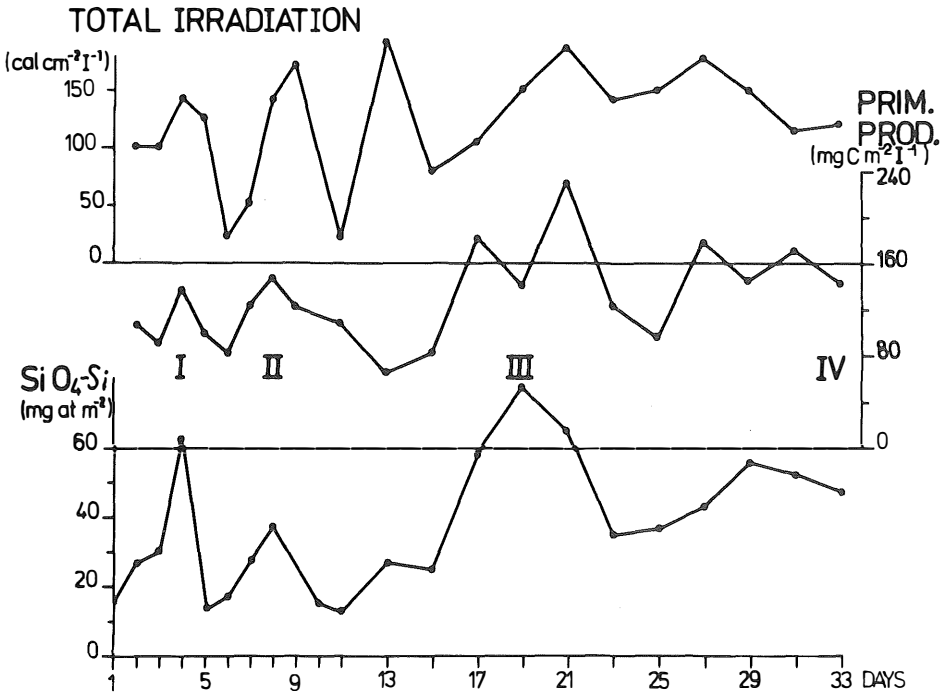

Fig. 2: Surface irradiation (cal m^{-2} I^{-1}) and primary production integrated for the 9 m water column (mg C m^{-2} I^{-1}) for the 4 hours of incubation time (I) and integrated values for silicate (mg at SiO_4 — Si m^{-2}) for the outside water.

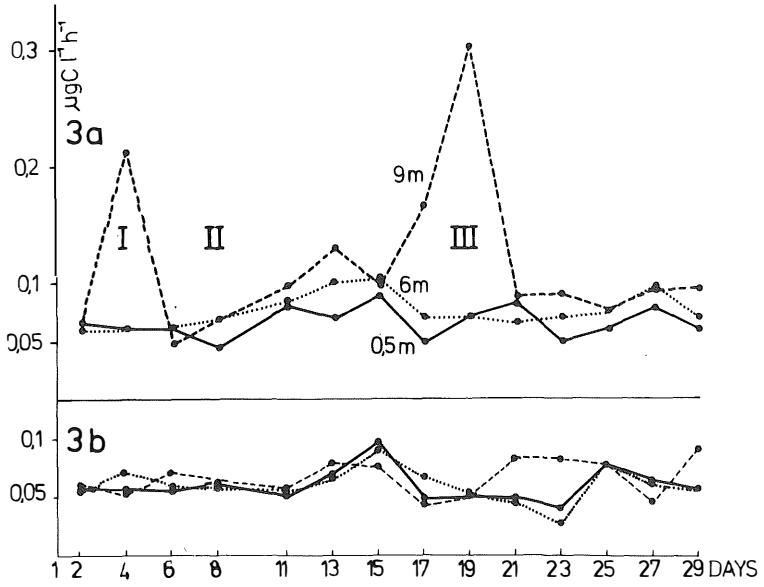

Fig. 3: Maximum uptake velocity of glucose (V_{max}) inside (3a) and outside the enclosure (3b).

Bacterial numbers and activity

Counts of viable bacteria (plate counts) showed that concentrations outside the enclosure (1000—3000 ml^{-1}) agreed well with data collected elsewhere in Kiel Bight for the summer months. Inside the enclosure, however, counts fluctuated greatly but were always higher, sometimes by up to two orders of magnitude. This was true for all three depths and no direct effect due to water exchange was noticeable. Surprisingly, data for potential heterotrophic microbial activity measured as maximum uptake velocity of glucose (V_{max}) were much the same inside and outside the enclosure with the exception of some 9 m values. V_{max} values are an indication of the size of the total active bacterial population, therefore it has to be assumed that total bacterial numbers were similar inside and outside the enclosure, apart from the bottom water in the enclosure. The increase in values of viable bacteria obtained by plate counts is probably due to a qualitative and not a quantitative change in the microflora within the enclosure.

V_{max} values for surface, 6 m and 9 m depths from outside and inside the enclosure have been depicted in fig. 3. Two major peaks — on days 4 and 19 — at the 9 m depth inside the enclosure are conspicuous, these peaks coincide exactly with the I and III flushing events, although no effect of the II flushing is evident. The measurements were carried out only till day 30, the IV flushing event (day 33) was not recorded. Apart from these peaks, rates of maximum glucose uptake by heterotrophic microorganisms recorded during the experiment (0.05—0.1 $\mu g\ C\ l^{-1}\ h^{-1}$) compare well with values for the same months recorded at other stations in Kiel Bight. Whereas values for the 3 depths showed no differences in the outside water, there was a noticeable increase in the uptake velocities from surface to bottom within the enclosure.

Per cent uptake of the pool of dissolved free amino acids per hour, depicted in fig. 4, did not vary much in the outside water during the experiment (4—12.5%, equivalent to a turnover time of 25—8 hours respectively), here also values for the 3 depths were similar. In contrast to this, considerable variability in turnover times of amino acids inside the enclosure are to be seen. Surface and 6 m values run parallel, the surface values being consistently lower. Both curves exhibit 3 distinct peaks, coinciding exactly with the 3 flushing events. The 9 m values show only 2 major peaks coinciding with the I and III flushing events and thus show basically the same tendency as the V_{max} data. The highest value recorded was 40% per hour — a turnover time of 2.5 hours.

Dark assimilation of CO_2, routinely estimated as a correction factor during ^{14}C primary production measurements, is mainly due to bacterial activity (Sorokin 1974). The values recorded at 9 m within the enclosure show the same picture as the V_{max} and per cent amino acid uptake data. However, apart from the major peaks during the I and III flushing events, a minor peak coinciding with the II flushing and a major one at the end of the experiment, during the IV flushing, are also present. Values from within the enclosure in between flushing events were similar to outside values (0.22 $\pm$ 0.08 mg C $m^{-3}\ h^{-1}$). Peak values during the II and the I, III and IV flushing events were 0.48 mg C $m^{-3}\ h^{-1}$ and 0.89 $\pm$ 0.04 mg C $m^{-3}\ h^{-1}$ respectively.

Dissolved organic carbon (DOC)

DOC values were fairly uniform at about 2.5 mg C l^{-1}, values below 2 mg C l^{-1} and above 3.5 mg C l^{-1} were recorded only occasionally. No noticeable difference was observed between values inside the enclosure and in the outside waters, and no relationship with any other parameter could be ascertained.

Discussion

Interaction between the water column and sediments in coastal ecosystems takes many forms. The role played by the sediments in supplying phytoplankton with nutrient salts is one of the most important aspects of this sediment / water interaction. Its significance for the functioning of the whole system has been recognised in recent years (v. BODUNGEN et al. 1975, ROWE et al. 1975).

The original intention behind the enclosure experiment described here was to quantify the processes comprising interaction between a water column and the patch of sediment underlying it. Leaks in the enclosure walls and the high permeability of the sediments which led to regular water exchange, prevented any budget calculations being made. In order to prevent water exchange, a stainless steel tub filled with sediment was used with great success in a subsequent enclosure experiment.

SMETACEK et al. (1976) described how, due to vertical density displacement, nutrients dissolved in interstitial water can be forced out of the sediments into the water column. They showed, taking silicate as an example, that only interstitial water with its heavy nutrient load could account for the rapid increases recorded in nutrient content of bottom water. VAN BENNEKOM et al. (1974), studying the silicate budget in the western Wadden Sea, reached a similar conclusion to explain their results. They presumed that an active mechanism for interstitial water exchange, in this case the 'subtidal pump' (the exchange of interstitial water by wave action) described by RIEDL et al. (1972), was behind the high silicate levels encountered by them in bottom water.

The results presented here show that the admixture of interstitial water to the water column leads to an increase in all nutrients and a depression in oxygen content. This effect was more pronounced within the enclosure, and therefore easier to study here, as large scale mixing and advection processes led to greater dilution in the outside water. Besides, it can be presumed that the original nutrient ratios in 'freshly flushed' water inside the enclosure were unchanged, as the phytoplankton content of this water was always very low, due to the filtering effect of the sediment. However, mixing processes outside lowered nutrient levels and also added phytoplankton to the 'freshly flushed' water; the phytoplankton biomass levels recorded here were essentially similar to surface values. Therefore, selective nutrient uptake by phytoplankton, only possible outside the enclosure, would lead to a change in original nutrient ratios. This is shown in table 1

Table 1

Nutrient atomic ratios during flushing

(9 m values)

flushing event	day	inside N : Si : P	outside N : Si : P
I	3	6.0 : 8.3 : 1	1.7 : 16.6 : 1
	4	7.7 : 14.2 : 1	1.4 : 12.4 : 1
II	7	6.7 : 13.2 : 1	1.2 : 16.2 : 1
	8	7.3 : 14.6 : 1	1.2 : 16.2 : 1
III	17	8.5 : 13.1 : 1	3.4 : 19.2 : 1
	19	7.3 : 13.4 : 1	2.3 : 19.7 : 1
	21	7.2 : 11.5 : 1	5.4 : 17.3 : 1
IV	31	7.3 : 11.2 : 1	1.1 : 20.3 : 1
	33	9.7 : 13.7 : 1	0.5 : 14.1 : 1

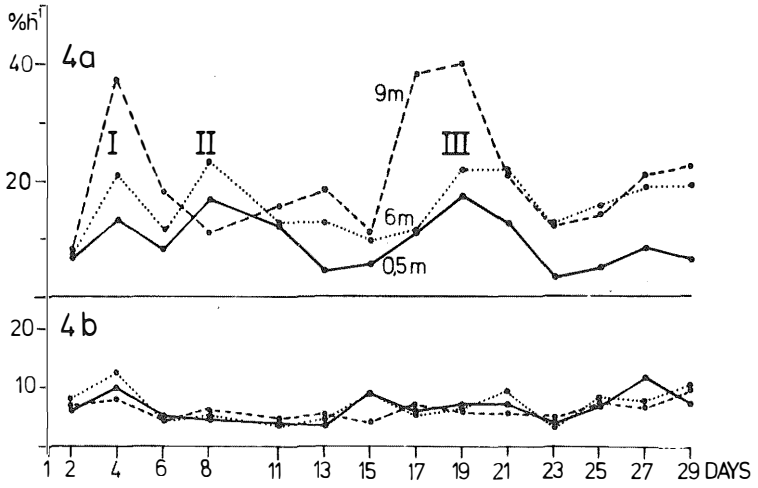

Fig. 4: Per cent uptake of the dissolved amino acid pool inside (4a) and outside the enclosure (4b).

where N : Si : P atomic ratios for the 4 flushing events from inside and outside the enclosure have been given. It can be assumed for the above reasons that the ratios within the enclosure are original values not altered much by phytoplankton uptake, as nutrient levels and their ratios remained fairly constant after flushing as long as higher salinity water remained within the enclosure. In contrast to this, the very low N : P and the higher Si : P ratios in the outside water are most probably due to very rapid uptake of ammonia as compared to phosphate and particularly silicate. Silicate can be regarded as the more conservative parameter here, as dinoflagellates increased and became dominant during the experiment both inside and outside the enclosure. There was accordingly more silicate present in relation to other nutrients in the outside water as compared to the enclosure.

Ammonia release from the sediments is a well documented fact (Rowe et al. 1975), so there is no reason to believe that ammonia input from the sediment outside the enclosure would be so much lower in proportion to other nutrients and oxygen as compared to within the enclosure; particularly as all these parameters, including ammonia, are indicators of remineralisation processes. Therefore the high degree of correlation of these parameters recorded within the enclosure is the normal situation, the lack of correlation with ammonia in the outside water can only be due to other factors not present within the enclosure at the 9 m depth. Obviously, rapid selective uptake of ammonia by phytoplankton can be the only explanation to account for this discrepancy.

The highly significant correlations between phytoplankton primary production and the nutrients silicate and phosphate and the lack of correlation with either ammonia or incident radiation in the outside waters is proof that ammonia was the limiting factor for primary production at the time. Dugdale and Goering (1967) reported that ammonia uptake by phytoplankton also takes place in the dark and, as ^{14}C-incubation was started at the same time that nutrients were measured (1200 hrs), it can be presumed that ammonia had indeed been taken up very rapidly by the phytoplankton.

The effect of flushing on bacterial activity in the water column is probably two-fold: Weise (1975) found that 47—51% of sediment bacteria in sand sediments of Kiel Bight were suspended in interstitial water and hence easily displaceable. Thus, flushing would directly increase bacterial numbers in the bottom water. Clark et al. (1972) found higher dissolved amino acid concentrations in interstitial water as compared to bottom water. Sediment flushing would increase concentrations of amino acids and probably also other labile DOC in bottom water and support growth of the microbial population there. The increase in labile DOC would not necessarily result in a noticeable increase in total DOC.

In other words, the high level of bacterial activity common for the sediments would continue in the water column till the depletion of the substrate and result in high bacterial standing stocks with high potential uptake rates. This might be the reason why bacterial numbers and uptake rates of amino acids increased so rapidly during flushing in the restricted enclosure but not in the outside water. The lack of a noticeable effect on the V_{max} and turnover time values during the II flushing event at the 9 m depth cannot be easily explained, particularly as values for turnover times from the surface and 6 m depth changed during all 3 flushing events.

Per cent uptake rates are a measure of the relationship between available substrate concentration and size of the bacterial population taking up that particular substrate. The size of the bacterial populations within the enclosure and outside are similar as shown by the V_{max} data. Therefore, the higher per cent uptake rates at the 0.5 and

6 m depths within the enclosures could be explained by a lower substrate concentration (amino acids) than in the outside water. However, there is no reason to believe that considerable differences in the amino acid concentrations in enclosure and outside water were present. The significantly higher numbers of viable bacteria within the enclosure indicate a qualitative change in the bacterial flora. This, presumably, led to an increase of bacteria which are better adapted to amino acids and therefore to higher uptake rates of this substrate. Evidently, the very high uptake rates at the 9 m depth within the enclosure (fig. 4, I and III) are due to the rapid increase in the bacterial number caused by the flushing events.

This assumption is supported by the data for dark assimilation of CO_2 from the 9 m depth during flushing within the enclosure. The high values recorded here, equivalent to 21 mg C m^{-3} d^{-1}, are most probably due to facultative anaerobic and obligate chemoautotrophic bacteria (PARSONS and TAKAHASHI 1973). Oxygen levels during flushing were very much lower inside the enclosure than outside and anaerobic conditions were recorded during the III and IV flushing events. It therefore seems likely that chemosynthetic bacteria, utilizing various reduced substances as substrates were able to continue CO_2 —assimilation in enclosure bottom water after displacement from the sediments.

The immediate effect of flushing on phytoplankton primary production is an excellent example of sediment/water interaction. Concentration of particulate organic matter on the bottom due to sedimentation increases its rate of remineralisation and hence the release of inorganic nutrients. Some of these nutrients enter the contact water, but a considerable amount is released into the interstitial water. A mechanism by which the latter nutrients can be returned to the water column is sediment flushing due to density displacement. The rapidity with which this process can take place and its frequency in a mesohaline ecosystem subject to changes in salinity is demonstrated by the results of the experiment described here. Presumably, other shallow water bodies similar to Kiel Bight like estuaries would exhibit the same dynamics of sediment nutrient release and its direct effect on phytoplankton primary production.

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