

Sedimentation of particulate organic matter and silicium during spring and summer in Lindåspollene, Western Norway

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ABSTRACT: Sedimentation of organic and inorganic matter was determined at 18, 38, 70, and 85 m between 17 March and 8 October 1982, in the land-locked fjord, Lindåspollene. Rates of sedimentation were highest during spring, with 2 peaks in sedimentation following the first spring diatom bloom and a second bloom not dominated by diatoms. About half of the biomass (C and N) formed during these 2 blooms apparently sedimented out from the euphotic zone. Based on the vertical structure of the plankton community, it is concluded that sedimenting material during summer mainly originates from the deeper part of the euphotic zone containing a chlorophyll maximum layer. Sedimentation of organic matter was correlated with sedimentation of particulate silicium both during spring and summer, suggesting that sinking of diatom frustules is a major transport mechanism for vertical flux of organic material. Recovery of particulate silicium in sediment traps compared to seston content was lower than for organic material. This indicates rapid dissolution of silicium, most of which apparently occurred within the sediment traps. Decreasing sedimentation flux of organic material with depth below the euphotic zone, and concomitant decrease in the N/C ratio and increase in the P/C ratio, are interpreted to reflect substantial mineralization and associated microbial growth on the sinking material.

INTRODUCTION

Sedimentation of spring phytoplankton blooms has been reported for many coastal areas (Smetacek et al. 1978, Smetacek 1980a, Bodungen et al. 1981, Peinert et al. 1982, Wassmann 1983, Davies & Payne 1984, Schnack et al. 1984). This appears to be a general phenomenon, related to the relatively low biomass of overwintering zooplankton in shallow coastal waters (Smetacek 1984). The response of the zooplankton to the rapidly increasing primary production in spring is slow, and grazing impact on the spring bloom is usually limited (Lännergren & Skjoldal 1976, Dagg et al. 1982, Franz & Gieskes 1984, Schnack et al. 1984). A large part of the accumulated phytoplankton biomass therefore sinks out from the euphotic zone in a late senescent stage of the bloom.

Lindåspollene is a land-locked fjord in western Nor-

way with a maximum depth of 89 m (Dahl et al. 1973). Sedimentation of the spring bloom in this system was inferred by Lännergren & Skjoldal (1976, Skjoldal & Lännergren 1978) and later confirmed by Wassmann (1983). Apart from representing an input of matter and energy to deeper water and benthos, deprivation of nutrients from the euphotic zone through sedimentation of the spring bloom has consequences for the further plankton development. This could be of particularly great importance in Lindåspollene due to the high stability of the water column and limited upward transport of nutrients from deeper water.

The mechanisms behind sinking of algal cells in general, and sedimentation of spring blooms in particular, are not well known, but nutrient starvation is probably involved. Bienfang et al. (1982) found that silicate depletion elicited a marked increase in sinking rates of 4 diatom species. Nitrogen or phosphorus depletion (2 d starvation), on the other hand, caused a decrease in sinking rate for 3 of the species. Thus, the response in sinking rate towards nutrient depletion is evidently complex, depending on the limiting nutrient

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and algal species and probably also on the degree of limitation and the light conditions. Silicate is often, but not always, the main limiting nutrient for the spring diatom bloom in Lindåspollene (Lännergren & Skjoldal 1976, Skjoldal unpubl. results). Towards the end of the bloom, the accumulated biomass is concentrated in the lower part of the euphotic zone, and sinking is therefore probably determined by a combination of nutrient and light limitation. Whether and to what extent the algae sink out as dying cells or as spore-forming cells are further complicating questions. Accelerated sinking rate of diatom populations has been suggested to be part of the life cycle strategy of bloom diatoms as these enter a resting or seeding stage (Smetacek 1985).

Dying and dead phytoplankton cells are rapidly colonized and degraded by bacteria (Fukami et al. 1981a, b, 1985a, b, Newell et al. 1981, Bauernfeind 1985). It is therefore possible that some of the bound nutrients are remineralized before the phytoplankton material sink out from the euphotic zone (Newell & Linley 1984). In order to obtain more information on the loss of organic material and bound nutrients from the euphotic zone in Lindåspollene, we measured sedimentation rates of total particulate material (TPM), plant pigments, particulate silicium (PSi), inorganic material (PIM), organic carbon (POC), organic nitrogen (PON) and total phosphorus (PTP) during spring, summer and early autumn in 1982. Seston concentrations were also measured. This allows calculations of relative sedimentation rates and evaluation of the importance of sedimentation as a pathway for removal of suspended biomass.

MATERIALS AND METHODS

All samples were collected at a central station over the deepest part (89 m) of Spjeldnesosen, the mid-basin of Lindåspollene (see Fig. 1 in Wassmann 1983).

Water samples were collected with Nansen bottles. Temperature was recorded with reversing thermometer and salinity was determined with an Autolab 601 MK III salinometer. Oxygen and hydrogen sulphide were determined by titration methods (Grasshoff 1976). Inorganic phosphate, nitrate, nitrite and silicate were analysed with Chemlab autoanalyser (Føyn et al. 1981) on samples preserved with chloroform and stored refrigerated (Hagebö & Rey 1984). Triplicate samples for chlorophyll and POC/PON analyses were collected on precombusted Whatman GF/C filters. Duplicate samples of particulate silicium (PSi) were collected on 0.6 µm Nuclepore filters (Paasche 1980).

Sediment traps containing chloroform as preservative were deployed at 18, 38, 70, and 85 m depth as

described by Wassmann (1983). The traps were deployed during 9 periods between 17 March and 8 October 1982, the exposure periods ranging from 9 to 50 d with an average of 22 d. The content of each trap was transferred along with 2.8 l of overlying seawater to a glass bottle and thoroughly mixed prior to removal of subsamples. Duplicate samples for total particulate matter (TPM) and particulate inorganic matter (PIM) and triplicate samples for particulate total phosphorus (PTP) analyses were filtered onto precombusted Whatman GF/C filters. Samples of plant pigments, POC/PON and PSi were taken in triplicate and duplicate as described above. The filters for POC/PON and TPM/PIM analyses were examined by eye and visible zooplankters were removed by forceps prior to analysis.

Chlorophyll *a* and phaeopigments were extracted with 90 % acetone and analysed fluorometrically (Strickland & Parsons 1972). The results from sediment traps have been expressed as chlorophyll *a* equivalents (Chl *a* equiv.). TPM and PIM were determined by weighing following successive drying and combustion, and POC and PON were determined with a Carlo Erba elemental analyser (for further details see Wassmann 1983). PTP was analysed as described by Grasshoff (1976). PSi was analysed as silicate (Strickland & Parsons 1972) following digestion with NaOH (Krause et al. 1983).

The variability between the replicate samples was on average highest for PTP (coefficient of variation [CV] = 13.6 %, with standard deviation [SD] = 12.8 %) and lowest for TPM (CV = 4.9 %, SD = 4.8 %). The variabilities for PON, POC, and Chl *a* equiv. were intermediate with CV = 10.8 % (SD = 13.3 %), 10.8 % (SD = 9.6 %), and 7.2 % (SD = 4.2 %), respectively.

RESULTS

Hydrography

Lindåspollene receives freshwater from a watershed area of 35 km² (Lännergren 1975). This freshwater input strongly influences the hydrography of Lindåspollene, resulting in a stratified and stable water column. The salinity of the surface layer fluctuates considerably as precipitation varies, but the effect of this does not penetrate deep in the water column. The observed salinities at 0.5 m in 1982 ranged from 24.4 to 30.1 ‰, whereas the salinities at 20 m changed by only 0.3 ‰ (from 30.68 to 30.98 ‰). The distribution of salinity with depth showed a more or less gradual increase without any marked halocline (Fig. 1A).

The restricted vertical mixing of the water column is also shown in the temperature distribution (Fig. 1B). During summer the surface water warmed to more than

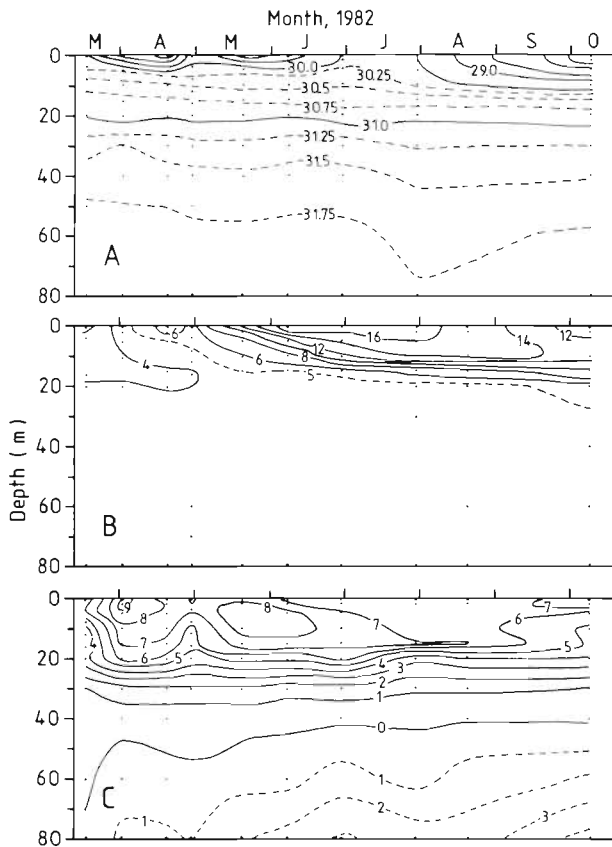


Fig. 1. Distribution of (A) salinity (‰), (B) temperature (°C), and (C) oxygen and hydrogen sulphide (broken isolines) (ml l⁻¹)

16 °C. The effect of this warming penetrated gradually to below 10 m, but the warming at 20 m between spring and autumn was only about 1 °C.

The deeper part of the water column was hypoxic or anoxic (Fig. 1C). During the winter 1978/79 there was renewal of the bottom water in Spjeldnesosen with

oxygen content of about 5 ml l⁻¹ (Aksnes & Magnesen 1983). After that the oxygen condition gradually deteriorated and this trend continued during 1982. The content of H₂S in the bottom water increased and the interface between O₂ and H₂S became displaced upwards to about 40 m (Fig. 1C).

Between the hypoxic mid-water and the well oxygenated upper water layer there was a marked O₂ gradient between 20 and 30 m. The temporal changes in the O₂ content of the upper layer were characterized by a maximum in early April, a minimum by late April, and a second maximum by late May (Fig. 1C).

Nutrients

Vertical profiles of nitrate, inorganic phosphate and silicate at 5 dates between 17 March and 15 June are shown in Fig. 2. The concentrations of PO₄ and Si increased with depth to about 7 and 75 μM, respectively, at 80 m. NO₃, on the other hand, decreased below 30 m and was virtually absent from the anoxic water.

The nutrient concentrations in the surface layer on 17 March were lower than the concentrations at 10 to 20 m, indicating that the first spring bloom had started just prior to this date. Up to 1 April there was a substantial consumption of all nutrients, but particularly of Si which was almost totally depleted from the upper 15 m. NO₃, in contrast, still occurred at concentrations of 3.4 and 6.2 μM at 10 and 15 m (Fig. 2). From these results it is evident that the major bloom took place between 17 March and 1 April and that Si was the main limiting nutrient.

The most notable change between 1 and 19 April was a marked increase in PO₄ concentration in the upper 10 m (Fig. 2). This indicates substantial re-

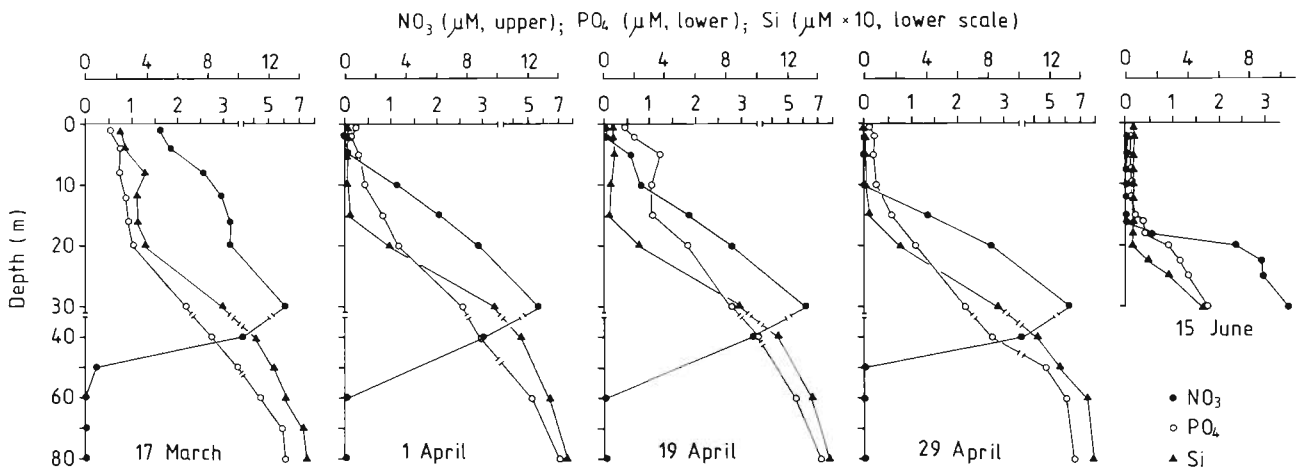


Fig. 2. Vertical profiles of nitrate, inorganic phosphate and silicate at 5 dates between 17 Mar and 15 Jun, 1982. Note the changes in depth, PO₄ and Si scales

generative activity during this period following the spring bloom. Unfortunately, we have no NH_4 data and cannot therefore verify this in terms of nitrogen regeneration. The concentration of Si in the upper 10 m also increased during this period from about 0.5 to $2 \mu\text{M}$.

Between 19 and 29 April there was again marked consumption of nutrients (Fig. 2). NO_3 was depleted from the upper 10 m and PO_4 was lowered from between 0.5 and $1.2 \mu\text{M}$ to about $0.2 \mu\text{M}$. This reflected the development of a second bloom, as evident from the distributions of POC and chlorophyll *a* (see Fig. 3A, B). At this time the summer nutricline, typically located around 15 m (Lännergren 1975, 1978), was being formed. The gradient in Si on 29 April was situated below the gradient in NO_3 . This was also the case on 15 June when a very sharp gradient in NO_3 occurred between 16 and 20 m whereas the gradient in Si started at 20 m (Fig. 2).

Seston and plankton development

The sampling frequency of chlorophyll and seston was low, but provides, together with the information from the nutrients data, a general outline of the major features of the plankton development.

PSi showed a pronounced maximum of $8.2 \mu\text{g-at Si l}^{-1}$ at 20 m on 1 April (Fig. 3C). There were also maxima of POC and chlorophyll (Chl *a* + phaeopigments) in the deeper part of the euphotic zone on this date (Fig. 3A, B). These maxima ($270 \mu\text{g POC l}^{-1}$ and $4.5 \mu\text{g chlorophyll l}^{-1}$) were, however, not impressive for a spring diatom bloom. Furthermore, the content of phaeopigments was about equal to that of Chl *a* in the upper 20 m. From these results and the strong depletion of Si at this date (Fig. 2), it is evident that the first spring diatom bloom had already culminated and was in its decline phase.

On 19 April there was a minimum in POC with $<100 \mu\text{g l}^{-1}$ at 10 and 15 m, and also chlorophyll and PSi showed minima on this date (Fig. 3A to C). As indicated by the increase in PO_4 up to 19 April (Fig. 2), this period was probably characterized by a build-up of the heterotrophic components of the plankton. A second bloom occurred thereafter, as evidenced by marked maxima in POC and chlorophyll on 29 April (Fig. 3A, B). There was only a slight increase in PSi (Fig. 3C), which suggests that diatoms contributed little to this bloom.

After the second bloom there were no further pronounced temporal maxima in either POC, chlorophyll or PSi, although the values varied somewhat during the summer. A consistent feature in the chlorophyll distribution was a more or less marked maximum between 15 and 20 m (Fig. 3B). Also PSi and, to a lesser

degree, POC exhibited deep maxima during the summer period (Fig. 3A, C).

The distribution of PON reflected the same major features as POC. The difference between them is illustrated by the N/C atomic ratio (Fig. 3D). During the

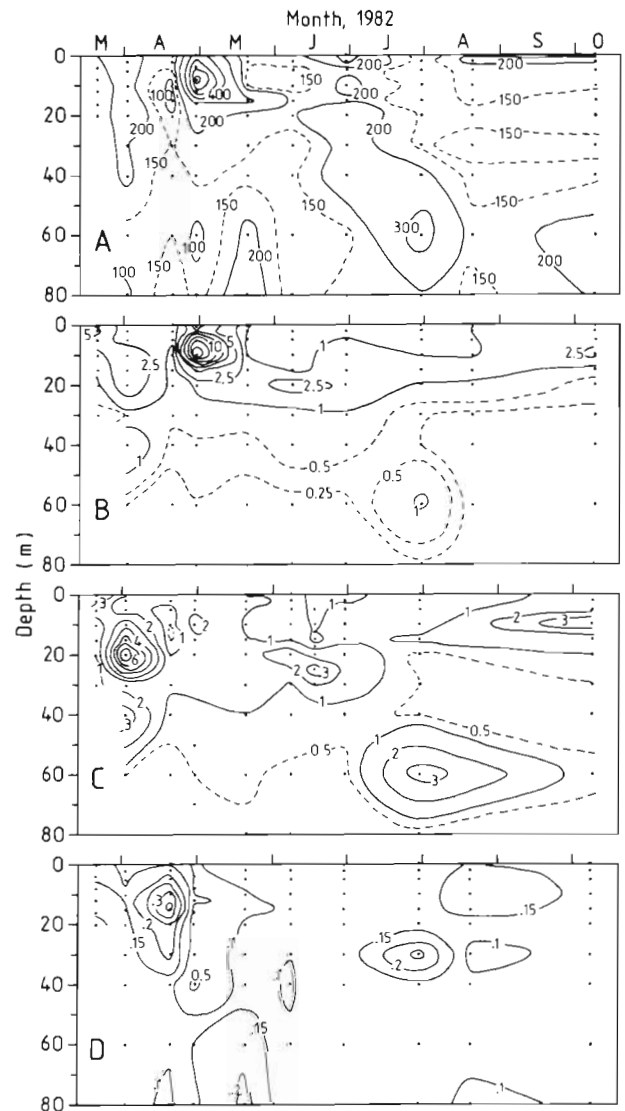


Fig. 3. Seasonal distribution of seston in the water column. (A) Particulate organic carbon ($\mu\text{g l}^{-1}$). (B) Chlorophyll *a* plus phaeopigments ($\mu\text{g l}^{-1}$). (C) Particulate silicium ($\mu\text{g-at Si l}^{-1}$). (D) N/C atomic ratio

decline of the first bloom (1 April) the ratio was about 0.14. Thereafter the ratio increased to >0.2 associated with the biomass minimum in the upper 20 m on 19 April. On 29 April, during the second bloom, the ratio was low, about 0.09. During summer the ratio was fairly constant with most values between 0.10 and 0.13 in the upper 20 m.

Sedimentation

Mean daily sedimentation rates for each measurement period are shown in Fig. 4. The rates at 70 m were in general quite similar to those at 85 m and are not included in the figure. Exceptions to this were much higher sedimentation rates of P*Si* and Chl *a* equiv. at 70 m than at 85 m between 1 and 19 April, as shown by the stippled columns in Fig. 4F, I.

Sedimentation in relation to depth

Decreasing sedimentation with increasing depth seems to be a characteristic of poll environments

(Wassmann 1983, 1985). This was also the case in the present study for the components TPM, PIM, POC and PON (Fig. 4). Sedimentation during the period from 17 March to 8 October is summarized in Table 1. The percentage decrease in sedimentation between 18 and 85 m ranged from 83 % for PON to 70 % for TPM. In contrast, sedimentation of P*Si*, PTP and Chl *a* equiv. tended to increase with depth (Table 1).

There were some obvious seasonal differences in sedimentation in relation to depth. To illustrate this we have divided the investigation period into a 62 d spring period (17 March to 18 May) and a 143 d summer period (including early autumn; 18 May to 8 October). The decrease in sedimentation of TPM,

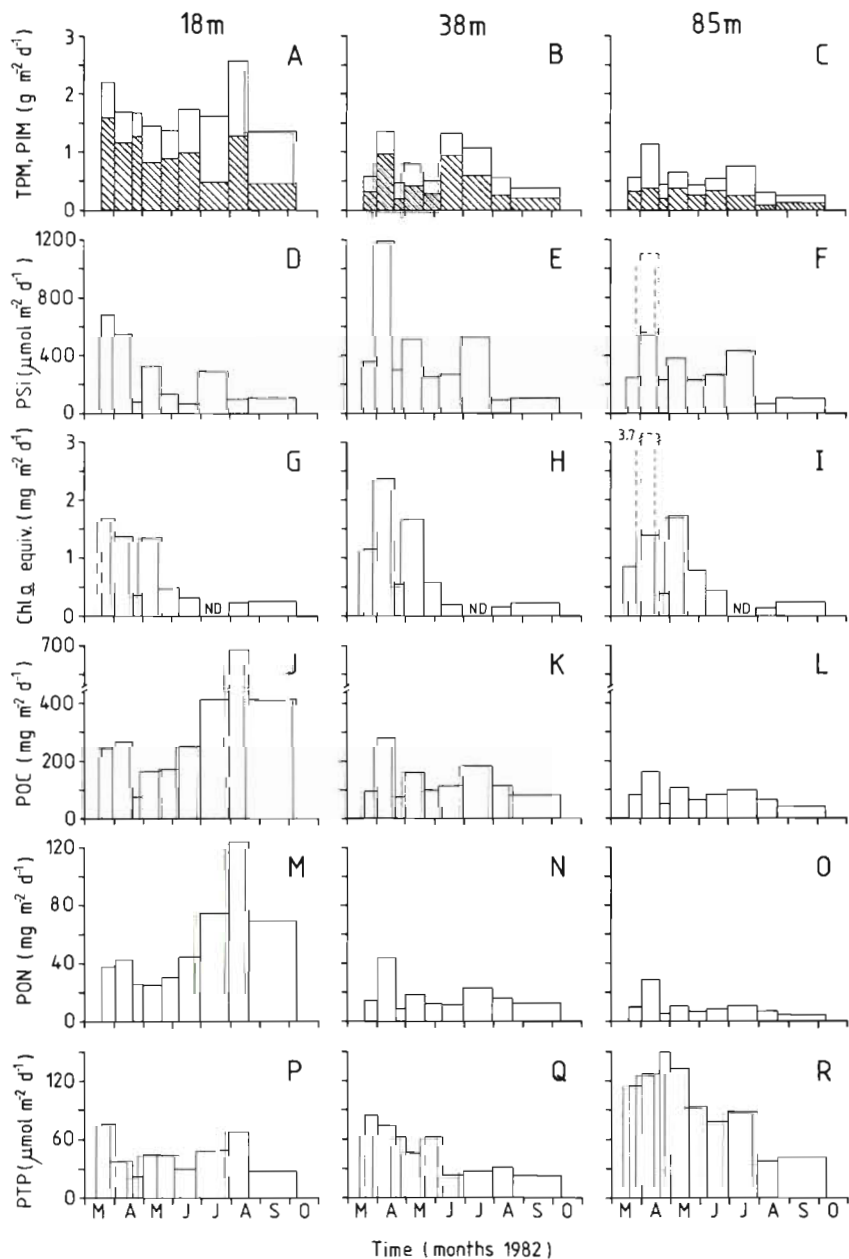


Fig. 4. Mean daily sedimentation rates at 18, 38, and 85 m during 9 successive measurement periods between 19 Mar and 8 Oct 1982. (A to C) total particulate material (TPM) and particulate inorganic material (PIM; hatched columns); (D to F) particulate silicium; (G to I) chlorophyll *a* plus phaeopigments, expressed as chlorophyll *a* equivalents; (J to L) particulate organic carbon (POC); (M to O) particulate organic nitrogen (PON); (P to R) particulate total phosphorus (PTP). Stippled columns in F and I show sedimentation rates at 70 m. ND: no data

Table 1. Sedimentation during the period 17 Mar to 8 Oct 1982 and sedimentation in spring (17 Mar to 18 May) as percentage of sedimentation between 17 Mar and 8 Oct. TPM: total particulate material; PIM: particulate inorganic material; PSi: particulate silicium; POC and PON: particulate organic carbon and nitrogen; PTP: particulate total phosphorus; Chl a equiv.: chlorophyll a plus phaeopigments

Component	Sedimentation 17 Mar – 8 Oct					Sedimentation in spring (%)			
	18 m	38 m	70 m	85 m	Decrease between 18 and 85 m (%)	18 m	38 m	70 m	85 m
TPM (g m^{-2})	345	157	102	107	70.0	32	35	47	43
PIM (g m^{-2})	177	92	52	49	72.3	42	35	52	44
PSi (mmol m^{-2})	48	74	73	53	-10.4	58	54	47	44
POC (g m^{-2})	69.3	26.9	19.2	16.4	76.3	18	39	44	42
PON (g m^{-2})	12.0	3.6	2.4	2.0	83.3	18	41	48	47
PTP (mmol m^{-2})	8.7	8.5	12.8	17.2	-97.7	34	49	49	47
Chl a equiv. (g m^{-2})	0.12	0.13	0.17	0.13	-8.3	66	74	69	61

PIM, POC, and PON with depth was less pronounced during spring than during summer (Fig. 5A to D). The measured sedimentation of PTP and Chl a equiv. tended to increase with depth for both the spring and summer periods (Fig. 5E, F). Sedimentation of PSi increased between 18 and 38 m and showed no marked difference between the 2 periods (Fig. 5A, B).

Sedimentation in spring as percentage of sedimentation from 17 March to 8 October ranged at 18 m from 66 and 58 % for Chl a equiv. and PSi, respectively, to 18 % for POC and PON (Table 1). The percentage sedimentation in spring tended to increase with depth for POC, PON, and TPM and to decrease with depth for PSi. This resulted in a diminished difference between

spring sedimentation of the various components in the bottom water. Thus, with the exception of Chl a equiv., spring sedimentation was in the narrow range of 42 to 47 % at 85 m (Table 1).

A diagrammatic matrix of linear correlations based on the temporal patterns of sedimentation is shown in Fig. 6. In the diagonal region of this diagram are correlations between sedimentation at the 4 depths for each separate component. For TPM, PIM, POC, PON, and PTP, sedimentation at 18 m was not correlated with sedimentation at 38, 70, and 85 m. Sedimentation at 18 m of Chl a equiv. and PSi was, on the other hand, significantly correlated with sedimentation at greater depths. With few exceptions, the sedimentations at 38,

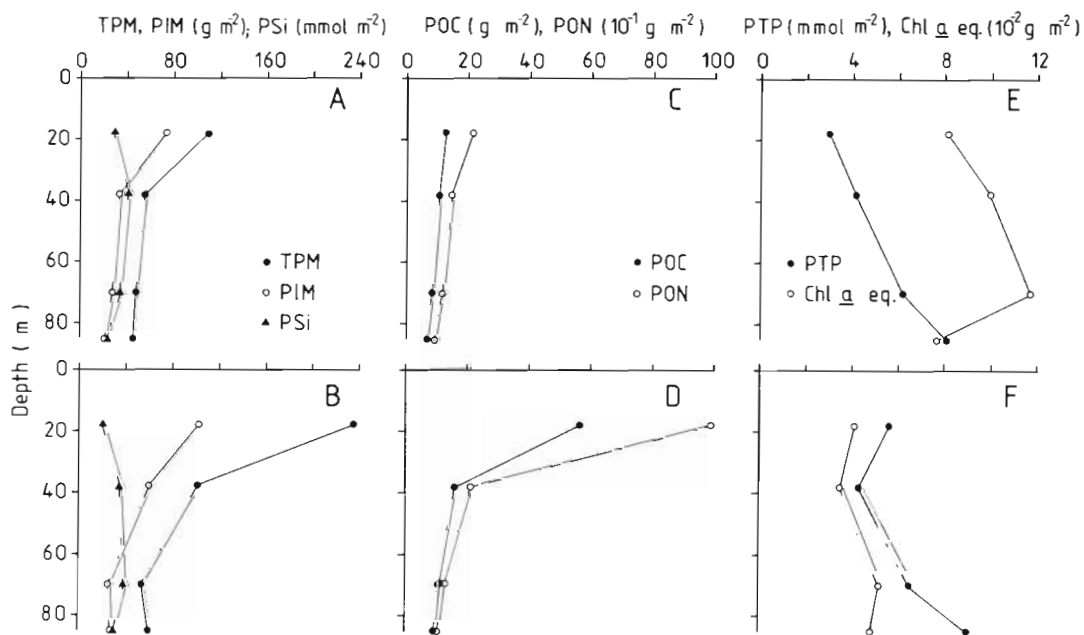


Fig. 5. Sedimentation during spring (17 Mar to 18 May; A, C, E) and summer (18 May to 8 October; B, D, F). (A, B) total particulate material (TPM), particulate inorganic material (PIM) and particulate silicium (PSi); (C, D) particulate organic carbon (POC) and nitrogen (PON); (E, F) particulate total phosphorus (PTP) and chlorophyll a plus phaeopigments (Chl a equiv.).

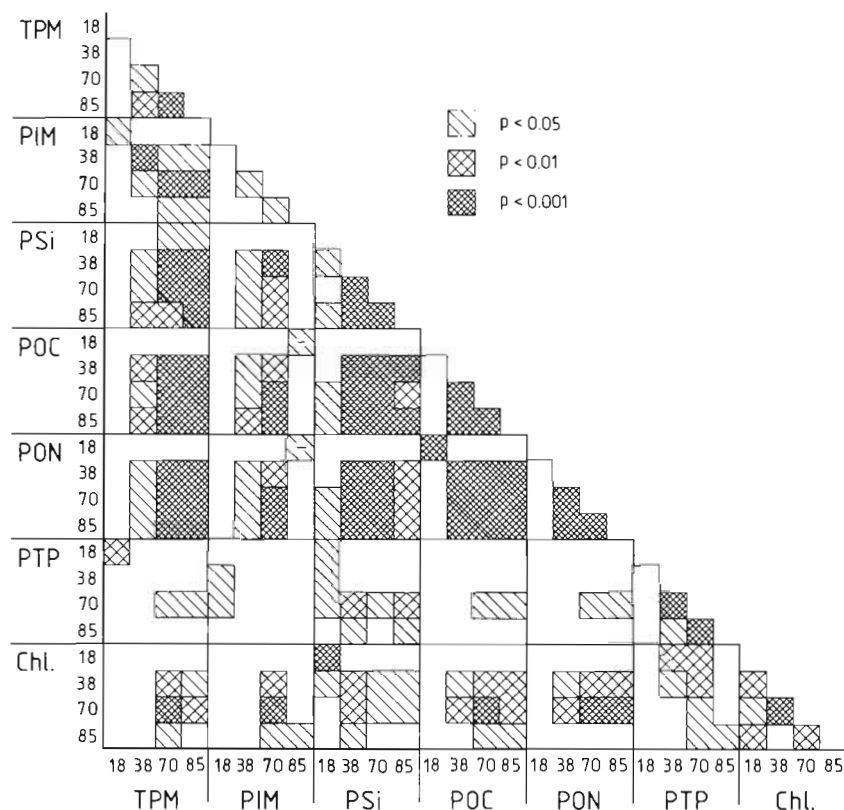


Fig. 6. Matrix of correlations between sedimentation rates at 18, 38, 70, and 85 m of total particulate material (TPM), particulate inorganic material (PIM), particulate silicium (PSi), particulate organic carbon (POC) and nitrogen (PON), particulate total phosphorus (PTP), and chlorophyll *a* plus phaeopigments (Chl.). Unless specified by -, correlations are positive. Significance levels (see text) correspond to $r > 0.63$, 0.76 and 0.87 for $p < 0.05$, 0.01 and 0.001 , respectively

70, and 85 m were positively correlated for all components (Fig. 6), with particularly high correlation coefficients for PSi ($r = 0.93$ to 0.96) and POC and PON ($r = 0.96$ to 0.99).

Temporal patterns of sedimentation

The 2 phytoplankton blooms during spring were reflected in the rates of sedimentation. The first diatom bloom between 17 March and 1 April resulted in elevated rates of sedimentation between 17 March and 19 April at 18 m and between 1 and 19 April at 38 to 85 m (Fig. 4). The second bloom, which was dominated by non-diatoms and probably culminated shortly after 29 April (Fig. 3), could be traced as a second peak in sedimentation in the ensuing period up to 18 May (Fig. 4).

The 2 spring peaks in sedimentation rates were most pronounced for Chl *a* equiv. (Fig. 4G to I), but they were also clear for PSi sedimentation (Fig. 4D to F) and for sedimentation of TPM, PIM, POC and PON below the euphotic zone (Fig. 4B, C, K, L, N, O). Sedimentation of PSi was much higher after the first diatom bloom than after the second bloom (Fig. 4D to F).

Sedimentation of POC and PON at 18 m increased to high levels during summer and early autumn (Fig. 4J, M). Below 18 m there was a third peak in sedimentation of PSi, POC and PON during July (Fig. 4E, F, K, L,

N, O). With the exception of sedimentation of POC and PON at 18 m, the rates of sedimentation tended in general to decrease from spring to autumn (Fig. 4).

Relations between sedimentation of the various components

The correlation matrix (product moment correlation coefficients; Sokal & Rohlf 1981) shown in Fig. 6 is based on the temporal patterns of sedimentation. It should be noted that the significance levels for the correlations apply to single comparisons and are not strictly correct when comparing many correlation coefficients. With 2 exceptions (sedimentation of POC and PON at 18 m vs PIM at 85 m), all 'significant' correlations were positive.

At 18 m the only 'significant' correlation coefficients were those for TPM vs PIM and PTP, PSi vs PTP and Chl *a* equiv., and POC vs PON (Fig. 6). In comparisons involving 18 m and some greater depths, the most notable feature was that sedimentation of PSi at 18 m was correlated with sedimentation below 18 m of most other components (i.e. with Chl *a* equiv. at 38 m, PTP at 38 and 70 m, and TPM, POC and PON at 70 and 85 m; Fig. 6).

In comparisons between 38, 70, and 85 m, there were in general many and high correlations (Fig. 6). Fewest and lowest correlations were shown by sedimentation

of PTP, with PIM and Chl *a* equiv. sharing the second rank in this respect. The highest correlations were those between POC and PON, but also TPM and PSi showed many high correlations with other components. These latter correlations tended to be highest for TPM at 70 and 85 m and for PSi at 38 and 70 m.

The correlations between sedimentation of PSi and organic matter below the euphotic zone are noteworthy. Although spring sedimentation was important in this respect, a correlation also appeared to exist during summer. This is exemplified in Fig. 7 for the relation between POC and PSi sedimentation.

Amount and composition of sedimented material in relation to seston

The peaks in sedimentation following the 2 spring blooms (Fig. 4) coincided with maxima in seston POC at 60 and 80 m on 19 April and 19 May (Fig. 3A). The third peak in sedimentation of organic material and PSi in July (Fig. 4) also corresponded to a maximum in POC that apparently sank slowly through the deeper water during July (Fig. 3A).

The daily rates of sedimentation at 18 and 38 m were calculated as percentages of the average seston content in the upper 20 m for each measurement period (Fig. 8). Since we missed the peak of the first diatom bloom in our sampling program, an estimated peak biomass (see Table 2 and 'Discussion') was used in calculating the average biomass for the first period (17 March to 1 April). The first bloom appeared as a peak in sedimentation which for POC represented an average daily loss of about 8 % of the seston content in

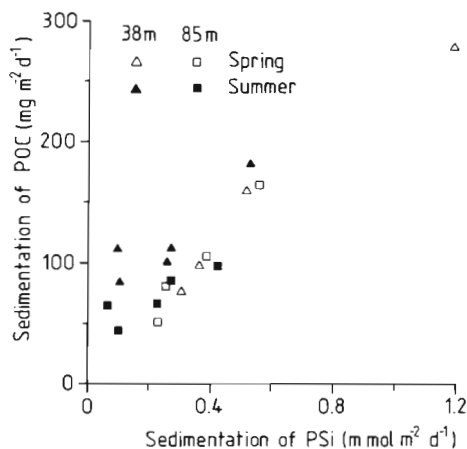


Fig. 7. Relation between sedimentation of particulate organic carbon (POC) and particulate silicium (PSi) at 38 and 85 m for spring (17 Mar to 18 May) and summer (18 May to 8 Oct) periods. Correlation coefficients (r) were 0.98, 0.89, and 0.94 at 38 m, and 0.98, 0.84, and 0.89 at 85 m for the spring ($n = 4$), summer ($n = 5$) and total period ($n = 9$), respectively

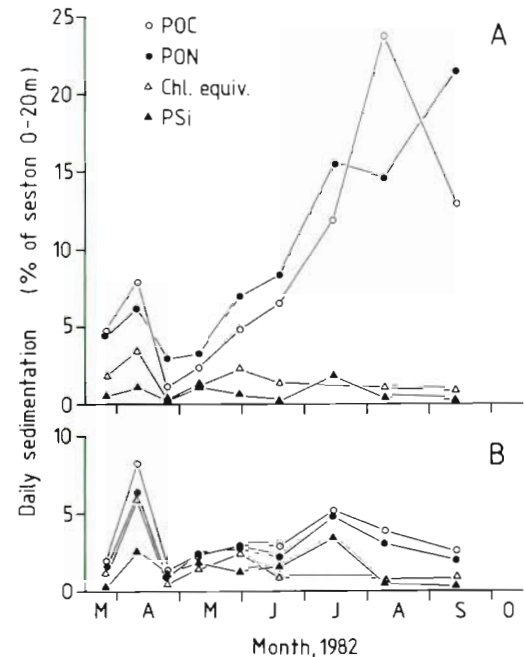


Fig. 8. Daily rates of sedimentation at (A) 18 m and (B) 38 m as percentages of average seston standing stock in the upper 20 m for each measurement period. POC and PON: particulate organic carbon and nitrogen, respectively; Chl. equiv.: chlorophyll *a* plus phaeopigments; PSi: particulate silicium

the euphotic zone (Fig. 8). The second bloom was not apparent in this representation, partly because of the high seston content on 29 April. During summer the daily loss of seston, measured as sedimentation at 18 m, increased to a maximum of about 20 % for POC and PON (Fig. 8A). A similar increase was also apparent in the sedimentation at 38 m, where maximum daily sedimentation losses of POC and PON of about

Table 2. Estimates of nutrients consumed and biomass produced during the first spring bloom, compared with sedimentation at 38 m during and just after this bloom. See text for further details

Nutrient consumption up to 1 Apr	
NO ₃	109 mmol m ⁻²
Si	184 mmol m ⁻²
Biomass produced	
PON	1530 mg m ⁻²
POC	9600 mg m ⁻²
PSi	5160 mg m ⁻²
Chlorophyll <i>a</i>	144 mg m ⁻²
Sedimentation at 38 m between 17 Mar and 19 Apr	
PON	1008 mg m ⁻²
POC	6524 mg m ⁻²
PSi	755 mg m ⁻²
Chl <i>a</i> equiv.	60 mg m ⁻²

5 % were recorded in July (Fig. 8B). The sedimentation loss at 38 m was in general highest for POC, slightly lower for PON, and lowest for P*Si* and Chl *a* equiv. (Fig. 8B).

The N/C atomic ratio of the sedimented material tended with few exceptions to decrease with increasing depth of collection (Fig. 9A). The ratios at 38 m to 85 m showed maxima in early April, associated with the peak in sedimentation resulting from the first diatom bloom. During this bloom fairly high N/C ratios of the seston were recorded (Fig. 3D). The second bloom in late April had a lower N/C ratio, as had also the sedimented matter collected following this bloom (Fig. 3D & 9A). The N/C ratios of both seston in the euphotic layer and sedimented material collected below tended to remain low during summer and to increase somewhat during early autumn. In contrast, the N/C ratio of the material collected at 18 m was considerably higher than that of the seston (Fig. 9A).

The P/C ratio of the sedimented material showed the opposite trend to that for the N/C ratio, increasing consistently with increasing depth of collection (Fig. 9B). The pattern of temporal variation in the P/C ratio was generally similar at all depths, although the range of variation increased with increasing depth. Associated with the 2 sedimentation peaks in early April and May were minima in the P/C ratios. During summer the P/C ratios tended to decrease (Fig. 9B).

Other ratios characterizing the sedimented material and seston are shown in Fig. 10 as average values for the spring and summer periods, respectively. The relative PIM content of the TPM varied from 44 to 67 %, being higher during spring than during summer. It tended furthermore to decrease with increasing depth (Fig. 10A). The POC content of the particulate organic material (POM = TPM - PIM) tended also to decrease with depth, varying from 27 % at 85 m to 47 % at 38 m during spring (Fig. 10A).

The Si/C ratio for seston showed a maximum at about 20 m for both the spring and summer periods, decreasing more or less gradually with increasing

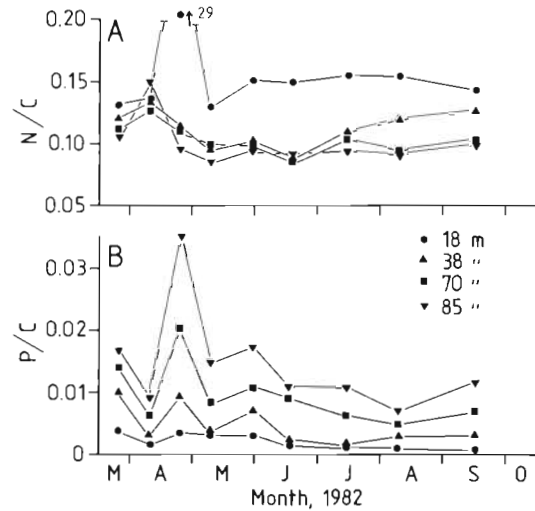


Fig. 9. (A) N/C and (B) P/C atomic ratios of sedimented material collected at 18, 38, 70, and 85 m

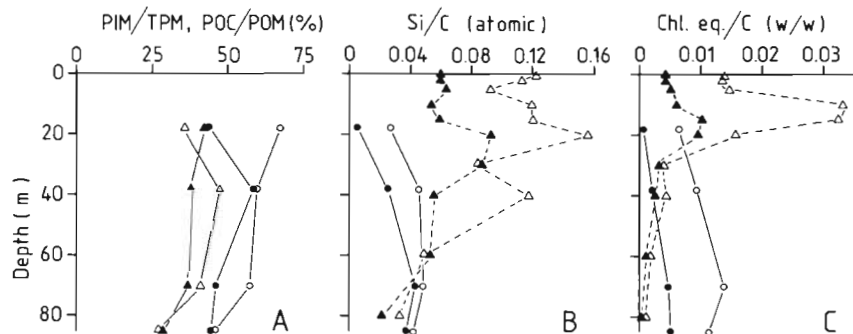
depth below this maximum (Fig. 10B). The Si/C ratio for the sedimented material, on the other hand, tended to increase from 18 to 70 m. The ratios for material which sedimented at 18 and 38 m were considerably lower than the corresponding seston ratios, whereas the sedimentation and seston ratios showed better agreement in the deep water. The Si/C ratios for both sedimented material and seston were higher during spring than during summer (Fig. 10B).

The Chl *a* equiv./C ratios showed much the same trends as the Si/C ratios. The most notable differences were a more pronounced decrease in the seston Chl *a* equiv./C ratio between 20 and 30 m and a greater difference in the sedimentation ratio between spring and summer (Fig. 10C).

DISCUSSION

The reliability of results obtained with sediment traps depends on their sampling efficiency, which

Fig. 10. Vertical profiles of ratios characterizing sedimented material (solid lines) and seston (broken lines). Average values for spring (open symbols) and summer (filled symbols) periods. (A) Particulate inorganic material (PIM) as percentage of total particulate material (TPM) (○, ●), and particulate organic carbon (POC) as percentage of particulate organic matter (POM = TPM - PIM) (△, ▲). (B) Si/C atomic ratio based on contents of particulate silicon and POC. (C) Chl *a* equiv./C ratio based on contents of chlorophyll *a* plus phaeopigments and POC



again is influenced by factors such as trap design, hydrographical conditions and properties of the sedimenting particles. Despite an extensive number of recent methodological studies, there are still uncertainties involved in sediment trap methodology. Aspects of these difficulties pertinent to our trap design, environmental conditions and measured components of sedimenting material have been discussed by Wassmann (1983, 1985).

The present results are generally in good agreement with those obtained previously (1981) in Lindåspollene by Wassmann (1983). He explained the decrease in organic sedimentation with increasing depth (Table 1, Fig. 5) as reflecting pelagic remineralization in the virtual absence of resuspension of sediment below the euphotic zone in this hydrographically stable poll environment. Mineralization or solubilization has been used to explain similar observations in many other sedimentation studies (e.g. Knauer et al. 1979, Suess 1980, Urrère & Knauer 1981, Honjo et al. 1982, Lorenzen et al. 1983, Karl & Knauer 1984, Karl et al. 1984). The labile nature of sedimenting material has been confirmed experimentally. Thus, Iseki et al. (1980) observed rapid decomposition of sedimenting POC in a coastal environment, with average loss coefficients decreasing with depth from 0.29 d^{-1} at 10 m to 0.02 d^{-1} at 50 m. Lorenzen et al. (1983) found that material collected between 250 and 900 m lost about 30 % of its POC content during 5 d *in situ* incubation.

Dying cells and debris of phytoplankton are rapidly colonized and degraded by bacteria (Iturriaga 1979, Fukami et al. 1981a, b, 1985a, b, Newell et al. 1981, Bauernfeind 1985). The degradation usually proceeds in 2 phases, with rapid initial degradation of labile compounds followed by slower mineralization of more refractory fractions (e.g. Fukami et al. 1981b, Newell et al. 1981, Garber 1984). The N/C ratio of detritus can show an initial increase during decomposition, reflecting the generally high N/C ratio of bacteria (Fukami et al. 1981b, Newell & Linley 1984). This effect is countered by low bacterial carbon conversion efficiency (Newell et al. 1981), and degradation of older detritus is therefore usually associated with a decrease of the N/C ratio (Fukami et al. 1981a, b). The small but regular decrease in the N/C ratio of the sedimented material between 38 and 85 m (Fig. 9A) is therefore consistent with microbial degradation during sedimentation of not quite fresh detritus.

Chl *a* equiv. and PTP showed the opposite trend to that of POC, PON, and TPM, with rates of sedimentation generally increasing with increasing depth (Table 1, Fig. 5). This has also been found in another poll, Nordåsvannet, and, for Chl *a* equiv., was thought to reflect the influence of the changing oxygen tension on the decomposition and leaching of plant pigments

within the sediment traps (Wassmann 1985). Similar phenomena involving adsorption and desorption are also possible as an explanation for the increase in PTP sedimentation. Alternatively, this increased flux of PTP could have reflected microbial growth during the descent of sedimenting material.

Detritus in surface waters contains apparently little phosphorus (Sakshaug et al. 1983), probably reflecting a rapid loss of phosphorus from newly formed detritus (Garber 1984). Bacteria degrading such detrital material would therefore be likely to take up phosphorus from the surrounding seawater. Development of bacteria on sedimenting detritus could therefore have contributed to the increases in sedimentation flux of PTP and P/C ratio with increasing depth (Fig. 5E, F & 9B). Fairly large microbial populations associated with sedimenting material have been documented by microscopy (Iturriaga 1979, Ducklow et al. 1982) and by measurements of ATP (Iturriaga 1979, Fellows et al. 1981, Karl & Knauer 1984, Karl et al. 1984).

A major feature of our results is the difference in the sedimentation regimen between spring and summer. The spring period was characterized by plankton blooms and generally high sedimentation rates that were fairly uniform throughout the water column. In contrast, the summer period was characterized by greater stability in the plankton and lower rates of sedimentation below the euphotic zone (Fig. 3 to 5).

Sedimentation in spring

The 2 spring phytoplankton blooms were followed by peaks in sedimentation (Fig. 3 & 4). The first diatom bloom occurred in late March and on 1 April it was evidently already in its decline phase (Fig. 2 & 3). Since we missed the peak of the bloom in our sampling program, we have estimated its magnitude from the consumption of nutrients up to 1 April (Table 2). The amounts of PON and P*Si* produced during the bloom were calculated from the decreases in the contents of NO_3 and Si in the upper 20 m, assuming homogeneous concentrations of $9 \mu\text{M NO}_3$ and $11 \mu\text{M Si}$ prior to the bloom. Production of POC and Chl *a* were estimated using conversion factors. A value of 0.136 for the N/C atomic ratio was used, based on average ratios in the upper 20 m of 0.131 on 17 March and 0.142 on 1 April. The corresponding Chl *a*/C ratios on 17 March and 1 April were 0.0147 and 0.0069, respectively. During the spring bloom in 1981, a ratio of 0.0154 was obtained at a POC concentration of $640 \mu\text{g l}^{-1}$ (Skjoldal unpubl. results). A value of 0.015 was chosen as the Chl *a*/C conversion ratio.

The estimates of bloom biomass have been compared with the amounts that sedimented at 38 m

between 17 March and 19 April (Table 2). Sedimentation of PON and POC comprised about 67 % of the bloom biomass. The average N/C ratio of this sedimented material was 0.132, which is only slightly lower than the estimated ratio for the bloom (0.136). The recovery of Chl *a* equiv. in the sedimented material was 42 % and thus lower than for PON and POC. However, more Chl *a* equiv. was found in the trap at 70 m (79 mg m^{-2}), representing 55 % of the estimated bloom content. The recovery of P*Si* was quite low, with only 15 % of the estimated bloom content being collected at 38 m (Table 2).

Sedimentation from the euphotic zone of 67 % of the bloom PON and POC is probably an overestimate since grazing and background sedimentation have been ignored. Using the sedimentation rate for the period from 12 October to 20 January as a correction for sedimentation in the absence of phytoplankton growth, the above estimate is reduced to about 50 %. This is in better agreement with the estimate of bloom chlorophyll sedimentation. Apparently, therefore, about half of the spring bloom biomass sedimented out from the euphotic zone, with the remainder being remineralized in the upper water layer.

Our data provide little new insight into the mechanisms behind this sink-out from the euphotic zone. It is noteworthy, however, that the algae did not appear to be extremely starved for nitrogen, as judged from the quite high N/C ratios of both seston and sedimented material (Fig. 3D & 9A). It is possible, therefore, that the sink-out was caused by some biochemical or physiological response to deteriorating environmental conditions, prior to the cells becoming severely limited (Barlow 1984, Smetacek 1984, 1985). Since Si was the main limiting nutrient (Fig. 2), increased sinking rate elicited by Si depletion (Bienfang et al. 1982) could have played a role in this respect.

The low recovery of P*Si* in the sedimented material (Table 2) indicates more rapid dissolution of P*Si* than mineralization of PON and POC. Rapid dissolution of P*Si* in near-surface waters was reported by Nelson & Goering (1977). Kamatani (1982) showed that dissolution of diatom frustules was strongly dependent on organic coating, surface texture, temperature, and diatom species. *Skeletonema costatum*, which typically dominates the spring bloom in Norwegian coastal waters (Lännergren & Skjoldal 1976, Braarud & Nygaard 1980, Hegseth 1982, Erga & Heimdal 1984), displayed the most rapid dissolution with a rate coefficient of $1.3 \times 10^{-3} \text{ h}^{-1}$ at 10°C . However, since shaking increased the dissolution rate by about an order of magnitude for 2 other species (Kamatani 1982), the rate coefficient could be as high as about 10^{-2} h^{-1} for sinking frustules of *Skeletonema costatum*. Rates in the range 10^{-3} to 10^{-2} h^{-1} represent dissolution of 15 to

81 % of the P*Si* in 1 wk. The concentration of dissolved Si in the upper water layer increased after 1 April (Fig. 2), but not enough to account for the low recovery (15 %) of P*Si* in the sedimented material. It is therefore likely that most of the dissolution of P*Si* took place inside the sediment traps during the 19 d exposure period.

Sedimentation following the second spring bloom in late April (Fig. 3) was less pronounced than after the first bloom, particularly in terms of PON and P*Si* (Fig. 4). The low N/C ratios of the seston towards the end of the bloom (Fig. 3D) and of the sedimented material (Fig. 9A) indicate that nutrient starvation caused the culmination and sedimentation of this mainly non-diatom bloom. The presence of phytoplankters such as thecate dinoflagellates, characterized by inherently low N/C ratios, is an alternative explanation. We consider this unlikely, however, since microscopic examination revealed no dinoflagellates in the sedimented material.

The contents of POC and PON in the upper 20 m decreased by 6.4 g m^{-2} (from 10.3 to 3.8) for POC and by 0.65 g m^{-2} (from 1.10 to 0.45) for PON between 29 April and 19 May. By comparison, 3.2 g POC m^{-2} and $0.36 \text{ g PON m}^{-2}$ were collected at 38 m during the same period. About 50 % of the POC and PON which disappeared from the euphotic zone was therefore apparently remineralized before reaching 38 m.

Sedimentation in summer

The pattern of sedimentation at 18 m tended to be dissimilar from the more uniform patterns at 38 to 85 m (Fig. 6). This reflected mainly the high sedimentation rates of POC, PON, and TPM at 18 m during summer (Fig. 4 & 5). The rate of POC sedimentation was more than $400 \text{ mg m}^{-2} \text{ d}^{-1}$ from 29 June to 8 October (Fig. 4J), which is equivalent to the total water column primary production (Lännergren 1976). This sedimentation furthermore represented a daily loss of 15 to 20 % of the POC and PON in the euphotic zone (Fig. 8A), which is much higher than reported for other coastal environments (Nakajima & Nishizawa 1972, Burns & Pashley 1974, Taguchi & Hargrave 1978). In addition, the N/C ratios of the collected material were exceptionally high, exceeding those for the seston (Fig. 3D & 9A).

The most likely explanation for the high sedimentation rates and N/C ratios at 18 m is contamination by zooplankton in this trap situated just below the maximum in zooplankton abundance (Lie et al. 1983), despite our effort to remove them from the filters prior to analysis. Collection of actively swimming zooplankton in poisoned traps has been found to be a serious

problem also in many other studies (Smetacek et al. 1978, Knauer et al. 1979, Fellows et al. 1981, Honjo et al. 1982, Karl & Knauer 1984). For this reason, we consider the sedimentation measured at 38 m as the most reliable estimate for the sedimentation loss from the euphotic zone during summer. This sedimentation usually amounted to a daily loss of less than 5 % of the euphotic zone seston content (Fig. 8B). The N/C ratio of the material collected at 38 m was fairly similar to the ratios for seston and material sedimenting in the deeper anoxic water (Fig. 3D & 9A). This, and the low zooplankton abundance (Lie et al. 1983) in the hypoxic water (Fig. 1C), suggest that any contamination by zooplankton in the 38 m samples was minor.

The rates of sedimentation below the euphotic zone tended to be lower during summer than during spring (Fig. 4). Other studies have also revealed low sedimentation rates associated with the seasonal development of zooplankton and maturing of the pelagic system (Iturriaga 1979, Smetacek 1980a, b, 1984, 1985, Peinert et al. 1982, Wassmann 1983). This is apparently in contrast to the view that vertical flux of fecal pellets represents a major mechanism for loss of organic material from the upper water layer (Turner & Ferrante 1979). Reasons for this might be the great importance of coprophagy (Paffenhöfer & Knowles 1979, Turner & Ferrante 1979, Hofmann et al. 1981, Lorenzen et al. 1983) and lower *in situ* sinking rates of fecal pellets than predicted from laboratory determinations (Smetacek 1980b, Krause 1981, but see also Lorenzen & Welschmeyer 1983). Several direct comparisons have shown that flux of fecal pellets constituted only a small fraction of total carbon flux (Knauer et al. 1979, Urrère & Knauer 1981, Honjo et al. 1982). This points to the possible greater importance of other types of aggregates such as marine snow (Shanks & Trent 1980) and amorphous fecal material (Bishop et al. 1977, 1978).

Vertical flux of fecal pellets is strongly influenced by the size composition and vertical distribution of the zooplankton community (Paffenhöfer & Knowles 1979, Hofmann et al. 1981). Using a theoretical approach, Hofmann et al. (1981) calculated that less than 10 % of the fecal pellets produced daily, or about 0.2 % of the average daily primary production in terms of nitrogen, reached the seafloor at 35 m for a coastal community dominated by *Paracalanus*.

Studies on the vertical distribution of zooplankton in Lindåspollene in summer have revealed distinct stratification, with little evidence for any substantial diel vertical migration of the small and dominant species (Lie et al. 1983, Skjoldal et al. 1983). The zooplankton community is apparently 2-layered (Magnesen, Aksnes & Skjoldal unpubl.). Cladocerans, appendicularians, and the small copepods *Acartia*

spp., *Paracalanus parvus* and *Centropages hamatus* occur mainly in the upper 5 m where most of the primary production also takes place (Lännergren 1976, Skjoldal et al. 1983). Below, with centers of distribution at 10 to 15 m, occur the copepods *Temora longicornis*, *Pseudocalanus elongatus*, *Oithona similis* and *Oncaea* spp., which together comprise the bulk of the zooplankton biomass.

The phytoplankton in the upper layer during summer is dominated by small flagellates and monads (Lännergren 1976, 1978, Skjoldal et al. 1983), which typically have very low sinking rates (Takahashi & Bienfang 1983, Bienfang & Harrison 1984). Slowly sinking cells as well as fecal pellets and other aggregates produced in the upper layer would have to pass through the dense layer of small copepods below. Heavy grazing would probably allow little of this material to sediment out directly from the euphotic zone.

During June 1981, the average zooplankton biomass between 5 and 15 m was 30 and 28 mg ash-free dry weight m^{-3} for the 2 size fractions 75 to 250 and 250 to 1000 μm , respectively (Lie et al. 1983, Skjoldal & Magnesen unpubl.). The mean individual dry weight over both size fractions was 1.7 μg at the biomass maximum at 10 m (Lie et al. 1983). Copepods of this size can ingest more than their own body weight per day at high food densities (Frost 1980). Using ingestion rates in the range 50 to 100 % of the body weight d^{-1} for both size fractions, their combined ingestion would be 140 to 280 mg C $m^{-2} d^{-1}$ for the 5 to 15 m layer. The corresponding production of fecal pellets would be 40 to 80 mg C $m^{-2} d^{-1}$, assuming 70 % assimilation efficiency (Paffenhöfer & Knowles 1979). These estimates are lower than the average sedimentation rate of 115 mg C $m^{-2} d^{-1}$ at 38 m during summer (Fig. 4K).

Coprophagy would reduce the amount of fecal material which could sediment out from the euphotic zone. In this respect we would like to point to the possible importance of members of the genus *Oncaea*, which are among the dominant copepods in Lindåspollene (Lie et al. 1983, Skjoldal et al. 1983) as well as in other coastal environments (Beers et al. 1977, Dagg et al. 1980, Paffenhöfer 1983). The feeding ecology of *Oncaea* is virtually unknown, although it has been speculated that it is omnivorous or carnivorous (Walsh 1983). *Oncaea* is often found associated with large particles such as abandoned appendicularian houses (Alldredge 1972). Paffenhöfer (1983) found a positive correlation between the abundance of late copepodites and adults of *Oncaea* and concentration of particulate matter. It is interesting to note that in such widely different environments as Lindåspollene, the eastern Gulf of Mexico, and off the coast of northern Peru, *Oncaea* tended to be distributed just beneath the bulk

of herbivorous small calanoids (Smith et al. 1981, Hopkins 1982, Magnesen et al. unpubl.). It is therefore possible that *Oncaea* feeds on fecal pellets, acting as a filter for fecal pellets produced by the herbivores in the water column above them.

The chlorophyll maximum layer (CML) in Lindåspollene during summer (Fig. 3B) is located at the nutricline (Fig. 2) below the zone of maximum copepod abundance. This appears to be a pattern of vertical organization often found in water columns with a developed nutricline and a deep CML (Longhurst 1976, Herman et al. 1981, Longhurst & Herman 1981). There is also vertical organization within the CML in Lindåspollene, as evidenced by the difference in gradients between NO_3 and Si (Fig. 2) and by *in situ* chlorophyll fluorescence profiles and microscopic analysis of samples obtained in June 1982 (Skjoldal & Erga unpubl.). This latter study revealed a dominance of small diatoms and silicoflagellates in the CML.

Cells sinking out from the CML could be a source for sedimentation to greater depths. The steep nutriclines signify that nutrients transported upwards are utilized in this layer. The gradient in NO_3 between 18 and 20 m on 15 June (Fig. 2) was 2.7 mmol m^{-1} . Combined with a coefficient of turbulent diffusivity of $0.04 \text{ cm}^2 \text{ s}^{-1}$ (Aure 1972), this yields an estimate of upwards transport of about $7 \text{ mg N m}^{-2} \text{ d}^{-1}$. This is equivalent to a C fixation of about $60 \text{ mg C m}^{-2} \text{ d}^{-1}$ and indicates that CML production has the potential to contribute substantially to the observed sedimentation at 38 m during summer. The CML is located at about the 1% light level. In summer, therefore, the midday light intensity varies from about 2 to $15 \mu\text{E m}^{-2} \text{ s}^{-1}$ between heavily overcast and clear days. This variation at low light intensities could to a great extent determine the rate of primary production, resulting in pulses of production and subsequent sedimentation.

The CML is not devoid of zooplankton and some grazing undoubtedly occurs. The material which sinks out from the lower part of the euphotic zone could therefore be a mixture of algal cells and fecal pellets. Few intact fecal pellets were detected in sedimented material, most of which was amorphous detritus (Wassmann 1983). However, rapid disintegration of pellets (Honjo & Roman 1978, Turner & Ferrante 1979) could be one reason why they were not observed more frequently.

The high correlations between P_{Si} and organic sedimentation (Fig. 6 & 7) suggest sinking diatom frustules, whether or not these are associated with fecal pellets (Ferrante & Parker 1977, Turner 1984), to be an important transport mechanism for organic material to the deeper water. The relation between sedimentation of P_{Si} and organic material was particularly strict in spring, but existed also during the summer and early

autumn period (Fig. 7). Due to the presumably high contribution of diatoms and silicoflagellates to the production in the CML, and the low proportion of diatoms in the surface layer, this lends further support to our suggestion that most of the material which sedimented out during summer originated in the deeper part of the euphotic zone.

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