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Sedimentation of organic and inorganic particulate material in Lindåspollene, a stratified, land-locked fjord in western Norway

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ABSTRACT: Sedimentation of particulate material to the bottom (90 m) was measured in Lindåspollene, a land-locked, highly stratified, west Norwegian fjord, receiving fresh water from a small glacier free watershed. Five cylindrical sediment traps positioned at 10, 20, 40, 70, and 85 m below the surface were exposed from April to November. Organic material comprised 40 to 60 % of the sedimented matter. Sedimentation rates of particulate inorganic material (PIM) and particulate organic carbon (POC) decreased from 229 and 111 at 20 m to 71 and 22 g m^{-2} yr^{-1}, respectively, in the deeper water. Possible reasons for the low sedimentation in the stagnant water below 40 m are high mineralization rates in the upper 40 m and the lack of resuspension in the water below. Three pulses of POC and PON (particulate organic nitrogen) reached the bottom related to phytoplankton blooms in April and May. The pulse in April was the largest and the sedimented material consisted of unidentified aggregates, diatoms and some few fecal pellets. Few recognizable structures were found in the samples below 20 m except in April. This might indicate a low zooplankton grazing efficiency in April, but a high efficiency during the rest of the investigation period.

INTRODUCTION

Little is known about seasonal and depth-related changes in sedimentation of particulate material in Norwegian fjords. Wassmann (1981) and Gulliksen (1982) applied sediment traps to measure the supply of particulate material to the sediment surface in respectively Fanafjorden and Balsfjorden, whereas Skei (1983) measured the sedimentation in the poll Framvaren.

I present here the first data concerning the supply of particulate material to the sediment of Lindåspollene, a west Norwegian, highly stratified, land-locked fjord (Fig. 1). The supply of particulate matter to the sediment depends partly on changes in the structure and function of the pelagic system. Monitoring the sedimentation cycle is, therefore, one important step towards the understanding of marine ecosystems (Smetacek, 1980a). The investigation is part of a project at the Institute of Marine Biology, University of Bergen. The ultimate aim of this project is to develop a dynamic mathematical model of the flows of energy and matter in the ecosystem (Dahl et al., 1973).

The settling of particles through the water column and onto the sea bed has been subject of thorough investigations in different parts of the world for about 2 decades (Table 5). This flux represents a loss of particulate organic matter from the euphotic zone and the main source of food and energy for the benthos and planktonic organisms living below this zone. The sinking of particles is also of interest for chemical and geochemical processes in the water column as well as in the sediment.

Small, land-locked fjords ('polls') are very common along the west coast of Norway. Despite extensive investigations of 'polls' in the twenties and thirties (Gaarder, 1932; Gaarder and Bjerkan, 1934 ; Ålvik, 1934; Strøm, 1936) little research has been done in Norway on such ecosystems until the sixties (e.g. Dybern, 1967; Lännergren, 1975, 1976, 1978; Dale, 1978; Skjoldal and Lännergren, 1978).

Land-locked fjords have specific topographic, hydrodynamic and biological characteristics, such as shallow sills, limited water exchange and stagnant bottom waters, and food chains which differ from those of more open fjords (Matthews and Heimdal, 1980).

Land-locked fjords differ so much from typical fjords that it has been suggested that the Norwegian word

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'poll', which means land-locked fjord, should be recognized and used internationally (Matthews and Heimdal, 1980). This term has previously been used in English articles by Klavestad (1957), Dybern (1967) and Lännergren (1975, 1976, 1978) and will be used throughout this publication.

MATERIALS AND METHODS

Lindåspollene, situated about 40 km north of Bergen (Fig. 1), consists of 3 basins separated by shallow sills. Lindåspollene is connected to the outer fjord (Lurefjorden) by 3 narrow sills less than 3 m deep. The restricted water exchange between the fjord outside and the basins leads to periodically anoxic conditions in Straumsosen and Spjeldnesosen at long-term intervals. Exchange of bottom water was not observed during the present investigation. Below 20 m the water is rather homogenous in salinity and temperature (Aure, 1972), but the oxygen content at the sampling site (Fig 1) declined from 5.5 to 6.5 ml $O_2\,l^{-1}$ at 18 m to 0.6 to 1.4 ml $O_2\,l^{-1}$ at 30 m (Fig. 2). H_2S was found in the bottom water below 70 m.

Lindåspollene has a small, glacier-free watershed of about 35 km^2 and receives about 70 10^6 m^3 freshwater yr^{-1} (Lannergren, 1976) from a number of small streams. This discharge corresponds to about 50 % of the total volume of the poll. During winter, Lindåspollene is most often ice-covered. The tidal range is about 50 cm and the water exchange during one tidal cycle about 2 % of the total volume (Dahl et al., 1973). The poll receives negligible amounts of domestic sewage.

Sedimentation of particulate material was measured at 10, 20, 40, 70, and 85 m depth at a central station with a water depth of 90 m (Fig. 1). Single traps were deployed during 12 periods, ranging from 6 to 31 d (average: 14 d) with one exceptional period of 57 d (July to August), from April (end of ice cover) to

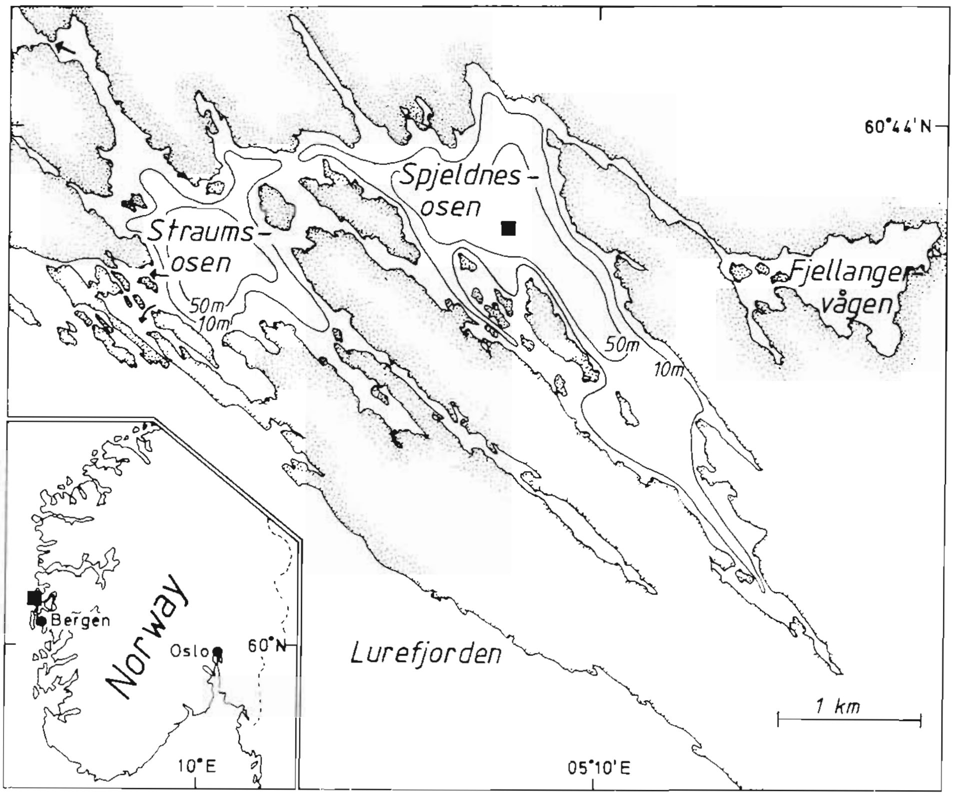

Fig. 1. Study area, Lindåspollene. Arrows indicate outlets from Straumsosen to outer fjord. ■ Sampling site

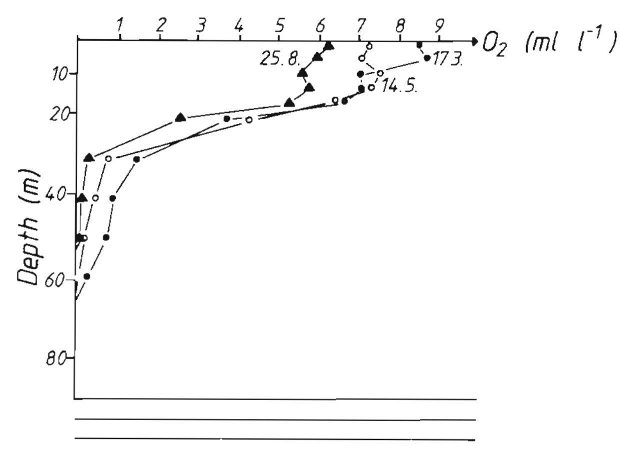

Fig. 2. Oxygen profiles in Lindåspollene between March and August 1981

November 1981. Cylindrical sediment vessels made of stainless steel und with a hight of 500 mm and a diameter of 100 mm (i.e. a H/D-ratio of 5) were held in position by wire, clamps, anchor and subsurface floats (Wassmann, 1981).

In most short-term sedimentation measurements moored traps of various design have been used (Ansell, 1974; Webster et al., 1975; Hargrave et al., 1976; Knauer et al., 1979; Lorenzen et al., 1981). Despite continuing discussions on the use of traps for sedimentation measurements (Bloesch and Burns, 1980; Iseki et al., 1980; Blomqvist and Håkanson, 1981), under moderate hydrodynamic conditions the use of cylindrical sediment vessels with a height/diameter greater than 3 seems to give reliable results (Hargrave and Burns, 1979; Blomqvist and Kofoed, 1981). To reduce degradation of trapped organic material inside the sediment vessels chloroform was added beforehand.

The collected material was suspended in 2.8 l of seawater and kept homogenous by agitation. Subsamples (25 to 250 ml) for the analyses described below were taken from the agitated suspension and filtered onto pre-ashed Whatman GF/C (glass fiber) filters.

Total particulate material (TPM) was determined in triplicate on pre-weighed filters. The filtered material was rinsed twice with 20 ml destilled water to remove salts and dried at 105 °C for 24 h. The fraction of particulate organic material (POM) and particulate inorganic material (PIM), respectively, was determined by weight loss on ignition at 450 °C for 3 h (Dean, 1974).

Particulate organic carbon (POC) and nitrogen (PON) were determined with a CHN-analyser (Carlo Erba Strumentatione 1106). To remove any carbonates the filters were treated with HCl prior to analysis.

A 100 ml subsample was preserved with buffered formaline (5 %) for microscopic examination; 20 ml of this subsample were examined at 60 × magnification. In the following text sedimentation rates are presented as per m^2 and day/year. The average sedimentation rate for the period December to March was assumed equal to that for the investigated period April to November when calculating the annual rates.

RESULTS

All sedimentation rates measured with traps represent gross sedimentation rates, including both primary settling material and secondary settling material (resuspension, turbulent upward transport, and active transport by animals). If nothing else is mentioned sedimentation means gross sedimentation in this context.

Sedimentation in relation to depth

Fig. 3b shows the mean sedimentation rates of TPM, PIM, POC and PON as functions of depth. Sedimentation was greatest at 20 m, decreasing markedly below, especially between 20 and 40 m. Sedimentation rates at 20 m were from 3 (PIM) to 8 (PON) times greater than those at 85 m (Table 1).

The extent to which sedimentation differs vertically in the water column can be assessed by analyzing the coherence between sedimentation rates at various depths. Table 2 shows product moment correlation coefficients (Sokal and Rohlf, 1981) between seasonal sedimentation rates at the various depths. Only 5 out of 40 regressions were significantly curvilinear. It is therefore assumed that linear regression sufficiently describes the relation between the seasonal sedimentation rates at different depths. The sedimentation rates at 10 m were closely correlated with those at 20 m. Also, the correlations between sedimentation rates at 40, 70, and 85 m were high, especially for POC and PON. On the other hand, the correlations between the sedimentation rates at 10 or 20 m and those at 40, 70, and 85 m were considerably lower. These results indicate different sedimentation regimes in the upper

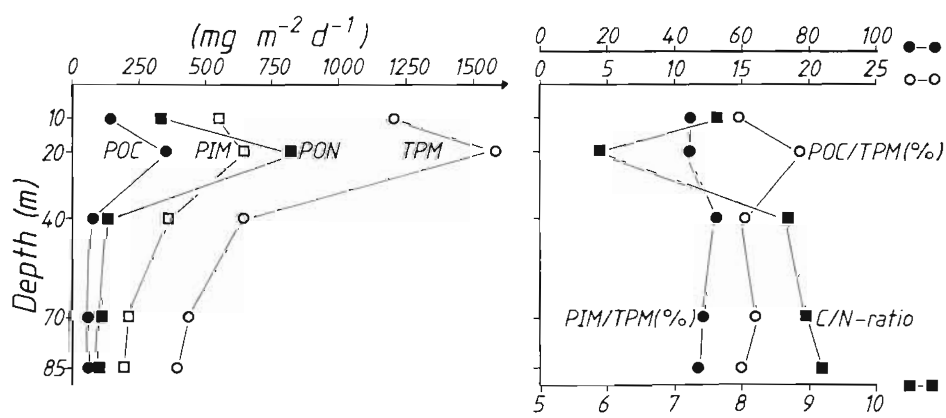

Fig. 3. (a) Mean sedimentation rates of total particulate material (TPM), particulate inorganic material (PIM), particulate organic carbon (POC), and particulate organic nitrogen (PON; units 15^{-1}) in relation to depths. (b) POC/PON-ratio (weight) of sedimented material, POC/TPM (%) and PIM/TPM (%) in relation to depth

Table 1. Annual gross-sedimentation rates of total particulate material (TPM), particulate inorganic material (PIM), particulate organic carbon (POC), and particulate organic nitrogen (PON) at different depths in Lindåspollene in 1981, and decrease in sedimentation between 20 m and 85 m expressed as a percentage of that at 20 m

Source	Sedimentation ($g\ m^{-2}\ yr^{-1}$)					Percent decrease in sedimentation between 20 and 85 m
	10 m	20 m	40 m	70 m	85 m	
TPM	424.0	536.3	224.0	155.6	146.6	72.8
PIM	191.3	228.6	128.1	75.1	70.9	69.0
POC	52.9	110.5	29.3	25.8	22.9	79.3
PON	8.2	19.9	3.4	2.8	2.5	87.5

Table 2. Product moment correlation coefficients (r) comparing seasonal sedimentation rates of total particulate material (TPM), particulate inorganic material (PIM) (n = 12), particulate organic carbon (POC), and particulate organic nitrogen (PON) (n = 11) at different depths in Lindåspollene in 1981. * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Significant curvilinear regressions underlined

Source	Depth (m)	20	40	70	85
TPM	10	0.922***	0.302	0.626**	0.567*
	20		0.578*	0.781**	0.760**
	40			0.742**	0.769**
	70				0.984***
PIM	10	0.623*	0.208	0.563*	0.517
	20		0.718**	$\underline{0.755^{**}}$	$\underline{0.780^{**}}$
	40			0.654*	0.708**
	70				0.942***
POC	10	0.956***	0.515	0.480	0.552
	20		0.572	0.556	0.586*
	40			0.972***	$\underline{0.933^{***}}$
	70				$\underline{0.968^{***}}$
PON	10	0.977***	0.618*	0.619*	0.656*
	20		0.697*	0.712**	0.719**
	40			0.962***	0.883***
	70				$\underline{0.961^{***}}$

and lower layers of Lindåspollene, with a looser coupling between the two layers than within each of them.

Seasonal patterns of sedimentation

The seasonal patterns of sedimentation of TPM, PIM, POC, and PON were not similar (Fig. 4). With regard to depth, the period of investigation can be separated into 2 main periods. In April and May the time variations in sedimentation, especially of POC and PON, were similar at all depths. For the rest of the period of investigation the sedimentation at 10 and 20 m differed markedly from that at greater depths. From July to November sedimentation rates for all components were fairly high at 10 and 20 m, but low at 40, 70, and 85 m. Time variations were almost uniform in the lower part of the water column during the last period.

Three maxima of phytoplankton biomass (as suspended chlorophyll *a*) in April and May in Lindåspollene (Skjoldal, unpubl.; no measurements available for the rest of 1981) coincided with 3 pulses of deposition of POC and PON at 20, 40, and 70 m, indicating that particulate material derived from phytoplankton is transferred rapidly to the deeper part of the poll. Only 1 peak of sedimentation of POC and PON reached the depth of 85 m and coincided with the first and main phytoplankton bloom. Particulate organic material from the upper part of the water column was not rapidly transferred to the stagnant part of the water column from July to November, a period of maximum stratification. This implies a high decomposition rate in the water mass above the oxycline (30 m) or export of POM out of the area during this period.

Nature of sedimented material

Microscopic examination revealed that most of the material found in the traps, especially below 20 m,

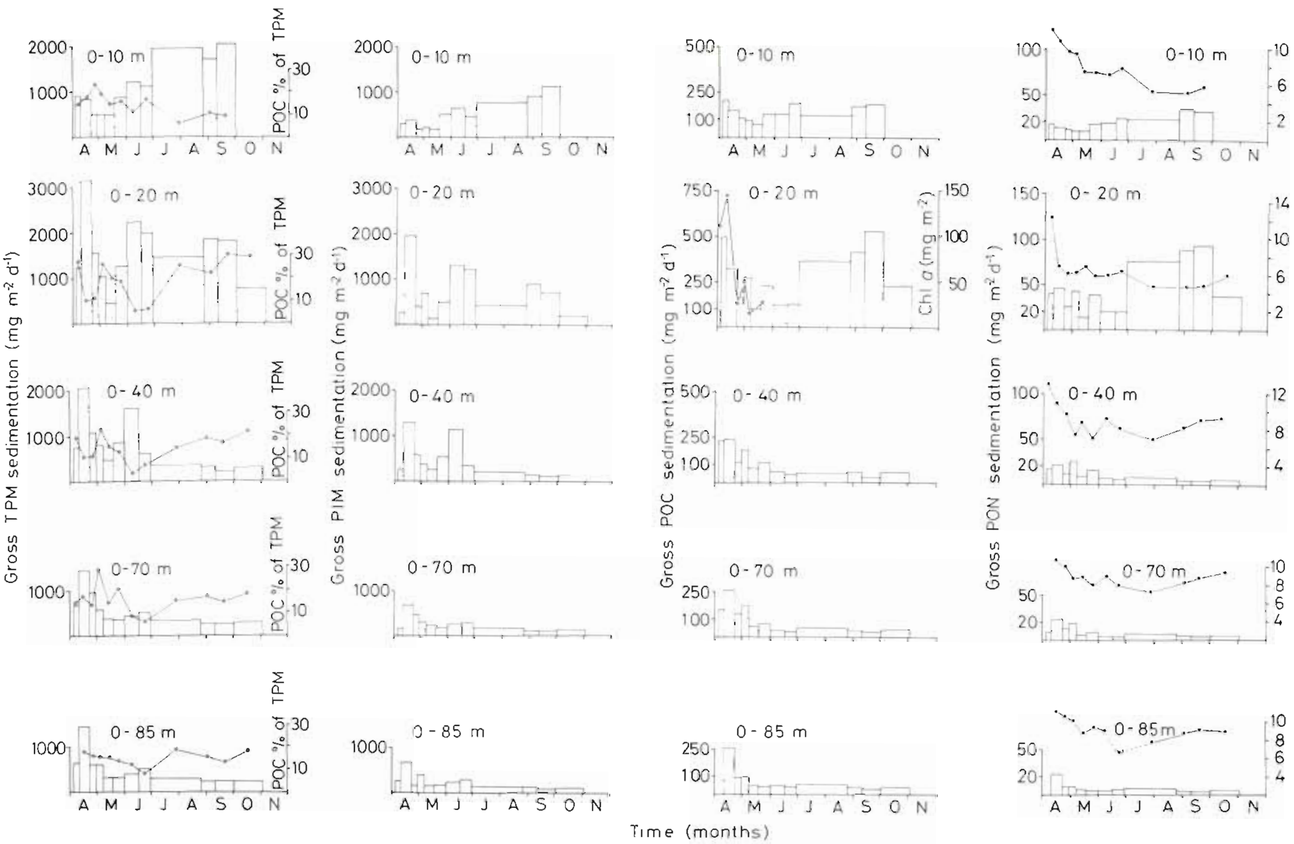

Fig. 4. Sedimentation rates of total particulate material (TPM), particulate inorganic material (PIM), particulate organic carbon (POC), and particulate organic nitrogen (PON) and the POC/PON-ratio (weight) and POC/TPM (%) of the sedimented material at 10, 20, 40, 70, and 85 m in the period April to November 1981 in Lindåspollene. Also shown is the chlorophyll *a* content in the upper 40 m of the water column

consisted of small aggregates and flakes without any recognizable structures. It is not clear, however, to what extent the preservation of the deposited material during exposure of the traps and during storage of the samples has influenced its appearance. Recognizable structures were mainly fecal pellets and diatoms, whereas dinoflagellates were rarely found.

Diatoms such as *Skeletonema costatum, Thallassiosira* sp., *Chaetoceros* sp. and *Rhiizosolenia* sp. were found at all depths during the peaks in sedimentation of POC and PON following the spring bloom. During the summer period, on the other hand, diatoms were rarely found in the traps below 20 m.

Organic material (ash free dry weight) comprised in general more than 50 % of the TPM deposited (Table 1). The relative content of POC varied between 4 and 30 % with an average of 16 % (Fig. 4).

Significant ($p < 0.001$) product moment correlations between precipitation (run-off from land) and the sedimentation rates of particulate material were found for the samples from 10 m depth, but not for the samples from 40 m and below (Table 3). Moreover, recognizable allochtonous material, such as leaves etc., was never found in the traps, indicating that particulate allochtonous material is of minor importance for the annual supply.

The relative POC content of the TPM showed greatest seasonal variations at 20 m and least variation at 10 and 85 m (Fig. 4). The patterns of variation were similar for the 20, 40, and 70 m samples, while being different for the samples from 10 and 85 m. Since organic material represents a major part of the TPM

Table 3. Product moment correlation coefficients (r) comparing precipitation (river run-off) and sedimentation of total particulate material (TPM), particulate inorganic material (PIM), particulate organic carbon (POC), and particulate organic nitrogen (PON) at 10, 20, and 40 m in Lindåspollene in 1981. * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Significant curvilinearity was not found

Depth (m)	TPM	PIM	POC	PON	n
10	0.893***	0.924***	0.951***	0.926***	10
20	0.605*	0.362	0.665*	0.627*	11
40	0.244	0.216	0.397	0.441	11

deposited and primary production is the main source of this organic material (Table 4), differences in the POC content of phytoplankton will influence the seasonal variations in the POC content of the TPM deposited. Diatoms and coccolithophorids, which contain much non-combustible material, showed blooms in April and June, respectively. Minima in the relative POC content at 20 m and below coincide with these blooms. The POC content of the sedimented matter was high and increasing from July to November at 20 m and below, despite the presumably high mineralization efficiency in the plankton during this period. Possibly, different sources for sedimentation of PIM and POC can also have caused seasonal variations in the POC content of the TPM.

The POC/PON-ratio of the sedimented material varied both with season and depth (Fig. 3b and 4), revealing changes in the composition of the organic material. The mean POC/PON-ratios at the different depths show the reverse trend to that of sedimentation (Fig. 3b). The ratio decreased slightly from 10 to 20 m, indicating less nitrogen depletion of deposited material at 20 m. The POC/PON-ratio increased markedly between 20 and 40 m, but only slightly between 40 and 85 m. The pattern of seasonal variation in the POC-PON-ratio were generally similar at all depths, with maximum values found in early April. Thereafter the ratios decreased to minima in July/August followed by a slight increase. The high POC/PON-ratios in April coincided with relatively high sedimentation rates at all depths. This indicates that the diatoms which comprised much of the sedimented material during this period were strongly nitrogen depleted.

Table 4. Annual supply and loss of POC in the upper 40 m of Lindåspollene (g m^{-2} yr^{-1})

SUPPLY:	
Photosynthetic production[a]	95
River discharge[a]	
flocculation of DOC[b]	7
particulate[c]	16
Sum supply[d]	118
LOSS:	
Sedimentation[e]	29
Export, Respiration[f]	89

[a] Lännergren (1976)
[b] Based on a mean concentration of DOC in fresh water of 10 mg C l^{-1} (Garrels and Mackenzie, 1971) and mean flocculation rate of fresh water DOM in sea water (Sholkovitz, 1976)
[c] Based on mean POC values from 45 Scandinavian and North American rivers (Karlström, 1978; Newbern, 1981)
[d] Few algae and macrophytes are found along the shores of Lindåspollene. No account is given for this supply. Release of sewage to the poll is low (Lännergren, 1976)
[e] Measured (Table 1)
[f] Calculated by difference

Flux of organic material to the sediment

Annual sedimentation rates from Lindåspollene (based on daily mean sedimentation rates) were calculated to compare those rates with annual sedimentation rates given in the literature (Table 1); 29 g POC m^{-2} yr^{-1} are supplied to the stagnant water mass of the poll. A rough calculation of the supply and loss of POC in the upper 40 m at the central station (Table 4) shows that only 24 % of the POC supply is transferred to the stagnant water. This implies that planktonic consumption and export are the most significant pathways for the POC flux in the upper part of the water column in Lindåspollene (Table 4).

Only 22 g POC m^{-2} yr^{-1} are supplied to the sediment (Table 1). This supply is in part used by the benthos as energy source and most of the refractory matter is accumulated in the sediment. Anaerobic benthic metabolism, i.e. sulfate reduction, does exist in the sediment of Lindåspollene. Therefore, the accumulation rate of POC has to be lower than 18 % of the POC supply of the upper 40 m of the poll. Supposing a sediment water content of 94 % (Pamatmat and Skjoldal, 1974; Skjoldal, unpubl.) and a specific weight of 2 g cm^{-3} dry sediment, the TPM sedimentation rate at 85 m (Table 1) is equivalent to sediment accumulation of less than 1.5 mm yr^{-1}.

The seasonal variation in sedimentation implies that the benthos at the sampling site receives more than 20 % of its annual supply of POC during 5 wk in April/May. For the rest of the year the sediment receives POC at almost steady state rate (about 60 mg POC m^{-2} d^{-1}).

DISCUSSION

The decrease of sedimentation with depth in Lindåspollene (Fig. 3a and 4) is in contrast to the increase with depth found in other environments (Steele and Baird, 1972; Ansell, 1974; Hargrave and Taguchi, 1978; Platt, 1979; Smetacek, 1980a; Gulliksen, 1982). The increase in sedimentation rate with increasing depth is usually interpreted as a result of resuspension, but other explanations might also be *in situ* autotrophic production, fecal pellet production by migrating zooplankton (Hargrave and Taguchi, 1978), the morphology of fjords and bays (sediment focusing) (Hargrave and Kamp-Nielsen, 1977) and currents.

The decreasing sedimentation with depth in Lindåspollene could be an artifact caused by different sampling efficiencies of the traps. The 5 sediment vessels are presumably subjected to different turbulence regimes at the various depths. In stagnant water a sediment vessel would catch the actual downward flow of particulate material regardless of the vessel design. The cylindrical traps used here have hydrodynamical qualities which, according to Hargrave and Burns (1979), Gardner (1980a, b), Blomqvist and Kofoed (1981) and Blomqvist and Håkanson (1981), give reliable results under the hydrodynamic conditions of this study. In a laboratory flume where the water current did not exceded 9.5 cm s^{-1}, Gardner (1980a) showed that a cylindrical sediment vessel with an H/D-ratio of 2.3 collected particles at a rate equivalent to the downward flux. Bröckel (pers. comm.), however, found that increasing water flow resulted in increased sedimentation rates up to a specific water current velocity, which flushes the whole sediment vessel and thus results in a lower sedimentation rate. The mean turbulent energy per unit time supplied to the water below 40 m depth in Lindåspollene is only about 3 % of the mean turbulent energy per unit time supplied to the top layer (0 to 10 m) (Aure, 1972). The turbulent diffusion is, therefore, of minor importance below 40 m and the sediment vessels below 40 m are situated in almost stagnant water. Sediment vessels at 10 and 20 m are subjected to turbulence and the collecting efficiencies might be reduced. Compared to other coastal environments, where sedimentation vessels with an H/D-ratio of 5 were used (Hargrave and Burns, 1979; Blomqvist and Kofoed, 1981), the influence of water movement in Lindåspollene is thought to be of minor importance. The decrease in sedimentation with depth can, therefore, not be explained by different catchment efficiencies.

The retrieval of the traps represents a critical step in this study because the traps were not closed during this operation. The effect of this was presumably small, however, since particles were never observed in the water above the deposited material on the bottom of the traps.

Due to the low oxygen content below 40 m (Fig. 2) most planktonic organisms have to stay above this depth. The consumption and the respiration of planktonic herbivores will lead to a decrease in particle concentration which can settle to the sediment. High zooplankton respiration rates directly above intense oxygen minimum zones are known from British Columbia fjords (Devol, 1981). The high concentration of animals in the upper 40 m of the water column in Lindåspollene produces a 'shadow effect' (Devol, 1981) reducing the sedimentation rate between 20 and 40 m (compare Fig. 2 and 3a).

In Lindåspollene resuspension is supposed to be of little importance at depths greater than 40 m since little turbulent energy is supplied to the water below (Aure, 1972). Therefore, the amount of collected matter at 20 and 40 m is supposed to reflect deposition of particulate material under conditions of turbulence and non-turbulence. From this point of view a diagram was made that illustrates differences in the deposition of POM in fjords and polls (Fig. 5). POM is produced in the euphotic zone of both water bodies. Due to this production net-sedimentation (primary settling material) increases down to the bottom of the euphotic zone if consumption is not excessive. Below this depth consumption by pelagic organisms leads to a decrease in net sedimentation in both areas. The turbulent water

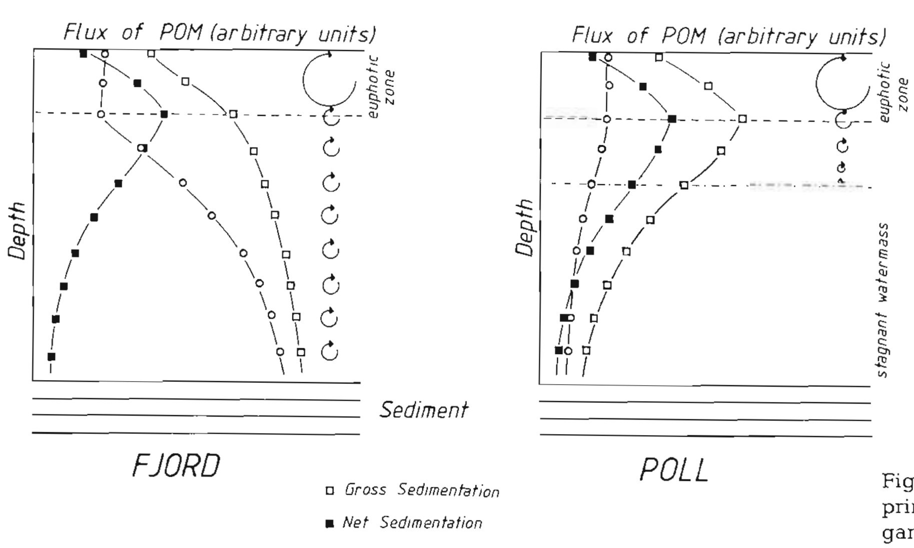

Fig. 5. General diagram showing the principal differences of particulate organic matter deposition in fjords and polls

transport (indicated by arrows), which is strongest in the upper part of the water column, leads to resuspension of particulate material from the bottom and the sides in fjords. This resuspended material is mixed with primary settling material. Turbulent water movement can also cause primary settling material to pass the same depth horizon several times in the course of its overall progress downwards. Thus turbulent water movement gives rise to increased quantities of material settled in collecting vessels. The consequence in fjords is an overall increasing sedimentation with depth. This is not the case in polls. Here turbulent water movement and resuspension are restricted to the upper part of the water column. As turbulent water transport decreases downwards, so does the resuspension (Fig. 5). The diagram gives a possible explanation why gross sedimentation increases in fjords and many other coastal environments down to the seafloor. In polls, however, gross sedimentation increases down to the bottom of the euphotic layer, but decreases below this depth. In the stagnant water, mass gross sedimentation and net sedimentation are close to each other if turbidity flows and sediment focusing do not occur.

Since resuspension is very low below 40 m sedimentation rates at 40, 70, and 85 m represent the actual downwards flux of particulate material. Gross sedimentation rates at 10 and 20 m have to be corrected for the amount of secondary sedimentation before the actual downwards flux can be obtained.

If we look at the period April to November in Lindåspollene as a whole a loose connection seems to exist between the upper 20 m and the water column below 40 m (Table 2). In April and May, however, these 2 layers are tightly coupled since pulses of POM settled quickly to the seafloor (Fig. 4). During summer and autumn the particle flux in Lindåspollene is characterised by two regimes of sedimentation. The sedimentation in the upper 20 m seems to be influenced by freshwater run-off, especially at 10 m depth (Table 3). Little of this material gets deposited at 40 m and below. The freshwater supplied material and minor phytoplankton blooms triggered by dissolved nutrient supply from freshwater are, therefore, either consumed in the upper layer or exported out of the area. The influence of this particulate material can also be seen in the increase and decrease of respectively POC/PON-ratio and POC/TPM (%) at 10 m depth compared to 20 m depth (Fig. 3b) since the freshwater supplied particles can be characterised as poor in nitrogen and high PIM-content.

In many coastal areas during some periods imbalances between the primary and secondary production have been reported (Fransz, 1976; Gieskes and Kray, 1977; Smetacek, 1980a; Peinert et al., 1982). This is often caused by low overwintering zooplankton biomass. Diatom populations from the spring phytoplankton bloom sink, therefore, ungrazed to the bottom. With the presence of a richer zooplankton community in summer and autumn much of the organic material gets recycled in the water column. Most fjords are deep enough for the overwintering of larger zooplankton organisms, such as *Calanus finmarchicus*, which immediately graze the spring phytoplankton bloom. In polls, however, larger zooplankton organisms are excluded from overwintering due to low oxygen concentration in the deeper parts and due to the shallowness of the sills.

The decrease in dissolved nutrients and especially in silicate brings the spring phytoplankton bloom to an end (Lännergren and Skjoldal, 1976). Skjoldal and Lännergren (1978) observed that major parts of the spring phytoplankton bloom in Lindåspollene disappeared from the water column during 8 d in late April. They suggested that the bloom sank to the bottom, which implies sinking rates of about 10 m d^{-1}. The results of this study show that this actually takes place. The coincidence of phytoplankton blooms (chlorophyll *a* concentrations, Fig. 4) and elevated POC- and PON-sedimentation rates in April and May show that the blooms sank to the bottom in about 7 to 14 d (exposure time of the traps). This implies sinking rates of 6 to 10 m d^{-1}.

There is considerable disagreement in the literature about *in situ* sinking rates of phytoplankton ranging from some cm to several tenths of m per day (Lännergren, 1979; Bienfang, 1981; Bodungen et al., 1981). 'Marine avalanches' (Bröckel, 1983), sinking about 10 or even 100 m d^{-1} and including parts or the whole phytoplankton bloom, have been described by several authors (Bodungen et al., 1975; Skjoldal and Lännergren, 1978; Smetacek et al., 1978; Bodungen et al., 1981). This phenomenon coincides with lack of dissolved nutrients and is caused by poor physiological state of the phytoplankton (Bienfang, 1981; Bröckel, 1983). Silicate depletion elicited by far the greatest increase in sinking rates of diatoms (Bienfang, 1982). Biochemical aspects of silicate metabolism of diatoms, which seem to be of more importance than density-related variations in the amount of silicate per cell (Bienfang, 1982), and low grazing pressure of zooplankton seem to be the main causes for the supply of phytoplankton biomass to the sea bed at the end of vernal blooms.

During summer and autumn, small forms like flagellates predominate the phytoplankton in Lindåspollene (Lännergren, 1976). These organisms manage well at low dissolved nutrient concentrations. The recycling of dissolved nutrients by the rich zooplankton community is sufficient for the phytoplankton in summer and autumn since its biomass is low. During those periods primary and secondary production in the upper part of the water column is tightly coupled. Good physiological state of phytoplankton organisms lead to balanced growth, which is reflected in POC/PON-ratios (moles) around 7 (Sakshaug et al., 1983). The balance between the phytoplankton growth rate and the remineralization rate during summer and autumn is reflected in the low POC/PON-ratios of the deposited material in the sediment vessels at all depth (Fig. 3a and 4). During blooms, however, lack of dissolved nutrients leads to nitrogen depletion and high POC/PON-ratios (Fig. 4). The results from Lindåspollene seem to indicate that 'new production' (April) and 'recycled production' (summer and autumn) (in the sense of Dugdale and Goehring, 1967) are well reflected in respectively high and low POC/PON-ratios of the deposited material.

The use of nitrogen content of detritus as an indicator of nutritional value has been criticised by Rice (1982) since much nitrogen accumulated under detritus decomposition is non-labile humic nitrogen rather than microbial protein. In Lindåspollene most of the organic material supply is due to photosynthesis (Table 4) and since the POC/PON-ratios can be used as reliable parameter characterising the physiological state of phytoplankton communities when corrected for detritus (Sakshaug et al., 1983) the ratio seems to be useful in explaining changes in the nature of the deposited material in this study.

In contrast to the results of Steele and Baird (1972), Seki et al. (1974), Bishop et al. (1977), Honjo and Roman (1978) and Spencer et al. (1978) fecal pellets seem to be of minor significance for the flux of the POM to the sea bed in Lindåspollene. Even in periods when zooplankton were abundant, fecal pellets were scarce, especially below 20 m. Also in Kiel Bight (Smetacek, 1980a) small amounts of fecal pellets were found in the sediment traps. The small contribution of fecal pellets in the sedimented material can be interpreted as a result of coprophagy (Turner and Ferrante, 1979), neutral buoyancy (Krause, 1981) and microbial attack on fecal pellets (Paffenhöfer and Knowls, 1979; Smetacek, 1980b; Hofman et al., 1981). If the particle diameter of suspended POM decreases severely in the lower part of the upper water column in Lindåspollene, i.e. due to the effect of grazing herbivores, coprophagy, resuspension of fecal material after the dissolution of the pellicula etc., the sedimentation rate would decrease markedly since the sinking rate of a particle decreases exponentially with decreasing diameter (McCave, 1975). Such a delay in sedimentation would lead to higher pelagical mineralization rates in the water column and, therefore, result in a lower amount of sedimenting material and lower numbers of recognizable particles.

Table 5 compares gross-sedimentation rates from different coastal areas with the results of this study. The deposition rates in Framvaren (Skei, 1983) and Lindåspollene are low compared to those from other areas. Polls, therefore, seem to be characterised by low sedimentation rates. The organic content of the deposited material, however, is quite high compared to the results of other studies (Table 5), indicating that inorganic material is of relatively minor significance for the total sedimentation in Lindåspollene.

According to Parsons et al. (1977), 30 to 40 % of the planktonic primary production settles to the sea floor every year in coastal areas. Other sources, such as sewage, allochtonous material, macrophytes etc., might also be of importance. Only 19 % of the POC-supply of Lindåspollene is supplied to the sea-bed at the sampling site (Table 1 and Table 4). Low deposition rates of POC are also known from lakes (Kimmel and Goldman, 1977; Wissmar et al., 1977) and from the glacial embayment Bedford Basin (Hargrave and Taguchi, 1978), where 15 % of the total supply reached the bottom. In contrast to Bedford Basin, where the tidal exchange is large and 57 % of the POC-supply is exported to the sea, the export of POC from Lindåspollene must be of minor importance. The surface water is highly stratified most of the year and only 2 % of the total water volume is exchanged during one tidal cycle; 28 % of the POC-supply is consumed by planktonic organisms in Bedford Basin. In Lindåspollene, however, planktonic consumption represents probably the main sink for POC supplied to the upper 40 m (Table 4). Planktonic mineralization rates (% of primary production) have been estimated for coastal waters like Narragansett Bay (Oviatt et al., 1981: 59 %), open ocean areas (Suess, 1980: 60 %), upwelling areas (Lee and Cronin, 1982: 90 %), tropical areas (Petersen and Curtis, 1980; Taguchi, 1982: 51 %), and from the oxic part of the water column of the Black Sea (Deuser, 1971: 80 %). Thus, it is probable that the planktonic mineralization rate in Lindåspollene is rather high since export is thought to be of minor importance. Compared to a west Norwegian fjord, where the net-sedimentation rate of POC close to the bottom comprised 38 % of the primary production (Wassmann, 1981), the flux of POC to the sediment in Lindåspollene comprised only 24 % of the primary production (Table 1 and Table 4). The assumption of Matthews and Heimdal (1980) that planktonic poll communities (characterised by nanoflagellates and small copepods) have at least during certain periods low ecological efficiencies compared to fjords (characterised by a predominance of diatoms and larger copepods) cannot be true for Lindåspollene on an annual basis since the remineralization efficiency of the planktonic community seems to be quite large. The specific structure of the planktonic food-chain and the hydrography of any poll

Table 5. Annual gross-sedimentation rates of total particulate material (TPM), particulate organic carbon (POC), and POC/TPM (%) in different coastal environments

Location and reference	Depth of trap (m)	Sedimentation ($g\ m^{-2}\ yr^{-1}$) TPM	POC	POC/TPM (%)
Depature Bay				
Stephens et al. (1967)	30	3000	200	6.7
Loch Ewe				
Steele & Baird (1972)	30		58	
Loch Etive				
Ansell (1974)	40		106	
	54		247	
St. Margareth's Bay				
Webster et al. (1975)	60	1500	118	7.9
Loch Thurnaig				
Davies (1975)	30		28	
Bedford Basin				
Hargrave et al. (1976)	20	791	58	7.3
	30	984	71	7.2
	40	1076	78	7.2
	50	1019	75	7.4
	60	1356	92	6.8
Monterey Bay				
Knauer et al. (1979)[a]	50[b]		158	
	250[b]		92	
	50[c]		33	
	250[c]		19	
Western Kiel Bight				
Smetacek (1980a)[d]	15	643–1681	39– 80	4.6–5.9
	18	611–1811	36–104	4.8–6.1
Dahob Bay				
Lorenzen et al. (1981)	50		70	
Kanehohe Bay				
Taguchi (1982)	15	1990	165	8.3
Fanafjorden				
Wassmann (1981)	60	825	96	11.6
	90	885	107	12.1
Framvaren				
Skei (1983, in press)	40	90		
Lindåspollene (this study)	10	424	53	12.5
	20	538	110	20.5
	40	224	29	12.9
	70	156	26	16.7
	85	147	23	15.6

[a] Based on daily flux rates from measuring periods between 19 and 21 d
[b] Under upwelling
[c] Under downwelling
[d] 3 yr study

or fjord have to be carefully considered before general statements on the recycling efficiencies of those areas can be made.

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