

Particle flux, and composition of sedimenting matter, in the Greenland Sea

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Abstract

Vertical flux of particulate material was recorded with moored sediment traps during 1988/1989 in the Greenland Sea at 72°N, 10°W. This region exhibits pronounced seasonal variability in ice cover. Annual fluxes at 500 m water depth were 22.79, 8.55, 2.39, 3.81 and 0.51 g m⁻² for total flux (dry weight), carbonate, particulate biogenic silicate, particulate organic carbon and nitrogen, respectively. Fluxes increased in April, maximum rates of all compounds occurred in May–June, and consistently high total flux rates of around 100 mg m⁻²d⁻¹ prevailed during the summer. The increasing flux of biogenic particles measured in April is indicative of an early onset of algal growth in spring. Small pennate diatoms dominated in the trap collections during April, and were still numerous during the high flux period when *Thalassiosira* species were the most abundant diatoms. During May–June, up to 22% of the *Thalassiosira* cells collected were viable-looking cells. The faecal pellet flux increased after the May–June event. Therefore we conclude that the diatoms settled as phytodetritus, most likely in rapidly sinking aggregates. From seasonal nutrient profiles it is concluded that diatoms contribute 25% to new production during spring and 50% on an annual basis. More than 50% of newly produced silicate particles are dissolved above the 500 m horizon. High new production during spring does not lead to a pronounced sedimentation pulse of organic matter during spring but elevated vertical export is observed during the entire growth period.

1. Introduction

Both the amount and composition of particulate matter settling to the ocean floor are highly variable in space and time. They thus reflect regional and seasonal differences in primary particle formation and modification in the pelagic realm in general, and the productive layer in particular (Wefer, 1989). The vertical export of the primary product, e.g. phytoplankton cells, depends on both the recycling efficiency in the watercolumn and their modification into larger,

fast-sinking particles. Formation of aggregates (marine snow) and production of faecal pellets are regarded as the two major processes by which sufficiently fast-sinking particles (with sinking speeds of > 100 m d⁻¹) are produced, that may escape destruction and degradation by the pelagic communities (Lorenzen and Welschmeyer, 1983; Alldredge et al., 1987; Asper, 1987; Banse, 1990). However, even these particles with potential sinking velocities of > 100 m d⁻¹ can be subject of considerable modification due to the activity of heterotrophic organisms. Smith et al. (1992) re-

ported high hydrolytic enzyme activity on marine snow particles, which implied rapid loss of organic compounds from these particles. Due to coprophagy, coprorhexy and coprochaly faecal material may be reingested and destroyed by zooplankton and thus exposed to enhanced remineralisation in the water column. (Lampitt et al., 1990; Noji, 1991; Noji et al., 1991).

Nevertheless, aggregation of diatoms into large marine-snow particles during the decline of the spring bloom can result in rapid transfer of biogenic particles from the euphotic zone to the seafloor (Billet et al., 1983; Smetacek, 1985; Peinert et al., 1989). Grazing and faecal pellet production of organisms occurring in dense swarms have been observed to cause recurring and sporadic sedimentation events (Bodungen, 1986; Bathmann, 1988; Wefer et al., 1988).

A third mode of rapid sedimentation to the seafloor is the settling of organisms themselves. Bathmann et al. (1990, 1991) and Antia et al. (1993) recorded distinct sedimentation events of foraminifers, radiolaria, pteropods and acantharia. From annual sediment trap moorings, distinct aggregates cannot generally be differentiated from the collections, whereas faecal material and hard parts of many organisms can be identified, and thus can be used to interpret trap collections with respect to pelagic processes.

Only few measurements of particle flux have been conducted in the partly ice covered areas of the ocean, where a distinct seasonality of pelagic processes can be expected. (Fischer et al., 1988; Honjo, 1990; Hebbeln and Wefer, 1991; Wassmann et al., 1991; Hargrave et al., 1993).

The use of sediment traps in determining the particle flux has been subject to criticism during recent years, as their collection efficiency might be biased by physical and hydrodynamical factors as well as the trap design (Butman, 1986; Bueseler, 1991; Gust et al., 1992; Honjo et al., 1992). This applies particularly for traps deployed in the surface mixed layers. During long incubation times collected matter in the cups may be lost and/or modified by a variety of processes. Measurements of dissolved properties in the supernatant water can be used for a conservative estimate of loss of particulate matter during incuba-

tion time (Bodungen et al., 1991a; Smith et al., 1992; Körtzinger et al., 1994). However, despite these possible drawbacks sediment traps are, up to the present, the only tool that allows a continuous record of quantity and quality of particles settling through different water layers.

Here we report on results obtained with moored sediment traps deployed in the Greenland Sea at a 72°N, in the Jan Mayen Current which is influenced by the East Greenland Current and its drifting ice fields. For the interpretation of trap collections, watercolumn data from several cruises to this area are included. The results presented here are part of the project "Particle flux from the pelagial" of the Sonderforschungsbereich 313 of Kiel University.

2. Methods

Sedimentation of particulate matter in the Greenland Sea was recorded using sediment traps deployed in a long term mooring at 72°34.8'N, 10°30.5' W at a water depth of 2241 m in the Jan Mayen Current from 5.9.1988–27.6.1989 (Fig. 1). Modified versions of the "Kiel-type" sediment traps (Zeitzschel et al., 1978) were moored in 500, 1000 and 2000 m depth. Sampling intervals of 14 and 30 days were selected for the periods of April to October and November to March respectively. However, due to technical failures the last cup of the 500 m trap sampled for a period of 49 days (18.5–27.6). In the 1000 m and 2000 m traps, the electronics failed completely so that only one cup sampled over the entire mooring period (5.9.1988–27.6.1989). These integrated values are presented as an approximation for the decrease of vertical flux with depth. In order to obtain a full annual cycle (Sept. 1988–Sept. 1989) we include data of a short-term mooring (29.6.1989–8.7.1989) and the results from the first sampling intervals of the long-term mooring 1989–1990. These moorings were deployed close to the positions of the mooring 1988/1989. Samples were poisoned *in situ* with HgCl₂ (end concentration 0.07%). After recovery of the traps samples were refrigerated until further treatment. After return to the lab, samples were split into aliquots by

means of a rotating splitter. Dry weight, carbonate, particulate biogenic silicate (PSi), particulate organic carbon (POC) and particulate organic nitrogen (PON) were determined by the procedures as described in Bodungen et al. (1991a).

Particulate silicate values were corrected by adding the increase of dissolved silicate (DSi) in the supernatant water, assuming that this DSi originates from dissolution of sedimented matter. This correction accounted for up to 50% of total

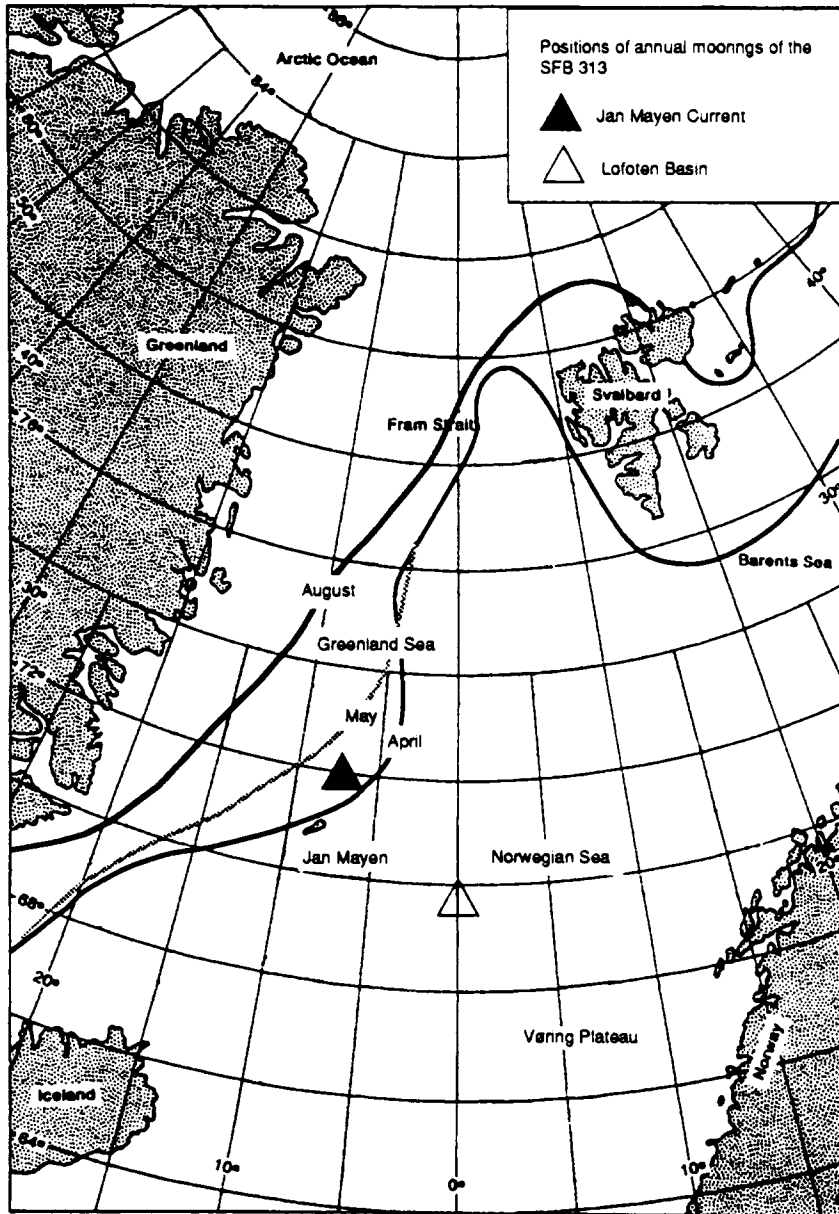


Fig. 1. Positions of annual sediment trap moorings of the SFB 313 in the northern North Atlantic (redrawn from Koeve, 1992). Mean position of the ice edge during April, May and August are indicated [depicted from data of the Bundesanstalt für Seeschiffahrt und Hydrographie (BSH), ice survey].

PSi values during times of low PSi flux; however it was in the range of 2–5% during periods of elevated PSi flux (Puch, 1990; Bodungen et al., 1991a). Microscopic analysis of the trap samples was carried out by means of an inverted microscope using the “Utermöhl-technique” (Utermöhl, 1958). The same method was used for the analysis of the phytoplankton composition and biomass in samples preserved with lugol’s solution and taken during *Meteor* cruise 10/3 to the Greenland Sea (June 6th–July 12th 1989).

In the trap samples only intact faecal pellets,

or particles that were identified as fragments of pellets, were counted in different size categories. For the calculation of faecal pellet volume (FPV), the pellets, or the volume of faecal pellet fragments, were converted to standard pellets. This was done by using an empirically obtained width/length relationship (Bathmann et al., 1987; U.V. Bathmann pers. commun., 1992). The volumes of oval-shaped and round pellets were calculated on the basis of spheres and ellipsoids respectively. The faecal pellet carbon content (FPC) was estimated from faecal pellet volume by

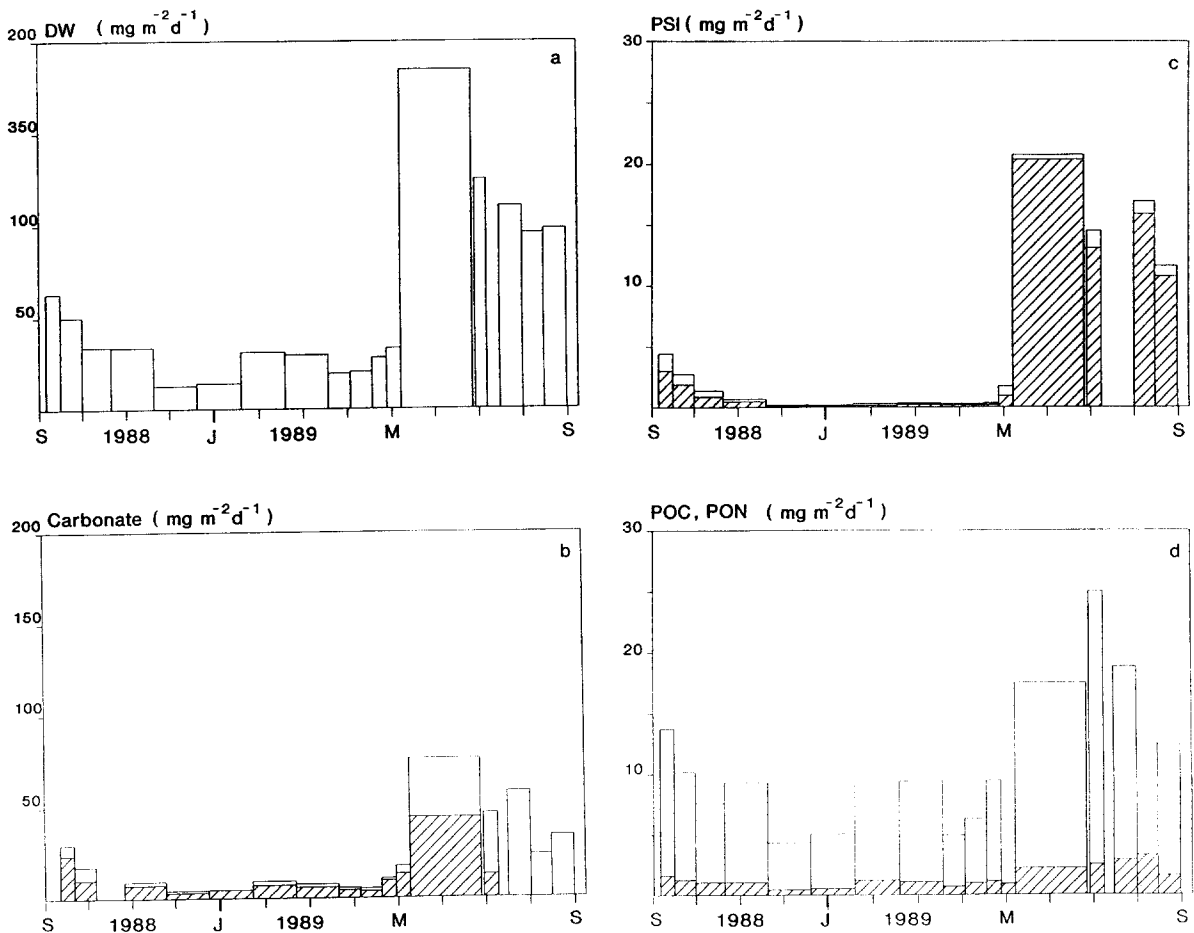


Fig. 2. Sedimentation pattern of particulate matter and its components in the Greenland Sea at 500 m depth as observed from September 1988–September 1989. a. Total flux as dry weight. b. Carbonate flux, hatched area = size fraction < 63 μm (no size fractionation in last 3 samples). c. Flux of particulate silicate (hatched) corrected for the dissolved fraction. d. Flux of POC and PON (hatched). All values in $\text{mg m}^{-2} \text{d}^{-1}$.

applying the conversion factor of 0.11 which may, however, result in an overestimation of FPC (Bathmann et al., 1987).

3. Results

3.1. Sedimentation of total particulate matter

In September 1988, total flux (dry weight) to 500 m amounted to 40–60 mg m⁻² d⁻¹ and decreased during winter to 20–40 mg m⁻² d⁻¹. A distinct increase to maximum flux rates of 184 mg was not observed before May 1989 (Fig. 2a). Thereafter total flux fluctuated around values of ≈ 100 mg m⁻² d⁻¹. For the period September 1988–September 1989 we calculated a total flux of 22.8 g m⁻². Of this flux, 39% was recorded during the 49 day period in May–June and 69% in May–September.

3.2. Composition of sedimented matter

Fluxes for carbonate, PSi, POC and PON showed similar seasonal patterns when compared to total flux. Carbonate sedimentation contributed significantly (25%–53%) to total flux during the whole mooring period (Fig. 2b), with a large proportion in the size fraction < 63 μm. Flux of carbonate increased 5-fold in May–June as compared to the preceding months; approximately 44% of the annual carbonate flux was recorded during that period (8.5–27.6.1989) (Table 1). In the same period, the increase in PSi flux was even more pronounced. Particulate silicate flux increased from low winter values (≈ 0.3 mg m⁻² d⁻¹) to > 1 mg m⁻² d⁻¹ in the beginning of May and to > 20 mg m⁻² d⁻¹ in May–June and remained at high levels (13–18 mg m⁻² d⁻¹) until September 1989 (Fig. 2c). Of the annual PSi flux of 2.39 g m⁻² a⁻¹ 42% were

Table 1

Sampling schedule, sedimentation rate (mg m⁻² d⁻¹) at 500 m and annual flux (g m⁻²) of particulate matter in the Greenland Sea at 72°N in the period September 88–September 89. (DW = dry weight, PSi = Particulate biogenic silicate corrected for the dissolved fraction, POC = particulate organic carbon, PON = particulate organic nitrogen, % = share of sedimentation during May/June 89, nv = no value)

| Sampling intervals | DW | Carbonate | PSi | POC | PON |
|----------------------------------|--------|-----------|-------|-------|------|
| 05.09.88–15.09.88 | 63.02 | 29.57 | 4.45 | 13.72 | 1.61 |
| 15.09.88–30.09.88 | 50.10 | 23.49 | 2.75 | 10.16 | 1.26 |
| 30.09.88–20.10.88 | 33.95 | 16.37 | 1.38 | 7.62 | 1.05 |
| 20.10.88–19.11.88 | 33.65 | 9.25 | 0.69 | 9.30 | 1.05 |
| 19.11.88–19.12.88 | 12.73 | 4.26 | 0.20 | 4.33 | 0.46 |
| 19.12.88–18.01.89 | 14.12 | 4.66 | 0.19 | 5.04 | 0.54 |
| 18.01.89–19.03.89 | 29.71 | 7.73 | 0.36 | 9.39 | 1.08 |
| 19.03.89–03.04.89 | 19.48 | 5.76 | 0.30 | 4.90 | 0.70 |
| 03.04.89–18.04.89 | 20.52 | 5.40 | 0.28 | 6.29 | 0.97 |
| 18.04.89–28.04.89 | 28.02 | 13.22 | 0.35 | 9.44 | 1.12 |
| 28.04.89–08.05.89 | 33.14 | 17.60 | 1.72 | 6.18 | 0.89 |
| 08.05.89–27.06.89 | 184.64 | 76.30 | 20.72 | 17.52 | 2.22 |
| 29.06.89–08.07.89 | 1.187 | 0.88 | 0.17 | 0.24 | 0.02 |
| 15.07.89–01.08.89 | nv | nv | nv | nv | nv |
| 01.08.89–15.08.89 | 95.68 | 23.65 | 17.10 | 12.64 | 3.31 |
| 15.08.89–01.09.89 | 97.96 | 34.00 | 11.63 | 12.39 | 1.58 |
| annual flux (g m ⁻²) | | | | | |
| 500 m | 22.79 | 8.56 | 2.39 | 3.81 | 0.51 |
| | 39% | 38% | 42% | 22% | 21% |
| 1000 m | 10.50 | 3.30 | 1.20 | 1.30 | 0.20 |
| 2200 m | 12.96 | nv | 0.43 | 0.33 | 0.04 |

recorded during the 49 day period in May–June and 85% in May–September.

The seasonal changes in POC and PON fluxes, although following the same general pattern, were less pronounced. Winter flux varied between 5–9 $\text{mg C m}^{-2} \text{d}^{-1}$ and 0.03–0.08 $\text{mg N m}^{-2} \text{d}^{-1}$ for POC and PON respectively. Similar to POC the flux of PON was highest in June and July (Fig. 2d). Annual sedimentation of PON amounted to 0.51 $\text{g m}^{-2} \text{a}^{-1}$ with 21% occurring in the high-sedimentation period during May–June 1989.

4. Microscopic analysis

4.1. Diatoms

Among the recognizable part of the sedimented matter, diatoms and their remains dominated. Numbers of diatoms varied from a minimum of 2000 cells $\text{m}^{-2} \text{d}^{-1}$ to $1.44 \times 10^6 \text{ m}^{-2} \text{d}^{-1}$ (Fig. 3a). The mean sedimentation rate from September 1988–April 1989 was 7200 cells $\text{m}^{-2} \text{d}^{-1}$; it increased more than ten-fold by end of April and by three orders of magnitude during May–June 1989 ($1.44 \times 10^6 \text{ cells m}^{-2} \text{d}^{-1}$). After this period, sedimentation fluctuated between $0.5\text{--}0.9 \times 10^6 \text{ cells m}^{-2} \text{d}^{-1}$. During the period of low sedimentation (September 1988–April 1989) organisms of the genera *Thalassiosira*, *Coscinodiscus* and unknown small centric diatoms (diameter, 20–30 μm) were the most abundant forms. Other species present at this time were *Proboscia alata* (November–December 1988), *Rhizosolenia hebetata f. semispina* and *Asteromphalus robustus* (October–November 1988). Cells of *Chaetoceros cf. concavicornis*, *Chaetoceros decipiens*, *C. atlanticum*, *C. boreale* and other unidentified *Chaetoceros* species sporadically were present in low numbers. Small pennate diatoms of the genus *Nitzschia* and *Navicula* were the dominating diatoms in trap collections during the end of April, when sedimentation started to increase. The same pennate diatoms were still observed in high numbers in the period of highest diatom sedimentation, when *Thalassiosira* species dominated the sedimented diatoms composition ($\approx 55\%$ by numbers). Besides these genera, *Rhi-*

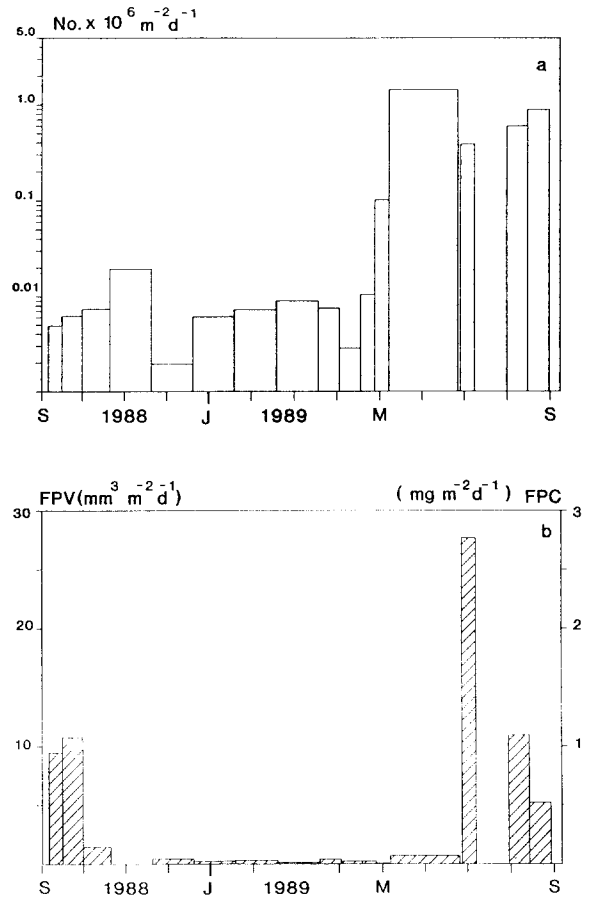


Fig. 3. Flux of diatoms and faecal pellets at 500 m. a. Sedimentation of diatoms given as numbers $\text{m}^{-2} \text{d}^{-1}$, note the logarithmic scale. b. Sedimentation pattern of faecal pellets given as volume (FPV, $\text{mm}^3 \text{m}^{-2} \text{d}^{-1}$) and faecal pellet carbon (FPC, $\text{mg C m}^{-2} \text{d}^{-1}$).

zosolenia hebetata f. hiemalis and *R. hebetata f. semispina* were observed in increasing numbers toward September 1989, sedimentation rates of these species in July–August ranged between 30–40,000 and 60,000 cells $\text{m}^{-2} \text{d}^{-1}$, respectively. Cells and resting spores of *Proboscia alata* were also observed in this period, albeit in low numbers.

Later analysis of the trap samples by scanning electron microscopy revealed the following *Coscinodiscus* and *Thalassiosira* species: *C. radiatus*, *T. antarctica*, *T. anguste-lineata*, *T. eccentrica*, *T. gravis* (A. Kohly, pers. commun.). Over the mooring period mainly empty frustules of diatoms

were found in the trap samples. Only in late April to June 1989 “viable-looking” diatom cells with plasma and chloroplasts were numerous. During May–June these “viable” cells amounted to 12% of total number of diatoms encountered and were up to 22% of the *Thalassiosira* cells during May–June.

4.2. Other biogenic particles

Among the non-diatomaceous particles observed were dinoflagellates, silicoflagellates (mainly *Dictyocha speculum*), empty lorica of tintinnids and radiolarians. Sedimentation of radiolarians was generally $< 500 \text{ ind. m}^{-2} \text{ d}^{-1}$, although highest numbers of radiolarians were observed in August 1989, when the sedimentation rate increased to a maximum of $15,000 \text{ ind. m}^{-2} \text{ d}^{-1}$. This number refers to intact skeletons of organisms belonging to Spumellarians and Nassellarians. However, the in situ-flux of radiolarians certainly was higher because variable amounts of fragmented remains of the skeletons of larger radiolarians (*Sagoscena sp.*), which we were not able to ascribe to individual organisms, were noticed regularly in the samples.

Coccolithophorids and foraminifers were also present in the samples, but were not quantified. Whole coccospheres of *Coccolithus pelagicus* as well as coccoliths of the same species were noticed. Coccolithophorids are known to form a major part in the phytoplankton assemblages of the Nordic Seas (Smayda, 1958; Ramsfjell, 1960; Samtleben and Bickert, 1990); this might explain the high carbonate flux of which $> 50\%$ was due to particles $< 63 \mu\text{m}$ during most of the time (Fig. 2).

Table 2
Sedimentation rates in the East Greenland Sea in the period 1985/1986 at 74°N ($\hat{\wedge}$) and 75°N ($\hat{\wedge}$) as given by Honjo, 1990. All values in g m^{-2} . Abbreviations see Table 1

| Depth | DW | carbonate | opal | POC | PON |
|---------------------------------|-------|-----------|------|-----|------|
| $881 \text{ m}^{\hat{\wedge}}$ | 8.79 | 2.59 | nv | 0.9 | 0.16 |
| $2833 \text{ m}^{\hat{\wedge}}$ | 10.21 | 3.28 | 2.61 | 0.4 | 0.06 |

Standing stock and sedimentation of foraminifera were examined during a drift study and by means of a short-term mooring from June 28th–July 8th 1989, where a flux of up to $5000 \text{ foraminifera m}^{-2} \text{ d}^{-1}$ was observed in 500 m (Bock, 1990). In August–September 1989, sedimentation of Acantharian cysts ($> 2000 \text{ m}^{-2} \text{ d}^{-1}$) was observed (Antia et al., 1993).

4.3. Faecal pellets

The annual sedimentation pattern of faecal pellets is given in Fig. 3. There was a sharp decrease in faecal pellet sedimentation to less than $0.5 \text{ mm}^3 \text{ m}^{-2} \text{ d}^{-1}$ ($< 100 \text{ pellets m}^{-2} \text{ d}^{-1}$) during late autumn 1988 and remained low through the winter and spring. A sharp increase to maximum flux rates of faecal pellets was observed by end of June ($27.6 \text{ mm}^3 \text{ m}^{-2} \text{ d}^{-1}$, $> 6000 \text{ faecal pellets m}^{-2} \text{ d}^{-1}$) after the maximum of diatom sedimentation. In August–September sedimentation rates declined to $1000\text{--}2000 \text{ faecal pellets m}^{-2} \text{ d}^{-1}$ ($\approx 10 \text{ mm}^3$) and then decreased to the low winter values. Converted to carbon (FPC), $3 \text{ mg FPC m}^{-2} \text{ d}^{-1}$ sedimented in the period of highest faecal pellet sedimentation and thus contributes 12% to total POC flux. In the preceding period with highest diatom sedimentation, the contribution of FPC to the POC flux was $< 1\%$. ($0.07 \text{ mg m}^{-2} \text{ d}^{-1}$).

In the entire mooring period faecal pellet composition was dominated by cylindrical pellets ($80\text{--}160 \mu\text{m}$ diameter) which can be attributed to copepods (Noji, 1991). Round and oval-shaped pellets were also present throughout the year, usually in low numbers; except in May–June 1989 when $\approx 20\%$ of the faecal pellet volume was due to this type of pellets. We did not consider pellets $< 50 \mu\text{m}$ although these “minipellets” were present in some of the trap samples (A.N. Antia, pers. commun., 1993). For this reason and because an unknown amount of faecal pellets may have been destroyed through breakage of the peritrophic membrane during splitting and storage, the reported faecal pellet flux can be regarded as a minimum.

5. Discussion

The observed annual sedimentation rate of total particulate matter and its components in the traps at 500 and 1000 m in the Greenland Sea at 72°N during 1988/1989 are comparable to the rates reported by Honjo (1990) at 74°35'N in 1985/1986 (Tables 1 and 2). The seasonal pattern of sedimentation, with a sudden increase in May–June at 72°N observed during our study, seems to be different compared with the neighbouring area where highest sedimentation occurred later in the year (Honjo, 1990). During the study in 1988/1989 at 72°N, 50% and 10% of the annual flux of POC recorded at 500 m reached the traps in 1000 m and in 2000 m, respectively (≈ 300 m above the seafloor).

The annual flux of POC and PON at 500 m in the Greenland Sea in 1988/1989 was comparable to flux rates in the Norwegian Sea (Bodungen et al., 1991b) despite considerable differences in the hydrographical regimes and phytoplankton–zooplankton relationships between both areas of the northern North Atlantic. Measurements of the particle flux in the Fram Strait in 1988/1989 revealed a strong influence from the presence and duration of ice cover on the amount as well as on the composition of sedimenting matter (Hebbeln and Wefer, 1991). Low total rates ($2.9 \text{ g m}^{-2} \text{ a}^{-1}$) were observed at a permanent ice-covered position. At a location in the Fram Strait covered by ice for approximately six months Hebbeln and Wefer (1991) found considerably higher flux rates, which were three times higher than at 72°N in the Greenland Sea, where similar ice conditions are encountered. Although a high amount of lithogenic components was observed in the sedimented matter in the Fram Strait, the share of biogenic particles increased during times when the ice edge was located close to the positions of the sediment traps. This is similar to the conditions we observed in the Greenland Sea at 72°N.

The mooring site in the Greenland Sea was permanently ice covered from November 1988 to February 1989. Ice charts of the study site, kindly provided by R. Ramseier, showed that the area first became ice free as early as late February.

Subsequently till the middle of June ice conditions varied from ice free conditions to ice coverage of 60–80% with the ice edge (ice coverage < 10%) moving several times across the mooring position. These highly variable ice conditions are caused by the constantly ice covered East Greenland current, which transports water of arctic origin to the south and feeds the easterly flowing Jan Mayen Current (Johannesen, 1985).

Marginal ice zones are regions of enhanced biological productivity, and of high biomass (Rey and Loeng, 1985; Smith et al., 1985; Smith and Sakshaug, 1990). The same certainly holds true for the highly variable ice conditions for the “repeatedly receding ice edge” in the Jan Mayen Current, which may favour phytoplankton growth early in the year. Growth of phytoplankton is reported to start about two months earlier in the partly ice-covered Greenland Sea than in the neighbouring Norwegian Sea which stays ice free throughout the year (Braarud, 1935; Paasche, 1960; Ramsfjell, 1960).

Our data, demonstrating an elevated particle flux starting in April, and showing a ten-fold increase in the sedimentation of diatoms in May–June indicate an onset of plankton growth, as early as April. This high flux of diatoms is mirrored in the high silicate flux in 500 m that contributed 42% to the annual POC flux at the same period (Fig. 2, Table 1).

In regions covered by ice, algal growth starts in, or at the bottom of the ice; at this early stage species composition is dominated by pennate diatoms, which are typical for ice algae communities (Horner, 1985). Growth of phytoplankton starts, when, due to the breakage and melting of ice, the nutrient-rich layer underlying the ice becomes stratified as the light intensity increases (Legendre et al., 1981; Sakshaug and Holm-Hansen, 1984). Below the ice, only planktonic algae adapted to low irradiances are able to grow. However, in drifting pack-ice, during ice melt and at the ice edge, light intensity fluctuates over a wide range. Organisms adapted to this fluctuating light regime are favoured under these conditions. *Thalassiosira* species generally show light saturation from low to high levels. Species of this genus are also known to grow well at low temperatures,

and to be characteristic species for diatom associations dominating during the first phase of phytoplankton succession in cold regions (Guillard and Kilham, 1977; Sakshaug, 1989; Baumann, 1990; Aletsee and Jahnke, 1992).

The pattern of diatom sedimentation in the Greenland Sea, exhibiting a succession from pennate species at the end of April to the dominance of *Thalassiosira* species during the high-sedimentation period, leads us to the conclusion that the formation of primary biomass was due to pelagic algae rather than to the growth of ice-associated algae.

In May–June 1989 a considerable portion of the diatoms, mainly *Thalassiosira*, sedimented as “viable” cells (10–22%). We take this as indicative of rapid sedimentation of these particulate material. As in the Greenland Sea rapid mass sedimentation of a spring *Thalassiosira* bloom has been reported in Antarctic waters (Bodungen et al., 1986). However, the authors reported that the majority of sedimented cells were resting spores which were not observed during our study in the Greenland Sea.

Because increased sedimentation of faecal pellets was observed after the maximum flux of diatoms (Fig. 3) we deduce that early spring phytoplankton development in the Greenland Sea is not controlled by zooplankton, and that the majority of phytoplankton sediments ungrazed. Elevated sinking velocities of diatoms in May–June 1989, were therefore probably achieved through the formation of aggregates. The coincidence of elevated POC flux and the increase in sedimentation of faecal pellets from the end of June on, when 12% of POC flux was due to faecal pellets, corroborates with the reported annual maximum abundance of copepods during June–July (Dawson, 1978; Smith et al., 1985; Smith and Sakshaug 1990; Smith and Schnack-Schiel, 1990). Although daily copepod herbivory in June–July 1989, as measured by gut clearance rate, was generally less than 1% of phytoplankton standing stock (Zeller, 1990), the large faecal pellets of *Calanus hyberboreus* (120–160 μm in diameter) contributed significantly to the POC flux in 500 m.

The flux of carbonate, that was the largest component of the total annual flux, was domi-

nated by the small size fraction ($< 63 \mu\text{m}$) during almost the entire mooring period. This is indicative of a considerable presence, and sedimentation of coccolithophorids. The increasing amount of carbonate particles $> 63 \mu\text{m}$ in May–June (Fig. 2) can be ascribed to increased sedimentation of foraminifera, which rapidly settled after reproduction (Bock, 1990).

The observed annual sedimentation pattern in the Greenland Sea appears to resemble patterns found in both coastal and oceanic waters, where sedimentation of the spring phytoplankton bloom occurs after the depletion of nutrients (Billet et al., 1983; Smetacek, 1985; Deuser, 1986; Peinert et al., 1989; Wassmann, 1990). However, none of the inorganic nutrients was depleted in the Greenland Sea at the time of trap recovery in June 1989. At the position of the mooring we measured 3.2, 4.8 and 0.43 μM of the inorganic dissolved nutrients, nitrate, silicate and phosphate, respectively. Phytoplankton composition at that time was dominated by non-diatomaceous organisms, with about 98% of phytoplankton biomass, *Phaeocystis pouchetii* being the dominant organism.

The observed pattern of diatom sedimentation in the Greenland Sea may be strongly influenced by the frequency of stabilization and destabilization in the euphotic zone during changing ice conditions; this was described as the “paradox of stability” by Legendre (1981). Through this mechanism sedimentation of phytoplankton may be triggered in the following way: early in the growth season, phytoplankton start to grow within a thin stabilized layer below the ice or between the ice floes where nutrients can become exhausted in a short time. In such shallow layers, particle concentrations may well be dense enough for aggregation to occur when phytoplankton, and in particular diatoms, secrete mucus under low nutrient concentrations (Smetacek, 1985). Consequently, a part of the early phytoplankton population may sink out of the surface layer. During periods of destabilization, nutrients will be mixed into the formerly nutrient-exhausted surface layer, thus restoring favourable conditions for phytoplankton growth during the next period of stabilization. This pattern of growth is corroborated by the

nutrient profiles, which showed deviations of winter values to far below the euphotic zone (Koeve, 1992). Thus, one may speculate that the onset of vernal growth in variable ice conditions represents a sequence of short biomass accumulation events and sinking pulses.

Thus the combination of light and the sequence of periods of stabilization and destabilization may well have triggered the sedimentation of non-motile phytoplankton in May–June 1989. However, we are not able to define exactly the onset and nature of the period of elevated sedimentation, as we only collected an integrated sample (49 days) for the period in question.

The magnitude of the export of organic matter from the euphotic zone to deeper water layers is strongly dependent on the amount of new production. On an annual basis the new production equals the vertical export through the base of the euphotic zone, which is often termed export production (Eppley, 1989). Composition and settling velocities of particles as well as biological activity in mid water layers are decisive for that portion of this export production which settles out of the winter mixed layer (Banse, 1990; Riebesell and Wolf-Gladrow, 1992)

Annual and seasonal new production at 72°N in the Greenland Sea was calculated from seasonal differences in nutrient profiles by Koeve (1992). Using the Redfield conversion he estimated an annual new production of 34.5 g C m⁻²a⁻¹. Of this annual new production, about 75% (≈ 26 gC m⁻²) took place before June. During the spring season approximately 3–4% of the spring new production settled through the 500 m depth horizon, which equals 28% of the annual export (Koeve, 1992), which amounts to 11% of the annual new production.

The contribution of diatoms to new production was estimated via Si:N ratios from the differences in the seasonal nutrient profiles and by application of an average molar ratio of Si:C = 0.13 for conversion into diatom new production of carbon. This ratio was determined from culture experiments with 27 different marine diatom species by Brzezinski (1985) and is similar to ratios found in natural populations by Paasche (1980). According to these calculations diatoms contributed ≈ 50%

to annual new production but surprisingly low 25% to new production during spring (until June).

Due to decomposition of carbon and dissolution of silicate during sinking and due to the fact that carbon losses in the collector cups during trap deployment cannot be corrected for estimations of the contribution of diatoms to vertical export cannot be quantified properly. Rapid dissolution of diatom frustules in the upper water column is evident from comparisons between nutrient profiles and measured flux rates. The difference between concentrations in winter and at the end of the growth season (October–November) would yield an annual “new production” of particulate silicate of 6.72 g m⁻² (Koeve, 1992). Recorded annual Si-flux in the trap at 500 m of 2.39 gm⁻² indicate that more than 50% of the particulate silicate is dissolved above this depth.

The contribution of diatoms to new production in spring at 72°N in the Greenland Sea is as low as the percentage of new production exported to deeper water layers, which is much lower than the annual average. During our investigations in this area during spring and summer 1989 high biomass of *Phaeocystis* was encountered (up to 98% of the phytoplankton biomass). The growth of *P. pouchetii* early in the year has been reported from high latitude waters (Braarud, 1935; Paasche, 1960; Bodungen et al., 1986; DeMaster et al., 1992). Recent investigations reveal that in some years even the spring bloom may be dominated by this organism (Rey and Loeng, 1985; Wassmann et al., 1990; Smith et al., 1991). Wassmann and his co-workers also describe the sedimentation of *Phaeocystis* in the Barents Sea. They were only able to follow sedimentation to 100 m, but found a marked decrease between 50 and 100 m that they ascribed to “dissolution, breakdown and grazing” (Wassmann et al., 1990). *Phaeocystis* is well known to form large aggregates which may not be readily consumed by zooplankton (Estep et al., 1990) but rather indicate a potential high sinking velocity. We observed *Phaeocystis* at the same mooring station during May–June 1990 in the trap at 500 m water depth. However, the role of *Phaeocystis* in vertical export is not very well understood. Our study indicates that spring production in the seasonally

ice-covered south-western Greenland Sea does not lead to high vertical export and much of the production is apparently recycled within the pelagic food web. Albeit the high percentage of annual new production in spring (75%) and the sharp increase in Si-flux in May (Fig. 2c), the vertical export of POC and PON (Fig. 2d) does not exhibit a pronounced spring pulse but rather elevated flux rates over the entire growth period of phytoplankton.

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