

Seasonal variation of vertical flux of phytoplankton and biogenic matter at Nordvestbanken, north Norwegian shelf in 1994

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The seasonal magnitude and biochemical composition of vertical flux of biogenic matter and phytoplankton at the north Norwegian shelf break was investigated at 14 depths between 20 and 200 m depth. Data of vertical flux were collected for 24 hours at monthly intervals using free- drifting sediment traps. Samples were analysed for particulate organic carbon and nitrogen (POC and PON), chlorophyll *a* (Chl *a*), phaeopigments (Phaeo) and phytoplankton composition. Two main periods of POC and PON vertical flux were observed in May and July with sedimentation rates ~ 300 mg POC $\text{m}^{-2} \text{d}^{-1}$ at 200 m depth. During the other periods vertical flux was ~ 100 mg POC $\text{m}^{-2} \text{d}^{-1}$ at 200 m depth. Vertical flux of Phaeo and POC had maxima in concert and Phaeo was always larger than Chl *a* vertical flux. Chl *a* vertical flux was low. The largest vertical flux was recorded in the upper water column in May and June ($0.4\text{--}0.7$ mg Chl *a* $\text{m}^{-2} \text{d}^{-1}$ at 20 m) and decreased rapidly with depth. The highest Chl *a* flux at depth was recorded during June and August ($0.2\text{--}0.5$ mg Chl *a* $\text{m}^{-2} \text{d}^{-1}$). Flagellates dominated the vertical plankton flux throughout the investigation and contributed significantly to the vertical POC flux (5–30 %). Net plankton ($> 20 \mu\text{m}$) and ciliates never contributed significantly to vertical POC flux. Biological processes were most important in regulating the vertical flux of biogenic matter which was regulated and controlled by the abundance of some key species of mesozooplankton.

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INTRODUCTION

The quantity and quality of sinking material is a result of the prevailing structure and function of the pelagic system (Wassmann 1998). Direct sedimentation of autotrophs and high flux are typical of new production regimes with low grazing pressure (e.g. Smetacek & al. 1984; Heiskanen 1998). Small herbivore biomass and slow reproduction response of advected and overwintering mesozooplankton populations typically prevents rapid pelagic exploitation of phytoplankton blooms (Kiørboe 1993; Peinert & al. 1989; Tande 1991). As a result extensive sedimentation of ungrazed phytoplankton and phytodetritus may take place during the senescent stage of the bloom. Export of phytoplankton may happen through sinking of single cells, chains or aggregated cells (Alldredge & Silver 1988; Kiørboe & Hansen 1993).

High heterotrophic activity may, however, postpone or prevent increased vertical losses (Peinert & al. 1989;

Wassmann 1998). Copepods, for example, may control the accumulation of phytoplankton biomass during the spring bloom if there is a large overwintering stock or a high import of zooplankton (Bathmann & al. 1990a). A match of the timing of copepods abundance and the onset of the bloom is crucial and determines the fate of the vernal bloom in the eastern regions of the Nordic Seas: export or retention in the upper layer (Peinert 1986; Bathmann & al. 1990a; Wassmann & Slagstad 1993). However, in the presence of a complex food web, the relationship between grazing and sedimentation is not simple (Silver & Gowing 1991) and depends on the all-over composition and function of the heterotrophic community. Swarm feeders (salps and krill) may graze effectively upon a bloom, giving rise to rapid sedimentation through fast sinking pellets. Other taxa such as copepods may actively recycle pellets through coprophagy, coprochaly and coprorhexy (Lampitt & al. 1990; Noji 1991) and retain material in the mixed layer. The complexity of the pelagic community may influ-

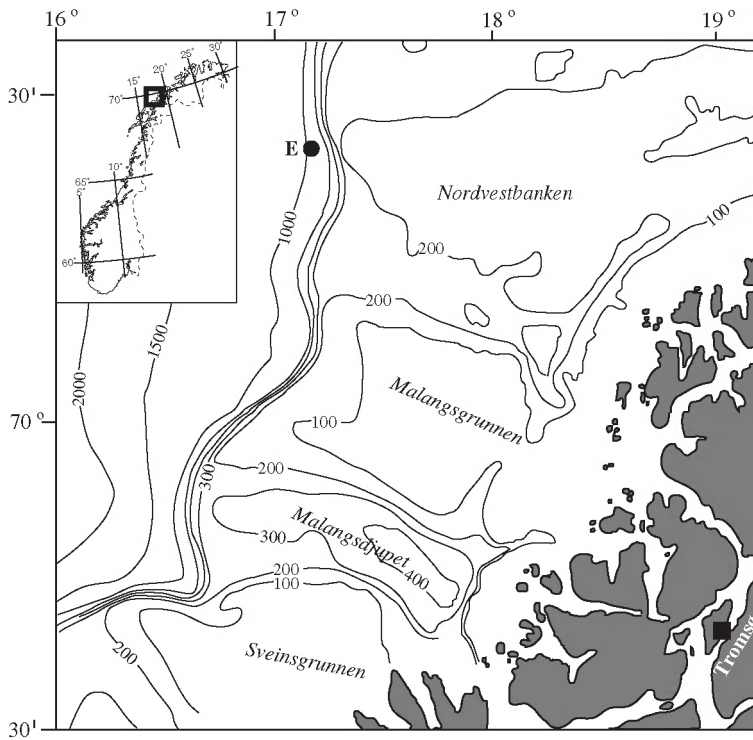


Fig. 1. Map of the sampling area with position of the start station for sediment trap deployment and the depth contours (m).

ence the relationships between primary production, grazing and vertical flux (Silver & Gowing 1991) and top down effects may be important in structuring the planktonic ecosystems in concert with abiotic factors (Verity & Smetacek 1996).

Extensive investigations regarding the vertical flux of organic matter have been carried out in the fjords of northern Norway (Keck & Wassmann 1996; Reigstad & Wassmann 1996; Wassmann & al. 1996) and at depth in the Norwegian Sea (Bathmann & al. 1987; Peinert & al. 1987; Bathmann & al. 1990b). However, only one short-term investigation of vertical flux has so far been carried out on the north Norwegian shelf, close to the Lofoten islands (Peinert 1986). To the best of our knowledge, no seasonal study of vertical flux has so far been carried out in our study area.

The present investigation is part of the Ocean Margin EXchange project (OMEX) which takes into account the specific features of European marine environments and settings. It concerns essentially the study of fluxes and processes occurring along European shelf break facing the North Atlantic Ocean. To study the main biological processes involved in the pelagic domain in northern Norway, the shelf and the shelf break NW of

the city of Tromsø, Nordvestbanken, was selected (Fig. 1). For an overview of the topography, hydrography, nutrients, suspended biomass and phytoplankton abundance of Nordvestbanken in 1994, see Nordby & al. (1999); Wassmann & al. (1999a) and Ratkova & al. (1999). The aim of the present study is to describe the seasonal magnitude and biochemical composition of vertical flux with particulate emphasis on phytoplankton-derived matter on the shelf and in great vertical detail. Data regarding the vertical flux of faecal pellets are presented by Urban-Rich & al. (1999) and Wassmann & al. (1999b).

MATERIAL AND METHODS

Data were collected at monthly intervals onboard R/V *Jan Mayen* from April to September 1994 at the shelf break off Nordvestbanken, northern Norway (Fig. 1). The shelf and shelf break off northern Norway are characterised by strong currents (Moseidjord & al. 1999) and is also a major area for trawl fishery. Free drifting sediment traps which reduce the problems of biased collection associated with high current velocities as well as the risk of loss due to local trawl fishing, were selected

as the best available tool for collecting sinking particles at the shelf break. A drifter (Fig. 2) equipped with 9 sediment traps between 20 m and 100 m and 5 sediment traps between 100 m and 200 m (each separated by 20 m) was applied. The sediment traps (KC maskiner og laboratorieudstyr, Denmark) were parallel cylinders mounted in a gimballed frame equipped with a vane. The traps were 0.072 m in diameter and 0.45 m high (H/D ratio = 6.25). They were deployed for 24 hours and no poison was applied during the deployment. Therefore grazing and bacterial decomposition might have taken place inside the sediment traps during exposure.

The drifter was deployed 6 times at approximately the same position (70°25.30'N, 17°08.00'E) at the shelf break (Fig. 1). This position is equivalent to the main plankton investigation site Stn E in Wassmann & al. (1999a). The ship followed the drifter while logging the position and taking CTD-profiles (Neil Brown Mk III) and water samples at regular intervals.

After recovery the content of the sediment traps was transferred to bottles, and kept cold and dark. Samples were never kept more than 6 hours before subsampling. Each sample was thoroughly mixed prior to subsampling. Duplicate samples (200–300 ml) from each cylinder were taken and filtered for analysis of particulate organic carbon and nitrogen (POC and PON), chlorophyll *a* (Chl *a*) and phaeopigments (Phaeo) on pre-combusted Whatman GF/F filters. Larger swimmers were removed by means of forceps on all filters. Samples for microscopic examination were taken from 20, 60, 100, 160 and 200 m depth and fixed with a ethanol-glutaraldehyde-Lugol solution (Rousseau & al. 1990) in order to amend the preservation of flagellates and mucilaginous matter.

Samples for Chl *a* and Phaeo were analysed immediately after subsampling using a Turner Design AU-10 fluorometer according to Holm-Hansen & al. (1965). This method is based on the assumption that Chl *b* exists in small amounts and does not interfere with the results (Holm-Hansen & al. 1965; Lorenzen 1981). Because of increasing fluorescence after acid addition some filters were rejected or set to zero (in cases where all parallels showed increase in fluorescence). This was mainly recorded in some or all parallels at six depths in May and at two depths in July. The results suggest the presence of Chl *b*, a possible underestimation of Chl *a* and overestimation of Phaeo (Welschmeyer 1994). A comparison of phytoplankton carbon estimates based on POC/Chl *a* ratios and phytoplankton biovolume conversion gave rise to greatly similar results (Wassmann & al. 1999a). There is thus little reason to expect a major underestimation of Chl *a*.

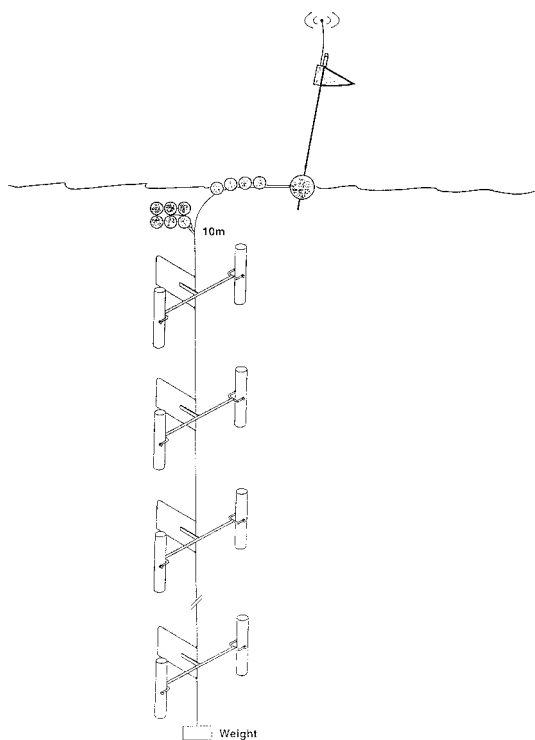


Fig. 2. Schematic illustration of the drifting buoy with sediment traps.

POC and PON samples were stored in a freezer and were later analysed on a Leeman Lab CEC 440 CHN analyser after removal of carbonate with fumes of concentrated HCl.

Phytoplankton was counted with a non-inverted light microscope furnished with a counting stage (Semina 1978). Counting of picoplankton and the most abundant nanoplankton algae was carried out in a Fuchs-Rosenthal counting chamber with a magnification of 400. Samples were allowed to settle for a week and the supernatant was slowly decanted through a glass tube covered with two layers fine-meshed nylon gauze. After gentle mixing the remaining sample was removed with a pipette and placed into a 0.05 ml chamber. Cells were counted under a magnification of 200. In order to count rare (usually larger) forms, a special 1.0 ml chamber was used, but as it is rather thick, only a low-power objective (magnification of 10) could be used. The volume of algae cells was calculated from the volume of appropriate stereometrical bodies (Smayda 1978) and average cell volume of each group was used to calculate the carbon content of the cells according to Strathmann (1967) and Edler (1979). For the calculation of pico-, nano- and microplankton contribution to sinking POC we used total pico-, nano- and microplank-

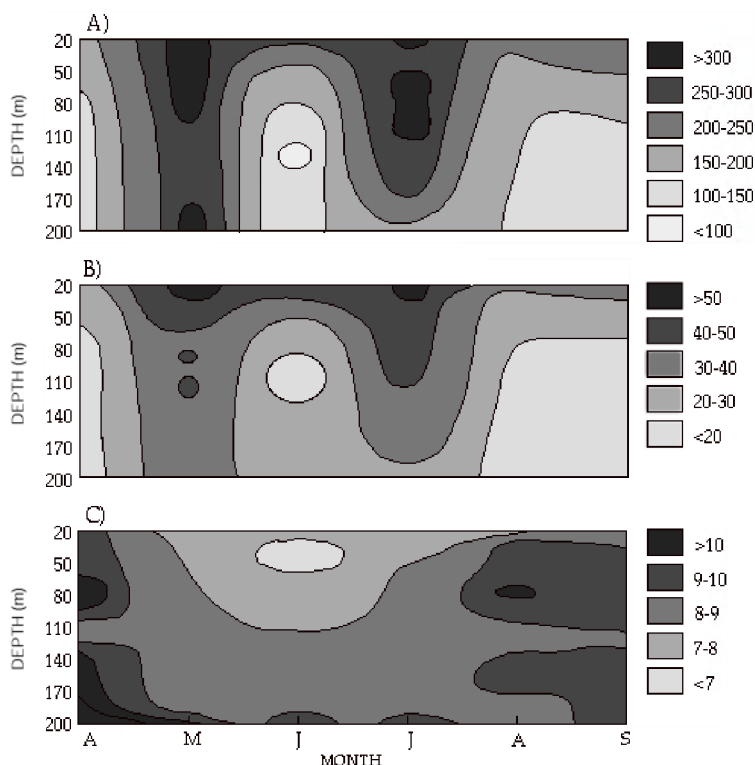


Fig. 3. Vertical flux of POC (A) and PON (B) at 20–200 m depth ($\text{mg m}^{-2} \text{d}^{-1}$). Also shown are the C/N (a/a) ratios of the exported material (C).

ton carbon (PNMC). Calculations of net phytoplankton carbon (NPC) (autotrophic cells $> 20 \mu\text{m}$) were conducted excluding the ciliate and positively identified heterotrophic dinoflagellate biomass.

Daily loss rates (%) and specific sinking rates (m d^{-1}) were calculated according to Hargrave & Taguchi (1978) using integrated concentrations (0–100 m) of POC, PON, Chl *a* and Chl *a* equiv. (Chl *a* + Phaeo) (data in Wassmann & al. 1999a) and vertical flux of the corresponding compounds at 100 m depth.

RESULTS

The dominating wind direction during all cruises was between south-west and south-east. Wind speed ranged predominantly from $5\text{--}10 \text{ m s}^{-1}$ with maxima up to 14 m s^{-1} in April. The drift pattern of the sediment traps in April, June, July and September was mainly south-west to north-east along the shelf edge. Excursions away from and towards the shelf break resulting in an eddy-shaped drift were encountered. In May the traps drifted towards the south-west along the shelf edge, while in August they moved towards north-west away from the shelf.

VERTICAL FLUX OF PARTICULATE MATTER (POC AND PON)

Two main periods of POC and PON sedimentation were identified (Fig. 3A, B). May and July had the highest POC and PON vertical flux with POC vertical flux ranging from $> 300 \text{ mg C m}^{-2} \text{d}^{-1}$ at 20 m to $\sim 250 \text{ mg C m}^{-2} \text{d}^{-1}$ at 180 m in both months. PON followed the same trends ($> 50 \text{ mg N m}^{-2} \text{d}^{-1}$ at 20 m, $\sim 35 \text{ mg N m}^{-2} \text{d}^{-1}$ at 180 m). In May the vertical flux increased to more than $300 \text{ mg C m}^{-2} \text{d}^{-1}$ and $36 \text{ mg N m}^{-2} \text{d}^{-1}$ at 200 m, while in July the POC vertical flux decreased to $185 \text{ mg C m}^{-2} \text{d}^{-1}$ and $23 \text{ mg N m}^{-2} \text{d}^{-1}$ at 200 m depth.

During the remaining periods vertical flux of POC and PON was lower. The decrease of POC and PON vertical flux with depth was more pronounced. April and August were the two periods with lowest vertical POC and PON flux throughout the water column (Fig. 3A, B). The vertical flux was $\sim 200 \text{ mg C m}^{-2} \text{d}^{-1}$ and $\sim 25 \text{ mg N m}^{-2} \text{d}^{-1}$ at 20 m and decreased with depth to $120\text{--}130 \text{ mg C m}^{-2} \text{d}^{-1}$ and $12\text{--}17 \text{ mg N m}^{-2} \text{d}^{-1}$ at 200 m. June and September had higher vertical flux in the upper 40 m ($> 230 \text{ mg C m}^{-2} \text{d}^{-1}$ and $> 20 \text{ mg N m}^{-2} \text{d}^{-1}$), but the vertical flux decreased clearly between 20–60 m and less so from 60 m and downwards. The POC verti-

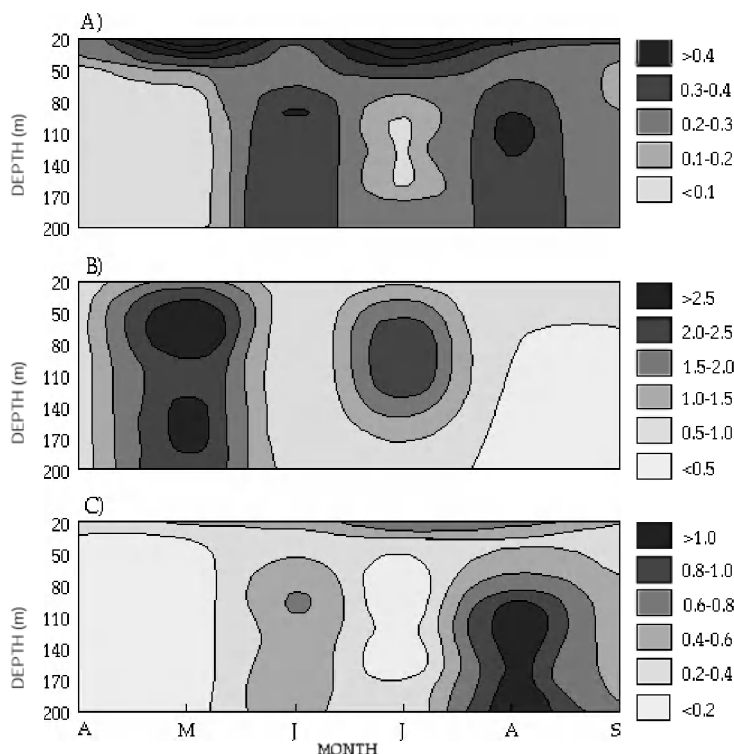


Fig. 4. Vertical flux of Chl *a* (A) and Phaeo (B) at 20–200 m depth ($\text{mg m}^{-2} \text{d}^{-1}$). Also shown are the Chl *a*/Phaeo (w/w) ratios of the exported material (C).

cal flux was similar to that of April and August ($130\text{--}150 \text{ mg m}^{-2} \text{d}^{-1}$), while PON vertical flux was higher in June ($13\text{--}24 \text{ mg N m}^{-2} \text{d}^{-1}$) compared to April, August and September.

VERTICAL FLUX OF PIGMENTS

April was characterised by the lowest vertical flux of Chl *a* during this investigation with $< 0.1 \text{ mg m}^{-2} \text{d}^{-1}$ and little variation with depth (Fig. 4A). The highest vertical flux of Chl *a* was recorded in May and June with $0.4\text{--}0.7 \text{ mg m}^{-2} \text{d}^{-1}$ at 20 m. The vertical flux of Chl *a* decreased rapidly with depth in both months to $< 0.2 \text{ mg m}^{-2} \text{d}^{-1}$ at 50 m in May and at 80 m depth in June. Below these depths the Chl *a* flux was low, generally $< 0.1 \text{ mg m}^{-2} \text{d}^{-1}$.

Two main events of Chl *a* flux to deeper water were recorded in June and August which ranged from $0.2\text{--}0.5 \text{ mg m}^{-2} \text{d}^{-1}$ throughout the entire water column. September experienced a vertical Chl *a* flux of $< 0.2 \text{ mg m}^{-2} \text{d}^{-1}$ with no reduction of Chl *a* flux with depth below 40 m.

Vertical flux of Phaeo (Fig. 4B) was larger than the flux of Chl *a* in all months except August. The vertical flux of Phaeo was similar in April, June, August and

September, ranging between $0.5\text{--}1.0 \text{ mg m}^{-2} \text{d}^{-1}$ throughout the water column. In April and June there was no significant variation with depth, while there was a slight decrease with depth in August and September. The main episodes of Phaeo vertical flux were in May and July, similar to POC vertical flux. May experienced the highest vertical flux of Phaeo with $> 2.4 \text{ mg m}^{-2} \text{d}^{-1}$ below 30 m. Vertical flux increased to maximum $3.4 \text{ mg Phaeo m}^{-2} \text{d}^{-1}$ at 60 m; below 60 m Phaeo flux was $2.5\text{--}3.0 \text{ mg m}^{-2} \text{d}^{-1}$.

VERTICAL FLUX OF PICO-, NANO-, AND MICROPLANKTON

Flagellates dominated the vertical plankton flux throughout the investigation both in terms of numbers ($1.0 \times 10^9\text{--}1.3 \times 10^{10} \text{ cells m}^{-2} \text{d}^{-1}$) and carbon (Fig. 5). On average 90 % or more of the plankton carbon were flagellates in April, May, August, and September (Table 1). June and July had lower percentages of flagellates with 80 and 50 % of the plankton vertical flux, respectively. The vertical flux of flagellates appeared to be highest in May and August ($2.1 \times 10^9\text{--}1.3 \times 10^{10} \text{ cells m}^{-2} \text{d}^{-1}$), and lowest in July ($1.1 \times 10^9\text{--}8.0 \times 10^9 \text{ cells m}^{-2} \text{d}^{-1}$). Flagellates contributed significantly to



the total vertical flux of POC (5-30 %). The lowest contribution by flagellates to POC vertical flux was in July (1-8 %).

Net plankton and ciliates never contributed significantly to the vertical flux of organic matter, with a maximum of 6 % of vertical POC flux (average 1.3 %). Diatoms (1.9×10^6 - 1.6×10^8 cells $m^{-2} d^{-1}$) were the second most abundant group in the vertical flux of microplankton, with highest biomass (Fig. 5) at 20 and 60 m in May and all depths in June/July (~12 % of PNMC). Dinoflagellates were only abundant in the upper traps in July (7.6×10^6 - 1.8×10^7 cells $m^{-2} d^{-1}$). *Phaeocystis pouchetii* colonies were very rare and never comprised a significant share of the vertical export of PNMC. Larger protozoa (ciliates and tintinnids) contributed most to the vertical flux in June/July (3.4×10^5 - 1.6×10^7 cells $m^{-2} d^{-1}$).

Table 1. The contribution of pico-, nano- and microplankton carbon (PNMC) to the total flux of carbon and the contribution of flagellates to POC and PNMC flux (%).

Month	Depth	% PNMC of POC	% flag. of POC	% flag. of PNMC
April	20	30	29	97
	60	8	6	74
	100	11	10	96
	160	8	7	87
	200	11	11	94
May	20	12	10	82
	60	13	10	80
	100	20	20	98
	160	10	10	94
	200	8	7	93
June	30	5	5	86
	60	20	14	70
	100	18	13	68
	160	17	14	83
	200	18	16	90
July	20	12	7	55
	60	17	8	48
	100	4	1	32
	160	10	7	65
	200	7	5	72
August	20	12	10	87
	60	23	20	90
	100	21	19	93
	160	31	28	91
	200	9	7	84
September	20	5	5	87
	60	15	14	96
	100	12	11	93
	160	16	15	94
	200	31	29	93

BIOCHEMICAL COMPOSITION OF SINKING MATTER

The POC/PON ratios (a/a) of the sinking material were highest in spring (April) and autumn (August/September) (9-12), while minimum ratios were recorded in the upper half of the water column in June (< 7) (Fig. 3C). POC/Chl *a* (w/w) ratios of the sinking material were high at all depths during the entire investigation period (> 300). The highest ratios (> 1000) were recorded at all depths in April, below 20 m in May and June, and at 60 m in September. NPC/Chl *a* ratios were relatively high in April, May and July (average NPC/Chl *a* ratios > 26), indicating that net plankton probably contributed the sinking of autotrophic phytoplankton. However the NPC/Chl *a* ratios were low in June, August and September (average NPC/Chl *a* ratios < 10) indicating that other sources than net plankton were responsible for the majority of sinking Chl *a*.

LOSS AND SINKING RATES

The daily loss rates (Table 2) of suspended POC and Chl *a* at 100 m were low in all months. Only minor variations from month to month were recorded. POC loss rates were highest in May and July with 1.8 and 1.6 % daily loss of suspended POC, respectively. The lowest daily loss rates were recorded in June and September with 0.7 %. Highest loss rate of Chl *a* was recorded in August with 1.8 % while June and September had loss rates in the range 0.9-1.1 %. The other months had loss rates in the range 0.2-0.3 %. Loss rates of total pigment or Chl *a* equiv. (Chl *a* + Phaeo) showed higher daily loss rates (1.5-2.9 %) during all periods, especially in May, June and July, indicating that sinking of degraded Chl *a* was a faster and more important pathway of vertical loss compared to sinking of undegraded pigments. Specific sinking rates for POC and Chl *a* were low throughout the investigation, ranging between 0.7-1.8 $m d^{-1}$ for POC and 0.2-1.8 $m d^{-1}$ for Chl *a* (Table 2).

DISCUSSION

To relate the vertical flux at Nordvestbanken with the pelagic community during the sojourn is based on the assumption that the pelagic community was fairly similar along the shelf, as quasi-contemporaneous comparisons of nutrients and suspended biomass on the shelf and shelf break south of Nordvestbanken indicate (I.J. Andreassen & P. Wassmann, unpubl. results). An obvious weakness in the present investigation is the lack of continuous measurements which would have been impossible at the shelf break. It is thus impossible to figure out if the observed vertical flux was characteristic for a longer time span, for example a month. Figs 3 and 4 may give the impression of continuity over time, but

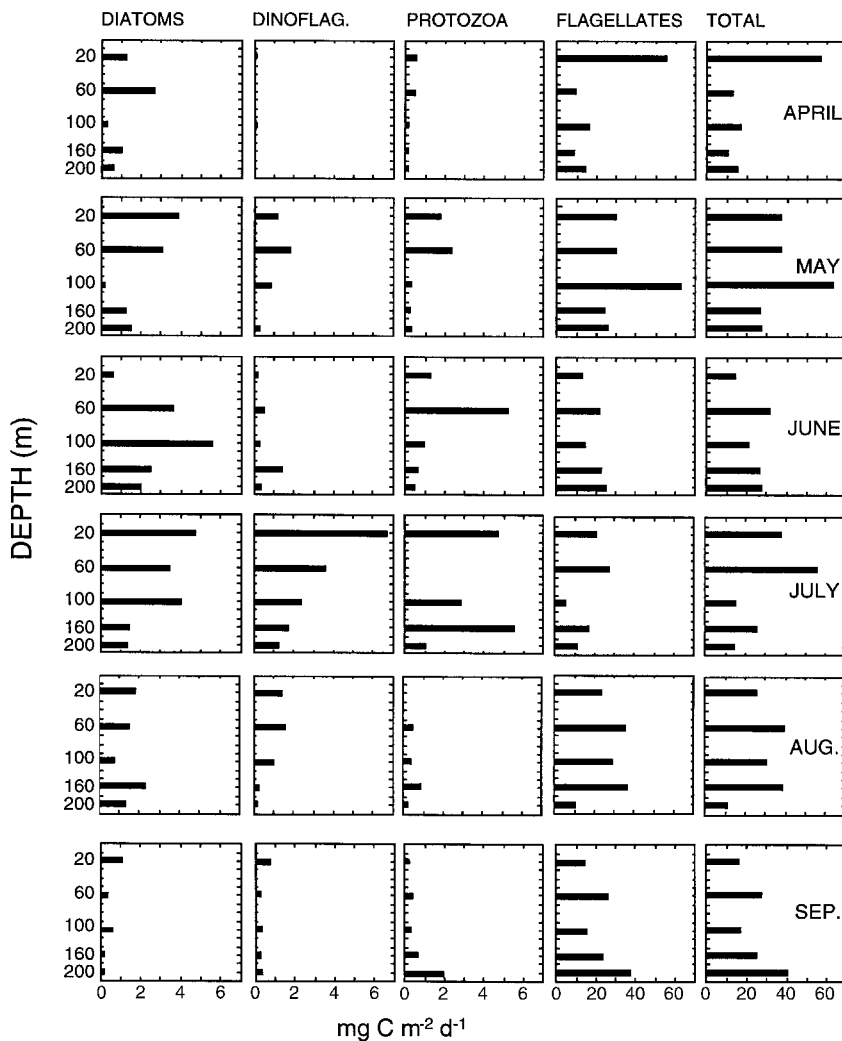


Fig. 5. Vertical carbon flux of diatoms, dinoflagellates, protozoa, flagellates and the total carbon flux ($\text{mg C m}^{-2} \text{d}^{-1}$) of pico-, nano- and microplankton (PNMC) at 20, 60, 100, 160, and 200 m depth. Notice the different scales for flagellates and total carbon flux.

Table 2. Daily loss rates of POC, PON, Chl *a* and Chl *a* equiv. at 100 m expressed as % of integrated biomass (0-100 m). Also shown are the specific sinking rates of POC and Chl *a* in the upper 100 m.

	Daily loss rate POC (%)	Daily loss rate PON (%)	Daily loss rate Chl <i>a</i> (%)	Daily loss rate Chl <i>a</i> (equiv.) (%)	Specific sinking rate POC (m d^{-1})	Specific sinking rate Chl <i>a</i> (m d^{-1})
April	1.19	1.46	0.26	1.73	1.2	0.3
May	1.82	1.95	0.20	2.89	1.8	0.2
June	0.66	0.79	1.10	1.46	0.7	1.1
July	1.64	2.50	0.18	2.56	1.6	0.2
Aug.	0.93	1.15	1.81	2.42	0.9	1.8
Sept.	0.66	0.72	0.92	1.45	0.7	0.9



the figure format was preferentially selected for technical reasons in order to present a large number of rates in a condensed and simple plot. Due to our rather limited knowledge of the annual and interannual dynamics of the food web on the north Norwegian shelf (Wassmann & al. 1999a) it must remain speculative to point out the exact causes for the vertical flux, let alone its episodicity.

The speed and direction of the drifter was similar to the general water flow predicted by a physical model of the investigation area (Moseidjord & al. 1999). In the upper 200 m current speed and direction is more or less similar at the shelf break. The hydrographic and biological features of the water masses did not vary significantly during the drift (I.J. Andreassen, unpubl. results), indicating that the drifter probably followed the same water mass during the sojourn. However, the exact current speed across the mouth of the traps cannot be demonstrated although it is likely to be small. Major amounts of larger swimmers such as calanoid copepods inside the traps, were rarely observed. This is the usual case in non-poisoned, short-term exposed traps in the investigated area. These swimmers were removed after visual examination of the samples. The smaller swimmers have been quantified microscopically and their biomass could have been estimated by biovolume conversion. However, it is not evident which of the smaller zooplankton taxa in sediment traps were swimmers, i.e. artefacts, and which belong to particle associated fauna, i.e. to the true vertical flux (Silver & al. 1991). Vertical carbon flux estimates derived from a 3D physical-biological coupled model for Nordvestbanken revealed very similar rates, both per day as well as integrated for the productive season (Slagstad & al. 1999). We thus believe that the vertical flux estimates derived in our study have an acceptable accuracy although they were not obtained according to the most elaborate proposition of analytical and hydrodynamical protocols for sediment traps (e.g. Bloesch 1995).

VERTICAL FLUX OF PHYTOPLANKTON

Large phytoplankton cells and especially highly silicified phytoplankton species such as diatoms are known to have higher sinking rates than small cells. This is both due to their size (Kiørboe & Hansen 1993) as well as mineral burden (Smayda 1970). Diatoms have a larger probability of forming aggregates due to production of sticky transparent exopolymer particles and the size and form of cells and chains (Kiørboe & Hansen 1993; Passow & al. 1994), in particular in areas or periods with high new production. Estimates of new production at Nordvestbanken based on nutrient consumption showed a minimum new production rate of $> 75 \text{ g C m}^{-2} \text{ year}^{-1}$ of which $> 25 \text{ g C m}^{-2} \text{ year}^{-1}$ was due to

diatoms (Wassmann & al. 1999a). However, no spring bloom as indicated by accumulation of phytoplankton was observed and the phytoplankton community was dominated by naked flagellates throughout the entire investigation (Ratkova & al. 1999; Verity & al. 1999).

Even though net plankton and especially diatoms were found in low concentrations in the water column (Ratkova & al. 1999) we did expect net plankton to contribute more to the sinking fraction of phytoplankton than flagellates. A diatom bloom may grow and decline in a short time (Smetacek 1985; Passow 1991), but no indications of such events were observed at Nordvestbanken in 1994 in terms of suspended biomass accumulation (Ratkova & al. 1999; Wassmann & al. 1999a), the decline of dissolved silicate concentrations (Wassmann & al. 1999a) or increased vertical flux of large cells (Fig. 5). Net plankton contributed generally less than 2 % to total vertical carbon flux and was not important for the total flux of matter in any month. Only in June net plankton contribution to vertical C flux was larger at some depths, but not $> 9 \%$. We could have missed episodic events of increased diatom sedimentation, but also the mathematical model (Slagstad & al. 1999) does rather suggest retention than export of diatoms. The lack of an accumulation of phytoplankton biomass in general and a diatom biomass in particular must thus be explained by other processes than sinking. The high mesozooplankton biomass found during this investigation (E. Nordby & K.S. Tande, pers. commn) and the intense grazing by microzooplankton (Slagstad & al. 1999) suggests that the phytoplankton community was controlled by micro- and mesozooplankton grazing (Verity & al. 1999).

A most conspicuous feature of our investigation was the high contribution of nano- and picoplankton to the vertical flux. Naked flagellates were responsible for up to 30 % (average 12 %) of the total POC flux during this investigation. July was the only month where flagellates contributed less than 8 % to the POC flux (Table 1). This was also the month when concentrations of flagellates were lowest in the water column (Ratkova & al. 1999). The contribution of small flagellates to vertical flux implies specific sinking rates in the same range as Chl *a* and POC (i.e. $1\text{--}2 \text{ m d}^{-1}$; Table 2). However, these specific sinking rates are much larger than expected for single cells (Kiørboe 1993). A possible explanation for the large contribution of small flagellates to the vertical flux might be that they sank as a part of detritus aggregates. Auto- and heterotrophic nano- and picoplankton were important in the pelagic ecosystem during the entire investigation period (Verity & al. 1999). They presumably colonised detrital matter, being a part of the diverse microbial communities characteristic for marine snow. However, to what

extend vertically exported flagellates were heterotrophic is not known, although the low Chl *a* sedimentation rates may support this assumption.

The phenomenon of heterotrophic flagellates colonising organic aggregates is known from sewage plants (Curds & Hawkes 1975), and Nygaard (1995) speculates that similar mechanisms may be involved in natural marine waters. Heterotrophic flagellates can induce flocculation of diatoms in cultures (Nygaard 1995) and are commonly associated with sinking detritus or aggregates (Patterson & al. 1993). Small aggregates may thus have been an important source for naked, small auto- and heterotrophic flagellates found in the sediment traps. The important role these flagellates had for the vertical flux is in contrast to the common assumption that a community dominated by small flagellates mainly will function as a retention system and not contribute much to the vertical flux (Bathmann & al. 1990b; von Bodungen & al. 1995). Short-term vertical flux measurements based on non-poisoned traps and combined with detailed planktonic investigations of fractions not adequately quantified by the commonly applied Utermöhl technique, have to the best of our knowledge not been carried out previously. If vertical export of naked flagellates is pertinent to the north Norwegian shelf in 1994 only remains unknown, but identical investigations in north-Norwegian fjords, the western Mediterranean and the central Barents Sea suggest that this is more general phenomenon (P. Wassmann, unpubl. results).

INFLUENCE OF ZOOPLANKTON ON VERTICAL FLUX

Phaeopigment dominated the pigment flux below 50 m depth during the entire season. This implies that export of phytoplankton biomass through faecal material and detritus was more important than phytoplankton sinking, supporting the hypothesis that grazing was responsible for the major loss of phytoplankton (Ratkova & al. 1999; Verity & al. 1999). The potential importance of faecal pellets for vertical flux (Wassmann & al. 1999b) is also indicated by the positive relationship between POC and phaeopigment flux.

The seasonal variation in mesozooplankton biomass at the shelf break was surprisingly modest (E. Nordby & K.S. Tande, pers. commn), but there was a pronounced succession in the species composition (Halvorsen & Tande 1999). The peak abundance of *Calanus finmarchicus* was observed in May, correspondent with maximum faecal pellet production in the > 500 µm fraction of the zooplankton (Urban-Rich & al. 1999). The importance of faecal matter for vertical flux of POC during this period is reflected by the high vertical faecal pellet carbon flux in May (Urban-Rich & al. 1999; Wassmann & al. 1999b). Adult *C.*

finmarchicus disappeared in June and during the summer period smaller and omnivore species of copepods dominated (Halvorsen & Tande 1999). The production of pellets by the larger zooplankton (> 500 µm) decreased correspondingly due to the reduction in numbers of zooplankton, and the contribution of these pellets to vertical flux did as well (Urban-Rich & al. 1999; Wassmann & al. 1999b). In July there was a maximum in the abundance of *Oithona similis* (Halvorsen & Tande 1999) and a generally higher production rate of faecal pellets due to higher abundance of zooplankton. The total flux of pellets increased, but the contribution of faecal pellets to vertical POC flux was not higher compared to June and August (Urban-Rich & al. 1999). This reflects probably the small size of *O. similis* faecal pellets, their fluffy nature as well as faecal pellet destruction. During late summer and autumn *Limacina retroversa* dominated the zooplankton biomass (Halvorsen & Tande 1999) and the faecal pellets from this species gave a large contribution to the vertical flux in the upper water column (Wassmann & al. 1999b). In general, the vertical flux of faecal pellets seems to be less related to mesozooplankton in terms of biomass, but rather to the succession and composition of the zooplankton community.

Faecal pellets were generally a larger contributor to vertical flux than phytoplankton, but the origin of the bulk of vertical carbon flux was unaccounted for. In general faecal pellet production is greater than their vertical export, indicating an active retention of pellets through coprophagy, coprochaly, coprorhexy or microbial degradation (Jacobsen & Azam 1984; Lampitt & al. 1990; Noji 1991). The large fraction of unidentified matter contributing to the vertical flux may therefore be due to slow sinking detritus from destroyed faecal pellets. This seems to be reflected by the low specific sinking rates (Table 2). The contribution of faecal pellets to vertical flux as described by Urban-Rich & al. (1999) and Wassmann & al. (1999b) must thus be considered as minimum rates.

Microzooplankton grazing can prevent large signals in the vertical export of carbon or phaeopigment which often characterise scenarios where mesozooplankton is the main herbivore (Buck & Newton 1995; Andreassen & Wassmann 1998). Minipellets were observed at all stations, depths and throughout the observation period, but due to small size they did not contribute greatly to vertical flux (Wassmann & al. 1999b). The importance of protozooplankton in regulating vertical flux is difficult to evaluate with the limited direct knowledge regarding their role at Nordvestbanken. Model evaluations indicate that they are significant herbivores and that mesozooplankton persistently feed more on microzooplankton than on phytoplankton (Slagstad & al.



1999). The generally high C/N ratio of the sinking matter suggests that the sinking matter was strongly degraded. Resuspension might have been a source of both suspended and sinking matter, but the importance of the total heterotrophic community in biogenic matter retention made it difficult to evaluate the importance of this source.

COMPARISON WITH RESULT FROM ADJACENT AREAS

Spring bloom sedimentation followed by reduced loss rates has been encountered in the Norwegian Coastal Current region (Peinert 1986), fjords (Lutter & al. 1989; Keck & Wassmann 1996; Reigstad & Wassmann 1996) and also in the Barents Sea (Wassmann & Slagstad 1993). The seasonal magnitude of vertical flux in north Norwegian fjords is usually rather large with vertical POC flux ranging roughly between 100 and 800 mg C m⁻² d⁻¹ (Keck & Wassmann 1996, Reigstad & Wassmann 1996). At Nordvestbanken vertical POC flux never approached the high daily sedimentation rates that have been observed in the inshore waters of northern Norway. The vertical export of Chl *a* was particularly low. Both the rates and the composition showed obvious similarities with vertical export in the Norwegian Sea (e.g. Bathmann & al. 1987; Peinert & al. 1987; Bathmann & al. 1990b). For example, a spring sedimentation pulse of phytodetritus with a high diatom contribution does usually not take place at the Vøring Plateau (Bathmann & al. 1990a).

High concentrations of mesozooplankton exerting a substantial grazing pressure on large phyto- and protozooplankton seem to be a prevalent feature of both the shelf and off-shelf area of northern Norway (Peinert &

al. 1987), for example at Nordvestbanken. There seems to be a tighter coupling between primary and secondary production on the shelf and the off-shelf area compared to the fjords, delaying and reducing the vertical flux of biogenic matter. This is mainly caused by the high and continuous advection of larger zooplankton along the eastern slopes of the Norwegian Sea, high nutrient supply due to extensive mixing and continuous high new production in the shelf break region (Slagstad & al. 1999). The Norwegian Sea and Nordvestbanken appear to share similarities with high nutrient/low chlorophyll (HNLC) regions of Antarctica and the subarctic and equatorial Pacific. However, in the case of the north Norwegian shelf the low phytoplankton standing stock is rather due to grazing than nutrient limitation. Top-down control was the most important factor in regulating the vertical flux of biogenic matter at Nordvestbanken in 1994, but we suggest that our results are representative for the general cycling of biogenic matter along the north Norwegian shelf and adjacent areas.

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