

SEDIMENTATION IN MARIAGER FJORD, DENMARK: THE IMPACT OF SINKING VELOCITY ON SYSTEM PRODUCTIVITY

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ABSTRACT

Mariager Fjord (east coast of Jutland, Denmark) is a sill fjord with a central, permanently stratified basin. The upper mixed layer of the water column shows unusually high levels of primary production and phytoplankton throughout the summer season. Plankton blooms takes place at intervals of 2-3 weeks during the entire growth season although the external load of mineral nutrients is not very high. It is shown here that the high production results from overall low sedimentation rates and consequently long retention times of suspended particulate matter within the mixed layer. The low sinking velocities of suspended particles thus constitute the base for an efficient *in situ* re-mineralization and high regenerated production. Plankton community structure is therefore more important for system productivity than is the external nutrient load *per se*.

Key words: Sedimentation, sinking velocity, pelagic retention, system productivity.

INTRODUCTION

The fertility of ecosystems is partially given by its capability of retaining nutrients. Both in terrestrial and in aquatic systems the force of gravity plays an important role for nutrient loss. But where the drain of nutrients in terrestrial systems is mainly associated the water flow, the movement exerted by the gravitational force on particles is mostly responsible for the leaking of nutrients in pelagic systems. Pelagic systems are continuously impoverished because of the sinking of plankton particles. Sedimentation usually exhibits strong seasonality reflecting the succession of the planktonic community. In coastal temperate regions the classical succession pattern of phytoplankton proceeds from a spring bloom dominated by large

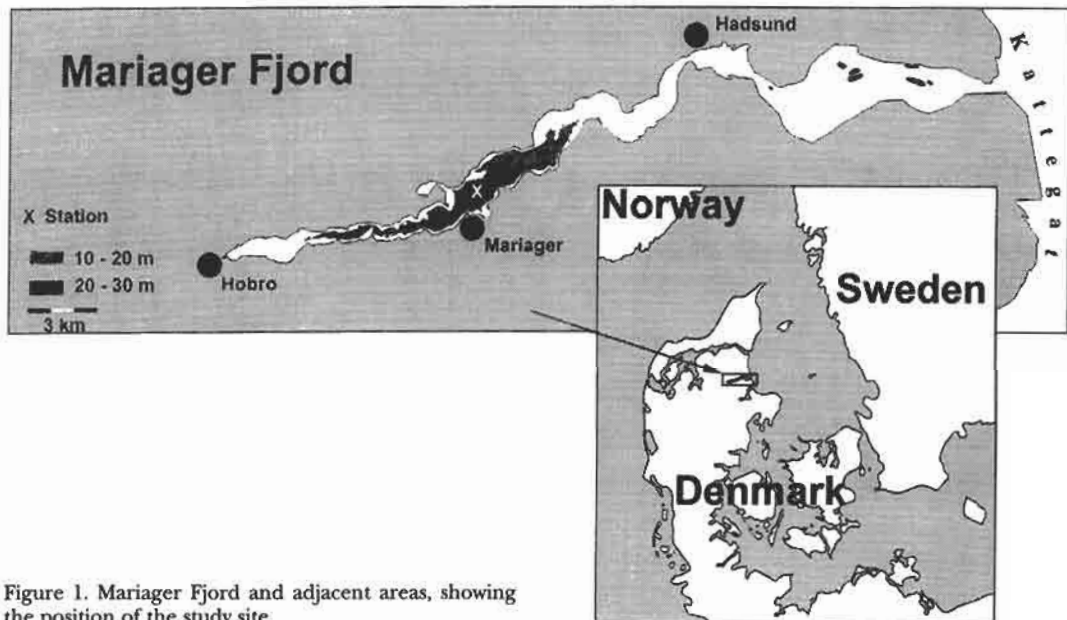


Figure 1. Mariager Fjord and adjacent areas, showing the position of the study site.

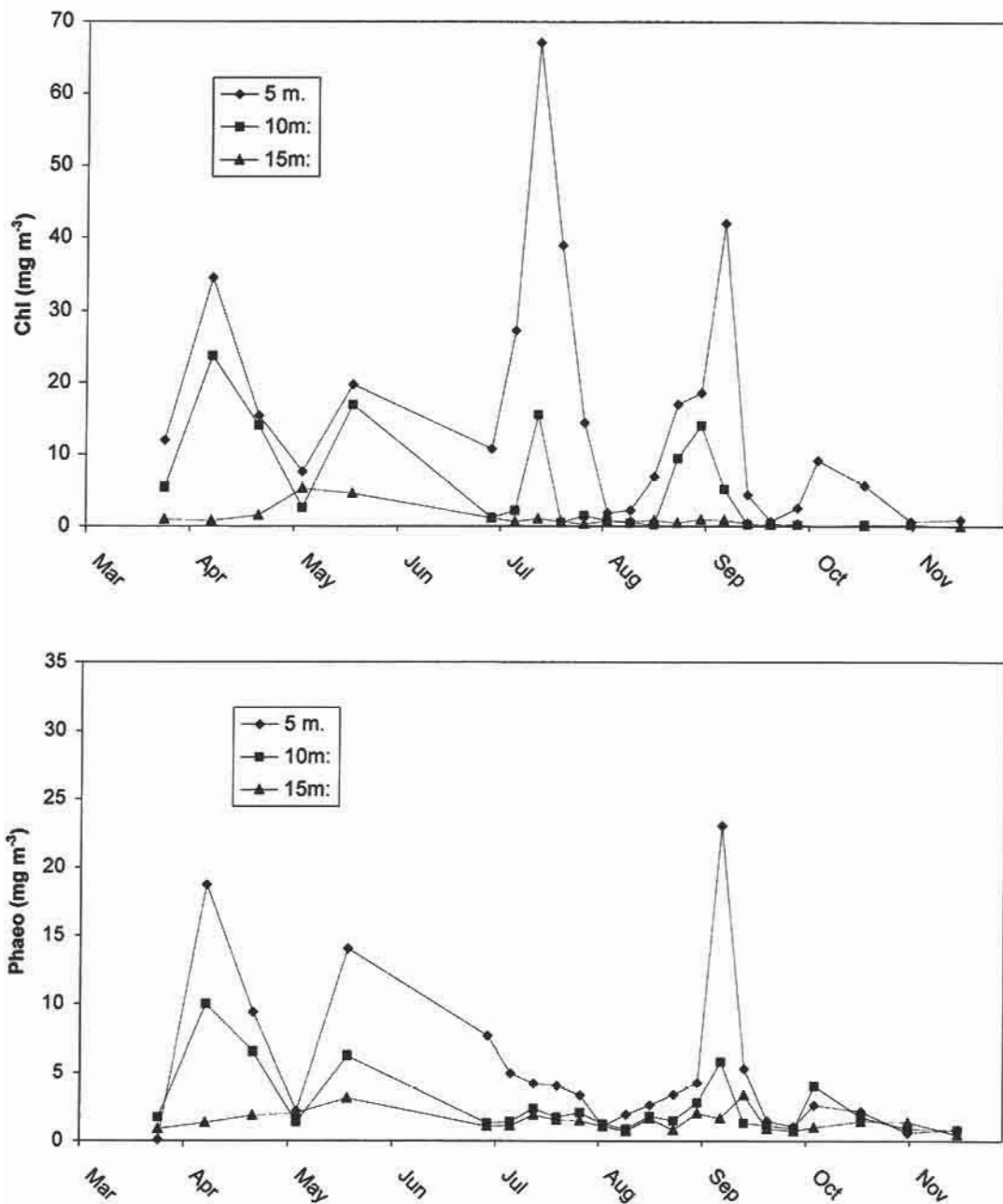


Fig. 2. Vertical and temporal distribution of chlorophyll *a* and phaeopigment in Mariager Fjord in 1999 (March - November 1999).

diatoms to a low biomass of small flagellates during summer (Margalef 1978, Smayda 1980). In late summer outbreaks of dinoflagellates or filamentous cyanobacterial blooms may occur (Nielsen 1991, Kahru et al. 1994). The termination and decay of the spring

bloom is usually associated with high sedimentation rates of diatoms (Smetacek 1985). A substantial fraction of the spring bloom production may, however, be grazed by meso- and microzooplankton, which subsequent may retard the loss of material from the productive

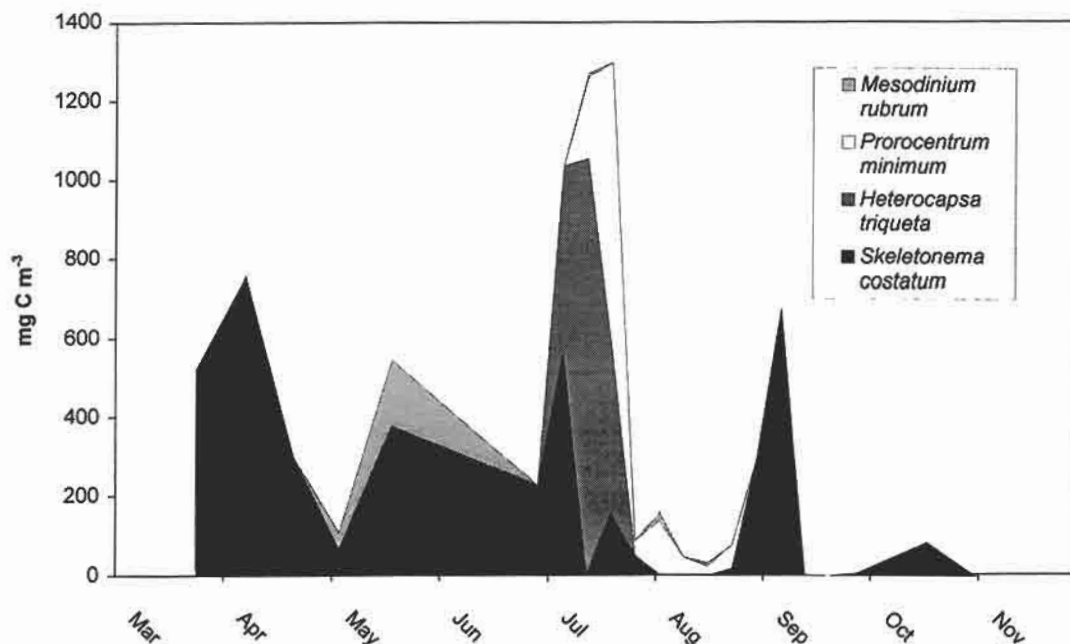


Fig. 3. The development of dominating phytoplankton species in Mariager Fjord through the productive season (March- October) of 1999. The estimates of carbon biomass are based on microscopic counting and measures of linear dimensions on samples from 5m depth.

surface layer. A longer retention time will potentially lead to a more effective remineralization of organic material in the pelagic system, to the benefit of the following summer primary production (Legendre & Le Fèvre 1989). The nano and pico-sized phytoplankton typical for the regenerating systems prevailing during summer is usually considered not to sink. Feeding activities by meta- and protozoa, however, seem to accelerate the export of organic matter during summer (Peinert et al. 1989, Lundsgaard & Olesen 1998). Blooms of dinoflagellates and cyanobacteria in late summer seldomly sink in bulk as do diatoms, but rather disintegrate in the water column (Sellner et al. 1994, Olesen 1995). Phytodetrital material, on the other hand, may contribute significantly to sedimentation (Lundsgaard et al. 1999).

The present study site differs in many respects from the above description. Mariager Fjord (Fig. 1) is characterized by frequent phytoplankton blooming during the whole productive period (March - November). Blooms are formed at intervals of 2-4 weeks. It may be hypothesized that sedimentation from the mixed layer plays a significant role for the decay of the blooms. Because of the stable pyc-

nocline at 10-15 m depth this would imply a corresponding loss of nutrient from the euphotic zone. However, if sedimentation is responsible for the disappearance of the blooms it is difficult to understand the nutritional basis for the following bloom. On a longer time scale, e.g., the annual cycle, export will equalize import of matter to the mixed layer (Eppley et al. 1983). Seasonal sedimentation can thus be used as a proxy of new production where advective net transport is negligible. Bulk sedimentation of autochthonous matter over time therefore reflects the external supply of nutrients rather than the planktonic food web structure. Day to day sedimentation, however, is temporally more or less decoupled from new production and biomass. Planktonic community organization and physiological state has been shown decisive for the sinking rate of autochthonous material and thus for the nutrients retention in the mixed layer (Noji 1991, Heiskanen et al. 1996, Waite et al. 1997, Boyd & Newton 1999). The size of regenerated production must therefore depend not only on how fast nutrients are remineralized, but also how long they are retained in the productive layer. Hence, system productivity and sinking velocity is probably strongly coupled.

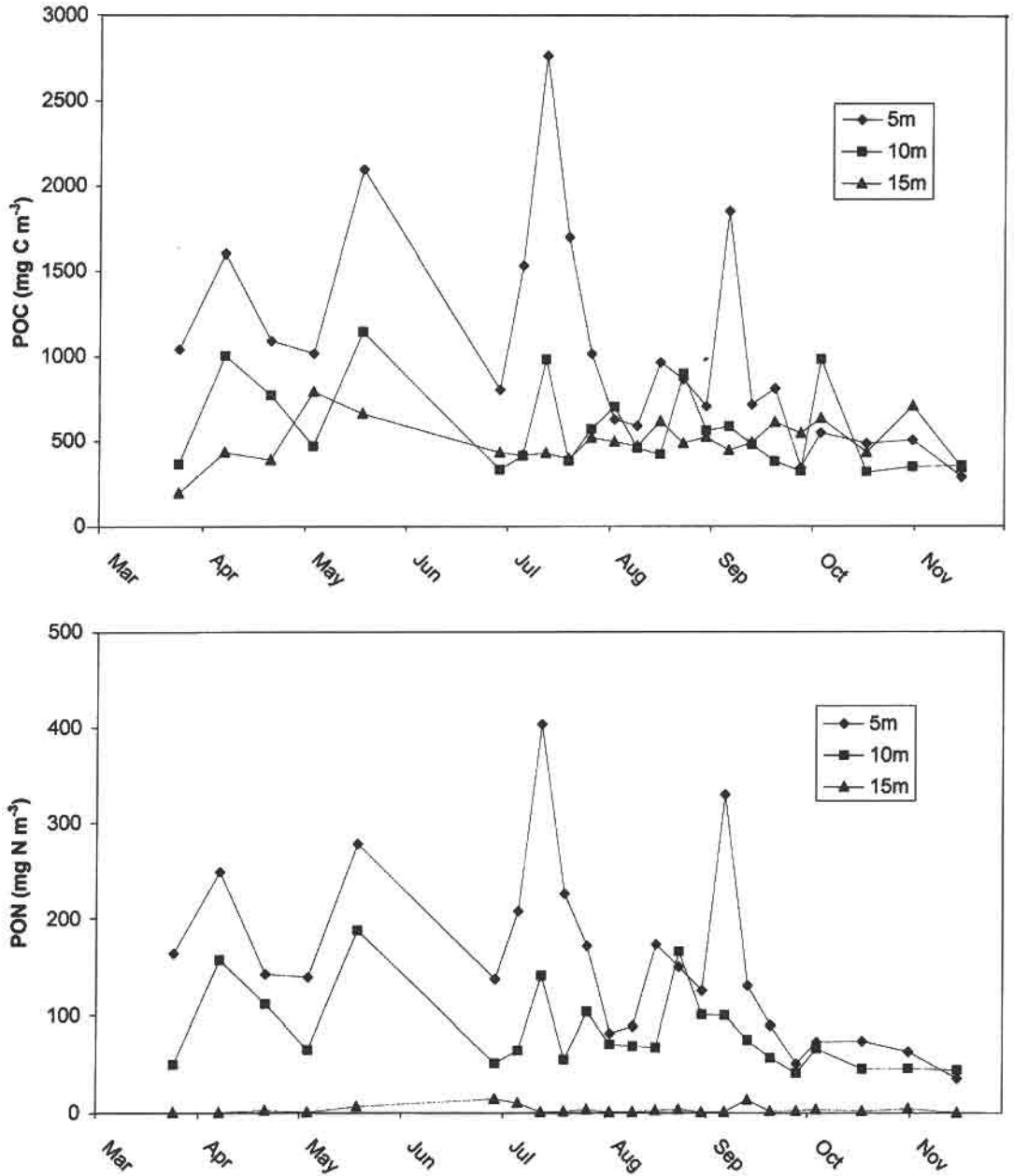


Fig. 4. Temporal variation of suspended particulate organic carbon, TPC and particulate organic nitrogen, PON from three depths in Mariager Fjord 1999.

Mariager Fjord has the highest recorded primary production (up to $1000 \text{ g C m}^{-2} \text{ y}^{-1}$) among coastal systems surrounding Denmark (Kaas et al. 1996). An annual production above 500 g C m^{-2} has to my knowledge not been recorded in other parts of the Baltic Sea system. The mean area specific terrestrial loading

of nutrients for the entire fjord ($25\text{-}35 \text{ g N m}^{-2} \text{ y}^{-1}$ and $5 \text{ g P m}^{-2} \text{ y}^{-1}$) is low to medium compared to other Danish coastal systems (Kaas et al. 1996). Accordingly, regenerated production comprises ca. 80% of the total production. Mariager Fjord is a sill fjord, which implies a relative low water exchange with adjacent sys-

tems, i.e., the Kattegat (Fig. 1). The long hydrological retention time may potentially result in a high degree of recycling of nutrients and thus production. The stable stratification of the fjord will on the other hand lead to reduce vertical exchange of biogenic matter and nutrient elements such as N and P.

A high systemic primary production requires a high plant biomass to catch and turn the incoming solar radiation into new biomass. Because phytoplankton is often subject to high loss rates (grazing and sedimentation) plant biomass in marine systems seldomly reaches levels that make an efficient light exploitation possible. Usually only a minor fraction (<10%) of the solar energy entering the surface layer is fixed into organic compounds. Due to the unusually high primary production, Mariager Fjord seems to have a much more efficient exploitation of the incoming photosynthetic radiation. In order to understand the background for the high standing stocks of phytoplankton in the mixed layer and thus the background for the high levels of regenerated production in Mariager Fjord the process of sedimentation has been investigated

RESULTS

Water column biomass and phytoplankton succession. – The phytoplankton distribution (5, 10 and 15 m) expressed as chlorophyll *a* (Chl) concentration was characterized by several distinct blooms in the mixed layer (0 - 12 m) throughout the year (Fig. 2). At least five blooms with maximum chlorophyll *a* concentrations between 10 and 70 $\mu\text{g l}^{-1}$ at 5 m depth were identified during the investigation period in 1999 (10/3 - 18/11). The pigment concentration at 10 m reflected the seasonal pattern at 5 m while the concentration at 15 m below the pycnocline was always low (typical less than 1 $\mu\text{g Chl l}^{-1}$). Blooms were dominated by the chain-forming diatom *Skeletonema costatum* (Fig. 3), but occasionally the dinoflagellates *Heterocapsa triquetra* and *Prorocentrum minimum* and the phototrophic ciliate *Mesodinium rubrum* took over. A starting *Skeletonema* bloom in July 1999 was taken over by *Heterocapsa triquetra*, which then developed the highest recorded biomass this year (Fig. 3). During the decay of the *Heterocapsa* bloom a minor bloom of *Prorocentrum* took place.

Phaeopigment (Phaeo) followed the temporal pattern of chlorophyll *a* with approximately half of the Chl concentration level (Fig. 2).

There was a remarkable discrepancy between the concentration of Phaeo and Chl in July 1999. Since this was not observed in the sediment traps (cf. next section) the lack of accordance is ascribed to methodological errors.

The mean pigment concentrations in the mixed layer in 1998 and 1999 were 7.3 $\mu\text{g l}^{-1}$ and 9.3 $\mu\text{g l}^{-1}$, respectively for chlorophyll *a* and 4.1 $\mu\text{g l}^{-1}$ and 3.5 $\mu\text{g l}^{-1}$, respectively for phaeopigment. TPC (total particulate carbon, Fig. 4) and PON (particulate organic nitrogen, Fig. 4) in the surface layer showed the same seasonal distribution as the chlorophyll *a* concentration, indicating that phytoplankton was responsible for most of the organic matter above the pycnocline. The average concentration of TPC and PON during the investigation period in 1999 was 790 $\mu\text{g C l}^{-1}$ and 118 $\mu\text{g N l}^{-1}$. This corresponds to a C/N-ratio of 6.7 (w/w), which is close to the Redfield ratio (5.7, w/w). In 1998 the average TPC and PON concentrations were 857 $\mu\text{g C l}^{-1}$ and 128 $\mu\text{g N l}^{-1}$, respectively which, as in 1999, gave a C/N ratio of 6.7.

The corresponding measurements of TPC and Chl in the water are depicted in Fig. 5. Although the relationship is not significant for the 15 m sampling depth, the slope of the regression lines of all three depths (ca. 30 w/w) indicates a relative high content of chlorophyll *a* in the algal cells, which probably reflects an adaptation to the poor light conditions prevailing in the mixed layer because of the high biomass. The intercept of the regression line (400-500 $\mu\text{g C l}^{-1}$) expresses particulate organic matter in the mixed layer not directly belonging to phytoplankton (non algal TPC = detritus and heterotrophs). This value corresponds to the TPC levels in the phytoplankton-depleted layer below the pycnocline (Fig. 5).

Sedimentation of particulate organic matter. – The sedimentation across the pycnocline (Figs. 6 and 7) shows a temporal pattern similar to that of the standing stock in the mixed layer (Figs. 2 and 4) during the productive season (March - October) in 1998 and 1999. Although the sedimentation signal relative to the changing biomass in the water column was blurred by relative long deployment periods (7-14 d) some temporary differences could be recognized. There seems to be a delay of one to two weeks between the succession in water and the occurrences in the trap suspended at 15 m. The average sedimentation rates at 5 and 10 m were

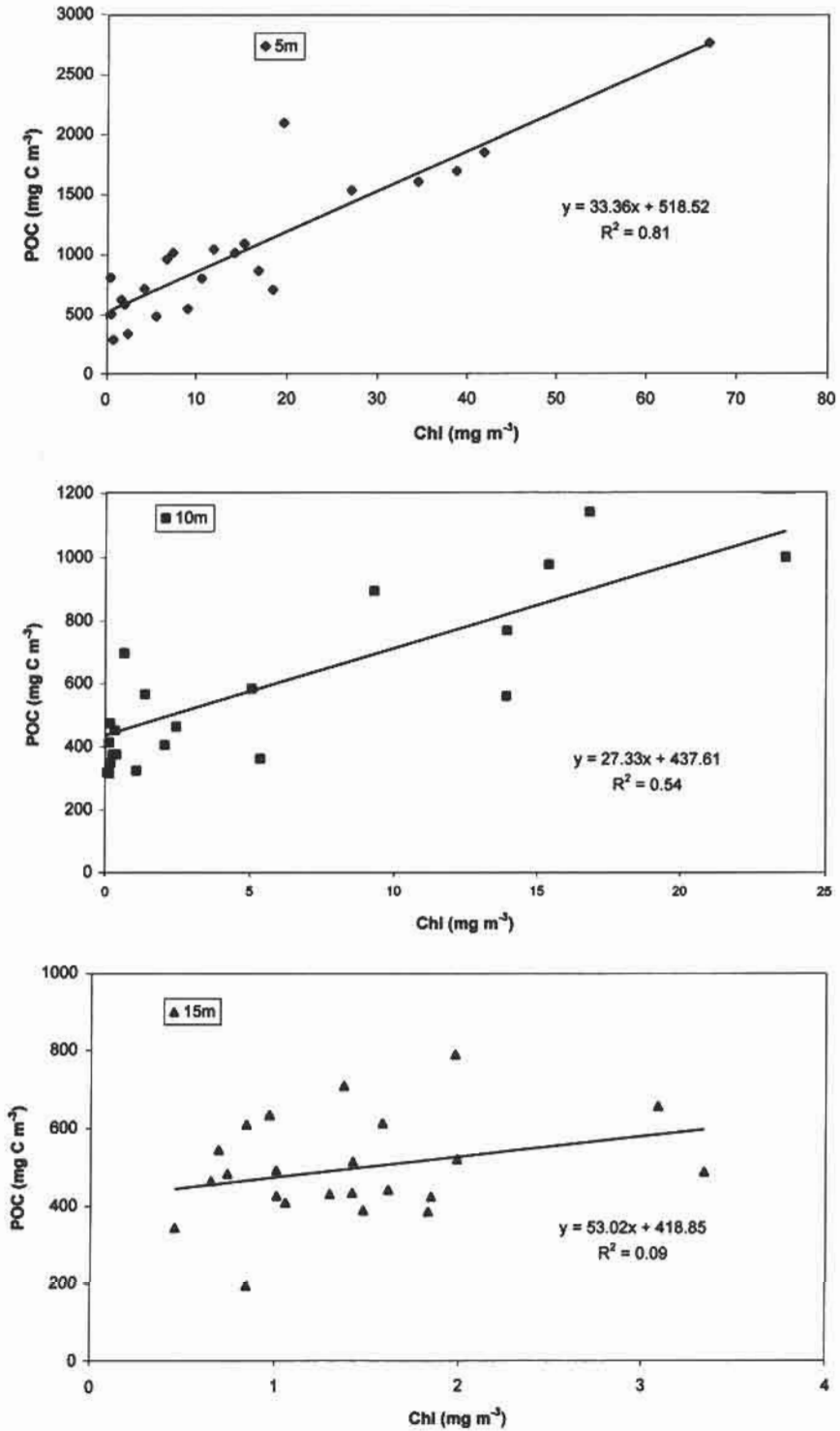


Fig. 5. The relationships between suspended particulate organic carbon (TPC) and chlorophyll *a* (Chl) for the three sampling depths (5m, 10m and 15 m). The equation of the regression line and the correlation coefficient (r^2) are shown.

Table 1. Standing stock, sedimentation and vertical export rates in 1998 and 1999, Mariager Fjord (inner fjord). Mean value of TPC, PON, chlorophyll *a* and phaeopigments. Mean value of sedimentation weighted according to the period of deployment

| | Standing stock Mixed layer (0-12 m) mg m^{-3} | | Sedimentation rate 15 m $\text{mg m}^{-2} \text{d}^{-1}$ | | Sinking loss rate $\% \text{d}^{-1}$ | |
|----------------------|--|------|--|------|---|------|
| | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 |
| TPC | 857 | 790 | 172 | 183 | 1.7 | 1.9 |
| PON | 128 | 118 | 25.4 | 26.4 | 1.7 | 1.9 |
| C/N | 6.8 | 6.7 | 6.8 | 6.9 | | |
| Chlorophyll <i>a</i> | 7.3 | 9.3 | 2.18 | 2.30 | 2.5 | 2.1 |
| Phaeopigment | 4.1 | 3.6 | 1.98 | 1.87 | 4.0 | 4.3 |

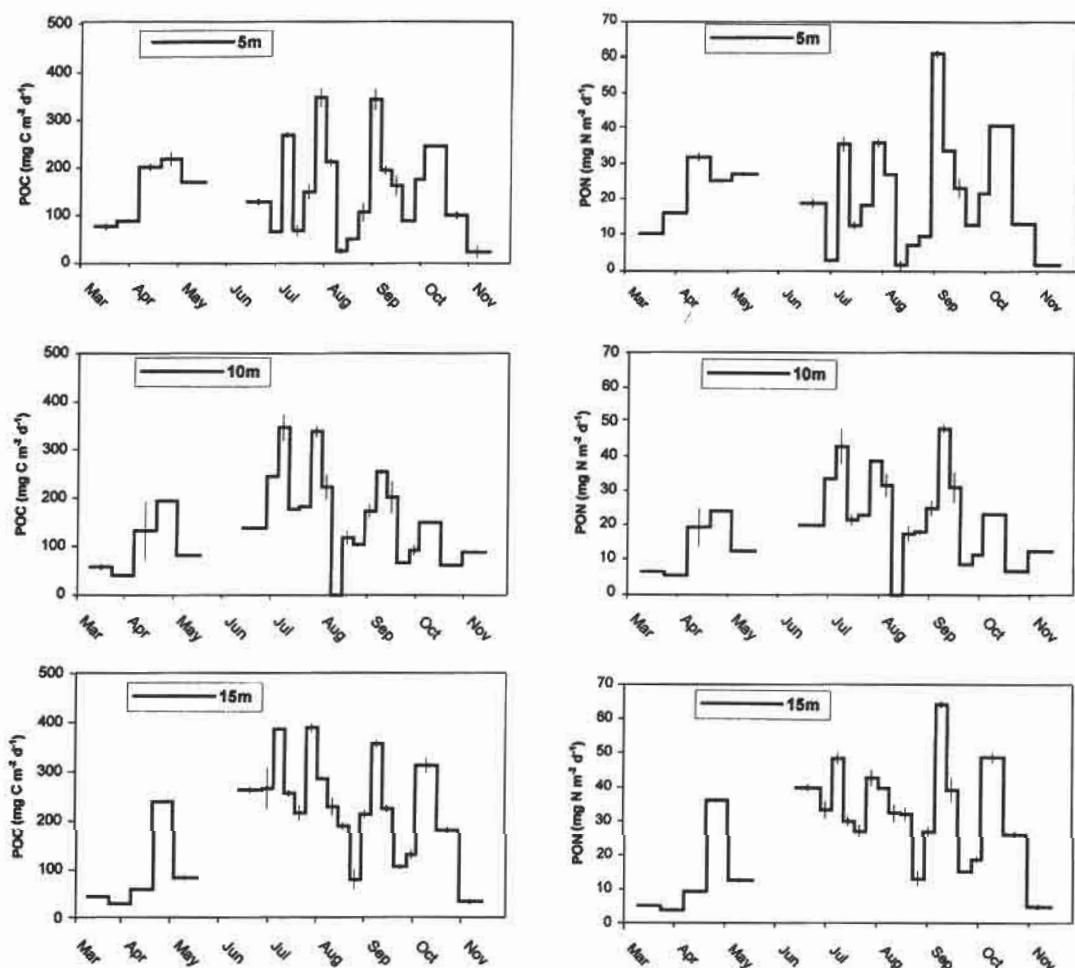


Fig. 6. Sedimentation rates of particulate organic carbon, TPC (left panels) and particulate organic nitrogen, PON (right panels) in Mariager Fjord (1999) for three deployment depths (5m, 10m and 15m). The rate measurements are based on matter collected in parallel sediment traps deployed for periods of one or two weeks. Error bars are indicated.

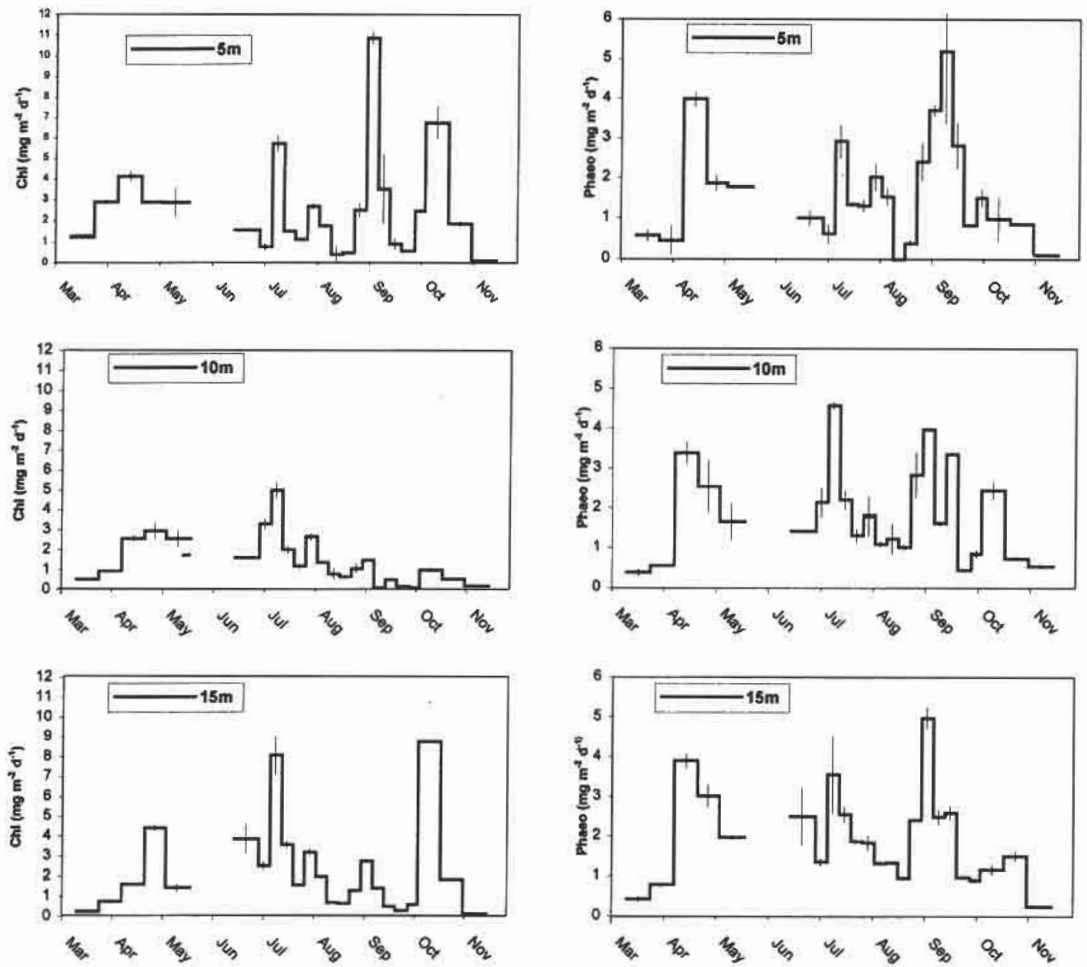


Fig. 7. Sedimentation rates of chlorophyll *a* (Chl, left panels) and phaeopigments (Phaeo, right panels) in Mariager Fjord (1999) measured in three depths (5m, 10m and 15m). The rate measurements are based on matter collected in parallel sediment traps deployed for periods of one or two weeks. Error bars are indicated.

identical and corresponded to $146 \text{ mg C m}^{-2} \text{ d}^{-1}$ and $21 \text{ mg N m}^{-2} \text{ d}^{-1}$ in 1999. The sedimentation at 15 m was generally higher. In 1999 the average sedimentation rate at 15 m was $183 \text{ mg TPC-C m}^{-2} \text{ d}^{-1}$ (range $50 - 400 \text{ mg C m}^{-2} \text{ d}^{-1}$) and $26 \text{ mg PON-N m}^{-2} \text{ d}^{-1}$ (range $5 - 70 \text{ mg N m}^{-2} \text{ d}^{-1}$, Table 1). These rates were close to the mean sedimentation in 1998 (Table 1). The generally lower mean sedimentation at 5 and 10 m relative to 15 m is ascribed to a faster decomposition of settled material in the mixed layer than in the anoxic layer below the pycnocline (see below).

The sedimentation of chlorophyll *a* and phaeopigments (Fig. 7) followed the same pat-

tern as for TPC and PON although the amount of Chl was highest at 5 m. The relative larger proportion of chlorophyll *a* in the 5-m trap was primarily due to a distinct sedimentation in the beginning of September 1999. One week later sedimentation reached a maximum at 10 and 15 m but had a significantly higher TPC to chlorophyll *a* ratio. The mean sedimentation of chlorophyll *a* and phaeopigment at 15 m was 2.3 and $1.9 \text{ mg m}^{-2} \text{ d}^{-1}$, respectively in 1999 and 2.2 and $2.0 \text{ mg m}^{-2} \text{ d}^{-1}$, respectively in 1998 (Table 1). The amount of phaeopigments relative to total measured pigment is higher in the traps (45%) than in the water (28%) in 1999.

A significant correlation between the col-

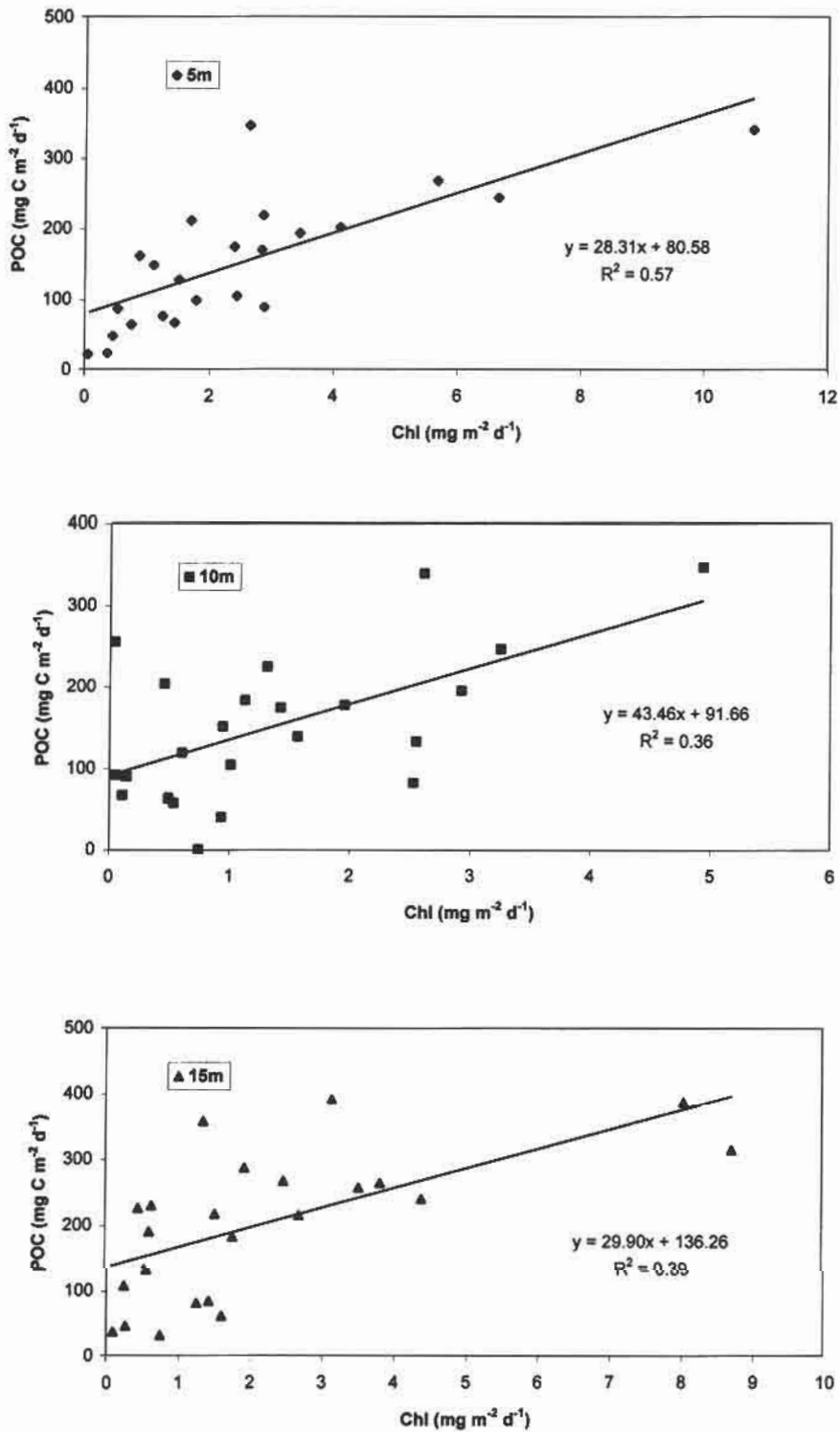


Fig. 8. The relationships between sedimented matter of particulate organic carbon (TPC) and chlorophyll *a* (Chl) for three deployment depths (5m, 10m and 15 m). The equation of the regression line and the correlation coefficient (R^2) are shown.

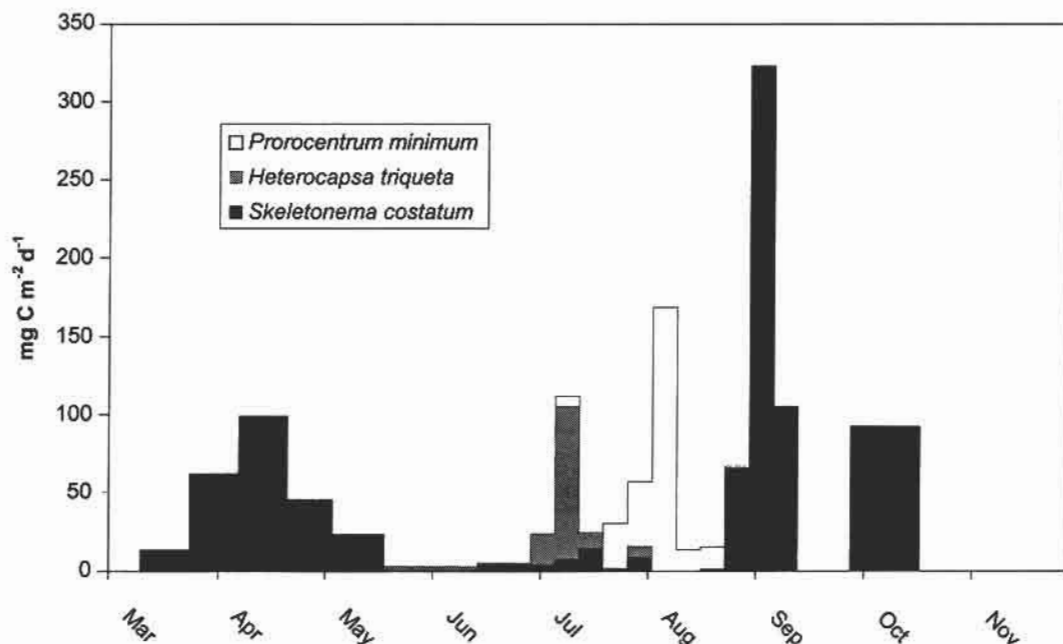


Fig. 9. The sedimentation of dominating phytoplankton species in Mariager Fjord throughout the productive season (March-October) of 1999. The microscopic enumerations were made on trap material already preserved during the deployment. Traps from 5 m was used for the counting of *Skeletonema costatum* whereas traps from 15 m was used for the motile cells; see text for further explanation.

lected material of TPC and Chl was found at all three depths of sediment traps (Fig. 8). The correlation was, however, less good than for the suspended matter in the mixed layer probably because the materials in the traps were relative more decomposed than in the water. The intercepts for the settled material (ca 100 mg C m⁻² d⁻¹) reflect the vertical flux of non-algal carbon and the average slope (34 w/w) of the linear regressions between TPC and Chl indicates the C/Chl ratio of sedimenting algae (Fig. 8).

Sinking losses and sinking velocities. – The average sinking velocities were almost constant throughout the investigation periods. Specific sinking velocity for chlorophyll *a* was < 0.25 m d⁻¹ in 1999 whereas phaeopigments were sinking faster (average sinking velocity of 0.4 m d⁻¹). This yielded average specific loss rates from the mixed layer in 1999 of 2.1% Chl d⁻¹ and 4.3% Phaeo d⁻¹ (Table 1). The mean specific sinking velocity of TPC and PON in 1999 were 0.23 m d⁻¹ and 0.22 m d⁻¹, respectively which resulted in lower integrated loss rates than chlorophyll *a* (< 2% d⁻¹).

Deposition, vertical migration and decomposition in sediment traps with and without preservation. –

Microscopic investigations revealed a considerable difference in the composition of algal material between the traps with and without preservative added. Especially during summer there seems to be a fast decomposition of *Skeletonema* cells in the traps above the pycnocline (5 and 10 m) because the unpreserved traps consisted of less intact *Skeletonema* cells than found in the preserved traps. The largest difference was found at 5 m in August - September 1999 during a period with the highest recorded temperature (18°C). In three subsequent samplings at 1-week intervals the unpreserved cylinder contained about half of the amount of *Skeletonema* cells than the parallel cylinder with preservation. If sedimentation rate was constant during the deployment period this correspond to a decomposition rate of 18% d⁻¹. Other studies have reported mineralization rates of particulate organic carbon to be 5% d⁻¹ (Iturriaga 1979, Olesen & Lundsgaard 1996). Mineralization may obviously lead to serious underestimation of the integrated sedimentation when sediment traps are employed for several days without preservation. In the traps below the pycnocline (15 m) no such difference between preserved and

unpreserved traps was seen. During the spring period (March–April) there was only a minor difference between the two types of cylinders in the traps above the pycnocline (5 and 10 m) with respect to *Skeletonema* cells. The three other dominating phytoplankton species (*Heterocapsa triquetra*, *Prorocentrum minimum* and *Mesodinium rubrum*) are all motile which explains why these cells appear in up to 10 fold higher numbers in the preserved traps in the mixed layer (5 and 10 m). The vertical migration of these cells apparently resulted in an “over catch” in traps with preservation whereas unpreserved traps did not prevent them to leave the traps. No such differences was seen in the composition of cells between the 15 m-trap cylinders with and without preservation indicating that the vertical migration seems restricted to the layer above the pycnocline. Poisoned traps may in presence of motile organism seriously overestimate the amount of settling material.

The influence of both microbial degradation and actively swimming organism was of less importance in the 15 m trap due to the anoxic conditions prevailing in the bottom water. The sedimentation rate across the pycnocline is likely not affected by differences in chemical composition between the two water layers. Measurements obtained from the unpreserved 15 m trap are therefore considered as the most reliable estimates of the vertical flux of TPC, PON and Chl. Likewise, only the trap deployed below the pycnocline was suitable for measuring sedimentation of motile species of phytoplankton, while the 5 m trap with preservation were used for estimates of *Skeletonema* sedimentation (Fig. 9)

Composition of settling matter. – The microscopic examinations demonstrate that the sedimenting material mainly consists of phytoplankton. *Skeletonema* cells constitute the major part of sedimentation in terms of carbon in 1998 and 1999 (Fig. 9), but *Heterocapsa triquetra* and *Prorocentrum minimum* dominated sedimentation during two of the five recorded bloom periods in 1999. It is noticeable that the pronounced sedimentation of *Prorocentrum* cells in August 1999 (Fig. 9) was accompanied by a similar increase in sedimentation of TPC but not of chlorophyll *a* (Fig. 7). This discrepancy reflects a remarkable change in the C/Chl ratio of the sedimenting phytoplankton. While the C/Chl for *Skeletonema* and *Heterocapsa* can be estimated to be about 30, the C/Chl ratio is

apparently >100 for *Prorocentrum minimum*. Because of the co-occurrence of *Heterocapsa* and *Prorocentrum* in the bloom formation it was not possible to distinguish between the C/Chl ratios of these two species directly in the water. Microscopic counting of faecal pellets in trap material during the period of investigation showed that faecal pellets never contributed more than 5% of the sedimented carbon. This represents an overestimate because it assumes a C-content of 0.11 mg C mm⁻³, which is high compared to other studies in the boreal region (c.f. Gonz ales et al. 1994). The insignificant contribution of faecal pellets on sedimentation is due to the low abundance of copepods in Mariager Fjord (Fallesen et al. 2000).

DISCUSSION

The fate of phytoplankton. – It seems natural to assume that sedimentation is responsible for the fast disappearance of phytoplankton following a bloom. However, no increases in specific sinking speed of phytoplankton were observed during the decay of the blooms in Mariager Fjord. Nor was any increased sedimentation of heterotrophic compounds like faecal pellets or amorphous aggregates observed. Sedimentation rates remained low and rather constant with overall specific loss rates below 5% d⁻¹ of the standing stock in the mixed layer. The impact of sedimentation on the planktonic system can be demonstrated by relating sedimentation to the changes in biomass between the samplings (Fig. 10). Because the exchange of inorganic carbon between the surface layer and the atmosphere is difficult to predict, considerations on the fate of phytoplankton are based on the mass balance of nitrogen. The Δ PON values (Fig. 10) shows the net-changes of particulate nitrogen corrected for sedimentation over a seven day or fortnight period. Positive values thus represent net-biomass-production including particulate matter lost via sedimentation. Negative values indicate disappearance of particulate matter in the mixed layer, which cannot be explained by sedimentation. Assuming a zero horizontal net-exchange of matter due to lateral advection, then the calculated negative values of Δ PON must result from transformation of particulate matter into dissolved organic or inorganic compounds. The highest net-transformation of particulate matter was found in July 1999 and shows that net 1.7 g m⁻² PON was transformed

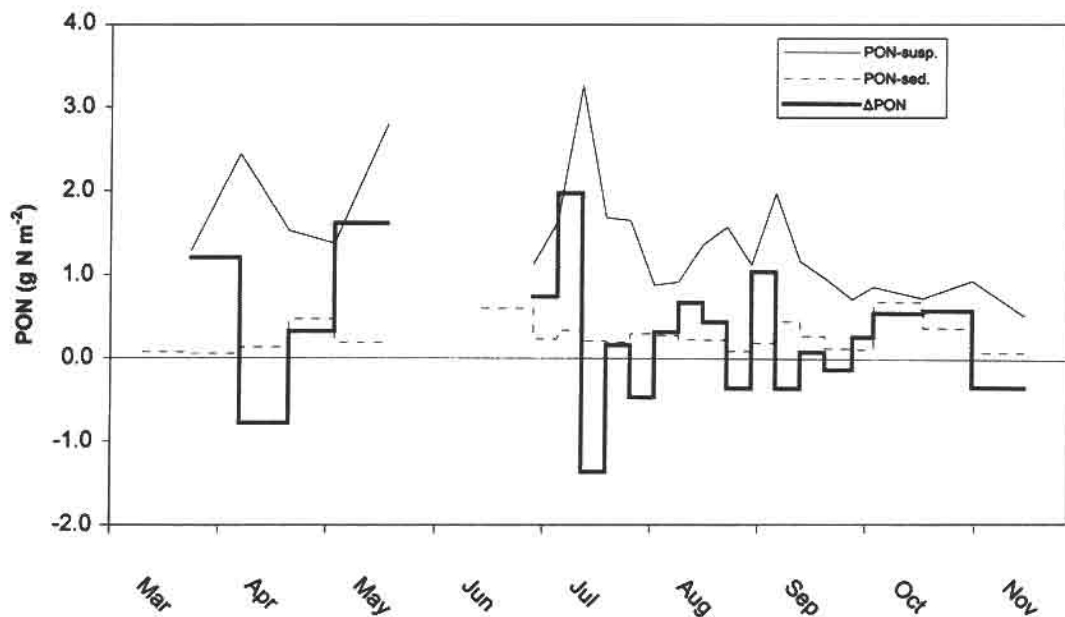


Fig. 10. Periodic net-allocation of particulate organic nitrogen (Δ PON) in the mixed layer based on temporal changes of the standing stock of suspended PON (PON-susp.) and on the vertical loss due to sedimentation (PON-sed.). Negative values represent loss of PON in the mixed layer that cannot be attributed sedimentation, and therefore presumably represent net-increase in DON. Positive values represent the net increase in PON (including sedimentation).

within the mixed layer during one week corresponding to $1.4 \text{ g C m}^{-2} \text{ d}^{-1}$ (applying a Redfield ratio of 5.7). Since accumulation of inorganic nitrogen in the surface layer is not likely, a transformation into dissolved organic matter seems to be the temporary fate of the phytoplankton in the mixed layer during summer. The labile part of the DON stock will then gradually degrade and thus create the nutritive background for a new bloom. Bacterial activity was not measured, but according to these considerations bacteria and maybe virus are expected to dominate the heterotrophic activity of the mixed layer in Mariager Fjord. Increasing emphasis has recently been drawn on such scenarios (Fuhrman 1999, Wommack & Colwell 2000).

Sinking velocity and aggregation. – The calculated sinking velocities are typical for free cells or chains (Smayda 1970) and indicates that phytoplankton is not forming aggregates, which would increase sinking velocities (Allredge and Silver 1988). The apparent insignificant aggregation was supported by the microscopic examinations of sedimenting matter where phytoaggregates occurred rarely. Unattached cells or chains of phytoplankton always domi-

nated the composition of the specimen. Aggregation was measured during a spring and summer period in Mariager Fjord in 1994 in 1995 (Lundsgaard & Olesen, in prep.). In spite of a very dense and almost monospecific occurrence of *Skeletonema costatum* ($> 100 \mu\text{g Chl l}^{-1}$) combined with a turbulent environment (shear rates ranging between 0.01 and 0.1 m^{-1}) the suspended phytoplankton chains remained unattached. According to coagulation theory (Jackson 1990) these conditions should favor collisions between phytoplankton cells. Absence of aggregates can therefore only be explained by the inability of the phytoplankton cells to adhere to one another. This is surprising because especially diatoms are assumed to be sticky (Kjørboe et al. 1990). The reason for the low stickiness is unknown, but aggregates do not play a similar role for sedimentation in Mariager Fjord as observed in other marine systems (Allredge and Silver 1988).

Low sedimentation – high primary productivity. – The total loss due to sedimentation of TPC and PON from the mixed layer was ca. 50 g C m^{-2} and ca. 7 g N m^{-2} for both of the productive seasons (Mar–Nov) of 1998 and 1999 (Table 2). The daily average sedimentation rate of ca. 180

Table 2. Cumulated loss of biogenic material due to sedimentation from the mixed layer throughout the productive period (marts - November, 275 days for 1998 and 1999, Mariager Fjord (inner fjord). For the missing period of investigation the mean value has been applied.

| | TPC g C m ⁻² y ⁻¹ | PON g N m ⁻² y ⁻¹ | Chloro- phyll <i>a</i> g Chl m ⁻² y ⁻¹ | Phaeo- pigment g Phaeo m ⁻² y ⁻¹ |
|------|--|--|--|---|
| 1998 | 47.2 | 7.0 | 0.60 | 0.55 |
| 1999 | 50.3 | 7.3 | 0.63 | 0.52 |

mg C m⁻² d⁻¹ and 25 mg N m⁻² d⁻¹ is comparable to the vertical flux reported from other, but more open coastal waters of the Baltic area (Olesen & Lundsgaard 1995, Lundsgaard et al 1999). The relative low sedimentation rates found in Mariager Fjord is in accordance with calculations of the carbon demand of the anoxic bottom water (Fenchel et al. 1995). The anaerobic mineralization was estimated to 144 mg C m⁻² d⁻¹ which, assuming steady state conditions, should equalize net import of organic matter.

Based on estimates for growth and biomass of the dense populations of the bivalve *Mytilus edulis* covering the slopes between 0 and 9-10 m of Mariager Fjord the benthic community account for a consumption that roughly equals sedimentation (Fallesen et al. 2000). The load of inorganic nitrogen to the fjord during the last decade was 25-35 g N m⁻² y⁻¹. In 1998 and 1999 the external supply of nitrogen has been estimated to 33-34 g N m⁻² y⁻¹ (Århus Amt & Nordjyllands Amt 2000). One third of this discharge is exported to Kattegat in the form of dissolved inorganic N during winter and another 15-20% leaves the fjord as incorporated in planktonic matter during summer (Larsen et al. 1992). The annual new production of the fjord based on the terrestrial loading can thus be estimated to range between 100 and 130 g C m⁻² y⁻¹ corresponding to 17 - 23 g N m⁻² y⁻¹. The total primary production between 1990 and 1999 varied between 800 and 1000 g C m⁻² y⁻¹ (Århus Amt & Nordjyllands Amt 2000). The regenerated production of the fjord therefore accounts for more than 80% of the total production. This high value can only be achieved through an efficient recycling of matter and is likely to be a result of the long retention time of suspended matter in the mixed layer. The retention time can be calculated as the inverse to the specific sinking loss rate, revealing a mean retention

time of suspended matter in the mixed layer of Mariager Fjord of 20 days in 1998 and 1999. The real figure is probably higher since estimates only include the particulate but not the dissolved organic matter of the mixed layer. A similar calculation for the Kattegat shows a mean retention time of 5-6 days implying a four fold higher mean sinking velocity of planktonic material than in Mariager Fjord (Olesen & Lundsgaard 1995). The low sinking velocities of phytoplankton and detrital matter is likely to be the reason for the efficient regeneration of nutrients and thus for the extreme high regenerated production of Mariager Fjord.

MATERIAL AND METHODS

Study area. - Mariager Fjord connects with northwestern Kattegat (Fig. 1). The inner part of Mariager Fjord consists of a basin separated from the Kattegat by a shallow (1 - 2 m) outer part functioning as a sill (Fig. 1). The study site was situated at 56°39.08'N, 9°58.50'E. The basin is permanently stratified and reaches a maximum depth of 30 m. Bottom water (20-25 psu) is separated from the mixed surface layer (15-20 psu) by a distinct pycnocline at depths of ca. 12 m (usually ranging between 10 and 15 m). The renewal of bottom water with high saline water from the Kattegat only happens at intervals of several years; therefore almost permanent anoxic conditions prevail below the pycnocline (Fenchel et al. 1995). The temperature of the bottom water remains below 10°C while temperatures above 20°C are found during summer in the mixed layer. The residence time of the surface water is about 7 months. Because of the relative long retention time of the water and a weak tidal amplitude (< 20 cm) the horizontal circulation plays a rather insignificant role for the vertical mixing. Wind is therefore the major mechanism for the mixing of water

Field studies. - The principal station (Fig.1) was visited once fortnightly during early spring (Mar-May) and fall (Oct-Nov) and weekly during summer (May-Sept) in 1998 and 1999. Sampling was performed from R V "Maria" on one-day cruises. Water samples were taken at the same depths as the sediment trap samples. Water for counting phytoplankton and measuring nutrients, total particulate carbon (TPC), particulate organic nitrogen (PON) and chlorophyll *a* were sampled with a 10-

Niskin water sampler (General Oceanic). Samples for microscopic examination and counting were preserved with Lugol's solution (1% final concentration) or glutaraldehyd (1% final concentration). Sedimenting particles were collected using sediment traps on an anchored mooring. Traps were deployed for one or two weeks at depths of 5, 10 and 15 m. Each trap array consisted of two cylindrical sampling tubes with a diameter of 5.35 cm and an aspect ratio of 5.7. The attachment to the mooring line was gimbaled and the drag force was equal above and below the pivot point with the center of gravity situated near the bottom of the cylinders.

In order to assess the decomposition of matter collected in the traps a preservative (1% final concentration of Lugol's solution in a 20 psu solution) was added before deployment to one of the parallel trap cylinders. The higher salt concentration in the poisoned cylinder relative to the ambient water could bias the efficiency of collecting settling particles. This would especially be the case in the mixed layer where salinity generally varies between 15 and 18 psu (at 15 m the salt concentration is around 20 psu). Assuming a relative low density of sinking particles of 1.080 g cm^{-3} (Smayda 1970) the differential cell density will decrease from 0.068 g cm^{-3} at 15 psu to 0.064 g cm^{-3} at 20 psu. According to Stokes law this could reduce the sinking velocity with ca 6%. Compared to the standard errors this change in settling velocity is not considered as a serious error of the estimation of the vertical flux rates.

The poisoned trap content was adjusted to 500 ml and collected into containers for later microscopic analysis. The content of traps without preservations was adjusted to 600 ml and subsamples were preserved with Lugol's solution (1% final concentration) or glutaraldehyd (1% final concentration). Other subsamples from the unpreserved cylinders were analyzed for Chl, TPC and PON contents (similar analysis was not performed on the preserved material because of the denaturation of the organic matter due to the preservative). Ship collision with the mooring resulted in loss of results for almost one month in May-June 1999 and technical problems resulted in a lack of coherence in the measurement during spring and late summer 1998. Sedimentation for the periods without moored traps was estimated as the average between the values of the last and first measurements surrounding the period.

Analysis. - For pigment analysis water and sedi-

ment trap samples were filtered onto Whatman GF/C filters and extracted in 96% ethanol. Samples were frozen (-18°C) and stored for max 2 months. The extract was centrifuged (4000 G) and measured on a Unicam SP 1800 spectrophotometer at 665 nm before and after acidification with 2 ml 0.06 N HCl per 10 ml of extract. Concentrations of Chl and phaeopigments were calculated according to Lorenzen (1967) using an absorption coefficient of Chl in 96% (v/v) ethanol of 83.4 g l cm^{-1} (Wintermans & DeMots 1965). For TPC and PON measurements water and sediment trap samples were filtered onto precombusted (450°C 6 h) Whatman GF/F filters and stored at -18°C . Filters were dehydrated at 80°C for 12 h before analysis on a Carlo Erba CHN-elemental analyzer (model 240 C) the

Phytoplankton and faecal pellets in water and sediment trap samples fixed in Lugol's solution were counted with an inverted microscope (Olympus CK 2) by the Utermöhl technique. Biovolume of phytoplankton was calculated and converted to organic carbon equivalents according to Edler (1979) based on cell size determinations. Estimates of the carbon content of the faecal pellets were achieved by assuming a carbon volume ratio of $0.11 \text{ mg C mm}^{-3}$ (Johannes & Satomi 1966).

Data processing. - Sedimentation rates (S ; $\text{mg m}^{-2} \text{ d}^{-1}$) were calculated as $S = (c_s - c_w)V/(At)$, where c_s is the biomass concentration (mg ml^{-1}) in the sediment trap, c_w the average concentration (mg ml^{-1}) in the ambient water during deployment, V the resuspended volume (ml) of the sediment trap sample, A the collection area of the sediment trap (m^2) and t the deployment time (in days, d). The sinking loss rate (SL , $\% \text{ d}^{-1}$) and sinking velocity (SV , m d^{-1}) were calculated as $SL = (S_p/C_a)100$ and $SV = S_p/C_v$ where S_p is the sedimentation rate across the pycnocline (15 m trap), C_a is the average integrated biomass (mg m^{-2}) and C_v is the average volume biomass (mg m^{-3}) for the mixed layer during the deployment.

The decomposition rate of settled material is estimated by comparing the number of non-motile cells in the preserved and unpreserved traps. Assuming a constant sedimentation rate (S) during the deployment period (t) the accumulation of cells in the cylinder with preservation can be expressed as $N = St$ and in the untreated cylinder as $N' = S/\mu(1 - \exp^{-\mu t})$ where μ is the decomposition rate; μ is found by equating the two expressions.

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