

Seasonal variation of nutrients and suspended biomass on a transect across Nordvestbanken, north Norwegian shelf, in 1994

Paul Wassmann, Inger J. Andreassen & Francisco Rey

SARSIA



Wassmann P, Andreassen IJ, Rey F. 1999. Seasonal variation of nutrients and suspended biomass on a transect across Nordvestbanken, north Norwegian shelf, in 1994. *Sarsia* 84:199-212.

Nutrient consumption in the uppermost, well-mixed 100 m of Nordvestbanken in 1994 started in March across the entire shelf. Significant nitrate reduction in the euphotic zone was reached in June at the inner and middle shelf, but not until September at the shelf edge. The variations of nutrient concentrations were generally similar for nitrate, silicate and phosphate. Increased stratification, giving rise to a pronounced nutricline around 40 m depth, was observed from August to October at the shelf edge, but not on the middle and inner shelf. The maximum carbon equivalent of cumulative nitrate consumption in the upper 100 m at the inner, middle and outer shelf was about 72, 52, and 55 g C m⁻² and occurred in June, August, and July, respectively. The suspended chlorophyll *a* concentrations were generally low throughout the transect and never higher than 2.4 mg m⁻³. Maxima were observed in June and July. Suspended phaeopigment concentrations were generally lower than 1 mg m⁻³. The concentration of suspended organic carbon was moderately high, varying between about 100 to 450 mg m⁻³. Maxima were found in the upper 40 m from May/June to October and in the entire water column in October.

New production, as reflected by the decrease of nutrients, is not exactly quantifiable in the present context. Thus the carbon equivalent of cumulative NO₃ disappearance, was interpreted as a minimum approximation of the new production rate. Estimates of new production were far greater on the inner shelf than generally assumed for adjacent north Norwegian coastal waters and are probably > 75 g C m⁻² y⁻¹. However, a concomitant accumulation of large quantities of phytoplankton in the water column did not take place, probably due to grazing, as reflected by low chlorophyll *a*, relative high phaeopigment and high POC concentrations as well as high POC/PON ratios (about 6-16). Increased POC/PON ratios throughout the water column in March and during July and August at depths up to 40 m indicate supply of degraded organic matter from the sides or below, probably due to resuspension from the slope and the shelf bottom.

Paul Wassmann & Inger J. Andreassen, Norwegian College of Fishery Science, University of Tromsø, N-9037 Tromsø, Norway. – Francisco Rey, Institute of Marine Research, PO Box 1870 Nordnes, N-5817 Bergen, Norway.

E-mail: paulw@nfh.uit.no – i-andrea@online.no – francisco.rey@imr.no

Keywords: Nutrients; biomass; seasonal variation; north Norwegian shelf.

INTRODUCTION

In a recent calculation of global marine primary productivity Longhurst (1995) estimates that the ocean margins, covering 11 % of the ocean surface, account for 29 % of the global total. The possible role of these productive regions as a sink of CO₂ from the atmosphere is nonetheless uncertain (Wollast & al. 1993) with estimates of organic material export from the shelf to abyssal depths (and thus carbon sequestration) ranging from > 90 % (Walsh 1991) to < 5 % (Biscaye & Anderson 1994) of primary production. Evidence from the North Pacific indicates that, basin-wide, about half of the benthic carbon utilisation occurs within 500 km of the ocean margin (Jahnke 1990), pointing to the im-

portance of shelf and slope export and its role in the ocean's biogeochemistry.

While extensive investigations regarding the dynamics of pelagic organisms and the fate of organic matter have been carried out in the inner coastal zone and the fjords of northern Norway, astonishingly little is known about plankton dynamics and biogeochemistry of the north Norwegian shelf, let alone shelf export. The most prominent plankton species composition and the seasonal variation in primary production in north Norwegian fjords and neritic waters have been reviewed by Tande (1991) and Wassmann & al. (1996). The population dynamics of the principal herbivores, the seasonality in biomass and productivity of the species at the north-eastern fringe of the northern Norwegian

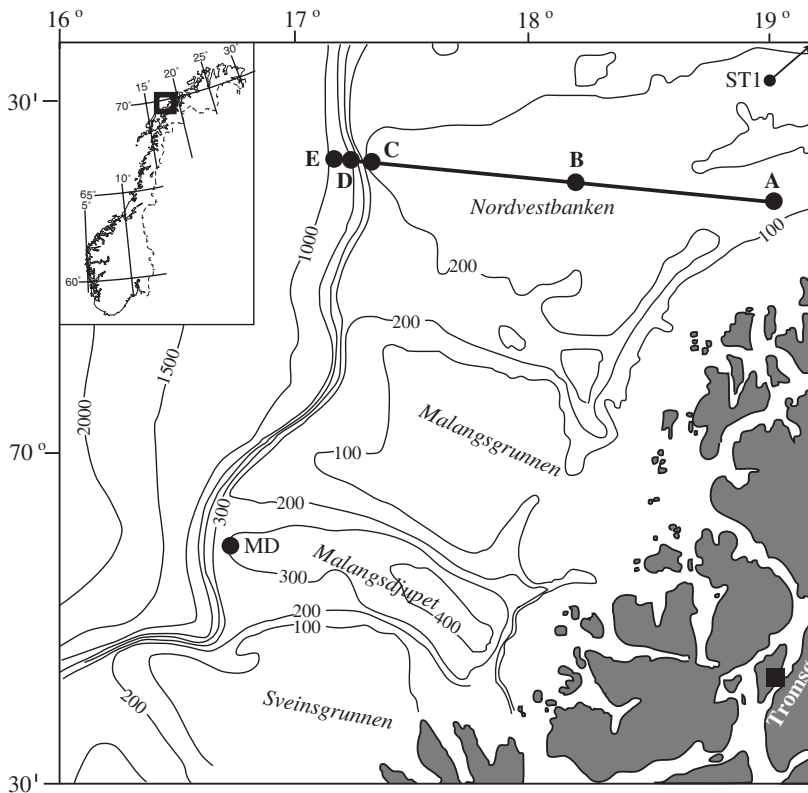


Fig. 1. Investigation area and the sampling stations A-E along the cross section over Nordvestbanken. Also shown are the stations ST 1 and Malangsdjupet (MD) where investigations of phytoplankton were carried out in 1988-1989 and 1991-1993 by Evensen (1994) and Hegseth & al. (1995), respectively.

Sea has been described by Hopkins & al. (1989) and reviewed by Tande (1991). Some off-shore investigations were carried out after the Second World War in the Norwegian Sea (e.g. Halldal 1953; Sverdrup 1953; Braarud & al. 1958; Lie 1968). More than 15 years ago the Norwegian Coastal Current was the subject of a major Norwegian investigation (Sætre & Mork 1981), including the study of pelagic processes (e.g. Rey 1981a, 1981b). Some investigations of plankton dynamics of the north Norwegian shelf close to the Lofoten islands were also carried out by Peinert (1986) and Peinert & al. (1987). However, to the best of our knowledge, no study of the cycles of nutrients, phytoplankton, and suspended matter throughout the entire productive season, has so far been carried out on and off the north Norwegian shelf.

The Norwegian Atlantic Current (NAC) transports Atlantic water northwards along the Norwegian continental shelf, thereby creating a marine environmental continuum which extends from the southern Norwegian Sea into the Barents Sea and further northwards to the

eastern coast of Spitsbergen (Blindheim & Loeng 1981). The coast of northern Norway is characterised by narrow and broad fjords and shallow banks, and the shelf break dominates the outer coastal zone in this area (Fig. 1). The Norwegian Coastal Current (NCC), characterised by decreased salinity due to fresh-water run-off from the fjords and the Baltic Sea, flows northward between the NAC and the coast. Fjords continue by trenches penetrating to the shelf break, separating the shelf into shallow coastal banks, for example Malangsgrunnen, Sveinsgrunnen and Nordvestbanken (Fig. 1). Clockwise circulation patterns are found on the banks (Sundby 1984). With fairly homogeneous physical environmental conditions along and off the shelf break, it may be reasonable to expect a plankton community which is structured and functioning basically in the same way throughout this large area. However, due to the substantial differences in topography along the Norwegian coastline the vertical structure of pelagic communities is anticipated to differ in the fjords, on the shelf and deep water areas. Based on the current understanding

of the physical oceanography of the area (Sætre & Mork 1981; Sundby 1984) profound effects on the production and both the vertical and horizontal fluxes of biogenic material over the shelf and the shelf break of northern Norway were expected. Extensive variation in ocean climate is considered to influence the plankton dynamics of the north Norwegian coastal zone (Sundby 1984) and the adjacent Barents Sea (Midttun & Loeng 1987).

The present investigation is part of the project "Comparative fluxes of biogenic matter and trophodynamic interactions across the shelf break of northern Norway", which, in turn is a segment of the Ocean Margin EXchange programme (OMEX) which takes into account the specific features of the European shelf environments and settings. It concerns essentially the study of fluxes and processes occurring along European shelf break facing the North Atlantic Ocean. Its aim is to measure and model exchange processes at the ocean margin as a basis for the development of global models to predict the impact of environmental changes on the oceanic system and more specifically on the coastal zone. To study the pivotal biological processes involved in the pelagic domain in northern Norway, the shelf and the break NW of the city of Tromsø, the Nordvestbanken, was selected. The shelf break is situated 60 km from the outer coastal zone and the selected sites cover a depth profile from about 100 m close to the coast to about 200 m at the shelf break, which is steeply declining to more than 1000 m over a distance of a few km. For an overview of the topography and hydrography of Nordvestbanken in 1994, see Nordby & al. (1999) and Moseidjord & al. (1999). Here, we describe the seasonality of nutrients and suspended particulate material in the upper layers of a transect across the north Norwegian shelf and at the shelf break from March to October in 1994 (Fig. 1). Attempts were made to estimate the seasonal new production rate across the shelf from the depletion of nitrate (e.g. Minas & al. 1986). The ambient nutrient concentration is a function of (a) phytoplankton growth, (b) the amount of winter-accumulated nutrients of the body of water passing by, (c) episodic or continuous mixing with other water masses over the course of time, (d) up- and downwelling and (e) diffusion. As some of these processes were not quantified in the present context, the estimates can only represent approximations of the new production rate.

MATERIAL AND METHODS

Standard hydrographic sampling was carried out on board of R/V *Jan Mayen* with a Neil Brown Mk III CTD-profiler mounted with a General Oceanic Rosette Sampler equipped with 5 litre Niskin bottles. The rosette was also equipped with a SeaTech fluorometer.

Samples were taken at 10 depths ranging from 0 to 100 m at 5 stations (A: inner shelf, ≈ 120 m; B: middle shelf, ≈ 150 m; C: 200 m; D: 300 m; E: shelf break, 500 m) from 23 March to 10 October in 1994 (Fig. 1). The transect across Nordvestbanken extends between $70^{\circ}20.00'N$, $18^{\circ}58.00'E$ to $70^{\circ}25.30'N$, $17^{\circ}08.00'E$. The distance between Stns A, B, and C is 30 km, while the distance between Stns C, D, and E at the shelf break is only a couple of km. Samples for nutrients and suspended biomass were taken monthly. Nutrient samples for nitrate, silicate, and phosphate were handled and analysed by a Technicon autoanalyzer as described by Wassmann (1991) at the Institute of Marine Research, Bergen. Chlorophyll *a* (Chl *a*) and phaeopigments (Phaeo) were measured with a Turner Designs AU-10. 250-500 ml from each depth were filtered through a 25 mm Whatman GF/F glass fibre filter. The filters were extracted with 10 ml of methanol for 2 hours at room temperature in the dark (Holm-Hansen & Riemann 1978). The samples were analysed according to Holm-Hansen & al. (1965). Calibration was done with pure chlorophyll *a* from SIGMA Chemical Co. 250-500 ml of samples for particulate organic carbon (POC) and nitrogen (PON) were filtered through precombusted 25 mm Whatman GF/F glass fibre filters and stored frozen. Before analysing the samples, filters were dried and treated with HCl fumes to remove carbonate. The samples were analysed on a Leeman Lab 440 CHN elemental analyser.

Assuming pre-bloom nutrient concentrations which were 10 % higher than those recorded at the start of the investigation on 23 March the seasonal NO_3 and Si(OH)_4 consumption in the euphotic zone were calculated. The C equivalent of the NO_3 and Si(OH)_4 consumption was calculated using Redfield ratios of 6.63 and 7.1, respectively. The estimates were interpreted as new production and carbon production by diatoms, respectively. These calculations are based on 2 assumptions: that a similar water source is sampled over time (no lateral import or export of nutrients to the shelf break current) and that no events < 1 months took place.

RESULTS

NUTRIENTS

The seasonal variation of nitrate on Nordvestbanken is given in Fig. 2. Nitrate concentration varied between $> 12 \mu\text{M}$ and detection limit. The highest concentrations were found in March and August/September at Stn E. Generally speaking nitrate concentrations in surface waters varied most at Stn A and least at Stn E. Nitrate concentrations at Stn A (inner shelf) decreased throughout the water column from March to June. Significant nutrient reduction was recorded in the upper 60-80 m

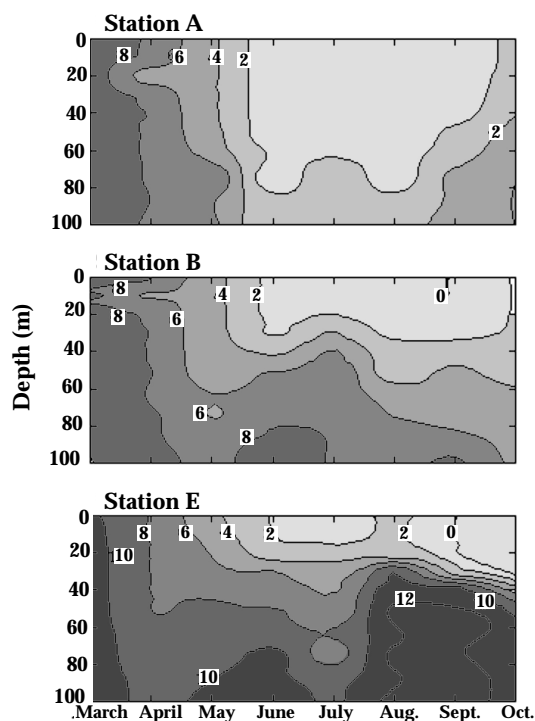


Fig. 2. Seasonal variation of nitrate (μM) in the upper 100 m at the sampling sites A (inner shelf), B (mid shelf) and E (shelf break) from March to October 1994.

from June to October while nitrate concentrations below this depleted layer varied between 2–4 μM , with a shoaling of the nitracline in September–October.

At Stn B (mid shelf) a similar pattern was found (Fig. 2). Nitrate concentrations decreased in the upper 100 m of the water column between March and April. However, nitrate was depleted only to about 30 m and just a slight increase in concentrations in surface water was recorded in October. Nutrient concentrations at depth during summer were at times elevated.

At Stn E (shelf edge) nitrate concentrations decreased rapidly in the water column in March and April (Fig. 2). The variability in nitrate concentrations was similar to that of Stn B, but nitrate depletion took place only in the upper 10 m in June/July and to 25 m in September/October. Also, there was a shoaling (Stns A and B) and a steepening of the nitrate cline from August and onwards. The nitracline was situated between 30–40 m with a distinct concentration gradient ranging from 2 to > 10 μM . Phosphate concentrations (not shown) followed the same pattern as nitrate.

In general, the dissolved silicate concentrations at Nordvestbanken revealed a variation similar to that of

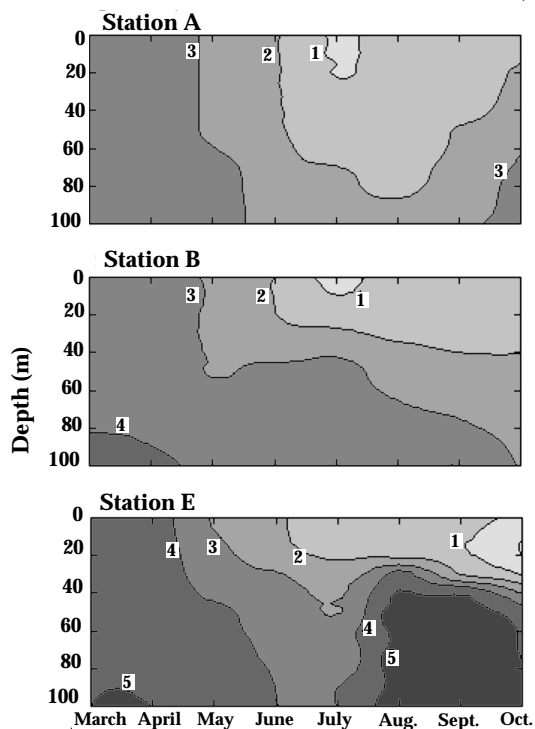


Fig. 3. Seasonal variation of silicate (μM) in the upper 100 m at the sampling sites A (inner shelf), B (mid shelf) and E (shelf break) from March to October 1994.

nitrate. Silicate varied between 5 to less than 1 μM , but the latter was rarely recorded. A major difference was the apparent lack of dissolved silicate uptake in March: while nitrate concentrations decreased between March and April, those of dissolved silicate were more or less unchanged (see also Fig. 8C). The highest concentrations were again recorded at depth and at the mid-shelf and shelf edge stations. At Stn A dissolved silicate concentrations decreased steadily throughout the upper 100 m from March to June. Dissolved silicate concentration was < 2 μM from June to August in the upper 80 m. A slight increase in concentrations was recorded in the lower 20 m from August to October.

Also at Stn B dissolved silicate concentrations decreased slowly in the upper 100 m of the water column from March to May (Fig. 3). However, dissolved silicate concentrations decreased slowly at depth and major increases in concentrations in surface water were not recorded for the rest of the investigation period. There were tendencies for increased dissolved silicate concentrations at depth during summer which may reflect increased supply at depth.

At Stn E the highest dissolved silicate concentrations

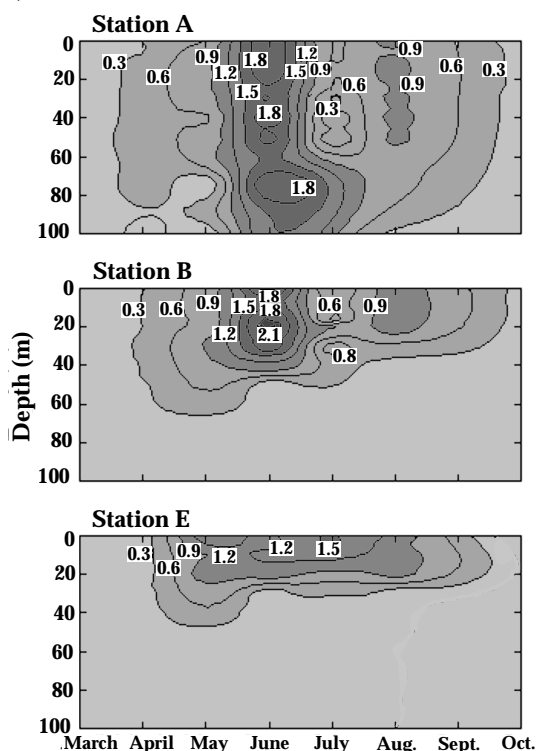


Fig. 4. Seasonal variation of Chl *a* (mg m^{-3}) in the upper 100 m at the sampling sites A (inner shelf), B (mid shelf) and E (shelf break) from March to October 1994.

were found (Fig. 3). Concentrations $< 1 \mu\text{M}$ were only recorded in surface waters in late autumn. Dissolved silicate disappeared from the water column relatively slowly from March to May. The variability in dissolved silicate concentrations was similar to that of Stn B, but silicate concentrations $< 2 \mu\text{M}$ were only recorded in the upper 20–30 m from June and onwards. The silica-cline was situated between 30–40 m from August and onwards, with a distinct concentration gradient ranging from 2 to $> 5 \mu\text{M}$.

It is interesting to note that nutrient concentrations at Nordvestbanken were depleted to a depth of more than 100 m. The complete seasonal nutrient decrease in the upper layer can thus not be depicted. This has in particular consequences for budgets of seasonal nutrient consumption. These budgets (see below) probably underestimate the total nutrient consumption by an unknown proportion.

PIGMENTS

The variation in Chl *a* is shown in Fig. 4. The most obvious result at Nordvestbanken were the low Chl *a* concentrations which never exceeded 2.4 mg m^{-3} . Most

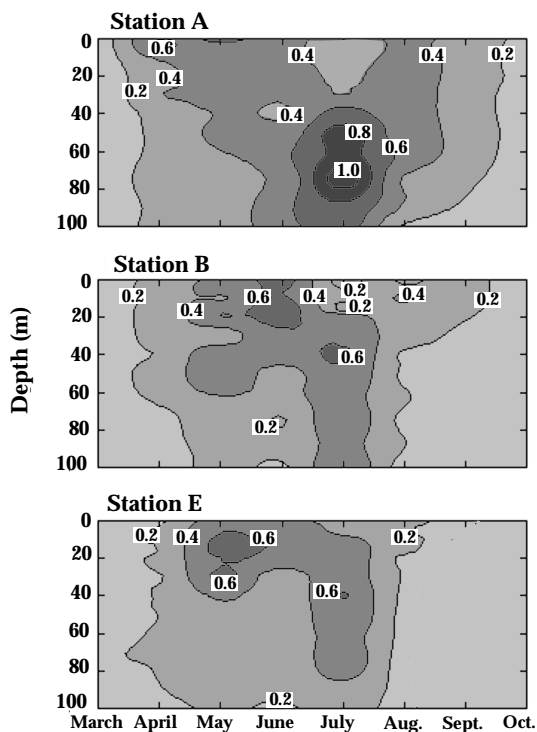


Fig. 5. Seasonal variation of Phaeo (mg m^{-3}) in the upper 100 m at the sampling sites A (inner shelf), B (mid shelf) and E (shelf break) from March to October 1994.

of the time and over most of the transect Chl *a* concentrations were lower than 1 mg m^{-3} . There was a general trend of decreased Chl *a* concentration towards the shelf edge. At Stn A Chl *a* was uniformly distributed throughout the upper 100 m. A gradual increase was recorded from March to June where a seasonal Chl *a* maximum was found. From July and onwards Chl *a* concentrations decreased again gradually.

At Stn B Chl *a* concentration in March and October was $< 0.3 \text{ mg m}^{-3}$ throughout the water column. Also here a maximum was recorded in June, slightly $> 2.0 \text{ mg m}^{-3}$ in the upper 30 m. Below 50 m depth the Chl *a* concentrations were always $< 0.6 \text{ mg m}^{-3}$. A second smaller maximum $> 0.9 \text{ mg m}^{-3}$ was found in August.

The Chl *a* concentration pattern recorded at Stn E had similarities with Stn B. Also here Chl *a* concentration in March and October were low. The water column below 30 m had always Chl *a* concentrations $< 0.6 \text{ mg m}^{-3}$ and $< 0.3 \text{ mg m}^{-3}$ below 40 m. Shallow maxima in the upper 10 m of the water column were recorded in May and June/July.

Also the Phaeo concentrations were low throughout the investigated period and the transect (Fig. 5). Con-

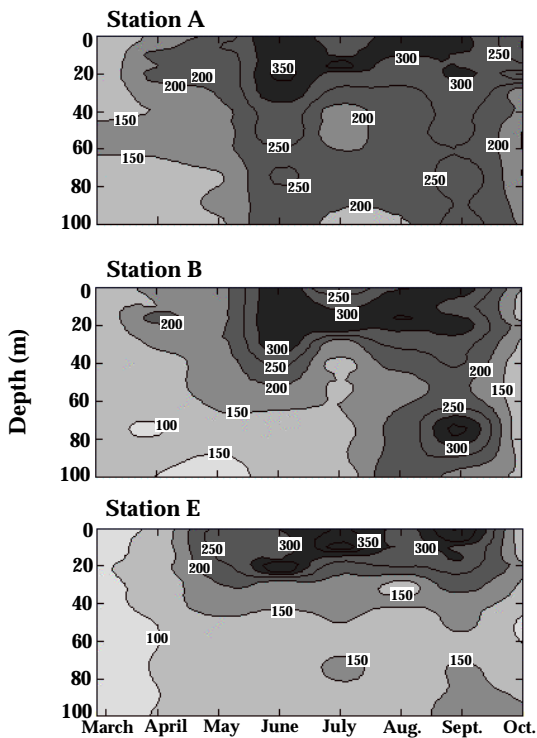


Fig. 6. Seasonal variation of POC (mg m^{-3}) in the upper 100 m at the sampling sites A (inner shelf), B (mid shelf) and E (shelf break) from March to October 1994.

concentrations $< 0.2 \text{ mg m}^{-3}$ were found in March and October at all stations. A general increase in concentrations was recorded throughout the water column in July at all stations. At Stn A Phaeo increased gradually towards July when a maximum of $> 1.0 \text{ mg m}^{-3}$ was recorded at 75 m depth, after which concentrations decreased again gradually. At Stn B the trend in the variability of Phaeo concentrations was similar. However, maximum concentrations were smaller and maxima were found in surface waters in June and at 40 m depth in July. Stn E had strong similarities with Stn B, but the concentrations were generally lower, in particular in August. Also, the annual maximum was found in May already at depths between 10 and 30 m. The Chl *a*/Phaeo ratio was frequently > 1 throughout the water column at Stn A, and at Stns B and E roughly in the upper 50 m. At greater depth the Chl *a*/Phaeo ratio was generally < 1 at Stns B and E. Most of the Chl *a* readings below 40 m depth from summer and early autumn were “negative” (data not included in Fig. 5), shedding doubts on the analysis of both Chl *a* and Phaeo.

Integrated Chl *a* concentrations ranged between 6–193 (average $55 \pm 104 \text{ \% S.D.}$), 7–82 (average 32 ± 64

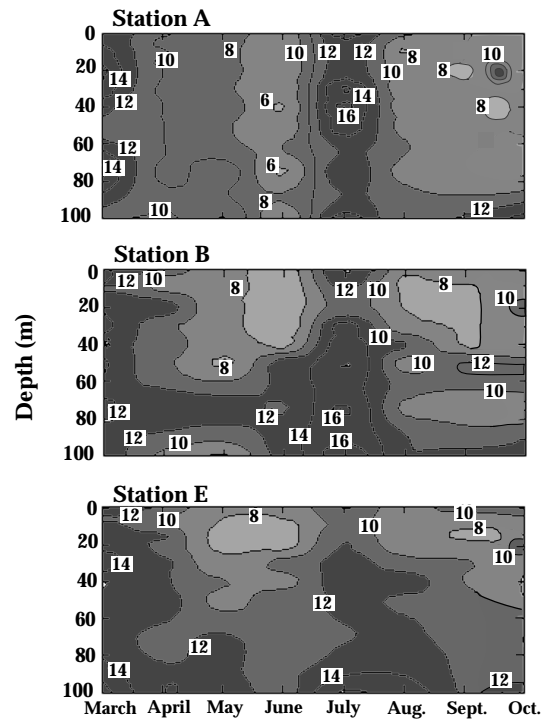


Fig. 7. Seasonal variation of the POC/PON ratio (a:a) or (w:w) in the upper 100 m at the sampling sites A (inner shelf), B (mid shelf) and E (shelf break) from March to October 1994.

\% S.D.) and 9–44 (average $27 \pm 57 \text{ \% S.D.}$) $\text{mg Chl } a \text{ m}^{-2}$ at Stns A, B, and C, respectively.

POC AND PON

In general POC concentrations were relatively high throughout the investigated period and the transect, ranging between 100 and 450 mg m^{-3} (Fig. 6). The seasonal pattern of POC concentrations at Stns A, B, and E were relatively similar. The lowest concentrations up to about $< 150 \text{ mg m}^{-3}$ were recorded in March and April. Maxima ($> 450 \text{ mg m}^{-3}$) were mainly recorded in the upper 20–30 m from May to September and throughout the water column in October. POC was more evenly distributed throughout the upper 100 m at Stn A while at Stn B and, in particular at Stn E, less suspended POC was found below 30–40 m. The POC/PON ratio varied greatly between about 6 to 16 (Fig. 7). Ratios < 8 were recorded in May–June and September–October. High ratios were found in March and July (> 14) throughout the transect and in particular at Stns B and E in the deeper part of the water column. There were indications of increased POC/PON ratios in July/August along with the development of the nutricline at Stn E, probably reflect-



ing resuspension of organic matter at depth. A similar phenomenon was recorded at Stns A and B.

The integrated suspended POC concentrations along the transect ranged widely between 6.2 and 31.9 g C m⁻² with maxima in June, August and September (21.8, 21.6 and 23.9, respectively; Fig. 8A). POC concentrations along the transect increase steeply and linearly from March to June, with average POC concentrations levelling off between 20 and 25 g C m⁻² thereafter. Integrated POC concentrations decreased finally in October. A considerable inter-station variability was recorded, in particular from June and onwards. There was a tendency towards decreasing suspended POC concentrations from the inner shelf towards the shelf edge.

NUTRIENT CONSUMPTION AND CARBON EQUIVALENTS

The carbon equivalents of the cumulative seasonal nitrate consumption across the transect are indicated in Fig. 8B. The maximum carbon equivalents of the cumulative seasonal nitrate consumption at the 5 stations were recorded between June and August and ranged widely between 40 and 72 g C m⁻² cumulative months⁻¹. As for the integrated suspended POC, the carbon equivalents of the seasonal nitrate consumption increased steeply and linearly from March to June after which they levelled off albeit with a wide range (about 20–70 g C m⁻² cumulative months⁻¹) and decreased slowly towards October. There must have been additional nutrient supply through the nutricline from July and onwards which is not reflected in nutrient concentrations. The carbon equivalents of the seasonal nitrate consumption were highest at Stn A with lower rates around the shelf edge.

The carbon equivalents of the cumulative seasonal silicate consumption across the transect are indicated in Fig. 8C. The average carbon equivalents of the seasonal dissolved silicate consumption at the 5 stations increased steeply and linearly from March to June, had a maximum (17 g C m⁻²) in July and decreased to about 12 g C m⁻² in October. The values ranged widely from 6 to 23 g C m⁻² in the latter part of the year. Again, the carbon equivalents of the cumulative seasonal dissolved silicate consumption were highest at Stn A with lower rates around the shelf edge. Dissolved silicate consuming phytoplankton organisms, preferentially diatoms, contribute at the maximum in summer about 30.7 ± 8 % SD. to the carbon equivalents of nitrate consumption.

DISCUSSION

The coastal area with its enhanced productivity and under the influence of continental input is an important source of dissolved and particulate matter for the open ocean (Monaco & al. 1990; Mantoura & al. 1991). On the other hand, deep, nutrient rich ocean waters are

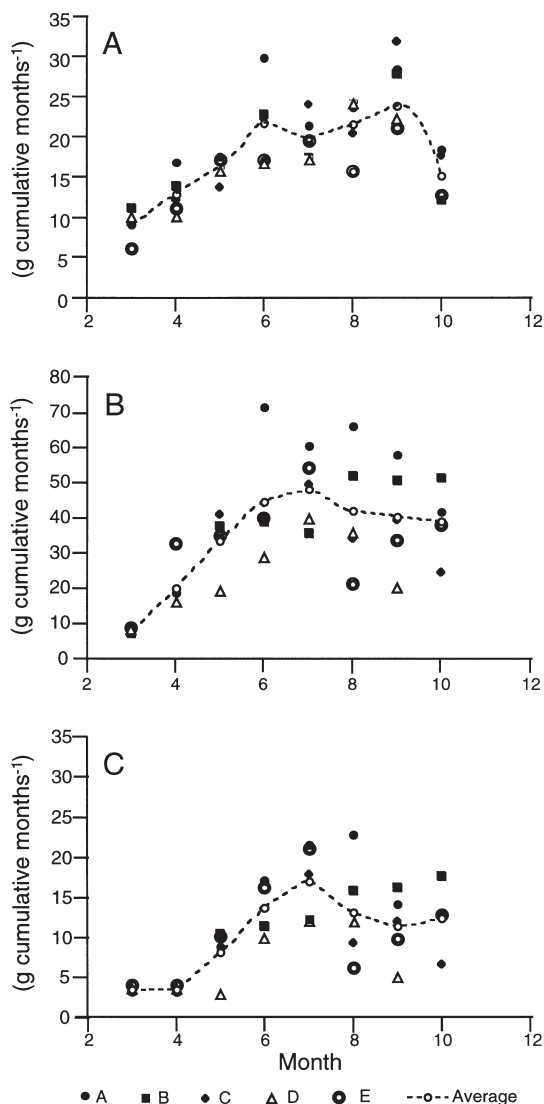


Fig. 8. A. Seasonal variation of integrated suspended POC (0–100 m; g m⁻²) from March to October at Stns A–E. Also shown is the average concentration (line). B. Seasonal variation of integrated carbon equivalents of nitrate consumption as related to winter accumulated concentration (0–100 m; g C m⁻²) from March to October at Stns A–E. Also shown is the average concentration (line). C. Seasonal variation of integrated carbon equivalents of silicate consumption as related to winter accumulated concentration (0–100 m; g C m⁻²) from March to October at Stns A–E. Also shown is the average concentration (line).

transferred across the shelf edge and help to sustain the high productivity of biota in the coastal zone and shelf seas (Walsh 1988). The quantification of fluxes at and across the ocean margin (Huthnance 1995) is thus a fun-



damental requirement for the evaluation of the carbon budget and nutrients between the continents, the coastal zone and the open ocean. What is the production regime on the north Norwegian shelf? Is it a shelf of high productivity and biomass accumulation and how does this margin and the adjacent continental slope enhance productivity and biologically-mediated transport?

NUTRIENT CONSUMPTION AND NEW PRODUCTION

The dynamics of nutrients and suspended biogenic matter on Nordvestbanken in 1994 were characterised by conditions which make this shelf area unique with regard to plankton dynamics so far recorded in coastal regions of northern Norway and the Barents Sea shelf. Nutrient consumption was substantially greater compared to fjords or the Barents Sea. The chlorophyll *a* concentrations were remarkably low, despite of the implicit high new production which may be twice as high as in fjords or the Barents Sea. Assuming a POC/Chl *a* ratio of 60 (E. Sakshaug, pers. commn) for small-celled phytoplankton such as prymnesiophytes and under light-limiting conditions (Hewes & al. 1990; Verity & al. 1991), the integrated phytoplankton carbon varied between 0.18 and 12 g C m⁻² (average: 2.25 ± 93 % g C m⁻²). This comprises on average only about 12 % of the average integrated seasonal POC across the transect (range: 9.1-23.9 g C m⁻²). What are the processes which give rise to such a large new production, a considerable accumulation of suspended POC and significantly decreased phytoplankton biomass?

The plankton dynamics are subjected to the strong current regime over the shelf, and in particular, at the shelf break were the average residual current speed parallel to the shelf break is well above 20 cm s⁻¹ (Moseidjord & al. 1999). Compared to the inner shelf with its prevailing eddies (Sundby 1984), the residence time of the water is supposed to be lower at the shelf edge as the current is both faster and more or less unidirectional (Moseidjord & al. 1999). Simulation indicates that particles starting to drift at the 200 m isobath will meander along the shelf at a velocity of about 300-400 km per month (Wassmann & Slagstad 1995). Particles off the shelf edge are either caught by eddies in the Norwegian Sea or move along the 1000 m isobath towards Spitsbergen at a velocity of about 200 km per month. The water over the shelf and the shelf break was only weakly stratified from March to July (Nordby & al. 1999). This probably implies strong mixing and extensive vertical excursion of surface water during a major part of the productive period until the development of stratification during late summer and onwards (August to October). Stratification is caused by the spreading of the NCC in late summer (50-100 m deep) which covers the shelf as well as intrusion of NAC water

at depth over the shelf break.

For major parts of the year water from far deeper than the euphotic zone can be transferred by mixing into the upper layers, providing substantial nutrient resources to the phytoplankton community. Simultaneously suspended particles, among those phytoplankton, may be subjected to extensive vertical excursions into the aphotic zone. Extensive vertical mixing will retard phytoplankton growth. However, weak stratification did not hinder strong phytoplankton growth as reflected by the substantial nutrient consumption across the shelf (Fig. 8B & C). On the contrary, mixing seemed to promote continuous phytoplankton growth over a major part of the productive period through increased nutrient supply. Scenarios of strong spring bloom development in almost non-stratified waters are not rare and have also been encountered in north Norwegian fjords (Eilertsen 1993; Wassmann & al. 1996), boreal shelves (Townsend & al. 1992; Hegseth & al. 1995), the open Norwegian Sea (Halldal 1953) and in the Atlantic sector of the Barents Sea (Skjoldal & Rey 1989; Wassmann & al. 1999b), suggesting that the phenomenon is widespread and rather the rule than an exception in many boreal and sub-polar environments. In the present case the bloom was reflected in nutrient consumption, but not in phytoplankton accumulation.

Wind strength and direction during early spring, along with the light regime, appears to play a crucial role for the onset, development and fate of the spring bloom (Sakshaug & al. 1995). The seasonal lateral oscillation of the coastal water has been attributed to upwelling events forced by north-westerly and north-easterly winds (Sætre & al. 1988). The wind speed at Nordvestbanken in 1994 was generally low and the main direction during all cruises was from the south-west, implying downwelling, rather than upwelling. To what extent up- and downwelling episodes due to wind-forcing has influenced the plankton dynamics on Nordvestbanken in 1994 is not precisely known.

Phytoplankton growth developed slowly, steadily and linearly with an average NO₃ consumption rate of about 125 mmol m⁻² month⁻¹ (equivalent to 10 g C m⁻² month⁻¹) until stratification and depleted nutrient reserves at depth reduced further growth. Additional diffusive supply of nitrate and dissolved silicate from below added to the available nutrients which are not reflected in the decline of nutrient concentrations. The question arises to what extent the data presented in Fig. 8B reflect the new production regime on Nordvestbanken? The processes which give rise to the variability of nutrients cannot be quantified in the present context as for example episodic or continuous mixing with other water masses over the course of time, up- and downwelling and diffusion were not determined. Phytoplankton new production, as re-

flected by the decrease of nutrients, is thus not exactly quantifiable. Confronted with the lack of direct investigations of new production the decrease of nutrients has been used in order to estimate or approximate new production, similar to previous approaches (e.g. Minas & al. 1986; Eppley, 1989). It can be argued that nutrient consumption must have been greater than the apparent decrease in ambient nutrient concentrations as (a) mixing and diffusion are supposed to be important processes determining the amount of available nutrients and (b) decreases in nutrient concentrations exceeded the maximum sampling depth of 100 m. Thus, the data shown in Fig. 8B may give an impression of the minimum new production rate across the transect. Also, as turbulent mixing and processes such as upwelling are supposed to be far more intensive at the shelf break compared to the inner shelf, the carbon equivalent of NO_3 consumption at Stn E appears to be far lower than the actual new production rate. The carbon equivalent of NO_3 consumption at Stn A, however, is probably closer to the respective new production rate on the entire shelf. With the hydrodynamic differences across the transect and the presumed seasonal variability in mind, any attempt to calculate precisely the new production rate at Nordvestbanken based on the present data set will be fruitless. Despite this complication, an estimate of the new production range may be approximated by investigating the maximum nitrate consumption rates and by extrapolating the curves in Fig. 8B from June and onwards. Having in mind that (a) the average line in Fig. 8B underestimates the real new production rate, (b) that the maximum carbon equivalent at Stn A comes closer to the new production rate because turbulent mixing, diffusion and upwelling are supposed to be less important compared to the shelf edge and (c) assuming that a cumulative new production curve will level off from mid summer, a new production rate of $> 75 \text{ g C m}^{-2} \text{ y}^{-1}$ on Nordvestbanken does not seem unrealistic. Similar evaluations with regard to dissolved silicate reveal that the carbon production based on average dissolved silicate may be $> 25 \text{ g C m}^{-2} \text{ y}^{-1}$, i.e. 1/3 of the new production rate.

Compared to other coastal and shelf areas, these rates reflect a high productivity. Data from Peinert (1986) revealed that significant nitrate reduction across the Norwegian shelf south of the Lofoten Islands in spring and early summer was equivalent to a range of new production rates between $40\text{--}60 \text{ g C m}^{-2}$, supporting the results presented here. Additional evidence for the supposedly high new production rates at Nordvestbanken is based on the average POC vertical flux at 100 m depth ($\approx 42 \text{ g C m}^{-2}$ productive season $^{-1}$; Andreassen & al. 1999) and the suspended POC from primary production which remained in the upper 100 m in October (15 g C m^{-2} ; Fig. 8A). Obviously, new production rates greater than

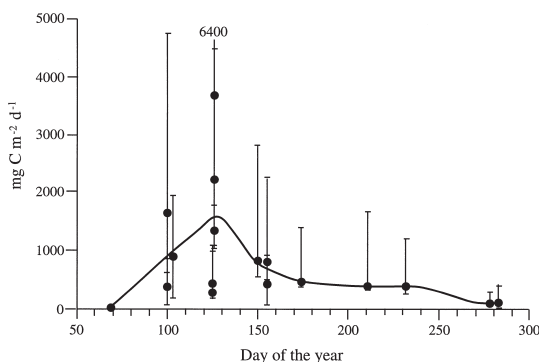


Fig. 9. Primary production estimates based on 320 measurements (1975–78) from Hekkingen Lighthouse and the North Cape ($\text{mg C m}^{-2} \text{ d}^{-1}$). Averages and standard deviations from 13 cruises are shown. Data from Rey (1981a).

$60 \text{ g C m}^{-2} \text{ y}^{-1}$ at the shelf break seem to be reasonable. Compared to the fjords, the shelf of northern Norway encounters thus an enhanced productivity and is an important source of biogenic matter. However, the influence of continental input with regard to nutrients and particulate biogenic matter is small in northern Norway (Wassmann & al. 1996). Here it must be mainly the deep ocean waters from the NAC, which by crossing the shelf edge help to sustain the high productivity of biota of shelf seas and in the coastal zone.

Primary production was not recorded during the survey. Rey (1981a) presented primary production data from the shelf between Hekkingen lighthouse (close to the city of Tromsø) and the North Cape from 1975–78. A total of 320 measurements were carried out during 13 cruises from March to October (Fig. 9). Not surprisingly, a tremendous variability in primary production rates was encountered, in particular in April/May. The integrated primary production from the north Norwegian shelf based on the average rates presented in Fig. 9 revealed an annual production of 126 g C m^{-2} . This rate suggests that the primary production rate on the north Norwegian shelf may be similar to that of north Norwegian fjords (e.g. Eilertsen & Taasen 1984), but not particularly high compared to many other shelf ecosystems (e.g. Walsh 1988). As new production rates seem to be high (Fig. 8B; Peinert & al. 1986), the seasonal f-ratio should be greater than 0.5. Because new production determines the maximum biomass which can be extracted from an ecosystem (e.g. Iverson 1991), a high f-ratio points to the fact that the north Norwegian shelf has a high net production although the gross production may be moderate, implying an effective food chain.

Due to the wide range of primary production rates on the north Norwegian shelf, reflecting substantial spatial, interannual and seasonal variability, any reasonable es-

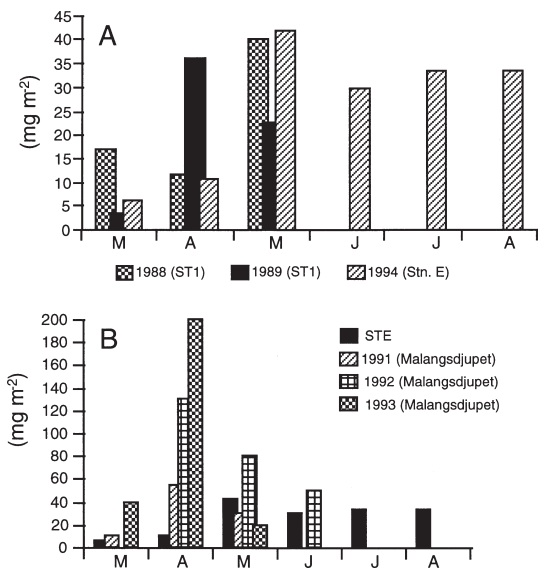


Fig. 10. A. Seasonal variation of integrated Chl *a* concentrations in the upper 50 m at Stn E in 1994 as compared with data from station ST 1 in 1988 and 1989 (Evensen 1994). B. Seasonal variation of integrated Chl *a* concentrations in the upper 50 m at Stn E in 1994 and from Malangsdjupet in 1991-1993 (Hegseth & al. 1995). Observe the obvious difference in April.

time would probably have to be based on modelling. Such a model from the OMEX area is available (Slagstad & al. 1999), revealing that primary production and new production along the transect of Nordvestbanken in 1994 ranged between 140-165 and 90-112 g C m⁻² y⁻¹, respectively. Obviously, primary and in particular new production on the north Norwegian shelf is high. The present approach to estimate a minimum annual new production resulted in approximations which were 17-33 % lower. Similar model estimates of the C-equivalents of Si consumption ranged between 31.4 and 33.4 g C m⁻² y⁻¹ at Stns A and E, respectively (Slagstad & al. 1999). Assuming that the annual silicate based carbon production on the shelf was > 25 g C m⁻² y⁻¹ (Fig. 8C), the present approach represents an underestimate of about 21-25 %.

SPATIO-TEMPORAL VARIABILITY OF CHLOROPHYLL *a*

Since new production is high, the reason for the low Chl *a* biomass at Nordvestbanken must be high vertical loss rates, degradation, migratory flux by zooplankton or grazing. The latter assumption finds support by the relatively high phaeopigment and POC concentrations (Figs 5 & 6). Also Evensen (1994) recorded low Chl *a* and high phaeopigment concentrations on the north Norwegian shelf during spring and early summer. Results on faecal pellets (Urban-Rich & al. 1999; Wassmann & al. 1999a),

mesozooplankton (Halvorsen & Tande 1999), heterotrophic nanoflagellates (Verity & al. 1999) and protozooplankton (Ratkova & al. 1999) further support the hypothesis that grazing may indeed be the main cause for the low Chl *a* standing stock. Migratory flux of Chl *a* cannot be substantial as daily vertical migration by mesozooplankton was not prominent. Also the vertical export of Chl *a* was low (Andreassen & al. 1999). However, on average only 45 % of the pico-, nano-, and microplankton on the shelf were autotrophic (Ratkova & al. 1999) while small heterotrophic cells often dominated the plankton community which was entirely dominated by small cells (Verity & al. 1999). The north Norwegian shelf in 1994 was thus characterised by high productivity, small cells size and low chlorophyll concentrations which is typical for systems subjected to extensive grazing. Nordvestbanken shares similarities with several large regions of the global ocean, e.g. the high nutrient/low chlorophyll (HNLC) in Antarctica (e.g. Froneman & Perissinotto 1996), the subarctic Pacific (e.g. Frost 1987; Dagg 1993) and the equatorial Pacific (Dam & al. 1995). The north Norwegian shelf belongs thus to the many high productivity areas where zooplankton grazing is supposed to play a pivotal role for the fate of phytoplankton-derived matter.

A comparison with integrated Chl *a* concentrations in the vicinity of the transect across Nordvestbanken was used to evaluate the questions if (a) the low Chl *a* concentrations may be characteristic for the entire north Norwegian shelf and if (b) there were significant spatial and inter-annual variability in accumulated phytoplankton in the euphotic zone. Fig. 10B compares data from a station in the Malangsdjupet area (see Fig. 1) with data from Stn E. Generally, Chl *a* concentrations were low, but there is an obvious difference in April where the integrated Chl *a* concentration at Stn E were far lower in 1994 compared to the 1991-1993 variability recorded by Hegseth & al. (1995). In 3 out of 4 months the concentrations at Stn E in 1994 were lower compared to the 3-year interval at Malangsdjupet, but in May the concentrations at Stn E were in the mid range. A comparison of the integrated Chl *a* concentrations with a station to the north reported by Evensen (1994) revealed that also here Chl *a* concentrations were low throughout spring and the lack of a seasonal pattern was similar to that of Stn E (Fig. 10A). Data from the upper 35 m layer of north Norwegian fjords indicate that maximum Chl *a* concentrations ranged between 50-80 and 150 mg Chl *a* m⁻² in Malangen and Balsfjorden, respectively (Reigstad & Wassmann 1995; Wassmann & al. 1996). The Chl *a* concentrations in spring are distinctively higher at the inner shelf along the entire north Norwegian coastal zone (Rey 1981b; Babichenko & al. 1999). Again increased grazing on the shelf and in particular at the shelf break seems to be a plausible explanation for the Chl *a* con-

centration and distribution. The comparison reveals that low Chl *a* volume concentrations appears to be a characteristic feature of the north Norwegian shelf, but not excessively in adjacent fjords, implying that extensive removal of phytoplankton takes place throughout the productive season, over the entire shelf.

If the variability between years and areas depicted in Fig. 10 reflects differences in the timing of the vernal bloom between years or spatial differences in production/degradation or both is impossible to conclude. The March and April results from Evensen (1994) and Hegseth & al. (1995), respectively, seem to imply that inter-annual differences may play a role on the north Norwegian shelf. This could imply differences in phytoplankton growth, but probably points at inter-annual differences in grazing pressure. Although the interaction between physical and biological processes for temporal-spatial variations in the distribution of zooplankton has been characterised and discussed for fjords (Falkenhaus 1997), unfortunately there are no zooplankton time series available from the shelf which could substantiate this hypothesis.

The lack of phytoplankton biomass accumulation despite significant new production points at a high degree of match between primary and secondary producers, implying an efficient trophic transfer. Despite this efficiency in biomass transfer, there must be a substantial vertical loss from the epipelagic zone through faecal pellets. This is the case (e.g. Urban-Rich & al. 1999; Wassmann & al. 1999a). The high degree of match highlights the importance of the mesopelagic zone as mediator of the vertical particle fluxes in the oceanic and shelf environments of the Norwegian Sea.

HOW DYNAMIC ARE NUTRIENT CONCENTRATION AND SUSPENDED BIOMASS ON THE NORTH NORWEGIAN SHELF?

The hydrodynamic and concomitant pelagic scenarios encountered across Nordvestbanken are supposed to be subject of significant changes over periods of time which are far shorter than the monthly sampling carried out during the present investigation. This implies that the present data can be misinterpreted as they are discussed as characteristic for the entire months in which sampling took place. Detailed and continuous investigations of the pigment distribution in the upper 30 m of the euphotic zone along 5 cross sections in the Malangs-djupet area in 1995 using the LIDAR technique of Babichenko & al. (1993) revealed notable differences in concentrations over time intervals of a few days only (Babichenko & al. 1999). This implies that an interpretation of the hydrodynamics and plankton ecology on Nordvestbanken based on monthly investigations should be interpreted with great care, as the short-term variability could be significant. With no more detailed data

at hand it was presumed that the data reflect the average monthly variation in nutrients and pigments. Considering the scarcity of seasonal variability data from the north Norwegian shelf, the present investigation is a first, but not more than an initial step towards a dynamic comprehension of plankton ecology in this area.

Given the complexity and the hydrodynamic variations of the north Norwegian shelf, the question can be raised as to what extent a number of measurements on nutrients and suspended matter at a given date and site are representative for more than a scale of a day and litres. The obtained samples represent unknown time and space integrals. This can be illustrated by approximating the horizontal displacement of surface water along the north Norwegian shelf. Assuming a constant and unidirectional average current speeds of 20–50 cm s⁻¹ at the shelf break (Sundby 1994; Moseidjord & al. 1999), the monthly horizontal displacement varies between 500–1300 km. This simple calculation exemplifies the basic problem of interpreting water bottle data from dynamic shelf regions: over the year the source areas for nutrients, suspended biogenic matter and plankton may differ remarkably. Each quantity of water and its constituents reflects a non-quantified life-story, resulting in large differences between the time and area of particle formation and where they were recovered, consumed or deposited. The dynamics of the pelagial on the north Norwegian shelf and the NAC probably differ from year to year (e.g. Ådlandsvik & Loeng 1991; Sakshaug & al. 1995), reflecting a particular and interannually-variable “blend” of physical events and biological processes. Great care must be taken to interpret data of suspended biomass and species composition as long as the timing and inter-annual variability of advective transports from various source areas are unknown, in particular when the sampling frequency of nutrients and suspended mass is infrequent or sporadic.

CONCLUSION

Deep ocean waters from the NAC, transferred across the shelf edge of northern Norway, the elevated availability of incident light during the productive season at 70°N and the low vertical stability of the water column all support a substantial supply of new nutrients and a high productivity of the biota. The magnitude of this productivity and its inter-annual variability is at present not well known, but new production rates are significantly higher than in adjacent fjords and on the Barents Sea shelf. They are probably also higher than other shelves fringing the eastern North Atlantic which are not exposed to upwelling and eutrophication. The rates and forms of biological activity on the north Norwegian shelf directly reflect the overwhelming importance of physical forcing in this area.



The concentration and dynamics of nutrients and suspended biogenic matter at Nordvestbanken indicate:

- A high primary production as reflected in large scale NO_3 reduction over the shelf, suggesting new production rates $> 75 \text{ g C m}^{-2} \text{ y}^{-1}$.
- Despite a high new production rate no major spring bloom as reflected by large scale accumulation of chlorophyll *a* is recorded.
- Low chlorophyll *a* concentrations and relative high phaeopigment and POC concentrations suggest extensive grazing and degradation of phytoplankton.
- About 1/3 of the phytoplankton carbon produced may be due to diatoms.

REFERENCES

- Ådlandsvik B, Loeng H. 1991. A study of the climatic system in the Barents Sea. *Polar Research* 10:45-49.
- Andreassen IJ, Wassmann P, Ratkova TN. 1999. Seasonal variation of vertical flux of phytoplankton and biogenic matter at Nordvestbanken, north Norwegian shelf in 1994. *Sarsia* 84:227-238.
- Babichenko S, Poryvkina L, Arikese V, Kaitala S, Kuosa H. 1993. Remote sensing of phytoplankton using laser induced fluorescence. *Remote Sensing of the Environment* 45:43-50.
- Babichenko S, Wassmann P, Poryvkina L, Andreassen IJ. 1999. Small time and spatial scale variability of phytoplankton biomass on the north Norwegian shelf in 1995. *Sarsia* 84:293-302.
- Biscaye PE, Anderson RF. 1994. Fluxes of particulate matter on the slope of the southern Middle Atlantic Bight: SEEP-II. *Deep-Sea Research* 41:459-509.
- Blindheim J, Loeng H. 1981. On the variability of Atlantic influence in the Norwegian and Barents Sea. *Fiskeridirektoratets Skrifter Serie Havundersøkelser* 17:161-189.
- Braarud T, Gaarder KR, Nordly O. 1958. Seasonal changes in the phytoplankton at various points off the Norwegian west coast. *Fiskeridirektoratets Skrifter Serie Havundersøkelser* 12:1-77.
- Dagg M. 1993. Grazing by the copepod community does not control phytoplankton production in the Subarctic Pacific Ocean. *Progress in Oceanography* 32:163-183.
- Dam HG, Roman MR, Youngbluth MI. 1995. Downward export of respiratory carbon and dissolved inorganic nitrogen by diel-migrating mesozooplankton at the JGOFS Bermuda time-series station. *Deep-Sea Research* 42:1187-1197.
- Eilertsen HC. 1993. Spring blooms and stratification. *Nature* 363:24.
- Eilertsen HC, Taasen JP. 1984. Investigations on the plankton community of Balsfjorden, northern Norway. The phytoplankton 1976-1978. Environmental factors, dynamics of growth and primary production. *Sarsia* 69:1-15.
- Eppley RW. 1989. New production: History, methods and problems. In: Berger WH, Smetacek VS, Wefer G, editors. *Productivity of the ocean: present and past*. New York: John Wiley & Sons Ltd. p. 85-97.
- Evensen A. 1994. *Planteplankton i Barentshavet: Artssammensetning og suksesjon. Regionale variasjoner i vår-oppblomstringen relatert til miljø* [Cand.scient. thesis]. Tromsø, Norway: University of Tromsø. 137 p.
- Falkenhaus T. 1997. *Studies of spatio-temporal variations in a zooplankton community* [PhD thesis]. Tromsø, Norway: University of Tromsø. 46 p.
- Froneman P, Perissinotto R. 1996. Microzooplankton grazing in the Southern Ocean: Implications for the carbon cycle. *Pubblicazioni delle Stazione Zoologica di Napoli I, Marine Ecology* 17:99-115.
- Frost BW. 1987. Grazing control of phytoplankton stock in the open subarctic ocean: a model assessing the role of meso-zooplankton, particularly the large calanoid copepods *Neocalanus* spp. *Marine Ecology Progress Series* 39:49-68.
- Halldal P. 1953. Phytoplankton investigations from weather ship M in the Norwegian Sea, 1948-49. *Hvalrådets Skrifter* 38:1-91.
- Halvorsen E, Tande KS. 1999. Physical and biological factors influencing the seasonal variation in distribution of zooplankton across the shelf at Nordvestbanken, northern Norway, 1994. *Sarsia* 84:279-292.
- Hegseth E, Svendsen H, Quillfeldt CH von. 1995. Phytoplankton in fjords and coastal waters of northern Norway: environmental conditions and dynamics of the spring bloom. In: Skjoldal HR, Hopkins C, Erikstad KE, Leinaas HP, editors. *Ecology of fjords and coastal waters*. Amsterdam: Elsevier Science. p 45-72.

ACKNOWLEDGEMENTS

The assistance of the crew of R/V *Jan Mayen* is gratefully acknowledged. Chrisje van Ek, Lena Hansen and Frida Tønning helped during the cruises. Jane Strømstad analysed the nutrient samples. The skilful and dedicated expertise of Sigrd Øygarden during the cruises and in particular in the laboratory contributed to the success of this investigation. Comments by H. Dam and an anonymous referee are gratefully acknowledged. This work was supported by the Research Council of Norway (project no. 101323/410 and 108085/122) and the European Union in the framework of the MAST programme, contract no. MAS2-CT93-0069 and MAS3-CT96-0056 (Ocean Margin EXchange - OMEX).



- Hewes CH, Sakshaug E, Reid FMH, Holm-Hansen O. 1990. Microbial autotrophic and heterotrophic eukaryotes in Antarctic waters: relationships between biomass and chlorophyll, adenosine triphosphate and particulate organic carbon. *Marine Ecology Progress Series* 63:27-35.
- Holm-Hansen O, Lorenzen CJ, Holmes RW, Strickland JDH. 1965. Fluorometric determination of chlorophyll. *Journal du Conseil International pour l'Exploration de la Mer* 30:3-15.
- Holm-Hansen O, Riemann B. 1978. Chlorophyll determination: improvement of the in methodology. *Oikos* 30:3-15.
- Hopkins CCE, Grotnes PE, Eliassen J-E. 1989. Organisation of a fjord community at 70° north: The pelagic food web in Balsfjord, northern Norway. *Rapports et Procès-Verbaux des Réunions Conseil permanent International pour l'Exploration de la Mer* 188:146-153.
- Huthnance JM. 1995. Circulation, exchange and water masses at the ocean margin: the role of physical processes at the shelf edge. *Progress in Oceanography* 35:353-431.
- Iverson R. 1991. Control of fish production. *Limnology and Oceanography* 35:1593-1604.
- Jahnke RA, Reimers C, Craven DB. 1990. Intensification of recycling of organic matter at the sea floor near the ocean margins. *Nature* 348:50-55.
- Lie U. 1968. Variation in the quantity of zooplankton and propagation of *C. finmarchicus* at station M in the Norwegian Sea 1959-66. *Fiskeridirektoratets Skrifter Serie Havundersøkelser* 14:121-128.
- Longhurst AR. 1995. Seasonal cycles of pelagic production and consumption. *Progress in Oceanography* 36:77-167.
- Mantoura RFC, Martin J-M, Wollast R, editors. 1991. *Ocean Margin Processes in Global Change*. Chichester: John Wiley & Sons. 469 p.
- Midttun L, Loeng H. 1987. Climatic variations in the Barents Sea. In: Loeng H, editor. *The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea*. Proceedings 3rd Soviet-Norwegian Symposium; Institute of Marine Research, Bergen, Norway. p 13-27.
- Minas HJ, Minas M, Packard TT. 1986. Productivity in upwelling areas deduced from hydrographic and chemical fields. *Limnology and Oceanography* 31:1180-1204.
- Monaco A, Biscaye PE, Soyer J, Pocklington R, Heussner S. 1990. Particle fluxes and ecosystem response on a continental margin: the 1985-1988 Mediterranean ECOMARGE experiment. *Continental Shelf Research* 10:809-839.
- Moseidjord H, Svendsen H, Slagstad D. 1999. Sensitivity studies of circulation and ocean-shelf exchange off northern Norway. *Sarsia* 84:191-198.
- Nordby E, Tande KS, Svendsen H, Slagstad D. 1999. Oceanography and fluorescence at the shelf break off the north Norwegian coast (69°20'N-70°30'N) during the main productive period in 1994. *Sarsia* 84:175-189.
- Peinert R. 1986. Production, grazing and sedimentation in the Norwegian Coastal Current. In: Skreslet S, editor. *The role of freshwater outflow in coastal marine ecosystems*. NATO ASI Series, Vol G7. Berlin: Springer Verlag. p 361-374.
- Peinert R, Bathmann U, Bodungen B von, Noji TT. 1987. The impact of grazing on spring phytoplankton growth and sedimentation in the Norwegian Current. In: Degens ET, Izdar EI, Honjo S, editors. *Particle flux in the ocean*. Mitteilungen des Geologisch-Paläontologischen Instituts der Universität Hamburg, Sonderband 62, SCOPE/UNEP. p 149-164.
- Ratkova TN, Wassmann P, Verity PG, Andreassen IJ. 1999. Abundance and biomass of pico-, nano-, and microplankton on a transect across Nordvestbanken, north Norwegian shelf, in 1994. *Sarsia* 84:213-225.
- Reigstad M, Wassmann P. 1995. The importance of advection for the pelagic-benthic coupling in north Norwegian fjords. *Sarsia* 80:245-257.
- Rey F. 1981a. Primary production estimates in the Norwegian Coastal Current between 62°N and 72°N. In: Sætre R, Mork M, editors. *The Norwegian Coastal Current*. University of Bergen. p 640-648.
- Rey F. 1981b. The development of the spring phytoplankton outburst at selected sites off the Norwegian coast. In: Sætre R, Mork M, editors. *The Norwegian Coastal Current*. University of Bergen. p 649-680.
- Riebesell U, Reigstad M, Wassmann P, Passow U, Noji T. 1995. On the trophic fate of *Phaeocystis pouchetii*. VI. Significance of *Phaeocystis*-derived mucus for vertical flux. *Netherlands Journal of Sea Research* 33:193-203.
- Sætre R, Aure J, Ljøen R. 1988. Wind effects on the lateral extension of the Norwegian Coastal Water. *Continental Shelf Research* 8:239-253.
- Sætre R, Mork M. 1981. *The Norwegian Coastal Current*. University of Bergen. 795 p.
- Sakshaug E, Rey F, Slagstad D. 1995. Wind forcing of marine primary production in the Northern atmospheric low-pressure belt. In: Skjoldal HR, Hopkins C, Erikstad KE, Leinaas HP, editors. *Ecology of fjords and Coastal Waters*. Amsterdam: Elsevier. p 5-25.
- Skjoldal HR, Rey F. 1989. Pelagic production and variability of the Barents Sea ecosystem. In: Sherman K, Alexander LM, editors. *Biomass and geography of large marine ecosystems*. Boulder, CO: Westview Press. p 243-283.
- Slagstad D, Tande KS, Wassmann P. 1999. Modelled carbon fluxes as validated by field data on the north Norwegian shelf during the productive period in 1994. *Sarsia* 84:303-317.
- Sundby S. 1984. Influence of bottom topography on the circulation at the continental shelf of northern Norway. *Fiskeridirektoratets Skrifter Serie Havundersøkelser* 17:501-519.
- Sverdrup HU. 1953. On conditions for the vernal blooming of phytoplankton. *Journal du Conseil International pour l'Exploration de la Mer* 18:287-295.



- Tande KS. 1991. *Calanus* in high latitude environments. *Polar Research* 10:389-407.
- Townsend DW, Keller MD, Sieracki ME, Ackelson SG. 1992. Spring phytoplankton blooms in the absence of vertical water column stratification. *Nature* 360:59-62.
- Urban-Rich J, Nordby E, Andreassen IJ, Wassmann P. 1999. Contribution by mesozooplankton fecal pellets to the carbon flux on Nordvestbanken, north Norwegian shelf in 1994. *Sarsia* 84:253-264.
- Verity PG, Smayda TJ, Sakshaug E. 1991. Photosynthesis, excretion, and growth rates of *Phaeocystis* colonies and solitary cells. *Polar Research* 10:117-128.
- Verity PG, Wassmann P, Ratkova TN, Andreassen IJ, Nordby E. 1999. Seasonal patterns in composition and biomass of autotrophic and heterotrophic nano- and microplankton communities on the north Norwegian shelf. *Sarsia* 84:265-277.
- Walsh JJ. 1988. *On the Nature of Continental Shelves*. Academic Press Inc. 520 p.
- Walsh JJ. 1991. Importance of continental margins in the marine biogeochemical cycling of carbon and nitrogen. *Nature* 350:53-55.
- Wassmann P. 1991. Sampling and analysis of marine particles with PEBENOCO (Pelagic-Benthic Coupling in the Norwegian Coastal Zone), University of Tromsø, Norway. In: Hurd DC, Spencer DW, editors. *Marine Particles: Analysis and Characterization*. Geophysical Monograph 63. p 97-99.
- Wassmann P, Hansen L, Andreassen IJ, Wexels Riser C, Urban-Rich J. 1999a. Distribution and sedimentation of faecal pellets on the Nordvestbanken shelf, northern Norway, in 1994. *Sarsia* 84:239-252.
- Wassmann P, Ratkova TN, Andreassen IJ, Vernet M, Pedersen G, Rey F. 1999b. Spring bloom development in the marginal ice zone and the central Barents Sea. *Pubblicazioni delle Stazioni Zoologiche di Napoli I, Marine Ecology*. (in press)
- Wassmann P, Slagstad D. 1995. Drift patterns of sinking particles in the north Norwegian coastal zone. In: Floderus S, Heiskanen A-S, Olesen M, Wassmann P, editors. *Sediment trap studies in the Nordic countries* 3. Nurmi-järvi, Finland: NurmiPrint OY. p 52-69.
- Wassmann P, Svendsen H, Keck A, Reigstad M. 1996. Selected aspects of the physical oceanography and particle fluxes in fjords of northern Norway. *Journal of Marine Systems* 8:53-71.
- Wollast R, Mackenzie FT, Chou L. 1993. *Interactions of C, N, P and S Biogeochemical Cycles and Global Change*. NATO ASI Series, Vol. 14, Berlin: Springer-Verlag. 521 p.

Accepted 30 July 1998 – Printed 15 November 1999
Editorial responsibility: Tore Høisæter