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# Variations in hydrography, nutrients and chlorophyll *a* in the marginal ice-zone and the central Barents Sea

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#### Abstract

The project "Climatic variability and vertical carbon flux in the marginal ice zone in the central Barents Sea" was initiated to fill some of the gaps in our knowledge on the biological processes related to the dynamic hydrography in the Barents Sea. A previously modelled transect from the Atlantic waters, crossing the Polar Front into the Arctic waters and the MIZ in the central Barents Sea, was investigated to cover the zonal structure and different water masses. The present paper describes the hydrography, nutrients and Chl a distribution in March, May 1998 and July 1999 along this transect. Based on the nutrient consumption, the new production is estimated and discussed as related to topography, water masses and climate change. Atlantic water dominated in south with a Polar Front shaped by the bank topography, and water with more Arctic characteristics in north. A high, uniform nutrient regime in March was depleted giving a spring bloom in May with Chl a accumulation < 100 m in the Atlantic dominated region. The phytoplankton biomass was concentrated in the upper 30 m in the strongly stratified MIZ. The new production estimates for the period ranged 30-80 g C m<sup>-2</sup> (0.5-1.4 g C m<sup>-2</sup> day<sup>-1</sup>). New production rates were closely related to the mixing depth with highest rates in the deeper mixed Atlantic region and trenches where the Polar Front was located. Non-Si demanding species were more important for new production in the deeper mixed regions. Seasonal changes from May to July was most likely masked by interannual variations as the July cruise took place the following year, characterised as a warmer year than 1998 in the Barents Sea due to increased Atlantic inflow in 1999 A locally produced cold but saline water mass observed on Sentralbanken in March and May resulting from the freezing process in the waters above the bank was replaced by warmer waters in July and the strongly stratified MIZ was pushed further north. Interannually variable hydrographic regimes in different regions influence the new production and the biological community in the Barents Sea. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Barents Sea; Marginal ice zone; Hydrography; Nutrients; Chlorophyll a; New production; Seasonal and interannual variability

### 1. Introduction

The Barents Sea is a productive high-latitude marine ecosystem characterised by a relatively shallow shelf and a complex hydrography (Loeng, 1991; Loeng et al., 1997). The inflow and mixing of warm

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Atlantic with cold Arctic waters and a seasonally and interannually variable ice-cover, makes this a highly variable environment sensitive to climate. A climate change is expected to influence the inflow of Atlantic water into the Barents Sea and the ice cover through changes in the large scale thermohaline circulation or regional intensity and pathways of low pressures (Ådlandsvik and Loeng, 1991; Sakshaug et al., 1994). Knowledge of how primary productivity and carbon flux is influenced by different physical conditions through different seasons is therefore crucial to understand and model the possible effects of climate change which is expected to be prominent in the Arctic.

North of the Norwegian Coastal Current, Atlantic water from the north-east flowing branch of the North Atlantic Current (NAC) dominates the southern Barents Sea. The warm, north-east flowing Atlantic waters meet cold Arctic waters flowing south-west and gives rise to the Polar Front in the central Barents Sea. The north-eastern part of the Barents Sea is seasonally ice-covered. The primary production in the Barents Sea, as in all high latitude ecosystems, is strongly subjected to physical forces. Different physical conditions like ice cover, low pressure passage, mixing depth and the temperature of Atlantic and Arctic water as well as the structure, position and dynamics of frontal systems and the marginal ice zone, makes the Barents Sea a heterogeneous and dynamic system.

In the north, the annual production is initiated by the strong stratification developing as the ice melts and light becomes available. At the same time nutrients are rapidly depleted in the stratified waters due to low supply from deeper and more nutrient rich waters. New production in the Marginal Ice Zone (MIZ) is therefore high, but highly seasonal close to the ice edge, and lower in the nutrient depleted melt water in the southern part of the MIZ where a deep chlorophyll maximum layer develops. A major phytoplankton bloom can thus be observed close to the ice edge as the ice recedes north in late spring and summer. In the Atlantic waters stratification is close to absent in spring, and a weak stratification develops slowly from solar radiation during the course of summer. The bloom seen in Atlantic waters is therefore often weaker in terms of phytoplankton biomass present (in terms of concentrations) compared to the

MIZ due to the deeper mixing depth and the resulting deep excursion of phytoplankton cells (Wassmann et al., 1999b). However, the deeper mixing in these waters results in a steady supply of nutrients to the upper layer, and consequently the new production can be higher here (per surface area) compared to the more stratified and less mixed Arctic water (Slagstad and Wassmann, 1997; Wassmann et al., 1999b).

The phytoplankton productivity in the Barents Sea is thus strongly related to the variable physical environment determined by ice cover, wind induced vertical mixing, melting area and relative distribution of Atlantic and Arctic water (e.g. Sakshaug and Slagstad, 1991; Sakshaug et al., 1995). The ice-cover in the Barents Sea depends on the inflow of warm Atlantic water, related to the interannually variable NAO-index (Vinje in Falk-Petersen et al., 2000). Years with low Atlantic inflow give rise to increased ice-cover, and model simulation has shown that high ice-cover results in lower productivity and vertical carbon flux the following year (Slagstad and Wassmann, 1997). The complicated interplay between physics and biology requires integrated model simulations with relatively high spatial resolution of the physical processes involved and a detailed biological model. As the interannual variability is known to be high, investigations giving comparable data on the relation between the physics and the biological processes over several years are essential to validate and improve existing models.

The project "Climatic variability and vertical carbon flux in the marginal ice zone in the central Barents Sea" under the Norwegian Research Council ALV program was initiated to fill some of the gaps in our knowledge on the biological processes related to the dynamic hydrography in the Barents Sea. These gaps emerged when the first generation of 2-D and 3-D models were developed and validated (Wassmann and Slagstad, 1993; Slagstad and Wassmann, 1997) on the base of knowledge developed from the PRO MARE program (Sakshaug et al., 1991). A previously modelled transect from the Atlantic waters, crossing the Polar Front into the Arctic waters and the MIZ in the central Barents Sea (Wassmann and Slagstad, 1993) was investigated to cover the zonal structure and different water masses. Three cruises during different seasons provided information on the seasonal development of the pelagic and pelagic-benthic coupling. The chosen transect is similar to a previously investigated transect (Skjoldal et al., 1987; Wassmann and Slagstad, 1993; Wassmann et al., 1999b) which allows interannual comparison. The present paper describes the hydrography, nutrients and Chl *a* distribution in winter, spring and summer along this transect. Based on the nutrient consumption, the new production is estimated and discussed as

related to topography, water masses and climate change. This paper provides the hydrographic basis for contributions deriving from the same expedition which focus on the biological processes related to the hydrography (e.g. phytoplankton (Ratkova and Wassmann, 2002), zooplankton (Arashkevich et al., 2002; Pasternak et al., 2002; Sato et al., 2002; Verity et al., 2002; Wexels Riser et al., 2002), microbial cycling

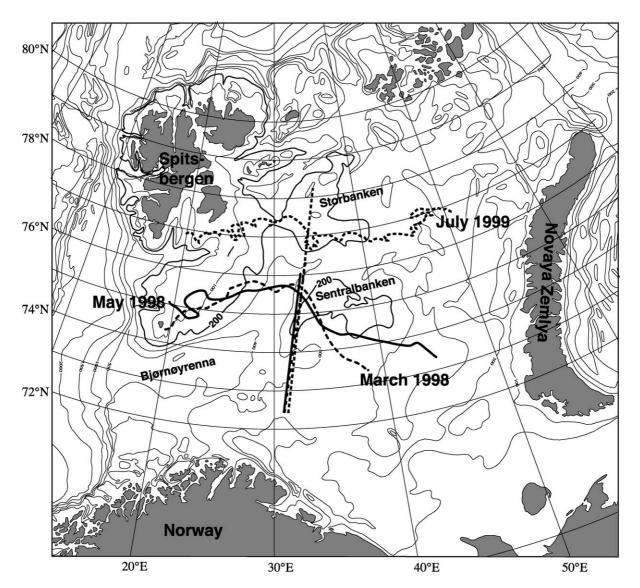


Fig. 1. The investigation area in the central Barents Sea and the investigated transects and ice edge locations during three cruises in March 1998, May 1998, and July 1999. Sentralbanken and Storbanken are indicated by the bold 200 m isobath.

(Allen et al., 2002; Howard-Jones et al., 2002), vertical flux regulation (Olli et al., 2002) and  $CO_2$  dynamics (Kaltin et al., 2002)).

#### 2. Material and methods

Data were collected along a transect during three cruises with R/V "Jan Mayen" to the MIZ and central

Barents Sea in March 1998 (17–19 March), May 1998 (18–20 May) and June/July 1999 (29 June–1 July, named July cruise in the text). The start point for the transect was the same every cruise (72°30′ N, 30°59′ E), and stations were sampled for hydrographical data (CTD), Chlorophyll a (Chl a) and nutrients every 20 nautical mile towards the north into the icecovered region. The winter cruise in March included 13 stations (northern most station at 76°23′ N,

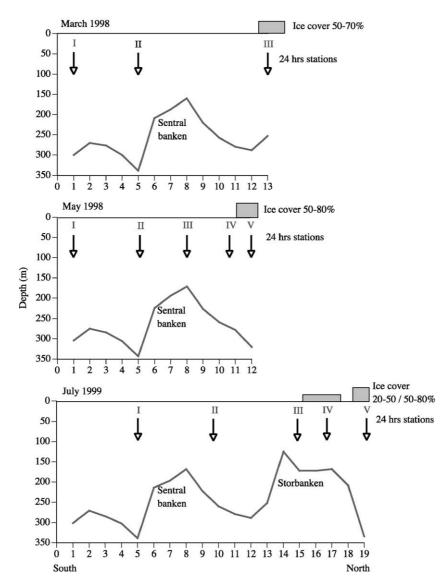


Fig. 2. Topography and ice cover along the investigated transect in the central Barents Sea in March and May 1998 and July 1999. Transect stations (x-axis) as well as the 24-h stations (roman numbers) are shown.

33°20′ E), the spring cruise included 12 stations (northern most station at 76°04′ N, 32°51′ E) and the summer cruise covered 19 stations (northern most station at 78°12′ N, 34°31′ E) due to the receded icecover and reduced ice-thickness. Twenty-four-hour stations for detailed biological process studies on phytoplankton and zooplankton (published elsewhere in this volume) were sampled along the same transect on the return from north to south. The investigation area with the transect and the ice distribution during the three cruises are shown at Fig. 1. The transect crossed the eastern edge of the Central Bank in March and May, and in July, also the Great Bank. The topography and the ice-cover (based on visual observations from the ship as well as satellite based information from the US National Ice Center (NIC); (www.natice.noaa.gov/) the transect stations (1-13/12/19 in March, May and July, respectively) and the 24-h stations are indicated in Fig. 2.

Standard hydrographic sampling was carried out with a Seabird CTD profiler mounted with a General Oceanic Rosette Sampler equipped with 5-l Niskin bottles. Water samples for analysis of nutrients and suspended pigments were obtained from 11 fixed depths (0, 10, 20, 30, 40, 50, 75, 90, 120, 150 and 200 m) or as deep as the station depth allowed sampling. Methods for analysis of nutrients and Chl *a* are described in Wassmann et al. (1990) and Wassmann (1991).

#### 3. Results

#### 3.1. Hydrography

The southern part of the investigated transect was characterised by Atlantic water. In March 1998, the temperatures were 2–3 °C in the surface layer and throughout the water column above the trenches (Fig. 3a). Salinities >34.9 were measured through the entire well mixed water column. On the Sentralbanken further north, cold but relatively saline waters (temperatures below 0 °C and salinity of 34.8–34.9) were found below 100 m, with cooled Atlantic waters characterised by higher temperature and salinity in the upper water column. In March, dense Sentralbanken water could be observed on the bank and the Polar Front was present on both sides of the Sentral-

banken as the topography allowed Atlantic water to enter the transect area through the deeper trenches on the northern and southern side (Fig. 3a). South of the bank, the front area (indicated by a well mixed water column) was observed around station 6. North of the bank, the front was tilted and laid below the typical Arctic waters observed in the surface. Cooled Atlantic water characterised the tilted front with dense Sentralbanken water in the deep layer. The deeper water was probably locally formed water with increased salinity resulting from freezing processes in the surface (cold, but with salinity of 39.8–35). The significant impact of Atlantic water in this area resulted from the trench north of Sentralbanken which allowed Atlantic waters to enter the area.

In May, 2 months later, the hydrographic profiles confirmed the pattern observed in March with Atlantic water in south, a meandering Polar front following the topography given by the trenches south and north of Sentralbanken (Fig. 3b). Cold, but relatively saline water (temperature < 0 °C, salinity of 34.8–34.9) was still dominating at depth on Sentralbanken. A developing spring situation was indicated by a weakly developed thermal stratification in Atlantic waters, and a stronger halocline from Sentralbanken and further north caused by melt water and Arctic water. The Arctic water region had moved south to Sentralbanken and was met at station 7.

In early July, the stratification in Atlantic waters had increased further with surface temperatures of 5–6 °C above 50 m depth (Fig. 3c). The deeper waters were warmer and more saline (temperature>3 °C and salinity>35) compared to the March and May scenarios. The cold and saline water mass observed on Sentralbanken in March and May was also warmer and more saline, indicating a stronger Atlantic influence. The Polar Front was pushed north to Storbanken, and Arctic water with temperatures below zero and salinities below 34.8 was only observed from Storbanken and further north. The surface waters in the northern part of the transect were still characterised by a strong melt water induced stratification down to 30 m.

#### 3.2. Nutrients

The nutrient concentrations measured in mid March 1998 were high and rather uniform at all depths along the transect (Fig. 4a). We assumed that they represent true winter concentrations at a time where no consumption had taken place. The total NO<sub>3</sub> and Si(OH)<sub>2</sub> depletion in May 1998 and July 1999 was calculated based on these concentrations. The C-equivalent of the NO<sub>3</sub> depletion (an approximation of new production) was calculated applying the Redfield ratio. Depletion of silicate (Si(OH)<sub>2</sub>) relative to nitrate

(NO<sub>3</sub>) can indicate whether the main consumers are silicate requiring groups such as diatoms.

The distribution of nutrients showed similarities to the hydrographic conditions through out the seasons. The nutrient concentrations confirmed that March represented a winter situation in the central Barents Sea and the MIZ. Nitrate, phosphate and silicate were >10.4, 0.75 and 4.5 µM, respectively, and were

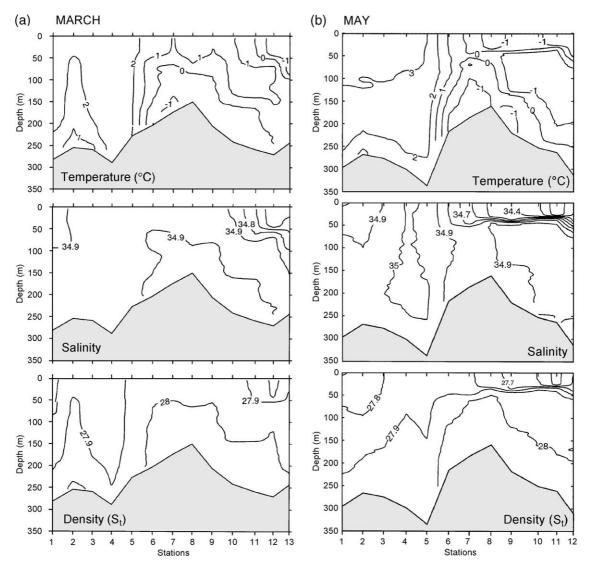


Fig. 3. Hydrography from the central Barents Sea to the marginal ice-zone in March (a), May 1998 (b), and July 1999 (c) showing temperature (°C), salinity and density (sigma t) from upper to lower panel. Topography is indicated.

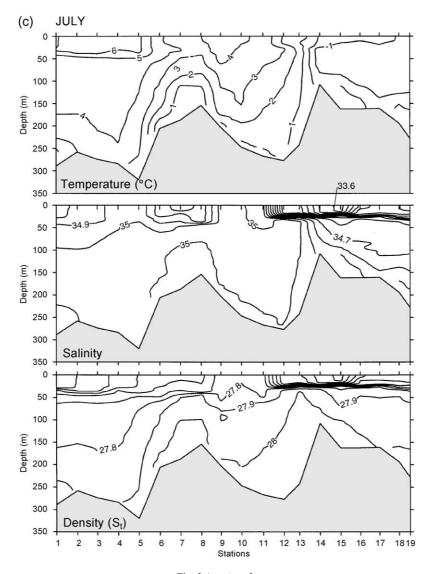


Fig. 3 (continued).

homogeneously distributed throughout the water column (Fig. 4a). No decrease in the upper layers, indicating phytoplankton production, was recorded. A nitrate versus silicate plot confirmed the homogeneity of nutrients along the transect reflecting that hardly any nutrients had been consumed by mid March (Fig. 5).

In May, the nutrient concentrations reflected a spring situation with depleted nitrate and phosphate concentrations in the surface waters along the entire transect (Fig. 4b). In the Atlantic waters, the depletion indicated deep mixing, as nutrients were reduced down to 100 m depth. In the melt water area, stratification was stronger and limited the mixing to the upper 30–40 m. This resulted in a stronger depletion of nutrients in the upper layer of Arctic compared to Atlantic waters. Higher nutrient concentrations in the MIZ compared to the melt water zone further south, indicated pre-bloom conditions at the ice edge in May. The topographic

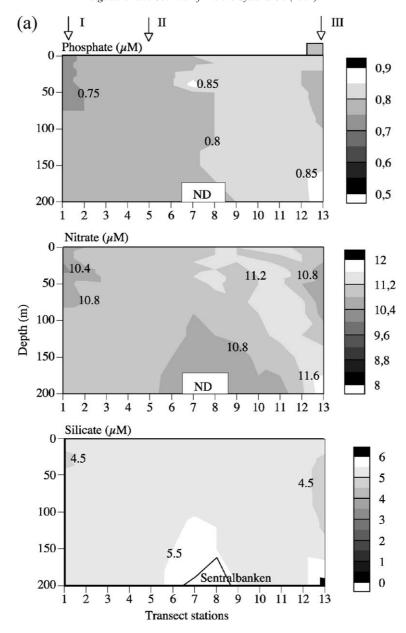


Fig. 4. Nutrient distribution ( $\mu$ M) from the central Barents Sea to the marginal ice-zone in March (a) and May (b) 1998 and July 1999 (c). Phosphate (PO<sub>4</sub>), nitrate (NO<sub>3</sub>) and (c) silicate (Si(OH)<sub>2</sub>) is shown from upper to lower panel, respectively. Topography above 200 m depth is indicated (black line) at the lower panel.

impact on nutrient distribution caused by differences in the mixing regime was demonstrated at the trench south of Sentralbanken (Fig. 4b, station 5). Here, vertical hydrographic profiles and a more homogenous nutrient distribution indicated strong and deep mixing.

Phosphate, nitrate and silicate were depleted in a similar, linear pattern on Sentralbanken and further

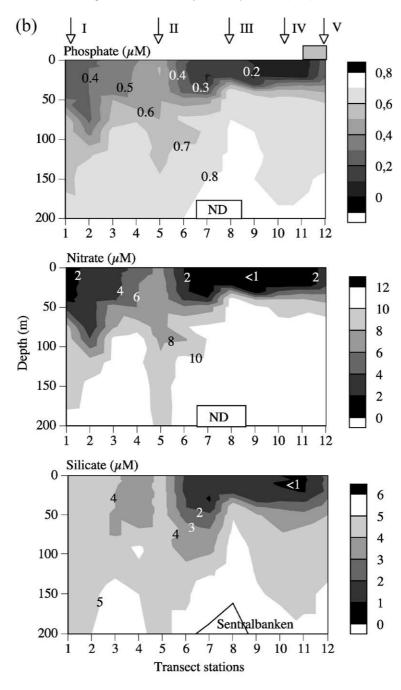


Fig. 4 (continued).

north, where the mixing depth was limited (Figs. 4b and 5). A contrasting, sigmoid depletion pattern was observed in the deeper mixed Atlantic waters, where

high silicate  $(3-5 \,\mu\text{M})$  and low nitrate and phosphate concentrations indicated low Si-consumption compared to the nitrate and phosphate uptake (Fig. 5,

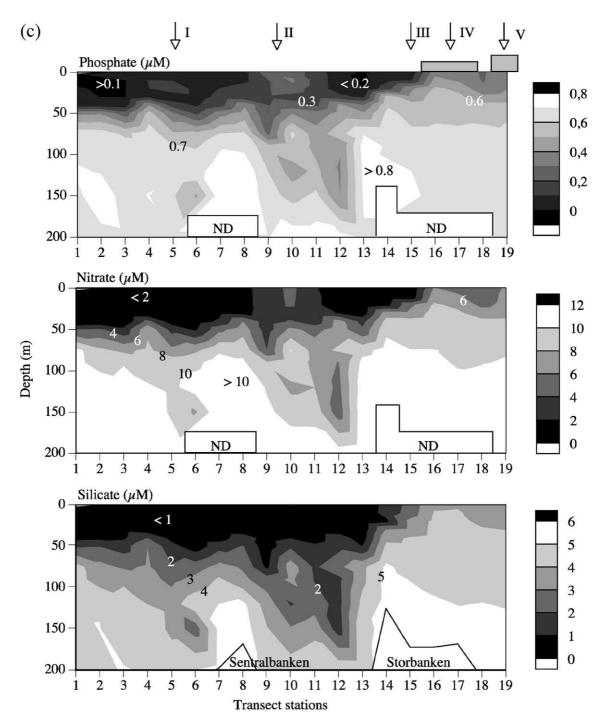
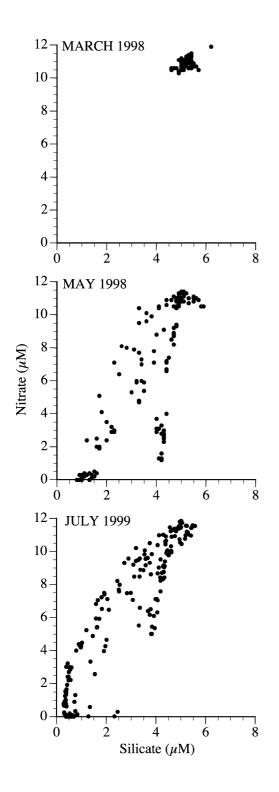


Fig. 4 (continued).



phosphate not shown). Silicate requiring algae may thus be more important in the stratified Arctic waters compared to the deeper mixed Atlantic water in May 1998.

In July 1999, all nutrients were strongly depleted in the surface waters in the Atlantic as well as the Arctic waters and up to the MIZ with concentrations mainly below 2, 0.2 and 1  $\mu$ M for nitrate, phosphate and silicate, respectively (Fig. 4c). The mixing depth in the Atlantic water (about 50 m) still exceeded that of the melt water area mixing depth (about 30 m). Higher nutrient concentrations in the northern marginal ice zone (stations 17–19) indicated an early stage of the bloom at the ice edge. The nitrate versus silicate plot for July shows similarities with that from May (Fig. 5). Again, stations characterised by low relative Si consumption were found.

#### 3.3. Pigments

The distribution of Chl a along the transect supported the fact that March represented a winter situation in the central Barents Sea and the MIZ (Fig. 6). The concentration of Chl a was very low ( $\leq$  0.04) at all stations and depths. Slightly higher concentrations close to the ice edge where a weak stratification appeared (station 11) could suggest some production, but such a low biomass was not reflected in the nutrient concentration.

High Chl a concentrations (6–14 mg m<sup>-3</sup>) along the entire transect during the spring cruise confirmed a spring bloom scenario in May. The pigment distribution reflected the hydrography and mixing regime which also were reflected in the nutrient distribution along the transect. Increased Chl a concentrations were recorded down to 100 m in the Atlantic region, to 150 m in the trench, and to 40 m only in the stratified melt water region. The highest Chl a concentrations were measured in the area with shallow mixing.

The pigment distribution in July reflected a summer situation with decreased Chl *a* concentrations indicating low algal biomass along the entire transect.

Fig. 5. Nitrate (NO<sub>3</sub>) versus silicate (Si(OH)<sub>2</sub>) concentrations ( $\mu$ M) in the central Barents Sea. Data from all stations and depths (0–200 m are included). Note the indications of nitrate depletion by non Siconsuming taxa (probably mass proliferation of *P. pouchetii*) at silicate concentrations about 4  $\mu$ M.

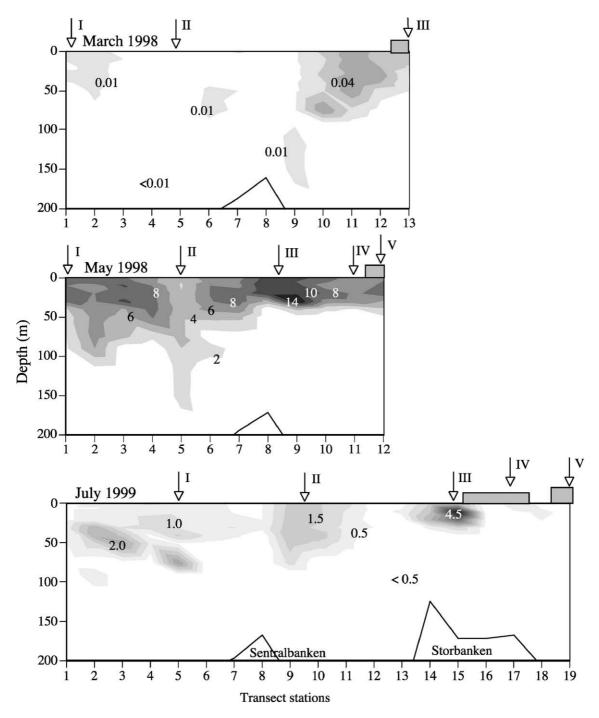


Fig. 6. Suspended chlorophyll a concentrations (mg Chl a m $^{-3}$ ) in the central Barents Sea and the marginal ice-zone in March and May 1998 and July 1999. Topography above 200 m is indicated (black line) along the x-axis.

In the Atlantic region, a deep maximum concentration of 2 mg Chl a m<sup>-3</sup> was measured at 50 m depth. The highest Chl a concentration along the transect in July was located just at the ice edge (4.5 mg Chl a m<sup>-3</sup>) reflecting an ice-edge bloom, while those under the ice were low and decreased towards the north.

#### 4. Discussion

The Barents Sea is an advective shelf system where warm Atlantic and cold Arctic waters meet and interact. The mosaic pattern of water masses and resulting hydrographic development is therefore suitable for an evaluation of how physical conditions can influence biological production during the productive season. These patterns depend on the topography, the inflow and distribution of Atlantic water as well as temperature and wind conditions, important for the ice distribution. Knowledge about how the plankton community is influenced by the physical conditions in the Atlantic relative to the Arctic regions and the MIZ is thus of outmost importance in order to comprehend how the Barents Sea productivity will respond to a climate change. The estimation of new production based on nutrient depletion gives the upper limit of the carbon export from the system (Dugdale and Goering, 1967; Eppley and Peterson, 1979), either through vertical export or harvestable resources. After an evaluation of the hydrographic, hydrochemical and hydrobiological conditions we attempt to approximate the new production by investigating the nitrate depletion.

#### 4.1. Ice distribution

The ice cover in the Barents Sea is at its maximum in late April and its minimum is normally in August. The seasonal and spatial variation is extensive, but can be exceeded by the major interannual variations observed (Vinje and Kvambekk, 1991). Ice can be transported into the Barents Sea from the Kara Sea and Arctic Ocean driven by north-easterly winds. South-westerly winds tend to push and pack the ice into a north-easterly direction, and the prevailing wind fields are thus important in determining the ice distribution, ice thickness and ice edge position.

The ice distribution in 1998, the year of the March and May cruise, corresponded to a normal/intermediate year. The ice edge was localised at just north of 76°N 32°E in mid May, and according to Vinje and Kvambekk (1991) the probability of this position in late April is close to 50%. Our July cruise took place in 1999, and the ice cover this year was significantly less compared to the same period the previous year (NIC; http://www.natice.noaa.gov/). The development and changes in hydrography and productivity on the different stations along the transect from March to July can thus not be regarded exclusively as a seasonal development, but represent also differences between years with more or less ice. Model simulations by Slagstad and Wassmann (1997) suggest up to 30% higher primary production and vertical export in years with decadal minimum ice coverage.

### 4.2. Seasonally changing water mass characteristics or interannual variability in Atlantic Water inflow?

The main changes in the hydrographic characteristics seen from March and May to July were the increased stratification in Atlantic as well as Arctic waters. The increased Atlantic Water impact along the transect in July was also prominent. The stratification in the Atlantic waters is induced by solar radiation (Skjoldal and Rey, 1989). The stratification of the vertically well mixed Atlantic waters after the winter is slow and the mixing depth in May 1998 was about 50 m, as indicated by the Chl a and nutrient distribution. Similar mixing depths were observed in July 1999, but with a stronger temperature and density gradient compared to May. In the northern area influenced by ice cover and Arctic water, stratification results from ice melt and the mixing depth in these waters was about 30 m only. The water masses in the trenches south and north of Sentralbanken remained well mixed through all the investigated seasons. The meandering Polar Front, separating Atlantic waters from Arctic or locally produced water, was localised related to these trenches and the situation was seasonally independent. This is in accordance with a circulation pattern proposed by Gawarkiewicz and Plueddemann (1995) suggesting that Atlantic Water flowing into the western Barents Sea is divided into two branches by Sentralbanken and that the northern branch is recirculated back to the Norwegian Sea

following the 250 m isobath north—west of Sentralbanken. The recirculation manoeuvre will cause the deep mixed water-column observed in the trench region south and north of Sentralbanken.

This implies different mixing regimes in (a) Atlantic waters, (b) trench/Polar Front region and (c) the melt water/Arctic water region. The three regions are controlled by different stratification mechanisms which has implication for the phytoplankton community development and primary production.

The second main difference observed through the three cruises was the increased impact from Atlantic Water in the central Barents Sea in July 1999 compared to March and May 1998. It is reflected in the increased salinity in the intermediate and deeper water (below 50-100 m) south of Storbanken. The water on Sentralbanken was characterised by low temperature but relatively high salinity compared to true Arctic water in March and May 1998 (i.e. Loeng, 1991). Quadfasel et al. (1992) suggests that this water is locally produced water resulting from the freezing process releasing salt and increasing the density. This dense water mass will remain quite stationary on Sentralbanken due to the Taylor column induced by the bank (Cushman-Roisin, 1994). The bank and the Taylor column act as a barrier and split the inflowing Atlantic water and prevent inflow on the bank. The cold and less saline waters observed on Sentralbanken in May 1993 by Wassmann et al. (1999a) were probably not a back-meandering of the Polar Front, but locally formed and relatively isolated Sentralbank water. The Sentralbanken water, in March and May 1998 characterised as cold, saline water, should persist also during summer. However, during our cruise in July 1999 the deep-water observed on Sentralbanken was warmer (>0 °C) and had a stronger Atlantic character. This was probably the result of a higher inflow of Atlantic water registered in 1999 compared to 1998 (Anon., 2000). Quadfasel et al. (1992) have identified changed water mass characteristics on Sentralbanken to be an interannual rather than a seasonal feature. They (op cit.) found a similar change in the Sentralbanken water during a year with high inflow of Atlantic Water (1982) where the inflow removed the low salinity surface layer and thus limited the freezing process inducing the dense water formation. The saline and cold deep-water was not observed until 1986, after a few years with moderate to low inflow of Atlantic Water. Similarly, the ice edge was located north of Sentralbanken in spring 2000 (NIC; http://www.natice.noaa.gov/), reflecting limited ice formation on Sentralbanken the following winter. The changed water mass characteristic on Sentralbanken observed during the July 1999 cruise could thus reflect an interannual variation rather than a seasonal development. Reduced ice formation change the hydrographic regime on Sentralbanken from being part of the MIZ to a deeper mixed system, more characteristic for the Atlantic region, with the implications this has for the biological production.

#### 4.3. Bloom development

The algal biomass reflected the depletion of nutrients along the transect in winter and spring. The low algal biomass (indicated by Chl a) measured in March could have been caused by grazing or extensive mixing reducing the concentrations, but the high and uniform nutrient concentrations supports the assumption of a winter scenario.

In the middle of May, the nitrate concentrations were depleted below a level were diatoms have been found to dominate in south and the melt water region (2 μM) (Egge and Aksnes, 1992). Chl a concentrations reflected a strong bloom and accumulation of phytoplankton. For the Atlantic region, this contrasts the scenario observed in spring 1993 where Wassmann et al. (1999b) measured low Chl a concentrations (<2 µM) in the Atlantic region, while in the Arctic region and the Polar Front the Chl a concentrations were similar both years (12-14 and 2-5 mg m<sup>-3</sup>, respectively). A higher grazing pressure in 1993 could explain the low accumulation of alga that year, on the other side a greater nutrient depletion in May 1998 suggests that the bloom had started earlier during the present investigation.

In July, accumulation of alga was mainly observed at the ice edge. The ice edge bloom is a continuos bloom resulting from melting, increased light availability and thus results in high new production in the nutrient-rich water (Sakshaug and Slagstad, 1991). The high nutrient concentrations measured in the ice-covered waters indicate that light was too weak for a bloom to develop. The low biomass present south of the ice edge, in the melt water as well as the Atlantic waters, is typical for summer (Fig. 6). We can

assume that the production in this area is mainly based upon regenerated production. Only above the trench between Sentralbanken and Storbanken, where the stratification was weaker, higher nutrient concentration indicated that deeper mixing supplied new nutrients from the deeper waters. However, also here the chlorophyll concentrations were low, probably reflecting grazing.

## 4.4. New production: depletion depth, regional variability and important producers in spring

New production is a measure of the fraction of the primary production which is based on nutrients supplied from the deep waters during the extensive mixing in winter and/or through deep mixing during the productive season (Dugdale and Goering, 1967). The depletion of nitrate has been widely accepted as a measure of new production as the recycling from ammonium back to nitrate takes place at depth. At steady state the new production represents the maximum export out of the system (Eppley and Peterson, 1979). New production was calculated based on the depletion of nutrients down to the bottom at each station. Because vertical mixing above trenches indicate nutrient depletion below 100 m, there was a significant variability in the new production estimates along the transect. The nitrate based C-production from winter till mid May was estimated to around 80 g C m<sup>-2</sup> in Atlantic water at the two southernmost stations, and to about 40 g C m<sup>-2</sup> in Arctic water at stations 9-11 (Figs. 2 and 7). A comparison between the C-production based on NO<sub>3</sub>-depletion in the upper 80 m or to the bottom revealed that the high new production at stations 1, 2 and 5 (in south and above the trench) was due to depletion below 80 m depth (Fig. 7). At all other stations the carbon consumption was comparable, implying that the new production utilised nutrients from the upper 80 m. Less stratified waters with deeper mixing can thus have twice as high new production compared to more stratified waters like the melt water zone in the northern Barents Sea. Such a difference is in agreement with model simulations from the area by Sakshaug and Slagstad (1992).

C-production based on silicate compared to nitrate depletion was calculated to approximate the share of diatoms in new production. Silicate demanding producers such as diatoms cause approximately the same magnitude and a similar pattern of nitrate and silicate based production. Flagellates and the important spring haptophyte *Phaeocystis pouchetii* would in contrast only cause nitrate depletion. The estimates indicate that the Si-based C-production was low in the Atlantic region (10–16 g C m<sup>-2</sup>), higher in the melt water region and at the ice edge (23–27 and 19 g C m<sup>-2</sup>, respectively; Figs. 7, 8). They were highest on Sentralbanken (34 g C m<sup>-2</sup> at stations 6 and 7). The Si-based new production took place in the upper 80 m as the estimates for 0–80 m and 0–bottom depletion were similar.

Si-demanding groups such as diatoms were more important for the new production in the more stratified Arctic region compared to the Atlantic region in spring 1998. However, the new production in the Arctic region was lower compared to the deeper mixed Atlantic region and trench areas. The flagellated or colonial P. pouchetii and other non-Sidemanding flagellates not only comprised an important group for the new production in the central Barents Sea, but were the major producers in the waters mixed below 80 m depth in spring 1998. The phytoplankton communities clearly reflect our interpretation of Si- versus NO<sub>3</sub>-depletion along the transect as P. pouchetii biomass dominated in the south and diatom biomass in the MIZ (Ratkova and Wassmann, 2002). These results support the hypothesis suggesting that diatoms tend to dominate in stratified and shallow mixed waters, while P. pouchetii is a more successful competitor when the mixing is deeper (Reigstad, 2000; Sakshaug and Walsh, 2000).

## 4.5. Seasonal or interannual variation in new production: a comparison between May 1998 and July 1999

New production in boreal and arctic waters is assumed to be most important in spring, as the supply of new nutrients from depth is limited by the increasing stratification favouring regenerated production (Smetacek et al., 1984; Sakshaug, 1997; Wassmann, 1998). Our investigation in the central Barents Sea revealed that compared to the new production estimates from May 1998, when the ice cover was close to maximum (stations 1–12), about 40% (on average) of the new production estimated for the period March–July took place later than mid May (Fig. 8). This could

be possible as Kristiansen et al. (1994) found that a significant influx of nitrate to the euphotic zone support a moderately high nitrate consumption in open and close pack ice after the spring bloom. However, as the present estimation was based on data sampled in two different years, a difference in the winter concentrations of 10–20% would have a significant impact on the new production estimates. Such a difference is realistic as winter concentrations during the PRO MARE program was reported to be higher compared to the present results (12–14 and 10–12  $\mu$ M nitrate, respectively) (Sakshaug et al., 1992). Such variations can be caused by increased impact of Atlantic water, generally showing higher nitrate concentrations in winter compared to Arctic water. Increased nitrate concentrations to 12 µM in March (10–20% increase compared to 1998 levels) increases the new production estimate for May 1998 with 40%. Thus, it is difficult to estimate the 1999 summer new production based on the 1998 winter concentrations as the 2 years investigated differed with a stronger Atlantic impact in 1999, and possible higher nitrate concentrations in March giving increased new production in the spring period this year (Fig. 8).

The higher Si-based C-production seen in July compared to May support the hypothesis on an interannual difference in the nutrient consumption pattern rather than a seasonal development. A seasonal argument require that 100% of the nitrate consumed from May to July was associated with a Si-uptake. However, from the phytoplankton data available (Ratkova and Wassmann, 2002) we know that non-Si-demanding species were important in July.

The pattern seen in May with high new production above the trenches was however supported by the July data giving maximum new production associated with the trench south of Sentralbanken and between Sentralbanken and Storbanken (88 and 120 g C m<sup>-2</sup>, respectively). This pattern is probably caused by the increased mixing in the trenches, but can also represent an overestimation caused by the impact of nutrient depleted Atlantic water advected from high production regimes in the Norwegian Sea/Barents Sea slope. Unfortunately, we did not have sediment traps measurements in this area which could have indicated the export production. However, model simulations gave a 100% increase in the primary production and vertical flux in this part of the transect when a very cold year (low inflow of Atlantic water) was compared to a warm one (Slagstad and Wassmann, 1997). The impact of Atlantic water is thus of outmost importance for the production regime and new production estimates in the central Barents Sea influencing the winter nutrient level as well as the strength of mixing and the resulting production.

According to the present estimates, the new production in the central Barents Sea in the period March–July varied from 15 g C m<sup>-2</sup> in the ice covered waters to 120 g C m<sup>-2</sup> at the trench between the banks (average 54 g C m<sup>-2</sup> for the entire transect), with an average of 68 g C m<sup>-2</sup> in the open waters south of the Polar Front. This is close to recent estimates of 62 g C m<sup>-2</sup> (winter–August) for the Greenland Sea by Rey et al. (2000). The slightly higher estimates for the central Barents Sea, can be explained by the deeper mixed layer present in the

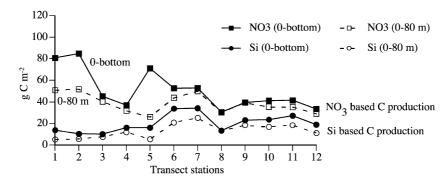


Fig. 7. New production estimates from March to May 1998 based on depth integration 0-80 m and 0-bottom.

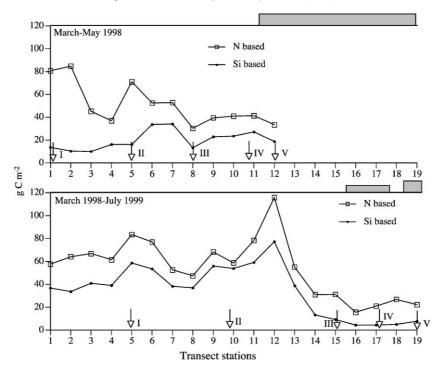


Fig. 8. New production estimates (g C m<sup>-2</sup>) (surface-bottom) from the central Barents Sea to the marginal ice-zone in May 1998 and July 1999 based on nitrate and silicate consumption calculated from measured March 1998 concentrations.

Atlantic region of the Barents Sea (50 m depth) and the topographically induced upwelling in the trenches supplying new nutrients, compared to the deeper Greenland Sea (strong stratification at 30 m depth; Rey et al., 2000).

4.6. Interannual variability and implications for new production estimates and model approaches

Interannual variability in species composition and bloom development in the central Barents Sea and MIZ is well known (Skjoldal et al., 1987; Wassmann et al., 1999b). The variability can be explained by several factors influencing the growth regime like variable inflow of Atlantic water and the wind conditions influencing the mixing depth, ice distribution and the available light as well as the seeding population present at the onset of the bloom.

On a daily scale, our estimates (1.2–0.2 g C m<sup>-2</sup> day<sup>-1</sup>, averaged for the March–July period) are well within the range obtained during other investigations from the area. Our lowest daily new production is

estimated at the northernmost stations characterised by pack ice. Kristiansen et al. (1994) measured new production rates ranging 0.22–3.51 g C m<sup>-2</sup> day<sup>-1</sup> in April using the <sup>15</sup>N technique in open and partly ice covered waters. Estimates of new production by Owrid et al. (2000) based on nitrate depletion from late June to late July along a comparable transect ranged from 0.36–0.0 from the productive ice edge in north to south of Storbanken. Taken into consideration that our daily estimates includes the spring period as well, the present results does not seem to be overestimates.

Two comparable investigations in the same period and along the same transect highlight the range of variability in the system. New production estimates from 1993 (Wassmann et al., 1999b) and annual new production estimated through modelling (Slagstad and Wassmann, 1997) gave only 50% of the new production estimates for spring 1998 presented in this paper. Wassmann et al. (1999b) estimated the new production from winter to mid May in 1993 to be considerably lower (32–12 g C m<sup>-2</sup>, average of 23 g C m<sup>-2</sup>) compared to the estimated new production in the same

period and transect in 1998 (ranging 32-60 g C m<sup>-2</sup> with average of 45 g C m<sup>-2</sup> using the same depth interval and winter conc. as Wassmann et al., 1999b). The ice conditions and the inflow of Atlantic water seemed to be quite similar these 2 years (Polar Front and ice edge localised in the same area). The mixing depth is however not known in 1993, as nutrients and pigments (used as indicator for mixing depth in 1998) only were measured down to 80 m. Strong mixing could have caused a higher new production in 1993 than reported if many stations where mixed below 80 m. Another striking difference that also can explain higher new production estimates in spring 1998 was the nutrient level (i.e. nitrate which was still high in May 1993; Wassmann et al., 1999b, but low in 1998; Fig. 5) and phytoplankton biomass (low in 1993; Wassmann et al., 1999b, and high in 1998; Fig. 6) along the transect. Kristiansen et al. (1994) suggest that primary production in the central Barents Sea is coupled to the standing stock of phytoplankton rather than nutrients. A higher and significant grazing pressure from herbivores reducing the phytoplankton standing stock enough to limit the primary production in 1993 could thus, as well as deep mixing, cause the patterns observed. This can perhaps explain a lower new production in the spring period in 1993.

The new production levels and patterns in the central Barents Sea and MIZ are thus influenced not only by physical factors like Atlantic water inflow, ice dynamics and wind important for the mixing depth, but also biological factors can be of importance. The phytoplankton community leaves different nutrient pattern "tracks" depending on whether Sior non-Si demanding species dominate (sigmoid Si versus NO<sub>3</sub> plots when Phaeocystis blooms are prominent, Fig. 4), and intensive grazing might delay the production or shape the microplankton community through selective grazing. Models can help us to understand the interplay and the impact of the variability in the physical and biological climate on the new production and consequently the export production. To get reliable models the most important factors has to be included, and this study has highlighted the importance of knowing the range of winter levels of nutrients to get correct new production estimates. Deeper mixing increases the new production, and seems to increase the importance of Phaeocystis, with the implication this has for the

nutrient pattern (low nitrate—high silicate) and C-transfer in the food web. The strength of Atlantic water inflow is important for both of these factors. Freezing and ice cover on Sentralbanken might be regulated by the Atlantic inflow and is essential for the hydrographic regime available during the productive period. The interannual variability is significant, and direct comparison of seasons investigated different years is therefor difficult.

Model approaches for calculation of the biological carbon pump potential, therefor need to include the interannual variability and its effect on the new production. At the same time, the high variability and range of scenarios present can teach us something about the effects of a climate change. If the consequence of global warming is reduced ice cover, the Atlantic impact can be expected to increase in the Barents Sea with the MIZ and the stratified waters moved northwards. Based on the present results increased Atlantic influence can increase the new production due to deeper mixing. Increased mixing depth can favour Phaeocystis dominance on the expense of diatoms. The implications for the trophic carbon transfer and C-sequestration are questions which are best answered through modelling.

## 4.7. Impact of bacterial nitrate consumption on new production estimates

Recent results from Allen et al. (2002) showed that there was a competition between bacteria and phytoplankton for nitrate, and that bacteria accounted for up to 40% of the total nitrate uptake in July. As bacteria need a C-source, we do not know if this is specific for the summer situation or if it is a general pattern in the Barents Sea. Anyhow, the nitrate depletion will not be new production in the sense of autotroph production as we have thought up to now, and our new production estimates are thus strongly overestimated. On the other hand, as bacteria need a carbon source, DOC, mucus or transparent exopolymer particles, this is available after the spring bloom as exudates from phytoplankton. Such exudates have been observed colonised by bacteria (Passow and Alldredge, 1994) and can provide excellent food packages for small heterotrophic organisms (Passow and Alldredge, 1999; Reigstad, 2000). As microzooplankton is an important food source for mesozooplankton (Slagstad et al., 1999) the nitrate is back in the traditional "fisheries food chain". The transfer of carbon is however less efficient going through the microbial food web compared to a direct transfer from phytoplankton to mesozooplankton. Nitrate depletion is thus still a measure of new production but the production is the sum of the autotrophic new production+the bacterial new production (times a transfer efficiency). Obviously new production and net productivity in the Barents Sea is surprisingly bad known in the light of the present results, <sup>15</sup>N-uptake studies (Allen et al., 2002) and model results (Slagstad and Wassmann, 1997).

#### 5. Conclusion

Our investigation covered hydrography, nutrients, Chl a and new production during three seasons in the Barents Sea typical for the winter, spring and early summer period. A characterisation of the seasonal development was however difficult as seasonal changes from spring to summer most likely were masked by interannual variations since the July cruise took place a warmer year with higher Atlantic inflow. Different mixing regimes in Atlantic waters, trench/ Polar Front region and the melt water/Arctic water region are structured by different stratification mechanisms which has implication for the phytoplankton community development and the new production. An interannually variable "atlantification" of the water mass on Sentralbanken changed the bank from being part of the MIZ characterised by melt water to a deeper mixed region. Si-demanding groups such as diatoms were important for the new production in the more stratified Arctic region compared to the Atlantic region in spring 1998. However, the new production in the Arctic region was lower compared to the deeper mixed Atlantic region and trench areas. These results support the hypothesis suggesting that diatoms tend to dominate in stratified and shallow mixed waters, while P. pouchetii is a more successful competitor when the mixing is deeper. Flagellated organisms seem to be important contributors to the new production.

Interannual differences in Atlantic inflow affecting nutrient winter concentrations and whether a region is characterised by deep or shallow mixing has implications for the new production estimates for the Barents Sea. Model approaches investigating the observed variability in hydrographic characteristics is necessary to understand implications of trends induced by a climate change for the biological community and production.

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#### References

Ådlandsvik, B., Loeng, H., 1991. A study of the climatic system in the Barents Sea. Polar Res. 10, 45–50.

Allen, A.E., Howard-Jones, M.H., Booth, M.G., Frischer, M.E., Verity, P.G., Bronk, D.A., Sanderson, M.P., 2002. Importance of heterotrophic bacterial assimilation of ammonium and nitrate in the Barents Sea during summer. J. Mar. Syst., this issue.

Anon., 2000. Havets miljø. Report. Institute of Marine Research, Bergen, Norway.

Arashkevich, E., Wassmann, P., Pasternak, A., Wexels Riser, C., 2002. Seasonal and spatial variation in biomass, structure and development progress of the zooplankton community in the Barents Sea. J. Mar. Syst., this issue.

Cushman-Roisin, B., 1994. Introduction to Geophysical Fluid Dynamics. Prentice-Hall, New Jersey, 320 pp.

Dugdale, R.C., Goering, J.J., 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. Limnol. Oceanogr. 12, 196–206.

Egge, J.K., Aksnes, D.L., 1992. Silicate as a regulating nutrient in phytoplankton competition. Mar. Ecol., Prog. Ser. 83, 281–289.
Eppley, R.W., Peterson, B.J., 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature 282, 677–680.

Falk-Petersen, S., Hop, H., Budgell, P.W., Hegseth, E.N., Korsnes, R., Løyning, T.B., Ørbæk, J.B., Kawamura, T., Shirasawa, K., 2000. Physical and ecological processes in the marginal ice zone of the northern Barents Sea during the summer melt period. J. Mar. Syst. 27, 131–159.

Howard-Jones, M.H., Ballard, V.D., Allen, A.E., Frischer, M.E., Verity, P.G., 2002. Distribution of bacterial biomass and activity in the marginal ice zone of the central Barents Sea during summer. J. Mar. Syst., this issue.

Gawarkiewicz, G., Plueddemann, A.J., 1995. Topographic control

- of thermohaline frontal structure in the Barents Sea Polar Front on the south flank of Spitsbergen Bank. J. Geophys. Res. 100 (C3), 4509–4524.
- Kaltin, S., Anderson, L., Olsson, K., Fransson, A., Chierici, M., 2002. Uptake of atmospheric carbon dioxide in the Barents Sea. J. Mar. Syst., this issue.
- Kristiansen, S., Farbrot, T., Wheeler, P.A., 1994. Nitrogen cycling in the Barents Sea—seasonal dynamics of new and regenerated production in the marginal ice zone. Limnol. Oceanogr. 39, 1630–1642.
- Loeng, H., 1991. Features of the physical oceanographic conditions of the Barents Sea. Polar Res. 10, 5–18.
- Loeng, H., Ozhigin, V., Ådlandsvik, B., 1997. Water fluxes through the Barents Sea. ICES J. Mar. Sci. 54, 310-317.
- Olli, K., Wexels Riser, C., Wassmann, P., Ratkova, T., Arashkevich, E., Pasternak, A., 2002. Seasonal variation in vertical flux of biogenic matter in the marginal ice zone and the central Barents Sea. J. Mar. Syst., this issue.
- Owrid, G., Socal, G., Civitarese, G., Luchetta, A., Wiktor, J., Nöthig, E.-M., Andressen, I., Schauer, U., Strass, V., 2000. Spatial distribution of phytoplankton, nutrients and new production estimates in the waters around Svalbard. Polar Res. 19, 155–171.
- Passow, U., Alldredge, A.L., 1994. Distribution, size and bacterial colonisation of transparent exopolymer particles (TEP) in the ocean. Mar. Ecol., Prog. Ser. 113, 185–198.
- Passow, U., Alldredge, A.I., 1999. Do transparent exopolymer particles (TEP) inhibit grazing by the euphausid Euphausia pacifica? J. Plankton Res. 21, 2203–2217.
- Pasternak, A., Wexels Riser, C., Arashkevich, E., Wassmann, P., 2002. Calanus spp. grazing affects egg production and vertical carbon flux (the marginal ice zone and open Barents Sea). J. Mar. Syst., this issue.
- Quadfasel, D., Rudels, B., Selchow, S., 1992. The Central Bank vortex in the Barents Sea: watermass transformation and circulation. ICES Mar. Sci. Symp. 195, 40–51.
- Ratkova, T., Wassmann, P., 2002. Seasonal variation and spatial distribution of phyto- and protozooplankton in the central Barents Sea. J. Mar. Syst., this issue.
- Reigstad, M., 2000. Plankton community and vertical flux of biogenic matter in north Norwegian fjords: Regulating factors, temporal and spatial variations. PhD Thesis. University of Tromsø, 88 pp.
- Rey, F., Noji, T.T., Miller, L.M., 2000. Seasonal phytoplankton development and new production in the central Greenland Sea. Sarsia 85, 329–344.
- Sakshaug, E., 1997. Biomass and productivity distributions and their variability in the Barents Sea. ICES J. Mar. Sci. 54, 341–350.
- Sakshaug, E., Slagstad, D., 1991. Light and productivity of phytoplankton in polar marine ecosystems: a physiological view. Polar Res. 10, 69–86.
- Sakshaug, E., Slagstad, D., 1992. Sea ice and wind. Effects on primary productivity in the Barents Sea. Atmos. Ocean 30, 579-591.
- Sakshaug, E., Walsh, J., 2000. Marine biology: biomass, productivity distributions and their variability in the Barents and Bering Sea. In: Nuttall, M., Callaghan, T.V. (Eds.), The Arctic: A Guide

- to Research in the Natural and Social Sciences. Harwood Academic Publishers, London, pp. 161–195.
- Sakshaug, E., Hopkins, C.C.E., Øritsland, N.A. (Eds.), 1991. Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, Norway, 12–16 May 1990. (Polar Res.) vol. 10, pp. 1–662.
- Sakshaug, E., Bjørge, A., Gulliksen, B., Loeng, H., Mehlum, F., 1992. Økosystem Barentshavet. NAVF, NFFR, MD, 304 pp.
- Sakshaug, E., Bjørge, A., Gulliksen, B., Loeng, H., Mehlum, F., 1994. Structure, biomass distribution and energetics of the pelagic ecosystem in the Barents Sea: a synopsis. Polar Biol. 14, 405–411.
- Sakshaug, E., Rey, F., Slagstad, D., 1995. Wind forcing of marine primary production in the northern atmospheric low-pressure belt. In: Skjoldal, H.R., et al. (Eds.), Ecology of Fjords and Coastal Waters. Elsevier, Amsterdam, pp. 15–25.
- Sato, M., Sasaki, H., Fukuchi, M., 2002. Stable isotope compositions of dominant copepods in the arctic and subarctic waters and implications to the feeding history. J. Mar. Syst., this issue.
- Skjoldal, H.R., Rey, F., 1989. Pelagic production and variability of the Barents Sea ecosystem. In: Sherman, K., Alexander, K.L. (Eds.), Biomass and Geography of Large Marine Ecosystems. Westview Press, Boulder, pp. 243–283.
- Skjoldal, H.R., Hassel, A., Rey, F., Loeng, H., 1987. Spring phytoplankton development and zooplankton reproduction in the central Barents Sea in the period 1979–1984. The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea; Proc. 3rd Sovjet–Norwegian Symposium. In: Loeng, H. (Ed.), Bergen Inst. Mar. Res, pp. 59–90.
- Slagstad, D., Wassmann, P., 1997. Climate change and carbon flux in the Barents sea: 3-D simulations of ice-Distribution, primary production and vertical export of particulate organic carbon. Mem. Natl. Inst. Polar Res., Spec. Issue 51, 119–141.
- Slagstad, D., Tande, K.S., 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.
- Smetacek, V., Bodungen, B.V., Knoppers, B., Peinert, R., Pollehne, F., Stegmann, P., Zeitzschel, B., 1984. Seasonal stages characterizing the annual cycle of an inshore pelagic system. Rapp. P.-V. Rèun. Cons. Int. Explor. Mer. 183, 126–135.
- Verity, P.G., Wassmann, P., Frischer, M.E., Howard-Jones, M.H., Allen, A.E., 2002. Grazing of phytoplankton by microzooplankton in the Barents Sea during early summer. J. Mar. Syst., this issue.
- Vinje, T., Kvambekk, Å.S., 1991. Barents Sea drift ice characteristics. Polar Res. 10, 59-68.
- Wassmann, P., 1991. Sampling and analysis of marine particles with PEBENOCO (PElagic-BEntic coupling in the NOrwegian COastal zone), University of Tromsø, Norway. Geophys. Monogr. 63, 97–99.
- Wassmann, P., 1998. Retention versus export food chains: processes controlling sinking loss from marine pelagic systems. Hydrobiology 363, 29–57.
- Wassmann, P., Slagstad, D., 1993. Sesonal and annual dynamics of particulate carbon flux in the Barents Sea. Polar Biol. 13, 363-372.

- Wassmann, P., Vernet, M., Mitchell, B.G., Ray, F., 1990. Mass sedimentation of *Phaeocystis pouchetii* in the Barents Sea. Mar. Ecol., Prog. Ser. 66, 183–195.
- Wassmann, P., Andreassen, I.J., Rey, F., 1999a. Seasonal variation of nutrients and suspended biomass on a transect across Nordvestbanken, north Norwegian shelf, in 1994. Sarsia 84, 199–212.
- Wassmann, P., Ratkova, T., Andreassen, I., Vernet, M., Pedersen,
- F., Rey, F., 1999b. Spring bloom development in the marginal ice zone and the central Barents Sea. Mar. Ecol. PZNI 20, 321–346.
- Wexels Riser, C., Wassmann, P., Olli, K., Pasternak, A., Arashkevich, E., 2002. Seasonal variation in production, retention and export of zooplankton faecal pellets in the marginal ice zone and the central Barents Sea. J. Mar. Syst., this issue.