Vernal export and retention of biogenic matter in the north-eastern North Atlantic and adjacent Arctic Ocean: The role of the Norwegian Atlantic Current and topography

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Abstract: The abundance of suspended chlorophyll a (Chl a) and particulate organic carbon (POC) and its vertical export was investigated on the shelf off northern Norway, off Spitsbergen and in the Barents Sea during biological spring. Accumulation of suspended Chl $a > 100$ mg m^{-2} was only observed in the Barents Sea marginal ice zone and at a distance from the shelf break. Suspended POC concentrations were less variable. Similar results were found for the vertical export of Chl a and POC from the upper layers. It is suggested that the high retention rates of suspended biogenic matter along the shelf break of the Norwegian Sea and the Arctic Ocean north of Spitsbergen, sites influenced by branches of the North Atlantic Current, are caused by top-down regulation of phytoplankton biomass by overwintered and advected zooplankton. Thus a tight coupling appears to exist between primary and secondary production on the shelf areas off northern Norway and Spitsbergen during spring. Classical vernal blooms are not the rule in the area and can only be observed when the distance to the shelf break is significant, advection of zooplankton occasionally is restricted and stratification supports rapid accumulation of phytoplankton.

1. Introduction

The dynamics of vertical flux of biogenic matter, and to a lesser extent also the composition of exported matter has been recurrently investigated in a variety of ecosystems. Major seasonal, as well as regional and inter-annual variations, have been encountered with regard to the quantity and composition of the material exported from the upper water column. Loss of organic matter from the upper water column mainly takes place through settling of phytoplankton cells, plankton-derived detritus and zooplankton faecal pellets. Regional, seasonal and interannual variations have thus been attributed to differences in primary production (Platt *et al.*, 1988) as well as retention and export food chains (*e.g.* Peinert *et al.*, 1989; Wassmann, 1998). The current understanding of the dynamics involved in daily and seasonal changes in vertical flux is though rudimentary. This is particularly true for sub-arctic and arctic areas, which experience large seasonal variations. In these areas the vertical flux is strongly dominated by episodic events on daily, weekly, seasonal and annual time scales (Wassmann *et al.*, 1996).

There are several oceanic areas where, in spite of high nutrient concentrations, phytoplankton is not abundant, *i.e.* high nutrient/low chlorophyll regions (HNLC).

Among those areas we find several pacific areas such as the Gulf of Alaska (Frost, 1987; Parsons and Lalli, 1988; Taniguchi, 1999) and the north-western Pacific Ocean (Odate, 1994; Taniguchi, 1999) or the Southern Ocean (Smith and Nelson, 1985; Martin *et al.*, 1990). Other factors than light and macro nutrient availability must be responsible for the lack of phytoplankton biomass accumulation. For example: water column stability (Nelson *et al.*, 1987; Townsend *et al.*, 1993; Huisman *et al.*, 1999), absence of essential micro nutrients (Martin and Fitzwater, 1988) or extensive grazing by zooplankton (Frost, 1991; Miller, 1993; Odate, 1994). Recent information reveals that similar scenarios are also encountered on the north Norwegian shelf (*e.g.* Wassmann *et al.*, 1999a). Here the new production was > 120 g C m^{-2} y^{-1} (Slagstad *et al.*, 1999), macro nutrients became hardly limiting at the shelf break (Wassmann *et al.*, 1999a) and phytoplankton biomass was low and entirely dominated by pico- and nanoplankton (Ratkova *et al.*, 1999; Verity *et al.*, 1999). The mesozooplankton biomass was high (Halvorsen and Tande, 1999) and vertical export of carbon was moderate to high and not dominated by phytoplankton, but faecal pellets and detritus (Andreassen *et al.*, 1999). The pelagic trophic structure obviously regulates the total suspended biomass, its species composition as well as the export of biogenic matter.

A major corollary of the traditional large organism food chain model is that each trophic level is primarily resource-limited. Enhanced nutrients supply at the bottom of the food chain will yield higher biomass of phytoplankton, zooplankton and fish (*e.g.* Legendre, 1990). This perspective has been challenged for its universal applicability (Verity and Smetacek, 1996). The food web structure on the north Norwegian shelf suggests that top-down control is as important as resource limitation: (a) a dearth of large phytoplankton, despite significant NO_3 and $Si(OH)_4$ consumption (Wassmann *et al.*, 1999a), (b) low abundance of large protozoans, despite tremendous abundances of their prey (Ratkova *et al.*, 1999); (c) high concentrations of mesozooplankton (Halvorsen and Tande, 1999) which cannot feed efficiently on small flagellates. The scenario implies that predation by the large copepods and euphausiids keep pace with the growth of large phyto- and protozooplankton, minimising their respective competition with and predation on small cells. The food web is thus characterised by joint regulation by resource availability and predation (Verity and Smetacek, 1996). This dual dependency indicates that the structure of the food web can indeed complicate relationships between primary production, grazing, and sedimentation (Andreassen *et al.*, 1996; Wassmann, 1998; Verity *et al.*, 1999).

The north Norwegian shelf shares similarities with HNLC regions. However, here the cause for the low phytoplankton stock is to be found in the substantial grazing pressure by overwintering mesozooplankton which is advected to the north by the Norwegian Atlantic Current. The question arises if the Nordic Seas, its encircling shelves and the adjacent Arctic Ocean are characterised by tendencies towards high nutrient/low chlorophyll conditions, which are caused by grazing? What consequences have the advection of Atlantic water and zooplankton for the production and fate of biogenic matter in the Arctic Ocean? In order to answer these questions, the present investigation reviews, compiles and recalculates published information by Andreassen *et al.* (1996), Andreassen and Wassmann (1998), Andreassen *et al.* (1999), Ratkova *et al.* (1999) and Wassmann *et al.* (1999a) on the suspended biogenic matter and its vertical export during biological spring along the pathway of the North Atlantic Current, *i.e.* the Norwegian shelf, the shelf of west and north of Spitsbergen and the adjacent Barents Sea.

2. Geographic and hydrographic description of the investigation area

The shelf off northern Norway is characterised by shallow banks and a steep shelf break. Fjords continue by trenches penetrating to the shelf break, separating the shelf into shallow coastal banks (Fig. 1). The shelf off northern Norway borders to the Norwegian
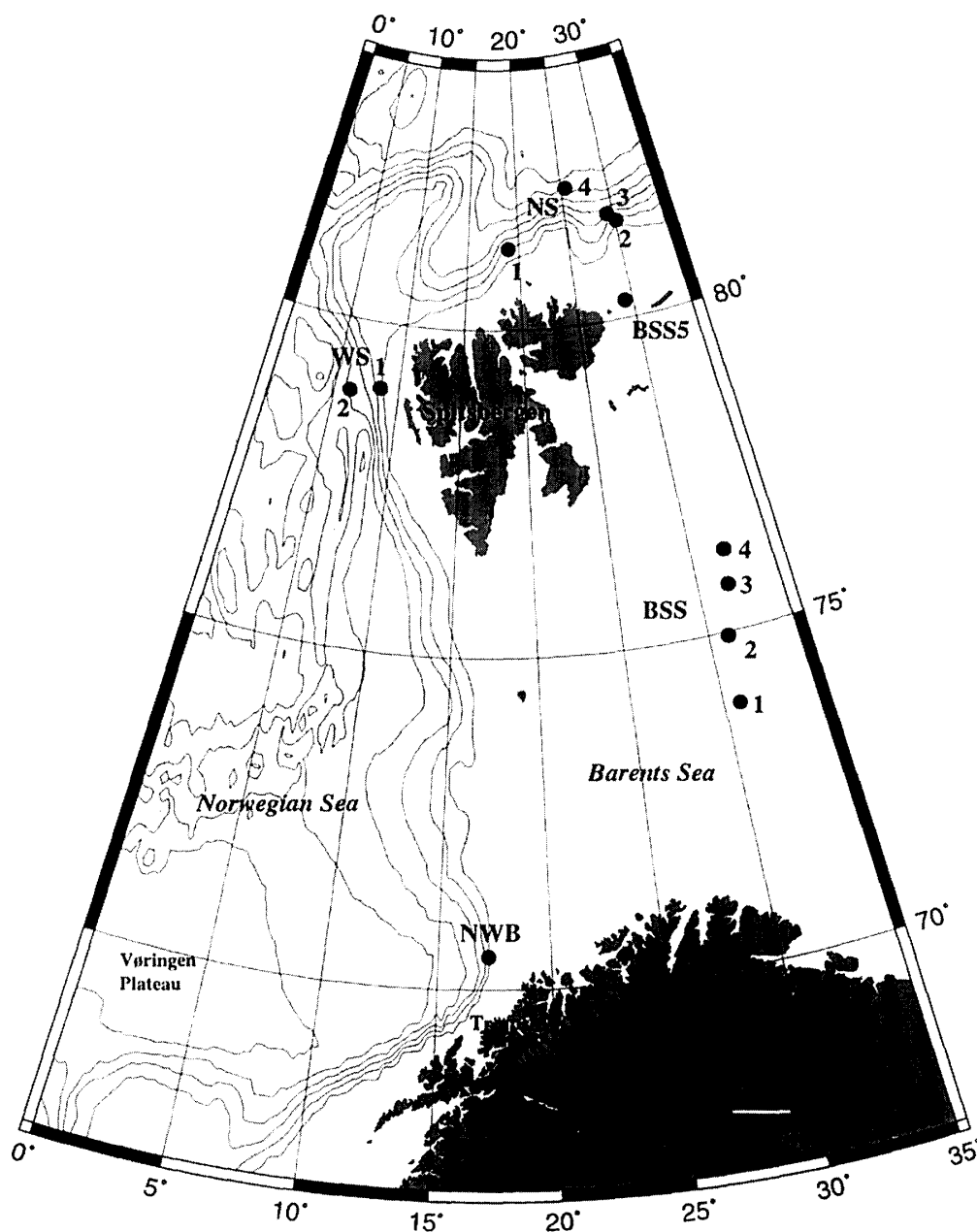

Fig. 1. The investigated and adjacent areas, the north Norwegian coast, the Barents Sea, the west-Spitsbergen shelf and the shelf of the Arctic Ocean north of Spitsbergen. The positions of the investigated sites are indicated. NWB = Nordvestbanken, WS = west Spitsbergen, NS = north Spitsbergen, BSS = Barents Sea shelf.

Sea. The Barents Sea, which is situated to the east of the Norwegian Sea between northern Norway and Spitsbergen, is part of the large shelf-seas bordering the Eurasian Arctic. This continental shelf is wide, with water depths ranging from 100 to 400 m. The shelf west and north off Spitsbergen is narrow, with penetrating trenches and a steep shelf break descending to more than 2000 m. This area shows great resemblance to that off northern Norway. To the north of Spitsbergen the shelf fringes the Arctic Ocean.

The investigation area is dominated by the Norwegian Atlantic Current (NAC), which transports warm Atlantic water northwards along the Norwegian continental shelf, to Spitsbergen, the Barents Sea and eastward along the Eurasian shelf edge of the Arctic Ocean (Fig. 2). The NAC splits into several branches. A broad tongue of the NAC flows eastward into the Barents Sea. Subduction under Arctic water takes place when the Atlantic water turns north. Another branch continues along the west side of Spitsbergen creating the West Spitsbergen Current (WSC). Also here subduction of Atlantic water occurs north of
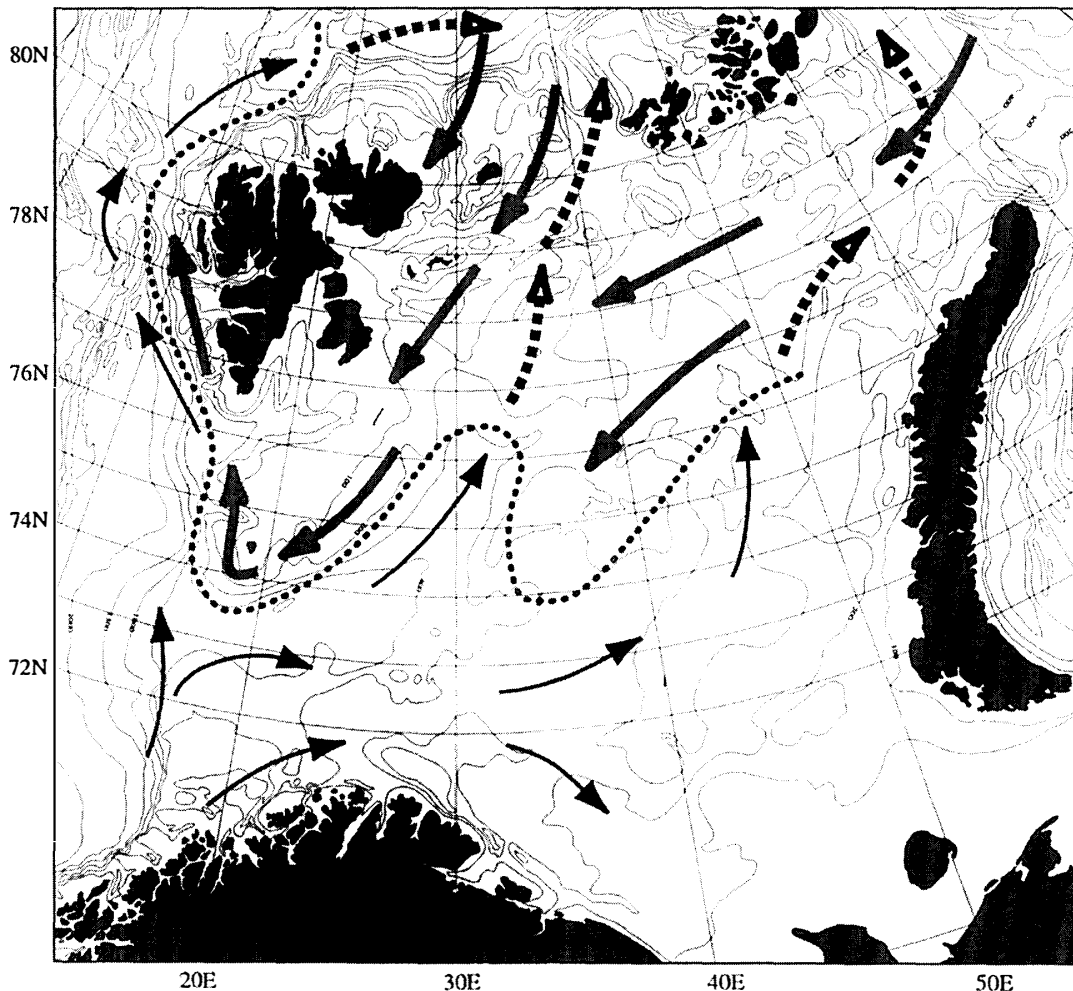

Fig. 2.   Main features of the surface current system in the investigated area. Dark, full lines: North Atlantic Current (NAC) and West Spitsbergen Current (WSC). Dark, dashed lines: Subducted NAC/WSC water. Grey lines: Arctic water. Also shown is the mean position of the Polar Front (dotted line).

Spitsbergen. At the Yearmark Plateau (north of Spitsbergen) the subducted WSC splits and the eastern branch continues along the shelf break, enters the Arctic Ocean and is joined by branches of Atlantic water from the Barents Sea through the Victoria and St. Anna troughs (west and east of Franz Joseph Land, respectively). The NAC hence creates a marine environmental continuum which extends from the south-eastern Norwegian Sea into the Barents Sea, along the western coast of Spitsbergen and to the Eurasian shelf break of the Arctic Ocean (Blindheim and Loeng, 1981; AMAP, 1998).

In the northern part of the Barents Sea cold Arctic waters from the north-east meets the warm Atlantic water flowing from the south-west, giving rise to a distinct front, the Polar Front, where the subduction of Atlantic water occurs. On the western side of Spitsbergen between the coast and the WSC, cold Arctic water flows north, creating the cold West Spitsbergen Coastal Current (WSCC). The water of the WSCC origins from the Arctic Ocean and flows between Nordaustland and Franz Josef Land as the East Spitsbergen Current (ESC) onto the Barents Sea shelf, and continues around the southern end of Spitsbergen as the WSCC.

Along the NAC/WSC continuum data from Nordvestbanken (NWB) (Andreassen et al., 1999; Ratkova et al., 1999; Wassmann et al., 1999a), the West Spitsbergen shelf (WS) (Andreassen et al., 1996) and the North Spitsbergen shelf (NS) (Andreassen et al., 1996) have been selected (Fig. 1). These data are contrasted by those derived from a north-south gradient crossing the Barents Sea (BBS) who is under the influence of the ESC and the MIZ (Andreassen et al., 1996; Andreassen and Wassmann, 1998).

3. Suspended biomass and vertical export

The suspended Chl a concentrations varied considerably between 10 to 400 mg m^{-2} during spring in the investigated area (Table 1). The highest concentrations were encountered in the MIZ of the Barents Sea while all shelf stations under the influence of the NAC had < 50 mg m^{-2}. Even on the north Norwegian shelf characterised by high new production, the Chl a concentrations were low. Thus the entire northern shelf region appears to be characterised by "blue water" scenarios despite of high nutrient depletion and productivity. The suspended POC concentrations varied less over the entire area: 3–18 g m^{-2}. They reflect both the accumulation of phytoplankton (for example at BSS4 in the MIZ) as well as nitrate depletion (which reflects new production) in various systems (far higher at NWS than at WS and NS). The vertical export of Chl a followed a similar pattern: low rates along the shelf, but high rates in the MIZ of the Barents Sea (Table 1). However, the range was an order of magnitude greater, from 0.03 to almost 5 mg Chl a m^{-2} d^{-1}. Similar to the suspended fraction, the range of vertical export rates of POC was less than that of Chl a: about 20 to 350 POC m^{-2} d^{-1}. The highest rates were encountered on the north Norwegian shelf and in the Barents Sea MIZ while the lowest rates were found west and north of Spitsbergen. This coincides with the high and nitrate depletion rates in these waters, respectively.

The daily loss rates of Chl a and POC reflect similar scenarios than those of presented above (Table 2): low loss rates along the NAC continuum (average 0.36 and 0.78% d^{-1} for Chl a and POC, respectively) while high rates prevail in the MIZ of the Barents Sea (average 1.95 and 3.0% d^{-1} for Chl a and POC, respectively). Maximum loss rates up to

Table 1. *Integrated suspended chlorophyll a (Chl a; mg m⁻²) and particulate organic carbon (POC; g m⁻²) (0-100 m, except BSS 1 (0-60 m). Vertical flux of chlorophyll a (Chl a) and particulate organic carbon (POC) at 100 m (60 m at BSS 5) (mg m⁻² d⁻¹). Data from two stations during April and May at NWB (1994), four stations during May at BSS 1-4 (1993) and July at BSS 5 (1991) and six station during June/July at WS and NS (1991) are shown.*

Station	NWB1	NWB2	WS1	WS2	NS1	NS2	NS3	NS4	BSS1	BSS2	BSS3	BSS4	BSS5
Suspended biomass													
Chl a	20	49	40	50	20	15	20	25	145	80	150	400	70
POC	11.1	17.2	11.6	12.2	7.0	3.3	5.2	8.5	8.7	4.8	9.0	24.0	6.1
Vertical export													
Chl a	0.1	0.2	0.05	0.05	0.03	0.2	0.03	0.03	0.35	4.8	2.8	1.2	0.9
POC	130	315	24	32	17	22	76	26	195	350	320	260	47

Table 2. *Daily vertical loss rates of chlorophyll a (Chl a) and particulate organic carbon (POC) at 100 m (% d⁻¹). Also shown is the residence time (d) of Chl a and POC in the upper 100 m (= 100/daily loss rate). Remark: 60 m at BSS 4 and 5.*

Station	NWB1	NWB2	WS1	WS2	NS1	NS2	NS3	NS4	BSS1	BSS2	BSS3	BSS4	BSS5
Daily vertical loss rates													
Chl a	0.5	0.4	0.1	0.1	0.2	1.3	0.2	0.1	0.2	6	1.9	0.3	1.3
POC	1.2	1.8	0.2	0.3	0.2	0.7	1.5	0.3	2.2	7.3	3.6	1.1	0.8
Residence time													
Chl a	200	250	1000	1000	500	77	500	1000	500	17	53	200	46
POC	83	56	500	333	500	143	67	333	45	14	28	55	75

7% d⁻¹ were encountered, clearly indicating the large-scale vertical export of biogenic matter in the MIZ. The residence times vary analogue to the daily loss rates. For Chl a they are several hundred days along the NAC continuum. They were as low as 14 and 17 days for Chl a and POC, respectively, in the MIZ of the Barents Sea.

Significant accumulation and vertical export of phytoplankton biomass were only encountered in areas at a distance to the main NAC current (*e.g.* the central Barents Sea) and the shelf edge. Stratification during spring will promote the vernal bloom development and vertical export (*e.g.* in the MIZ). In all other areas along the shelf of the NAC continuum, vernal blooms were not encountered. Vertical export of biogenic matter is thus not a simple function of nitrate depletion or standing stock. Below I will try to analyse why this is so and what general conclusions could be deduced from the data presented in Tables 1 and 2.

4. Physical environment, phytoplankton growth and vertical flux: The significance of bottom-up regulation

In arctic and sub-arctic seas, the environment is highly dynamic both on a seasonal and interannual times scale. Thus physical processes strongly influence the pelagic community and the vertical flux of biogenic particles (Wassmann *et al.*, 1996). It is widely accepted that the seasonal development of water column stabilisation, in combination with increasing solar radiation in spring, is a prerequisite of vernal spring blooms (Smetacek and Passow,

1990). In ice-covered environments, water column stability by ice melt, the depth of the stratified surface water as well as photosynthetic active radiation, control the magnitude and time development of the bloom (Sakshaug and Holm-Hansen, 1984; Sakshaug and Skjoldal, 1989). Melting sea ice is the only important source of fresh water in the entire region during spring. In contrast, the spring bloom on the north Norwegian shelves and in the southern part of the Barents Sea dominated by Atlantic water, takes place in almost non-stratified waters (Skjoldal and Rey, 1989; Wassmann et al., 2000). Limited vertical mixing appears to support cell growth, giving rise to a bloom (Eilertsen, 1993: Townsend et al., 1993). Wind strength and direction, along with radiation and ice cover, play a crucial role for the onset, development and fate of the spring bloom in arctic and sub-arctic waters (Sakshaug, 1997; Slagstad and Wassmann, 1997).

Vertical stability, mixing and upwelling determine the amount of nutrients available and thus the new production. The level of turbulence also influences the composition of primary producers (Margalef, 1978; Kiørboe, 1993). Turbulence and shear increase the collision rates of particles in the water column and may thus increase the aggregation of sticky particles (e.g. Kiørboe, 1993). Advection of water may influence the prevalence of zooplankton along with the NAC (e.g. Halvorsen and Tande, 1999; Slagstad et al., 1999) and the Barents Sea (e.g. Ådlandsvik and Loeng, 1991; Pedersen, 1995). The physical oceanography determines primarily the new production and hence the upper limit of export production from the euphotic zone (Platt et al., 1988). Physical oceanography determines further the dynamics of vertical flux indirectly through mixing, shear, timing of spring bloom, aggregation, phytoplankton species composition and through over-wintering, advection and retention of zooplankton (Wassmann et al., 1996).

The daily and seasonal changes of the vertical flux of biogenic matter are thus the result of complex interactions of biological and physical factors, which could be circumscribed as bottom-up regulation. The quantity and quality of sinking biogenic material reflects also the prevailing structure of the pelagic system, in particular zooplankton (Wassmann, 1998). The latter impact could be describes as top-down regulation, which will be discussed further in the next sections. Thus, both the complexities of the physical environment and the pelagic community are important in structuring planktonic ecosystems and influence vertical flux (Silver and Gowing, 1991; Verity and Smetacek, 1996).

5. Meso- and macrozooplankton and top-down regulation

The deep Norwegian Sea is an important area for over-wintering of meso- and macrozooplankton, and its early ascend in the Norwegian Sea has been shown to potentially control the early spring bloom (Bathmann et al., 1990). These zooplankton populations on the north Norwegian shelf are primarily advected into the area with the Norwegian Coastal Current (NCC) and the NAC (Slagstad and Tande, 1996; Halvorsen and Tande, 1999). As early as March, over-wintering mesozooplankton may be imported onto the shelf off northern Norway and further north (Slagstad and Tande, 1996). At NWB in March 1994 a mesozooplankton biomass of 0.3 $g\,C\,m^{-2}$ was recorded, and already in April mesozooplankton biomass at the shelf break ($\sim$4 $g\,C\,m^{-2}$; K. Tande, unpubl. res.) equalled levels which are usually reached in late summer in north Norwegian fjords (Tande, 1991; Falkenhaug et al., 1995; Pasternak et al., 2000). Mesozooplankton biomass attained

maxima up to 20 g C m^{-2} at Nordvestbanken in May and a high average biomass (2.3–3.4 g C m^{-2}) prevailed throughout summer and autumn (K. Tande, unpubl. res.).

The average seasonal grazing rate of mesozooplankton at NWB may have been 31–94 g C m^{-2} (Verity *et al.*, 1999), indicating that mesozooplankton grazing was sufficient to consume the entire new production in spring. The low Chl *a* concentration (Table 1), a high new production rate of about 120 g C m^{-2} y^{-1} (Slagstad *et al.*, 1999) and high grazing estimates (Verity *et al.*, 1999) all suggest significant top-down regulation of phytoplankton biomass at NWB in 1994. Due to the lack of more detailed information from West Spitsbergen, indications of grazing controlled phytoplankton biomass are not well support-ed by data, but low suspended Chl *a* stocks (Table 1) and the character of the sedimented material indicate that zooplankton grazing was important (Andreassen *et al.*, 1996). Thus the NAC/WSC continuum along the Norwegian Sea shelf supports top-down regulation of phytoplankton biomass.

Sedimentation of phytoplankton and ice algae was low in areas covered by multi-year ice north of Spitsbergen, as could be expected due to the low nutrient consumption and phytoplankton biomass (Andreassen *et al.*, 1996). Microscopic examination indicated that sedimentation of faecal pellets was more important for vertical flux of biogenic matter than sinking algae at all NS stations. This is supported by reports of relatively high mesozoo-plankton biomass in the area (González and Smetacek, 1994). Faecal pellets produced by sub-ice fauna may also be a source for sinking faecal pellets (Werner, 1997). Due to light-limited growth of phytoplankton even low grazing rates might have been sufficient to control the phytoplankton biomass. Zooplankton and sub-ice fauna were important factors in regulating the vertical flux in areas covered with multi-year ice by producing faecal pellets, also by controlling suspended and sinking phytoplankton biomass. It is suggested that a substantial fraction of the zooplankton present along and on the shelves fringing the Eurasian section of the Arctic Ocean is advected into the region by the NAC/WSC (Fig. 2). For an evaluation of this transport for the pelagic-benthic coupling in the Arctic Ocean, see below.

Although the concentration of suspended Chl *a* was higher in the Barents Sea compared to the Norwegian Sea shelf, the vertical flux data indicated retention of phyto-plankton biomass due to grazing also here (Andreassen and Wassmann, 1998). Thus even during "typical" vernal bloom conditions with "green" waters (Wassmann *et al.*, 1999b), retention of phytoplankton is significant. Calanoid copepods are regarded as the main herbivorous species during spring in the central Barents Sea (Båmstedt *et al.*, 1991; Tande, 1991). Experiments carried out by Hansen *et al.* (1996) indicated low copepod biomass and grazing rates in the euphotic zone at BSS 1–4 in spring 1993. Consequently the suspended Chl *a* concentrations were high. However, variability in overwintering and the concomitant grazing impact on phytoplankton development has a dominating impact on phytoplankton biomass and pelagic-benthic coupling (Peinert *et al.*, 1989; Wassmann and Slagstad, 1993). As a consequence, grazing pressure can be expected to vary with the magnitude of zooplankton present during early spring, giving rise to variable top-down control.

To the extent that the grazing potential of mesozooplankton has been estimated in the area at all, results are only available for the most dominant copepod species (Båmstedt *et al.*, 1991; Hansen *et al.*, 1996). The role of macrozooplankton species such as euphausiids, pteropods, amphipods and gelatinous taxa and under-ice fauna were so far rarely evaluated.

Euphausiids for example, are important contributors to zooplankton biomass in the south-western and western Barents Sea (Dalpadado and Skjoldal, 1991). Euphausiids have been shown to give rise to rapid sedimentation of organic matter through fast sinking pellets in the area (Bathmann *et al.*, 1991; Riebesell *et al.*, 1995).

Microzooplankton can, by high grazing rates, the production of small and slow sinking faecal pellets and coprophagy retain biomass and nutrients in the upper layers (Antia, 1991; Buck and Newton, 1995; Taniguchi, 1999). Their pellets were less prominent at NWB, reflecting pelagic retention (Wassmann *et al.*, 1999c). At BSS stations during spring 1993 microzooplankton grazing was shown to be higher than copepod grazing in the Barents Sea (Hansen *et al.*, 1996). Microzooplankton grazing was largest at BS4 and BS1 (Hansen *et al.*, 1996), both stations with low daily Chl *a* loss rates (Table 2). BS2 and BS3 experienced lower microzooplankton grazing pressure coinciding with larger vertical flux of Chl *a*. At NWB protozooplankton became a most significant prey of food-limited mesozooplankton (Verity *et al.*, 1999; Slagstad *et al.*, 1999).

The classical bottom-up view (*e.g.* Margalef, 1978) regards the hydrodynamic conditions as the most important factor in regulating phytoplankton biomass, species composition and consequently vertical export of biogenic matter. A top-down oriented perspective, however, explains the composition and biomass of phytoplankton species as a function of grazing pressure, escape from grazing and competition, in addition to dependence of light, nutrients and turbulence conditions (*e.g.* Kiørboe, 1993; Wassmann, 1998). Pico- and nanoplankton biomass is usually controlled by protozooplankton due to similar growth rates of predator and prey. Low over-wintering populations and slow reproductive response of mesozooplankton in relatively shallow coastal environments typically prevents a high grazing pressure on large phytoplankton cells, allowing an accumulation of phytoplankton biomass (*e.g.* the spring bloom). Spring blooms in shallow environments are therefore usually dominated by large phytoplankton forms and characterised by large-scale vertical export of ungrazed cells (Kiørboe, 1993). However, such scenarios are not encountered on the NAC/WSC-dominated shelves fringing the eastern Norwegian Sea and Arctic Ocean where zooplankton appears to play a pivotal role throughout the productive season.

6. Zooplankton advection and vertical export: Importance of interannual variation

Mesozooplankton exerting a substantial grazing pressure on phyto- and protozooplankton during spring, seems to be a prevalent feature of both the north Norwegian shelf and off-shelf areas (Peinert *et al.*, 1987; Slagstad *et al.*, 1999). A slow start of the spring bloom due to low water column stability on the shelf and large mesozooplankton biomass during early spring couple primary production and consumers tightly along the shelves flushed by the NAC (*e.g.* Andreassen *et al.*, 1996; Halvorsen and Tande, 1999; Wassmann *et al.*, 1999a). In contrast, zooplankton is obviously not able to prevent accumulations of phytoplankton during spring in fjords (Reigstad *et al.*, 2000) and in the Barents Sea (Skjoldal and Rey, 1989; Wassmann *et al.*, 1999b).

Interannual variation of vertical flux in the Barents Sea has been suggested due to variation in hydrography, ice-cover and advection of zooplankton from the Norwegian Sea (Wassmann *et al.*, 1996; Slagstad and Wassmann, 1997). Sensitivity testing of a simulation model for the Barents Sea indicated that the number of over-wintering and advected

copepods represents one of the most important variables in the Barents Sea ecosystem (Wassmann and Slagstad, 1993). The results presented here indicate that advection of zooplankton might have even greater implications at the shelf off Northern Norway, West-Spitsbergen, in the southern Barents Sea and probably also north of Spitsbergen, giving rise to control of both phytoplankton biomass, species composition as well as influencing the vertical flux. Earlier reports describing classical spring blooms on the shelf off Northern Norway (Rey, 1981; Hegseth et al., 1995), suggest that interannual variation exists. The NWB results from Nordvestbanken may thus indicate that top-down control may vary between years.

Both the timing of the onset of phytoplankton production and the size of the local over-wintering population or advected zooplankton biomass are thus important factors influencing the regulation of the vernal bloom and its vertical export. The late onset of reproduction and a long generation time of each mesozooplankton cohort typically gives rise to a mismatch between primary and secondary production in the central Barents Sea and in fjords in northern Norway (Eilertsen et al., 1989; Tande, 1991; Reigstad et al., 2000). An important key for the regulation of the vertical flux of phytoplankton in these areas is therefore the timing between advection of mesozooplankton and the development of phytoplankton growth during spring.

Variation in hydrodynamic conditions may influence the interannual magnitude of new production and zooplankton abundance (Slagstad and Wassmann, 1997; Vernet et al., 1998; Wassmann et al., 1999b). Thus both the potential vertical flux and retention of biogenic matter must vary interannually. The onset of the phytoplankton growth season is mainly confined to a time interval of a couple of weeks between April to June, varying slightly between different areas. The phytoplankton accumulation starts earlier and develops more rapid in the MIZ. This is due to earlier and stronger stratification compared to the southern Barents Sea and the shelf area off northern Norway, where phytoplankton blooms are caused by periodically reduced vertical mixing (Heimdal, 1974; Rey and Loeng, 1985). The MIZ region is also most remote to the major over-wintering areas for mesozoo-plankton in the Norwegian Sea. Consequently, advection of zooplankton to these areas may be more sporadic, dependent on transport time and usually occurs later in the season (e.g. Reigstad et al., 2000).

Long-term observations from weather ship M in the Norwegian Sea show that the ascent of copepods is characterised by considerable interannual variation. Maximum abundance may occur as early as April or as late as August (Lie, 1968). This suggests that the timing between primary production and advection of grazers may be subjected to strong interannual variations. Low over-wintering success of mesozooplankton in the Norwegian Sea, or changes in current pattern can also result in less advection of mesozooplankton onto and along the shelf, as has been suggested for the southern and central Barents Sea (Pedersen, 1995). Consequently, in years with low zooplankton abundance during spring, a classic phytoplankton bloom with a predominance of export food chains may develop on the shelf off northern Norway and result in stronger spring sedimentation of phytoplankton-derived matter. Accordingly, during years of strong and early zooplankton advection a similar situation as found at NWB may be expected in the southern Barents Sea and around Spitsbergen.

7. Advection of zooplankton into and top-down regulation in the Arctic Ocean?

Recent investigations of the physical oceanography of the Eurasian Basin imply that significant amounts of Atlantic water are annually advected into the basin, mainly along the shelf break north of Spitsbergen and through the St. Anna Trough between Franz Josef Land and Novaya Zemlya (AMAP, 1998). The flow through the Barents Sea varies between 2-3 Sv (Ådlandsvik and Loeng, 1991) while the boundary current close to the Lomonossov ridge is about 5 Sv (F. McLaughlin and E. Carmack, pers. com.). In addition, intermittent draining of several Sv of cool and salty water masses which accumulate in the Barents Sea basins during sea ice formation, adds to the discharge of Atlantic water into the Arctic Ocean (Midttun and Loeng, 1987). Water of NAC-origin flows as a boundary current subducted under the Arctic water and the halocline in a circular pattern along the Eurasian shelf break towards the east (Fig. 2). It crosses the Arctic Ocean along the Lomonosov or Alpha Ridge to the Canadian side and leaves, mixed with Arctic water, through the Fram Strait. At times modified Barents Sea water may penetrate along the entire Siberian coast into the Beaufort Sea area (F. McLaughlin and E. Carmack, pers. com.).

Many of the zooplankton species living in the subarctic region, have life cycles of one year or longer and overwintering at depth based on lipid reserves. It is suggested that the high abundance of zooplankton, which characterises the NAC (Noji et al., 1999), is advected through the Barents Sea and along the West- and North-Spitsbergen shelf into the Arctic Ocean, probably also in winter (Pedersen et al., 1995). Atlantic species have frequently been detected in the northern Barents Sea (e.g. Falk-Petersen et al., 1999) and north of Spitsbergen and Novaya Zemlya (Mumm, 1993). Some of the expatriates in these Arctic waters, for example the typical Atlantic species Calanus finmarchicus, is out of the temperature range favourable for spawning (Falk-Petersen et al., 1999). The consequent supply of allochthonous biomass from the south-west and north onto the Barents Sea shelf and from west to east along the Eurasian shelf into the Arctic Ocean is thus based on "down-stream" NAC/WSC production. It derives partly from the previous year. Similar scenarios with advection of Neocalanus plumchrus through Bering Straight into the western Beaufort Sea have been detected (S. Smith, pers. com.). Annual carbon budgets inside the Arctic Ocean can thus not be in balance with regard to meso- and macrozooplankton as only their contemporary grazing and growth, but not all of their biomass is based on the autochthonous production.

Massive differences in zooplankton standing stock have been detected along gradients between the NAC/WSC and East-Greenland Current (Noji et al., 1999), suggesting that far more zooplankton is advected into than out of the Arctic Ocean. This suggests a net loss of zooplankton biomass in the Eurasian basin, which could be caused by decreased spawning success by the expatriates, carnivory, or death. Similar to the net advection of zooplankton into the headwaters of fjords and estuaries (Lewis and Thomas, 1986), the ecological setting of zooplankton in the Arctic Ocean could be rephrased by the proverb "one foot in the grave" (Soetaert and Herman, 1994), which was applied for large-scale death of advected zooplankton in an estuary. The advective net flux of zooplankton into the Arctic Ocean is regulated by both the climatologically varying strength of NAC inflow, modifications in the Barents Sea and inter-annual differences in zooplankton abundance

outside the Arctic Ocean. The import of zooplankton also implies that at least the boundary current region of the Arctic Ocean may be top-down controlled as suggested by data from Andreassen *et al.* (1996). The Arctic Ocean is thus not an almost closed system with modest abiotic and biotic variability, but it is an open, variable, advective and circular system subject to considerable climatic and biogeochemical variability.

8. Conclusion

The hydrodynamic conditions on subarctic and arctic shelves off northern Norway, off Spitsbergen and in the Barents Sea play a major role in favouring export production out of the euphotic zone. The advection of variable magnitudes of NAC/WSC water, including nutrients and plankton, is of utmost significance for the function of the region. Advection is not only regulated by NAC/WSC mass flow, but also by the configuration of the shelf. Troughs, coastal banks and the shape of the slope and shelf break region modify the impact of the NAC/WSC on the pelagic ecosystem dynamics. Suspended biomass and vertical export are strongly modified by zooplankton grazing and *in situ* recycling. The present data suggest that biological and physical processes *in concert* regulate vertical flux of phytoplankton and biogenic matter along the NAC/WSC continuum. Significant accumulation of phytoplankton biomass during spring can be encountered at a distance to the shelf break (*e.g.* the central Barents Sea) or areas restrained from regular, large-scale water exchange (*e.g.* fjords). Stratification during spring will promote the vernal bloom development (*e.g.* the MIZ). In all other areas under the influence of the NAC, vernal blooms can only be encountered during events of insignificant zooplankton advection. The advection of zooplankton and its concomitant top-down regulation of suspended biomass and vertical export, calls for a new manner to study the plankton ecology of the north-eastern North Atlantic and adjacent Arctic Ocean. It calls for what Matthews and Heimdal (1980) call an "ecology of advection". It further points at the pivotal, but still not sufficiently reckoned role of zooplankton for global marine productivity (*e.g.* Banse, 1992, 1995).

Joint regulation by resource availability (bottom-up) and predation (top-down) offers a new conceptual framework in which the apparent regulation of the pelagic trophic structure and the pelagic-benthic coupling in subarctic and arctic areas in northern Norway, Spitsbergen, the Barents Sea and the Arctic Ocean may be resolved. Future studies need to expand the basic knowledge regarding the importance of pelagic key species, which shape the carbon flow. The entire size spectra of phytoplankton consumers, their role in structuring the pelagic carbon flow, their life cycles and where they were spawned, is essential to acquire a comprehensive understanding of the retention and export potential in the region.

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