Vertical export of particulate organic carbon: Attenuation, composition and loss rates in the northern Barents Sea

Marit Reigstad a,*, Christian Wexels Riser a, Paul Wassmann a, Tatjana Ratkova b

a Norwegian College of Fishery Science, University of Tromsø, N-9037 Tromsø, Norway
b Shirshov Institute of Oceanology, Russian Academy of Science, 36 Nahimovsky Prospekt, 117997 Moscow, Russia

A B S T R A C T

The fate of primary production (PP) is closely linked to the ecosystem structure in aquatic environments. High pelagic consumption and recycling reduce quantity and quality of vertically exported organic material, while low to moderate pelagic consumption allows more carbon of higher quality to reach benthic communities. To evaluate the driving forces influencing changes in quantity and composition of vertical flux with depth and environmental conditions in ice-covered waters, short-term sediment trap deployments at 6–8 depths from 20 to 200 m were conducted. Eleven stations in the northern Barents Sea were investigated during early, peak and late bloom scenarios in 2003–2005. Vertical particulate organic carbon (POC) export ranged 140–760 mg C m⁻² d⁻¹ at 30 m and 58–720 mg C m⁻² d⁻¹ at 90 m depth. Strongest vertical carbon flux attenuation was observed during peak bloom scenarios. The pycnocline always defined the depth of the strongest attenuation. The POC export was highly correlated with Chl a flux (r² = 0.89) and with a low POC/Chl a ratio, this indicates that fresh material is being exported to depth. A tight coupling between POC export at 90 m and particulate PP (r² = 0.61) was observed and suggests that on average 36% of daily PP was exported as POC. Deep vertical mixing observed in the Polar Front or less stable water masses did, however, enhance the vertical export and loss rates considerably. Annual estimates of vertical POC export to PP, suggests weaker retention, and thus stronger pelagic–benthic coupling in Arctic compared to the Atlantic region of the Barents Sea.


A R T I C L E I N F O

Keywords:
POC/PON ratio
Phytoplankton
Vertical flux attenuation
Mixing-induced vertical export
Barents Sea
Arctic shelf

1. Introduction

At high latitudes, seasonality is strong with ice cover and polar nights creating a narrow time-window of sufficiently available light, water-column stabilisation and nutrients that facilitate primary production (PP) (Sakshaug, 2004). Following ice melt, productivity can be intense and prominent blooms form. The ecosystem response is of vital importance for the fate of the bloom (Bauerfeind et al., 1997; Falk-Petersen et al., 2000; Michel et al., 2006). Vertical export of organic material represents often the remains of the pelagic PP after consumption and remineralisation (Peinert et al., 1989; Noji, 1991; Wassmann, 1998). An efficient pelagic food web reduces the quantity and quality of organic material exported, while processes promoting fast sinking, such as aggregation, enhanced particle density or physical processes, facilitate benthic utilisation and carbon sequestration (Grebiemeier and Barry, 1991; Wassmann, 1998; Turner, 2002; De La Rocha and Passow, 2007). Combined investigations of pelagic food webs and vertical carbon export are therefore powerful tools revealing major pathways of carbon flow through the ecosystem. To understand vertical flux regulation, identification of the key players and processes that control vertical export in different regions or seasons is required.

With increased focus on global carbon cycling and efforts to model marine ecosystems, the relevance of the model output depends on our ability to select and include the factors of importance (Boyd and Trull, 2007). This involves key organisms and processes as well as relevant biogeochemical rates and sufficient coupling between biology and physics. While carbon export in global models often is based on measurements > 500 m, the main regulating processes determining the carbon export are found in the upper part of the water column (Olli et al., 2001; Wassmann et al., 2003; Boyd and Trull, 2007). During the last decade, high-resolution sediment trap measurements in the upper 200 m have pointed to potentially high vertical carbon flux attenuation over short vertical distances in locations ranging from Arctic, sub-Arctic coastal and boreal coastal environments (Riebesell et al., 1995; Andreassen and Wassmann, 1998; Reigstad et al., 2000; Olli et al., 2001, 2002). The flux attenuation describes the retention as seen through the POC flux profile. The main cause...
for the attenuation was attributed to retention processes like grazing or remineralisation by the present pelagic community.

Vertical carbon flux data from Arctic ecosystems show an extensive variability both spatially and interannually (Wassmann et al., 2004). Carmack and Wassmann (2006) suggested a conceptual model of the carbon flux attenuation based on a physical–biological continuum where the primary productivity and the depth of the mixed layer and grazing efficiency are the main driving forces. To identify and verify such key driving forces, it is necessary to know the pelagic community as well as the physical conditions accompanying a given vertical flux scenario. Over a short-time period, investigations of ecologically contrasting Arctic scenarios are possible in the Barents Sea, due to its hydrographic complexity over short distances.

The Barents Sea is highly productive and the largest shelf sea of the Arctic Ocean (Wassmann et al., 2006a). Trenches and banks provide a complex topography ranging from 30 to 500 m in depth (mean depth of 230 m). The Barents Sea is an deep inflow shelf (Carmack and Wassmann, 2006) characterised by the inflowing Atlantic water (AW) in south and west, and the colder water in north and east being AW transformed through cooling, freezing and melting processes or water of Arctic origin (ArW) advected from north (Loeng, 1991; Schauer et al., 2002). The complex topography, the presence of seasonal sea ice and the advective impact from two water masses create hydrographic settings with considerable impact on the pelagic processes. The focus of the present investigation was the northern Barents Sea region where seasonal ice cover contributes to a production regime controlled by available light in early spring, and strong stratification resulting from ice melting restricting the input of new nutrients and the new production after the first bloom.

Within the multidisciplinary project ‘Carbon flux and ecosystem feedback in the northern Barents Sea in an era of climate change’ (CABANERA), we focus here on the vertical carbon export as part of the fate of PP and supply of food to benthos. We investigated in particular the most prominent depth intervals for vertical flux regulation, and the relative impact from primary productivity and ecosystem consumption versus physical forcing.

2. Material and methods

2.1. Sampling area

During three cruises with the ice-enforced R/V ‘Jan Mayen’ in 2003–2005, 11 stations were selected for 24-h vertical-flux studies in the northern Barents Sea and the shelf break to the Arctic Ocean (Fig. 1). Station depths ranged 150–3500 m, with sampling periods including May in 2005, and mid-July and late July in 2003 and 2004, respectively (Table 1). Stations were successively identified by Roman numbers (I–XVIII). The ice class of the ship and the need for sufficiently robust ice floes to anchor sediment trap arrays limited the sampling scenarios to stations with close to open-drift ice. Station XVIII was the only open-water station.

2.2. Suspended biomass and vertical export

Suspended material was collected at 12–13 depths during the first CTD profile (Seabird SBE9) at each station using 12 Niskin water bottles mounted on a rosette for the 90–200 m depths (90, 120, 150 and 200 m), followed by Go-Flo-bottle sampling for the upper 1–60 m (1, 5, 10, 20, 30, 40, 50, 60 m and Chl a max). Sub-samples for biological and chemical characterisation such as chlorophyll a (Chl a) and particulate organic carbon and nitrogen (POC, PON) were taken.

Sediment traps were deployed at 6–8 depths between 20 and 200 m or as deep as the station depth allowed (Table 1). In 2004, the mooring was lost at station IX and replaced with a shorter one of 90 m only at stations X and XI. Strong currents and drift over shallow regions spoiled the vertical flux measurement at station XIII. The array was anchored to a drifting ice floe and balanced to neutral weight with sub-surface buoys and a 40 kg weight in the lower end. At the open-water station XVIII, the mooring was balanced to float. The traps comprised a double set of cylinders at each depth (inner diameter = 72 mm, H/D ratio = 6.25) balanced in a gimbaled frame (KC Denmark A/S Research equipment). The traps were deployed for ~24 h (Table 2) without baffles or addition of any preservatives. The sediment traps have previously been calibrated against thorium (234Th) in the Barents Sea where 234Th-based estimates of vertical POC export corresponded to the sediment trap-based POC export with 70–100% trapping efficiency (Coppola et al., 2002). After retrieval, the content of the traps was transferred to 5-L bottles and gently mixed before sub-samples were taken for microscopic analysis and biogeochemical characterisations of Chl a, POC and PON.

Samples for phytoplankton determination (100–250 mL) were preserved with a Lugol-glutaraldehyde mixture (Rousseau et al., 1990) to enhance the preservation of flagellates. In 2005, phytoplankton were determined based on staining with primuline and fixation with 3.6% glutaraldehyde and 10% glycerol according to modification of methods described by Nejstgaard et al. (2001) to enhance the trophic identification of the microplankton community (trophic data presented elsewhere). The phytoplankton data presented here include autotrophic and heterotrophic plankton in the size class of nano- and microplankton. For simplicity, we use the term phytoplankton.

2.3. Analysis

Water for Chl a determination was filtered onto 25-mm Whatman GF/F filters in triplicates per depth (100–200 mL),...
Ice cover is given according to standard ice categories (0 is open water, 4–7 is open drift ice and 9–10 is very close drift-ice ice). Sediment traps were deployed at 6–8 depths for periods of approximately 1 day. Ice-cover data were made available by H. Hop.

Table 2
Characteristics of stations categorised to four scenarios, with average depth of Chl a max, average POC/PON ratio in exported material, average loss rates of POC and Chl a and % POC export relative to primary production (PP).  

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Station</th>
<th>Average Chl a depth (m)</th>
<th>C/N ratio</th>
<th>POC loss %</th>
<th>Chl a loss %</th>
<th>% POC exported/PP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early bloom</td>
<td>IV, VII, XVII</td>
<td>7 (1–10)</td>
<td>6.7 (5.5–7.7)</td>
<td>0.6 (0.5–0.7)</td>
<td>1.3 (0.7–2.1)</td>
<td>28 (17–38)</td>
</tr>
<tr>
<td>Peak bloom</td>
<td>II, III, X, XI, XIV, XVI</td>
<td>20 (10–28)</td>
<td>8.7 (7.8–9.9)</td>
<td>1.0 (0.5–1.5)</td>
<td>1.1 (0.6–2.0)</td>
<td>37 (24–52)</td>
</tr>
<tr>
<td>Late bloom</td>
<td>I</td>
<td>37</td>
<td>8.5</td>
<td>0.5</td>
<td>0.2</td>
<td>24</td>
</tr>
<tr>
<td>Deep mixing</td>
<td>XVIII</td>
<td>10</td>
<td>6.9</td>
<td>4.0</td>
<td>4.5</td>
<td>72</td>
</tr>
</tbody>
</table>


3. Results

3.1. Sampling region

The investigation area included the southern-to-northern marginal ice zone of the western Barents Sea and the shelf break to the Arctic Ocean (Fig. 1). Hydrographically, stations were clustered according to their location and dominating water mass according to Sundfjord et al. (2007) and Wexels Riser et al. (2008). The Northern Shelf Break Stations included stations VII and XIV. They were characterised by surface melt water and ArW overlying eastward-flowing AW. Station XIV located in the steeper part of the shelf break, had a deeper mixed layer and deeper pycnocline, were warmer, more saline and denser compared to the more northern station VII. The interior stations II, III, X and XI located at the shelf were dominated by ArW. Low-salinity melt water characterised the upper 25–30 m, and modified AW could be found in the deeper regions. In the southern Barents Sea, AW advected from south-west crosses the Polar Front and subducts below the ice and ArW coming from the north-east. The water masses at the southern MIZ Stations I, IV, XVI and XVIII showed AW characteristics modified depending on the distance from the Polar Front. All stations but one were ice covered, with surface melt water above the density gradient. Station XVIII was located in the Hopen depth, and had no signal of previous ice cover. Owing to strong winds during sampling of this station in 2005, the weak pycnocline initially present broke down resulting in a homogenisation of the water column >200 m (Sundfjord et al., 2007). In 2003, station I was located in the same region, but extensive ice distribution the previous winter placed this station within the ice-covered region that year.

Detailed water-mass characteristics, current patterns and hydrographic description of the stations are presented and discussed in detail in Kiviäinen (2007) and Sundfjord et al. (2007) for stations I–IV and VII–XVIII, respectively.
3.2. Bloom scenarios and spatial heterogeneity

The similarities in ice conditions at the selected stations restricted the variability of ecological scenarios to different phases of the spring bloom, ranging from early bloom to peak bloom and late bloom. Each year, the investigated stations represented two or more of the hydrographical regions and different bloom stages. The stations also were grouped according to their blooming stage based on nutrient conditions, level and vertical pattern of PP, Chl a max (Hodal and Kristiansen, 2008) (Table 2) and dissolved oxygen (Hancke, 2007). For further description of bloom-stage determination, see Hodal and Kristiansen (2008). The early bloom stations included stations IV, VII and XVII, while station I was the only late bloom station with depleted nutrients and a deep Chl a max.

Station XVIII was exposed to strong wind-induced mixing during sampling. This caused a deepening of biomass distribution and re-fertilisation of the upper layer with nutrients (Hodal and Kristiansen, 2008). This station is considered a mixed station due to its potential for continued blooming.

3.3. Vertical carbon export

The high vertical resolution of POC and PON export measurements provided detailed insight to the changes in daily fluxes in the upper 200 m (Fig. 2). The vertical POC flux profiles for all 11 stations showed a pronounced decrease in the export of organic carbon within the upper 200 m, and the strongest decrease was observed in the depth range of 30–60 m, close to the depth of the pycnocline (Fig. 2). Maximum POC flux was observed at 20–40 m depth, and minimum was observed from 90 to 200 m depth. One station from each investigated year fell into the early bloom group (Table 2). These stations (stations IV, VII and XVII) had generally lower POC flux and a less pronounced decline in flux compared to the peak bloom stations. Maximum POC flux at the early bloom stations ranged 195–275 mg C m$^{-2}$ d$^{-1}$, with minimum of 40 mg C m$^{-2}$ d$^{-1}$ observed at the northern shelf break station VII (minimum of 40–145 mg C m$^{-2}$ d$^{-1}$, including all early bloom stations).

Two stations from each investigated year were considered peak bloom stations (Stns II, III, X, XI, XIV and XVI; Table 2). During peak bloom, highest vertical carbon flux were measured in the upper layers with maximum of 870 mg POC m$^{-2}$ d$^{-1}$, at 20 m on the southern MIZ station XVI (Fig. 2). Despite high fluxes above the pycnocline, stronger attenuation of the POC flux curve was seen during peak bloom, leaving only 120–220 mg POC m$^{-2}$ d$^{-1}$ ($n = 6$) to be exported at 90–200 m depth.

Only station I was characterised as a late bloom station. The curvature and flux rates resembled the early bloom stations with POC fluxes ranging 230–110 mg C m$^{-2}$ d$^{-1}$ at 20 and 200 m, respectively. Owing to the mixing event at station XVIII, characteristics of this station according to bloom stage were...
complicated. The vertical mixing induced nearly uniform vertical flux rates in the upper 90 m, and the rates were as high as surface fluxes during the peak bloom with \(-750 \text{ mg C m}^{-2} \text{d}^{-1}\). Even at 200 m, POC flux were \(400 \text{ mg C m}^{-2} \text{d}^{-1}\) and twice the POC export measured at the peak bloom stations.

### 3.4. Contribution from algal material

Contribution from PPC to the vertical POC flux was examined for three bloom scenarios (early, peak and late bloom represented by station XVII, II and I, respectively) and the well-mixed station XVIII (Fig. 3). Although the vertical POC flux profile of the early bloom station XVII in the eastern Barents Sea and late bloom station I in the Hopen Trench was comparable with respect to vertical export of POC and shape of profile, they differed in composition. In the early bloom scenario, PPC contributed up to 65% of the POC flux, mainly through flagellates and diatoms (Table 3). At the late bloom scenario (station I), PPC contributed <7% of the POC flux, with *Phaeocystis pouchetii* cells and heterotrophic flagellates dominating the export. During the peak bloom, diatoms (mainly *Thalassiosira* spp.) dominated the export with up to 90% of the PPC carbon (Table 3), but the attenuation was strong in the 30–40 m depth region. The most efficient vertical export of phytoplankton material was measured at the deeper mixed station. High PPC flux (ranged 530–230 mg C m\(^{-2}\) d\(^{-1}\)) was revealed from 20 to 200 m depth, suggesting fast export and low retention of algal material. Although the POC export was higher at station XVIII than at any other station, 30–70% of the particulate carbon export was due to PPC.

The vertical POC export was highly correlated with the Chl a export when all investigated depths and stations were included \((R^2 = 0.89, n = 52; \text{Fig. 4B})\). The correlation was weaker for the suspended POC and Chl a \((R^2 = 0.65, n = 156; \text{Fig. 4A})\), indicating a non-algal POC fraction not contributing to the vertical export. According to regressions, the overall POC/Chl a ratio of the suspended material was estimated to 46, while it was 54 in the vertically exported material.

### 3.5. POC/PON ratios in suspended and exported organic matter

The C/N ratio indicates the quality of organic material, as degradation increases the elemental composition from the Redfield ratio of 6.6 assumed for phytoplankton biomass. No general trend with increased POC/PON (C/N) ratio was observed with depth for the suspended or the exported material, suggesting fast export and low degradation of the exported material. The mean C/N ratios of the exported material varied between stations, with the early bloom stations VII and XVII having the lowest rates together with the deep mixed station XVIII (Table 2). The C/N (atomic) ratio in the particulate suspended material, including all

[Fig. 3. Vertical flux of phytoplankton carbon (PPC) with the total POC flux during four different scenarios: early bloom, peak bloom, late bloom and a deep-mixed station (stations XVII, II and XVIII, respectively). The vertical flux at eight depths from 20 to 200 m is shown.]

depths and stations sampled, ranged 3.5–24.6 (Fig. 5A), with a mean of 7.9±0.4 (95% CI). No difference from the suspended material was measured for the C/N ratio of exported particulate organic material, with a corresponding mean and CI of 7.9±0.2 (95% CI). The variance of the suspended material was higher compared to the exported material (Fig. 5A and B) due to C/N ratios >10.5 at the early bloom station IV. Here and at depth of the late bloom station I, appendicularian houses were observed in the water column and detrital remains might have influenced the suspended C/N ratio. The vertical flux did not show increased C/N ratios at these stations, indicating that the signal came from unidentified non-sinking material, as appendicularian houses are assumed to settle. No houses, however, were observed in the traps at those stations.

3.6. Integrated biomass, daily loss and export rates

The integrated biomass 0–90 m of POC and Chl a varied considerably between the stations and ranged from 9 to 39 g POC m⁻² and from 12 to 590 mg Chl a m⁻². The early bloom station VII located at the northern shelf break had lowest biomass, while the highest biomass was measured at the interior peak bloom station XVI (Fig. 6). Integrated POC and Chl a biomass showed similar patterns at most stations with POC/Chl a ratios of the integrated biomass ranging 60–145, but at the early and late bloom stations IV, VII and I, the biomass was carbon-dominated with POC/Chl a ratios of 427–763.

Except for the deep mixed station XVIII, daily loss rates were generally low, ranging 0.5–1.5% for POC and 0.2–2.1% for Chl a. The
pattern did not reflect scenarios of high or low suspended biomass, but average POC loss rates were slightly higher for peak bloom compared to early bloom stations (Fig. 6, Table 2). The average loss of Chl \(a\) always exceeded the POC loss, except the late bloom station (Table 2), implying the export of Chl \(a\) containing material was favoured. The deeper mixed station XVIII was clearly different with loss rates exceeding 4% of suspended biomass per day. High vertical export at this station also was reflected in the export percentage of daily PP. Hodal and Kristiansen (2008) measured particulate PP to be about 1000 mg C m\(^{-2}\) d\(^{-1}\) at station XVIII, the second highest of all investigated stations. The carbon flux at 90 m corresponded to 72% of the PP at Station XVIII, while ranging from 17% to 52% at the other stations. No bloom stage related patterns were identified (Fig. 6, lower panel).

4. Discussion

The Barents Sea is a highly productive, but heterogeneous Arctic shelf sea characterised by Atlantic influence in the south-west, and more Arctic conditions with seasonal ice cover in the north and east (Wassmann et al., 2006a). Looking at the seasonal timing of peak organic carbon export in productive Arctic areas, Caron et al. (2004) concluded that the North Water polynya (NOW) peaked later (July) than the central Barents Sea (May, in Olli et al., 2002), but earlier than Frobisher Bay (August, in Atkinson and Wacasey, 1987). Moran et al. (2005) also reported peak fluxes during July and August rather than May–June in the Chukchi Sea, while annual carbon flux records in the North East Water polynya (NEW) showed highest export rates in August–October, clearly related to ice cover (Bauerfeind et al., 1997). The present investigation revealed that peak bloom conditions accompanied by high sedimentation rates as well as early bloom scenarios may occur within a wide period including mid-May to late July in the northern Barents Sea. The onset of the Arctic marine spring is closely linked to ice conditions, ice melt and snow cover regulating the light availability (Sakshaug, 2004). The timing therefore can be highly dynamic and variable in time and space (Ramseier et al., 1999), between as well as within areas, and closely related to climate. The key to understand organic carbon...
flux dynamics includes thus physical as well as modulating biological regulation mechanisms. The patterns of vertical carbon export observed in the northern Barents Sea during this study revealed a potential for strong pelagic regulation in the upper aphotic zone. The strongest retention, here seen as reduction in vertical flux, is associated with the pycnocline. There exist also a significant potential for high export (and consequently reduced retention) when strong wind and weak stratification short-circuited the retentive filter (sensu Wexels Riser et al., 2001) through mixing.

4.1. Vertical flux attenuation

While effort has been made to establish carbon flux rates at depth to look for global carbon sequestration patterns, less attention has been given to processes regulating the vertical flux from productive surface layers and grazing loss from the heterotrophic community through the twilight zone (Wassmann et al., 2003; Boyd and Trull, 2007). Buesseler et al. (2007) argues for an increased focus on the twilight zone in the 150–500 m depth range to detect how ecosystems enhance or retain the organic material from the productive layer. The 11 vertical flux profiles from the northern Barents Sea suggest that the most prominent vertical flux regulation takes place even further up in the water column than suggested by Buesseler et al. (2007). For an Arctic shelf sea like the northern Barents Sea, the depth interval of 30–60 m is extraordinary active. Here, a vertical hot spot is identified where flux retention takes place and where flux attenuation is most prominent (see also Wexels Riser et al., 2007). From 90 to 200 m depth, the vertical export was surprisingly stable, suggesting that the major retention and heterotrophic grazing takes place at shallower depths, and that slower remineralisation processes dominate below 90 m. This agrees well with findings from previous vertical flux studies in the central Barents Sea (Olli et al., 2002). A high correlation between surface-sediment pigments (at 195–503 m) and the vertical pigment flux at 90 m, supports limited loss below 90 m (Renaud et al., 2008). High vertical resolution of sediment traps at adequate depths for vertical flux attenuation is a prerequisite to detect specific attenuation layers. A study off the north-west coast of Spain using a similar approach detected high retention and a sharp vertical flux attenuation depth interval at around 60 m for an off-shelf upwelling system (Olli et al., 2001; Wexels Riser et al., 2001). Also sub-Arctic fjord-systems show similar vertical patterns (Reigstad et al., 2000).

The close correspondence between the maximum attenuation and the pycnocline depths observed in this study (Fig. 2) points to the importance of retention in this layer. The attenuation curves visualise the results of intensified ecological processes like grazing and remineralisation at the border between the illuminated upper mixed layer and the nutrient-rich water below. We suggest that this is not only the case in ice-covered regions, but typical also for other systems stratified at moderate depths. In order to quantify vertical flux regulation, increased attention has to be paid to and proportionate spacing of sediment traps introduced in the 20–200 m depth interval.

Comparison of the three different bloom phases in the Barents Sea reveals that the strongest vertical carbon flux attenuation is encountered during peak bloom scenarios, i.e. when suspended biomass and thus the potential flux are highest. This suggests that retention processes are highly efficient also during peak blooms in terms of preventing export, although the attenuation strength will be sensitive to the heterotrophic grazing capacity (Carmack and Wassmann, 2006). Grazing impact estimates from small mesozooplankton (estimated from gut fluorescence) as well as for *Calanus* spp. (estimated from egestion rates) (Pasternak et al., 2008; Wexels Riser et al., 2008) also had maxima during the peak bloom phases. At the same time, the POC export was doubled at 90 m compared to the early and late bloom scenarios, suggesting that the pelagic as well as the benthic food webs receive an important fraction of the annual energy demands during the spring bloom (on average about 35% of annual total supply (Table 5)).

The bulk POC flux profiles observed for the early bloom and late bloom stations showed the similar patterns and rates, but microscopy investigations revealed that the carbon flux during these two bloom phases differed extensively in composition during the two bloom phases (Fig. 3). A diverse group of phytoplankton contributed to the organic carbon flux during the early bloom, while faecal pellets were of minor importance (Wexels Riser et al., 2008). The late bloom carbon flux was dominated by detrital matter where hardly any phytoplankton or faecal pellets could be identified (Table 3, Wexels Riser et al., 2008). The different composition indicated that the two carbon flux profiles represented different ecosystem functioning. Top-down regulation was minor in the early bloom phase, leaving ungrazed phytoplankton cells to settle (20–80%; Table 3). In the late bloom phase, more efficient retention processes left only reworked detrital material to settle, characterised by low POC (2–7%), non-recognisable material, elevated C/N ratios (8.2; Table 2) and high Chl a/phaeopigment ratio (data not shown).

A striking feature was the high vertical export induced by a wind induced, strong mixing event observed at station XVIII. The loss rates for POC and Chl a were in general low for all phases of the bloom observed, but retention short-circuited when vertical mixing changed the export from passive gravitational sinking to also include actively transported POC export through mixing. A similar increased flux response to mixing was observed close to the Barents Sea Polar Front by Olli et al. (2002). Such events transform shallow biomass peaks to an evenly distributed biomass down to >90 m. Compared to the slow gravitational sinking rate <1 m d⁻¹ measured for Arctic phytoplankton (Mei et al., 2003) in columns with no turbulence, a mixing-induced elevator from 40 to 90 m speeds up the export with >50 days favouring fresh organic input to the benthic community. Facilitation of aggregate formation by turbulence will further increase the sinking speed and export (Kriese et al., 1994), and also facilitate export of small phytoplankton (Richardson and Jackson, 2007). We can therefore suggest that regions characterised by mixing induced by topography, fronts, low stratification and wind favours pelagic–benthic coupling through high-quantity and high-quality export.

4.2. Vertical carbon export: composition and characteristics

In spite of moderate loss rates (0.3–1.2% d⁻¹ during stratified conditions; Table 2), the vertical export of organic matter observed in the northern Barents Sea in 2003–2005 reflected a coupling between the pelagic and benthic community, with relatively high flux of material carrying signals of low degradation. An investigation of vertical carbon flux on the shelf surrounding Spitsbergen in 1991 (Andreasen et al., 1996) detected strong impact of multiyear-ice, resulting in low carbon flux, degraded matter as well as input of terrestrial material (as reflected by C/N ratios of 27). Some of these stations were revisited during the present investigations, but reflected a very different scenario where signals from multiyear-ice and terrestrial input where absent. At station 124 of Andreasen et al. (1996), located east of Nordaustlandet, corresponding to our station XI, vertical POC flux at 60 m was 50 and 220 mg POC m⁻² d⁻¹, in July 1991 and 2004.
respectively. The contribution from phytoplankton was <6% in 1991, compared to 7–81% in the present investigation. Although both stations were located in the northern marginal ice zone of the Barents Sea at the time of sampling, possible different physical conditions and heavier ice influence in 1991 versus seasonal ice in 2004 illustrate how reduced ice cover can influence the carbon flux through enhanced light and productivity. Chlorophyll-containing material explained most of the variability in the POC flux, with a stronger correlation between vertical POC and Chl $a$ flux ($R^2 = 0.89$, $p < 0.0001$) compared to the suspended material (Fig. 4A and B). The minor difference in POC/Chl $a$ ratios between suspended and exported material (45 and 54, respectively, estimated by regression) also suggest that the particles that carried on through the retention filter (Wexels Riser et al., 2001) were rapidly exported from the pelagic to the benthic community with high-quality food supply during the Arctic spring.

The wider range in the vertical export POC/Chl $a$ ratios reflect similar patterns seen from the microscopic examination of exported material, with high ratios and minor phytoplankton contribution after the peak bloom due to increased retention and degradation of organic matter. During the early and peak bloom scenarios, the grazing capacity of the zooplankton could not match the phytoplankton production, leaving ungrazed cells to settle and contribute up to 80% of the POC export. Diatoms were an important contributor to C flux at the early and peak bloom station, with a dominance of typical ice-associated pennate diatoms like Nitzschia frigida, Pauuliella taeniata and Navicula pelagica sinking during the early bloom, similar to sub-ice export in the Barrow Strait (Fortier et al., 2002). Typical spring bloom species like the centric diatoms Thalassiosira antarctica and T. nordenskioldii dominated the peak bloom phytoplankton export. Similar to findings during a seasonal study in the central Barents Sea (Olli et al., 2002), contribution from the colonial prymnesiophyte Phaeocystis pouchetii was important at the weaker stratified and deep mixed station. While the importance of Phaeocystis spp. for vertical carbon flux continuously is debated (Schömann et al., 2005), sediment trap evidence suggests that episodes of deep mixing is an efficient vehicle for vertical export of Phaeocystis spp. (Reigstad and Wassmann, 2007). Melosira arctica is described as an important species contributing to carbon export in other Arctic regions like the North East Water polynya (Bauerfeind et al., 1997) and North Water polynya (Caron et al., 2004). The lack of multiyear ice influence or too late sampling after the initial ice-melt may have influenced the minor impact of ice-algae for vertical flux during the present study. Stable isotopes indicated only few occasions were ice-algae contributed to the flux signal (Tamelander et al., 2008).

The C/N ratio in settling organic matter often has proved to be higher than the Redfield ratio. In the present study, the C/N ratio of the exported organic material was surprisingly consistent between stations and depths with an average of 7.9 ± 0.2. A similar ratio of 8.0 ± 0.9 was reported from traps measurements following the spring bloom in Disko Bay, West Greenland (Juul-Pedersen et al., 2006) and 8.3 at the marginal ice zone of northern Barents Sea (Andreasen et al., 1996), while Olli et al. (2002) reported C/N ratios > 10 in the ArW dominated region of the central Barents Sea. All studies reported C/N ratios well above the Redfield. Export production estimates are often based on new production calculated from NO$_3$-uptake (Eppley and Peterson, 1979), and nitrogen-based mathematical models need conversion factors to calculate carbon cycling and budgets, for which the Redfield ratio is frequently used. To get reliable estimates of export production as well as global carbon budgets, a first step should allow differential C/N ratios for production and export, with an export ratio closer to 8 rather than 6.6.

### 4.3. Particulate organic carbon flux as a function of primary production

There has been an increased awareness of the regulating impact ecosystems have on vertical carbon flux (Wassmann et al., 2003; Boyd and Trull, 2007; Buesseler et al., 2007), and a need to understand the driving forces determining the fate of the PP within a given system. Measurements of daily PP and vertical carbon flux during different seasons and years in the Barents Sea (Table 4) have been compiled to evaluate the carbon export ratio from PP in this highly productive Arctic shelf ecosystem (Fig. 7A). By regression (assuming a linear relationship), 36% of the PP was exported below 90 m, and that is close to the 35% export reported by Caron et al. (2004) for the productive period in the North Water polynya. The relatively high correlation suggests that the two processes, PP and vertical export, are linked, but not necessarily linearly, and there is also variability induced by variable time scales and phasing. PP, in particular new production, fills up the suspended matter pool from which vertical export derives. There is a delay between PP and suspended biomass, and there can also be a delay between the suspended biomass and vertical export. The delay will depend on the nutritional and physiological status of the algal community and the physical environment (i.e. light, mixing).

A considerable part of the variability in vertical export is not explained by PP rates, but by other processes regulating the vertical carbon export (Fig. 7B). The range in % POC exported relative to the PP is illustrated by the low export during late bloom where retention and degradation of the settling matter was high, and the high export associated with deep mixing (Table 2). Stations with a vertical export rate > 600 mg POC m$^{-2}$ d$^{-1}$ were all situated in the weakly stratified AW region of the Barents Sea, where biomass was mixed below 90 m depth.

Retention of biomass reducing the vertical export relative to the PP, results from grazing and high degree of recycling within the upper layers (Wexels Riser et al., 2007). An increasing consciousness of the role and impact of the microbial food web (Azam et al., 1983; Karl, 2007) suggests that retention through the

<table>
<thead>
<tr>
<th>Year</th>
<th>Month</th>
<th>Data</th>
<th>Stations (n)</th>
<th>Location</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>May</td>
<td>PP</td>
<td>4</td>
<td>MIZ central Barents Sea</td>
<td>Vernet et al. (1998)</td>
</tr>
<tr>
<td>2001</td>
<td>July and August</td>
<td>PP and vertical flux</td>
<td>5</td>
<td>Arctic Ocean, Nansen basin</td>
<td>Olli et al. (2007)</td>
</tr>
<tr>
<td>2003–2005</td>
<td>July, July and May</td>
<td>Vertical flux</td>
<td>11</td>
<td>Northern Barents Sea</td>
<td>Present study</td>
</tr>
</tbody>
</table>
microbial community creates a basis of pelagic ecosystem functioning. This is better known for low latitudes, but increasing amounts of evidence points to similar functions at high latitudes (Levinsen et al., 1999; Lovejoy et al., 2002). Pasternak et al. (2008) have showed how grazing impact from the sub-mesozooplankton (<1 mm) equal the larger grazers. Similar can consumption from heterotrophic protozoans be within the same order of magnitude (Hansen et al., 1996; Tremblay et al., 2006). All these groups are assumed to promote retention rather than vertical export. Even assumed important faecal pellet producers like larger mesozooplankton such as *Calanus* spp. contributes on average only to 20% of the POC flux (Wexels Riser et al., 2008). Considerable vertical carbon export can thus be seen as the result of short-circuited retention, overflow or mismatch between the capacity of producers and consumers; scenarios mainly seen during a short Arctic spring period.

### 4.4. Annual particulate organic carbon export and export efficiency in ice-covered and open waters

The available daily vertical carbon flux measurements from this and previous investigations (Wassmann, 1989; Andreassen and Wassmann, 1998; Olli et al., 2002) have been used to give a rough estimate of the annual POC flux in the Arctic and Atlantic influenced regions of the Barents Sea (Table 5). In the shallow Barents Sea with extensive trawling, no reliable annual flux measurements from automatic traps are available. The present data do not allow high seasonal resolution, but the data represent the variable bloom phases, the most prominent vertical export periods in the two regions. Table 5 is thus an attempt to utilise the existing data to compose best possible estimates. The period October to April is regarded as winter. Nutrient and pigment data show homogenous nutrient distributions in March and a

![Graph](image)

**Fig. 7.** Particulate organic carbon (POC) flux at 90 m depth relative to the integrated primary production at 30 stations in the central and northern Barents Sea including seasons from March–July, and five from the Amundsen Basin, Arctic Ocean. Data included are published as referred to in Table 4. Stippled lines indicate how processes like grazing or vertical mixing can reduce or increase the fraction of primary production exported below 90 m depth.

### Table 5

<table>
<thead>
<tr>
<th>Period</th>
<th>Measurements</th>
<th>Periods</th>
<th>Estimates</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Daily export rates (mg POC m(^{-2}) d(^{-1}))</td>
<td>Monthly export rates (g POC m(^{-2}) month(^{-1}))</td>
<td></td>
</tr>
<tr>
<td></td>
<td>ArW (n)</td>
<td>AW (n)</td>
<td>ArW</td>
</tr>
<tr>
<td>March</td>
<td>26 (1)</td>
<td>45 ± 21 (2)</td>
<td>0.8</td>
</tr>
<tr>
<td>May</td>
<td>325 ± 140 (8)</td>
<td>561 ± 258 (5)</td>
<td>10.1</td>
</tr>
<tr>
<td>July</td>
<td>165 ± 83 (10)</td>
<td>185 ± 30 (3)</td>
<td>5.0</td>
</tr>
<tr>
<td>August*</td>
<td>100</td>
<td>100</td>
<td>3.1</td>
</tr>
<tr>
<td>Annual POC export (g C m(^{-2}) yr(^{-1}))</td>
<td>31.8</td>
<td>44.4</td>
<td></td>
</tr>
<tr>
<td>Simulated annual primary production (g C m(^{-2}) yr(^{-1}))</td>
<td>68</td>
<td>130</td>
<td></td>
</tr>
<tr>
<td>Simulated new production (g C m(^{-2}) yr(^{-1}))</td>
<td>50</td>
<td>80</td>
<td></td>
</tr>
<tr>
<td>e(_{90}) ratio(^{d})</td>
<td>0.47</td>
<td>0.34</td>
<td></td>
</tr>
<tr>
<td>e(_{90}) ratio(^{*})</td>
<td>0.63</td>
<td>0.55</td>
<td></td>
</tr>
</tbody>
</table>

Monthly and annual POC export in the two regions of the Barents Sea are estimated from these data. Export ratio (e ratio) of primary production is calculated based on the estimated annual POC export production and simulated total primary production. Simulated new production was used to calculate the *e* ratio. Vertical flux measurements are from previously published data (Wassmann, 1989; Andreassen and Wassmann, 1998; Olli et al., 2002) and the present study.

* Wassmann (1989), 60 m depth, sampling in AW water only.
* Wassmann et al. (2006b).
* Calculated from *f*-ratios for Atlantic and Arctic waters: 0.62 and 0.74 (D. Slagstad, personal communication).
* e ratio = export production/total primary production.
* *e* ratio\(_{90}\) = export production/new production.
continuous nutrient drawdown and pigment increase from early May in the central Barents Sea and marginal ice zone (Reigstad et al., 2002; Olsen et al., 2003). Based on data from 1980 to 1984 and model applications, Kristiansen et al. (1994) and Wassmann and Slagstad (1993) suggest mid-April as the onset of the productive period in open waters.

The mean vertical carbon flux in the Atlantic influenced region exceeded that of the Arctic region during all periods, although the variability between stations was high. May was the most important month in terms of export, contributing 31% and 38% to the annual vertical flux for Atlantic and Arctic waters, respectively. The total annual carbon flux estimated was 32 and 44 g POC m$^{-2}$ for the Arctic and Atlantic regions, respectively.

The export production that leaves the euphotic zone and passes through the most efficient part of the retention filter (here we select 90 m depth) can be related to PP through the $e$ ratio ($e = \text{export production/total PP}$; $e_{90}$, Table 5). The $e$ ratio indicates the effect of two different retention effects that complicate interpretation: that of recycled production in the euphotic zone and vertical export retention in the aphotic zone. Compared to a simulated, annual PP of 130 and 68 g m$^{-2}$ for the Atlantic and Arctic regions (Wassmann et al., 2006b), the $e_{90}$ ratio was 0.34 and 0.47, respectively. For the Arctic region, this is close to predictions for the Atlantic boreal coastal zone (Wassmann, 1990). A shorter productive period such as in ice-covered waters generally comes with increased $f$ and $e$ ratios (Wassmann, 1990; $f = \text{export production/new production}$) and this is reflected in an $e_{90}$ ratio that is 38% higher in Arctic compared to the Atlantic region of the Barents Sea. Close to the North Pole and for August the $e$ ratio was even higher: 0.59 (Olli et al., 2007).

In order to omit the effect of recycled production that per definition cannot support vertical export, the $e$ ratio may be introduced. This ratio relates vertical export to new production (i.e. it represents the upper limit of vertical organic carbon export). The $e$ ratio largely reflects the retention of organic carbon in the retention filter. The $e_{90}$ in the Atlantic and Arctic regions of the Barents Sea were 0.55 and 0.63, respectively (Table 5), while the $e$ ratio for the North Pole (assuming $f = 0.8$) is 0.73. In summary, these calculations suggest that a decreasing percentage of the potential export production (45%, 37% and 27% for the Atlantic and Arctic regions of the Barents Sea and the Arctic Ocean close to the North Pole, respectively) is retained in the upper water column. This suggests that marine Arctic ecosystems have a stronger pelagic–benthic coupling and that retention is increasingly reduced. The $e$ ratios support the hypothesis that the pelagic–benthic coupling in seasonally ice covered and Arctic regions are stronger than open water regions (Carroll and Carroll, 2003; Wassmann et al., 2006a).

5. Conclusions

The 11 sites represent detailed snapshots of the pelagic–benthic coupling, which in concert indicate how vertical export varies during different phases of a bloom in the MIZ of the northern Barents Sea. The plethora of vertically exported quantities, their composition and regulation thus results in a complexity that is demonstrated here, and which deserves more in-depth, future study. Some prominent features can be identified and highlighted from the present investigation on processes and factors of importance for vertical carbon flux during bloom conditions in the seasonally ice-covered Barents Sea:

- The most important flux reduction (attenuation) is associated with the pycnocline.
- Vertical POC export changes through bloom phases in magnitude as well as composition.
- The change is not controlled by primary production alone, but related to various degrees of retention.
- Vertical mixing can short-circuit the retention filter promoting extensive vertical export of high quality POC.
- The $e$ and $e_{90}$ ratio estimated from simulated annual production and estimates of annual export suggest decreasing retention of carbon towards more Arctic waters.

Acknowledgements

We greatly appreciate assistance in field from H. Hodal and M. Sturluslon with Chl a analyses, L. Souteh with CHN analysis and M. Daase for preparations of the map. A. Balvik, J. Larsen, the captain and crew of FF "Jan Mayen" contributed with valuable practical assistance related to the fieldwork. We also thank H. Hop for making ice-cover estimates available for the CABANERA group. We appreciate the detailed primary production data supplied by P. Matrai from 1993, 1998 and 1999, and comments and suggestions from C. Svensen on the manuscript. We also thank T. Noji and one anonymous reviewer for constructive and helpful comments. This investigation resulted from the projects “Carbon flux and ecosystem feedback in the northern Barents Sea in an era of climate change” (CABANERA: project no.: 155936/700), Marine Climate and Ecosystems in the Seasonal Ice Zone (MACESIZ; project no. 159545/700) and contributions from iAOOS Norway: Closing the loop (project no. 176096/530), all financed by The Research Council of Norway.

References


