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Fate of pelagic organic carbon and importance of pelagic–benthic coupling in a shallow cove in Disko Bay, West Greenland

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ABSTRACT: Biomass and production of phytoplankton, bacteria, proto- and mesozooplankton together with vertical flux of particulate organic carbon, sediment oxygen demand and biomass of macrozoobenthos were estimated over 2 wk in spring and 2 wk in autumn 2003 in a shallow cove in Disko Bay, West Greenland. In spring, bloom conditions were encountered with high phytoplankton concentrations of 20 to 30 mg chlorophyll *a* m^{-3}. The zooplankton community associated with the spring bloom could not control the developing bloom, which resulted in high sedimentation rates of 1438 mg C m^{-2} d^{-1}, of which 518 mg C m^{-2} d^{-1} could be related to chlorophyll *a* (chl *a*). The settling phytoplankton was ingested by filter-feeding as well as deposit-feeding bivalves. In autumn, the water column was stratified and nutrient levels reduced, resulting in a phytoplankton biomass below 0.5 mg chl *a* m^{-3}. The vertical flux of particulate carbon was reduced to 235 mg C m^{-2} d^{-1}. Compared to spring, benthic mineralisation rates had increased. Ingestion of chl *a* was reduced in filter-feeding and in deposit-feeding bivalves. The pronounced seasonal shift in production and mineralisation pathways clearly highlights the importance of the spring bloom in the costal waters of subarctic Greenland. Analysis of local sea ice conditions from 1979 to 2003 suggests that the mismatch between primary producers and copepods observed during 2 wk in spring could be related to an earlier than usual break-up of sea ice in 2003, which illustrates how climate can influence pelagic–benthic coupling.

KEY WORDS: Carbon flux · Greenland · Pelagic–benthic coupling · Vertical flux · Sea ice

INTRODUCTION

Arctic marine systems are characterised by the presence of sea ice, which confines primary production to a short period during summer. The majority of the annual primary production takes place during the weeks following the break-up of sea ice, when nutrient-rich water is exposed to light and a phytoplankton bloom develops. Due to solar heating of the surface layer combined with freshwater flow from land and melting sea ice, the water column becomes increasingly stratified, resulting in an upper mixed layer, which eventually becomes nutrient-depleted. In areas with strong stratification and no upwelling, nutrient depletion occurs within 2 to 3 wk. During this short period, up to 50% of the annual new production takes place (Sakshaug 1997). The fate of the bloom is strongly dependent on whether the timing of the bloom coincides with large stocks of the dominant grazers *Calanus* spp. Dominant species such as *C. finmarchicus* and *C. hyperboreus* spend the winter at 500 to 1000 m depth, but migrate to the surface in April (Hirche 1998, Madsen et al. 2001). When vertical migration of copepods matches the timing of the spring bloom, grazing efficiently reduces phytoplankton stocks. A large fraction of the new production is

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thereby channelled through the pelagic food web. On the other hand, if the bloom sets in before copepods have ascended from deeper waters, most of the production sediments to the sea floor and becomes available to the benthic community. Interannual variation in sea ice dynamics thus plays an important role in determining the magnitude of the spring bloom, the annual primary production and whether production is predominantly consumed by the pelagic or the benthic community (Fortier et al. 2003, Wassmann et al. 2004).

The general decrease in Arctic sea ice cover observed during the last few decades (Parkinson & Cavalieri 2002) highlights the importance of improved understanding of the relationship between sea ice dynamics, primary production and the relative importance of pelagic and benthic pathways, especially in coastal waters around Greenland, where fishing of a few species comprises more than 95% of the national export. Climate change combined with overfishing necessitated a shift from cod fishing to shrimp fishing in 1960–1990 in West Greenland and showed that changes in ecosystem carbon flow can have significant socioeconomic impacts (Hamilton et al. 2003). A prerequisite for understanding the relative importance of pelagic and benthic compartments of the food web in Arctic areas is a detailed description of both during years with different ice regimes. Such information is available for the pelagic part of the highly productive Disko Bay, West Greenland. Here, studies have documented the importance of the pelagic food web (Nielsen & Hansen 1995). A seasonal change in the dominating pathways of the carbon flow is observed with high grazing impact of copepods, predominantly *Calanus* spp., in spring and early summer, followed by a transition to microbial food web dominance in late summer (Levinsen & Nielsen 2002). The latter results in an efficient retention of production in the water column and little vertical export of organic matter (Nielsen & Hansen 1999, Levinsen et al. 2000). The studies of Nielsen & Hansen (1999) and Levinsen et al. (2000) were mainly conducted over the deep troughs at the entrance to the bay at depths of 250 to 300 m. In the present study we seek to add to the descriptive knowledge of carbon cycling in Disko Bay by describing the fate of pelagic primary production and pelagic–benthic coupling over a total of 4 wk in spring and autumn in a shallow cove. This was achieved through quantification of (1) phytoplankton biomass and production, (2) biomass and production of pelagic bacteria, (3) composition, biomass and grazing of dominant zooplankton, (4) vertical transport of particulate carbon, (5) benthic mineralisation of organic matter and (6) gut content, biomass and composition of selected macrozoobenthos.

MATERIALS AND METHODS

Study site and sampling. The study was conducted in a small cove, Engelskmandens Havn, approximately half a nautical mile off the Qeqertarsuaq harbour in Disko Bay, West Greenland (69° 15′ 36″ N, 53° 34′ 61″ W) (Fig. 1). Sampling was conducted from the RV 'Porsild' (Arctic Station, University of Copenhagen) on 5 occasions in spring and autumn, 28 April to 6 May and 10 to 18 September 2003, respectively, at a 50 m deep station in the middle of the cove. Vertical profiles of water temperature, salinity and fluorescence were obtained down to 45 m using a SeaBird SBE25 equipped with a fluorometer. Sampling depths for chemical and biological variables were 1, 5, 10, 15, 20, 30 and 45 m and the depth of maximum fluorescence, if present. Sampling was omitted at 20 m in autumn. All sampling was conducted around noon and water samples were kept dark and cold during transport to the laboratory, where subsamples were taken for analysis.

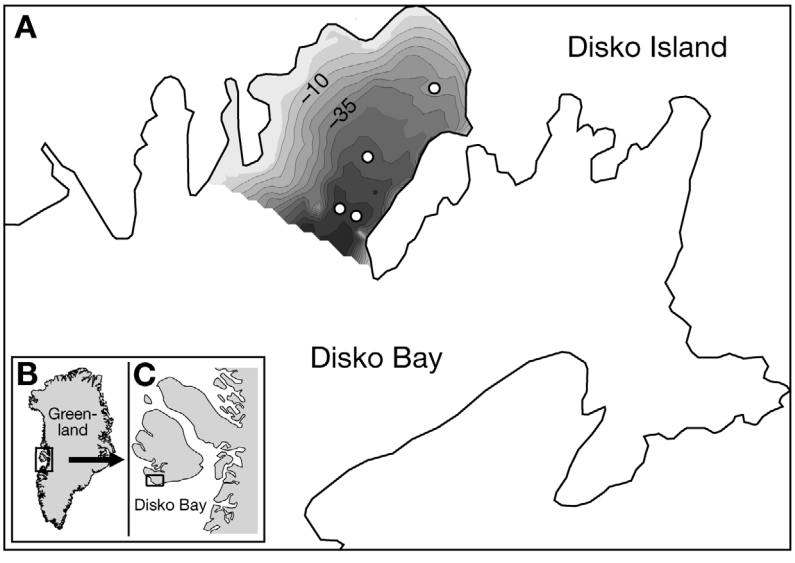

Fig. 1 (A) Shallow cove in Disko Bay, West Greenland, where sampling was conducted in spring and autumn 2003. Contours show 5 m depth intervals in the cove Engelskmandens Havn. Small white dots represent sampling stations for benthic macrofauna, the large white dot indicates main sampling station. Inserts show location of (B) Disko Bay and (C) the cove

Water chemistry. The concentration of NO_3^- was determined on an NO_x analyser (Model 42C, Thermo Electron Corporation). PO_4^{3-} and Si were determined by standard calorimetric methods and analysed automatically on a robotic sample processor coupled to a spectrophotometer (Tecan RSP-5051 & Camspec M330, Tecan AG). Dissolved inorganic carbon was measured using a CO_2 analyser (Coulometer CM5012, UIC).

Phytoplankton biomass and production. Chlorophyll *a* (chl *a*) and phaeopigments (phaeo) were measured on 100 to 500 ml triplicate samples filtered onto GF/F filters, extracted for 24 h in 96% ethanol and analysed on a Turner 770h fluorometer (Turner Designs), calibrated against a chl *a* standard. The net primary production was measured *in situ* for 4 h around noon using the ^{14}C method. Triplicate samples from each of the depths 1, 5, 10, 15 and 20 m in spring and 1, 5, 10, 15 and 30 m in autumn, were incubated in 2 clear and 1 dark 100 ml Jena bottles with 4 µCi $NaH^{14}CO_3^-$ (45889778 disintegrations per min [dpm] per ampoule, International Agency for ^{14}C Determination). Incubated samples were kept dark until processing. The entire volume of each bottle was vacuum-filtered through GF/F filters. Filters were placed in scintillation vials and inorganic ^{14}C was removed by adding 200 µl 1 N HCl. The filters were kept frozen until further processing. Ten ml Filter-count (PerkinElmer) were added to the samples and counting was carried out on an automatic scintillation counter (Beckman LS1801, Beckman Instruments). Filters were placed under a hood for a minimum of 24 h to allow excess inorganic ^{14}C to evaporate before counting.

Bacteria. For quantification of bacteria, 10 ml samples from each depth were preserved with 1 ml formalin in 20 ml glass vials and stored cold (but not frozen) until processing. The bacteria were enumerated on a FACS Calibur flow cytometer (Becton Dickinson) after staining with the nucleic acid stain SYBR Green 1 (Molecular Probes). Number of cells was converted to biomass (mg C m^{-3}) applying 20 fg C $cell^{-1}$ according to Lee & Fuhrman (1987). Bacterial production and growth were obtained by incubating four 10 ml seawater samples from each sampling depth with 10 nM ^3H-thymidine and 50 nM ^{14}C-leucine for 2 h. One replica served as control sample and was fixed with 500 µl trichloroacetic acid (TCA), 100%, before addition of isotopes. The samples were filtered onto 0.2 µm cellulose-nitrate filters and washed with ice-cold TCA, 5%. The filters were kept frozen (–18°C) in clean 20 ml plastic vials before addition of 10 ml Ecoscint (National Diagnostics), and processed on an automatic scintillation counter (Beckman LS1801). Thymidine incorporation was converted to cell production (mg C m^{-3} d^{-1}) by the factor 1.1×10^{18} cells mol^{-1} ^3H incorporated (Riemann et al. 1987). Leucine incorporation was converted to protein production by using the fractions 0.073 leucine/protein and 0.86 C/protein according to Simon & Azam (1989). For the ^{14}C-leucine incorporation to carbon production calculation, a dilution factor of 2 was applied, as some isotope dilution is always present (Simon & Azam 1989), as well as the correction factor 1.27 because of the dual labelling approach with ^3H-thymidine and ^{14}C-leucine (Chin-Leo & Kirchman 1988). The bacterial carbon demand was calculated based on an estimated growth efficiency of 0.33, which is within the range of earlier reports from marine areas (del Giorgio & Cole 1998).

Sediment/water exchange of O_2 and nutrients. Within each season, 8 sediment cores were taken from a 0.1 m^2 box corer using 30 × 5.3 cm Plexiglas tubes to sample 22 cm^2 of the sediment surface. Sediment cores were kept dark and cold during transport to the laboratory, where cores were submersed in a tank filled with bottom water and kept in darkness at *in situ* temperature. Mixing was provided by Teflon-coated magnets rotating at about 60 rpm and placed 5 cm above the sediment surface in each core. All cores were preincubated for at least 12 h before further processing to minimise disturbance from coring and transport. Studies of exchange rates of O_2, NO_3^-, PO_4^{3-}, Si and NH_4^+ between water column and sediment were initiated by closing cores with gas-tight lids and incubating for approximately 30 h. During incubation, 8 samples were collected to verify the linear change in concentrations over time. Water samples were analysed for nutrients as described above for the water column, and O_2 concentrations were analysed by Winkler titration. Oxygen consumption was transformed to carbon mineralisation using an oxygen-to-carbon ratio of 1:1 (Rysgaard et al. 1998).

Proto- and mesozooplankton. For analysis of protozooplankton, 300 ml water from each sampling depth was fixed with 6 ml Lugol's solution to a final concentration of 2%. Samples were kept in the dark at room temperature until processing. Subsamples of 50 to 250 ml were left for at least 24 h before sedimented material was quantified by inverted microscopy. Ciliates and heterotrophic dinoflagellates (HDF) were categorised by functional group and size class. Length and width of cells were measured to determine biovolume. Carbon content was estimated as pg C $cell^{-1}$ = 0.76 pg C × cell $volume^{0.819}$ for HDFs and ciliates according to Menden-Deuer & Lessard (2000). Grazing potentials of HDFs and ciliates were estimated according to Hansen et al. (1997) assuming maximum ingestion and clearance in spring and autumn, respectively. Growth of protozooplankton at *in situ* temperature was estimated using Q_{10} = 2.8 and assuming an average growth efficiency of 0.33 (Hansen et al. 1997). The ver-

tical distribution of mesozooplankton was determined by filtering 12 to 15 l of seawater through a 45 µm screen. Samples were preserved in buffered formalin for later determination. Faecal pellets were counted in samples from the water column and the sediment traps. From the sediment traps 300 ml samples were collected and preserved with Lugol's solution. From the water column, 500 ml samples were analysed until a minimum of 20 pellets had been counted. Faecal pellet volume was estimated from length and width measurements using a dissecting microscope (Olympus SZ40, 40× magnification). The volume of intact pellets was estimated using the equation for a cylinder with half-spherical ends. For fragmented pellets the equation for a cylinder was used. Faecal pellet volume was converted to carbon biomass using a factor of 69.4 µg C mm^{-3} (Riebesell et al. 1995).

Mesozooplankton were collected by vertical net hauls (0 to 45 m) using a modified WP-2 net equipped with a 45 µm mesh net. On all sampling occasions, triplicate samples were taken. The samples were concentrated on a 45 µm filter, rinsed into a beaker, preserved in 2 to 4% formalin, and stored for later enumeration and biomass estimation. The samples were split using a plankton splitter to obtain sample sizes of approximately 500 individuals, and all identifiable zooplankton were identified to either species or genus and development stage. Prosome lengths were measured on 10 individuals from each copepodite stage and total body length was measured on 25 to 50 nauplii. Carbon content was estimated from length–weight regressions from the literature (summarised in Thor et al. 2005). The grazing impact was not measured, but estimated from the specific rates from the bloom period presented in Madsen et al. (2001).

Sedimentation traps. The vertical flux of particulate carbon was studied using parallel acrylic cylinder sediment traps (KC Denmark) deployed for 6 h at depths of 5, 15, 30 and 45 m. Traps were 0.45 m in height (H) and 0.072 m in diameter (D) (ratio H:D = 6.25) giving a trap area of 0.0041 m^2 per cylinder. Before deployment, traps were filled with 0.2 µm-filtered bottom water. Upon recovery, duplicate trap samples from each depth were pooled before subsamples were taken for analysis of faecal pellets, particulate organic carbon (POC) and chl *a*. Sedimentation rate was calculated according to Knap et al. (1996). Sinking velocity was calculated after Kiørboe et al. (1994).

Carbon (POC, DOC). POC was measured on precombusted GF/F filters after filtration of 200 to 500 ml of seawater from the water column and 300 to 500 ml from sediment traps (volume depending on season). Filters were analysed on an elemental analyser (Roboprep-CN, Europa Scientific). POC was divided into 3 fractions according to Juul-Pedersen et al. (2006): particulate organic carbon associated with phytoplankton (PPC), faecal pellets (FPC) and a remaining unidentified amorphous fraction (APC). The fraction associated with phytoplankton was estimated from the regression of chl *a* on POC in the water column. The faecal pellet fraction was estimated from faecal pellet volume estimates (see subsection 'Proto- and mesozooplankton') and the remaining detritus fraction was estimated as POC – (FPC + PPC). Water samples for determination of dissolved organic carbon (DOC) were filtered through precombusted fibreglass filters (Whatman GF/F) and frozen (–18°C) in acid-washed 20 ml vials until analysis on a Shimadzu TOC-5000 analyser.

Gut content of bivalves. To analyse phytoplankton material contained in the gut of bivalves, the soft parts of 20 individual bivalves collected at 50 m depth were homogenised, and plant pigments were extracted in 96% ethanol for at least 6 h from each separate bivalve. Extraction volume depended on individual specimen size. After centrifugation, the supernatant was analysed spectrophotometrically for chl *a* and phaeopigments. The content of total pigments (phaeo + chl *a*) per individual was used as a measure of phytoplankton gut content.

Macrozoobenthos. Sampling was conducted in autumn at 3 stations in the cove at increasing depth (20, 40 and 50 m). Three 0.25 m^2 Van Veen grab samples were collected at each station. Samples were sieved through a 0.5 mm screen and retained material was fixed in buffered formaldehyde and transferred to 70% alcohol for later identification. All sampled specimens were identified to main groups and dominant taxa to species level. Biomass (ash-free dry weight, AFDW) was determined by drying at 110°C for 24 h, and weighing and then burning at 520°C for 24 h before weighing again. Biomass was converted to carbon using taxa-specific conversion rates according to Brey (2001). To estimate the annual carbon demand of macrozoobenthos, the approach of Klages et al. (2003) was applied, whereby somatic production is estimated using an empirical model developed by Brey (1999).

RESULTS

Hydrography and nutrient distribution

Distinct seasonal differences in temperature and water chemistry were observed between spring and autumn (Figs. 2 & 3). In spring, sampling took place approximately 3 wk after the break-up of sea ice, and ice floes were still present in the cove. Air temperatures were below freezing at the beginning of the sampling period, followed by several days of sun with temperatures of 5 to 10°C. Water temperature was initially

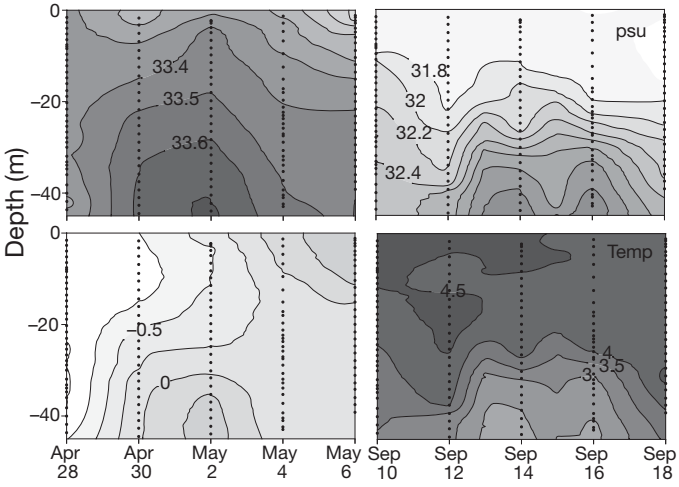

Fig. 2. Development of temperature (°C) and salinity (psu) at the 50 m station during spring and autumn. Dotted lines represent sampling points

–0.75°C and salinity 33.3 to 33.4 psu, after which an inflow of warmer and more saline and nutrient-rich bottom water was observed (Figs. 2 & 3). The inflowing water was characterised by concentrations of PO_4^{3-}, Si and (especially) NO_3^- well above those of the surface water. The surface water was not depleted of nutrients, however, and measurable levels of PO_4^{3-}, NO_3^- and Si were detected. In autumn, the water column was clearly stratified. Surface-water (0 to 25 m) temperature had increased to 4.5°C and salinity was below 32. Close to the bottom (25 to 45 m) temperature was around 3°C and salinity above 32.5. Compared with spring concentrations, autumn nutrients were depleted in the upper 30 m. The Si concentration was below 1 µM vs. 8 µM in spring and PO_4^{3-} was 0.1 µM vs. 0.7 to 0.8 µM in spring. NO_3^- concentrations were lower in the surface water in autumn, as illustrated by the average depth of the 2 µM contour, which was approximately 10 m in spring and 25 m in autumn (Fig. 3). For all nutrients, highest concentrations in autumn were found near the bottom.

Production and biomass of phytoplankton

Spring sampling was conducted during the spring bloom. High chl *a* concentrations were found near the surface, where nutrients were not yet depleted. The highest chl *a* concentration was observed on 28 April at 10 to 15 m with a maximum of 30 mg chl m^{-3} (Fig. 3). On 30 April and 2 May, the inflow of bottom water shifted the chl *a* maximum closer to the surface, but it returned to 10 to 15 m a few days later. Integrated primary production showed large variation, ranging from 107 to 413 mg C m^{-2} d^{-1} with an average of 195 ± 54 mg C m^{-2} d^{-1}. Maximum production was found during sunny and calm conditions from 30 April to 4 May at depths between 1 and 5 m (data not shown). Diatoms dominated the bloom at this time, and the size fraction larger than 50 µm increased from 20 to 40% during the spring sampling period (Fig. 4). In autumn, the chl *a* concentration was below 0.5 µg l^{-1}. Only 10% of the chl *a* was comprised of cells larger than 50 µm.

Distribution of POC and DOC

POC showed a strong linear relationship with chl *a* in the water column, as expressed by the equation

$$POC = 43.3 \pm 4.4 \times \text{chl } a + 194.5 \pm 14.6 \quad (1)$$
$$(r^2 = 0.76,\ n = 34,\ p < 0.001)$$

The slope of the regression line was used for converting chl *a* measurements to PPC in the water column. Since fresh faecal pellets contain chl *a*, this

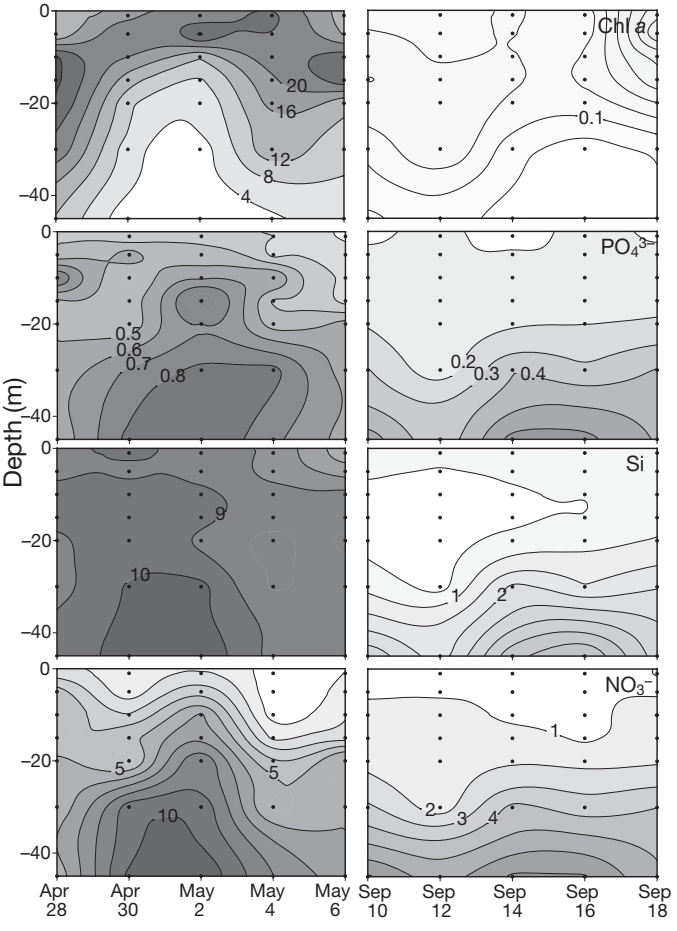

Fig. 3. Distribution of chlorophyll *a* (mg m^{-3}) and nutrients (µM) at sampling stations during spring and autumn. Dotted lines represent sampling points

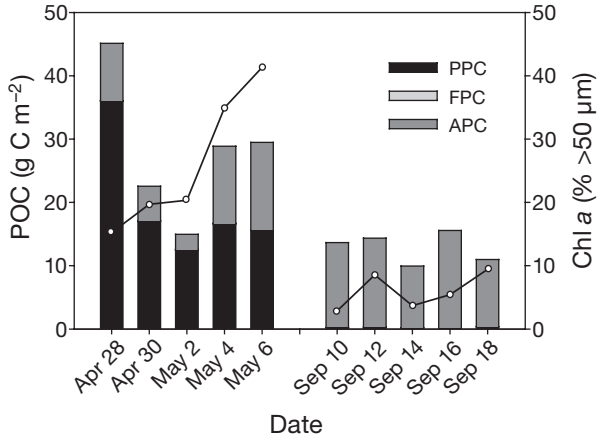

Fig. 4. Distribution of integrated (0–45 m) particulate organic carbon (POC) at the sampling station in spring and autumn (bars). PPC: phytoplankton carbon; FPC: faecal pellet carbon; APC: amorphous particulate carbon (all in g C m^{-2}). Superimposed is proportion of chlorophyll *a* (chl *a*) that could be attributed to cells >50 µm

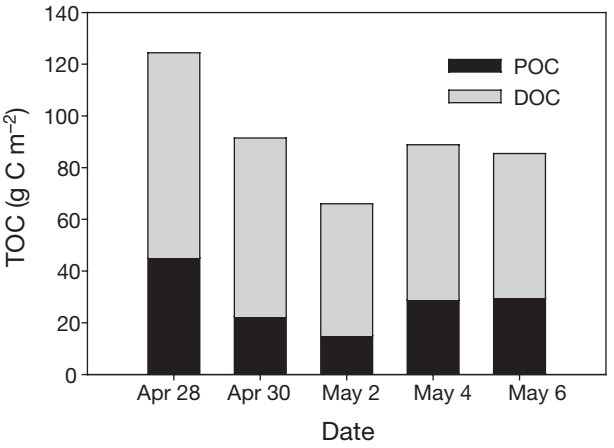

Fig. 5. Total integrated (0 to 45 m) organic carbon (TOC) content divided into 2 fractions: dissolved organic carbon (DOC) and particulate organic carbon (POC)

method can result in overestimation of the 'true' PPC fraction, especially when pellet density is high relative to phytoplankton. The maximum integrated POC content of 45 g C m^{-2} in the water column (0 to 45 m) was observed on 28 April (Fig. 4). The inflow of bottom water with low chl *a* concentration resulted in a decrease to about 20 g C m^{-2}. The concentration increased to 30 g C m^{-2} at the end of the spring period. In September, the POC was dominated by the unidentified fraction (APC), with concentrations around 10 g C m^{-2}. During spring, the PPC fraction constituted 70 ± 12% (mean ± SD, n = 5) compared with 2.2 ± 0.9% (mean ± SD, n = 5) in autumn. FPC constituted 0.2 ± 0.2 and 0.2 ± 0.3% (mean ± SD, n = 5) in spring and autumn, respectively. The concentration of DOC was only measured in spring (Fig. 5), when 70 ± 6.1% of the total amount of organic carbon (DOC + POC) was found to be dissolved. Mean concentration (±SD, n = 34) of DOC was 126 ± 47 µM with a range of 77 to 235 µM.

Production and biomass of bacteria

Bacterial biomass increased during spring from 0.6 to 1.20 g C m^{-2} (Fig. 6). In autumn, bacterial biomass ranged from 0.8 to 1.1 g C m^{-2}. Mean bacterial biomass was not significantly different between seasons (Student's *t*-test, p = 0.62; df = 8). Bacterial production varied greatly in spring from 47 to 185 mg C m^{-2} d^{-1}. Production was generally lower in autumn (22 to 73 mg C m^{-2} d^{-1}) but the difference between seasons was not statistically significant (*t*-test, p = 0.13; df = 8).

Proto- and mesozooplankton

The protozooplankton were dominated by naked dinoflagellates (*Gymnodinium*/*Gyrodinium* and *G. spirale*) and naked oligotric ciliates (genera *Strombidium*, *Strobilidium* and *Tontonia*) in both seasons. These 2 groups contributed equally to the integrated biomass with 217 ± 41 and 131 ± 39 mg C m^{-2} for dinoflagellates and ciliates, respectively (Fig. 6). In spring, production was 16 ± 0.8 mg C m^{-2} d^{-1} for ciliates and 9.4 ± 0.2 mg C m^{-2} d^{-1} for dinoflagellates. Ingestion during the same period was 48 ± 3 mg C m^{-2} d^{-1} for ciliates and 29 ± 0.6 mg C m^{-2} d^{-1} for dinoflagellates. Protozooplankton composition in autumn was comparable with that of the spring community. The dinoflagellates and ciliates contributed equally to the microzooplankton biomass with 723 ± 63 and 710 ± 110 mg C m^{-2} for the 2 groups, respectively. Ingestion and production of the 2 groups corresponded to 13 ± 2 and 56 ± 19 mg C m^{-2} d^{-1} and 4.4 ± 0.7 and 19 ± 6 mg C m^{-2} d^{-1}, respectively. During the spring investigation there was a pronounced change in the mesozooplankton community. At the first sampling, the community was dominated by small copepods e.g. *Pseudocalanus* spp., *Acartia longiremis*, *Oithona* spp. and *Calanus* spp. nauplii and biomass was 35 ± 4 mg C m^{-2}. This plankton composition is typical for winter plankton that dominates the surface layer and shallow coastal areas prior to the arrival of *Calanus* spp. After the first sampling, the water masses in the cove were replaced with saltier, more nutrient-rich water from the bay proper (Figs. 2 & 3). In association with the advection of bay water, *Calanus* spp. was introduced to the cove and the copepod biomass increased by several orders of magnitude to 3068 ± 814 mg C m^{-2} on the last sampling occasion. Unfortunately, the mesozooplankton samples from the autumn investigation were lost, but to estimate

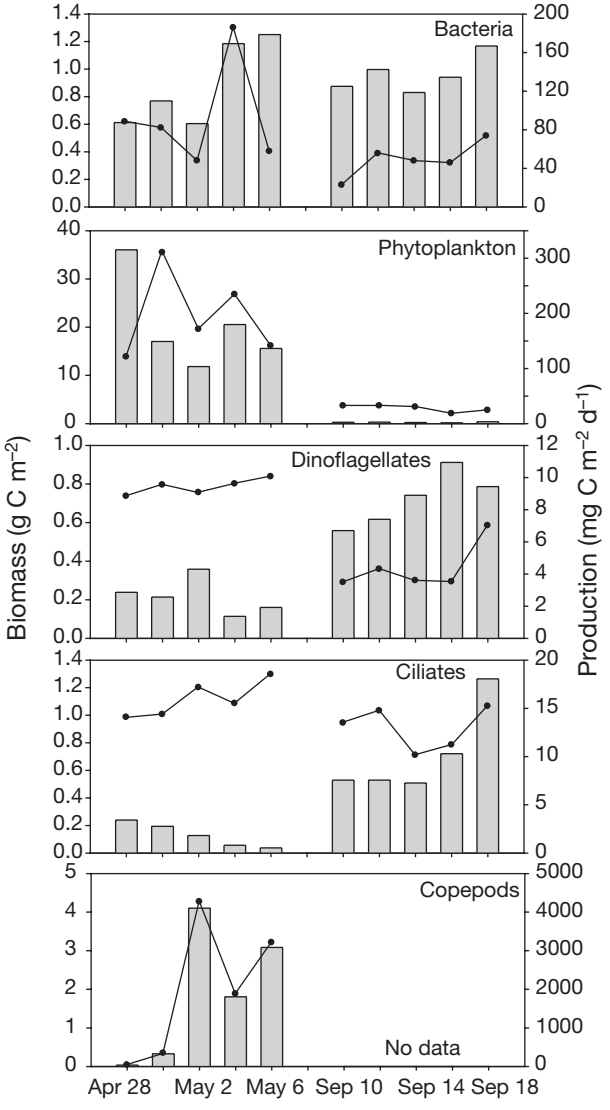

Fig. 6. Integrated (0 to 45 m) biomass (bars; g C m^{-2}) and production (curves; mg C m^{-2} d^{-1}) of bacteria, phytoplankton, heterotrophic dinoflagellates, ciliates and copepods during spring and autumn

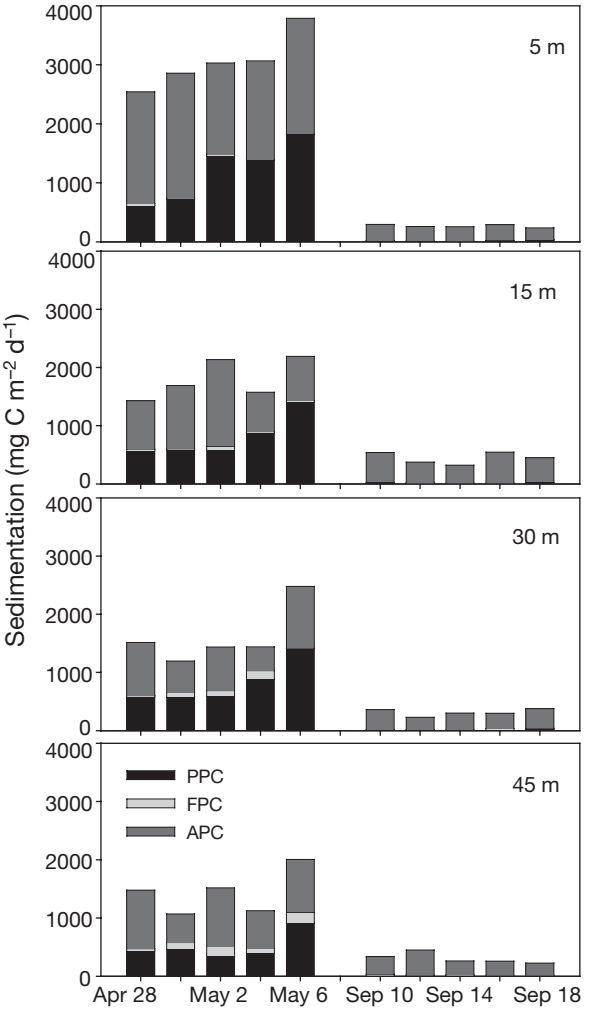

Fig. 7. Sedimentation rates of particulate organic carbon measured from short-term sediment trap deployments at 4 different depths. Carbon was identified as 3 fractions: phytoplankton carbon (PPC), faecal pellet carbon (FPC) and amorphous particulate carbon (APC)

the potential role of these organisms, the average biomass from September 1997 of 158 ± 59 mg C m^{-2} originating from Madsen et al. (2001) was included in the carbon budget (Madsen et al. 2001). The grazing impact was assessed from a specific egg production rate of 3% d^{-1} measured during a *Calanus* spp.-dominated spring bloom (Madsen et al. 2001) and of 7% d^{-1} during a small-copepod scenario in September (Madsen et al. unpubl. data). Assuming a growth efficiency of 33% (Hansen et al. 1997) the grazing impact of the copepod community was estimated at 168 ± 70 and 33 ± 12 mg C m^{-2} d^{-1} for the spring and autumn investigations, respectively.

Sedimentation

Vertical transport differed markedly between spring and autumn (Fig. 7). In spring, vertical transport showed a decreasing trend with increasing water depth. Maximum vertical transport (3055 mg C m^{-2} d^{-1}) was recorded at 5 m depth and minimum transport (1438 mg C m^{-2} d^{-1}) at 45 m depth. In autumn, rates were lower and changed little with depth, ranging from 206 to 342 mg C m^{-2} d^{-1}. As in the water column, the POC content in sediment traps was separated into 3 fractions: PPC, FPC and the remaining fraction, APC. The following relationship between POC and chl *a* was found in the traps:

$$\mathrm{POC} = 58.2 \pm 13.1 \times \mathrm{chl}\ a + 407 \pm 127 \quad (2)$$
$$(r^2 = 0.52,\ n = 40,\ p < 0.001)$$

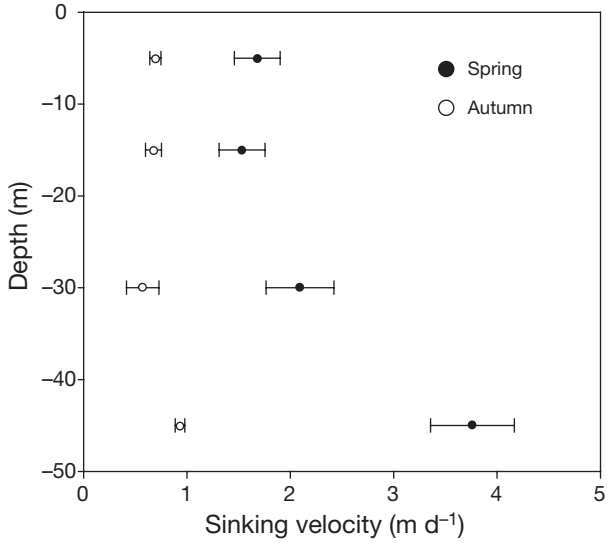

Fig. 8. Sinking velocity (mean ± SE, n = 5) of phytoplankton carbon intercepted in short-term sedimentation trap deployments during spring and autumn

During spring, the bloom conditions resulted in high vertical transport of chl *a*-associated carbon. About 30 to 50% of the total carbon content in traps was attributed to chl *a* (PPC), while the remainder was made up mainly of the unidentified (amorphous) fraction (APC, see above). FPC were most abundant in the traps at 45 m, where a maximum of 178 mg C m^{-2} d^{-1} was found. In autumn, the only significant fraction was APC. Sinking velocity of PPC showed a significant increase (ANOVA 1-way: F = 5.66, $p < 0.01$, df = 19) with increasing depth in spring (Fig. 8). Average values close to 1.5 m d^{-1} were found at 5 and 15 m, increasing to 3.7 ± 0.4 m d^{-1} at 45 m. In autumn, the sinking velocity of PPC was constant at all trap depths (ANOVA 1-way: F = 1.74, p = 0.20, df = 19), ranging from 0.6 to 0.9 m d^{-1}. Because of low numbers in autumn the sinking velocity of faecal pellets could only be estimated in spring. In spring, no trend was observed as a function of sampling date or trap depth, and mean sinking rate was 77.8 ± 6.8 m d^{-1} at all depths (mean ± SE, n = 20). Settlement of resuspended matter in sediment traps can cause significant overestimation of vertical flux rates (Blomqvist & Larsson 1994), and resuspension could have contributed to the sedimentation measured, although to what extent cannot be determined. The fact that sedimentation rates did not increase closer to the bottom indicates that sedimentation caused by resuspension was not dominant, and that the measured sedimentation can be considered a valid estimate of the primary settling of carbon originating from the euphotic zone.

Sediment/water exchange of O_2 and nutrients

Sediment oxygen uptake increased from 6.1 mmol m^{-2} d^{-1} in spring to 27.4 mmol m^{-2} d^{-1} in autumn. A similar seasonal trend was also found for nutrients, where highest efflux rates were observed in autumn (Table 1).

Gut content of bivalves

The filter-feeding *Clinocardium ciliatum* and the deposit-feeding *Macoma calcarea* both contained fresh phytoplankton in their gut when collected in spring. Intestine colors were dark green in spring compared to a more brownish color in autumn. In both species the amount of pigment extracted was significantly correlated to shell size (Fig. 9). The mean shell length of specimens collected in spring and autumn was not significantly different for either *C. ciliatum* (*t*-test; p = 0.42, df = 38) or *M. calcarea* (*t*-test; p = 0.72, df = 38). Differences in mean pigment content between seasons were tested for each species. Mean pigment contents were higher in spring (*t*-test) for *C. ciliatum* ($p < 0.001$, df = 38) and *M. calcarea* ($p < 0.001$, df = 38).

Macrozoobenthos

The biomass of macrozoobenthos decreased from 73.8 ± 7.7 g (mean ± SE, n = 3) AFDW m^{-2}, approximately equivalent to 38.2 ± 4.0 g C m^{-2} at 20 m and to 18.2 ± 9.7 g AFDW m^{-2} (9.4 ± 5.0 g C m^{-2}) at 50 m. This was especially due to the reduction in bivalve biomass (Fig. 10). Abundance showed less variation with depth, ranging between 5000 and 7000 ind. m^{-2} at all depths. However, the composition of benthos changed greatly. Bivalve abundance peaked at 20 m with 2604 ± 395 ind. m^{-2} (mean ± SE, n = 3), decreasing to 258 ± 35 ind. m^{-2} at 50 m. The dominant bivalve species were *Macoma calcarea*, *Hiatella arctica* and *Mya truncata*. Polychaetes increased in abundance with increasing

Table 1. Mean ± SE sediment metabolism (mmol m^{-2} d^{-1}) in spring and autumn in Disko Bay

Parameter	Spring	Autumn
Sediment uptake		
O_2	6.07 ± 1.51	27.37 ± 4.14
Sediment efflux		
Si	0.86 ± 0.16	9.03 ± 1.06
NH_4^+	0.15 ± 0.07	0.76 ± 0.32
NO_3	0.16 ± 0.10	0.35 ± 0.07
PO_4^{3-}	0.005 ± 0.004	0.09 ± 0.02

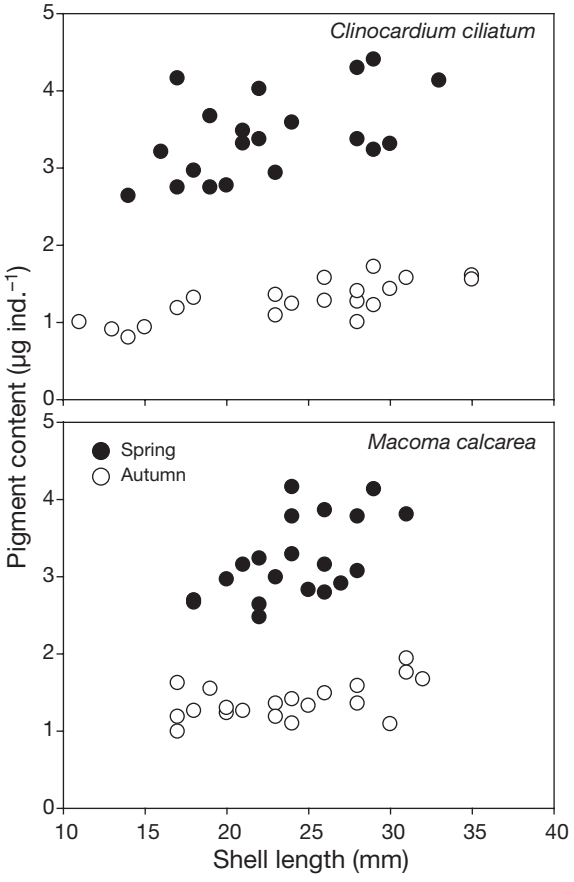

Fig. 9. Total chlorophyll *a* content of individual bivalves as a function of individual shell length for suspension-feeding *Clinocardium ciliatum* and deposit-feeding *Macoma calcarea* during spring and autumn

depth from 4125 ± 908 to 6648 ± 1357 ind. m^{-2} at 20 and 50 m, respectively. The dominant species were *Euchone analis* and *Pectinaria granulata.* The latter was most abundant at 20 m and contributed to the high polychaete biomass found at this depth. Taxa not belonging to either bivalves or polychaetes were predominantly gastropods and amphipods at 20 m. From the biomass of benthos at 50 m the estimated carbon demand was 39 mg C m^{-2} d^{-1}. This was assumed to change relatively little between seasons because of the dominance of multiyear species, which keep biomass relatively constant.

DISCUSSION

Carbon flow in spring and autumn in Disko Bay

The carbon budget (Fig. 11) is based on mean values from 2 wk of sampling in spring and 2 wk in autumn. Although the data are influenced by advective processes, we believe that the overall pattern illustrates the seasonal differences in the area. This assumption is corroborated by data from seasonal studies 1 nautical mile from this locality by Levinsen et al. (2000) and Madsen et al. (2001). In late April and early May, bloom conditions were encountered and phytoplankton biomass and production greatly exceeded values in September. The bloom resulted in high vertical transport of carbon, of which 36% was in the form of phytoplankton compared to only 4% in autumn. Bacterioplankton biomass and production in the water column did not show distinct variation between seasons. The zooplankton was

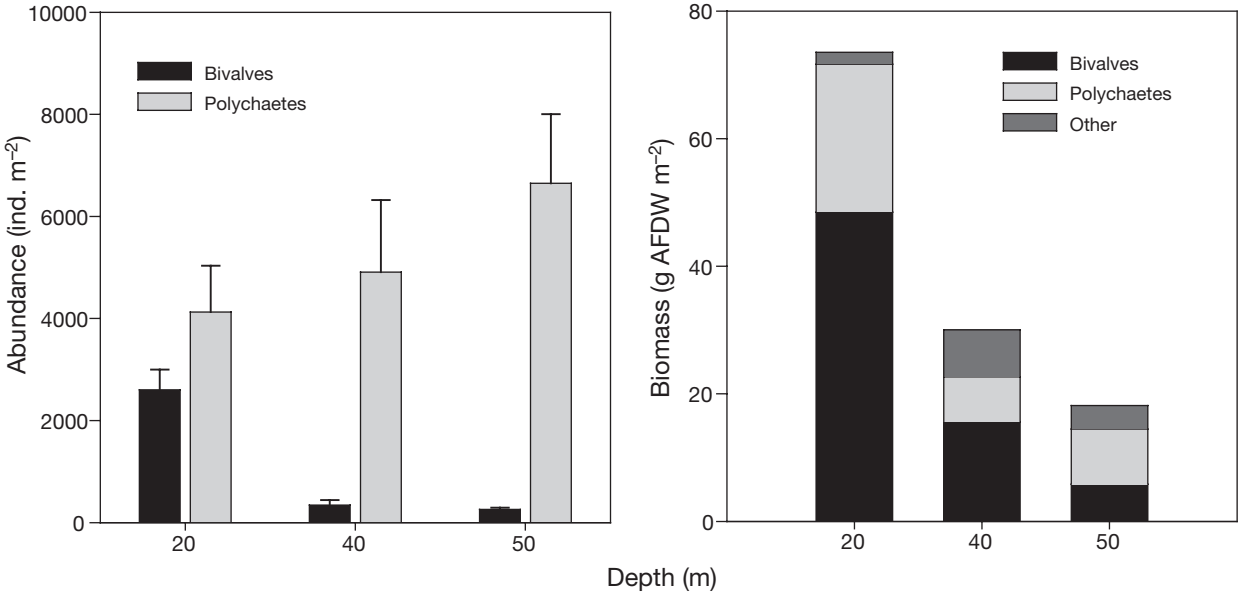

Fig. 10. Benthic abundance (±SE) and biomass at the 3 macrobenthos sampling stations. AFDW: ash-free dry weight

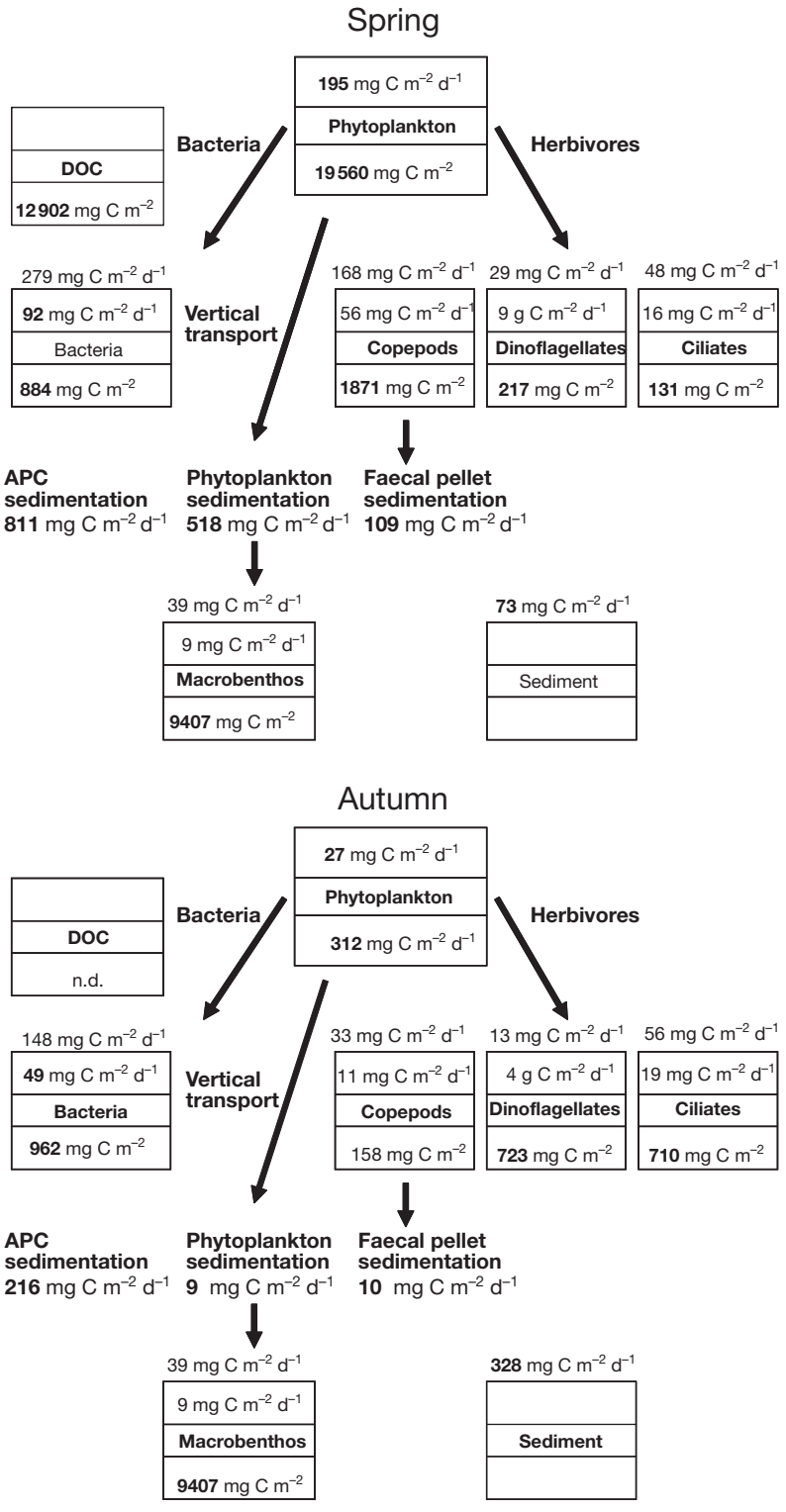

Fig. 11. Carbon flow scenarios during short-term field studies in spring (28 April to 6 May) and autumn (10 to 18 September) in Disko Bay. Inside boxes, values at bottom and top indicate biomass (mg C m^{-2}) and production (mg C m^{-2} d^{-1}), respectively; outside boxes, values represent carbon demand (mg C m^{-2} d^{-1}). Values in boldface were measured and represent average values of 5 sampling days, other values were estimated from empirical relations. Biomass of copepods in autumn estimated from Madsen et al. (2001). n.d.: no data

dominated by copepods in spring and sedimentation of faecal pellets constituted 8% of total vertical flux. In autumn, ciliates and dinoflagellates dominated the zooplankton and the contribution of pellets to the vertical flux was reduced to 4% of the total. Despite the strong sedimentation in spring the total sediment oxygen demand was highest in autumn. Sedimentation of fresh organic carbon has been shown to elicit a rapid increase in mineralisation rates in Arctic sediments (Rysgaard et al. 1998). However, a part of the settling bloom may consist of viable cells that are not directly available to assimilation by macrofauna, and pass intact through the gut. This fraction might also be resistant to microbial degradation, and decoupling of peak chl *a* concentration and sediment oxygen uptake rates have also been observed in temperate areas (Ståhl et al. 2004). However, the high vertical transport in spring was utilised by both suspension- and deposit-feeding bivalves, which exhibited increased gut content of chl *a* in spring compared with autumn. The biomass of macrobenthos was relatively high and comparable with estimates of benthic biomass from the highly productive part of the Bering Sea (Grebmeier et al. 1988). Consequently, macrobenthic carbon demand (39 mg C m^{-2} d^{-1}) was also considerably above estimates obtained by similar methods from the Kara Sea (15.5 to 21.7 mg C m^{-2} d^{-1}; Klages et al. 2003) and Young Sound, NE Greenland (15 mg C m^{-2} d^{-1}; Sejr & Christensen 2007), indicating that productivity is high in Disko Bay. Despite high biomass, the carbon demand of macrobenthos was relatively low compared with that of the pelagic community.

Formation and fate of spring bloom

The spring bloom was initiated by the break-up of sea ice during the first week of April. When sampling was conducted, the bloom was established and phytoplankton production and biomass were concentrated in the upper 20 m. Nutrients had not yet been depleted, partly due to the intrusion of nutrient-rich bot-

tom water which added new nutrients to the surface water. High chl *a* concentrations of 20 to 30 mg m^{-3} were measured; these are among the highest chl *a* concentrations reported from Disko Bay, as typical concentrations of chl *a* in summer are less than 10 mg m^{-3} (Levinsen et al. 1999, Nielsen & Hansen 1999). The biomass of copepods was initially very low in spring, but increased to 3–4 g C m^{-2}. In Disko Bay, the major part of the copepod community spends the winter at 300 to 400 m depth and then return to the surface water in late May and early June when the integrated biomass in the upper 50 m typically reaches 3 to 4 g C m^{-2} (Madsen et al. 2001, Juul-Pedersen 2006). The observed increase in copepod biomass in spring could thus be related to the beginning ascent of the wintering population combined with advection of water into the cove. It indicates that the bloom was initiated before significant quantities of copepods were present in the cove. The large increase in copepod biomass during the 2 wk in spring caused the grazing of the pelagic herbivores to exceed primary production at the end of the period. The vertical transport during the spring bloom was characterised by very high sedimentation rates. Average sedimentation of POC at 45 m was 1438 ± 168 mg C m^{-2} d^{-1} in spring. This is comparable with maximum sedimentation rates reported from the Barents Sea (409 to 1090 mg POC m^{-2} d^{-1} at 20 to 200 m, Andreassen & Wassmann 1998) and the North Water Polynya (155 to 1104 mg POC m^{-2} d^{-1} at 50 m, Michel et al. 2002). Approximately 36% of the vertical transport of carbon at 45 m could be related to the PPC fraction. The vertical transport of PPC was most probably stimulated by aggregation of individual cells (Kiørboe et al. 1994), as indicated by the increase in sinking velocity with increasing depth (Fig. 8). The loss rate of the PPC fraction due to sedimentation (2.5% of integrated biomass d^{-1}) thus exceeded the loss due to the combined grazing of the pelagic compartments (1% d^{-1}). It is likely, therefore, that we sampled during the peak of the bloom, when the appearance of copepods combined with the effect of aggregation eventually caused the loss of phytoplankton from the water column to exceed production. The termination of the spring bloom in Disko Bay was studied by Juul-Pedersen et al. (2006) in June 2001. They encountered a situation in which the surface water was depleted of nutrients and phytoplankton biomass was rapidly being reduced over a 3 wk period. The lower phytoplankton biomass reduced the average sedimentation to 628 mg POC m^{-2} d^{-1}. Copepods played a more important role, as their grazing resulted in a phytoplankton loss rate of 18% d^{-1}, and faecal pellets contributed on average 29% to the total vertical flux.

The abundance of bacterioplankton was similar to that previously reported for the area (Nielsen & Hansen 1995, 1999). Although bacterial biomass corresponded to only 5% of phytoplankton biomass in spring (Table 2), bacterial production was 50% of the phytoplankton production. High phytoplankton stocks supplying the present pool of DOC provided ample substrate for bacteria. Hence, the spring turnover rates of bacteria (bacteria production, BP:bacteria biomass, BB) were relatively high (10%, Table 2). Turnover rates of <5% have previously been reported during summer (Nielsen & Hansen 1999). Ciliates and heterotrophic dinoflagellates were present in concentrations typically encountered in June and July and provided a significant potential grazing pressure of 39% of primary production.

Factors influencing fate of pelagic primary production in Disko Bay

The spring sampling conducted during this study was performed over only 2 wk, but nevertheless showed the flow of carbon to be quite different from that previously described for the area. The apparent mismatch between phytoplankton and copepods observed probably contributed to the high chl *a* concentrations measured. As a result, we observed an export system displaying a close benthic–pelagic coupling rather than a system that efficiently retained carbon in the water column, as previously reported for the summer by Nielsen & Hansen (1999). The difference in carbon flow compared with previous studies is most probably related to 2 factors: our study was conducted (1) at shallow depths and (2) during a year when sea ice broke up earlier than usual. The shallow depth of this study (50 m) compared with depths of 200 to 300 m in previous studies probably increased pelagic–benthic coupling. Bacteria and protozooplankton have less time to degrade sinking particles in shallow water than in deep water, which increases the fraction of primary production reaching the benthos. Also, copepods, which spend the winter near the bottom in the deeper parts of the bay, probably return later in spring

Table 2. Mean ± SE. Integrated biomass (g C m^{-2}) and production (mg C m^{-2} d^{-1}) of bacteria and phytoplankton during spring and autumn

Parameter	Spring	Autumn
Phytoplankton biomass (PB)	20 ± 4	0.3 ± 0.1
Phytoplankton production (PP)	195 ± 34	27 ± 3
Bacteria biomass (BB)	0.88 ± 0.14	0.96 ± 0.06
Bacteria production (BP)	92 ± 24	49 ± 8
BB:PB	0.05	3.2
BP:PP	0.5	1.8

to shallow coastal areas. At 200 to 300 m in the middle of the bay, copepods would have intercepted the sinking spring bloom.

Shallow depth also increases chances of mixing events, which add new nutrients to the photic zone, as observed in spring. Møller & Nielsen (2000) found increased production in August near small islands in the central part of the bay, where bottom topography induced upwelling. A similar situation is probably found along the coast and in the cove, where this study was conducted. Finally, the shallow depth of the studied cove allows the macrobenthos to feed directly on the subsurface chl *a* maximum. This allows benthic suspension feeders to compete directly with pelagic grazers for resources. The high abundance of bivalves at 20 m combined with the typically high biomass of benthic macrozoobenthos generally support the idea that annual primary production is high near the coast, and that much of the production is available to the benthic community. The decrease in macrobenthic biomass with increasing depth matches the sedimentation pattern in spring and the frequent observation of subsurface blooms in summer. Peaks in benthic biomass and especially suspension-feeding bivalve biomass near the pycnocline have previously been documented in Greenland fjords (Sejr & Christensen 2007).

Sea ice conditions in Disko Bay as inferred from satellite imagery (Gloersen et al. 1990, Maslanik & Stroeve 2004) show large year-to-year variability (Fig. 12). In 2003, when this study was conducted, the ice cover in spring and on an annual basis was the lowest recorded since 1979. Sea ice break-up is usually reported to occur in late April or early May (Andersen 1981, Madsen et al. 2001), but sometimes occurs as late as June (Nielsen & Hansen 1995, Nielsen et al. 2001). In 2003, the sea ice broke up during the first week of April and we probably observed a bloom that formed at least 3 to 4 wk earlier than previously reported. It is well known that sea ice plays an important role in the timing of the spring bloom in the Arctic as well as in the year-to-year variation in the vertical flux (Fortier et al. 2003, Wassmann et al. 2004). As copepods previously have been reported to ascend in late May and early June in Disko Bay (Madsen et al. 2001), the unusual ice conditions could have been a contributing factor to the low biomass of copepods recorded on the first 2 sampling dates in spring.

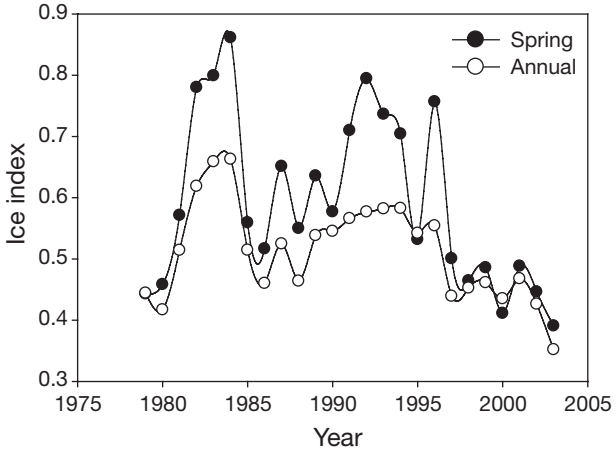

Fig. 12. Index of sea ice cover from satellite images of Disko Bay, West Greenland 1979 to 2003, showing annual sea ice index and spring index for months April, May and June

When comparing the carbon flow scenarios obtained in this study with the carbon flow in Young Sound, NE Greenland, important differences can also be related to sea ice conditions. Young Sound is a high-arctic fjord with approx. 9 mo of ice cover. Here, annual phytoplankton production is only 10 g C m^{-2} (Rysgaard et al. 1999) compared with estimates from 26 g C m^{-2} (Levinsen & Nielsen 2002) to 90 g C m^{-2} (Andersen 1981) in Disko Bay. As sea ice usually breaks up in early July, light availability is important to annual primary production in Young Sound while nutrient availability is more important in Disko Bay. The low productivity in Young Sound makes carbon inputs from land and the Greenland Sea relatively important (Rysgaard & Sejr 2007). Furthermore, the short open-water season in Young Sound does not leave room for the protozooplankton community to comprise the dominant grazers, because copepods are present throughout the summer. The obvious importance of sea ice for year-to-year variation and geographic differences in carbon flow makes speculation on impacts of projected sea ice changes necessary. Assuming that the future will bring a decrease in sea ice cover and an earlier ice break-up in spring, the following inferences can be made based on the present study. Annual primary production can be expected to increase due to increased light availability. Previous studies have found significant productivity associated with subsurface blooms or upwelling events even when nutrients were depleted in the upper mixed layer (Nielsen & Hansen 1999, Møller & Nielsen 2000). This indicates that nutrients are available to sustain increased production. Approximately 10 to 15% of the annual sunlight is received in April (Nielsen et al. 2001) and will be available to primary producers if sea ice breaks up in early April instead of May. A key question related to the fate of the increased production is whether changing ice conditions will increase the occurrence of years with a mismatch between copepods and the spring bloom. If so, a large proportion of the production could settle to the sea floor, as observed in this study, and the amount of carbon transported through the copepods could actually decrease despite increased primary production. The exact mechanisms controlling the emergence from dia-

pause are still unresolved, but if settling phytoplankters are involved, as suggested by Ringuette et al. (2002), copepods in Disko Bay should be able to respond to changing ice conditions and, over time, eventually match their ascent to the spring bloom. In a scenario such as this, increased primary productivity would predominantly benefit pelagic grazers.

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LITERATURE CITED

Andersen OGN (1981) The annual cycle of phytoplankton, primary production and hydrography in the Disko Bugt area, West Greenland. Medd Grønl, BioScience 6:1–65

Andreassen IJ, Wassmann P (1998) Vertical flux of phytoplankton and particulate biogenic matter in the marginal ice zone of the Barents Sea in May 1993. Mar Ecol Prog Ser 170:1–14

Blomqvist S, Larsson U (1994) Detrital bedrock elements as tracers of settling resuspended particulate matter in a coastal area of the Baltic Sea. Limnol Oceanogr 39: 880–896

Brey T (1999) A collection of empirical relations for use in ecological modelling. Naga, ICLARM Q 22:24–28

Brey T (2001) Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. Available at: http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/navlog/index.html

Chin-Leo G, Kirchman DL (1988) Estimating bacterial production in marine waters from the simoultaneous incorporation of thymidine and leucine. Appl Environ Microbiol 54:1934–1939

del Giorgio PA, Cole JJ (1998) Bacterial growth efficiency in natural aquatic systems. Annu Rev Ecol Syst 29:503–541

Fortier M, Fortier L, Michel C, Legendre L (2003) Climatic and biological forcing of the vertical flux of biogenic particles under seasonal Arctic sea ice. Mar Ecol Prog Ser 225: 1–16

Gloerson PD, Cavalieri WJ, Campbell B, Zwally J (1990) Nimbus-7 SMMR polar radiances and Arctic and Antarctic sea ice concentrations. National Snow and Ice Data Center, Boulder, CO. Available as CD-ROM

Grebmeier JM, McRoy CP, Feder HM (1988) Pelagic–benthic coupling on the shelf of northern Bering Sea and Chuckchi Seas. I. Food supply source and benthic biomass. Mar Ecol Prog Ser 48:57–67

Hamilton LC, Brown BC, Rasmussen RO (2003) West Greenland's cod-to-shrimp transition: local dimensions of climatic change. Arctic 56:271–282

Hansen PJ, Bjørnsen PK, Hansen BW (1997) Zooplankton grazing and growth: scaling within the 2–2000 µm body size range. Limnol Oceanogr 42:687–704

Hirche HJ (1998) Dormancy in three Calanus species (*C. finmarchicus*, *C. glacialis* and *C. hyperboreus*) from the North Atlantic. Ergeb Limnol 52:359–369

Juul-Pedersen T, Nielsen TG, Michel C, Møller EF and 5 others (2006) Sedimentation following the spring bloom in Disko Bay, West Greenland, with special emphasis on the role of copepods. Mar Ecol Prog Ser 314:239–255

Kiørboe T, Lundsgaard C, Olesen M, Hansen JLS (1994) Aggregation and sedimentation processes during a spring phytoplankton bloom: a field study to test coagulation theory. J Mar Res 52:297–323

Klages M, Deubel H, Rachor E (2003) Organic carbon consumption of the Kara Sea macrozoobenthos: a first assessment. In: Stein R, Fahl K, Fütterer DK, Galilmov EM, Stepanets OV (eds) Siberian river run-off in the Kara Sea. Elsevier Science, Amsterdam, p 267–280

Knap A, Michaels A, Close A, Dusklow H, Dickson A (eds) (1996) Protocols for the Joint Global Ocean Flux Study (JGOFS) core measurements. JGOFS Rep No. 19 Reprint of the IOC manuals and guides No. 29. UNESCO 1994, p 1–170

Lee S, Fuhrmann JA (1987) Relationships between biovolume and biomass of naturally derived marine bacterioplankton. Appl Environ Microbiol 53:1298–1303

Levinsen H, Nielsen TG (2002) The trophic role of marine pelagic ciliates and heterotrophic dinoflagellates in arctic and temperate coastal ecosystems: a cross latitude comparison. Limnol Oceanogr 47(2):427–439

Levinsen H, Nielsen TG, Hansen BW (1999) Plankton community structure and carbon cycling on the western coast of Greenland during the stratified summer situation. II. Heterotrophic dinoflagellates and ciliates. Aquat Microb Ecol 16:217–232

Levinsen H, Turner JT, Nielsen TG, Hansen BW (2000) On the trophic coupling between protists and copepods in arctic marine ecosystems. Mar Ecol Prog Ser 204:65–77

Madsen SD, Nielsen TG, Hansen BW (2001) Annual population development and production by *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in Disko Bay, western Greenland. Mar Biol 139:75–93

Maslanik J, Stroeve J (2004) DMSP SSM/I daily polar gridded brightness temperatures, July 1987 to October 2004. National Snow and Ice Data Center, Boulder, CO. Available as CD-ROM

Menden-Deuer S, Lessard EJ (2000) Carbon to volume relationships for dinoflagellates, diatoms and other protist plankton. Limnol Oceanogr 45:569–579

Møller EF, Nielsen TG (2000) Plankton community structure and carbon cycling off the western coast of Greenland, with emphasis on sources of DOM for the bacterial community. Aquat Microb Ecol 22:13–25

Nielsen TG, Hansen B (1995) Plankton community structure and carbon cycling on the western coast of Greenland during and after the sedimentation of a diatom bloom. Mar Ecol Prog Ser 125:239–257

Nielsen TG, Hansen BW (1999) Plankton community structure and carbon cycling on the western coast of Greenland during the stratified summer situation. I. Hydrography, phytoplankton and bacterioplankton. Mar Ecol Prog Ser 16:205–216

Nielsen N, Humlum O, Hansen BU (2001) Meteorological observations in 2000 at the Arctic Station, Qeqertarsuaq (69° 15' N), central West Greenland. Dan J Geogr 101: 155–157

Parkinson CL, Cavalieri DJ (2002) A 21 year record of arctic sea ice-ice extents and their regional, seasonal and monthly variability and trends. Ann Glaciol 34:441–446

Riebesell U, Reigstad M, Wassmann P, Noji T, Passow U (1995) On the trophic fate of *Phaeocystis pouchetii* (Hariot): VI. Significance of *Phaeocystis*-derived mucus for

vertical flux. Neth J Sea Res 33:193–203
Riemann B, Bjornsen PK, Newell S, Fallon S (1987) Calculation of cell production of coastal marine bacteria based on measured incorporation of ^{3}H thymidine. Limnol Oceanogr 32:471–476
Ringuette M, Fortier L, Fortier M, Runge JA, Bélanger S, Larouche P, Weslawski JM, Kwasniewski S (2002) Advanced recruitment and accelerated population development in Arctic calanoid copepods of the North Water. Deep-Sea Res II 49:5081–5099
Rysgaard S, Sejr MK (2007) Vertical flux of particulate organic matter in a High Arctic fjord: relative importance of terrestrial and marine sources. In: Rysgaard S, Glud RN (eds) Carbon cycling in Arctic marine ecosystems: case study Young Sound. Medd Grønl Biosci 58:109–121
Rysgaard S, Thamdrup B, Risgaard-Petersen N, Fossing H, Berg P, Christensen PB, Dalsgaard T (1998) Seasonal carbon and nutrient mineralisation in a high-arctic coastal marine sediment, Young Sound, Northeast Greenland. Mar Ecol Prog Ser 175:261–276
Rysgaard S, Nielsen TG, Hansen BW (1999) Seasonal variation in nutrients, pelagic primary production and grazing in a high-Arctic coastal marine ecosystem, Young Sound, Northeast Greenland. Mar Ecol Prog Ser 179:13–25
Sakshaug E (1997) Biomass and productivity distributions and their variability in the Barents Sea. ICES J Mar Sci 54: 341–350
Sejr MK, Christensen PB (2007) Growth production and carbon demand of macrofauna in Young Sound with special emphasis on the bivalves *Hiatella arctica* and *Mya truncata*. In: Rysgaard S, Glud RN (eds) Carbon cycling in Arctic marine ecosystems: case study Young Sound. Medd Grønl Biosci 58:121–137
Simon M, Azam F (1989) Protein content and protein synthesis rates of planktonic marine bacteria. Mar Ecol Prog Ser 51:201–213
Ståhl H, Tengberg A, Brunnegård J, Bjørnholm E and 7 others (2004) Factors influencing organic carbon recycling and burial in Skagerrak sediments. J Mar Res 62:867–907
Thor P, Nielsen TG, Tiselius P, Juul-Pedersen T and 5 others (2005) Post-spring bloom community structure of pelagic copepods in the Disko Bay, Western Greenland. J Plankton Res 27(4):341–356
Wassmann P, Bauerfeind E, Fortier M, Fukuchi M and 8 others (2004) Particulate organic carbon flux to the Arctic Ocean sea floor. In: Stein R, MacDonald RW (eds) The organic carbon cycle in the Arctic Ocean. Springer-Verlag Berlin, p 101–138

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