

Pivotal role of sea ice sediments in the seasonal development of near-shore Arctic fast ice biota

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ABSTRACT: The impact of sea ice sediments on the seasonal development of sea ice biota was assessed in Alaskan nearshore fast ice. Ice, water, and seafloor sediment were sampled in spring 2002 and 2003 at 2 locations. Light in the sediment-loaded sea ice location (total particle load = 106 g dry mass, DM, m⁻²) was reduced by more than 99% compared to the clean ice location (total particle load = 6 g DM m⁻²). Strong bottom ice algal blooms developed in sediment-free fast ice, reaching their maximum of 330 µg chl a l⁻¹ (36 mg chl a m⁻²) in late May. Pigment levels in sediment-laden ice never exceeded 9 µg chl a l⁻¹ (1 mg chl a m⁻²). In the water column, pigment levels remained below 1 µg chl a l⁻¹ (<5 mg chl a m⁻²) under both clean and sediment-laden ice. With increasing ice algal biomass, the δ¹³C ratio of sea ice particulate organic matter (POM) in clean ice increased from -25‰ in February to -16‰ in May, while no and little enrichment was observed in sediment-laden ice and pelagic POM, respectively. The abundance of ice metazoans in clean ice increased with progressing season from 17 700 (Feb) to 276 200 ind. m⁻² (May), dominated by nematodes and ice-associated polychaete juveniles. In sediment-laden ice, maximum abundance was 16 600 ind. m⁻² (May). Abundances of meroplanktic polychaete juveniles were at least one order of magnitude below abundances in the ice, suggesting sea ice is an important feeding habitat for these young life stages. Sediment within the ice had a profound impact on sea ice biota, and delayed or inhibited the spring bloom development.

KEY WORDS: Arctic sea ice · Sea ice sediments · Ice algae · Ice fauna · Particulate organic carbon · POC · Particulate organic nitrogen · PON · Stable isotope ratio

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INTRODUCTION

Light is generally accepted as the most important variable responsible for the enormous seasonality in many biological processes in polar oceans (Kirst & Wiencke 1995, Sakshaug 2004). In sea ice, additional environmental conditions such as space availability, temperature and salinity not only reach extreme values but also vary considerably with season (Eicken 2003). These settings make the brine channel network in sea ice a habitat that is extreme, highly variable and distinctly different from any other polar marine environment (Weissenberger et al. 1992, Gradinger 2002). With the return of light in early spring, ice algal blooms form at the bottom of the ice prior to any increase in phytoplankton productivity, and ice algae are a main food source for herbivores early in the season (Horner & Schrader 1982, Horner 1985).

Over the course of the spring, diatoms, flagellates, ciliates, nematodes, turbellarians and copepods build up considerable abundances within the bottom section of the sea ice, and amphipod and copepod crustaceans frequent the ice/water interface (e.g. Lønne & Gulliksen 1991, Gradinger & Bluhm 2004, Bluhm & Gradinger 2008). In coastal fast ice locations, a plentiful assemblage of meroplankton, pelagic larvae of benthic invertebrates, augments the sea ice faunal inventory, e.g. copepod nauplii and copepodites, and larvae and juveniles of benthic polychaetes and mollusks (Carey & Montagna 1982, Cross 1982, Kern & Carey 1983, Grainger et al. 1985). The ice algal productivity is not only used by the ice-related fauna, but also by zooplankton and benthic feeders, specifically during periods of ice melt (e.g. Michel et al. 2002, Leventer 2003, Bluhm & Gradinger 2008).

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The dominance of the light regime in regulating primary production in sea ice is well documented from field and laboratory experiments (e.g. Gradinger et al. 1991, Arrigo 2003, Gradinger 2009). For ice algal growth, major abiotic modifiers of available light are seasonality, ice thickness and snow cover (Maykut 1985). Only recently has sediment, incorporated within the ice, been studied with regard to its ability to modify the albedo and attenuation properties of sea ice (Light et al. 1998). Sediment occurs in concentrations above 100 g m^{-2} in Arctic sea ice (e.g. Nürnberg et al. 1994), and such sediment-rich patches are particularly common in the Chukchi and Beaufort Seas (Barnes et al. 1982, Osterkamp & Gosink 1984, Eicken et al. 2005), forming so-called 'dirty ice' or 'sediment-laden ice'. Up to 50% of the entire Arctic ice cover can contain visually detectable amounts of sediment (Pfirman et al. 1989, Reimnitz et al. 1993, Nürnberg et al. 1994), which is transported across the offshore Arctic with the ice drift.

Sea ice sediments located in the top 20 to 30 cm of the ice alter the spectral albedo, whereas total sediment load affects light transmission (Light et al. 1998). Osterkamp and Gosink (1984) observed, for example, about 10-fold higher attenuation coefficients for sediment-laden fast ice compared to clean ice. Previous studies have demonstrated that modulation of light by snow cover is a major factor responsible for horizontal patchiness in sea ice physical and biological variables (e.g. Gosselin et al. 1986, Grossi et al. 1987, Steffens et al. 2006). In this study, we hypothesized that sea ice sediment load should also have a pronounced effect on the seasonal development of sea ice biota due to its alteration of the light regime. We expected significantly higher maximum biomass values for ice algae and higher sea ice meiofauna abundances in clean ice compared to sea ice with sediment. This hypothesis is specifically important for Arctic seas, as changing sediment loads are likely to occur in the near future as a result of increased coastal erosion and sediment suspension with decreasing sea ice regimes (Stierle and Eicken 2002).

MATERIALS AND METHODS

The fast ice along the Alaskan coastline forms in November/December and reaches a thickness of 1.5 to 1.8 m by April (Macdonald et al. 1999, Mahoney et al. 2007a,b). Break-up usually occurs between late June and mid-July (Mahoney et al. 2007b). Attached to the shore and anchored to the sea floor by up to 20 to 25 m deep keels (Macdonald 2000), the ice extends several km out onto the Chukchi and Beaufort shelves.

Two sites (Fig. 1) were selected during our first field phase (April 24 to 28, 2002) while the main experiment included 3 sampling periods February 12 to 17 (pre-bloom), April 1 to 5 (maximum ice algal bloom) and May 27 to 30 (end of bloom) of 2003. We selected 2 clean (no visible sediment incorporation) sites in 2002 for ice-core sampling to check for differences between sites. Both sites were approximately 200 m offshore in a water depth of 5 to 5.6 m and we only sampled in level, un-ridged areas to minimize spatial variability (e.g. Steffens et al. 2006). Having sampled 2 sites gave us flexibility in 2003 in finding areas of clean and sediment-laden ice. This flexibility was needed given the substantial year to year variability in the fast ice regime in this region (Mahoney et al. 2007a, b). In 2003, we sampled clean (without visible sediment load) ice at Site 1 ($71^{\circ}20' \text{ N}$, $156^{\circ}42' \text{ W}$), while all cores from Site 2 ($71^{\circ}22' \text{ N}$, $156^{\circ}24' \text{ W}$) exhibited substantial amounts of sediment in the top 40 to 44 cm of the ice cores (for example see Fig. 2).

Physical properties. At each location, snow depth was determined at 10 locations in a perimeter of 1 m around the site. Air, snow surface, snow/ice interface and ice temperatures were measured with a Traceable thermometer (accuracy of 0.05 K). Ice cores were collected with an ice auger (9 cm diameter) and the total ice thickness was recorded from a minimum of 4 cores per site for each sampling event. Ice temperature was measured immediately after coring in 1 ice core per site in 10 to 20 cm intervals over the entire ice thickness. Temperature and salinity of the water column were determined with a YSI 85 sensor (YSI Inc.) at 1 m intervals. Freezing of the T/S sensor head due to cold air temperatures caused malfunction of the salinity readings in February and April 2003.

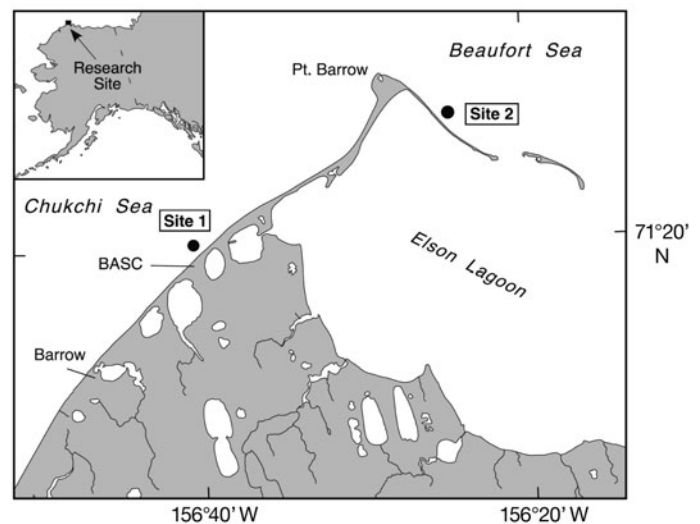


Fig. 1. Location of project sampling sites. Site 1: sediment-free ice, Site 2: sediment-loaded ice



Fig. 2. Complete ice core collected at sediment-laden Site 2 on February 16, 2003. Note gray coloration due to incorporated sediments in top part of ice core, while remaining parts of the ice are nearly sediment-free. Additional ice cores (already processed) on top of fast ice

At each station and sampling date around solar noon, the PAR (photosynthetically active radiation; 400 to 700 nm) photon flux density was measured with a LI-COR underwater 4π sensor at 1 m intervals through a separate core hole which was covered with snow prior to readings. A 2π sensor that remained at the ice surface provided a reference to eliminate changes due to cloud cover. Measurements were otherwise not corrected for variations in weather between sampling periods. To ensure accurate depth readings, for both light and T/S, the sensors were attached to marked fiberglass rods. In May 2003, we also determined the spectral composition of the incoming radiation on the surface of the sea ice and the downwelling radiation under the sea ice to a spectral resolution of 2 nm using a calibrated OceanOptics radiometer equipped with a 3 m long fiber-optic cable.

Biological properties. Biological samples were taken from sea ice, water column and sea floor sedi-

ment in 4 replicates per site, season and variable, unless otherwise specified. Due to logistical constraints, the treatments 'sediment-laden' versus 'sediment-free' were not replicated. Based on the observed variability within the replicates of the 2002 sampling event and assuming a difference of at least a factor of 5 between clean and sediment-laden ice biological properties, an *a priori* power analysis (using SYSTAT 11) revealed that 3 replicates would be sufficient to detect significant differences between the sediment-free and sediment-laden locations.

Eight ice cores were taken at each site, 0.3 to 2 m apart from each other. Of these 8 cores, we only analyzed the bottom 10 cm, as these generally contain the highest algal and meiofauna abundances (Horner 1985, Schünemann & Werner 2005). In April 2003, a ninth, entire ice core from the sediment-free location was analyzed for algal pigment concentrations; the thickness of the analyzed sections was 1 to 10 cm. In April 2003, an additional entire ice core from each location was used to determine the total seston content. Melted cores were filtered onto pre-weighted and pre-combusted GF/F filters and stored frozen until later analysis of total particulate matter by weighing the filter in the home laboratory.

For resampling the sites after the first sampling event, a handheld GPS was used to find the location, and sampling took place within a 25 m radius of this location.

The bottom 10 cm sections of Cores 1 to 4 were melted directly in the dark. After complete melt, 50 ml sub-samples were filtered onto Whatman GF/F filters and subsequently frozen (-20°C) for algal pigment analysis. Another set of 50 ml sub-samples was filtered onto pre-combusted GF/F filters, and frozen (-20°C) for later determination of total particulate organic carbon (POC), nitrogen (PON) and stable carbon and nitrogen isotope composition.

The bottom sections of Cores 5 to 8 were melted in the dark after addition of 1 l of $0.2\ \mu\text{m}$ -filtered seawater to avoid osmotic stress for the biota (Garrison & Buck 1986). After complete melt, samples were concentrated over $20\ \mu\text{m}$ gauze. Metazoan ice meiofauna was sorted and counted fresh or after fixation in 4% formaldehyde using a Wild M3 dissecting microscope. Areal abundances (ind. m^{-2}) were calculated by dividing the number of counted animals by the surface area of the ice corer.

Four replicate water samples were taken through the core holes from an intermediate water depth (3 m) with a Kemmerer water sampler. For analysis of algal pigments, total organic and inorganic matter, and stable isotope composition, 0.2 to 0.5 l each was filtered onto GF/F filters and treated in the same way as the melted ice samples.

Vertical plankton hauls were taken with 20 and 200 μm mesh nets. Samples were sorted either live or after preservation in formaldehyde (4% final concentration), and specimens were counted by species/taxon using a Wild M3 dissecting microscope. Areal estimates were calculated by dividing the number of animals counted by the area of the net opening.

Benthic sediment samples were collected with a benthic corer (6 cm diameter) with an attached extension deployed through an ice core hole. The top 5 cm of the sediment cores were collected, thoroughly mixed, and sub-samples frozen for determination of algal pigments. We did not succeed in collecting depth-stratified samples within the top 5 cm due to difficulties with core collection and extraction at the partially extremely cold temperatures. Due to the methodological problems, we were not able to calculate areal estimates for sediment variables.

Algal pigment concentrations were determined in all 3 realms. Ice and water column samples were extracted with 7 ml of 90% acetone for 24 h in the freezer (Arar & Collins 1992). In the case of the sediment samples, 15 ml of 90% acetone were added to approximately 1 g (wet weight) of sediment (Conde et al. 1999). After extraction of the sediment samples, 7 ml of acetone were transferred into a borosilicate tube and centrifuged for 20 min at 1500 min^{-1} . Pigment concentrations (chlorophyll *a*, chl *a* and phaeophytin) were determined fluorometrically with a Turner Designs fluorometer. Phaeophorbides were determined collectively as phaeophytin. Following the pigment extraction, the sediment was dried at 60°C for 24 h, and weighed. Chl *a* concentrations in sediment are therefore presented per g dry weight sediment. Our chl *a* estimates are unlikely to be strongly influenced by the presence of chl *b*, as ice algal communities are typically dominated by diatoms (Gradinger 2002). Thus we assume that the effect of underestimating chl *a* and overestimating phaeophorbides did not have a substantial impact on our data (<5%, Arar & Collins 1992).

Filters for stable isotope analysis were dried in a drying oven at 65°C for 1 to 2 d. All filters were then HCl-fumed in a vacuum chamber for 24 h and dried again. The filters were folded into tin cups and analyzed on ThermoFinnigan Delta mass spectrometers for their $\delta^{13}\text{C}$ (analytical error: 0.05‰) and $\delta^{15}\text{N}$ (analytical error: 0.06‰) values and total POC and PON masses with carbon PDB and atmospheric N_2 as standards.

For sea ice, we converted the volumetric algal pigment and POC estimates of melted sea ice to areal estimates using an average density for submerged first year ice (0.91 Mg m^{-3} ; Timco & Frederking 1996) for the bottom 10 cm of our ice cores. For sea water data, we assumed a integration water depth of 5 m.

RESULTS

Physical properties

Snow thickness varied between 3 and 7 cm within and among sampling events and stations. Due to an ice break-off on December 23, 2002, ice thickness at the clean ice site was less (0.8 m) than at the sediment-laden ice site (1.2 m) in February 2003. Ice thickness increased over time to maximum values of 1.3 m at the clean ice site and 1.7 m at the sediment-laden ice site in May 2003. The variability of ice thickness between replicate cores at each site and each sampling event was <5 cm.

Ice temperatures were lowest at the top of the fast ice and increased to seawater temperature at the bottom with no differences between the 2 sites (Fig. 3a,b). The coldest air and ice temperatures were encountered in February 2003, with minimum ice temperatures of -25°C at the ice surface and air temperatures of -30°C . Ice temperatures in April 2003 ranged from -13°C at the top of the ice cores to -1.9°C at the bottom. In late May, ice temperatures had increased to between -0.2 and -2°C at the ice surface. The temperature profiles in the water column (not shown) exhibited neither seasonal patterns nor any indication of vertical stratification: values ranged between -1.4 and -2°C . Water column salinity in May varied between 30.6 and 31.9.

The incident PAR increased with season at Sites 1 and 2 from February (34 and $138 \mu\text{E m}^{-2} \text{ s}^{-1}$) to April (393 and $642 \mu\text{E m}^{-2} \text{ s}^{-1}$) and May (886 and $1402 \mu\text{E m}^{-2} \text{ s}^{-1}$). The higher values at Site 2 are due to differences in the weather conditions during sampling. Relative light intensities at the ice/water interface under sediment-laden sea ice were 2 orders of magnitude below those under sediment-free ice, and never exceeded an absolute value of $0.4 \mu\text{E m}^{-2} \text{ s}^{-1}$ (Fig. 3c,d). At the clean ice Site 1, absolute irradiance increased with time, but the relative irradiance levels in the ice/water interface region decreased from February to April and remained low in May. Distinct differences were evident in the spectral light composition between sediment-laden and sediment-free sea ice (Fig. 3e,f). At the sediment-free site, attenuation was highest in the blue and red wave bands, where chlorophyll has its absorbance maxima. In contrast, the spectral composition at the sediment-laden site did not indicate any preferential absorption in the PAR range (400 to 700 nm).

The dry mass (DM) of particulate matter over the entire ice thickness was 15.3 times higher at sediment-laden ice Site 2 ($102.41 \text{ g DM m}^{-2}$) than at clean ice Site 1 (6.67 g DM m^{-2}). The analysis of 4 replicate bottom sections revealed that approximately 0.9% of the total particle load was localized in the bottom 10 cm at the sediment-laden site ($0.9 \pm 0.1 \text{ g DM m}^{-2}$), while the

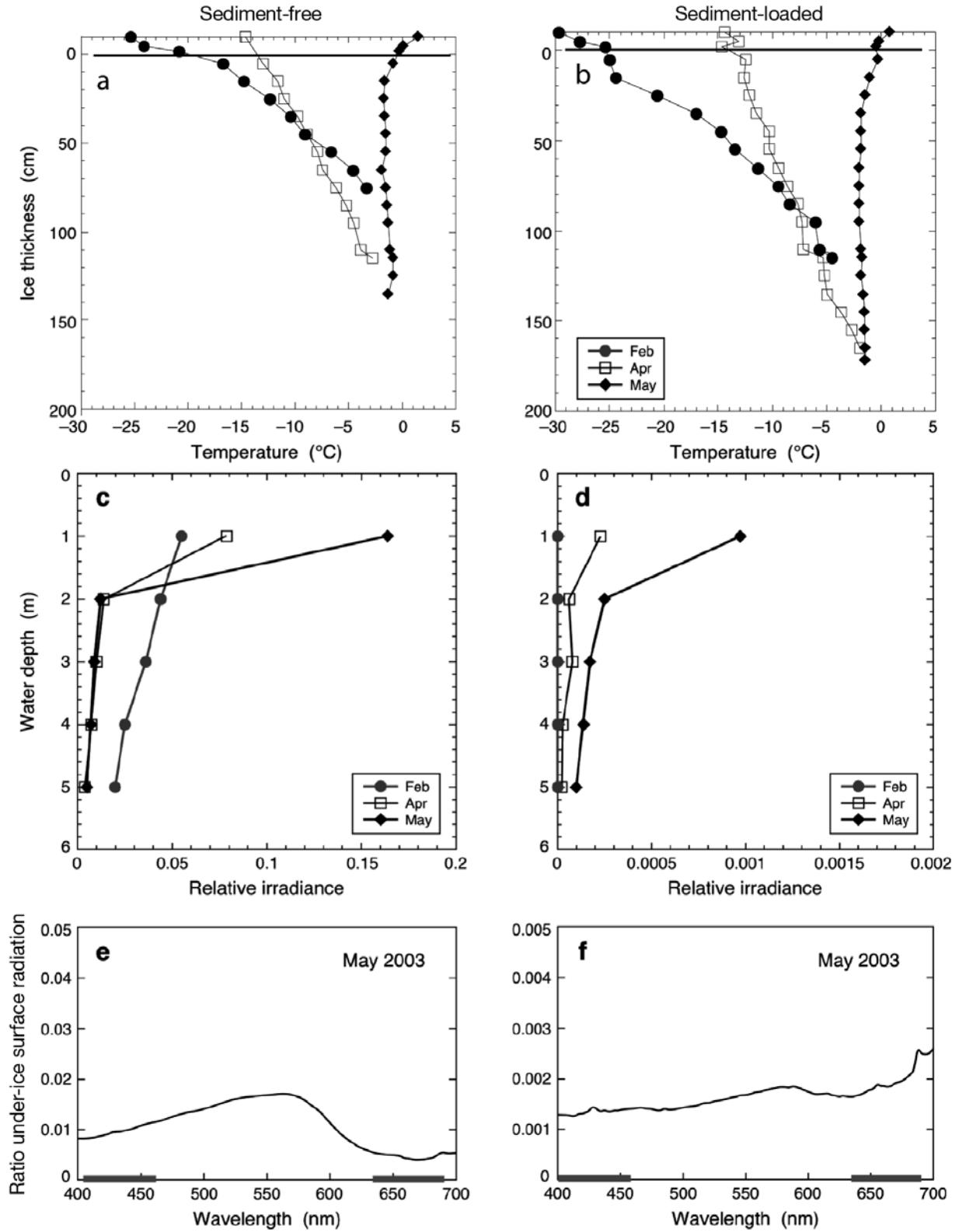


Fig. 3. Environmental variables at 2 coastal fast ice sites with no sediment (left) and high sediment load (right) in sea ice cover in 2003. (a,b) Sea ice temperatures. Horizontal line: top of ice floe; measurements above the line were made in air and snow. (c,d) Sub-ice irradiance (ratio $4\pi:2\pi$ sensor) in February, April and May 2003. (e,f) Spectral light composition in May 2003. Thick gray lines along the x-axis: ranges of maximum chlorophyll absorption. Note differences in axis scales

fraction at the clean ice site was considerably higher at 46.5% ($3.1 \pm 0.9 \text{ g DM m}^{-2}$).

Biological properties

Our data from April 2002 revealed high ice algal pigment concentrations in clean ice at both locations with a maximum concentration of $246.8 \pm 23.5 \mu\text{g chl a l}^{-1}$ at

Site 2 (Fig. 4; note that Site 2 had clean ice in 2002). Analysis of algal pigment concentration at Site 1 over the entire ice thickness in April 2003 demonstrated that the bottom 10 cm contained 93% ($7.72 \text{ mg chl a m}^{-2}$) of the entire integrated pigment content ($8.31 \text{ mg chl a m}^{-2}$) (Fig. 5). Seasonal changes in ice algal biomass in the bottom 10 cm segments (given as mean \pm SD plus areal estimate based on the mean) were observed at both sampling locations. At the clean ice

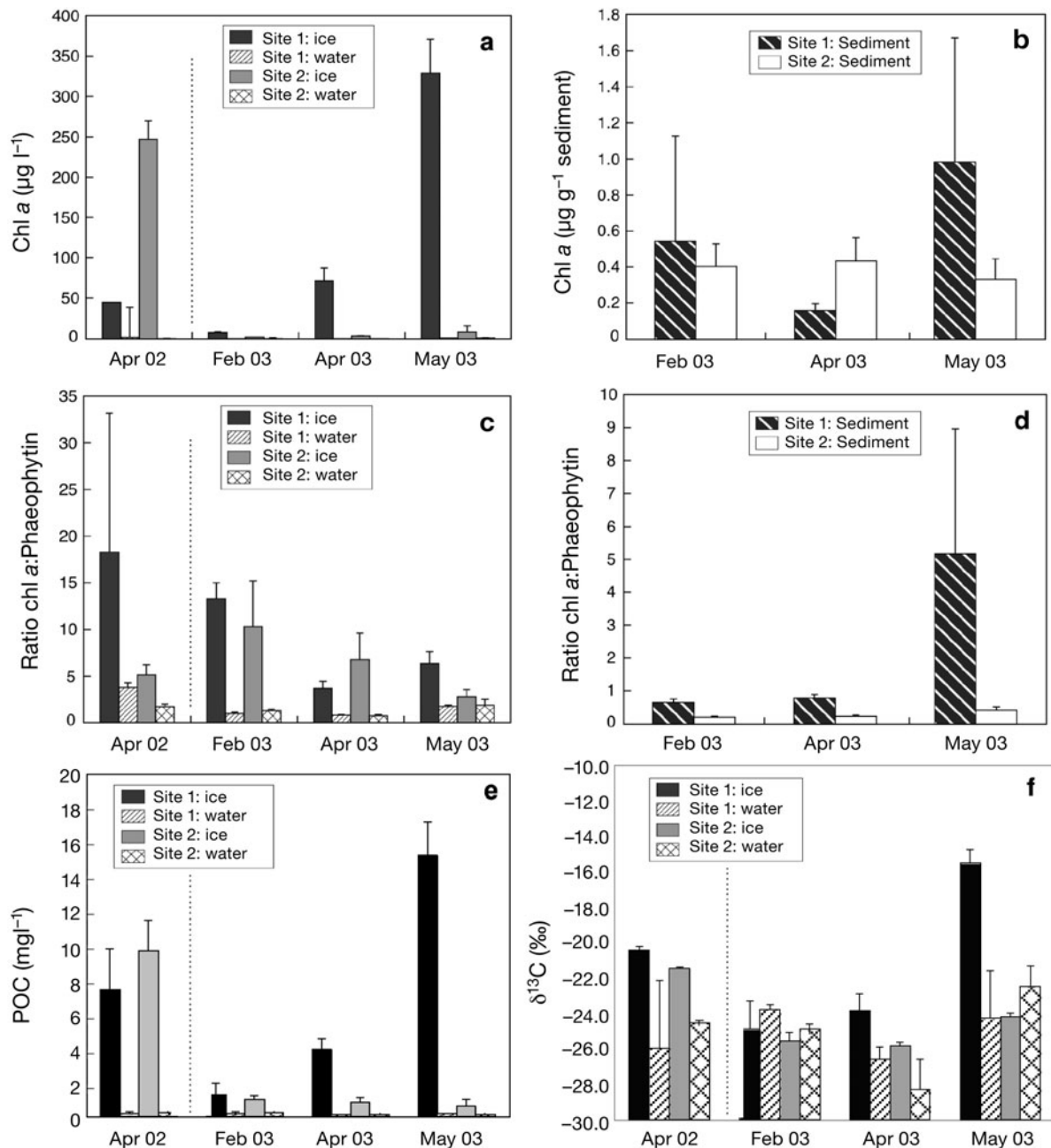


Fig. 4. Biological variables at 2 coastal fast ice sites with no sediment (Site 1) and high sediment load (Site 2) during sea ice cover in 2003. (a,b) Algal pigment concentrations and (c,d) pigment ratios (chl a:phaeophytin) in ice, water and sediment. (e,f) POC and $\delta^{13}\text{C}$ in sea ice and water samples. Dotted vertical lines separate the 2002 and 2003 sampling events. Error bars represent the standard deviations

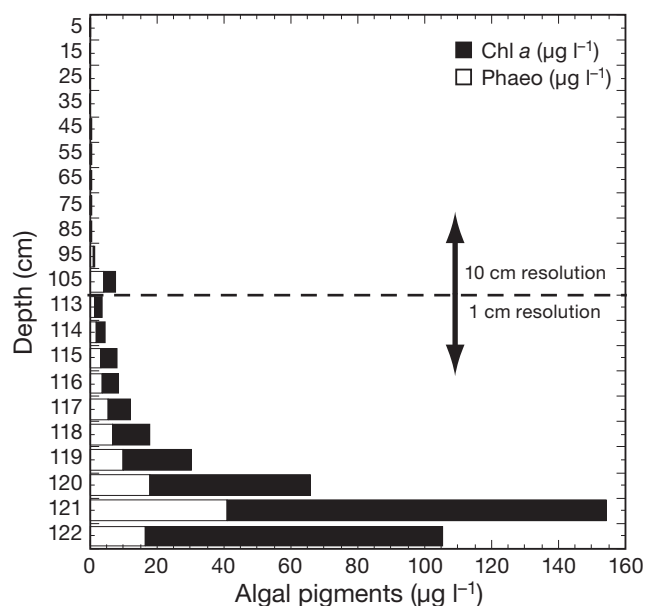


Fig. 5. Algal pigment concentration in April 2003 at Site 1. Note that the vertical resolution changes from 10 cm sections (top 112 cm) to 1 cm sections in the bottom 10 cm of the core. Depth represents the midpoint between the upper and lower end of a section

Site 1 in 2003, algal pigment content in the bottom 10 cm of the sea ice increased by 2 orders of magnitude from February ($7.4 \pm 0.7 \mu\text{g chl a l}^{-1}$; $0.8 \text{ mg chl a m}^{-2}$) to May 2003 ($329.3 \pm 42.0 \mu\text{g chl a l}^{-1}$; $36.2 \text{ mg chl a m}^{-2}$) (Fig. 4a). In the sediment-laden sea ice (Site 2 in 2003), pigment concentration increased slightly from $1.9 \pm 0.0 \mu\text{g chl a l}^{-1}$ ($0.2 \text{ mg chl a m}^{-2}$) in February to $8.3 \pm 7.0 \mu\text{g chl a l}^{-1}$ ($0.9 \text{ mg chl a m}^{-2}$) in May 2003. The chl a:phaeophytin ratios decreased at both locations with progressing season from February (13.3 ± 1.7 at Site 1, and 10.3 ± 4.9 at Site 2) to May (6.3 ± 1.3 at Site 1, and 2.7 ± 0.8 at Site 2) (Fig. 4c). Visual inspection of the ice cores immediately after coring revealed no indication of internal or surface pigment maxima in any of the cores.

Compared to sea ice algal concentrations, phytoplankton pigment levels remained low ($<1 \mu\text{g chl a l}^{-1}$; $<5 \text{ mg chl a m}^{-2}$) throughout the 2003 study period at both locations (Fig. 4a). The chl a/phaeophytin ratios at the 2 sites were lowest in April 2003 (0.7 ± 0.1) and highest in late May 2003 (1.8 ± 0.6) with no significant site-specific differences (Fig. 4c). The ratio of the mean chl a concentrations in sea ice relative to the water column increased with progressing season from 150 to 370 at the clean ice site, while it decreased from 47 to 9 at the sediment-laden ice location. Ratios of integrated algal pigments between ice and water ranged from 3.3 (February) to 16.8 (April) at Site 1, and from 0.2 (May) to 1.0 (February) at Site 2.

Mean chlorophyll concentrations in benthic sediment varied between <0.2 and $>1.0 \mu\text{g chl a g}^{-1}$ dry sediment throughout the sampling period at both sites. The pigment concentrations in the sediment varied considerably between replicates at the sediment-laden ice site, where the coarse sediment was difficult to sample with our corer. No seasonal trend in pigment concentrations and chl a:phaeophytin ratios was observable at the sediment-laden ice location, but they increased at the clean ice site in May when the ratio was 5.2 ± 3.8 (Fig. 4b,d).

The sea ice POC concentrations increased at the sediment-free location by a factor of 12 during the 2003 sampling period (Fig. 4e) from $1.3 \pm 0.6 \text{ mg l}^{-1}$ (0.14 g m^{-2}) in February to $15.2 \pm 1.9 \text{ mg l}^{-1}$ (1.68 g m^{-2}) in May. C:N ratios in clean ice (not shown) varied between 7.4 ± 0.1 (April 2002) and 12.1 ± 2.4 (May 2003) with no clear seasonal trend. At the sediment-laden ice site, POC decreased from February ($1.0 \pm 0.2 \text{ mg l}^{-1}$; 0.11 g m^{-2}) to May ($0.6 \pm 0.1 \text{ mg l}^{-1}$; 0.06 g m^{-2}). The C:N ratios at this site were >10 in both February and April 2003. No C:N ratio is available for Site 2 in May 2003. Water column POC concentrations remained below 0.2 mg l^{-1} (1.06 g m^{-2}) at both sites throughout the study period (Fig. 4e). The ratio of the integrated POC values between ice and water increased at the clean ice site from 0.2 in February to 2.6 in May. At both locations, C:N ratios in the water column decreased over the progressing season with maximum change at the clean ice site from 18.4 ± 11.8 in February to 6.9 ± 0.6 in May.

The $\delta^{13}\text{C}$ in the clean sea ice became increasingly enriched with progressing season from $-24.9 \pm 1.6\text{‰}$ in February to $-15.5 \pm 0.8\text{‰}$ in May (Fig. 4f). In contrast, the $\delta^{13}\text{C}$ signature remained below -25‰ at Site 2 in February and April, and increased slightly to $-24.2 \pm 0.2\text{‰}$ in May. This relationship between $\delta^{13}\text{C}$ (‰) and POC ($\mu\text{g l}^{-1}$) pooled for the entire data set was highly significant:

$$\delta^{13}\text{C} = -25.964 + 0.0007 \times \text{POC} \quad (1)$$

$(r^2 = 0.899, n = 18, p < 0.0001)$

At both sites, $\delta^{13}\text{C}$ ratios in the water column samples were depleted in April (clean ice site: $-26.6 \pm 0.7\text{‰}$, sediment-laden ice site: $-28.3 \pm 1.7\text{‰}$) relative to February (clean ice site: $-23.8 \pm 0.3\text{‰}$, sediment-laden ice site: $-24.9 \pm 0.3\text{‰}$) and May (clean ice site: $-24.3 \pm 2.7\text{‰}$, sediment-laden ice site: $-22.5 \pm 1.2\text{‰}$).

The abundance of meiofauna within the sea ice followed the changes of the ice algal biomass (Fig. 6a,b). In the sediment-free ice, mean total abundance increased from $18\,000 \text{ ind. m}^{-2}$ sea ice in February to $276\,000 \text{ ind. m}^{-2}$ in May. In contrast, mean total abundances in the sediment-laden ice remained below $17\,000 \text{ ind. m}^{-2}$ throughout the study period in 2003 with no seasonal trend. This cannot be attributed to site

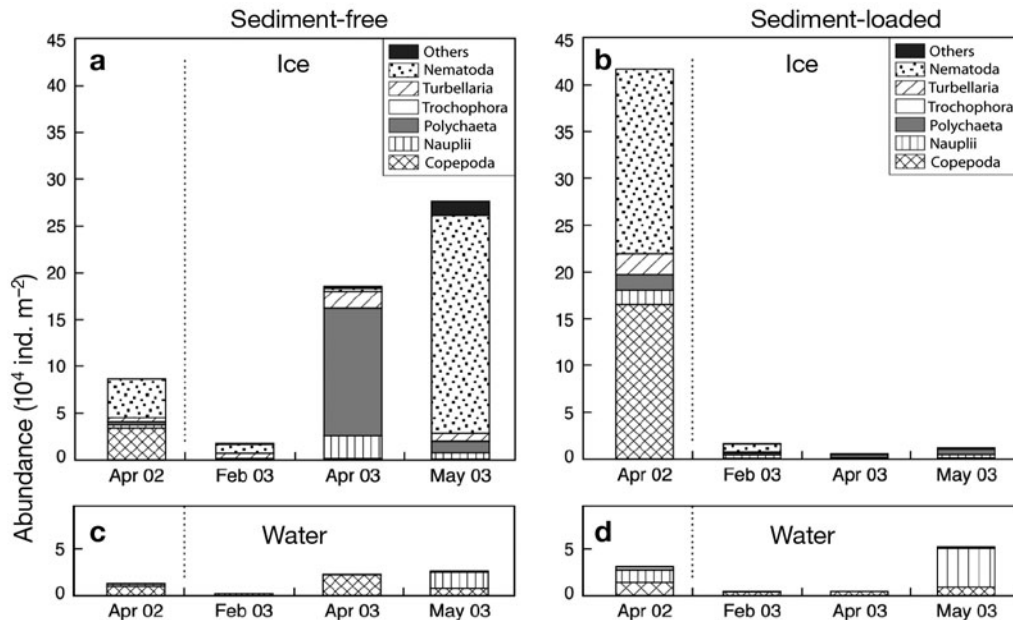


Fig. 6. (a,b) Abundance and composition of metazoans within the sea ice and (c,d) in the water column beneath the sea ice in April 2002 to May 2003 in and under sediment-free ice (Site 1) and sediment-loaded ice (Site 2). Dotted vertical lines separate the 2002 and 2003 sampling events

effects, as the April 2002 mean abundance of the same location without sediment load was 416 700 ind. m^{-2} . Ice meiofauna was dominated by polychaete juveniles, nematodes, copepods (calanoid, cyclopoid and harpacticoid), copepod nauplii and turbellarians. Taxa less frequently found (listed as others, Fig. 6) included unidentified larvae, rotifers and cnidarians. Unicellular meiofauna taxa (ciliates and flagellates) occurred regularly but were not quantified. The high abundance of nematodes in May was related to active reproduction: we observed juveniles hatching out of egg cases in the laboratory while counting the samples.

Zooplankton abundances in the water column showed a seasonal increase of similar relative magnitude at both sites in 2003 (Fig. 6c,d). Values increased between February and May from 2140 ind. m^{-2} to 28360 ind. m^{-2} at the clean ice Site 1 and from 4730 ind. m^{-2} to 56300 ind. m^{-2} at the sediment-laden

ice Site 2. At all sampling dates, the zooplankton (Fig. 6c,d) was dominated by copepods, with nauplii starting to occur in late April (2002) and May (2003). The total abundance of polychaete juveniles in the water column was <700 ind. m^{-2} at any of the sampling events and, thus, at least one order of magnitude below sea ice values in April and May (3520 to 136600 ind. m^{-2}) of the clean ice site.

Using the means for all variables of the complete sea ice data set from both sampling sites and all dates, the correlation analysis (Table 1) revealed significant relationships between various ice biota biomass and abundance variables. Chl *a* and POC were highly significantly correlated, and the relationships between ice meiofauna abundance and chl *a* and POC were significant at the levels of $p < 0.01$ and $p < 0.05$, respectively. The $\delta^{13}C$ ratios were significantly correlated with chl *a* and POC values.

Table 1. Correlation matrix for the entire sea ice data set based on mean values of each variable for each sampling date. Significant relationships in **bold** (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Light 4 π (%) is the ratio of the PAR level at the ice-water interface compared to the surface 2 π reading. C:N = carbon:nitrogen ratio

	Chl <i>a</i> ($\mu g\ l^{-1}$)	Meiofauna abundance (ind. m^{-2})	POC ($\mu g\ l^{-1}$)	C:N	Light 4 π (%)	Light 2 π ($\mu E\ m^{-2}\ s^{-1}$)
Meiofauna abundance (ind. m^{-2})	0.887**					
POC ($\mu g\ l^{-1}$)	0.941***	0.801*				
C:N	-0.184	-0.505	-0.267			
Light 4 π (%)	-0.035	-0.064	-0.048	0.227		
Light 2 π ($\mu E\ m^{-2}\ s^{-1}$)	0.214	0.207	0.115	-0.117	-0.556	
$\delta^{13}C$ (‰)	0.858**	0.637	0.961***	-0.204	-0.039	0.170

DISCUSSION

Our study demonstrates that sediment within the ice delays the seasonal development of the sea ice biota. In the region of high sediment load, the biological development of the spring algal bloom was retarded, and abundance of sea ice fauna was greatly reduced compared to a clean ice location. In the following, we will first discuss the biological observations at the clean ice site, and then focus on the effect of the sediment load on sea ice biological properties.

Seasonal development of ice biota through a spring bloom cycle at a clean ice site

Field and modeling efforts clearly demonstrate that increasing day length and, hence, irradiance and ice temperatures initiate the formation of the spring ice algal bloom in the bottom 10 cm of the sea ice (Horner & Schrader 1982, Welch et al. 1991, Jin et al. 2006, this study).

In general, the timing and the amplitude of the ice algal spring bloom (in terms of chl *a*) observed at our clean ice site followed the pattern observed in previous Alaskan fast ice studies (Alexander 1974, Horner & Schrader 1982). With progressing season, under-ice PAR intensities increased from 1.5 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in February to 7.7 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in late May. Ice algae, in general, are adapted to low-light conditions (Cota & Smith 1991, Cota et al. 1991, Kirst & Wiencke 1995, Mock & Gradinger 1999), with ice algal spring bloom formation starting at PAR threshold values of about 2 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Horner & Schrader 1982). Thus, light alone likely explains the low concentrations of algae in February 2003, when light intensities were just approaching the threshold. PAR values exceeded the threshold later in the season, which coincided with the observed biomass increase.

Temperature also has a major impact on ice algal growth. First, low ice temperatures, down to -25°C in Barrow fast ice in February 2003, directly reduce physiological process rates. One of the very few studies on temperature effects on ice biota revealed Q_{10} values of about 1 to 5 for Antarctic ice algae (Kottmeier & Sullivan 1988). Second, low temperatures result in high brine salinities and, therefore, osmotic stress with coupled additional metabolic costs for osmoregulation for sympagic biota (Assur 1958, Gradinger 2002). Salinities >100 , occurring at temperatures $<-6^{\circ}\text{C}$, retard or completely inhibit ice algal growth (Grant & Horner 1976, Zhang et al. 1999, Arrigo 2003). We measured such low temperatures in the upper parts of the ice cores taken in February and April (Fig. 3). The relatively warm and constant temperatures at the bottom

of the sea ice (around -1.8°C) put no thermal restrictions on the formation of the bottom ice community, which contributed 93% to the total integrated algal pigment content in April 2003 at Site 1. Although we did not determine nutrient concentrations within the ice, other studies suggest that the final biomass accumulated is a function of the nutrient supply from the water column (e.g. Cota et al. 1987, Gradinger 2009).

In April 2003, algal pigment concentrations were 20-fold higher than in February, which is similar to data from other areas, where biological values increased by about 10 for algal and bacterial biomass, and over 50 for primary and bacterial production (Horner 1980, Smith et al. 1988, Gradinger et al. 1991, Haecky & Andersson 1999). The POC values exhibited the same temporal trend as the chl *a* concentrations, resulting in the significant correlation to chl *a*. By April 2003, the integrated algal biomass at Site 1 ($8.3 \text{ mg chl } a \text{ m}^{-2}$) was higher than in pack ice of the transpolar drift system in the spring (Gradinger 1999a and unpubl. data; median = $1.4 \text{ mg chl } a \text{ m}^{-2}$), but even during its maximum in May 2003 ($36.2 \text{ mg chl } a \text{ m}^{-2}$), it was lower than in other near-shore studies, where maximum values exceeded $300 \text{ mg chl } a \text{ m}^{-2}$ (Smith et al. 1990). By the end of May 2003, a final biomass of $15.2 \pm 1.9 \text{ mgC l}^{-1}$ was reached within the bottom 10 cm of the ice. The integrated POC value of 1.7 g m^{-2} in May 2003 represents the net biomass accumulation over the entire spring bloom. This is less than the yearly primary production estimates for fast ice off Barrow (5 gC m^{-2} ; Alexander 1974, Horner 1984) but more than further east in the Beaufort Sea off Narwhal Island (0.7 gC m^{-2} , Horner & Schrader 1982).

Assuming that loss terms such as grazing or sedimentation are minor during the build up of the ice algal spring bloom (Gradinger 1999b, Nozais et al. 2001, Michel et al. 2002), the chlorophyll increase over the 103 d between the February and May sampling converts into an algal growth rate of 0.037 d^{-1} , or an algal doubling time of 18.8 d. This estimate is in accordance with data from other field studies on Arctic (Gradinger et al. 1991: 10 d) and Antarctic pack ice (Grossi et al. 1987: 10 d) under natural snow-cover conditions. Spring ice algal growth rates at other Arctic locations like Resolute are significantly higher, as observed by Michel et al. (1996: growth rate of 0.14 d^{-1} between May 4 and May 14, 1992) or modeled by Lavoie et al. (2005: mean of 0.15 to 0.18 d^{-1}). All rates, however, were well below the empirical potential growth rate maximum of 0.52 d^{-1} for a temperature of -2°C (Eppley 1972), indicating ignored substantial loss terms, or, more likely, sub-optimal growth conditions (e.g. light, temperature and nutrient limitation) under *in situ* conditions. The latter exert substantial environmental stress on fast ice algae in our study area, as

expressed in sub-optimal photochemical yields (Manes and Gradinger 2009). Differences between regions (e.g. Barrow versus Resolute) are likely due to differences in water column nutrient concentrations and strength of tidal currents causing regional gradients in ice algal development (e.g. Gradinger 1999a, 2009, Bluhm & Gradinger 2008).

Sea ice algae exceeded the algal pigment concentrations of both phytoplankton and microphytobenthos, likely due to the very low light intensities under the sea ice (Horner & Schrader 1982, Glud et al. 2002). For microphytobenthos Glud et al. (2002) estimated a minimum photon flux density (PFD) of $>4.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ for positive net photosynthesis, which was never exceeded in our study region at 5 m water depth where we measured a PFD range of 0.8 (February) to $3.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ (May 2003) at Site 1. Our observations indicate that no substantial primary production occurred during our period of investigation in the plankton and benthic habitat in these nearshore Arctic waters, in agreement with Horner and Schrader (1982).

The small-scale spatial patchiness based on the variability of the chl *a* concentrations between the 4 replicates at each sampling date (SD/mean = 9 to 23%) is similar to that of studies in other areas, where the small-scale patchiness was $<15\%$ in constant environmental settings, especially regarding snow depth (Steffens et al. 2006). In contrast, larger-scale variability between stations in a geographical area can exceed 50% in the same season (Gosselin et al. 1997, Gradinger 1999a, Haecky and Andersson 1999), again related to environmental variables, in particular light availability and nutrient supply (Sullivan et al. 1985, Gosselin et al. 1986, Cota & Horne 1989, Gradinger et al. 1991, Legendre et al. 1991). Light availability also explains the difference between the 2 sites in April 2002, as relative under-ice light levels were 1.3 times higher at the higher biomass Site 2 (0.5% of surface irradiance) compared to Site 1 (0.38%).

Ice algae are considered to be generally isotopically heavier than phytoplankton (Hobson et al. 1995, Naidu et al. 2000, Schubert & Calvert 2001). Our data reflect the wide range of possible $\delta^{13}\text{C}$ ratios in ice algae and sea ice POC, ranging from $-24.9 \pm 1.6\%$ in February to $-15.5 \pm 0.8\%$ in late May. While the February sea ice POC data were close to those of Arctic phytoplankton (Hobson et al. 1995, Schubert & Calvert 2001, this study), the signatures became significantly enriched with increasing POC concentration (Tremblay et al. 2006, this study). The water column $\delta^{13}\text{C}$ ratios, in contrast, showed little enrichment over the time of our study (see discussion below). Consequently, sea ice POC $\delta^{13}\text{C}$ ratios deviated from water column signatures over time, and the ratio of ice to water values decreased from 1.0 in February to 0.6 in May and might

be used as an indicator for the temporal development of an ice algal bloom. The dynamic nature of $\delta^{13}\text{C}$ sea ice signatures stresses the need to apply them with caution in food web studies (Hobson et al. 1995), as the values may vary greatly depending on the state and magnitude of the algal bloom at the time of release of this food source to the pelagic and benthic realms. This scenario is further complicated by the slow isotopic turnover in Arctic fauna (Kaufman et al. 2008).

Ice meiofauna abundance in this study was similar to that of other near-shore Arctic studies, also with respect to seasonality and relative composition (e.g. Cross 1982, Kern & Carey 1983, Carey 1985, Grainger & Hsiao 1990, Nozais et al. 2001, Michel et al. 2002). Copepods (mainly harpacticoids and cyclopoids) and their nauplii, turbellarians, nematodes and polychaete juveniles formed the dominant metazoan ice meiofauna taxa. Ciliates, which can numerically dominate the sea ice fauna $>20 \mu\text{m}$ (Gradinger et al. 1991, Gradinger 1999b, Michel et al. 2002), were observed regularly, but were not quantified in our study.

The immigration of meroplanktic larvae of benthic copepods, polychaetes and gastropods into Arctic sea ice has been previously reported for near-shore Chukchi and Beaufort Sea waters (Carey & Montagna 1982, Cross 1982, Kern & Carey 1983, Nozais et al. 2001). The major immigration of larvae and juveniles of the polychaetes, in particular *Scolecopsis squamata* (Spionidae) occurred between February (40 ind. m^{-2}) and April ($137\,000 \text{ ind. m}^{-2}$). Food availability, mainly ice algae, is likely the major reason for the increase in polychaete numbers, as herbivory appears to be a widespread feeding strategy for ice meiofauna in general (Grainger & Hsiao 1990). At the time of the polychaete abundance maximum in the ice, the chl *a* concentration of the bottom ice community was 760 times higher than in the water column, and our data support the hypothesis that the larvae and juveniles use sea ice as a nursery ground (Carey 1992), whereas the adults inhabit the benthos. While counting the samples, we observed positive phototactic behavior of the polychaete juveniles, known from several polychaete species (e.g. McCarthy et al. 2002). This provides a mechanism for moving from the plankton into the brighter sea ice, a change from a meroplanktonic life style to one we define analogously as merosympagic. The density decrease of the ice-associated polychaete juveniles between April and late May suggests either active downward migration towards the sea floor or passive release through ice melt, as indicated by the warm ice temperatures in May. The slightly increased $\delta^{13}\text{C}$ values in the seawater POC (Fig. 4f) and higher chl *a*: phaeophytin ratios (Fig. 4d) in the sediment in May compared to April also point towards a release of organic matter from the ice into the water column and

sediment at the end of May, similar to that reported by Horner and Schrader (1982). On the other hand, polychaete juveniles might have out-grown the brine channel diameters by late May (Krems et al. 2000), forcing them out of the sea ice, or they may have changed to negative phototaxis (McCarthy et al. 2002). Although we did not measure the juvenile polychaetes, we observed that the majority were larger by late spring.

Nematodes are a well-documented major component of the Arctic sea ice meiofauna. In coastal areas, several investigators noted this taxon to be especially abundant in late spring/early summer (May to June; Kern & Carey 1983, Grainger et al. 1985, Carey 1992, this study). In agreement with our observations, Carey (1992) observed a seasonal shift in meiofauna composition from polychaetes (67% in March) to nematodes later in the season (77% of total abundance in May) in fast ice in Stefansson Sound in the Beaufort Sea. In the present study, the increase in nematode abundance was caused by major reproductive activity during the May sampling. It remains unclear whether the observed association of the nematode egg cases with microalgal aggregates was an artifact introduced by sample processing, or whether it reflects a natural preference.

The abundances of sympagic nauplii, copepodites and copepods followed the temporal trend of the sympagic polychaetes with peak abundances in April 2003, which is contrary to Carey's (1992) finding of a continuous increase in copepod abundance until the end of May. The comparatively high ratio of nauplii could have resulted either from immigration of early nauplii stages into the ice or reproduction of adults within the sea ice. Examples for both strategies are documented: pelagic Antarctic copepods use coastal sea ice as a nursery ground (e.g. Kurbjeweit et al. 1993, Schnack-Schiel 2003), while Arctic and Antarctic harpacticoid sympagic copepods reproduce within the sea ice (Kern & Carey 1983, Carey 1992).

Impact of sediment load on the sympagic regime

Considerable amounts of sediments are incorporated into fast and pack ice in the Arctic (e.g. Nürnberg et al. 1994, Eicken et al. 2005), with suspension freezing and incorporation of fine-grained sediments under turbulent conditions as the main process (Osterkamp & Gosink 1984, Kempema et al. 1989, Reimnitz et al. 1993, Eicken et al. 1997). In the present study, the homogenous distribution of fine-grained sediment in the top 40 cm of the ice cores at the sediment-laden ice site (see Fig. 2 for example) suggests suspension-freezing as the mechanism for sediment incorporation. The total particulate load at the sediment-laden ice site

was within the range of data reported from visibly discolored ice in the Transpolar Drift, and the Laptev and Beaufort Seas (100 to 200 g m⁻²; Reimnitz et al. 1993, Nürnberg et al. 1994, Eicken et al. 1997, 2000, 2005) while 'clean ice' had an approximately 20 times lower particle load (this study, references above).

Until now, the role of sediment for sea ice had only been studied from the perspective of ice albedo and attenuation, whereas biological consequences had not been evaluated. High particulate concentrations in sediment-laden sea ice have profound impacts on the light regime experienced by the sea ice biota and phytoplankton underneath (Osterkamp & Gosink 1984, Light et al. 1998, this study), similar to the shading effect of the snow cover (Maykut 1985, Gradinger et al. 1991). Over the period of our observations, irradiance at the sea ice/water interface at the sediment-laden ice location was reduced by 99.8 to 100% compared to the clean ice site, and PFD ranged between 0 and 0.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The spectral differences in the underwater light combined with our PAR data indicate that the high concentrations of ice algae not only increase the total PAR attenuation (e.g. Gradinger 2009) but also change the light spectrum, leaving a different signature compared to incorporated sediments (Maykut & Grenfell 1975, SooHoo et al. 1987, Light et al. 1998, Mundy et al. 2007).

The reduced PAR availability in sediment-laden sea ice explains the slow algal growth relative to the sediment-free site. Even in May, the PFD was still just approaching the threshold light intensity required for ice algal growth, as determined by Mock & Gradinger (1999), and was below levels where biomass build-up has been observed in the field (Horner & Schrader 1982). At comparable PFD levels of 0.3 to 0.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$, no algal growth was observed over 19 d in an artificially darkened Arctic pack ice area (Gradinger et al. 1991). Over the 4 mo of our observations, ice algal growth was much slower at the sediment-laden ice site (estimated doubling time of 49 d) compared to the clean ice site (doubling time of 19 d). We exclude factors other than sediment as a cause, as the snow load was similar at both sites and a rich algal bloom had formed at this site when it was sediment-free in April 2002. The observed reduction of PAR at the sediment-laden ice site is equivalent to the combined effect of a 50 cm snow load on 3 m thick sea ice (Maykut 1985), values that by far exceed any observed differences in these properties between Sites 1 and 2. We conclude that sediment incorporated within sea ice is a main factor controlling ice algal growth in Arctic sea ice which acts by modulating the available light intensities.

The reduction of algal growth caused by entrained sediment within sea ice has several broader implications. First, it suggests an overestimation of Arctic-

wide ice algal biomass and primary production estimates, as most biological studies did not include material collected from sediment-laden sea ice (e.g. Gosselin et al. 1997, Gradinger 1999a, 2009, Gradinger et al. 1999). The ice algal primary production in seasonally ice-covered waters is currently estimated to contribute 4 to 26% to total primary production (Legendre et al. 1992) and even above 50% in the permanently ice-covered central Arctic (Gosselin et al. 1997). According to the results of this study, these estimates need to be corrected downward. Based on the observed biomass accumulation in terms of POC, net production in sediment-laden sea ice was reduced to 4% of the clean ice values. Assuming that 40% of the sea ice in the Arctic may be sediment-laden (Pfirman et al. 1989, Reimnitz et al. 1993, Nürnberg et al. 1994, Tucker et al. 1999), the impact of sediment-laden ice would lead to a reduction of the estimates of total annual sea ice primary production by 38%. Considerable regional differences in the sediment load and consequently their biological impact need to be considered with highest incorporation rates in shallow shelf seas like the Chukchi Sea (50% of ice contained visible sediment) and lower concentrations (0 to 35%) in the central Arctic (Tucker et al. 1999). The interannual variation in sediment incorporation (Tucker et al. 1999) will contribute to the interannual variability of primary productivity in Arctic seas in addition to other oceanographical variables (Michel et al. 2006). Global climate change might further enhance the sea ice sediment load and its transport in the Arctic by increasing the frequency and strength of storms (Proshutinsky et al. 1999, Stierle & Eicken 2002), and cause further reduction of ice algal productivity on regional to basin-wide scales. Both arguments warrant a further evaluation of the impact of sediments on ice biological properties on an Arctic basin-wide scale.

Also, ice meiofauna abundance differed greatly between the 2 sites in 2003. The observed positive correlations between meiofauna density and POC and pigment concentrations suggest that the ice is primarily used as a feeding ground and may be less important as a habitat *per se*. Both functions have previously been discussed (Carey 1985, Grainger & Hsiao 1990, Krembs et al. 2000, Gradinger 2002, Schnack-Schiel 2003). The relevance as a food-bearing habitat is supported by the differences in absolute densities between the 2 sites in 2003: few individuals were attracted to sediment-laden ice that provided protection from potential predators, but little food. Again, we consider the location *per se* unlikely as a cause for these differences, as ice meiofauna concentrations were very high at Site 2 in April 2002 and zooplankton abundance in the water column was similar to that at the clean ice site.

In addition to the limited food availability in sediment-laden ice, the reduced light under the ice may have had an impact on the behavior and distribution of biota, mainly of polychaetes. McCarthy et al. (2002) reported ontogenetic changes in the phototaxis of meroplanktonic polychaete larvae. One day old larvae were positively attracted, while older larvae (28 d) responded negatively to light. We propose that the observed phototactic attraction of the polychaete juveniles in our study may allow them to avoid sediment-laden ice patches with low algal biomass. Attraction to the brightest spots of sea ice in early spring (February to March) prior to algal growth may select for best initial conditions for later algal growth. We do not know whether light quality (spectral composition) might provide additional clues for polychaetes during site selection. At present, we do not understand how reduced organic biomass accumulation in the ice due to sediment-laden ice impacts pelagic and benthic environments, as material released from sediment-free and sediment-loaded ice areas will be mixed and distributed in the water column. However, a further evaluation of this process seems worth consideration, as the early occurrence of the ice algal peak might be crucial for benthic and pelagic animals (Carey & Boudrias 1987, Grebmeier & McRoy 1989, Renaud et al. 2007, Bluhm & Gradinger 2008).

CONCLUSION

The coastal fast ice algae accumulate considerable amounts of biomass with seasonally increasing light intensities. The ice meiofauna, composed of taxa reflecting the benthic and pelagic communities, is more abundant than the zooplankton in the water column, where algal concentrations remain low until ice melts. Sediment in sea ice plays a pivotal role in controlling these biological processes in the sea ice in that sediment-laden fast ice drastically retards the spring bloom development. The reduced light intensities cause a domino effect along the sympagic food chain by reducing the build-up of ice algal biomass, causally followed by diminished development of ice meiofauna densities. This effect, moreover, alters the cryo-pelagic-benthic coupling processes in 2 ways: the input of organic matter from the sea ice to the realms below is greatly reduced, and sediment-laden ice has lower nutritional value for merosympagic larvae and juveniles.

Over the last decade, the Arctic ice cover has been shrinking and thinning, with minimum ice coverage in the Beaufort and Chukchi Seas (Walsh 2008). While implications of changes in the duration and characteristics of the ice cover have been discussed from various perspectives (e.g. Stirling & Derocher 1993, Gradinger

1995, Bluhm & Gradinger 2008), we propose that sediment effects need to be incorporated into future field studies and modeling efforts dealing with the productivity of the Arctic in general, and more specifically, with Arctic ice algae.

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