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Seasonal variation in benthic community oxygen demand: A response to an ice algal bloom in the Beaufort Sea, Canadian Arctic?

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Abstract

Understanding pathways of carbon cycling on Arctic shelves is critical if we are to evaluate the potential effects of climate change on these systems. We investigated the relationship between ice algal standing stock and benthic respiration between January and July 2004 at a time series station in the southeastern Beaufort Sea. Both ice algal chlorophyll *a* and benthic sediment oxygen demand showed >10-fold increases from between March and April. While some of the increase in oxygen demand can be attributed to bacteria and meio-fauna, most was due to the activities of macroinfauna. We also observed a trend toward lower sediment pigment content during the pulse in benthic carbon remineralization. While chl *a* sedimentation also increased by a factor of 7 during this period, fluxes were not sufficient to provide for the increased carbon demand. We suggest that sedimenting ice algae provided a cue for increased benthic activity, and that direct consumption of ice algae and increased oxygen availability in the sediment due to bioturbation by epifaunal organisms led to the enhancement in respiration rates. Seasonal patterns in primary productivity and the activity of resident epifaunal and infaunal communities are, thus, important factors in determining carbon cycling patterns on Arctic shelves.

Keywords: Beaufort Sea; Carbon cycling; Ice algae; Benthic–pelagic coupling; Respiration; Benthos; Sedimentation

1. Introduction

The Arctic is experiencing drastic climate change. Recent studies have documented significant air and ocean temperature increases, and reductions in ice cover, and it is predicted that these changes will accelerate over the next 50–100 years (Vinnikov et al., 1999; Intergovernmental Panel on Climate Change, 2001; Moritz et al., 2002; ACIA, 2004; Johannessen et al., 2004). It is unclear how these changes will impact ecosystems on the expansive continental shelves of the Arctic's marginal seas, but qualitative and quantitative shifts of many components and pathways of the carbon cycle are likely to occur (Walsh et al., 2004; Wassmann, 2004).

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Understanding current pathways may help to identify where impacts of climate change are most likely to be observed.

The Arctic Ocean and its marginal seas overlie 25% of the world's continental shelves. These shelf systems exhibit pronounced seasonality as ice cover and the polar winter limits the period of algal production. Strong seasonal pulses of phytodetritus to the benthos (Wefer, 1989; Honjo, 1990) fuel some of the richest benthic communities and fisheries in the world, indicating tight linkages between benthic and pelagic processes (e.g. Peterson and Curtis, 1980; Carey, 1991; Grebmeier and Barry, 1991; Ambrose and Renaud, 1995; Piepenburg et al., 1997; Wollenburg and Kuhnt, 2000). Additionally, a larger fraction of sedimenting carbon is buried in the Arctic Ocean than in many other areas of the world's oceans (Stein and MacDonald, 2004). Clearly, the benthos plays an important role in the carbon cycle of Arctic shelves.

Logistical difficulties due to ice cover have limited most studies of the sources and fate of carbon on Arctic shelves to the period from late spring to early fall. There has been some suggestion, however, that early season production by algae growing within and beneath the sea ice may represent a significant fraction of carbon flux to the benthos in these regions (Ambrose and Renaud, 1997; Bauerfeind et al., 1997; Hargrave et al., 2002). Ice algae communities are notoriously patchy (e.g. Gosselin et al., 1997; Rysgaard et al., 2001), but they have been suggested to account for a significant proportion of the total primary production in the Arctic (Horner and Schrader, 1982; Legendre et al., 1992; Gosselin et al., 1997). Since ice algae are known to sink rapidly upon release from the sea ice (Michel et al., 1997a,b) and can be processed by benthic fauna (Ambrose et al., 2001), it has been suggested that they are of particular importance to benthic communities (Ambrose and Renaud, 1995, 1997; Ritzrau, 1997; Ritzrau and Thomsen, 1997; Hargrave et al., 2002; Carroll and Carroll, 2003). Evidence for such importance, however, is largely circumstantial.

This study represents the first effort to quantify the response of a benthic community to an ice algal bloom. Taking advantage of the infrastructure provided by the Canadian Arctic Shelf Exchange Study (CASES), we were able to monitor the ice algal community and its export from the sea ice, sediment carbon and phytopigment content, and benthic community respiration from mid-winter to ice break-up. In this study, we ask: (1) What are the seasonal dynamics of the ice algal community? (2) How are these dynamics reflected in sediment biochemical parameters? and (3) What is the impact of ice algal seasonality on benthic community respiration?

2. Materials and methods

2.1. Study site

From December 2003 to June 2004, the Canadian Coast Guard icebreaker *Amundsen* was frozen into the annual shore-fast ice in western Franklin Bay, southeastern Beaufort Sea (70°02′N, 126°18′W; Fig. 1). Water depth at our sampling station was 231 m. The timing and magnitude primary productivity in this region vary considerably (Arrigo and van Dijken, 2004), and are linked to ice dynamics. Ice sampling was conducted in an undisturbed area approximately 1.5 km NE of the ship (70°04′N, 126°26′W). Ice thickness increased from 1.31 m in February to a maximum of 2.00 m at the end of May, and then decreased to 1.55 m on the last sampling day on 20 June. Near-bottom temperature, salinity, and transmissivity data were obtained from twice-daily CTD casts from the ship.

2.2. Ice algal measurements

Multiple ice cores were collected with a manual corer (Mark II coring system, 9 cm internal diameter; Kovacs Enterprise) at two sites representative of low (3.4±2.5 cm) and high (16.2±3.5 cm) snow conditions for analysis of ice algal communities. Ice thickness was recorded at the time of sampling. The bottom 4 cm of cores from each snow depth were cut and pooled together, and slowly melted in 0.2 μm filtered surface seawater to minimize osmotic stress (Garrison and Buck, 1986). Estimates of chlorophyll a biomass (chl *a*) on 10 cm sections over the total length of ice cores were performed on three occasions (25 March, 24 April and 4 May), showing that 94.6%±2.5% of the total integrated chl *a* biomass in ice cores was found in the bottom <10 cm section. Concentrations of chl *a* were determined fluorometrically (Turner Designs Model 10-AU) on duplicate subsamples filtered on Whatman GF/F filters after 24 h extraction in 90% acetone at 4 °C. The concentration of chlorophyll *a* was calculated according to Holm-Hansen et al. (1965).

2.3. Under-ice sedimentation and water column sampling

Vertical pigment fluxes were measured from February 23 to June 20, using sequential deployments ($n = 16$) of particle interceptor traps. The traps, which were PVC cylinders with a height/diameter ratio of 7 (10 cm diameter), were attached to a tripod on the sea ice and deployed at 1, 15, and 25 m from the undersurface of the

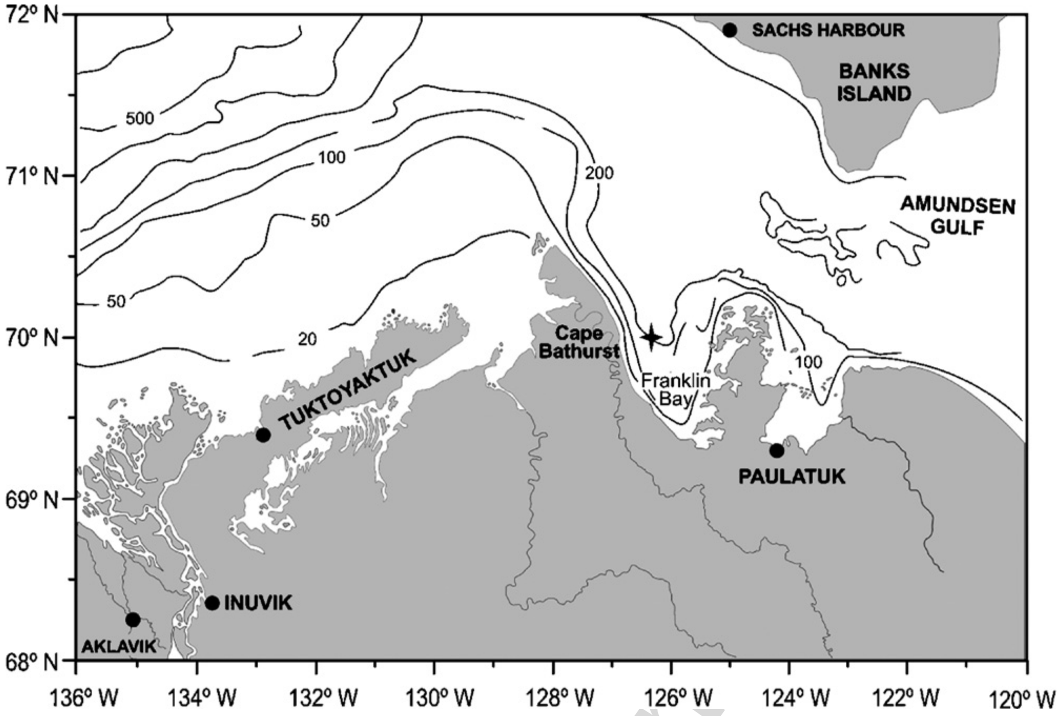

Fig. 1. Map of the southeastern Beaufort Sea. The study site for the time-series in Franklin Bay is identified by the cross. Depth is expressed in meters.

ice. Prior to deployment, the traps were filled with 0.22 μm filtered seawater collected well below the deployment depth to ensure higher water density in the traps compared to ambient water. The particle interceptor traps were deployed for 7.8 ± 0.8 days ($n = 6$) from March to mid-May, while the deployment time was reduced to 6.2 ± 0.4 days ($n = 8$) from mid-May to end of June, in response to higher sinking fluxes. Upon recovery, material from the traps was prefiltered through a 425 μm mesh prior to subsequent analysis in order to remove large swimmers. Samples were gently mixed to achieve homogenous subsampling. Water at the ice–water interface was collected using a hand pump with Tygon tubing attached to an adjustable arm that was held parallel to the undersurface of the ice. The tubing and pump were thoroughly rinsed with the sampled water prior to sample collection in sterile containers. Duplicate 100–500 mL subsamples from particle interceptor traps and interfacial water were analyzed for chlorophyll *a* and total pigments. These subsamples were filtered onto Whatman GF/F filters, and analysed as described above.

2.4. Sediment sampling and benthic respiration

Sediment was sampled on 5 dates between 14 January and 7 May 2004, and then again on 4 July 2004. On 6 April, sampling was performed through the "moon pool", an opening in the ship's hull that allowed sampling from within the ship while it was frozen into the ice. On this date we used multiple deployments of a small corer; but on all other occasions a spade corer (45 cm × 45 cm) was deployed through a hole cut in the sea ice near the ship. During winter and spring, only a single core was collected, due to the difficult and time-consuming logistics involved in cutting the sampling hole in ice that was up to 3 m thick near the ship. In July, when the area was ice-free, the box corer was deployed three times. Only cores with intact surface layers, indicated by surface 'fluff' or delicate epifauna, were used.

Replicate sub-cores (10 cm diameter × 20–25 cm deep with as much overlying water preserved as possible) were taken for estimating the respiration of the entire infaunal sediment community. While sub-coring may be viewed as pseudoreplication, our analyses indicated that variance in respiration rates among sub-cores from the same box core deployment was not different than the variance from different deployments at the same station (unpub. data). Incubation cores (3–4 per sampling date) were topped off with bottom water collected using the ship's rosette and bubbled to saturate the overlying water with oxygen. Control cores were filled with bottom water and bubbled. Cores were always kept in the cold room at 0–2 °C. All cores were sealed using tops that provided constant stirring. Oxygen concentrations were monitored during the incubations using a microelectrode (Unisense A/S; Aarhus, Denmark) inserted into a small sampling port in the core top. Incubations were terminated when 15–30% of the oxygen had been consumed (usually 30–48 h).

To estimate how much of the whole-core respiration was due to micro- and meio-fauna, we performed additional incubations ("minivials") following the methodology of Grant et al. (2002). Approximately 24 subcores (1.4 cm diameter × 2 cm deep) were taken on the 6 sampling dates. Macrofauna was removed as the sediment was transferred into pre-cleaned 24 mL glass scintillation vials. Vials were filled with Whatman GF/F-filtered near-bottom water to overflowing and sealed using caps with conical inserts to prevent air bubbles. All vials were shaken and the oxygen concentration in half the vials was determined after 0.5–1 h using a microelectrode. This time allowed for settlement of sediment, as well as chemical oxidation of reduced mineral species present in the top 2 cm of sediment. The remaining vials were incubated for 48–56 h, after which the oxygen concentrations were measured. The difference between time zero (t_0) and time final (t_f) is an estimate of oxygen consumption by the meio-fauna, protozoa, and bacteria in the sediment. After eliminating vials where macrofauna was found after the incubation, sample sizes ranged from 4 to 14 vials. The entire procedure was performed in a cold room (0–2 °C) under very low light.

2.5. Sediment analysis

Triplicate sub-cores for sediment pigments (5 cm diameter × 10 cm deep) and organic carbon and nitrogen (1.9 cm diameter × 2 cm deep) were taken during the winter; one of each type of sub-core was taken from each of the three replicate deployments in July. Pigments were analyzed fluorometrically according to Holm-Hansen et al. (1965). Each sub-core was extruded and sliced at 1 cm intervals. Half of each slice was frozen in 60 mL centrifuge tubes, which were then wrapped in foil. Within 3 weeks, this sediment was thawed and 20 mL of 100% acetone was added. Pigments were extracted in the freezer in the dark, during which tubes were shaken periodically. After 48 h, sediment was centrifuged (4000 rpm for 10 min at 0 °C) and the supernatant was analyzed in a Turner Designs model 10-AU fluorometer before and after acidification with 20% HCl.

Samples for organic carbon and total nitrogen content were stored at − 20 °C until analysis. Sediment was dried at 60 °C for 24–48 h and ground until homogeneous. A subsample (1 g) was acidified three times with 2 mL of 1 N HCl (drying and grinding between each acid treatment) to dissolve carbonates. Homogenized sediment was then run on a Fisons model 1108 CHN Analyzer with acetanilide as a standard.

2.6. Data analysis

Respiration, sediment pigment, carbon, and nitrogen data were analyzed by one-way analyses of variance (ANOVA) or Kruskal–Wallis (KW) tests (unequal variances), with sampling date as the discriminating factor, using the JMP-IN (SAS Institute) software package. Where ANOVA tests were significant, the Tukey HSD post-hoc test was performed to elucidate the differences. Bonferroni contrasts were performed following significant KW tests. Before performing the ANOVA tests, homogeneity of variances was tested using Bartlett's test (Sokal and Rohlf, 1995).

3. Results

3.1. Near-bottom hydrographic measurements

Values obtained from the CTD indicated a range in near-bottom (within 10 m) temperature from +0.2 to − 0.7 °C, and in salinity between 33.8 and 34.7 over the 6 month period of the study. It is interesting to note that temperature was relatively constant between +0.2 and +0.05 °C for the first 6 sampling dates and decreased to − 0.7 °C between May and July. Near-bottom transmissivity was variable, yet exhibited a noticeable decline in the period of 10 March to 20 April, when most readings (with one exception) were below the lowest measurements recorded outside this time interval (Fig. 4).

3.2. Surface and ice biomass and sinking export

There was a clear seasonal trend in the ice algae biomass in the bottom ice, as evidenced by monthly averaged chl *a* concentrations for high and low snow covers combined (Fig. 2a). Average bottom ice chl *a* concentrations were <0.3 mg chl *a* m^{-2} during the months of February–March. These concentrations increased by more 10-fold in April (avg = 5.6 mg chl *a* m^{-2}), and reached ca. 15 mg chl *a* m^{-2} in May. A strong decrease in bottom ice chl *a* was observed during the month of June, with average values of 2.5 mg chl *a* m^{-2}. KW tests on means showed statistically significant differences ($p < 0.001$) in ice algae concentrations among months, with post-hoc Bonferroni contrasts (at alpha = 0.05) indicating that May concentrations were higher than during any other time period. When the alpha-value was raised to 0.10, April values were also significantly higher than the average value for February–March. There were no phaeopigments observed in the bottom ice (values of 0 throughout the season).

While ice coring can potentially underestimate ice algal biomass (Ambrose et al., 2005), comparative

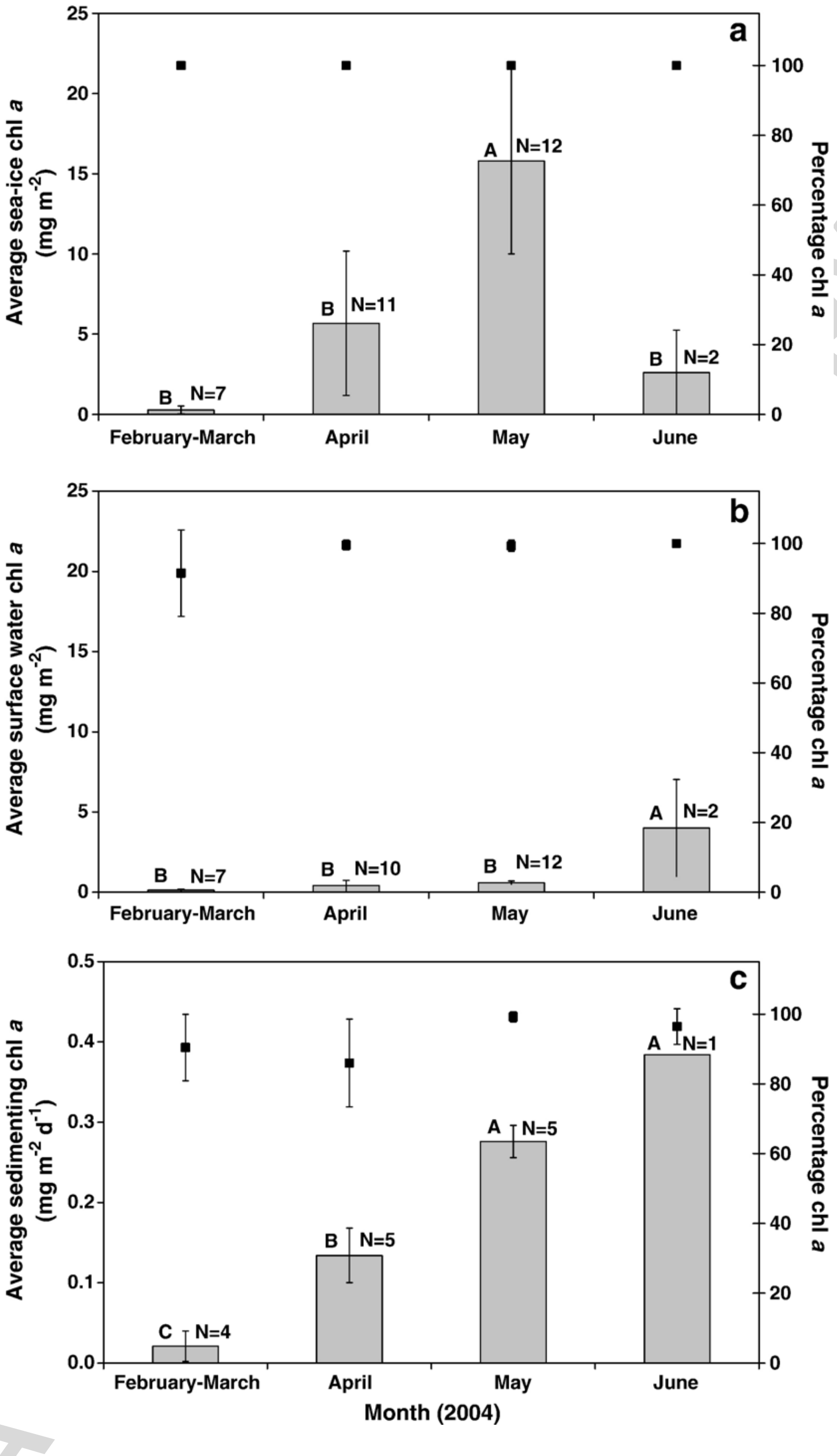

Fig. 2. Seasonal trends in average chlorophyll *a* concentration from (a) the bottom of the sea ice, (b) the top 1 m of seawater directly under the ice, and (c) particle interceptor traps deployed 1 m below the ice at a station in the southeastern Beaufort Sea. Data are averages of 1 or 2 months of samples in 2004. $N=$ number of samples represented by the means. All error bars represent ± 1 standard deviation. Black squares represent the average percentage of total pigments from each sampling period that was chlorophyll *a* (right axis). Date was determined to have a significant effect on chlorophyll *a* concentrations in all material ($p<0.001$; Kruskal–Wallis test); bars with the same upper case letter are not significantly different from each other (Bonferroni test at alpha = 0.05). Percent chlorophyll *a* was not significantly different among time periods in any of the material sampled ($p \gg 0.05$).

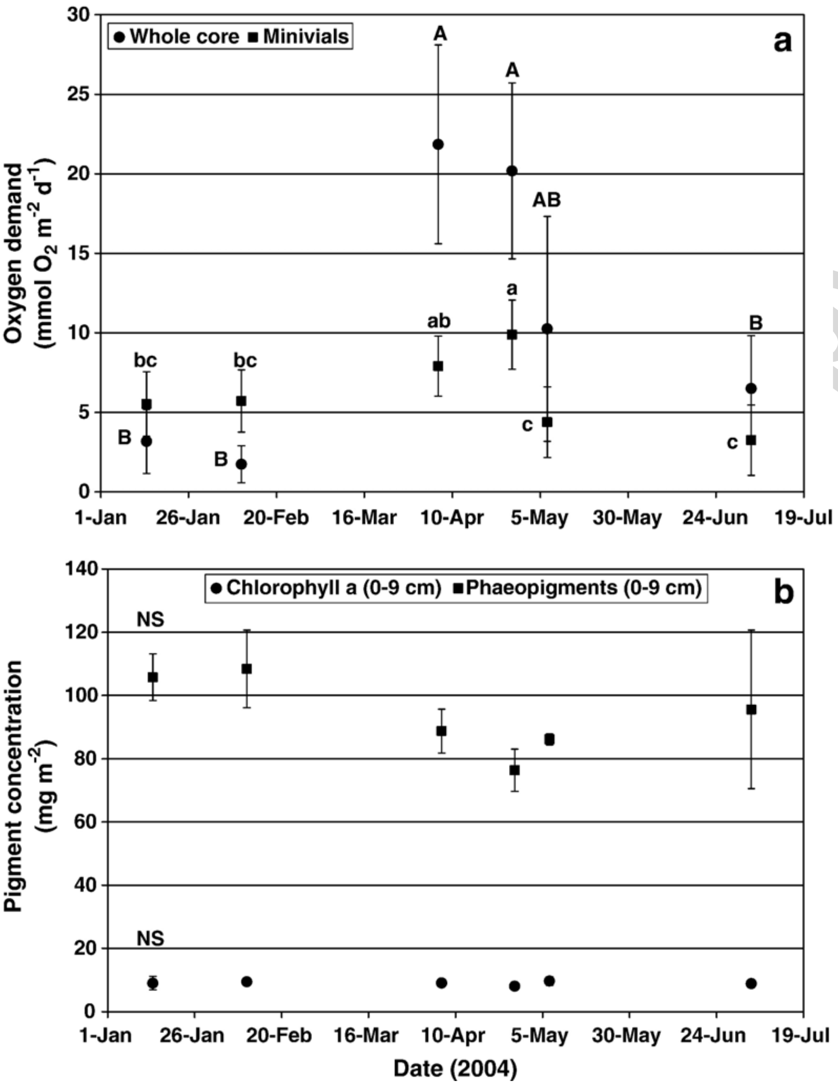

Fig. 3. Time-series measurements of (a) sediment oxygen demand from whole-core (circles) and minivial (squares) incubations, and (b) concentration of sediment chlorophyll *a* (circles) and phaeopigments (squares). When analysis of variance indicated significant date effects ($p < 0.05$), letters appear beside or above symbols. Symbols marked with the same letter are not significantly different by Tukey's HSD test. NS indicates that the measurements did not vary significantly among dates. In (a), upper case letters refer to results of statistical tests for whole-core incubations; lower case letters reflect results from minivial incubations. All error bars represent ± 1 standard deviation.

results from SIPRE cores and cores obtained by divers in Arctic first-year ice have shown that this underestimation primarily occurs at the time of ice melt, with the loosening of the ice algae community. During the period of ice growth, SIPRE and divers cores provide comparative results (Welch et al., 1988). During our study, ice growth was taking place from February to the end of May. Hence, we are confident that the ice algae biomass estimates for February to May are reasonable. For the month of June, when melt was taking place, there was a potential underestimation of the ice algal biomass, although it cannot be quantified. This possibility, however, does not change the seasonal trends presented here.

Surface water (top 1 m under the ice) chl *a* was consistently low (<0.60 mg chl *a* m^{-2}) until June, when average values increased to 4.0 mg chl *a* m^{-2} (Fig. 2b). Biomass values were significantly higher in June than during the previous periods ($p < 0.001$; KW). Chl *a* made up more than 90% of the total pigments in surface waters for the entire February to June period.

Seasonal trends for sinking fluxes of chl *a* at 1 m under the ice were similar to those for ice algae (Fig. 2c). Very low sinking fluxes of chl *a* were observed during February–March (average = 0.02 mg d^{-1}). These fluxes increased 7-fold in April (average = 0.13 mg chl *a* m^{-2} d^{-1}), and continued to increase during May and June, at a time when maximum sinking fluxes were observed (0.38 mg chl *a* m^{-2} d^{-1}). Means from all months were significantly different, except for May and June deployments when results were indistinguishable ($p < 0.001$;

ANOVA). Seasonal trends in the sinking fluxes of chl *a* at 15 and 25 m (not shown) closely followed those observed at 1 m beneath the sea ice. Sinking fluxes of pigments at 25 m made up, on average, 69% of pigment sinking fluxes observed at 1 m (% var=27% for the whole sampling season). The percent chl *a* in total pigments (chl *a*+phaeopigments) in the 1 m traps varied between 86 to 99% during the season, with no significant differences among sampling months ($p>0.11$; Fig. 2c).

3.3. Benthic respiration

Sediment-community oxygen demand varied by more than one order of magnitude (1.75 to 21.0 mmol O_2 m^{-2} d^{-1} between 10 February and 6 April) over the sampling period (Fig. 3a). Respiration rates measured on 6 April and 27 April were significantly higher than rates measured on 14 January, 10 February or 4 July ($p<0.0001$; ANOVA). Variances were not significantly different among sampling dates ($p>0.05$; Bartlett's test), supporting the use of ANOVA tests.

The range in oxygen demand by micro- and meiofauna in the minivial incubations was less than that for the entire community, only varying by a factor of two (Fig. 3a). The mean respiration rate on 27 April was significantly higher than rates measured in January, February, May, and July; the rate on 6 April was also significantly higher than on the last two sampling dates ($p<0.0001$; ANOVA). Bartlett's test again indicated an equality of variances ($p>0.05$).

3.4. Sediment parameters

Phytopigment (chlorophyll *a* and phaeopigments) concentrations in the top 9 cm of sediment at the overwintering station showed an opposite trend to that in the ice algae and respiration data. Phaeopigment concentration was highest from mid-January to mid-February. It decreased between February and early April, where it remained fairly stable until mid-May; it was slightly higher again during the July sampling (Fig. 3b). ANOVA failed to detect significant differences among sampling dates, but a *p*-value of 0.053, suggests a trend toward lower values during April and May. Chlorophyll *a* values in the top 9 cm showed no significant differences among sampling dates ($p>0.05$; ANOVA; Fig. 3b). Trends and results of statistical analyses of data from only the top 2 cm of sediment were virtually identical to that of the top 9 cm (data not shown). Bartlett's test indicated equality of variances for both analyses ($p>0.05$).

Organic carbon and total nitrogen content in the top 2 cm of the sediments did not vary among sampling dates. Organic carbon values ranged from 1.28% (SD=0.07) to 1.41% (0.14), and total nitrogen values varied between 0.13% (0.0005) and 0.16% (0.03). *P*-values for both ANOVAs were higher than 0.50.

4. Discussion

A sharp increase in benthic oxygen demand coincided with the onset of an ice algal bloom at our time series station in the southeastern Beaufort Sea (Figs. 2a and 3a). At the same time, there was a strong increase in the sinking flux of chl *a*, as measured from short-term particle interceptor traps deployed immediately underneath the ice (Fig. 2b). With interfacial water chl *a* concentrations more than one order of magnitude lower than those in the bottom ice during the months of April and May (Fig. 2a and b), it is most likely that the increase in chl *a* sinking flux observed at that time was from ice algae released from the bottom ice. The release of ice algae in early April cannot be explained by ice melt, since this was a period of ice growth. Phaeopigments were absent from the bottom ice and were found in very low concentrations in particle interceptor traps (Fig. 2a and c), indicating very little or no grazing under the ice. It is possible that ice algae were released from the bottom ice as a result of brine drainage (Melnikov, 1998). It is also possible that turbulence under the ice may have dislodged ice algae.

Increased chl *a* sedimentation and benthic oxygen demand were not accompanied by an increase in sediment pigments, organic carbon, or total nitrogen content (Fig. 3b and Section 3.1). In fact, there was a strong trend toward a significant decrease in sediment pigments during the short pulse in benthic respiratory activity (Fig. 3). These results suggest that, while the onset of ice algal growth and sedimentation coincided with the observed increased in sediment community oxygen demand, it is unlikely that the input of ice algae alone is sufficient to explain the ten-fold increase in respiration rates that we observed from early April to mid-May. While there is a growing body of evidence supporting the value of ice algae as an early-season food source for benthic macrofauna (see below), it is more likely that our results reflect a combination of direct consumption and indirect responses to ice algal sedimentation.

4.1. Direct response to ice algal deposition

There is something of a paradox to be addressed when discussing the coupling between the pelagic and benthic environments. It seems straightforward that processes in the two realms should be linked as benthic communities rely on production from the euphotic zone as their source of energy; and there are several extensive reviews documenting this linkage (Grebmeier and Barry, 1991; Carey, 1991; Graf, 1992). Alternately, textbook values for "typical" sinking rates and horizontal velocity fields suggest that, even on relatively shallow continental shelves, material reaching the benthos must come from tens of kilometers away. Indeed, there are studies that document the importance of advective processes (e.g. Tanaka, 2003). There is overwhelming support, however, to suggest that surface waters directly above a benthic sampling location have a tight link with community structure and/or sediment biogeochemical processes on Arctic shelves (Atkinson and Wacasey, 1987; Grebmeier et al., 1989; Grebmeier and McRoy, 1989; Ambrose and Renaud, 1995, 1997; Hobson et al., 1995, 2002; Piepenburg et al., 1997; Grant et al., 2002). Aggregation can result in sinking rates of greater than 200 m d^{-1} (Asper and Smith, 2003). While we do not claim that ice algae directly over our benthic sampling site led to benthic respiration patterns, we use the timing and magnitude of the ice algal bloom at this location as a proxy for regional patterns of ice algal production that are potentially responsible for our observations of benthic processes.

Ice algae have been proposed to be an important high quality food source for benthic communities, especially early in the season before pelagic production increases (Ambrose and Renaud, 1997; Hargrave et al., 2002; Carroll and Carroll, 2003). This is the first study, however, to simultaneously track ice algal community development and its sinking from the ice, and benthic processes. Recently, ice algae have been shown to be readily consumed and assimilated by benthic fauna as evidenced from addition experiments where pigments, fatty acids, and stable isotopes were monitored (McMahon et al., 2006). In that study, sediment chlorophyll and essential fatty acid content was increased by over 80% due to food additions, but decreased to background levels within 19 days. The rates of consumption and assimilation of ice algae were comparable to those in phytoplankton addition treatments. Clearly, ice algae are a potentially valuable early-season food source for at least some components of the benthic community, and elicit a rapid response upon arrival at the sediment surface.

Rysgaard et al. (1998), studying a fjord system in east Greenland, attributed much of the increase in benthic oxygen consumption he observed to microbial activity. Our data strongly suggest, however, that the enhanced community respiration we measured was due primarily to macroinfauna. Minivial incubations did indicate a doubling of micro- and meio-faunal respiration rates between February and late April, but this increase was modest compared with the 10-fold increase in rates for the entire community (Fig. 2b). Clough et al. (2005) found that the role of macrofauna was far greater than that of meio-fauna at depths shallower than 500 m in the Chukchi Sea in the summer. They also noted that benthic macrofaunal biomass explained 75% of the variability in benthic respiration rates. Grant et al. (2002) found a similar pattern in the North Water polynya (northern Baffin Bay).

Using a 1:1 stoichiometric relationship between oxygen and carbon utilization, and a respiration coefficient of 0.85 (Smith, 1978), we estimate the benthic carbon demand during the period of highest sediment oxygen demand at around 210 mg m^{-2} d^{-1}. Carbon fluxes

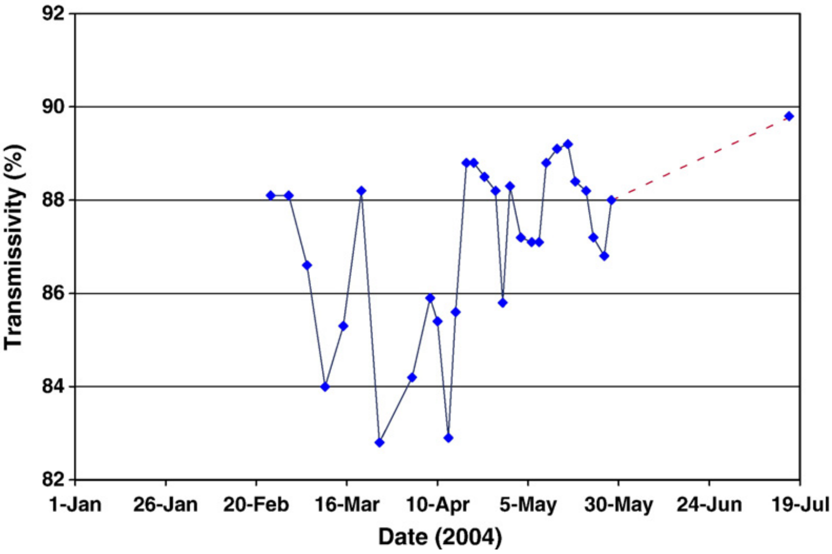

Fig. 4. Near-bottom transmissivity data from CTD casts at the time-series station.

measured in under-ice traps did not approach this value until June, and were between 20 and 28 mg m^{-2} d^{-1} from February to May (T. Juul-Pedersen et al., unpub. data). While some benthic fauna may derive a significant portion of their early-season food from sedimenting ice algae, it is unlikely that the pigment sedimentation rates we measured were sufficient to account for such a significant increase in benthic community respiration. It is possible, however, that the arrival of fresh phytodetritus at the sea floor served as a cue to benthic fauna to increase their activity. It follows directly then that we would not see an increase in sediment pigment concentrations at periods of peak respiration, but instead a trend toward a net loss in sediment pigments (Fig. 2b and c). Infauna stimulated directly by sedimenting ice algae may have consumed all the new ice algal material that was deposited plus pigmented matter from the sediment inventory.

4.2. Indirect response to ice algal deposition

Epifaunal invertebrates, primarily echinoderms (e.g. sea stars, brittle stars, sea cucumbers, sand dollars), are abundant and important components of Arctic shelf communities (Welch et al., 1992; Piepenburg and von Juterzenka, 1994; Piepenburg et al., 1995; Bluhm et al., 1998; Ambrose et al., 2001). With densities up to 700 individuals m^{-2}, ophiuroids alone can account for up to 80% of the total benthic-community metabolism (Piepenburg et al., 1995). Bottom photographs from our sampling station in the Beaufort Sea indicate that ophiuroid densities reach at least 60 individuals m^{-2} at this site (P. Renaud, pers. obs.). Furthermore, non-quantitative traps deployed at this station suggest that large epi-/hyper-benthic amphipods (e.g *Anonyx* spp.) are quite abundant, but are not effectively enumerated from bottom photography. Evidence from laboratory assays (Ambrose et al., 2001) and stable-isotope studies (Hobson et al., 1995, 2002) suggest that some of the most abundant ophiuroids and amphipods consume ice algae. Through their feeding activities, epibenthic organisms bioturbate the surface sediment, altering its biological (Ambrose, 1993) and geochemical (Lohrer et al., 2004; Solan et al., 2004; Wenzhöfer and Glud, 2004) structure. Klages et al. (2004) suggested that availability of dissolved oxygen may limit metabolic activity in Arctic sediments. Infaunal bioturbators enhance oxygen exchange in sediments by a factor of 1.5–3 (Glud et al., 2000), and it is likely that the large densities of epifauna at our study site would have a similar effect. As epifauna were excluded from our incubation cores, their direct contribution to benthic oxygen demand is not reflected in the data presented, but indirect effects of bioturbation would have been reflected in our measurements since the sediment would presumably have been exposed to bioturbation before collection. We propose, therefore, that any direct enhancement of sediment-community oxygen demand due to deposition of ice algae could have been augmented by the increased feeding and burrowing activities by epifauna, at least in part by ophiuroids, scavenging for the newly deposited phytodetritus.

In addition to cuing feeding and burrowing activities, arrival of fresh phytodetritus on the sea floor may stimulate reproduction-related events that could result in enhanced respiration. This has been observed for many benthic taxa that exhibit seasonal reproduction (e.g. Rokop, 1974; Tyler et al., 1982, 1992; Uitto and Sarvala, 1991; Blake, 1993). As food supply to the benthos is highly seasonal in the Arctic, the synchrony of reproductive events with phytodetrital input to insure adequate food for developing larvae or new recruits may be particularly important (Gage and Tyler, 1991, Ólafsson et al., 1994, Ambrose and Renaud, 1997).

4.3. Other potential factors

Our sediment-community respiration rates for January, February, May, and July are similar to rates measured on shelves throughout the Arctic (reviewed in Glud et al., 1998; Clough et al., 2005). These values are also similar to those from many temperate shelf areas, indicating that benthic systems in the Arctic are not significantly less productive than elsewhere. Although we observed order of magnitude increases in *both* ice algal standing stocks and benthic oxygen demand (Figs. 2a and 3a), it is possible that the respiration results in this study were due to factors unrelated to the onset of the ice algal bloom. Some of these factors may include deposition of phytoplankton, increased bottom temperatures, resuspension of bottom sediments, and advection of potential food from outside the local area.

The dramatic, order-of-magnitude increase in sediment-community oxygen demand in April (Fig. 3a) was unexpected, but not completely without precedent. For example, infauna are capable of respiration rates that vary by a factor of 7 over a diel cycle (Wenzhöfer and Glud, 2004). Additionally, Rysgaard et al. (1998) observed an increase in benthic respiration of a lesser magnitude in a shallow Greenland fjord, but that was much later in the season and attributed to a phytoplankton bloom initiated by ice break-up. It is highly unlikely that the increase in respiration we observe in this study was due to phytoplankton. Empirical studies from the southeastern Beaufort Sea indicate very low phytoplankton production during April, with spring blooms of highly variable magnitude taking place much later in the year (May/June, or as late as July; Arrigo and van Dijken, 2004; Carmack et al., 2004). Under-ice suspended chl *a* concentrations during our study period were very low from February through May (Fig. 2b). Additionally, the high proportion of chl *a* in the sedimenting pigmented material indicates that the sinking material was from a fresh algal source. Food, and not water temperature, has been proposed to be the most important limiting factor for benthic organisms on Arctic shelves (Rysgaard et al., 1998). This assertion has considerable support from two decades of research indicating strong linkages between sediment pigment content and community structure and function (Christensen and Kanneworff, 1985; Carey, 1991; Grebmeier and Barry, 1991; Ambrose and Renaud, 1995; Clough et al., 1997; Piepenburg et al., 1997; Grant et al., 2002). Indeed, over the first 5 sampling dates, including the period where we saw the large increase in benthic respiration rates, near-bottom temperatures only varied by approximately 0.1 °C.

The modest decrease in transmissivity observed in this study coincided with the onset of ice algal growth and the marked increase in benthic respiration (Figs. 2a, 3a, 4). It is possible that the transmissivity signal reflected a pulse of newly deposited ice algae and/or fecal pellets to the sediment surface. Alternatively, it may be evidence of a resuspension or near-bottom advection event. Advection of labile material from outside the local area may be an important mechanism providing food for benthic organisms (Dayton and Oliver, 1977; Rosenburg, 1995), and one that would confound the coupling of pelagic and benthic processes expected for this location.

The impacts of climate change on carbon cycling in Arctic marine communities are difficult to predict (Wassmann, 2004). This study suggests, however, that factors changing the patterns of ice algal production on Arctic shelves may have significant consequences for carbon processing and storage in benthic sediments. It is increasingly clear that the structure and seasonal activity of benthic faunal communities interact with the primary productivity regime to determine carbon preservation and regeneration patterns on Arctic shelves.

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