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Dissolved carbohydrates in Antarctic sea ice

L.-M. HERBORG[1], D.N. THOMAS[1]*, H. KENNEDY[1], C. HAAS[2] and G.S. DIECKMANN[2]

[1]School of Ocean Sciences, University of Wales-Bangor, Menai Bridge, Anglesey LL59 5EY, UK
[2]Alfred Wegener-Institut für Polar- und Meeresforschung, Am Handelshafen 12, D-27570 Bremerhaven, Germany
*Corresponding author: d.thomas@bangor.ac.uk

Abstract: Concentrations of dissolved monocarbohydrates (MCHO) and polycarbohydrates (PCHO) were analysed in a variety of ice habitats from summer Weddell Sea sea ice (surface ponds, ice cores, gap layers and platelet ice). The dissolved organic carbon (DOC) pool in these habitats was also measured and the contribution of carbohydrate to this pool was assessed. The DOC concentrations within all sea ice habitats were high compared to surface seawater concentrations with values up to 958μMC being measured. Total carbohydrates (TCHO) were highest in the ice cores and platelet ice samples, up to 31% of the DOC pool, a reflection of the high algal biomass in these two habitat classes. TCHO in the other habitats ranged between 10% and 29% of DOC. The ratios of MCHO to PCHO varied considerably between the ice habitats: in surface ponds and ice cores MCHO was 70% of the TCHO pool, whereas in gap layers and platelet ice there were lower PCHO concentrations resulting in MCHO being 88% of TCHO.

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Introduction

The annual formation, consolidation and subsequent melt of 16 x 10^6 km^2 of sea ice is the fundamental process in the Southern Ocean that has profound implications for biogeochemical cycles in the region. Over 200 taxa have been described living within sea ice with dominant groups being bacteria, diatoms, flagellates, fungi, foraminifers, ciliates, nematodes, polychaetes, or turbellarians (reviewed by Palmisano & Garrison 1993, Ackley & Sullivan 1994). Pennate diatoms are typically the most dominant component of sea ice assemblages, although *Phaeocystis* spp. are often present in large numbers. At times the number of proto- and metazoan grazers found within sea ice can be several orders of magnitude higher than that found in the water column as they exploit the highly concentrated ice algal stocks (Palmisano & Garrison 1993, and citations therein).

Bacteria are an important part of the assemblages formed within ice habitats, ensuring high rates of nutrient remineralisation (Grossmann & Dieckmann 1994, Grossmann *et al.* 1996, Helmke & Weyland 1995, Thomas *et al.* 1998). Some authors have suggested a symbiotic relationship between epibacteria and some ice diatoms (Sullivan & Palmisano 1984) which is based on carbohydrates produced by the diatoms (McGrath Grossi *et al.* 1984). Clearly the coupling of primary production and heterotrophic activity within the ice is mediated through the dissolved organic matter (DOM) pool, although to date, no studies, to our knowledge, have measured all three aspects at the same time.

It has long been assumed that levels of dissolved organic matter must be high in sea ice (Gradinger *et al.* 1992, Grossmann *et al.* 1996, Günther *et al.* 1999), and that these are central to the high heterotrophic activity within the ice and the subsequent remineralisation of inorganic nutrients. However, until recently, measurements of DOM have been lacking, and much of the discussion about the links between primary and secondary production in sea ice has been speculative. Thomas *et al.* (1998, in press a, in press b) have shown that dissolved organic carbon and nitrogen (DOC and DON) in sea ice are significantly enriched compared with surface waters often by several orders of magnitude. Concentrations of DOC are typically greater than 150 μMC, although up to 2 mMC have been measured, and likewise DON values up to 75 μMN have been recorded (Thomas *et al.* 2001b). However, when concentrations within the brine channel/pore space were calculated from estimated brine volumes, actual concentrations of DOC in sea ice brines were up to 23.3 mM and DON up to 2.2 mM, although mean values were 1.8 and 0.15 mM respectively (Thomas *et al.* in press b).

Thomas *et al.* (1995, 1998) concluded that much of this DOM originates from high grazing activity within the ice. In contrast Palmisano & Sullivan (1985a) have also measured release of more than 30% of photosynthetically fixed organic carbon as DOC. Likewise Smith *et al.* (1997) measured a significantly positive relationship between DOC and chlorophyll *a* (chl *a*), an indicator for an algal origin of the DOC within the ice. However, such relationships are not universal, and several studies have indicated poor correlation between algal biomass and DOC (Thomas *et al.* 1998, in press b). Only a few studies have investigated components of sea ice DOM, and due to the lack of bulk DOC and DON measurements their significance has been difficult to appreciate. Since a high percentage of carbon stored in ice algae is stored

as carbohydrates it is likely that carbohydrates will contribute a high percentage of the total DOC pool. Krembs (personal communtication 2000) have shown that sea ice diatoms release substantial quantities of microbially produced exopolymeric substances (EPS) that can alter brine pore structure around diatoms and protect them from ice crystal damage during freezing. The likelihood is that much of the DOM in sea ice is algal derived in the form of EPS.

Our understanding of microbial processes within sea ice is highly dependent on our understanding of the nature of the DOM pool. Thomas *et al.* (in press b) have measured total dissolved carbohydrates to be on average 36% of the total DOC pool of melted ice cores, although values up to 99% were found. The aim of this study was to develop these preliminary findings and determine the dissolved mono- and polycarbohydrate levels in various sea ice types, relating these to bulk DOC levels.

Materials and methods

Samples

The samples analysed were obtained on two different occasions. Ice cores were obtained during the research cruise ANT14/3 of the RV *Polarstern* to the Weddell Sea during summer, between 4 January 1997 and 19 March 1997. A detailed description of the ice conditions and sampling is given by Haas *et al.* (1998, in press). Ice cores were taken with a titanium ice corer (9 cm internal diameter). During coring and subsequent handling care was taken not to contaminate the ice, and it was handled as little as possible. Immediately after coring the cores were sawed with a clean stainless steel saw into ten centimetre sections, and these subsequently put into 1 litre opaque PVC containers. On board ship the ice sections were melted in the containers at 4°C in the dark. This process took no longer than 24 h and due to the porous nature of the ice the melting periods were often considerably shorter.

During the cruise several other sea ice habitats were sampled (Fig. 1). These included surface ponds, formed by flooding of the ice surface by seawater or the accumulation of meltwater or a combination of both. Sub-surface gap layers, quasi-continuous gaps flushed with seawater (Haas *et al.* in press) were also sampled. These liquid samples were collected with syringes, glass bottles and ladles. Any loose ice was sieved from the samples. Seawater (open water) samples were also collected from the edge of ice floes.

Platelet ice was sampled at Drescher Inlet, a 20 km long funnel shaped crack in the Riiser-Larsen ice shelf (72°52'S, 19°25'W) in the eastern Weddell Sea. The inlet is characterized by a stable fast ice cover lasting throughout the summer and an underlying platelet ice layer which can reach a thickness of > 20 m (Thomas *et al.* in press a). Platelets and interstitial water from between the platelets were collected through core holes. Platelets were separated from the interstitial water using a coarse sieve (mesh 1 mm^2). Platelets were melted in the same way as the ice cores described above.

Platelets and interstitial water were also sampled during the second sampling period during a five week ice camp at the Drescher Inlet during February 1998 (Thomas *et al.* in press a). Samples were taken at eight stations. At five of them interstitial water from the platelet layer between 20 cm and 1.75 m underneath the ice was collected using the ADONIS sampler which allowed high resolution sampling of the interstitial water within the platelet ice (Dieckmann *et al.* 1992). Platelet ice was collected and separated from interstitial water by sieving with a mesh size of 1 mm^2. Open ice-free water at three depths was collected from beneath the ice (30, 150, 400 m) by using Niskin bottles.

Sample processing

All samples were filtered through precombusted GF/F filters (Whatman, 450°C, 3 h). The filters were stored frozen until subsequent chl *a* analysis using a Turner fluorometer, after extraction overnight in the dark at 4°C (Evans & O'Reilly 1983). Filtrates were divided into precombusted glass ampoules (450°C, 5 h), that were then sealed and stored at -20°C until analysis. Dissolved organic carbon was measured by high temperature oxidation using an MQ1001 TOC Analyser (Qian & Mopper 1996).

The method used to determine the mono- and polysaccharide concentrations was based on the methods of Myklestad *et al.* (1997). The conditions for polycarbohydrate hydrolysis were altered to the following: temperature was reduced from 150°C to 100°C and the amount of HCl added was reduced from 400 µl to 100 µl, lowering the final molarity of the hydrolysis from 9.1 $x10^{-2}$ M HCL to 2.4 $x10^{-2}$ M HCL.

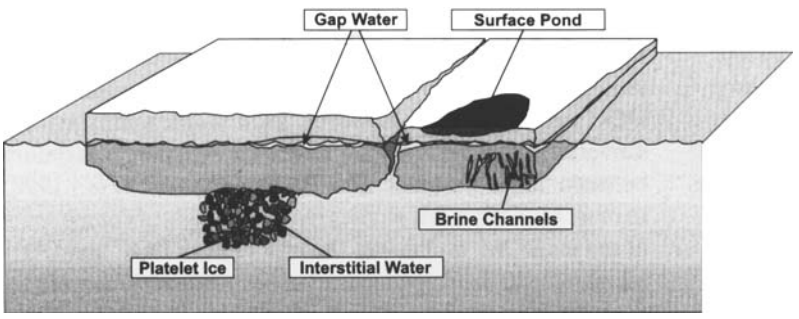

Fig. 1. Various types of sea ice habitats sampled for dissolved organic carbon (DOC) and carbohydrate analyses in summer Weddell Sea ice. When platelet ice was sampled the interstitial water between ice platelets was analysed separately.

Table I. The dissolved organic carbon (DOC), dissolved monocarbohydrates (MCHO), and polycarbohydrates (PCHO) content of samples from six different habitat classes associated with summer sea ice in the Weddell Sea. Algal biomass is given as chl *a* concentrations for each class. (Results are presented ± s e, and the numbers of samples analysed in each class is given by *n*).

Habitat	*n*	DOC μM C	MCHO μM C	PCHO μM C	TCHO μM C	chl *a* μg L^{-1}
Ice cores	8	254 ± 133	38 ± 19	15 ± 11	53 ± 22	74 ± 112
Platelet ice	9	124 ± 77	21 ± 19	3 ± 2	24 ± 16	114 ± 85
Interstitial water	18	143 ± 45	12 ± 7	2 ± 2	13 ± 8	31 ± 78
Surface ponds	7	338 ± 293	40 ± 26	17 ± 26	57 ± 34	25 ± 42
Gap water	15	257 ± 199	20 ± 14	3 ± 5	22 ± 18	11 ± 13
Open water	10	78 ± 50	7 ± 4	1 ± 1	8 ± 4	1 ± 1

Results

The DOC, mono-, polycarbohydrate concentrations (MCHO and PCHO respectively) and chl *a* content of all the habitat samples are shown in Table I. All of the various ice types had significantly elevated concentrations of DOC and dissolved carbohydrates compared with the open water samples (mean 78 μMC). The highest DOC and total dissolved carbohydrates (TCHO) concentrations were measured in the surface ponds in which up to 958 μMC (mean 338 μMC) DOC was measured. Similar concentrations of DOC were measured in the ice cores and gap waters (means 254 and 257 μMC respectively), which were significantly higher than concentrations measured in platelet ice and the interstitial water.

However, in the ice cores there were approximately twice the amount of carbohydrates than in the gap water samples. The concentrations of DOC in the platelet ice and interstitial water were lower than in the other ice habitats. The contribution of TCHO to the DOC pools therefore varied considerably between ice type, the highest contributions being in ice cores (29%) and platelet ice (31%) and surface ponds (22%). In interstitial waters, gap waters and open water TCHO ranged from 10 to 18% of the total DOC (Table II).

There were strikingly significant differences in the composition of the carbohydrates when the various sample types were compared. In open water mean values of MCHO were 90% of the TCHO concentrations. Similar mean percentage contributions (88%) were measured in the platelet ice, interstitial waters and gap waters. In contrast in the ice cores and surface ponds the PCHO fraction formed a greater proportion of the dissolved carbohydrate pool resulting in the mean contribution of MCHO being only 70% of the TCHO pool (Table I).

Table II. The mean average percentage carbon contributed by dissolved monocarbohydrates (MCHO), polycarbohydrates (PCHO), and total carbohydrates (TCHO) to dissolved organic carbon (DOC) pool in various sea ice habitat classes and open water.

Sample class	MCHO:DOC in %	PCHO:DOC in %	TCHO:DOC in %
Ice cores	21	8	29
Platelet ice	29	2	31
Interstitial water	9	1	10
Surface ponds	13	8	22
Gap water	14	1	15
Open water	17	1	18

The differences in DOC and TCHO levels did not correspond to differences in algal biomass indicated by chl *a* concentrations (Table I). The highest algal biomass were in fact found in the platelet ice (mean 114 μg chl $a\,l^{-1}$) and melted ice cores (mean 74 μg chl $a\,l^{-1}$), whereas the surface ponds and gap waters with higher DOC values supported a significantly lower algal biomass (means 25 and 11 μg chl $a\,l^{-1}$ respectively).

Since the surface ponds and gap waters can be influenced by processes quite separate from the confined ice habitats it was decided to consider the ice cores, platelet ice and interstitial water separately. In the ice cores and platelet ice TCHO varied as a function of increasing DOC concentrations (Fig. 2). This relationship was mostly due to the increasing concentrations of MCHO, PCHO levels having little trend with increasing DOC levels. There was no evident trend in the dissolved carbohydrates of the interstitial water with increasing DOC in the samples.

Discussion

The concentrations of DOC in the ice habitat samples measured in this study were considerably higher than the open water samples which are typical of Weddell Sea concentrations (Wedborg *et al.* 1998). But the concentrations of DOC in the ice habitats were not as high as the mM concentrations measured in other samples collected at the same time of year (cf. Thomas *et al.* 1998, in press a, in press b). It is not surprising therefore that the carbohydrate concentrations measured within the sampled ice habitats were also greater than those sampled from open oceanic waters, where TCHO concentrations typically vary from 5 to 35 μMC, on average 21 ± 7% of the DOC. However, values up to 35% of DOC have been recorded (Pakulski & Benner 1994, and citations therein). The range of values for the contribution of TCHO to the DOC pool measured in this study (10 to 31%) are similar to the range described by Pakulski & Benner (1994) and McCarthy *et al.* (1996) for open waters in different oceans. They were not as great as those measured by Thomas *et al* (in press b) where values of TCHO were up to 99% of DOC in ice core samples,

although the mean percentage contribution of TCHO to the DOC pool was 36%, and similar to the higher values in this study.

Whereas MCHO concentrations vary little with depth in open water, PCHO are evidently the dominant form of carbohydrate (up to 71 ± 18% of TCHO) in surface waters, concentrations decreasing markedly with depth (Benner *et al.* 1992, Pakulski & Benner 1994). PCHO in surface waters are therefore considered to be a very important component in the flux of carbon and energy through the microbial loop in surface waters (Pakulski & Benner 1994). Water from depths of 2–200 m in the Gerlache Strait contained between 5.6–1.0 μMC MCHO and 8.8 to 18.3μMC PCHO which comprised together up to 13 to 19% of the DOC (Pakulski & Benner 1994). The results from all of the ice habitats sampled here, as well as the 10 open water samples, are contrary to these findings, with the MCHO (70 to 90%) being a significantly higher contribution to TCHO than PCHO (10 to 31%).

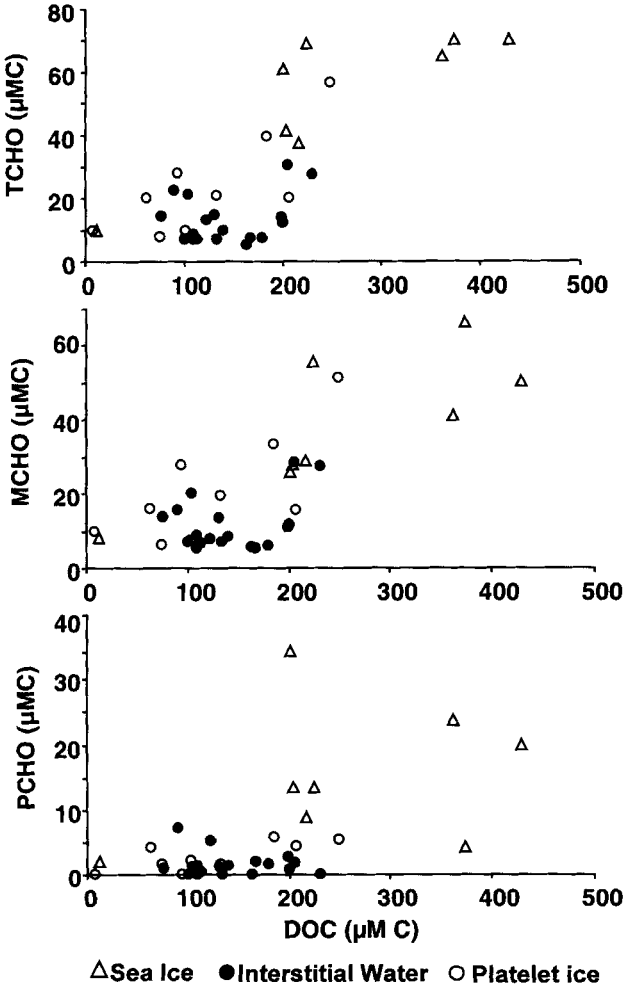

Fig.2. Relationship between dissolved organic carbon (DOC) and total carbohydrates (TCHO), Monocarbohydrates (MCHO) and polycarbohydrates (PCHO) in sea ice core, platelets and interstitial waters between ice platelets.

Correspondingly PCHO measured in this study had a lesser contribution (1 to 8%) to the DOC than the values (16 ± 9%) given by Pakulski & Benner (1994). This is somewhat anomalous if the sources of carbohydrate production in sea ice are considered, especially the high allocation of carbon stored as polysaccharide in sea ice algae, and the extracellular release of polysaccharides.

Irradiance, inorganic nutrient concentrations and growth state greatly influence the metabolic status in ice algae (Thomas & Gleitz 1993, and citations therein). Palmisano & Sullivan (1985b) showed that between 52 and 75% of photosynthetic carbon uptake is laid down as polysaccharides in the bottom-ice ice algae assemblages. In the interstitial water of the underlying platelet layer 26 to 28% of the carbon was as fixed polysaccharide. In floating ice and tidal cracks 27% of carbon uptake was assimilated into polysaccharides. McConville *et al.* (1985), Kottmeier & Sullivan (1987) and Smith *et al.* (1987) all measured high percentage allocation of photoassimilated carbon into polycarbohydrate pools (up to 46%) in field samples. In laboratory incubations Thomas & Gleitz (1993) showed that *Chaotoceros* sp. allocated 11 to 17% of the incorporated carbon into polysaccharides, whereas in *Nitzschia curta* values were up to 46%. The greatest proportion of carbon was metabolised into polysaccharides at a salinity of 50. Gleitz & Kirst (1991) suggest that production of storage carbohydrates is a direct function of the photon influx, and accumulation of reserve polysaccharides in ice diatoms is observed when photoassimilation of CO_2 provides more carbon than is required for metabolism.

It can be speculated that much of the production of DOM within sea ice is due to mechanical damage of organisms during the ice formation and consolidation (Gleitz & Thomas 1993). It has been contended that grazing by protozooplankton and zooplankton may result in the release of large amounts of DOC into the ice matrix (Thomas *et al.* 1998). However, osmotic adjustment may lead to the release of carbohydrates, and nutrient limitation, and changing growth stages result in the release of extracellular polysaccharides from algae (Penna *et al.* 1999, Guerrini *et al.* 1998). However, one of the greatest supplies of DOM into ice habitats will be microbial EPS (Decho 1990, and citations therein). The production of microbial EPS can reach such a magnitude that these substances can also interconnect pores and may significantly affect the hysteresis of brine pore space and the inpermeability for solutes and microorganisms (Krembs personal communtication 2000). Other ice active organic substances that roughen ice surfaces, are proposed to promote binding sites for attached species, or increase light scattering (Raymond 2000, Raymond *et al.* 1994). Polysaccharides are of primary importance for movement in pennate diatoms, and a whole range of extracellular polysaccharides in the form of threads, gelatinous capsules, mucilage, stalks, and tubes are produced by diatoms for attachment to surfaces and structural support with other cells (Round *et al.* 1989). Extracellular carbohydrates have also been described as having an inhibiting effect on grazing

by temperate water copepods (Malej & Harris 1993), and may be released in a similar fashion within the ice, where copepod and foraminifer grazing pressure can be high (Schnack-Schiel *et al.* 1998, 2001, in press, Thomas *et al.* 1998).

Considering the above it would be easy to speculate that PCHO concentrations in the sea ice samples should be high. However, evidently MCHO are the dominant fraction of the carbohydrate contribution to the DOC pool in the ice samples. Whereas PCHO showed no trend with increasing DOC levels (Fig. 2), MCHO increased significantly with increasing DOC concentrations in the ice core samples, again a reflection that MCHO are the more dynamic component of the ice core DOC.

Although at times the algal biomass was high, it was not exceptional for summer sea ice (Dieckmann *et al.* 1998). All samples were diatom based, predominantly *Fragilariopsis* and *Nitzschia* spp. Although bacteria numbers were high (up to 1 x 10^9 cells l^{-1}), they were not exceptional for sea ice samples either (Grossmann *et al.* 1996, Helmke & Weyland 1995). Stimulating effects of bacterial presence on algal growth and carbohydrate synthesis have been well demonstrated (Guerrini *et al.* 1998). Such symbiotic interactions could be based upon the exchange of cell products, such as carbohydrates, between the bacteria and algae (Fukami *et al.* 1997, Stewart *et al*, 1997, McGrath Grossi *et al.* 1984). Grossart (1999) observed a symbiotic relationship between specific bacteria and marine diatoms species under low inorganic nutrient conditions but with increasing organic matter, a likely scenario for closed sea ice. Guglielmo *et al.* (2000) observed particulate carbohydrate levels in Antarctic sea ice cores from Terra Nova Bay to increase strongly from the top to the bottom of the core (214.3 to 927.4 μgC l^{-1}). A similar increase with depth was measured for β-glucosidase concentrations and bacterial production. Skoog *et al.* (1999) investigated glucose and high molecular weight DOM turnover rates of bacteria in open surface waters. Glucose concentrations in the range of 12 to 90 nMC supported 5–30% of bacterial production, although glucose concentrations alone did not determine the glucose assimilation rate, as inorganic N availability increased the assimilation rate. The importance of glucose concentrations, three orders of magnitude lower than the concentrations of MCHO in the sea ice samples, for bacterial production illustrate the significance of the MCHO concentrations measured in this present study, for supporting bacterial activity within the ice.

Apart from the ice cores, the highest concentrations of DOC measured in this study were in the gap waters and surface ponds. These two habitats are characterized by having high incident irradiance in the summer. In particular, for the gap waters, there was exchange with the surrounding seawater. In both habitats there was significantly less algal biomass than in the other ice habitat classes, which is anomalous with the high DOC values. These high DOC levels in the surface features corroborate the findings of Kottmeier & Sullivan (1990) who measured significantly greater rates of bacterial activity in surface ponds and porewaters when comparing bacterial and phytoplankton carbon production in various pack ice associated habitats through the seasons. The greater amounts of PCHO in the surface ponds may be a consequence of UV radiation on photosynthesis of the surface pond assemblages which decreases the overall amount of carbon assimilated and lowers the rate of synthesis of MCHO in the storage carbohydrate pool (Goes *et al.* 1996).

There was no significant differences in the DOC content of melted platelets and the interstitial water between them. However, there were significant differences in the carbohydrate composition of this DOC. TCHO was 31% of DOC in the platelets, and 10% in the interstitial water. This may well be a reflection of the attachment of the bacteria and diatoms to the platelet surfaces, generating higher concentrations of CHO. A study comparing the bacterial and algal processes in the platelet ice layer (Grossmann *et al.* 1996) found that the bulk of bacterial biomass occurred attached to diatoms which grew on platelet ice rather than floated in the interstitial water. Günther *et al.* (1999) found that algal standing stock attached to the ice platelets was approximately on order of magnitude higher than in interstitial water. The lower concentrations of DOC and CHO in the platelet layer samples compared with the closed ice and surface pond samples are a likely result of exchange with seawater (Robinson *et al.* 1998), which in the latter two habitat classes will not be as great.

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