Proc. NIPR Symp. Polar Biol., **10**, 1–13, 1997

THE POTENTIAL ROLE OF MELTED "BROWN ICE" AS SOURCES OF CHELATORS AND AMMONIA TO THE SURFACE WATERS OF THE WEDDELL SEA, ANTARCTICA

Frederico P. BRANDINI[1] and Marcus E. M. BAUMANN[2]

[1]*Universidade Federal do Paraná, Centro de Estudos do Mar, Av. Beira Mar s/n, Pontal do Sul, Pontal do Paraná, CEP 83255–000, PR, Brasil*
[2]*Alfred-Wegener-Institut für Polar- und Meeresforschung, Postfach 120161, D-27515 Bremerhaven, Germany*

Abstract: The Antarctic sea ice is the site of production of great amounts of dissolved biogenic compounds of a very diverse nature, including potential chelators and reduced nitrogen which are introduced into adjacent surface waters in marginal ice zones during melting periods. The effect of melted brown ice on the development of surface phytoplankton in the Weddell Sea was tested experimentally using natural surface populations and cultured diatoms. The growth of natural and cultured diatoms was enhanced after various additions of melted brown ice. EDTA was also used as a standard chelator in order to compare the chelating capacities of surface water and melted ice. It was demonstrated that surface waters are not limited by lack of chelating compounds, which may originate from ice communities. The role of melted brown ice as a potential source of either ammonium or chelators affecting phytoplankton development in marginal ice zones is discussed.

1. Introduction

The release of algal cells from the ice during melting has been claimed to increase phytoplankton biomass in adjacent waters of coastal and offshore Antarctic regions (GARRISON and BUCK, 1985; FUKUDA *et al.*, 1986; GARRISON *et al.*, 1987). However, surface waters within marginal ice zones receive not only particulate material from the ice but also dissolved organic compounds, which are produced in great amounts by "brown ice" communities (KUOSA *et al.*, 1992). This makes the seeding process much more complex than has hitherto been assumed.

Dissolved organic substances present in brown ice are a very complex mixture of extracellular products of high and low molecular weight originating from biological activity within the ice community (MCCONVILLE, 1985). The chelating properties of large molecules play a crucial role in the primary production of upwelling regions, by enhancing the uptake of trace elements (BARBER and RYTHER, 1969). Amino acids, urea and ammonium are also abundant in the ice (GARRISON *et al.*, 1990; HARRISON *et al.*, 1990) and represent important sources of reduced nitrogen for phytoplankton (FLYNN and BUTLER, 1986; PALENIK *et al.*, 1990). How great an effect these compounds have on the growth of phytoplankton during the melting season is still an open question.

DUNBAR (1977) reported: "...very interesting experiments were done by BARNES

(1932), BARNES and JAHN (1933), and by HARVEY (1933), all showing that water recently melted from ice had a decidedly stimulating effect on the growth and multiplication of plant cells (*Spirogyra, Euglena, Nitzschia*)". The stimulating effect of melted ice on phytoplankton growth was reported more than 60 years ago; however, it has not been considered in studies during the past decades.

In this investigation we report the potential effect of melted brown ice enrichment on the composition and biomass accumulation in experiments with natural surface phytoplankton of the Weddell Gyre, and in cultures of Antarctic diatoms. We discuss the brown ice contribution of reduced nitrogen and chelators to the surface water during melting seasons.

2. Materials and Methods

In order to check the chelating capacity of melted ice we followed the increase of diatoms in natural water and in cultures of Antarctic diatoms after enrichments with filtrates of melted brown ice in comparison with enrichments with EDTA. The enhancement of phytoplankton abundance (as cell number) after EDTA additions was considered the control upon which the chelating effects of ice enrichments were compared.

2.1. Experiments with natural communities

Experiments were performed on board the RV "POLARSTERN" during the ANT IX/2 cruise in November/December 1990. Two brown ice samples (BI-1 and BI-2) and adjacent surface seawater were collected from two different sites in the Central Gyre of the Weddell Sea. BI-1 (67°50'S; 20°51'W) was dominated by *Phaeocystis* cf *antarctica* colonies and BI-2 (68°49'S; 17°55'W) by a mixture of *P.* cf *antarctica* and different species of pennate diatoms (*Navicula* sp, *Nitzschia longissima, Fragilariopsis curta, F. cylindrus*). The ice samples were transfered to beakers and maintained at 0°C in the dark until melting was completed after approximately one day. The melted ice samples were filtered through GF/F filters and the filtrates were added to unfiltered surface waters in order to set up the experiments described in Table 1.

No nutrients were added except for 2.72 mgEDTA/*l* in experiment 2 (VON STOSCH and DREBES, 1964) to check the chelating capacity of surface waters. All

Table 1. Experimental design to test the addition of melted brown ice and EDTA on the growth of natural phytoplankton in the Weddell Sea (R/V POLARSTERN–Nov./Dec. 1990).

Experiments	Description
1 (control)	800 m*l* SW+200 m*l* FSW
2	800 m*l* SW+200 m*l* FSW+EDTA
3	800 m*l* SW+200 m*l* melted BI-1
4	800 m*l* SW+200 m*l* melted BI-2

SW: surface water; FSW: filtered surface water.

experiments were run in duplicate; 200 m*l* of filtered sea water (FSW) was added to experiments 1 and 2. Experiments were run at 0 °C under 30 μmol m^{-2} s^{-1} of continuous light provided by fluorescent/daylight lamps.

Diatom counts were conducted at two day intervals during a 12 day incubation experiment. Aliquots of 50 m*l* at the beginning of the experiment and 10 m*l* at the end of the experiment were taken from the experimental bottles and filtered onto cellulose acetate filters (Sartorius, 0.8 μm pore size). A pre-determined filter area of 47.5 mm^2 was examined under the microscope in which all micro-size diatoms, *i.e.,* diatoms larger than 20 μm, were counted. The nano-size species, *i.e.,* those of less than 20 μm, such as *Fragilariopsis cylindrus* and *Chaetoceros dichaeta* were counted in transects of the filter area and the total number of cells in the same unit area as for the micro-size cells was calculated considering the appropriate factors. In the experiment with natural phytoplankton population cell counts are therefore expressed as absolute numbers within the filter area.

Samples for inverted microscope analyses (UTERMÖHL, 1958) were taken at the end of the experiment, for examining final species composition, cell densities per liter and biomass in terms of cell carbon per liter. The Baltic recommendations (EDLER, 1979) were followed to calculate cell carbon based on measurements of cell dimensions and plasma volume.

The initial species composition of the surface sea water used for the experiments was determined from net samples (50 μm mesh size) and from direct observations of nano-size cells retained by membrane filters (Sartorius 0.2 μm).

Autoanalyzer techniques were used onboard to determine nitrate, nitrite, ammonium, phosphate and silicate concentrations (KREST and Ross, 1992). Salinity of melted ice and surface water used for experiments was determined with a Guildline Autosal 8400A laboratory salinometer.

2.2. *Experiments with cultures using aged water*

The experiments with monoalgal cultures were set up as follows:

(i) Cultures of the Antarctic diatoms *Thalassiosira antarctica, Thalassiosira tumida* and *Fragilariopsis curta* were established from a single cell isolated during the ANT IX/2 expedition (Nov./Dec. 1990) to the Weddell Sea on board the RV "POLARSTERN".

(ii) Water from the Weddell Sea was kept in the dark at about 7°C for over a year. By this, bacterial activity was expected to decrease the concentration of organic compounds, reducing the chelating properties of the "aged" water.

(iii) A test was carried out in duplicate to check the chelating capacity of the aged water, following the development of *T. antarctica* in cultures with and without (controls) additions of EDTA. Vitamin and metal (Fe, Co, Mn, etc.) enrichments of the aged water were also performed according to VON STOSCH and DREBES (1964).

The chelating property of melted brown ice was tested with cultures of *T. tumida* and *F. curta* at the Alfred Wegener Institute, Germany, using the aged natural Antarctic seawater, filtered onto 0.2 μm cellulose acetate filters (Sartorius). The cultures were spiked with melted brown ice at a concentration of 2 m*l*/10 m*l* culture, and 3 levels (3, 6 and 9 m*l*/*l*) of EDTA (VON STOSCH and DREBS, 1964). We assume

that differences in the development of cultures with and without additions (=controls) of either melted brown ice or EDTA represents the recovery of the potential fertility of the aged water by any one of these compounds. The experiments were performed in Duran flasks under continuous light provided by fluorescent lamps (30 $\mu E \cdot m^{-2} \cdot s^{-1}$) and temperature controlled conditions (2°C±0.25°C) during 2 to 4 weeks. Samples of 10 m*l* were taken at two day intervals for counting cells with the inverted microscope (UTERMÖHL, 1958).

The same species were grown in a second experiment, in which Fe (as $Fe_2(SO_4)_3$) was added alone and in combination with melted ice and EDTA. Additions were based on the quantities prescribed by VON STOSCH and DREBES (1964).

2.3. Experiments with deep Antarctic waters

During the POLARSTERN cruise ANT X/7 in November 1992, water samples were taken from 600 m in the Weddell Gyre, with the purpose of testing the chelating capacity of deep warm waters. The water was filtrated onto GF/F filters and used for cultures of *Thalassiosira antarctica* at 0 °C under 30 μmol m^{-2} s^{-1} of continuous light provided by fluorescent/daylight lamps. Cultures were set up without (control) and with additions of EDTA. Cultures with EDTA were done in duplicate. The increase of cell densities were followed during four days by counting samples every day, with the sedimentation technique of UTERMÖHL (1958).

3. Results

3.1. Effect of ice enrichment on natural communities

The addition of melted ice with salinity around 6 ppt decreased the original salinity of surface water to approximately 28 ppt. It also decreased, although not to limiting levels, the initial concentrations of nitrate, phosphate and silicate in the experiments with melted ice (exps 3 and 4), since concentrations of these elements in the ice were much lower than in the surface water (Table 2).

The experiments started with very low phytoplankton stocks in surface water, around 0.3 μg Chl.$a \cdot l^{-1}$ (data not shown), typical for the Central Gyre of the Weddell Sea in late winter when ice melting started (NÖTHIG *et al.*, 1991). Initial cell densities (*i.e.*, the number of cells inside the unit filter area) in all experimental flasks varied from 252 to 364. Cell numbers increased only slowly in the first 120 hours, but after 240 hours cell densities were almost 3 times higher in the melted ice enriched flasks than in the controls (Fig. 1). The addition of EDTA did not stimulate the growth of diatoms in the natural seawater; final densities were comparable to those of the controls.

The initial phytoplankton assemblage of the adjacent water used for experiments was formed by nano-size diatoms (*F. cylindrus, Chaetoceros neglectus*) and flagellates of different taxonomic groups. The analyses of final species composition and cell densities on a water volume basis after 17 days revealed that the diatom community in the control was numerically dominated by *F. cylindrus*. However, the addition of EDTA and melted brown ice stimulated the development of other nano-size species such as *Chaetoceros dichaeta* and, to a lesser extent, *Fragilariopsis curta*, in BI-2

Table 2. Nutrient concentrations in the melted brown ice (BI-1 and BI-2), in the surface water (SW) and in the experimental flasks at the beginning of the experiment. Concentrations in μM.

Sample	SiO_2-Si	PO_4-P	(NO_3+NO_2)-N	NH_4-N
BI-1	33.1	0.70	4.1	5.9
BI-2	28.9	2.07	11.5	20.0
SW	71.0	2.06	28.9	0.4
1A	71.2	2.09	29.0	0.5
1B	71.0	2.07	28.9	0.4
2A	71.0	2.05	28.9	0.3
2B	70.8	2.04	28.8	0.4
3A	62.2	1.77	23.8	0.9
3B	62.6	1.77	23.7	0.7
4A	63.4	2.09	25.3	2.9
4B	63.4	2.09	25.4	2.5

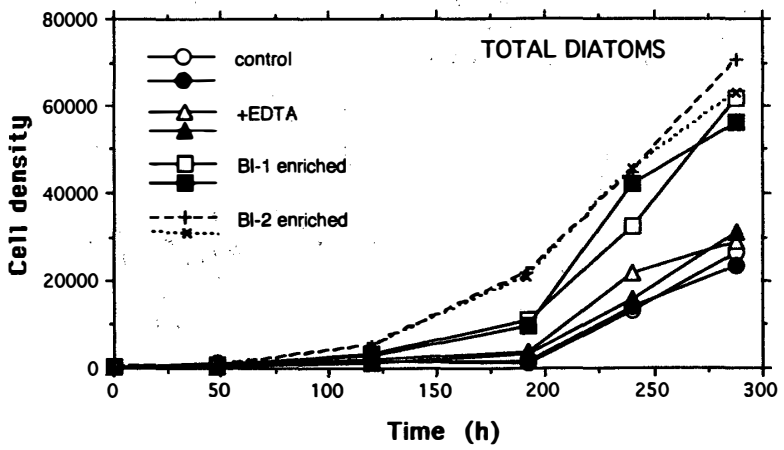

Fig. 1. Growth of natural phytoplankton with and without brown ice-enrichment (circle: controls; triangle: EDTA enriched; square: BI-1 enriched; cross: BI-2 enriched). Refer to text and Table 1 for details of experimental design.

enrichments (Fig. 2).

The results in terms of biomass depicted a similar pattern but with different species composition. Final carbon biomass in the ice melted enrichments was remarkably higher than in the control and the control+EDTA, mainly due to the contributions of *Chaetoceros neglectus, F. curta* and *Pseudonitzschia* sp. (Fig. 3).

3.2. Chelating properties of brown ice

The experiment to test the chelating property of aged water revealed that cultures of *Thalassiosira antarctica* without any sort of enrichment died in two days (Fig. 4). Only EDTA enrichment enhanced growth and supported healthy cells for

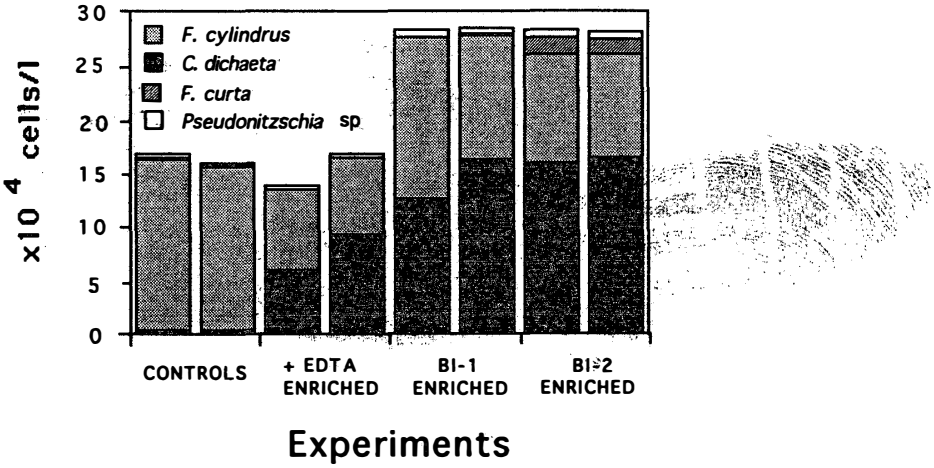

Fig. 2. Final species composition and abundance of diatoms in natural Weddell Sea water enriched with melted brown ice. Refer to Fig. 1 and text for legend.

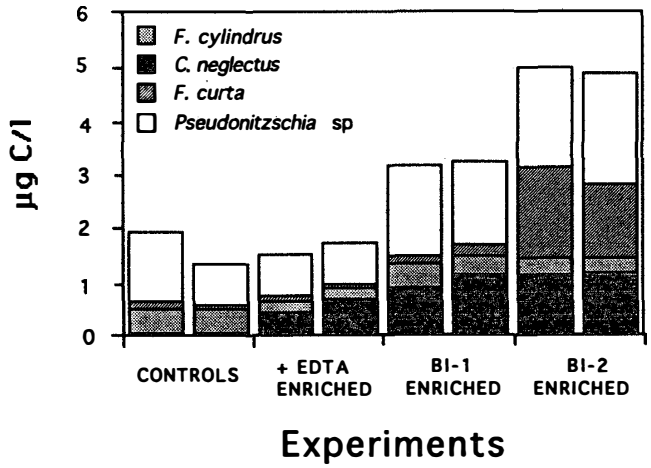

Fig. 3. Final carbon biomass of diatoms in natural Weddell Sea water with and without enrichments with melted brown ice. Refer to Fig. 1 and text for legend.

many days at the same level of complete enrichment (EDTA, metals and vitamins), suggesting that only the addition of chelators was sufficient to improve the capacity of the water to support growth of the diatom species.

The culture experiments with *Thalassiosira tumida* and *Fragilariopsis curta* showed the expected stimulating effect of brown ice additions on the potential fertility of aged Antarctic water. In both species, the addition of melted brown ice enhanced the growth in aged water, but not as in any of the three experiment with additions of EDTA (Fig. 5).

Additional experiments with the same diatom species revealed that growth was not enhanced by the addition of Fe alone (Fig. 6). Growth rates of *T. tumida* in enrichments with only brown ice and with brown ice+Fe were similar but represented

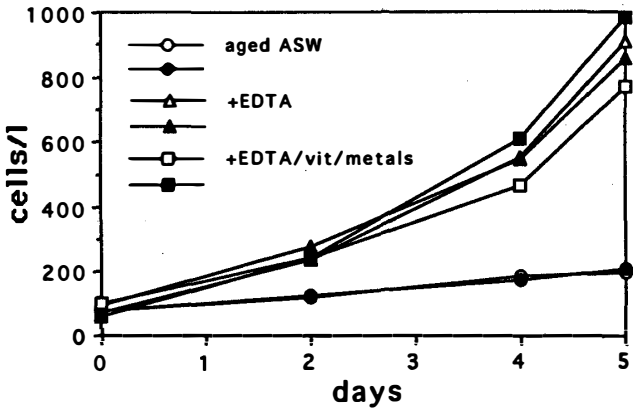

Fig. 4. Growth of Thalassiosira antarctica *in aged Antarctic water without any enrichment (circle), with additions of EDTA (triangle) and EDTA+ vitamins+trace elements (square).*

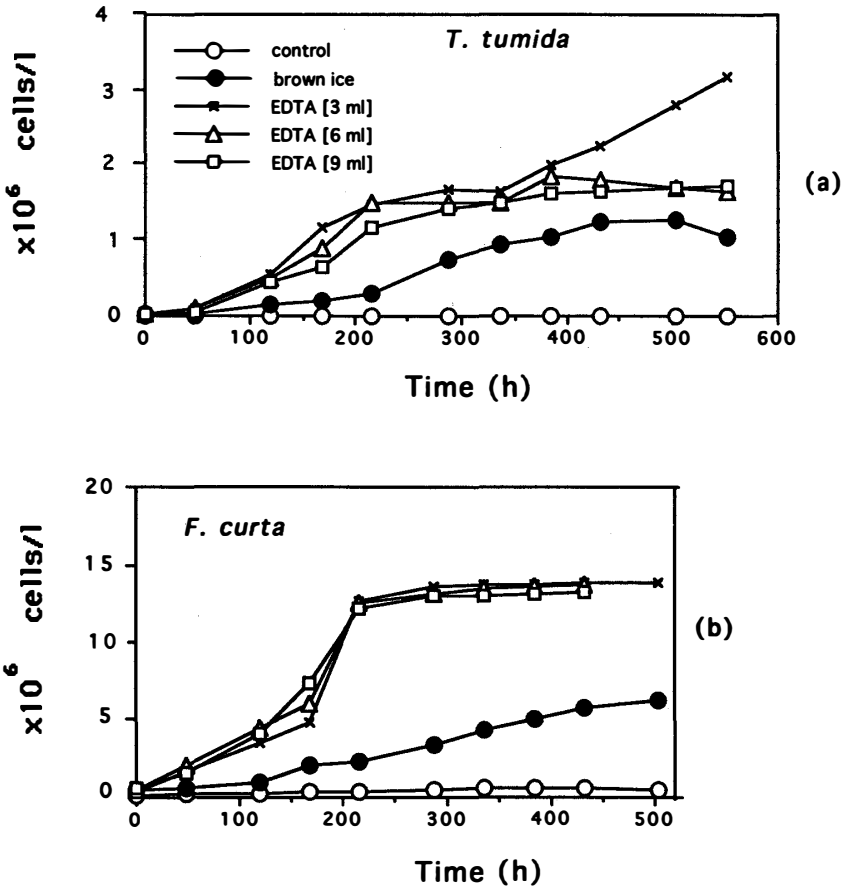

Fig. 5. Growth of Thalassiosira tumida *(a) and* Fragilariopsis curta *(b) using aged Antarctic water enriched with melted brown ice and different concentrations of EDTA.*

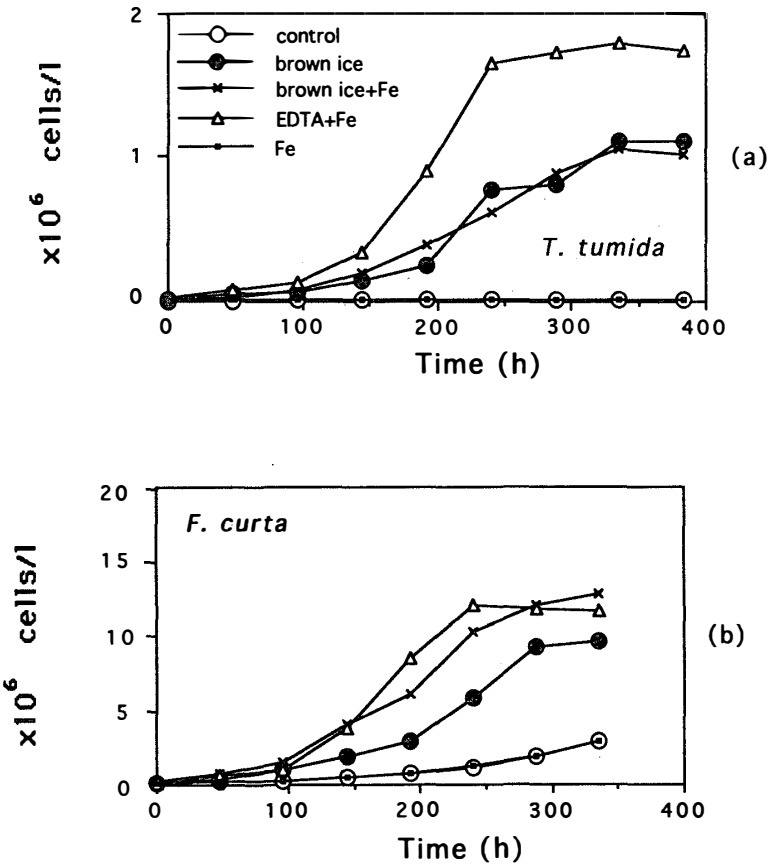

Fig. 6. Growth of Thalassiosira tumida *(a) and* Fragilariopsis curta *(b) using aged Antarctic water enriched with melted brown ice, EDTA and iron.*

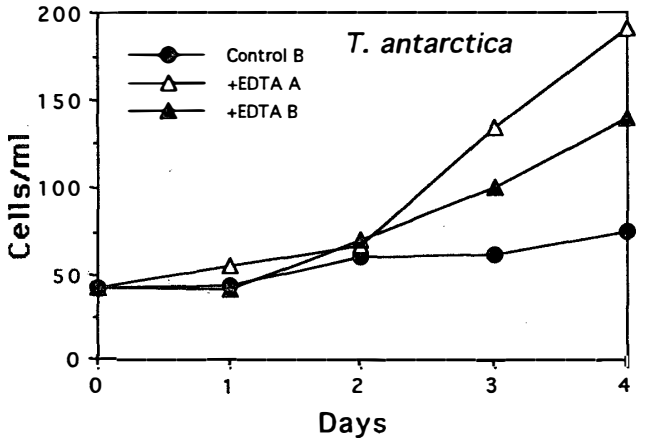

Fig. 7. Effect of EDTA enrichment on the growth of Thalassiosira antarctica *in Warm Deep Water.*

half the growth observed in enrichments with EDTA+Fe. In the case of *F. curta*, maximum growth rates were obtained upon enrichment with brown ice+Fe and EDTA+Fe, whereas the enrichments with only ice enhanced partially the growth rates compared to the control. The addition of only Fe did not show any effect on the growth of either diatom species.

3.3. Chelating capacity of deep Antarctic waters

The culture experiments with water from 600 (Antarctic Warm Deep Water) revealed that the deep water was inadequate for culturing *Thalassiosira antarctica* without the addition of EDTA (Fig. 7). After 4 days of experiment, cells did not grow in the deep water. However, duplicate experiments with addition of EDTA showed comparatively higher cell development.

4. Discussion

The experiments with natural phytoplankton demonstrated that the growth in the Weddell Sea was not limited by chelating compounds since cell development in EDTA enriched flasks was similar to controls. Therefore, the enhancing of cell development in the BI-1 and BI-2 enrichments depicted in Fig. 1 could not be associated with the chelating property of organic compounds in the brown ice. However, the experiments with cultures using aged sea water showed clearly that ice could be an important source of chelators, recovering the potential fertility of water bodies devoid of these compounds. The experiment carried out with deep waters aimed to test the potential fertility of Warm Deep Water, *i.e.*, the capacity of this water to support maximum growth of phytoplankton (see HARVEY, 1947). The Warm Deep Water is the main source of upwelled water in the Antarctic Divergence (SAKSHAUG and HOLM-HANSEN, 1984). It became clear that without the addition of EDTA, deep water was inadequate for culturing *Thalassiosira antarctica* (Fig. 7). BARBER and RYTHER (1969) demonstrated the importance of chelators for enhancing primary production in upwelling systems. It remains to be confirmed, however, whether this could be applied to the upwelling/divergence zones of the Antarctic and to what extent the stocks of dissolved organic matter from the brown ice represent important sources of chelators to improve the potential fertility of deep upwelled waters.

It has been argued that Antarctic phytoplankton preferentially utilize ammonium despite the high ambient nitrate concentrations (GLIBERT *et al.*, 1982; KOIKE *et al.*, 1986; RÖNNER *et al.*, 1983). Ammonium uptake most likely plays an important role in primary production of ice edge ecosystems (GOEYENS *et al.*, 1995), although predominance of nitrate uptake has been also observed (SMITH and NELSON, 1990). GOEYENS *et al.* (1991) observed a decrease in *f*-ratio (*i.e.*, the ratio of nitrate uptake to nitrate plus ammonium uptake) indicating an increasing uptake of ammonium as the summer progresses. Therefore, the initial supply of ammonium could also enhance biomass accumulation in the ice-enriched experiments with natural phytoplankton. The relationship between final carbon biomass in the experimental flasks (Fig. 4) and initial ammonium supply of each respective experiment (Table 2) showed a

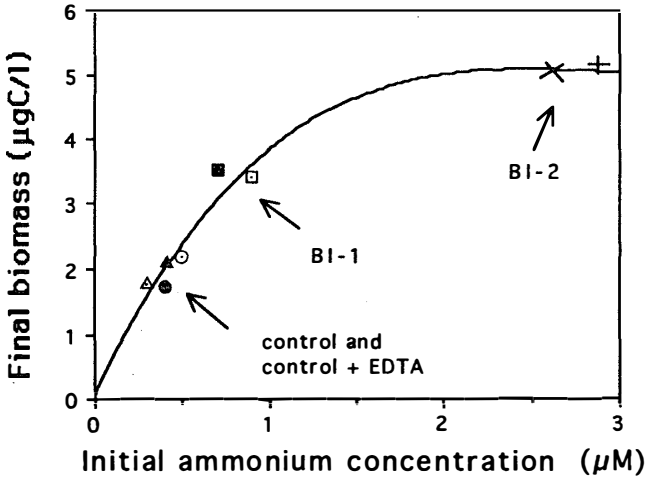

Fig. 8. Relationship between initial ammonium concentration and final carbon biomass of diatoms, in surface water from the Weddell Gyre enriched with EDTA and melted brown ice.

"Michaelis-Menten" type curve (Fig. 8). Initial ammonium supply and final biomass in the control and in the EDTA enriched experiments were similar. But initial ammonium supply in BI-1 and BI-2 enrichments was higher than in the control and in the enrichment with only EDTA. Moreover, the initial ammonium supply in BI-2 was on average three times higher than in BI-1 enriched experiments, as their respective final carbon biomasses were consistently different (Fig. 3). Since the experimental conditions were not axenic, bacterial regeneration of ammonium from the organic fraction of melted ice was probably another source of reduced nitrogen.

The high affinity for ammonium is confirmed by lower Ks values than the ones for nitrate; this holds particularly true for nano-size species (EPPLEY *et al.*, 1969). This does not necessarily imply enhancement of specific growth rate but it could have had some effect on the numerical dominance of *Fragilariopsis cylindrus* and *Chaetoceros neglectus* in our ice enriched flasks, although the final pool of carbon biomass has been shared among diatoms of the micro-size category (*e.g.*, *F. curta* and *Pseudonitzschia* sp). *Fragilariopsis cylindrus* is an important representative of phytoplankton assemblages in marginal ice zones (GARRISON *et al.*, 1987; RIEBESELL *et al.*, 1991) and usually numerically dominates culture experiments in which natural populations are used. KUOSA *et al.* (1992) have attributed this dominance to the release of cells from the ice. But in our experiments, the dominance of *F. cylindrus* or any other nano-size diatoms must be related to chemical factors (*e.g.*, ammonium and chelators) since there were no diatoms in the filtrates of melted ice used for the experiments.

The lowering of salinity in the melted ice enrichments might also have stimulated the growth rate of diatoms (BUNT, 1964). Nevertheless, the more or less 5 ppt difference in salinities between controls and ice melt enriched flasks may not be the only factor accounting for such large differences in final cell carbon biomass (Fig. 3).

5. Final Remarks

There is a general consensus that continental contributions of dissolved organic matter to the Antarctic Ocean are negligible (EWALD *et al.*, 1986). Therefore, apart from the input of all sorts of inorganic and biogenic particles, the considerable biological activity associated with the sea ice should be regarded as the main source of dissolved compounds to the upper euphotic layers during the melting season in the deep marginal ice zones. ROMANKEVICH and LJUTSAREV (1990) reported increasing surface concentrations of dissolved organic carbon from the divergence (*i.e.* upwelling) regions of the Weddell Sea toward the pack ice zone. KUOSA *et al.* (1992) measured concentrations of DOC in brown ice up to 50 $mg \cdot l^{-1}$ *i.e.*, 35 times higher than the mean concentrations in the euphotic layer (1.44 $mg \cdot l^{-1}$) reported by ROMANKEVICH and LJUTSAREV (1990). Approximately 15×10^6 km^2 of seasonal ice melts every spring/summer period in the whole Antarctic area (ZWALLY *et al.*, 1983; MAYKUT, 1985) and approximately 80% of this melts from November to January, which represents a mean of 130000 km^2 of ice per day within this period. Considering an average ice thickness of about 1 m and the maximum concentration of 50 $mgDOC \cdot l^{-1}$ reported by KUOSA *et al.* (1992), up to 6.5×10^6 tons of DOC may be released every day in marginal ice zones around the Antarctic Continent during the melting season. These figures may be overestimated since DOC is not distributed homogeneously in the sea ice. Other papers reported, on a regional scale, an ice retreat rate of approximately 9 km per day during December 1988 (LANCELOT *et al.*, 1993). But even if overestimated, the daily input of dissolved substances is certainly high enough to affect not only the bacterial activity in the water adjacent to ice, as reported by KUOSA *et al.* (1992), but also the autotrophic activity of phytoplankton in marginal ice zones.

On a quantitative basis our results may not reflect exactly what happens in the pack ice zone during the melting season. The supply of large amounts of a very diverse composition of organic compounds to the water column, as simulated in our experiment, does not happen within the temporal and spatial scales prevailing in the marginal ice zones during melting seasons. The physiological response of phytoplankton to the input of potential chelators or reduced forms of nitrogen can be faster (scales of minutes, hours) than the diffusion rates of these elements within the stable upper layers, typical of the MIZ. Even under high rates of diffusion, the continuous input of dissolved compounds during ice melting certainly affects the chemistry of the adjacent water and the physiological reactions of its phytoplankton population.

It remains to be clarified how different would be the structure and the functioning of the pelagic systems off MIZ if the sea ice were totally devoid of biological activity, being not a site of production and source of dissolved organic matter to the adjacent water during melting. Our limited data-set does not allow further speculation on this matter but it reveals the remarkable effect of dissolved compounds from the ice on adjacent phytoplankton populations. These effects deserve further investigation to provide a more detailed picture of the impact of a receding ice edge on the phytoplankton ecology in the MIZ.

Acknowledgments

The authors thank J. KREST and A. Ross for the analyses of nutrients on board. L. GOEYENS and two anonimous reviewers made valuable contributions to improve this paper. The first author was supported by the Alexander von Humboldt Foundation while working on this investigation in the Alfred Wegener Institute, Bremerhaven.

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(Received December 11, 1995; Revised manuscript accepted September 2, 1996)