Aus dem Institut für Polarökologie

der Christian-Albrechts-Universität zu Kiel

Sea-ice communities: structure and composition in Baltic, Antarctic and Arctic seas

Dissertation
zur Erlangung des Doktorgrades
der Mathematisch-Naturwissenschaftlichen Fakultät
der Christian-Albrechts-Universität
zu Kiel

vorgelegt von

Klaus Meiners

Kiel

2002

Referent: Prof. Dr. M. Spindler

Korreferent/in: . . . . . .

Tag der mündlichen Prüfung: . . . . . .

Zum Druck genehmigt: Kiel, ...

Der Dekan

Summary

Sea ice is an important structural component of polar marine ecosystems but also at lower latitude seas like e.g. the northern Baltic Sea. This study summarises observations on biological, chemical and physical characteristics of sea ice and under-ice water obtained during three expeditions to the Baltic Sea, the Fram Strait area (Arctic) and the Bellingshausen Sea (Antarctica). The study aimed at a better understanding and quantification of different components of the sea ice related food web. The seasonal Baltic sea ice is least studied and therefore the work in this area focused on an inventory determination of the abundance and biomass composition of the sympagic (= ice-associated) community of the Bothnian Bay and Bothnian Sea as well as on the importance of abiotic and biotic factors in the control of ice algal accumulation.

The work on the better explored polar sea ice focused on the abundance, distribution and characteristics of transparent exopolymer particles (TEP) in Arctic and Antarctic sea ice. TEP are a recently described class of exopolymeric particles, which are formed abiotically and biotically from polysaccharid-rich precursors. High amounts of TEP-precursors are released by bacteria and algae especially in response to environmental stress. In the pelagic realm TEP are important in the aggregation of diatom blooms, provide the matrix of macroaggregates and serve as substrate and habitat for attached bacteria. High concentrations of TEP have been recently described for Arctic sea ice and may have an important impact on carbon dynamics in sea-ice systems. The present study related TEP concentrations to biotic and abiotic sea ice parameters, potential modes of TEP formation were elucidated and the importance of TEP for the sea-ice habitat was discussed. It follows a short summary of the main findings in the different investigation areas:

Baltic sea ice: The Baltic sea ice was colonised by complex communities consisting of prokaryotes, protists and metazoa. Integrated biomass (mean relative contribution) was mainly formed by pennate diatoms (33 %), followed by centric diatoms (29 %), autotrophic flagellates (23 %), bacteria (8 %), heterotrophic flagellates (7 %) and metazoans (1 %). Only two metazoan taxa (rotifers, crustaceans) colonised the Baltic sea ice, while most of the sympagic taxa described for Arctic and Antarctic sea ice were lacking. This is in accordance with the generally low biodiversity of the brackish environment of the northern Baltic Sea. Sympagic metazoa consumed, on average, only 1.5 % of the ice algal standing stock per day, based on allometric calculations. The data suggest that the accumulation of autotrophic biomass in Baltic sea ice under investigation was controlled rather by abiotic factors (particularly nutrient availability), than by the heterotrophic component of the sympagic community.

Polar sea ice: The two investigations in the polar regions dealt with the quantification of TEP in the sea-ice system and provided an estimation of its relevance for the carbon cycle within sea ice. The work in Fram Strait (Arctic) quantified for the first time the vertical distribution of TEP in young, first-year and multi-year sea ice over the entire ice thicknesses. Median TEP abundances and TEP areas in the different ice types ($3.17–4.89 \times 10^6$ particles l^{-1} and 4.6–6.9 cm^2 l^{-1}, respectively) by far exceeded median concentrations in under-ice water (0.56×10^6 particles l^{-1} and 0.6 cm^2 l^{-1}, respectively). TEP concentrations were highest in the interior of the sea ice and were significantly correlated with chlorophyll *a* as well with the abundances of pennate diatoms, centric diatoms and bacteria. It is hypothesised that TEP peaked in the ice interior due to the more extreme living conditions in these layers. The abundance of TEP was inversely correlated with TEP size. TEP in sea ice and under-ice water showed distinct size-frequency distributions, which differed from those commonly reported in pelagic studies, in that they contained a large proportion of relatively large particles.

In Antarctic sea ice, TEP concentrations were higher with TEP abundance ranging between $10.22–260.45 \times 10^6$ particles l^{-1} and TEP area between 3.4–92.1 cm^2 l^{-1}. Median TEP con-

centrations in the ice (median abundance: 50.16×10^6 particles l^{-1}, median area: 21.3 cm^2 l^{-1}) exceeded under-ice values (median abundance: 3.56×10^6 particles l^{-1}, median area: 1.0 cm^2 l^{-1}) by one order of magnitude. TEP size distributions in Antarctic sea ice and under-ice water resembled those found in the Arctic. TEP size frequency spectra showed relatively flat slopes, indicating a considerable contribution of larger particles. This unique size-frequency distribution is possibly caused by different factors e.g., capsular mucus formation by bacteria and algae, disruption of biofilms and / or distinct physical characteristics of the sea-ice habitat (large internal surfaces, elevated shear rates). In addition to TEP concentrations and size distributions, the bacterial colonisation of TEP was examined in Antarctic sea ice. All TEP were colonised by bacteria. The median fraction of attached bacteria was 1.9 % and 14.8 % of the total bacterial number in the under-ice water and sea-ice samples, respectively. The combined data on Arctic and Antarctic sea ice indicate that pennate diatoms are the main TEP producers in polar sea ice.

Estimates of integrated sea-ice TEP carbon accounted for 14–32 % (average: 23 %) of integrated sea ice particulate organic carbon, which ranged between 38.8–2808.9 mg C m^{-2} and 437.3–3207.4 mg C m^{-2} in the Arctic and Antarctic sea ice, respectively. The data strongly suggest that TEP is an, until now largely neglected, integral component of Arctic and Antarctic sea-ice communities. The implications of the large TEP pool for the food web structure and for the turn-over of particulate organic matter within the sea-ice habitat are discussed.

Zusammenfassung

Meereis ist eine wesentliche, strukturierende Komponente polarer mariner Ökösysteme und ist auch in gemäßigten Zonen mit saisonaler Eisbedeckung, wie z.B. in der nördlichen Ostsee, von großer ökologischer Bedeutung. Diese Arbeit fasst biologische, chemische und physikalische Charakteristika von Meereis- und Untereiswasserproben zusammen, die während drei Expeditionen in die Ostsee, die Framstraße (Arktis) und in das Bellingshausen Meer (Antarktis) ermittelt wurden. Das Ziel der Untersuchungen war die Quantifzierung verschiedener Komponenten des eisassoziierten (= sympagischen) Nahrungsnetzes und ihrer Bedeutung für den Stoffumsatz im Meereis. In der bezüglich Meereis wenig untersuchten Ostsee wurde die Zusammensetzung sympagischer Gemeinschaften, die das saisonale Eis der Bottenwiek und der Bottensee besiedeln, untersucht. Im Vordergrund stand dabei die Abschätzung des Einflusses abiotischer und biotischer Faktoren auf die Akkumulation von Algen im brackischen Eis der Ostsee.

Die Arbeiten im bereits besser untersuchten Meereis der Arktis und Antarktis konzentrierten sich auf die Bestimmung der Häufigkeit, Verteilung und Charakteristik transparenter exopolymerer Partikel (TEP). TEP sind eine relativ neu beschriebene Klasse exopolymerer Partikel, die sowohl biotisch als auch abiotisch durch Koagulation polysaccharidreicher gelöster Substanzen entstehen. Diese Vorläufersubstanzen werden von Bakterien und Algen gebildet. Eine hohe Produktion der Vorläufer wurde speziell für Organismen beschrieben, die durch verschiedene Umweltfaktoren gestresst waren. Pelagische TEP haben eine große Bedeutung für die Sedimentation von Diatomeenblüten, bilden die Matrix für marine Makroaggregate und sind ein wichtiges Substrat und Habitat für angeheftete Bakterien. Hohe TEP-Konzentrationen wurden kürzlich in Bodensegmenten arktischen Meereises beobachtet, genauere Untersuchungen zur Verteilung von TEP im Meereis fehlten. In der vorliegenden Arbeit werden die Auswirkungen abiotischer und biotischer Parameter auf die Verteilung und Bildung von TEP im Meereis beschrieben. Die Bedeutung von TEP für die Meereislebensgemeinschaften und mögliche Modi der TEP-Bildung werden diskutiert. Es folgt die Darstellung der wichtigsten Untersuchungergebnisse der Regionen:

Meereis der Ostsee: Das Meereis der Ostsee war von komplexen Biozönosen besiedelt, die sich aus Prokaryoten, Protisten und Metazoen zusammensetzten. Die integrierte Gesamtbiomasse im Meereis wurde von pennaten Diatomeen dominiert (33 %), diesen folgten zentrische Diatomeen (29 %), phototrophe Flagellaten (23 %), heterotrophe Bakterien (8 %), heterotrophe Flagellaten (7 %) und Metazoen (1 %). Nur zwei Metazoentaxa (Rotatoria, Crustacea) besiedelten das Meereis der Ostsee. Typische, für arktisches und antarktisches Meereis beschriebene, Metazoen wurden nicht vorgefunden. Dies ist wahrscheinlich auf die generelle Artenarmut der brackischen, nördlichen Ostsee zurückzuführen. Für die sympagischen Metazoen wurden, mit Hilfe allometrischer Funktionen, maximale potentielle Ingestionsraten berechnet. Diese waren gering und deuten an, dass die sympagischen Metazoen im Mittel nur 1,5 % der gesamten Algenbiomasse des Eises pro Tag konsumieren. Die Studie belegt, dass abiotische Faktoren (speziell die geringe Nährstoffverfügbarkeit) und nicht der Fraßdruck der heterotrophen Gemeinschaft die autotrophe Biomasse im brackischen Eis der Ostsee kontrollieren.

Polares Meereis: Die Arbeiten in den Polargebieten befassten sich mit der Quantifizierung von TEP und der Abschätzung der Relevanz von TEP für den Stoffumsatz im Meereis. Die Arbeiten in der Framstraße (Arktis) konzentrierten sich auf die vertikale Verteilung von TEP in neugebildeten, einjährigen und mehrjährigen Meereis. Zum ersten Mal wurden dabei exopolymere Partikel über die gesamte Eisdicke arktischen Meereises quantifiziert. Die medianen TEP-Konzentrationen in den verschiedenen Meereistypen (3,17–4,89 $\times$ 10^6 Partikel l^{-1} und 4,6–6,9 cm^2 l^{-1}) waren wesentlich höher als die medianen Konzentrationen im Untereiswasser

($0{,}56 \times 10^6$ Partikel l^{-1} und 0,6 cm^2 l^{-1}). Die höchsten TEP-Konzentrationen wurden im Inneren des Meereises gefunden. Die TEP-Konzentration war signifikant mit der Konzentration der pennaten und zentrischen Diatomeen, der Chlorophyll *a*-Konzentration und mit der Gesamtbakterienzahl korreliert. Die hohen TEP-Konzentrationen in den internen Eishorizonten sind vermutlich auf die extremeren Umweltbedingungen im Inneren der Meereisschollen zurückzuführen. Die Anzahl der TEP-Partikel war negativ mit der Größe der TEP-Partikel korreliert. TEP im Eis und Untereiswasser zeigten distinkte Größenspektren, die aufgrund des hohen Anteils relativ großer Partikel von üblichen Größenspektren pelagischer Studien abweichen.

In der Antarktis wurden die für arktisches Meereis beschriebenen Untersuchungen fortgeführt. Die TEP-Konzentrationen im antarktischen Meereis waren extrem hoch und zeigten eine große Spannbreite (10,22–260,45 $\times 10^6$ Partikel l^{-1} bzw. 3,4–92,1 cm^2 l^{-1}). Die medianen TEP-Konzentrationen im antarktischen Meereis (50,16 $\times 10^6$ Partikel l^{-1} bzw. 21,3 cm^2 l^{-1}) waren eine Größenordung höher als die Werte im Untereiswasser (3,56 $\times 10^6$ Partikel l^{-1} bzw. 1,0 cm^2 l^{-1}). Die TEP-Größenspektren im Eis und Untereiswasser spiegelten die Ergebnisse der arktischen Studie wider. Sie zeigten flache Steigungen, die eine relativ hohe Anzahl größerer Partikel indizieren. Die Form der TEP-Größenspektren deutet auf einen speziellen Bildungmodus von TEP innerhalb des Meereises hin, der z.B. durch die Produktion von Schleimhüllen durch sympagische Organismen und / oder durch spezielle physikalische Charakteristika (hohe Scherungsraten, große innere Oberfläche) des Habitates beeinflußt wird. In den antarktischen Proben wurde zusätzlich die Besiedlung der TEP durch Bakterien ermittelt. Die mediane TEP-Besiedlung (angegeben als Prozent der Gesamtbakterienzahl) im Untereiswasser lag bei 1,9 %, während im Eis ein wesentlich höherer Anteil (14,8 %) der Gesamtbakterienanzahl TEP-assoziiert vorlag.

Ein Vergleich der Abschätzung der TEP-Produktion durch sympagische Bakterien und durch sympagische Diatomeen deutet daraufhin, dass Diatomeen sowohl im arktischen als auch im antarktischen Meereis die Hauptproduzenten von TEP sind.

Abschätzungen des integrierten TEP-Kohlenstoffes zeigen, dass dieser zwischen 14 und 32 % (Mittelwert: 23 %) zum integrierten partikulären organischen Kohlenstoff (POC) arktischen und antarktischen Meereises beiträgt. Die integrierten POC-Werte zeigten eine Spannbreite von 38,8 bis 2808,9 mg C m^{-2} in der Arktis und von 437,3 bis 3207,4 mg C m^{-2} in der Antarktis. Die Daten zeigen, dass TEP ein wesentlicher Bestandteil arktischen und antarktischen Meereises ist, der in bisherigen Studien weitgehend vernachlässigt wurde. Die möglichen Auswirkungen hoher TEP-Konzentrationen auf die Struktur des sympagischen Nahrungsnetzes und den Stoffumsatz im Meereishabitat werden diskutiert.

1 General introduction

Sea ice is an important structural element of polar marine ecosystems, but also in the Baltic, Caspian and Okhotsk Seas (Horner et al. 1992, Thomas and Dieckmann 2002). At its maximum, sea ice covers 13 % of the earth's surface, making it an important biome encompassing a similar area as deserts or tundra systems (Lizotte 2001). The sea-ice canopy greatly modifies the exchange of energy and material between the atmosphere and the sea (e.g. Wettlaufer 1991, Rahm et al. 1995, Haapala and Leppäranta 1997). Sea ice reduces the amount and quality of light in the water column and thus, strongly influences the onset and composition of pelagic spring blooms (Maykut 1985, Haecky et al. 1998).

The largest expanse and seasonal variation of sea ice occurs in the Southern Ocean which, during minimum extent (March), is covered by approx. 4×10^6 km^2 and during maximum extent (September) by approx. 20×10^6 km^2 (e.g. Zwally et al. 1983, Fig. 1.1). In the Arctic, sea-ice cover is seasonally less variable ranging between approx. 7×10^6 km^2 during minimum (September) and 14×10^6 km^2 during maximum extent in March (Maykut 1985). Most of the Antarctic sea ice is less than one year old (so-called first-year sea ice) and less than 1 m thick (Spindler 1990, 1994). Arctic sea ice in contrast shows a higher percentage of multi-year sea ice (= sea ice that survived at least one summer's melt season) and is generally thicker than 2 m (Spindler 1994). During average maximum extent in the Baltic Sea (March), ice covers the Bothnian Bay, parts of the Bothnian Sea and the Gulf of Finland (Strübing 1995, Leppäranta et al. 1998). On average approx. 45 % of the Baltic sea surface are ice-covered during winter (Leppäranta et al. 1998). The Baltic sea-ice canopy shows a high temporal and spatial variability.

When sea ice forms, a number of physical processes occur, which are basically understood. Under turbulent conditions, as occurring in wave zones, ice formation follows the so-called pancake-cycle (Lange et al. 1989, Lange and Eicken 1991): The freezing of seawater leads to the accumulation of large ice crystals (frazil ice) in the upper parts of the water column and the formation of so-called grease ice on the sea surface. Further freezing results in the consolidation of the grease ice and, under turbulent conditions, in the formation of pancake-like ice floes. Under calm conditions, so-called nilas ice forms directly on the surface. Pancake ice and nilas can reach thicknesses of several decimetres on time scales of days. Rafting of pancake ice and young sea ice may increase ice thickness very fast and is important for ice growth especially in the Southern Ocean.

The knowledge on sea-ice biota dates back to the first expeditions to polar seas, when sailors observed brownish or greenish discoloured ice floes. First investigations showed that the colouration was caused by high abundances of microalgae, and a period of the detailed taxonomic description of the algae started (historical review by Horner 1985b). Sea-ice research was long hindered by the ice itself and a new era of investigations started as recently as about two decades ago, when ice-going research vessels allowed access and sampling in heavily ice-covered seas.

During ice formation planktonic and detrital material are harvested from the upper water column and incorporated into the sea ice by various physical processes (Ackley 1982, Garrison et al. 1983, Shen and Ackermann 1990, Spindler 1994). After a short time needed to adapt to the new environment some organisms start growing and develop so-called sympagic communities, consisting of all major organism groups like viruses, bacteria, protists and metazoa (Horner 1985a, Horner et al. 1992, Gradinger 2002). The actual habitat of the organisms is a partially interconnected three-dimensional network of brine-filled channels constituting 1–30 % of the ice volume (Weeks and Ackley 1982, Weissenberger et al. 1992, Krembs et al. 2001). The brine volume is a function of ice temperature and ice bulk salinity (Frankenstein and Garner 1967, Leppäranta and Manninen 1988). The sympagic organisms are adapted to the environmental conditions in the brine channels and can use brine channel walls as sites for attachment, locomotion and grazing (Gradinger and Ikävalko 1998, Krembs et al. 2000). When the ice melts the sea ice derived material is released to the water column (Gradinger et al. 1999), where former sea-ice algae either continue to grow in the surface layer or are subject to elimination by sinking to greater depths (Carey 1987, Smith and Sakshaug 1990, Riebesell et al. 1991, Fortier et al. 2002).

Ice algal production contributes between 10–30 % to overall primary production in Arctic and Antarctic ecosystems (Legendre et al. 1992, Arrigo et al. 1997, Gosselin et al. 1997). The contribution is less in the

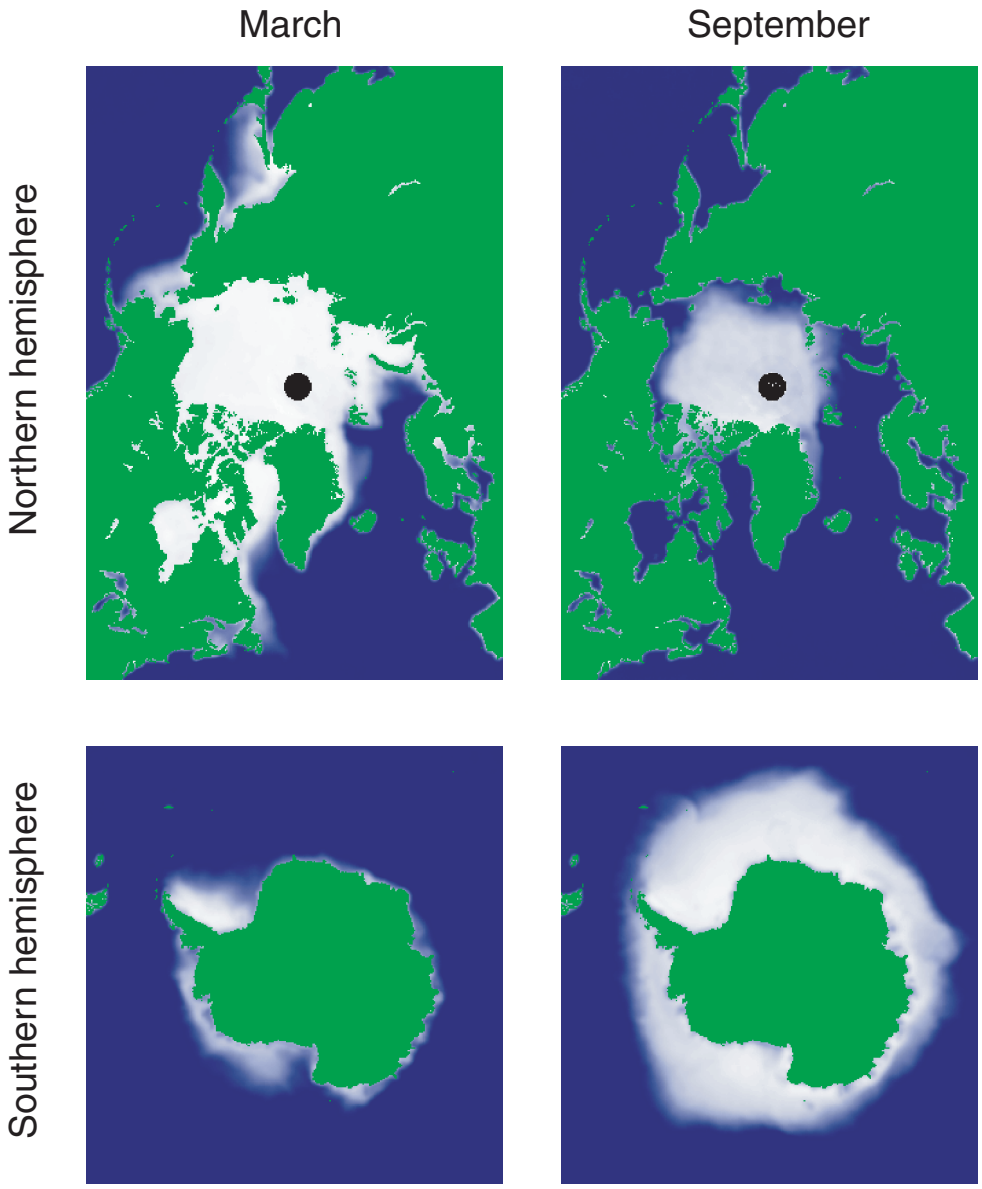

Fig. 1.1: Sea-ice distribution in March and September for the northern and southern hemisphere (monthly averages: 1978–1991). Modified after U.S. Geological Survey.

Baltic Sea, where ice algae production accounts for only approx. 1 % of total annual primary production due to the short ice-covered season (Haecky and Andersson 1999).

Most of the studies focused on the sea-ice algae and abiotic factors controlling primary production within the sea ice. Except for bacteria, relatively little is known about the heterotrophic organisms and the detrital component of the sea-ice assemblages.

Recent studies investigated the metazoan biomass and grazing impact in Arctic and Antarctic sea ice and give controversial results regarding the importance of metazoan grazing on primary producers and ice algae standing crop (Gradinger 1999a, Gradinger et al. 1999, Nozais et al. 2001). Norrman and Andersson (1994) observed high metazoan abundances in Baltic sea ice and assumed that metazoan grazing might be important in the Baltic sea-ice communities. However, it still remained unclear to which extent abiotic versus biotic factors control ice algal accumulation in the brackish Baltic sea ice.

Furthermore, there is currently substantial interest in the role of extracellular polymeric substances (EPS) in aquatic environments in general. In benthic habitats, especially pennate diatoms have been shown to produce copious amounts of EPS which serve the or-

ganisms in various functions, e.g. in adhesion, locomotion, biogenic habitat stabilisation as well as in protection against harsh environmental conditions (e.g. Hoagland et al. 1993, Cooksey and Wigglesworth-Cooksey 1995, Smith and Underwood 1998, Wetherbee et al. 1998). In the pelagic realm high concentrations of EPS consisting mainly of polysaccharides have been observed during and subsequent to diatom blooms (Passow et al. 1994, Leppard 1995). Alldredge et al. (1993) observed pelagic particles and gels formed of EPS and defined a new class of particles based on their staining capacity with the cationic dye Alcian Blue, which are referred to as transparent exopolymer particles (TEP). Several studies showed that TEP are important in the aggregation of diatom blooms, provide the matrix of marine snow and have a large influence on the particle flux in the ocean (Passow and Alldredge 1994, Mari and Kiørboe 1996, Engel and Schartau 1999, Passow et al. 2001). Many of the dominant ice algae such as pennate diatoms produce extensive extracellular mucilages and large quantities of exopolymeric substances have been suggested to occur within the sea-ice habitat (McConville 1985, Riebesell et al. 1991, Gradinger and Nürnberg 1996, Herborg et al. 2001). However their distribution and importance for the sea-ice habitat are largely unknown.

Thus, the major aims of the present study are:

- to describe the structure and composition of the community in the brackish Baltic sea ice
- to identify the importance of abiotic versus biotic factors in the control of algal accumulation in brackish Baltic sea ice
- to describe the concentration, vertical distribution and size frequency of transparent exopolymer particles (TEP) in different types of Arctic and Antarctic sea ice
- to understand the importance of sea-ice TEP and its implications for the sympagic organisms and the ice-covered ocean

This thesis combines results from three ice-covered seas of the world's oceans: the Baltic Sea, the Fram Strait (Arctic) and the Bellingshausen Sea (Antarctica). The results gathered during the different expeditions are presented in separate chapters. Chapter 2.1 deals with the abundance, biomass and composition of the Baltic sea-ice community. Chapter 2.2 summarises the occurrence and characteristics of TEP in Arctic sea ice of varying ages. Chapter 2.3 presents the results of an investigation of TEP and its bacterial colonisation in Antarctic sea ice. Chapter 3 discusses and compares the different habitats and their communities.

2 Chapters

2.1 Abundance, biomass and composition of biota in Baltic sea ice and underlying water (March 2000)

2.1.1 Introduction

In the Baltic Sea, ice formation normally starts in the northern Bothnian Bay in late November. The sea-ice cover extends southwards along the coastlines, with areas at the open sea freezing about one month later than coastal sites at corresponding latitudes (Leppäranta et al. 1998). On average, maximum ice extent is reached in March, when ice covers the Bothnian Bay, parts of the Bothnian Sea and the Gulf of Finland. The duration of the ice season is 4–6 months in the Bothnian Bay, 2–4 months in the Bothnian Sea and 1–3 months in the Gulf of Finland (Strübing 1995, Leppäranta et al. 1998).

Baltic sea ice forms generally according to the same principles described for the open ocean and consists of a mixture of ice crystals and brine (Leppäranta et al. 1998). However, the low salinities of the brackish environment result in small brine volumes compared to sea ice forming in high saline waters. Similar to Arctic and Antarctic sea ice, the brine filled interstices of Baltic sea ice are the habitat for diverse communities consisting of bacteria, cyanobacteria, protists and metazoa forming the so-called sympagic communities (e.g. Horner et al. 1992, Norrman and Andersson 1994, Ikävalko 1998a). In general, sympagic communities occur in the surface, the interior and in the bottom parts of sea ice (Horner et al. 1992, Gradinger 1999b). In the Baltic Sea, sympagic communities have been reported mainly from the interior horizons of the ice (Norrman and Andersson 1994, Ikävalko and Thomsen 1997, Ikävalko 1998a, Kaartokallio 2001).

Generally, abiotic factors, i.e. temperature, brine salinity, nutrient availability and light are considered to control ice algal growth and have been used to explain spatial and temporal distribution of the sea-ice autotrophs (Kirst and Wiencke 1995, Cota et al. 1991). Algal growth in annual Arctic sea ice is light limited at the early stage and nutrient limited at the later stage of the spring ice algal bloom (Gosselin et al. 1990, Cota et al. 1991). Haecky and Andersson (1999) report light-limitation for the early stage and nutrient (particularly phosphate) limitation for the bloom stage (mid of April) of the ice algal community in the Bothnian Bay. In the northern Baltic Sea, the contribution of ice algal production to total production supposedly accounts for approx. 10 % for the ice covered season and for 1 % for the annual primary production (Haecky and Andersson 1999).

With the exception of bacteria, the heterotrophic component of the sea-ice community has received much less attention than the autotrophic. Studies investigating the metazoan biomass and grazing impact in polar sea ice give controversial results regarding the importance of metazoan grazing on primary production and ice algae standing crop (Gradinger et al. 1999, Gradinger 1999a, Nozais et al. 2001). Norrman and Andersson (1994) observed high abundances of rotifers in sea ice of the northern Baltic Sea and concluded that these organisms are important consumers of ice algae. However, the information on metazoans of sea-ice communities is scarce and particularly poor for the Baltic Sea area.

It still remains unclear to which extent physical, chemical and biological parameters control the algal accumulation in Baltic sea ice throughout the ice season. In order to contribute to this discussion, this chapter presents the results of an interdisciplinary effort on the physical, chemical and biological properties of Baltic sea ice. For the first time biomass data for the entire community (bacteria, protists and metazoa) in Baltic sea ice are presented.

2.1.2 Material and methods

Site and sampling

Ice and under-ice water samples were collected in two areas in March 2000 (Fig. 2.1.1). Free-drifting pack ice (Sts. 67, 68 and 69) was sampled in the southern Bothnian Bay at about 64°07' N, 22°22' E during an expedition on RV *Aranda* (cruise 2000 / 3). These offshore stations were approximately 8 km apart from each other. Additional material was collected at three nearshore fast ice stations (Sts. 74, 77 and 81) in three dif-

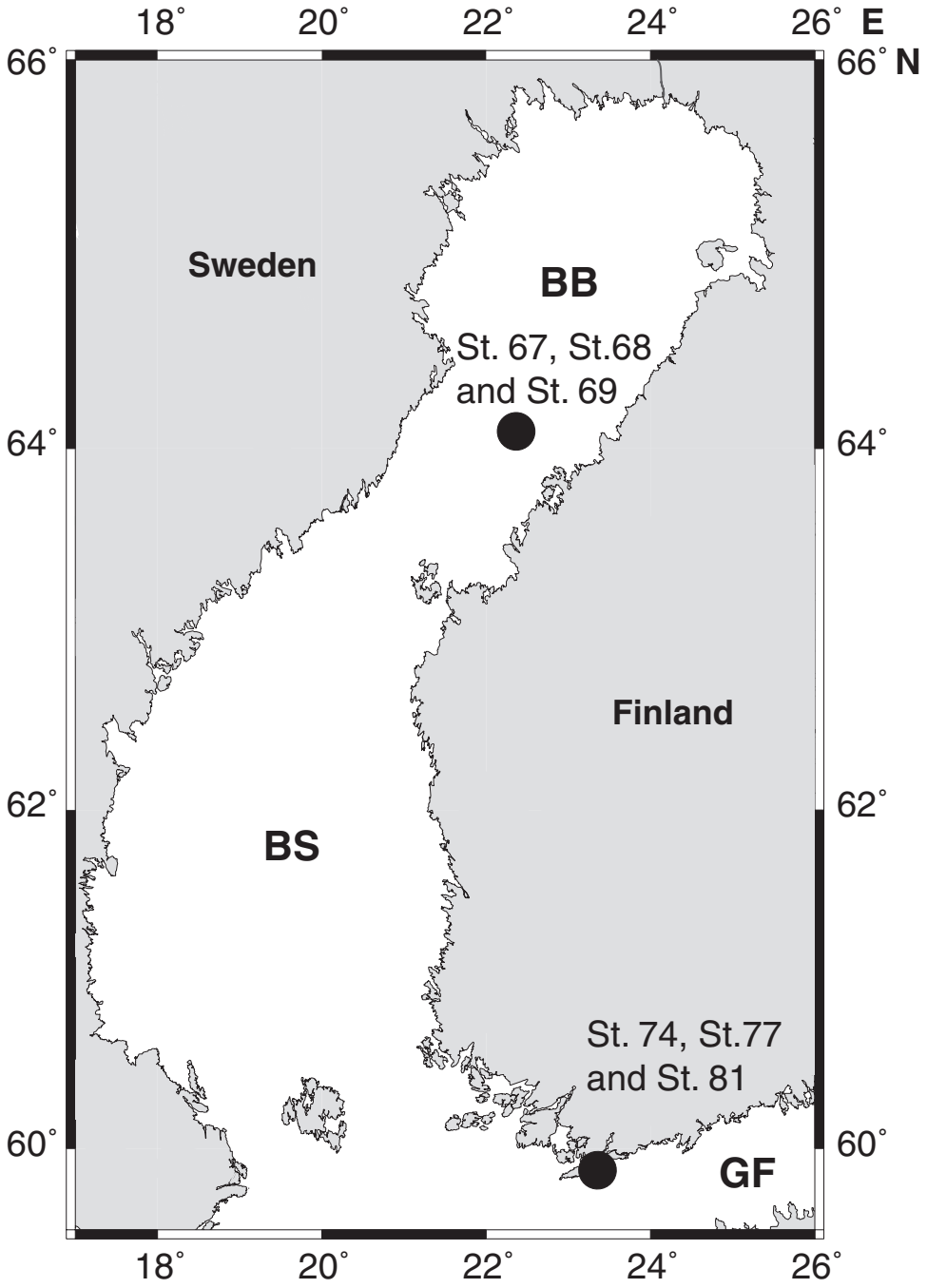

Fig. 2.1.1: Station map. Station number = day of the year. BB = Bothnian Bay, BS = Bothnian Sea and GF = Gulf of Finland

ferent bays (Santala Bay, Broarsbukten Bay, Predium Bay) in the vicinity of Tvärminne Zoological Station (59°50' N, 13°15' E) at the entrance of the Gulf of Finland.

Snow thickness was measured with a ruler at each sampling site prior to coring. At each station five ice cores (named A–E) were collected with a SIPRE-type ice auger (9 cm internal diameter) within an area of 1 m^2. Two complete cores (A, B) were sealed in clean plastic tubing and kept frozen (–20 °C) for later analysis of ice structure and stable oxygen isotopic composition. The remaining three ice cores were cut immediately into 1–10 cm sections, transferred into acid-washed polyethylene boxes and transported to the laboratory for analysis of salinity, inorganic nutrients (NO_3, NO_2, NH_4, PO_4, $Si(OH)_4$), pigments (chlorophyll *a* (chl *a*), pheopigments (pheo)) and for microscopical investigations. Under-ice water was sampled using a 10 m long polyethylene tube (4 cm internal diameter) with a valve at one end. The unequipped end

of the tube was lowered into the water with the valve open. At a depth of 5–10 m the valve was closed and the tube with the trapped water was retrieved. These integrated water samples were transferred to acid-washed containers and transported to the laboratory for further analysis.

Ice structure and stable oxygen isotopic composition

The ice structure of core A was determined by thin section analysis (Kawamura et al. 2001). Based on ice crystal size and orientation two stratigraphic units were distinguished: granular ice and columnar ice. Ice core B was cut into sections according to results of the structural analysis of core A. Sections were melted and used for the determination of $\delta^{18}O$ with a mass spectrometer (Finnigan MAT Delta E). Based on the combined structural and isotopic characteristics, ice cores were divided into three categories: snow ice, granular ice and columnar ice (Kawamura et al. 2001).

Temperature, salinity, nutrients and pigments

Ice temperature was measured with a Testo720-thermometer immediately after coring from small holes drilled in the core in 2–10 cm intervals. For the analysis of inorganic nutrients and the determination of pigments, ice core sections were melted in the dark at 4 °C. Inorganic nutrients (NO_3, NO_2, NH_4, PO_4 and $Si(OH)_4$) were determined using standard seawater procedures (Grasshoff et al. 1983). Salinity of melted ice and water samples was measured with a WTW LF 191 conductometer. For the determination of chlorophyll *a* (chl *a*) and pheopigment (pheo) concentrations, samples were filtered onto Whatman GF / F filters and analysed fluorometrically with a Turner Designs 10-AU digital fluorometer according to Arar and Collins (1997). Brine salinity was calculated as a function of ice temperature (Assur 1958); brine volume as a function of temperature and ice bulk salinity (Leppäranta and Manninen 1988). Nutrient concentrations in the ice core segments were normalised to the under-ice water salinity of the same station (e.g. Gleitz et al. 1995, Mock et al. 1997).

Abundance and biomass of bacteria, protists and metazoans

Ice core sections for the determination of organism abundance and biomass were melted by addition of 0.2 µm prefiltered seawater at 4 °C (Garrison and Buck 1986). Two subsamples (5–100 ml) of each melted ice and water sample were fixed with borax-buffered formalin (1 % final concentration). The first subsample (5–30 ml) was filtered onto a black 0.2 µm polycarbonate filter and stained with DAPI (Porter and Feig 1980). Filters were mounted and examined with a Zeiss Axiovert 135 epifluorescence microscope for bacterial and pico- and nanosized flagellate abundance and biomass. Estimates of bacterial biovolume were determined with a New Porton G12 grid (Graticules Ltd., UK) at a final magnification of 1000×. Bacterial biovolume was converted into bacterial carbon using the formula $CC = 88.6 \times Vol^{0.59} \times 1.042$ (Simon and Azam 1989), where CC (fg) and Vol (μm^3) are the average carbon content per cell and the average cell volume, respectively. Autotrophic (cells with chlorophyll autofluorescence) and heterotrophic pico- and nanosized flagellates were counted in four size classes (< 2 µm, 2–5 µm, 5–10 µm and 10–20 µm) at magnifications of 400–1000× on the same filter as the bacteria. The second subsample was used for the counting of protists > 20 µm (except ciliates) in Utermöhl chambers (Utermöhl 1958). Calculation of the biomass of protists < 20 µm and protists > 20 µm followed the recommendations of the Baltic Marine Environment Protection Commission (1988).

The rest of the indirectly melted ice and water samples (2000 ml) were poured through a 20 µm mesh and the concentrated metazoans were fixed with borax-buffered formalin (4 % final concentration). Metazoan samples were examined under a dissecting microscope equipped with a video camera. Specimens were videotaped and the size of the metazoans was measured using image analysis procedures (Friedrich 1997). Biovolume and biomass estimates of the collected rotifers and nauplii were calculated from length and width measurements as follows:

- Rotifers:

$V = 0.26 \times L \times B^2$, where V = volume ($\mu m^3$), L = length (µm) and B = width (µm). The volume was converted to wet weight assuming a density of seawater of 1.028 (salinity = 35 psu, temperature = 0 °C) (Gradinger et al. 1999). Wet weight was converted to carbon assuming a carbon content of 8 % of the wet weight (Beers and Stewart 1970).

- Nauplii:

The wet weight (WW; µg) of the nauplii was calculated according to Gradinger et al. (1999) with $WW = L \times B^2 \times 360\ \mu g\ mm^{-3}$, where L = length (mm)

and B = width (mm). The dry weight was estimated as 22.5 % of wet weight (Gradinger et al. 1999) and carbon content as constituting 40 % of dry weight (Feller and Warwick 1988).

In box plots, the total data range, the 25–75 % quartile range and the median are shown. Single data points were marked as outliers when they exceeded a value of V = UQ + 1.5 × IQD (UQ is the upper quartile, IQD is the interquartile distance).

2.1.3 Results

Abiotic parameters

Stations 67, 68 and 69 were situated in the southern Bothnian Bay at sites with water depths between 75 m and 104 m, whereas stations 71, 74 and 81 were located in nearshore environments (water depths: 7–9 m) at the entrance of the Gulf of Finland (Fig. 2.1.1). Snow thickness on the drifting pack ice floes (diameter: > 1 km) in the Bothnian Bay ranged between 5 cm and 6 cm, whilst the fast ice sampled in the coastal area was free of snow. Ice thickness was similar in both areas with 22–30 cm and 23–27 cm in the Bothnian Bay and the nearshore stations, respectively. Based on the stable oxygen isotope and thin section analysis, ice cores were divided into three successive structural classes (Fig. 2.1.2). The upper part of the ice consisted of so-called snow ice with a granular texture and minimum $\delta^{18}O$ values indicating the atmospheric origin of this part of the ice (Fig. 2.1.2a). The thickness of the snow ice varied between 3.9 cm and 10.0 cm and contributed between 16.6 % and 33.3 % of the total ice thickness. Below snow ice an intermediate ice layer (12.5–57.4 % of total ice thickness) occurred with higher $\delta^{18}O$ values, indicating the seawater origin for this ice type. It is referred to as granular ice. The lowermost 25.9–62.5 % of the ice showed a columnar structure (Fig. 2.1.2b).

A distinct difference in bulk salinity was observed in the sea-ice samples. Median ice bulk salinities in the Bothnian Bay (S = 0.5) were significantly higher than ice salinities at the nearshore stations (S = 0.3) (Mann-Whitney U-test: p = 0.0051). Vertical gradients also differed with higher salinities (S = 0.5–1.0) in the surface decimetres of the ice floes from the Bothnian Bay (Fig. 2.1.3). Under-ice water salinities were higher in the Bothnian Bay (range: 3.4–3.5) than at the coastal sites (range: 2.6–3.2), which were influenced by melting sea ice.

Ice temperature (data not shown) varied between −3.1 °C and −0.2 °C (median: −0.5 °C). Minimum temperatures were observed in the upper ice-horizons in the Bothnian Bay; ice temperatures were higher at the nearshore ice stations. Brine salinities calculated as a function of ice temperature ranged between 3.6 and 54.2 (median: 10.1). The relative brine volumes were

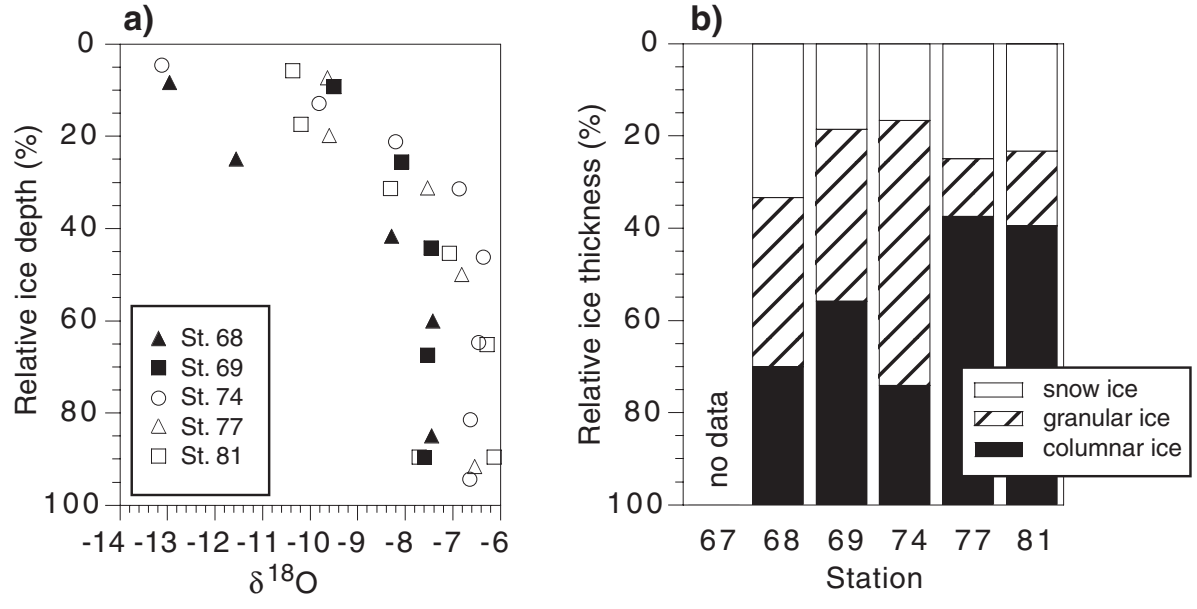

Fig. 2.1.2: a) Vertical distribution of $\delta^{18}O$-values (given against SMOW in per mil) from 5 stations. **b)** Vertical distribution of textural ice classes (for definitions see text)

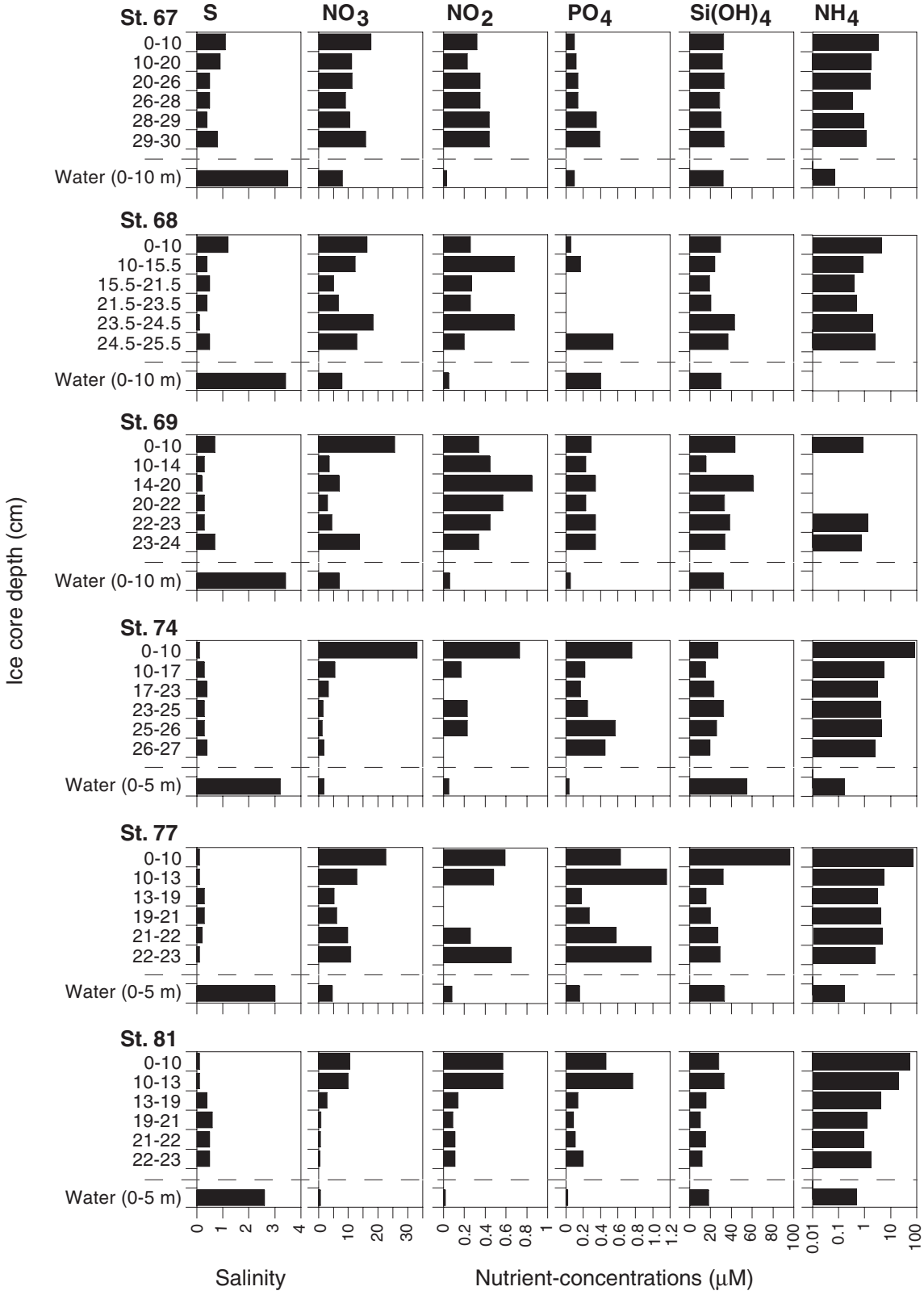

Fig. 2.1.3: Vertical distribution patterns of salinity, nitrate (NO_3), nitrite (NO_2), phosphate (PO_4), silicate ($Si(OH)_4$) and ammonia (NH_4) in sea ice and values for the underlying water. Note logarithmic scale for NH_4. All nutrient data from the ice core sections are normalised to the salinity of the under-ice water of the same station. NO_2, PO_4 and NH_4 were measured in all samples, but concentrations were below detection limits in few cases.

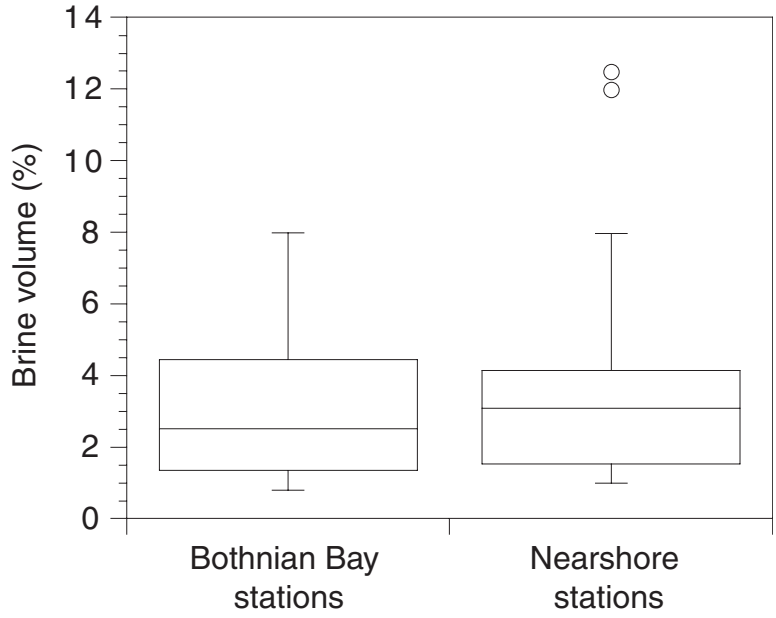

Fig. 2.1.4: Box plots for brine volumes (calculated according to Leppäranta and Manninen 1988) in the sea-ice segments of the Bothnian Bay and at the nearshore stations

small at both sampling sites (Fig. 2.1.4). Volumes ranged from 0.8–12.5 %, the median value for all stations was 3 %.

Vertical profiles of nutrient concentrations in the ice (normalised to under-ice water salinity of the same station) are shown in Fig. 2.1.3. NO_3 concentrations in the ice varied between 0.6 µM and 33.0 µM with maximum concentrations generally occurring in the uppermost horizons of the ice cover. Maxima at the ice-atmosphere interface were also observed for NH_4 concentrations. The median NH_4 concentration in sea ice was significantly higher at the nearshore stations (5.2 µM) than in the Bothnian Bay (1.2 µM, Mann-Whitney U-test: $p < 0.0001$). NO_2 and PO_4 concentrations in the ice and under-ice water ranged from below the detection limit to 0.8 µM and 1.1 µM for NO_2 and PO_4, respectively. Molar N / P ratios in the ice showed a wide range (10–373). Nutrient concentrations in the under-ice water were generally lower than those measured in the ice. The N / P-ratio of the under-ice water ranged from 19 to 141 in the Bothnian Bay and from 38 to 55 at the nearshore stations.

Chl *a* concentrations in the ice varied between 0.1 µg l^{-1} and 15.4 µg l^{-1} and peaked at the bottom as well as in the interior of the ice (Fig. 2.1.5). Concentrations in the Bothnian Bay ice (median: 0.8 µg l^{-1}) were significantly lower than concentrations in the nearshore ice (median: 1.9 µg l^{-1}) (Mann-Whitney U-test: $p = 0.0065$). Except for the uppermost layers of the ice cover, chl *a* concentrations in the ice exceeded those in water at five of six stations (Fig. 2.1.5). At station 74 high concentrations occurred also in the under-ice water. Integrated chl *a* concentrations of sea ice (range: 0.09–0.54 mg m^{-2}) were considerably lower than integrated water values (range: 2.10–22.50 mg m^{-2}, integration depth: 10 m at the Bothnian Bay stations and 5 m at the nearshore stations). Pheo / Chl *a* ratios varied between < 0.1 and 0.8. Water ratios exceeded ratios in the ice with the exception of station 67 (Fig. 2.1.5).

Abundance and biomass

Abundances of sympagic and planktonic biota consisting of bacteria, protists and metazoa are shown in Table 2.1.1. Crustaceans occurred only in snow and columnar ice, while all other taxa occurred in all structural ice classes. Total biomass (biomass of all taxa) was highest in the lowermost horizons of the ice cores with the exception of station 77, which had an internal biomass peak close to the sea-ice surface (Fig. 2.1.6). Total biomass in the Bothnian Bay ice ranged between 2.0 µg C l^{-1} and 311.8 µg C l^{-1} and was significantly lower than sea-ice biomass at the nearshore stations with a variation of 28.7–3349.5 µg C l^{-1} (medians: 30.6 µg C l^{-1} and 74.8 µg C l^{-1}, Mann-Whitney U-test: $p = 0.0026$). Integrated total

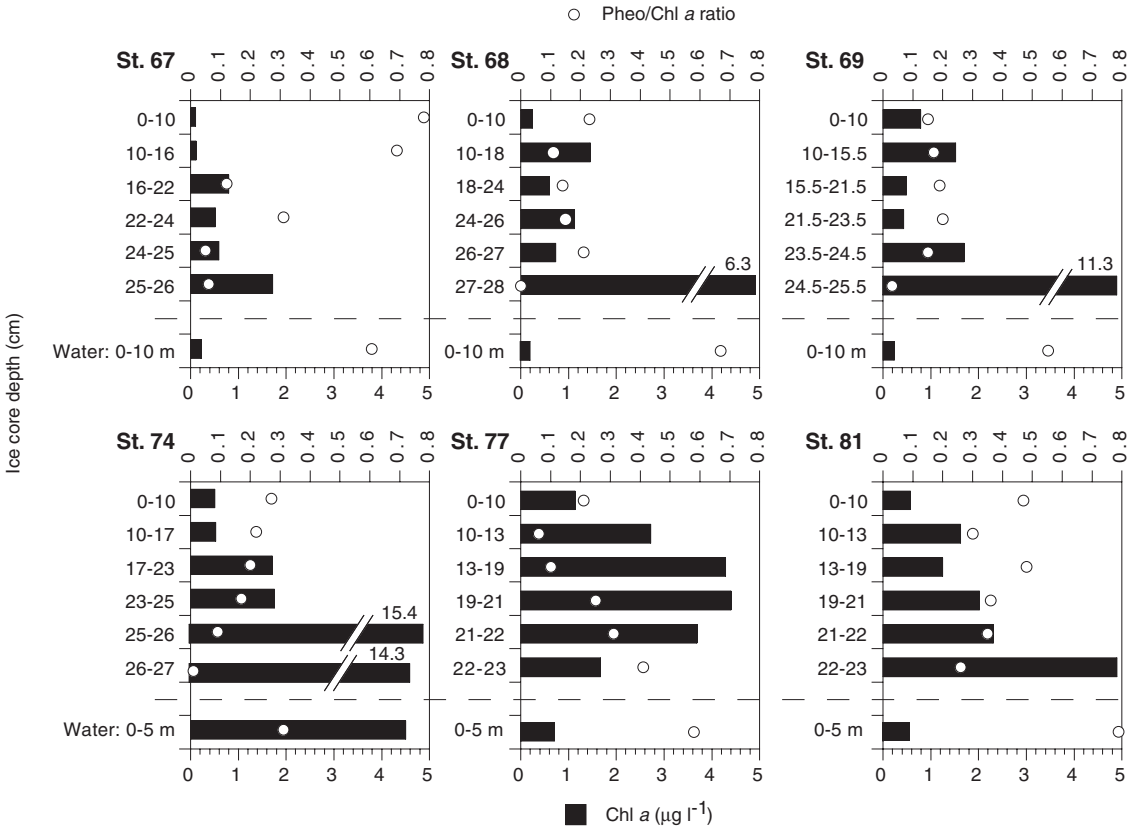

Fig. 2.1.5: Vertical distribution of chlorophyll *a* concentration (chl *a*) and the pheopigment / chlorophyll *a* ratio (= Pheo / Chl *a* ratio) in sea ice and underlying water

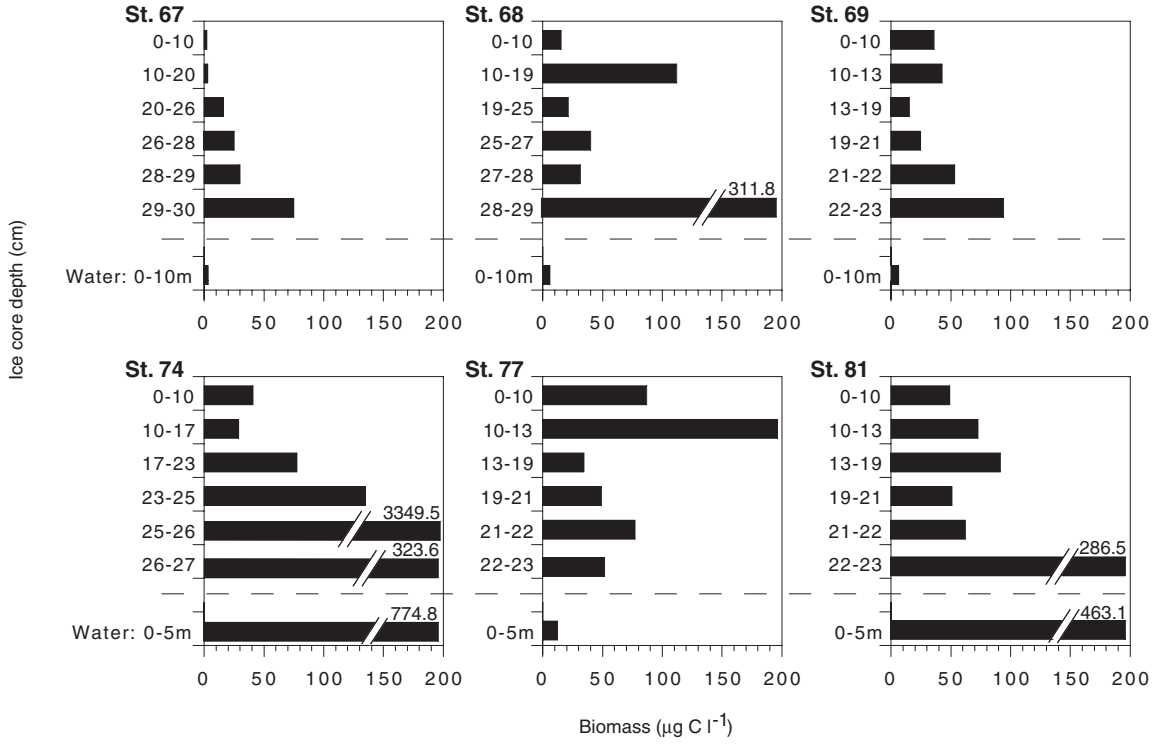

Fig. 2.1.6: Vertical distribution of total biomass of organisms in sea ice and underlying water

Table 2.1.1: Abundance and biomass values of different groups of organisms in sea-ice segments and underlying water (median values in parentheses)

	Ice		Water	
	Abundance	**Biomass**	**Abundance**	**Biomass**
Prokaryota	**(10^8 cells l^{-1})**	**(µg C l^{-1})**	**(10^8 cells l^{-1})**	**(µg C l^{-1})**
Heterotrophic bacteria	0.69–17.74 (2.09)	0.7–22.7 (3.6)	1.07–8.05 (3.51)	0.9–5.7 (3.6)
Cyanobacteria	0.0002–0.0152 (0.0016)	0.0–0.1 (< 0.1)	0.0009–0.0181 (0.0049)	0.0–0.1 (< 0.1)
Protista	**(10^6 cells l^{-1})**	**(µg C l^{-1})**	**(10^6 cells l^{-1})**	**(µg C l^{-1})**
Autotrophic nanoflagellates (< 20 µm)	0.03–1.30 (0.46)	0.7–27.0 (7.6)	0.03–0.78 (0.16)	0.2–5.2 (1.2)
Heterotrophic nanoflagellates (< 20 µm)	0.01–0.55 (0.17)	0.0–9.0 (2.0)	0.02–0.16 (0.05)	0.1–0.7 (0.2)
Autotrophic flagellates (> 20 µm)	0.00–0.36 (0.004)	0.0–126.6 (1.3)	< 0.001–0.03 (< 0.001)	0.0–14.6 (0.7)
Heterotrophic flagellates (> 20 µm)	0.00–2.29 (< 0.001)	0.0–325.9 (0.2)	< 0.001–0.001 (< 0.001)	0.0–6.6 (< 0.1)
Chlorophytes	0.00–0.01 (0.00)	0.0–0.2 (0.0)	0.00–0.02 (0.005)	0.0–0.4 (0.1)
Centric diatoms	0.00–1.41 (0.04)	0.0–194.3 (2.9)	< 0.001–3.97 (0.002)	0.1–733.2 (0.2)
Pennate diatoms	0.00–60.26 (0.05)	0.0–2963.5 (4.7)	< 0.001–0.11 (0.001)	0.1–7.4 (< 0.1)
Metazoa	**(organisms l^{-1})**	**(µg C l^{-1})**	**(organisms l^{-1})**	**(µg C l^{-1})**
Rotifera	0.0–194.1 (4.2)	0.0–1.1 (< 0.1)	2.0–32.0 (7.0)	< 0.1–1.0 (0.2)
Nauplii	0.0–149.3 (0.0)	0.0–6.2 (0.0)	1.0–11.0 (7.5)	< 0.1–4.3 (0.9)

biomass was lower in the Bothnian Bay sea ice when compared to the nearshore stations (Fig. 2.1.7). Integrated total biomass in the ice (range: 2.69–45.13 mg C m^{-2}) was identical to the biomass found in the upper 0.73–2.52 m of the water column in the Bothnian Bay and the upper 0.03–1.38 m of the water column in the coastal bays (range of the water biomass: 30.58–3834.28 mg C m^{-2}, integration depth: 10 m at the Bothnian Bay stations and 5 m at the nearshore stations).

Concerning biomass, dominating primary producers in both sea ice and under-ice water were diatoms. In sea ice, the contribution of pennate and centric diatoms to total integrated biomass of organisms was 9.6–70.6 % (average: 32.8 %) and 6.4–57.2 % (average: 28.8 %), respectively. *Achnanthes taeniata* Grunow, *Pinnularia* spec., *Fragilariopsis cylindrus* Grunow and *Nitzschia frigida* Grunow dominated the biomass of pennate diatoms in the sea ice. Dominating sympagic centric species were *Melosira arctica* (Ehrenberg) Dickie in the Bothnian Bay and *Chaetoceros* sp. at the nearshore stations. *Thalassiosira hyperborea* (Grunow) Hasle was found in high numbers in the sea ice at station 81. In under-ice water, biomass of centric diatoms exceeded that of the pennate taxa. In the water at stations 74 and 81 a bloom of *Skeletonema costatum* (Greville) Cleve occurred and contributed > 90 % to the total biomass (Fig. 2.1.7).

Autotrophic and heterotrophic flagellates showed important fractions of total integrated biomass in the sea ice and contributed 7.5–37.5 % (average: 22.7 %) and 1.6–16.9 % (average: 7.1 %), respectively. In the sea-ice samples, autotrophic flagellates > 20 µm were dominated by the dinoflagellate *Scrippsiella* sp.; the dominant heterotrophic flagellate was *Cryothecomonas armigera* Thomson Buck Bolt and Garrison. Compared to the ice habitat the relative biomass contribution of autotrophic and heterotrophic flagellates was low in the under-ice water with values of 0.6–20.3 % and 0.1–11.6 %, respectively. Dominant larger plank-

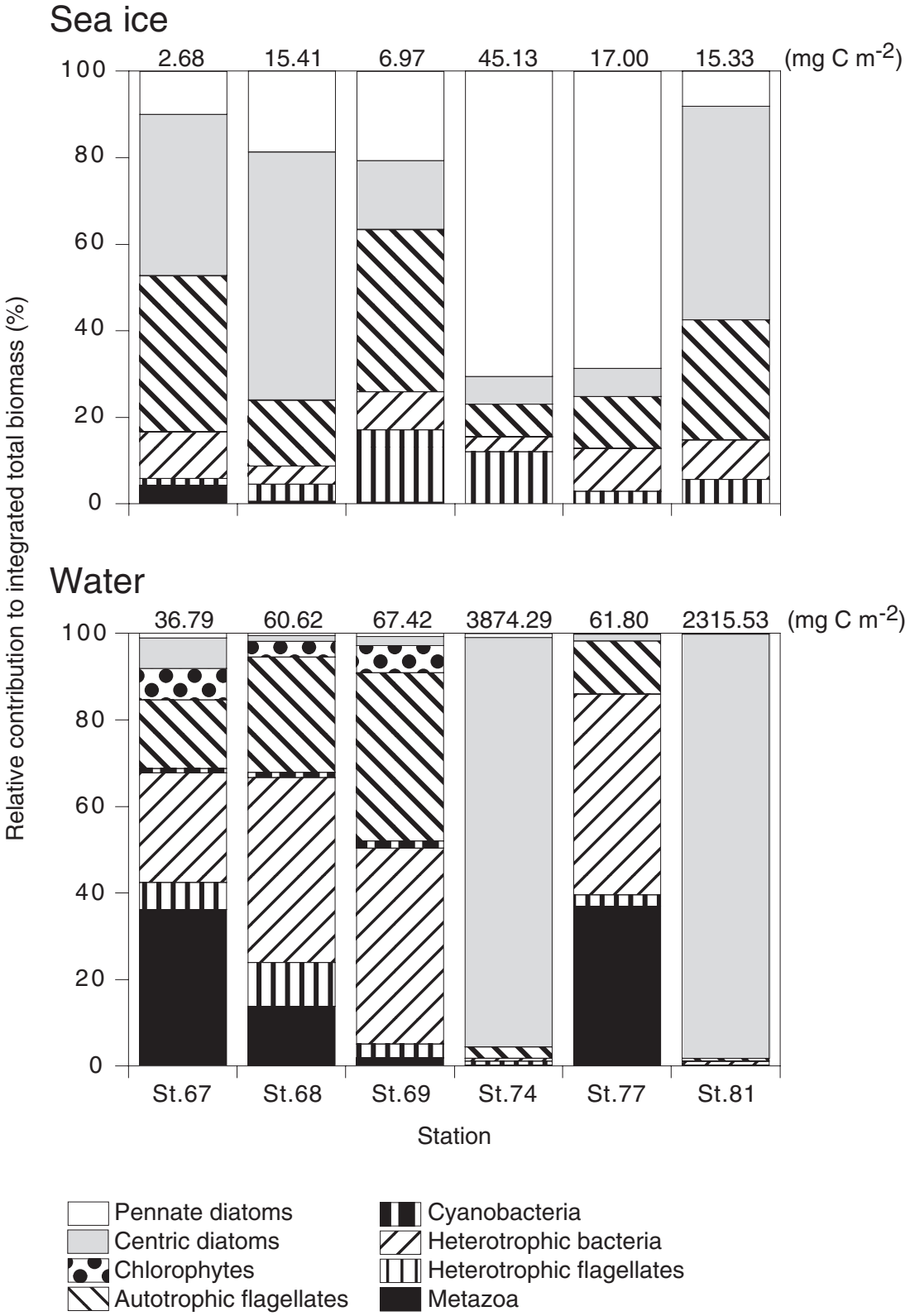

Fig. 2.1.7: Integrated total biomass and relative contribution of pennate diatoms, centric diatoms, chlorophytes, autotrophic flagellates, cyanobacteria, bacteria, heterotrophic flagellates and metazoa in sea ice and underlying water. Integration depth for sea ice: Station 67 = 30 cm, station 68 = 29 cm, station 69 = 23 cm, station 74 = 27 cm, station 77 = 23 cm and station 81 = 23 cm. Integration depth for water: Station 67, 68 and station 69 = 10 m, station 74, 77 and 81 = 5 m

tonic flagellates were the dinoflagellates *Scrippsiella* sp. and *Peridiniella catenata* (Levander) Balech. The chlorophyte *Monoraphidium contortum* (Thuret) Komárková-Legenerová contributed up to 7.3 % to the planktonic biomass in the Bothnian Bay.

Bacterial biomass in the ice varied between 0.7 µg C l^{-1} and 22.7 µg C l^{-1}. Median bacterial biomass was significantly higher in the ice of the nearshore stations (median: 8.2 µg C l^{-1}) compared to the Bothnian Bay (median: 2.2 µg C l^{-1}) (Mann-Whitney U-test: $p < 0.0001$). Integrated ice values (0.29–1.68 mg C m^{-2}) contributed 3.5–10.8 % (average: 7.7 %) to total integrated biomass of the ice cover. Integrated bacterial biomass in the under-ice water ranged between 9.33 mg C m^{-2} and 30.48 mg C m^{-2} (integration depth: 10 m at the Bothnian Bay stations and 5 m at the nearshore stations) and showed high relative portions of the planktonic biomass at the Bothnian Bay stations and at station 77 (Fig. 2.1.7).

Biomass of sympagic rotifers was low (0–1.1 µg C l^{-1}) and increased significantly towards the ice water interface (Spearman Rank-correlation: $\rho = 0.683$, $p < 0.0001$). Nauplii occurred only in the lowest two centimetres of the ice (columnar sea ice), with the exception of station 68 where nauplii were also found in the snow ice layer. Integrated metazoan biomass in the ice was < 0.01–0.12 mg C m^{-2} and contributed less than 4.3 % (average: 0.9 %) to the total integrated biomass. In the water, metazoan biomass varied between 1.30 and 22.80 mg C m^{-2} contributing 0.1–36.9 % to the total integrated biomass. Four rotiferan species were found in both ice and water samples: *Synchaeta* cf. *baltica* Ehrenberg, *Keratella quadrata quadrata* Müller, *K. cruciformis cruciformis* Levander and *K. cochlearis cochlearis* Gosse, with *Synchaeta* cf. *baltica* being the dominant species in the ice (up to 100 individuals l^{-1}) and water (maximum abundance: 32 individuals l^{-1}) at all stations.

Coccalean cyanobacteria occurred throughout the entire ice thickness, but biomass was close to the detection limit, not exceeding 0.1 % of integrated total biomass of the sea ice. Cyanobacteria added less than 0.1 % to 1.6 % to the total integrated biomass of under-ice water.

2.1.4 Discussion

Due to the late sea-ice formation in winter 1999 / 2000, sampled sea ice was relatively thin compared to the average maximum ice thickness (March / April) in the Bothnian Bay (50–80 cm) and Bothnian Sea (25–40 cm) (Mälkki and Tamsalu 1985). A distinctive feature of the sea ice was the high relative proportion of snow ice. As in other studies on Baltic sea ice high NO_3 and NH_4 peaks were always found in the snow ice layers, which suggests that atmospheric nitrogen accumulates in the upper parts of the sea ice (Norrman and Andersson 1994, Rahm et al. 1995, Kaartokallio 2001). Snow and snow ice layers are therefore assumed to have an important influence on the mass balance and nutrient dynamics in Baltic sea ice.

With the exception of the two lowermost centimetres of the ice cores taken at the nearshore stations 74 and 81, molar N / P ratios in both sea ice and under-ice water were higher than 16 (the Redfield-ratio) and indicate P-limitation of the sympagic and planktonic algae at both sites. These observations are in agreement with other studies in the Bothnian Bay and coastal sites of the Bothnian Sea, where P-limitation of sympagic and pelagic algal production is reported (Andersson et al. 1996, Haecky and Andersson 1999). The nearshore data contrast to observations of open water bodies in the Gulf of Finland which are generally N-limited (Wulff et al. 1986).

Potential ice algal pigment concentrations (calculated using the measured PO_4 data, a molar C / P ratio of 106 and a conversion factor of 1 mol C g^{-1} chl *a*, Redfield et al. 1963, Haecky et al. 1998) in the Bothnian Bay and at the nearshore stations ranged from 0.4 to 0.9 mg chl *a* m^{-2} and 0.5 to 0.6 mg chl *a* m^{-2}, respectively. These estimates are considerably lower than potential biomass calculations for coastal Bothnian Sea ice which range between 3.0 and 40.0 mg chl *a* m^{-2} (Haecky and Andersson 1999). Also the measured concentrations from both Bothnian Bay ice (0.09–0.30 mg chl *a* m^{-2}) and nearshore ice (0.26–0.54 mg chl *a* m^{-2}) are low compared to other Baltic sea-ice data which range between 1.5 and 10 mg chl *a* m^{-2} (Norrman and Andersson 1994, Haecky and Andersson 1999). Haecky and Andersson (1999) attributed high interannual changes of ice algal standing stock in the Bothnian Bay to large differences in the phosphate concentration trapped in the sea ice during its formation. In comparison to earlier studies, algal accumulation in the

Baltic sea ice was extremely low in the year 2000 and reflected the low phosphate concentrations in the under-ice water.

In addition to the interannual variability, seasonal variability affects the accumulation of Baltic sea-ice algae (Haecky and Andersson 1999) and is assumed to have influenced the results of this study. The early developmental stage of the sympagic and the pelagic communities in the Bothnian Bay is indicated by the low relative contribution of the integrated measured chl *a* concentrations to the integrated potential chl *a* concentrations (average contribution: 30 %). The nearshore stations in contrast showed a higher contribution (average: 75 %) and also elevated chl *a* concentrations in the interior of the ice cover, which generally occur during the time of the spring ice algae bloom (Huttunen and Niemi 1986, Norrman and Andersson 1994, Laamanen 1996, Ikävalko and Thomsen 1997, Haecky et al. 1998, Kaartokallio 2001). The difference in the algal succession can be attributed to differences in local climate and snow thickness. The presence of snow on the Bothnian Bay ice drastically reduced the transmittance of light. Snow cover of 5 cm and ice thickness of 30 cm reduced the down-welling irradiance in the PAR (= photosynthetic active radiation) range by approximately 50 % (Maykut 1985) and caused the light-limited low productive winter-stage of the sympagic and planktonic algal communities investigated in the Bothnian Bay. The different developmental stage of the sympagic and the pelagic communities in the Bothnian Bay and the Bothnian Sea is considered as the main reason for biomass differences between offshore pack ice and nearshore fast ice stations.

Despite its relatively high temperatures, the Baltic sea ice was characterised by low brine volumes, which are the result of the low bulk salinities of the brackish ice (Frankenstein and Garner 1967, Leppäranta and Manninen 1988). The median relative brine volume of 3 % is much smaller than average and median values reported for Arctic and Antarctic sea ice which range between 10–20 % (Weissenberger et al. 1992, Gradinger et al. 1999, Eicken et al. 1995). Small brine volumes in combination with a small internal ice-surface area have been discussed as limiting factors for sympagic communities (Maykut 1985, Krembs et al. 2000). In addition, low brine volumes result in small porosity and thus in a reduced permeability of sea ice (Freitag 1999). Golden et al. (1998) give a threshold of 5 % brine volume, below which sea ice becomes effectively impermeable for fluid transport. Since total accumulated biomass is mainly a function of nutrient-availability and import of nutrients from the water column into the ice is restricted by the low permeability, the small brine volume is considered as an important abiotic factor limiting ice algal accumulation in the low salinity regime of the northern Baltic Sea.

Studies from the Arctic and Antarctic indicate the wide adaptability of sea-ice algae and the highly variable response of their growth rates to changing salinities (Kirst and Wiencke 1995, Zhang et al. 1999). Growth of sea-ice algae has been demonstrated at salinities between 4 and 95 (Bartsch 1989, Zhang et al. 1999). Generally most ice algae are obviously more tolerant to decreasing rather than to increasing salinities (Kirst and Wiencke 1995). In this study brine salinities (range: 3.6–54.2) exceeded under-ice water salinities by a factor of approx. 1 to 20. It is therefore assumed that brine salinities, despite their relatively low absolute values, may limit growth of organisms adapted to the low salinities of the brackish environment in the northern Baltic Sea.

In agreement with earlier investigations, this study showed that Baltic sea ice serves as a habitat for a complex community consisting of prokaryotes, protists and metazoa (Huttunen and Niemi 1986, Norrman and Andersson 1994, Laamanen 1996, Ikävalko and Thomsen 1997, Haecky et al. 1998, Haecky and Andersson 1999). Dominant diatom species such as *Melosira arctica* and *Achnanthes taeniata* in both sea ice and under-ice water are part of the so-called Arctic relict-flora, a group of euryhaline species which mainly occur in the Arctic, but have been described also from the northern Baltic Sea (Lenz 1995). The sympagic metazoan community consisted only of rotifers and nauplii, which have been reported in earlier studies on Baltic sea ice (Norrman and Andersson 1994). Thus, on the basis of available observations, Baltic sea ice seems to lack the majority of metazoan taxa described for Arctic sea ice. It is assumed that this lack of metazoan taxa is most likely attributed to the reduced biodiversity in the brackish environment (Remane 1958, Lenz 1995).

Despite the peculiar characteristics of the ice habitat, protist species composition in the ice resembled that of the under-ice water, with the exception of some diatom species which were only found in the ice. Chengalath (1985) and Friedrich and De Smet (2000)

showed that benthic types dominate rotiferan abundance in Arctic fast ice, whereas pack ice is dominated by the generally planktonic genus *Synchaeta*. In contrast, both Baltic Sea pack and fast ice were dominated by planktonic protist and metazoan species and, despite shallow water depths, rather serve as additional temporal habitats for planktonic than for benthic organisms (Ikävalko and Thomsen 1997, Ikävalko 1998b).

Using general allometric equations (Moloney and Field 1989), the potential maximum ingestion rate of the metazoan community was estimated assuming a Q_{10}-value of 2 and a temperature of 0 °C. Metazoa in the ice and under-ice water consumed < 0.01–0.15 mg C m^{-2} d^{-1} (average: 0.07 mg C m^{-2} d^{-1}) and 2.04–11.42 mg C m^{-2} d^{-1} (average: 5.24 mg C m^{-2} d^{-1}), respectively. This corresponds to a daily consumption of < 0.1–6.8 % (average: 1.5 %) of the ice algal standing stock and a consumption of < 0.1–96.5 % (average: 5.2 %) of the planktonic algal standing stock. The relative consumption rates of the sympagic community meet estimates for the consumption of Arctic sea-ice meiofauna in northern Baffin Bay (average: 0.9 %) given by Nozais et al. (2001) and agree with results of Gradinger (1999a), who reported a low grazing impact by sea-ice meiofauna in Arctic and Antarctic sea ice.

The Baltic sea ice showed a very high proportion of autotrophic biomass (average: 84.3 %). Gasol et al. (1997) proposed that the ratio of heterotrophic biomass and autotrophic biomass (H / A-ratio) changes along gradients of autotrophic biomass and productivity. A high H / A-ratio indicates an "inverted biomass pyramid" associated with a high turnover of the autotrophic carbon pool and a high biomass specific activity of the autotrophs (Gasol et al. 1997). Gradinger et al. (1999) found a H / A ratio of 1.9 for Arctic pack ice, which is similar to the average of oligotrophic open ocean areas and indicates high P_B ratios of Arctic ice algal communities supporting high heterotrophic biomass. The sea ice observed in this study showed a H / A ratio of only 0.19, a value much smaller than the average (1.0) reported for coastal pelagic communities (Gasol et al. 1997). The ratio suggests that the ice algal community in this study was controlled bottom up, i.e. by abiotic factors, rather than by grazing. However, other characteristics of the sea-ice habitat like e.g. spatial refuges in the brine channel network (Krembs et al. 2000) might also influence the ratio and complicate the application of the pelagic model to the ice habitat. In the water, H / A ratios (range: < 0.1–6.1; average: 1.8) were very variable with extremely low values at stations 74 and 81 that showed planktonic blooms. H / A ratios of the planktonic communities in the Bothnian Bay (average: 1.7) were relatively high compared to the coastal average (1.0) and mirrored the low autotrophic biomass and the winter stage of these communities. During the winter stage autotrophic and heterotrophic metazoan biomass can be uncoupled due to e.g. special overwintering strategies of the heterotrophs (e.g. use of storaged lipids and / or reduced metabolism), which severely limit the use of this approach in this habitat. In addition, it is assumed that the H / A ratios of the underlying water were affected by sampling with the tube system and do not represent proper mesozooplankton biomass. Larger copepods were not found in the tube-samples, but contributed to the biomass in under-ice water (I. Werner, pers. comm.). Larger copepods can possibly escape when the tube is lowered, which would result in an underestimation of the H / A ratio.

The results demonstrate the regional and temporal variability in biomass of Baltic Sea pack and fast ice biota and in the underlying water. The data suggest that metazoan grazing in Baltic sea ice was low and did not control algal production. A combination of abiotic factors, especially the low permeability of the sea ice, rather than the heterotrophic component of the sea-ice biota, controlled the accumulation of autotrophic biomass in the brackish sea ice under investigation.

2.2 Vertical distribution of transparent exopolymer particles (TEP) in sea ice of the Fram Strait (Arctic) during autumn

2.2.1 Introduction

Exopolymeric substances (EPS) produced by microorganisms play important roles in various aquatic, porous and extreme environments. In benthic habitats especially pennate diatoms have been shown to produce copious amounts of EPS which serve the organisms in various functions, e.g. in adhesion, locomotion, biogenic habitat stabilisation as well as in protection against harsh environmental conditions (e.g. Hoagland et al. 1993, Smith and Underwood 1998, Wetherbee et al. 1998, Smith and Underwood 2000). In the plankton high concentrations of EPS consisting mainly of polysaccharides have been observed during and subsequent to diatom blooms (Passow et al. 1994, Leppard 1995). Alldredge et al. (1993) observed pelagic particles and gels formed of EPS and defined a new class of particles based on their staining capacity with the cationic dye Alcian Blue, which are referred to as transparent exopolymer particles (TEP). TEP can be formed biotically by bacteria and algae in the form of capsules and sheets, but also abiotically by coagulation of dissolved organic matter and colloidal precursors (Zhou et al. 1998, Passow 2000, Passow 2002). Different studies showed that TEP are important in the aggregation of diatom blooms, provide the matrix of marine snow and have a large influence on the particle flux in the ocean (Passow and Alldredge 1994, Mari and Kiørboe 1996, Engel and Schartau 1999, Passow et al. 2001).

Many of the dominant ice algae produce extensive extracellular mucilages and large quantities of exopolymeric substances have been suggested to occur within the sea-ice habitat (McConville 1985, Riebesell et al. 1991, Gradinger and Nürnberg 1996, Herborg et al. 2001). However, up to now quantification of TEP in natural sea ice was only performed in one study. Krembs and Engel (2001) investigated the lowermost 10 cm of Arctic first-year pack ice and report on high TEP concentrations at the ice-water interphase. However, no information was provided on the vertical distribution of TEP within the sea ice. Since Arctic pack ice can harbour productive and biomass-rich bacterial and algal communities also in its interior (Gradinger and Zhang 1997, Mock and Gradinger 1999), information on TEP over the entire ice thickness is needed to understand the importance of TEP for the sea-ice habitat and the ice-covered ocean.

This study reports on TEP in sea ice of varying age: young, first-year and multi-year sea ice. TEP was quantified and characterised over the entire ice thickness and compared to values observed in the under-ice water. It is hypothesised that the more extreme living conditions in the upper parts of the sea ice enhance TEP production, making TEP an important, until now largely neglected, source of organic carbon for the nutrition of sympagic animals and bacteria.

2.2.2 Material and methods

The material for this study was sampled during the expedition ARK XV-3 with RV *Polarstern* to the Fram Strait and Greenland Sea in September / October 1999 (for details see Schauer 2000). Five different sets of ice samples were obtained with a motor-powered SIPRE type ice auger (internal diameter 9 cm) at three locations (Fig. 2.2.1). For each set, two ice cores (named A and B) were sampled within 1 m^2 to minimise horizontal heterogeneity.

Core A was used for the determination of ice temperature, bulk salinity, nutrient concentrations and particulate organic carbon (POC) and nitrogen (PON). Ice temperatures were measured with a Testo720-thermometer immediately after coring inside small holes drilled into the core in 2–10 cm intervals. Thereafter core A was cut into 1–20 cm sections, which were placed in clean polyethylene boxes. Ice segments were transported to the ship and melted in the dark at 4 °C. Salinity of the melted segments was measured with a WTW 190 conductometer. Subsamples (30–50 ml) were analysed for NO_2, NO_3, PO_4 and $Si(OH)_4$ using automated nutrient analysis procedures (Grasshoff et al. 1983). The rest of the melted segments (70–1500 ml) was filtered onto pre-combusted Whatman GF / F filters and used for the determination of POC and PON with a CARLO ERBA NA 1500 CHN-Analyzer (Verardo et al. 1990).

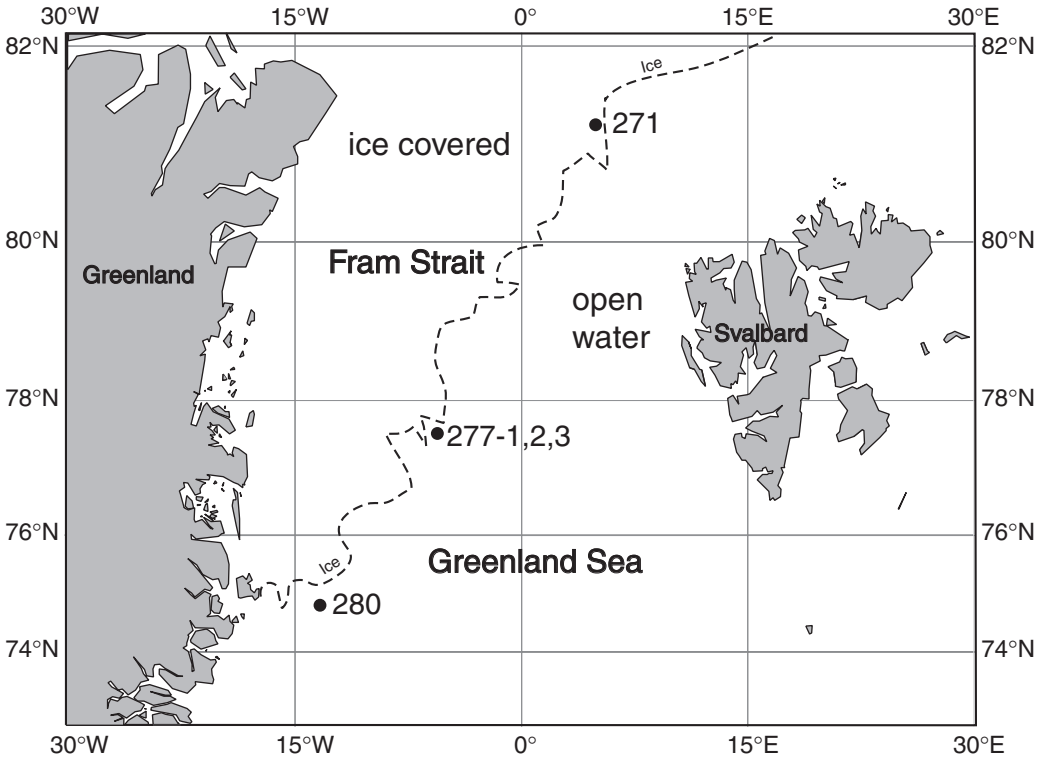

Fig. 2.2.1: Location of the stations in the Fram Strait area. Station numbers represent the day of the year. Dashed line indicates the ice edge on 20.9.1999 (day of the year = 263)

Ice core B was used for the microscopical investigation of bacteria, algae and TEP and for the determination of algal pigments. Ice core sections (1–20 cm) of this core were melted in the dark at 4 °C with an addition of 0.2 µm filtered seawater to avoid osmotic stress to the organisms (Garrison and Buck 1986, Spindler and Dieckmann 1986). Blanks of the filtered seawater were taken at each station and treated like the ice samples; the concentrations of blanks were insignificant for all parameters (cell counts, TEP and algal pigments). Immediately after the ice samples had melted, two 100 ml subsamples were fixed with 0.2 µm filtered borax-buffered formalin (1 % final concentration). 30–50 ml of the first subsamples were filtered onto a black polycarbonate filter (0.2 µm), stained with DAPI and mounted on a microscope-slide (Porter and Feig 1980). From this slide the total bacterial number was calculated from at least 400 cells counted on a minimum of 20 fields with a Zeiss Axiovert 135 microscope using UV excitation. The second subsample was used for the determination of the abundance of centric and pennate diatoms. Samples were counted in settling chambers (Utermöhl 1958) following the recommendations of the Baltic Marine Environment Protection Commission (1988).

For the determination of TEP, 30–50 ml unfixed subsamples of melted segments were filtered carefully onto polycarbonate filters (pore size 0.4 µm) supported with backing filters with a pressure difference of < 0.1 bar. Samples were stained with 0.2 µm pre-filtered Alcian Blue solution (Alldredge et al. 1993) and mounted on microscope slides. Relative cover of total TEP area on the filters was low (on average < 1 %). TEP abundance and size were measured semi-automatically at 400× magnification with a Leitz Aristoplan microscope connected to a Sony DXP-CCD video camera. A minimum of 500 TEP were videotaped and the videoframes were digitised. Contour lines of digitised TEP images were traced manually and the area of individual particles was determined with a LEICA QWIN 500 MC image analysis system. Individual TEP areas were converted to equivalent spherical diameters (ESD), which were assigned to eight logarithmically increasing size classes ranging from 3–60 µm ESD.

Particle size distributions are often described by power relations of the type $N = kd_p^{-\beta}$, or $dN/d(d_p) = kd_p^{-(\beta+1)}$, where dN is the number of particles per unit volume in the size range d_p to $\{d_p + d(d_p)\}$ (e.g. McCave 1984). The constant k depends on the

concentration of the particles and β describes the size distribution of the particles; the smaller β the larger is the fraction of large particles. A β of 3 denotes equal particle volumes in the logarithmically increasing size classes (McCave 1984). β+1 values were estimated from the regressions of $\log\{dN/d(d_p)\}$ versus $\log\{d_p\}$. The magnitude of β+1 allows comparison between TEP size frequency distributions at different stations and environments.

The rest of the meltwater of the sections of ice core B was used for determination of chlorophyll *a* (chl *a*) and pheopigments (pheo). Subsamples (200–2300 ml) were filtered onto Whatman GF / F filters and analysed fluorometrically with a Turner Designs 10-AU digital fluorometer according to Arar and Collins (1997).

Under-ice water was sampled at all locations through drill holes using a polyethylene tube (4.0 cm internal diameter) with a valve at one end. The unequipped end of the tube was lowered into the water with the valve open. At a depth of 10 m the valve was closed and the tube with the trapped water was hoisted. All parameters mentioned above were also determined for these integrated (0–10 m) water samples.

Based on the temperature and salinity measurements of core A, brine salinity was calculated as function of ice temperature (Assur 1958) and brine volume as function of ice temperature and ice bulk salinity (Frankenstein and Garner 1967, Leppäranta and Manninen 1988). Non-parametric Spearman-Rank-correlations were used to determine relationships between biogenic parameters. For testing on significant differences between median values the Kruskal-Wallis-test was applied (Sachs 1984). In box plots, the total data range, the 25–75 % quartile range and the median are shown. Single data points were marked as outliers when they exceeded a value of V = UQ + 1.5 × IQD (UQ is the upper quartile, IQD is the interquartile distance).

2.2.3 Results

Physico-chemical parameters

Drifting pack ice was sampled at 5 stations in the marginal ice zone of the East Greenland Current (Fig. 2.2.1). Ice thickness varied between 10 cm (St. 277-2) and 304.5 cm (St. 280), ice temperatures between −8.0 °C and −1.5 °C (Fig. 2.2.2a).

Sea-ice bulk salinities ranged between 0.1 and 12.3 (Fig 2.2.2b). Based on ice thickness and ice salinity profiles, ice cores were pooled into three different classes: Young sea ice (ice thickness: 10–38 cm, salinity: 5.7–12.3) was sampled at stations 277-1 and 277-2 (= nilas ice) in recently refrozen leads, first-year sea ice (ice thickness: 143–193 cm, salinity: 1.5–5.9) at stations 271 and 277-3, and multi-year sea ice (ice thickness: 302–304.5 cm, salinity: 0.1–4.9) was sampled at station 280. The highest bulk salinity was measured in the nilas ice (consolidated newly formed sea ice) sampled at station 277-2; minimum bulk salinities occurred in the upper ice horizons at station 280. Strong temperature gradients were observed in the upper parts of the ice, whereas temperatures in the lower parts were more homogenous and close to the freezing temperature of seawater.

Sea-ice brine salinities, calculated as a function of ice temperature, ranged between 27.0 and 128.9. Median brine salinity was highest in young sea ice (YSI, median = 79.9) followed by first-year sea ice (FSI, median = 40.8) and multi-year sea ice (MSI, median = 37.4) (Fig. 2.2.3a). The relative brine volume (calculated as a function of ice temperature and bulk salinity) varied from < 1.0 % to 22.4 %. The highest volumes occurred in YSI (median: 13.2 %), minimum brine volumes were observed in MSI (median: 9.6 %) (Fig. 2.2.3b).

Nutrient concentrations in sea ice showed a strong vertical variability (data not shown) and only PO_4 was significantly correlated with ice depth. Median concentrations of PO_4, NO_2 and NO_3 were highest in YSI followed by FSI and MSI data (Fig. 2.2.4a, b, c). Median $Si(OH)_4$ concentrations were similar in all ice types and in the under-ice water (Fig. 2.2.4d). NO_2 showed slightly elevated values in the YSI compared to the under-ice water concentrations. Median concentrations of NO_3 in the different ice classes (total range: < 0.1–1.7 µM) were lower than in the water (total range: 1.5–3.0 µM).

Biogenic parameters

Various biogenic parameters measured in the different ice classes and in the under-ice water are summarised in Table 2.2.1. Median POC concentrations of the sea-ice samples exceeded those in the under-ice water by factors of 3.3 to 5.6 (Fig. 2.2.5a). Median PON values were highest in YSI and decreased with increasing age of the sampled ice (Fig. 2.2.5b), causing an increase of

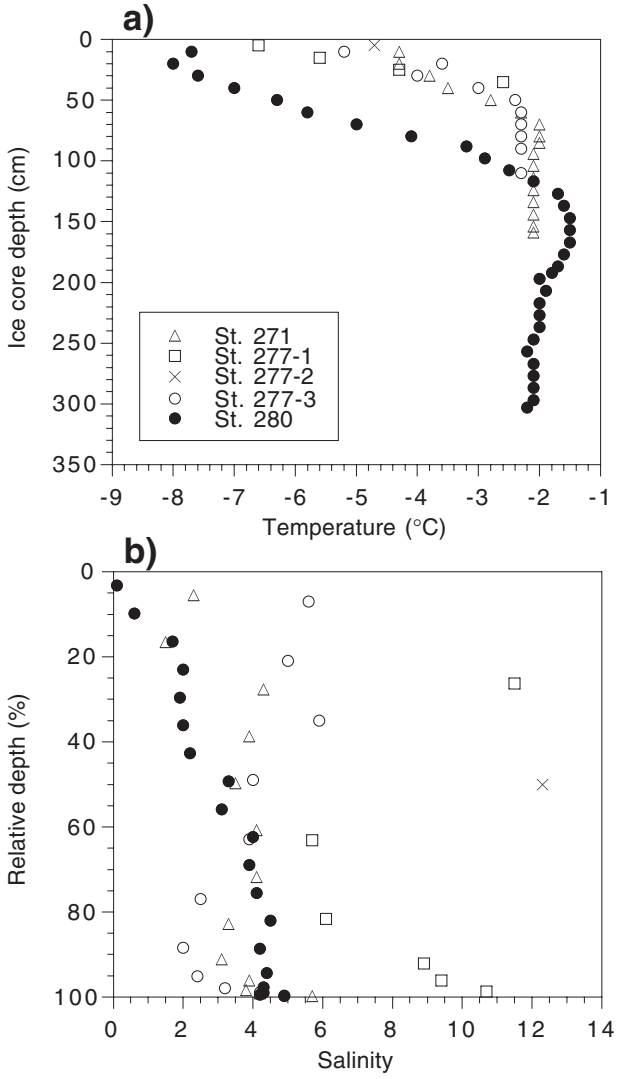

Fig. 2.2.2: a) Vertical temperature profiles in the sea-ice floes. **b)** Vertical profiles of sea-ice bulk salinity. Note relative scale on *y*-axis

the median C / N ratios with increasing age of the sea ice (Fig. 2.2.5c, Table 2.2.1).

Chl *a* concentrations in sea ice showed large vertical variations with peak concentrations occurring both at the bottom and in the interior of the ice (data not shown). The maximum chl *a* concentration (17.1 µg l^{-1}) was observed in the interior of young sea ice (St. 277-1). Also the highest median chl *a* concentration was found in this ice type, followed by FSI and MSI. Chl *a* concentrations in the under-ice water were low, with a median of 0.5 µg l^{-1} (Fig. 2.2.5d). The pheo / chl *a* ratio was highest in the MSI and water samples with a median of 0.7 and 0.5, respectively.

In this study TEP concentrations are reported in two ways: TEP abundance (particles l^{-1}) and TEP area (cm^2 l^{-1}). High concentrations of TEP were found in all sea-ice classes (Fig. 2.2.5e, f, Table 2.2.1). TEP abundance in sea ice varied between 0.43×10^6 and 14.93×10^6 particles l^{-1}, area of TEP between 0.6 cm^2 l^{-1} and 16.2 cm^2 l^{-1}. Vertical profiles of the TEP concentrations showed peaks in different layers, with maximum TEP concentrations always occurring in the interior of the ice (Fig. 2.2.6). With the exception of the upper 80 cm ice layer of the MSI (station 280), TEP abundance and area in sea ice were one order of magnitude higher than in the under-ice water (Fig. 2.2.6). This large difference is also reflected in the medians, which were considerably higher in the sea-ice environments than in the under-ice habitat. Differences of the medians were statistically significant for TEP area only (TEP area: Kruskal-Wallis-Test: $p = 0.0209$; TEP abundance: Kruskal-Wallis-Test: $p = 0.0505$). The median TEP / chl *a* ratio increased with the age of the sampled ice floes from YSI over FSI to MSI

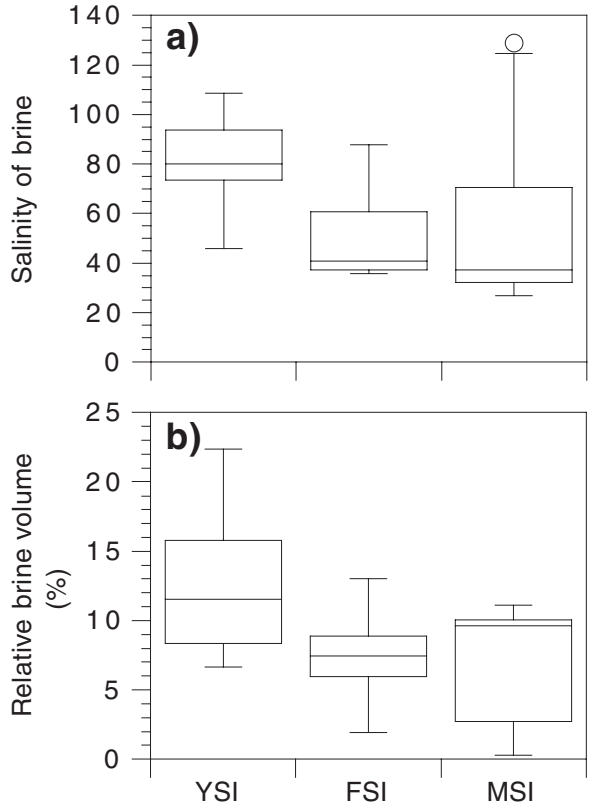

Fig. 2.2.3: a) Box plots for the salinity of brine (calculated after Assur 1958). **b)** Box plots for the relative brine volume (calculated after Frankenstein and Garner 1967, Leppäranta and Manninen 1988). YSI = young sea ice, FSI = first-year sea ice, MSI = multi-year sea ice

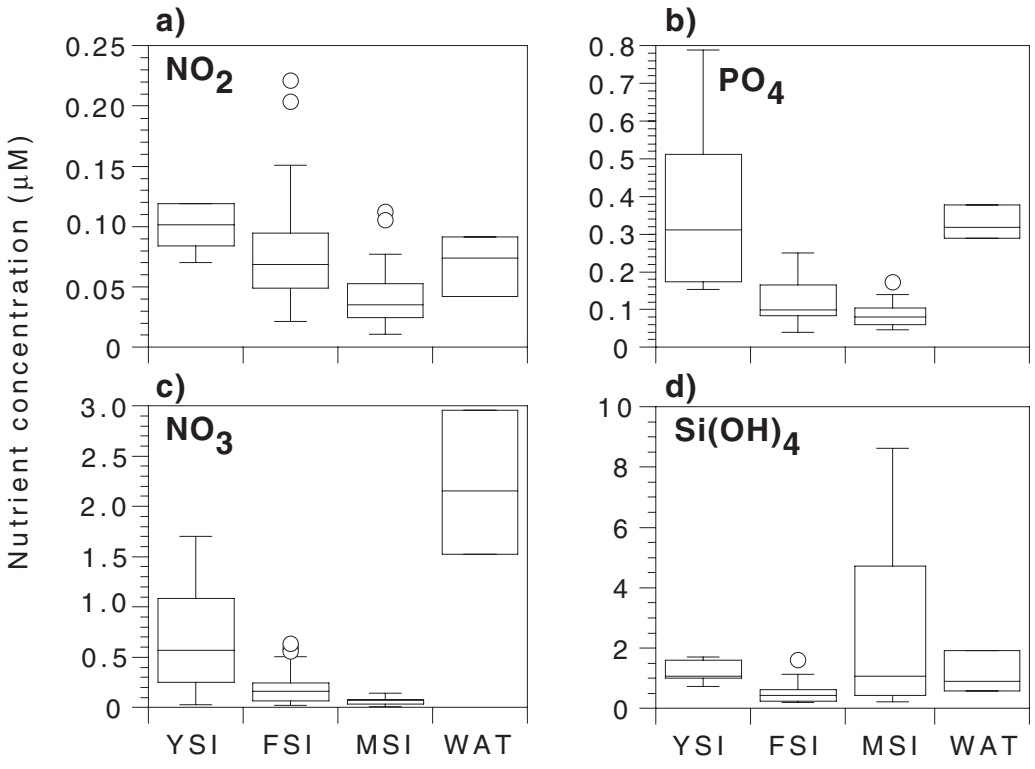

Fig. 2.2.4: Box plots of nutrient concentrations: **a)** NO_2, **b)** PO_4, **c)** NO_3, **d)** $Si(OH)_4$. YSI = young sea ice, FSI = first-year sea ice, MSI = multi-year sea ice, WAT = under-ice water

Table 2.2.1: Biological parameters of the different environments (range with median values in parentheses)

	Young sea ice	First-year sea ice	Multi-year sea ice	Water
Particulate organic carbon (mg l^{-1})	0.27–1.46 (1.07)	0.25–6.39 (0.63)	0.23–5.58 (0.88)	0.10–0.28 (0.19)
Particulate organic nitrogen (mg l^{-1})	0.04–0.31 (0.16)	0.03–0.54 (0.06)	0.01–0.34 (0.06)	0.02–0.05 (0.03)
Molar C / N ratio	4.0–10.7 (6.0)	6.3–19.5 (12.4)	12.3–50.2 (17.4)	5.7–7.0 (6.9)
Chlorophyll *a* (µg l^{-1})	1.0–17.1 (6.7)	0.1–10.2 (2.1)	0.1–12.1 (1.0)	0.3–0.8 (0.5)
Pheopigments (µg l^{-1})	0.4–3.8 (1.7)	0.1–1.7 (0.4)	0.1–3.2 (1.0)	0.2–0.4 (0.2)
Pheopigment / Chlorophyll *a* ratio	0.2–1.5 (0.3)	0.1–0.5 (0.2)	0.1–3.1 (0.7)	0.4–0.5 (0.5)
Pennate diatoms (10^3 cells l^{-1})	7.6–742.0 (140.2)	4.2–1323.9 (234.0)	1.8–2049.2 (456.2)	4.5–45.0 (5.9)
Centric diatoms (10^3 cells l^{-1})	2.8–2462.3 (59.4)	0.0–199.0 (3.1)	0.0–2.4 (0.0)	4.8–21.9 (21.2)
Bacteria (10^9 cells l^{-1})	0.21–1.20 (0.31)	0.22–0.94 (0.47)	0.11–2.49 (0.37)	0.26–1.06 (0.34)
TEP (10^6 particles l^{-1})	1.43–4.65 (3.17)	2.28–10.42 (4.15)	0.43–14.93 (4.90)	0.50–0.83 (0.56)
TEP (cm^2 l^{-1})	2.0–10.9 (5.9)	1.6–16.2 (6.9)	0.6–9.2 (4.6)	0.2–0.9 (0.6)
β+1	1.6–2.2 (1.7)	1.4–2.7 (2.0)	1.6–3.2 (2.3)	2.2–3.2 (2.2)

(Fig. 2.2.5g), which indicates the accumulation of TEP relative to autotrophs in the sea-ice habitat with time. The abundance of TEP was negatively correlated with size and followed a power law relationship except for a few samples, in which the smallest size class appeared to be underrepresented. The slopes of the size distributions were relatively flat with β+1 in the range of 1.4 to 3.2 in the ice core sections and 2.2 to 3.2 in the under-ice water (Table 2.2.1). Relative TEP size frequencies for the pooled data of YSI, FSI, MSI and water are shown in Fig. 2.2.7. Also the combined data showed flat size distributions with β+1 values in the range of 1.9–2.3, which indicates a very large proportion of larger TEP in all habitats.

Most important primary producers in sea-ice samples were pennate diatoms, whose abundances showed large vertical variations (data not shown). Median pennate diatom abundance was highest in MSI (median: 456.2×10^3 cells l^{-1}), cell numbers were lower in FSI and YSI (Table 2.2.1). The abundance of pennate diatoms in sea ice was significantly correlated with ice depth (Table 2.2.2). With the exception of YSI, abundances of centric diatoms in sea ice were much lower than cell numbers of pennate diatoms. Only in YSI and under-ice water samples, centric diatoms were more abundant than pennate species (Table 2.2.1).

Bacterial concentrations in sea ice showed a large variability and varied by a factor of 25. Minimum concentrations were observed in the upper horizons of the MSI, maxima occurred in the bottom sections of the same ice class (data not shown). Median bacterial concentrations of all ice types and under-ice water were relatively similar and varied from $0.31–0.47 \times 10^9$ cells l^{-1} (Table 2.2.1).

Spearman-Rank-correlations were used to explore relationships between parameters measured in sea-ice segments obtained from cores B (Table 2.2.2), due to different lengths and subsequently different vertical resolutions of cores A and B. TEP concentrations in sea ice correlated significantly with chl *a* concentrations as well as with the abundances of pennate diatoms, centric diatoms and bacteria (Table 2.2.2). The diatom abundance / bacterial abundance ratio showed a highly significant correlation with TEP area (Spearman-Rank correlation: $\rho = 0.477$, $p = 0.0007$).

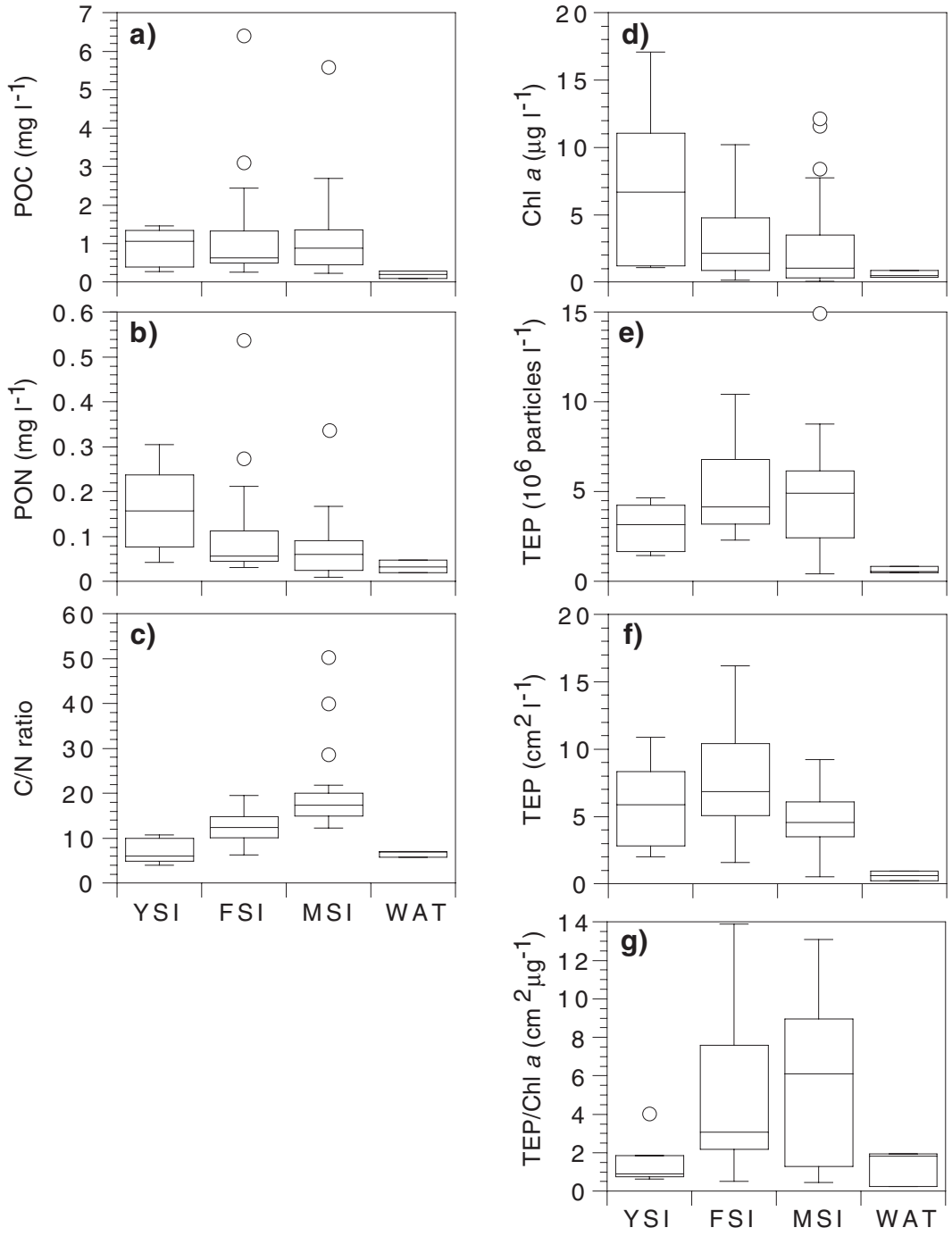

Fig. 2.2.5: Box plots for **a)** particulate organic carbon (POC), **b)** particulate organic nitrogen (PON), **c)** molar POC / PON ratio = C / N ratio, **d)** Chl *a* concentration, **e)** abundance of transparent exopolymer particles (TEP), **f)** TEP area and **g)** TEP / Chl *a* ratio in the different environments. YSI = young sea ice, FSI = first-year sea ice, MSI = multi-year sea ice, WAT = under-ice water

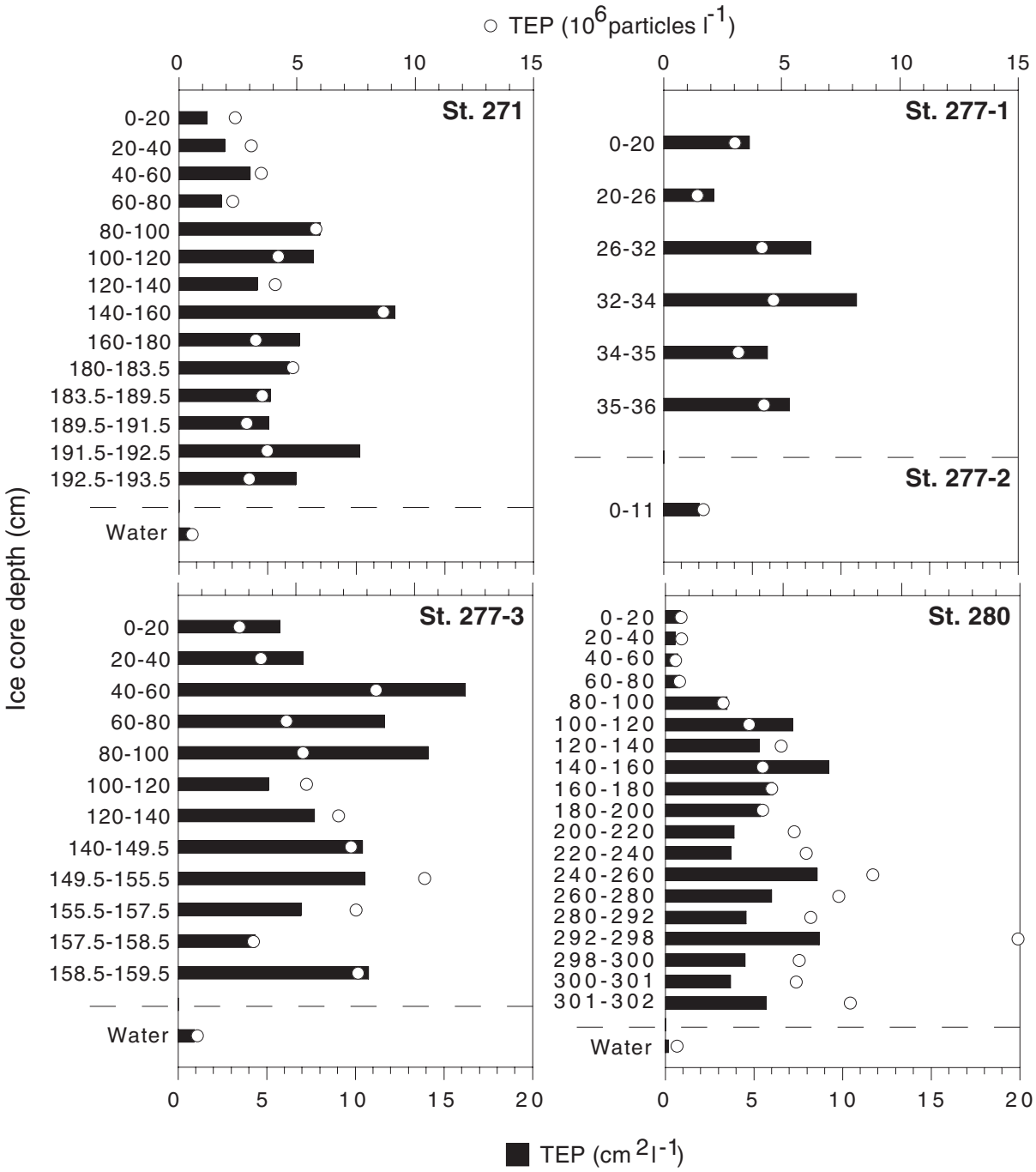

Fig. 2.2.6: Vertical distribution of transparent exopolymer particles (TEP): Concentration and area in sea ice and under-ice water

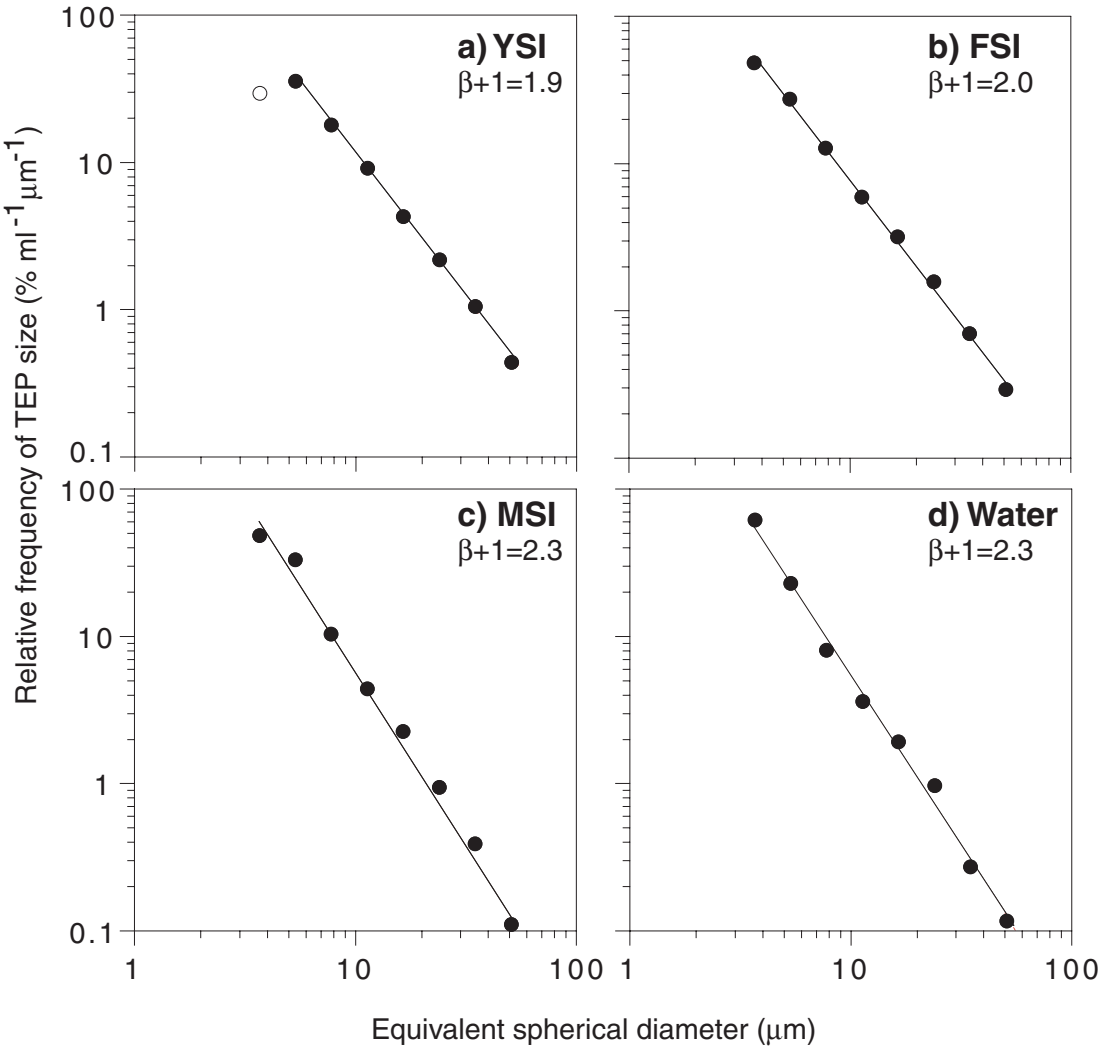

Fig. 2.2.7: Relative size frequencies of transparent exopolymer particles (TEP) (pooled data). **a)** YSI = young sea ice, **b)** FSI = first-year sea ice, **c)** MSI = multi-year sea ice, **d)** Water = under-ice water. Only filled dots were used for the regression lines and the determination of β+1 values

Table 2.2.2: Spearman-Rank correlations of biological parameters (bulk concentrations) of the pooled ice core data. Bold values are statistically significant ($p < 0.01$, $n = 49$). Chl *a* = chlorophyll *a*, PHEO = pheopigments, PEN = pennate diatoms, CEN = centric diatoms, BACT = bacteria, TEP (area) = area of transparent exopolymer particles

	DEPTH	**Chl *a***	**PHEO**	**PEN**	**CEN**	**BACT**
Chl *a*	0.371					
PHEO	**0.611**	0.334				
PEN	**0.375**	0.326	**0.500**			
CEN	0.139	**0.807**	0.248	0.211		
BACT	**0.424**	0.362	**0.506**	**0.509**	0.180	
TEP (area)	0.350	**0.621**	0.331	**0.488**	**0.463**	**0.511**

2.2.4 Discussion

This study gives first estimates of TEP concentrations in natural Arctic sea ice of varying age. Median TEP concentrations of the pooled sea-ice samples exceeded median TEP concentrations in the water by one order of magnitude, indicating the importance of TEP for the sea-ice habitat.

Producers of TEP

Diatoms are considered as important producers of exopolymeric substances in pelagic and benthic habitats (Decho 1990, Mopper et al. 1995, Smith and Underwood 1998). Especially benthic pennate diatoms produce copious amounts of exopolymeric substances, which serve in the adhesion and the motility of the organisms (Hoagland et al. 1993, Cooksey and Wigglesworth-Cooksey 1995). Krembs and Engel (2001) suggest pennate diatoms as the dominant TEP producers in bottom communities of Arctic pack ice during summer. In the present study, sea-ice TEP was correlated with the abundances of diatoms and bacteria, which both may significantly contribute to the TEP pool in sea ice. To estimate the importance of the two groups for the accumulation of polymeric substances in sea ice, the daily production rates of sea-ice diatoms and bacteria were calculated using cell-specific EPS production rates of temperate epipelic diatoms (6.31–31.46 pg glucan equivalents $cell^{-1}$ d^{-1}; average: 18.01 pg glucan equivalents $cell^{-1}$ d^{-1}; Smith and Underwood 2000) and temperate planktonic bacteria (4 amol C $cell^{-1}$ h^{-1}; Stoderegger and Herndl 1999). Rates of temperate species were used, due to a lack of data on cold-adapted and sympagic species. Neglecting temperature effects, estimated EPS production of sea-ice diatoms was on average 3.6 µg C l^{-1} d^{-1} (range: 0.1–18.7 µg C l^{-1} d^{-1}), estimated bacterial EPS production in sea ice averaged only 0.7 µg C l^{-1} d^{-1} (range: 0.1–2.9 µg C l^{-1} d^{-1}). The diatom EPS production / bacterial EPS production ratio was high and showed an average of 6.1 (range: 0.1–40.9). This high ratio and the striking dominance of pennate forms imply that pennate diatoms were the primary source of TEP in the sea ice under investigation. This idea is also supported by the highly significant positive correlation of the diatom abundance / bacteria abundance ratio with the TEP concentration.

TEP concentrations and characteristics

In this study high TEP concentrations were observed in young, first-year and multi-year sea ice, exceeding under-ice water values by one order of magnitude. The investigated TEP abundances in sea ice (10^5 and 10^7 particles l^{-1}) are similar to those reported during phytoplankton blooms in coastal areas (Passow et al. 1994, Mari and Kiørboe 1996). Krembs and Engel (2001) report TEP concentrations between below detection to 16 cm^2 l^{-1} with a median value of 2.9 cm^2 l^{-1} for the lowermost 10 centimetres of Arctic pack ice from the Laptev Sea during summer. TEP concentrations in this study showed a similar range, but median values of all ice types exceeded the median value given by Krembs and Engel (2001) by a factor of 2–3. This can be explained by the high concentrations in the ice interior, which was not studied in the other investigation. The same authors found a distinct size pattern of sea ice derived TEP, with a higher contribution of relatively large particles. Their calculated mean β+1 value of 1.86 agrees well with the average value of this study (2.1). The difference to values commonly reported for pelagic environments ($\beta+1 \approx 4$), demonstrates that sea ice contains a large fraction of relatively large particles, indicating differences in environmental factors affecting processes of TEP formation (coagulation) and in TEP losses (grazing, disaggregation) in sea ice and the pelagic realm. The large proportion of relatively large particles may also represent fragments of biofilms coating the surface of brine channel walls. The occurrence of sympagic biofilms has been suggested by Thomas and Dieckmann (2002). However, in this study also under-ice water samples showed reduced β+1 values (range: 2.2–3.2) when compared to TEP size spectra determined in other pelagic studies. It is therefore assumed that the under-ice water samples in the present study contained sea ice derived TEP and / or that elevated shear stress in the sub-ice water layer increased coagulation of particles and thus reduced β+1 values in this special habitat.

Already the newly formed nilas ice sample showed an increased TEP abundance compared to the under-ice water. Particles are incorporated into sea ice by various physical processes (e.g. Shen and Ackermann 1990, Grossmann and Dieckmann 1994, Spindler 1994). Gradinger and Ikävalko (1998) showed that the selectivity of incorporation processes of algae into newly forming sea ice is immense and proposed that not only particle size (Penny and Sullivan 1990), but

also surface characteristics of the particles (e.g. stickiness) are responsible for different incorporation rates. Gradinger and Ikävalko (1998) calculated an enrichment index I_S which allows the comparison of particle concentrations in newly formed sea ice and water based on salinity and concentration data. An I_S value of 1 indicates no differences in concentrations between the samples, increased values demonstrate elevated concentrations in the ice sample compared to the underlying water. Using their approach the enrichment indices for the abundances of pennate diatoms, bacteria and TEP were calculated for the nilas ice sample at station 277b (ice thickness: 11 cm). Pennate diatoms showed an enrichment index of 0.5, bacteria of 1.8 and TEP of 5.6. These values are relatively low compared to enrichment indices with median values of 7 for bacteria and 212 for pennate diatoms reported by Gradinger and Ikävalko (1998). Nevertheless, the data show that TEP was significantly enriched already in the initial stage of sea ice. The enrichment can be caused by coagulation of TEP and TEP precursors on ice surfaces, by biotically TEP formation of incorporated organisms exposed to severe environmental stress and by pure physical accumulation of TEP particles. Because abundances and enrichment of organisms were relatively low compared to TEP, it is assumed that physical incorporation was responsible for the enrichment in the newly formed sea ice. Grossmann (1994) proposed that bacteria are incorporated into newly forming sea ice via attachment to algae and algal mucus. Since TEP are sticky and serve in the coagulation of particles (Engel 2000, Passow et al. 1994), it is proposed that the presence of TEP in seawater from which the ice forms might also influence the incorporation of other particles (organisms and sediments) into newly forming sea ice, e.g. by enhanced adhesion of particles to crystal surfaces.

Many studies showed increased production of polymeric substances by planktonic and benthic algae under nutrient limitation, during senescence of algal blooms and in response to different environmental stress factors (Decho 1990, Myklestad 1995, Corzo et al. 2000, Staats et al. 2000, Liu and Buskey 2000, Wolfstein and Stal 2002). Aletsee and Jahnke (1992) report high concentrations of Alcian Blue stainable mucus in sea ice algal cultures exposed to cold temperatures. During the summer-winter transition rapidly decreasing light levels and the development of steep temperature and brine salinity gradients in ice floes create many challenges to the sympagic biota, which can response to the changes with the increased production of EPS (Thomas and Dieckmann 2002, Krembs pers. comm.). In this study day lengths decreased by ~30 min d^{-1} and the ice showed strong vertical temperature gradients with minimum temperatures of −8.0 °C. Low temperatures were accompanied by high brine salinities ranging between ~40 and ~130 in the middle and upper parts of the ice. Hence, harsh environmental conditions influence especially internal communities, which have been recently described for Arctic pack ice (Gradinger and Zhang 1997) and contribute significantly to ice algal biomass and primary production (Gradinger 1999b, Mock and Gradinger 1999). Interior communities were found in all ice cores of this study and are assumed as the source of the internal TEP peaks.

In addition to cold temperatures and salinities also restricted nutrient availability in the ice interior has been proposed (Cota et al. 1987, Gradinger et al. 1992), which may affect TEP production. Using bulk nutrient concentrations and brine volume calculations, nutrient concentrations in the sea-ice brine were calculated, i.e. the nutrient concentrations to which the sympagic organisms were exposed. Nutrient concentrations in the sea-ice brine were high (pooled ice data: $NO_2 + NO_3 > 0.24$ µM, $PO_4 > 0.56$ µM and $Si(OH)_4 > 2.4$ µM) and exceeded half saturation constants (k_S values) commonly reported for mixed natural phytoplankton assemblages (Sommer 1998). The data suggest that nutrients were not limiting sympagic algal production and that TEP production was not affected by nutritional limitation during the time of this investigation. Since exopolymeric material has been considered to be refractory, sea-ice TEP might accumulate as well over longer time-scales in different layers of the sea ice, and high concentrations observed in this study, may represent old signals of previous situations of environmental and/or nutritional stress. Further studies in different seasons are necessary to understand, if the bulk of the ice TEP is produced and accumulated during the productive spring and summer seasons when nutrients can be severely depleted (Gosselin et al. 1990, Cota et al. 1991), or are formed in response to the changing environmental conditions during the summer-winter transition. The accumulation of refractory material may also explain the poor relationship between median TEP concentrations and other median values of abiotic and biotic

parameters. Despite distinct differences between median nutrient concentrations, C / N ratios and chl *a* values, indicating the different environmental conditions in the three ice types observed, median concentrations of TEP in ice classes showed relatively little variation and did not resemble the variation of the other parameters. The good consistency of median TEP / chl *a* ratios and median C / N ratios is interpreted as indication of an accumulation of TEP in older sea ice. Beside production and accumulation, also bacterial breakdown of TEP as well as consumption by larger organisms have been suggested for the pelagic realm (Decho 1990) and might also significantly influence the TEP pool within Arctic sea ice.

Estimate of TEP carbon

Integrated POC levels in the sea ice varied between 38.0 mg C m^{-2} and 2808.9 mg C m^{-2}. Using the equation of Mari (1999) with TEP-C (µg C TEP^{-1}) = $0.25 \times 10^{-6} \times r^{2.55}$, where r is the equivalent spherical radius of the TEP particle (µm) and D is its fractal dimension, the integrated TEP carbon values were calculated. These ranged between 7.3 mg C m^{-2} and 564.8 mg C m^{-2} sea ice. This organic carbon accounts for 16 % to 32 % (average: 24 %) of the integrated POC values. Despite the problems related to the transfer of the carbon-size relationship of laboratory produced TEP to natural particles, the high values demonstrate that TEP represents an important, until now largely neglected, source of sea-ice carbon. The high TEP carbon concentrations may have implications for the sympagic food web and might serve as a food source for ice-associated protozoans and metazoans during the long and unproductive winter season when the autotrophic standing stock is low and food sources become scarce.

2.3 Abundance, size distribution and bacterial colonisation of transparent exopolymer particles (TEP) in Antarctic sea ice (Bellingshausen Sea)

2.3.1 Introduction

The annual formation, consolidation and subsequent melting of sea ice surrounding the Antarctic continent has a pivotal role in the biogeochemical cycles of the Southern Ocean (Lizotte and Arrigo 1998, Thomas and Dieckmann 2002). The interior of the sea ice is a habitat for sympagic communities inhabiting a brine-filled network of pores and channels (Horner et al. 1992, Gradinger 2002). Typically, Antarctic sea-ice communities are dominated by bacteria in terms of abundance and diatoms in terms of biomass (Palmisano and Garrison 1993, Thomas and Dieckmann 2002). Riebesell et al. (1991) showed that aggregate formation is a characteristic property of Antarctic sea-ice algae. Krembs and Engel (2001) report on high concentrations of TEP in the lower-most centimeters of Arctic sea ice in the Laptev Sea. The second chapter (2.2) of the present study demonstrated the vertical distribution and importance of TEP in Arctic sea ice of varying age. However, TEP data on polar ocean areas are still scarce (Hong et al. 1997) and up to now no data for TEP in Antarctic sea ice are available.

TEP also serve as substrate and habitat for bacteria (Passow and Alldredge 1994, Mari and Kiørboe 1996, Simon et al. 2002) and the attached bacteria may act in the formation as well as in the degradation of the aggregates (Smith et al. 1992, Ploug et al. 1999, Simon et al. 2002). High proportions of epiphytic and particle-attached bacteria have been frequently observed in Antarctic sea ice (Sullivan and Palmisano 1984, Palmisano and Garrison 1993, Ackley and Sullivan 1994, Archer et al. 1996), but detailed information on bacteria associated with sea-ice microaggregates like TEP particles is missing.

The scope of this chapter was therefore to describe the occurrence, abundance and size distribution of TEP in Antarctic sea ice and underlying water and to discuss the potential role of TEP for the Antarctic sea-ice habitat. A special focus was given to the bacterial colonisation of sea-ice TEP.

2.3.2 Material and methods

Site and sampling

Ice and under-ice water samples were collected during the expedition ANT XVIII-5b on RV *Polarstern* in the Bellingshausen Sea in April 2001 (Fig. 2.3.1, for details see Bathmann 2002). Snow thickness was measured with a ruler at each sampling site prior to coring. At each station 5 ice cores (named A–E) were collected with a SIPRE-type ice auger (9 cm internal diameter) within an area of 1 m^2. Two complete cores (A, B) were sealed in clean plastic tubing and kept frozen (−30 °C) for later analysis of ice structure and stable oxygen isotopic composition. The remaining three cores were cut immediately into 1–10 cm sections, transferred into acid-washed polyethylene boxes and transported in insulated boxes to the ships laboratory for further analysis of salinity, inorganic nutrients (NO_3, PO_4, $Si(OH)_4$), particulate organic carbon (POC) and nitrogen (PON), algal pigments (chlorophyll *a* (chl *a*), pheopigments (pheo)) and for microscopical investigations. Under-ice water was sampled using a 10 m long polyethylene tube (4 cm internal diameter) with a valve at one end. The unequipped end of the tube was lowered into the water with the valve open. At a depth of 10 m the valve was closed and the tube with the trapped water was retrieved. These 0–10 m integrated water samples were transferred to acid-washed containers and transported to the laboratory for further analysis.

Ice structure and stable oxygen isotopic composition

The ice structure of core A was determined by thin section analysis (e.g. Kawamura et al. 2001). Based on ice crystal size and orientation three stratigraphic units were distinguished: granular ice, columnar ice and intermediate granular / columnar ice. Ice core B was cut into sections according to results of the structural analysis of core A. Sections were melted and used for the determination of $\delta^{18}O$ with a mass spectrometer (Finnigan MAT Delta E). Based on the combined structural and isotopic characteristics, ice cores were divided into four categories: snow ice, granular ice columnar ice and intermediate granular / columnar ice.

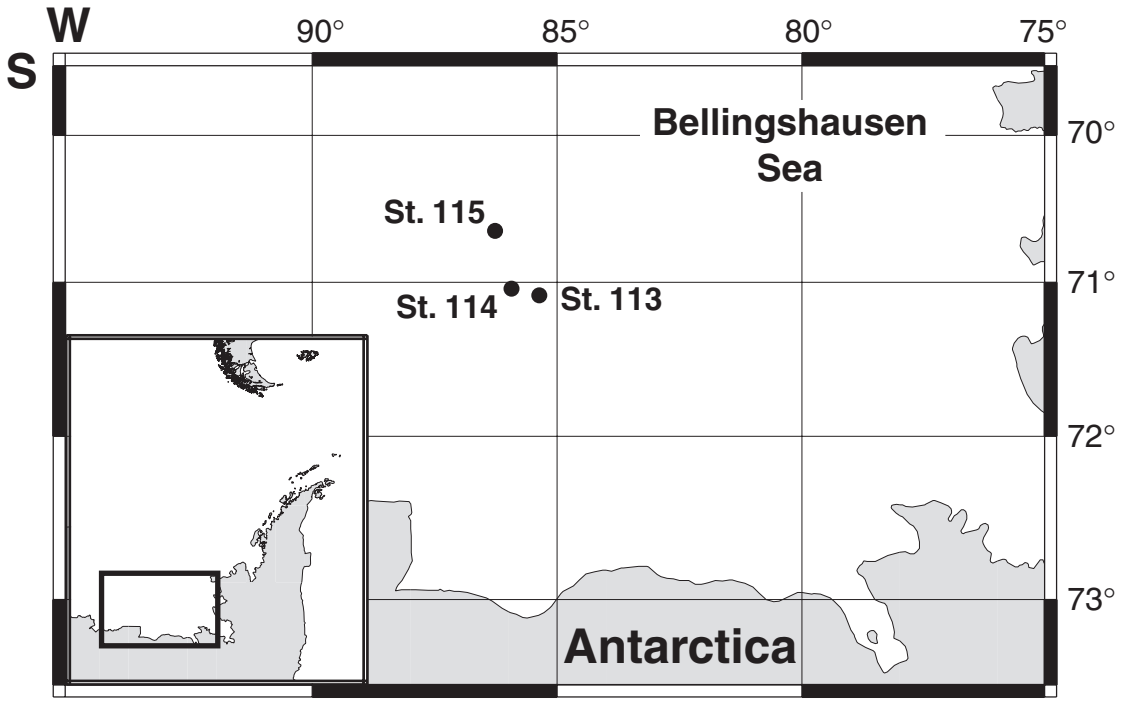

Fig. 2.3.1: Study area and location of the stations in the Bellingshausen Sea. Station numbers represent the day of the year

Temperature, salinity, chemical parameters and pigments

Ice temperature was measured with a Testo720-thermometer immediately after coring from small holes drilled in the core C in 5–10 cm intervals. To prevent cooling of the ice core, these measurements were performed in a temperature-insulated plastic tube. For the analysis of salinity, inorganic nutrients, algal pigments (ice core C) and particulate organic carbon (POC) and nitrogen (PON) (ice core D) sections of ice cores were melted in the dark at 4 °C. Salinity of melted ice and water samples was measured with a WTW LF 191 conductometer. Subsamples (50 ml) were fixed with $HgCl_2$ (Kattner 1999) and stored frozen (–20 °C) until analysis for the concentration of NO_3, PO_4 and $Si(OH)_4$ using standard seawater procedures (Grasshoff et al. 1983). For the analysis of POC and PON, melted ice and water samples were filtered onto precombusted Whatman GF / F filters and combusted in a CARLO ERBA NA 1500 CHN-Analyzer (Verardo et al. 1990). For the determination of chl *a*- and pheo concentrations, samples were filtered onto Whatman GF / F filters and analysed fluorometrically with a Turner Designs 10-AU digital fluorometer according to Arar and Collins (1997).

Abundance and biomass of bacteria and diatoms

Ice core E was used for the microscopical investigation of bacteria, algae and TEP and for the determination of the bacterial colonisation of TEP. Ice core sections (1–10 cm) of this core were melted in the dark at 4 °C with an addition of 0.2 µm filtered seawater to avoid osmotic stress (Garrison and Buck 1986, Spindler and Dieckmann 1986). Blanks of the filtered seawater were taken at each station and treated like the ice samples; the concentrations of blanks were insignificant for all parameters (bacteria, algae and TEP). Immediately after the ice samples had melted, 250 ml subsamples were fixed with 0.2 µm filtered borax-buffered formalin (1 % final concentration). Subsamples (30–100 ml) were filtered onto black 0.2 µm and 0.8 µm polycarbonate filters, stained with DAPI and mounted on microscope-slides (Porter and Feig 1980). For the calculation of the total bacterial number and bacterial biomass (0.2 µm filter) at least 400 cells were counted on a minimum of 20 fields. Estimates of bacterial biovolume were determined from length- and width measurements of 100 cells per samples with a New Porton G12 grid (Graticules Ltd., UK) at a final magnification of 1000×. Bacterial biovolume was converted into bacterial carbon using the formula $CC = 88.6 \times Vol^{0.59} \times 1.042$ (Simon and Azam 1989), where CC (fg) and Vol (μm^3) are the average carbon

content per cell and the average cell volume, respectively. The second filter (0.8 µm) was used for the counting of centric and pennate diatoms. Calculation of the diatom biomass was based on cell measurements and followed the recommendations of the Baltic Marine Environment Protection Commission (1988).

Determination of TEP

For the determination of TEP, 2–30 ml subsamples were filtered carefully onto 0.4 µm polycarbonate filters supported with backing filters with a pressure difference of < 0.1 bar. Samples were stained with 0.2 µm pre-filtered Alcian Blue solution (Passow and Alldredge 1994) and mounted on Cyto-Clear slides (Poretics Corp., USA) (Logan et al. 1994). Relative cover of total TEP area on the filters was low (< 4.5 %). TEP abundance and size were measured semi-automatically at 400× magnification with a Leitz Aristoplan microscope connected to a Sony DXP-CCD video camera. A minimum of 500 TEP were videotaped and the videoframes were digitised. Contour lines of digitised TEP images were traced manually and the area of individual particles was determined with a LEICA QWIN 500 MC image analysis system. Individual TEP areas were converted to equivalent spherical diameters (ESD), which were assigned to eight logarithmically increasing size classes ranging from 3–60 µm ESD.

Particle size distributions are often described by power relations of the type $N = kd_p^{-\beta}$, or $dN/d(d_p) = kd_p^{-(\beta+1)}$, where dN is the number of particles per unit volume in the size range d_p to $\{d_p + d(d_p)\}$ (e.g. McCave 1984). The constant k depends on the concentration of the particles and β describes the size distribution of the particles; the smaller β the larger is the fraction of large particles. A β of 3 denotes equal particle volumes in the logarithmically increasing size classes (McCave 1984). β+1 values were estimated from the regressions of $\log\{dN/d(d_p)\}$ versus $\log\{d_p\}$. The magnitude of β+1 allows comparison of the TEP size frequencies at different stations and environments.

Bacterial colonisation of TEP

For the determination of the number of bacteria attached to TEP, 5–30 ml subsamples of the fixed samples were filtered onto 0.4 µm polycarbonate filters and double-stained with Alcian Blue and DAPI. After staining, filters were mounted on Cyto-Clear slides (Poretics Corp., USA) (Logan et al. 1994). For each sample, bacteria associated with 24 individual TEP were enumerated by switching between bright field and UV illumination. The individual TEP were sized (see above) and associated bacteria were counted. Because TEP are three-dimensional, the entire volume of each TEP was examined by changing the microscopes focal plane during the observation. Hence, both bacteria on the surface and embedded in TEP were counted (Mari and Kiørboe 1996). A potential error (5–15 %) in this enumeration is free-living bacteria retained by the filter beneath the examined TEP (Mari and Kiørboe 1996). Assuming that TEP are spherical and solid, TEP area was used to calculate the projected spherical enclosed volume $PSEV = 4/3\pi r^3$, with $r = 1/2$ ESD. The volume estimates were used to calculate bacterial concentration per aggregate volume. In order to estimate the fraction of total bacteria attached to TEP, a relationship between TEP size and the number of attached bacteria was calculated for each sample. The number of attached bacteria can be fitted to a power law function $n = ad_p^b$, where n is the number of bacteria per TEP, d_p is the ESD of the TEP and a and b are constants for a given sample. Numbers of associated bacteria were plotted versus ESD in log-log coordinates and gave estimates of a and b. The fraction of attached bacteria was calculated by combining this relationship, the size spectra of TEP and the total bacterial numbers in the samples (Passow and Alldredge 1994, Mari and Kiørboe 1996).

Brine salinity was calculated as a function of ice temperature (Assur 1958); brine volume as a function of temperature and ice bulk salinity (Frankenstein and Garner 1967). Non-parametric Spearman-Rank-correlations were used to determine relationships between biogenic parameters. For testing on significant differences between median values the Mann-Whitney U-test was applied (Sachs 1984).

2.3.3 Results

Temperature, salinity, chemical parameters and pigments

Free-drifting pack ice and under-ice water were sampled in the marginal ice zone of the Bellingshausen Sea during late austral autumn 2001. Ice thickness at the sampling sites was very variable and ranged between 49–79 cm, 56–68 cm and 47–65 cm at St. 113, St.

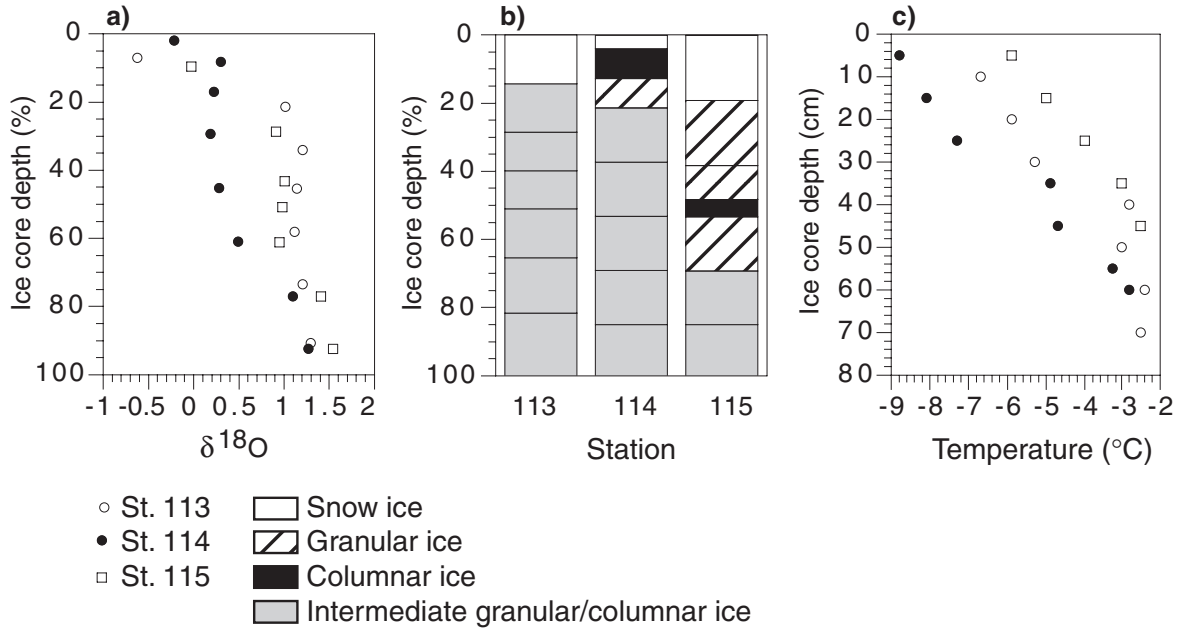

Fig. 2.3.2: a) Vertical distribution of $\delta^{18}O$-values (given against SMOW in per mil). **b)** Vertical distribution of textural ice classes (for definitions see text). **c)** Vertical profiles of sea-ice temperature

114 and St. 115, respectively. All stations were snow covered, with snow thickness varying between 4–20 cm. The sea-ice texture was dominated by intermediate granular / columnar and granular ice, indicating dynamic, turbulent conditions during sea-ice formation (Fig. 2.3.2). Snow ice, characterised by minimum $\delta^{18}O$ values (Fig. 2.3.2a) was found at all stations and contributed between 4–19 % to total ice thickness (Fig. 2.3.2b). Station 113 and 114 showed an internal porous layer, which upper boundary was located approx. 10–15 cm below the freeboard level of the ice floes (freeboard-levels: St. 113: 2.5 cm, St. 115: 1.5 cm). Ice temperatures ranged from −8.8 °C to −2.4 °C and showed typical linear winter profiles with lowest temperatures in the uppermost parts of the ice (Fig. 2.3.2c). Brine salinities, calculated as function of ice temperature, were high with values between 42.5 and 132.8 (median: 79.9, data not shown). Vertical profiles of sea-ice bulk salinity are presented in Fig. 2.3.3. Bulk salinities ranged between 6.4 and 14.2 (median: 9.5). Bulk salinity and temperature measurements were used to calculate brine volumes, i.e. the fluid phase of the sea-ice system in which dissolved matter is enriched and which serves as the actual habitat for the sea-ice biota. Brine volumes ranged between 6.7 % and 24.6 % (median: 11.9 %, data not shown).

Vertical profiles of nutrient concentrations in the ice and under-ice water values are shown in Fig. 2.3.3. With the exception of NO_3 concentrations, which were positively correlated with ice depth (Spearman-Rank correlation: $\rho = 0.545$, $p = 0.0046$), nutrient concentrations in the sea ice were neither correlated to ice depth nor to ice bulk salinity. NO_3 concentrations in the ice were highly variable and ranged between 0.7 µM and 9.4 µM. PO_4 concentrations in the ice varied from 0.3–9.2 µM (median 3.8 µM). $Si(OH)_4$ concentrations in the ice of stations 113 and 114 showed extremely high peaks in the ice interior, coinciding with peak values of algal pigments and biomass (Fig. 2.3.3, Fig. 2.3.4). Maximum $Si(OH)_4$ concentrations measured in this study are 5–6 times higher than maximum values reported in other studies on Antarctic pack ice (Dieckmann et al. 1991, Garrison and Buck 1991, Gleitz et al. 1995) and may result from dissolution of diatom frustules in the nutrient samples, which were not filtered before fixation with $HgCl_2$. Despite careful fixation, storage and analysis of the samples the extremely high $Si(OH)_4$ data are therefore probably erroneous. Except for NO_3, sea ice at stations 113 and 114 showed much higher nutrient concentrations than St. 115. Nutrient concentrations in the water were rather similar at all stations, with the exception of the high NO_3 concentration at St. 113.

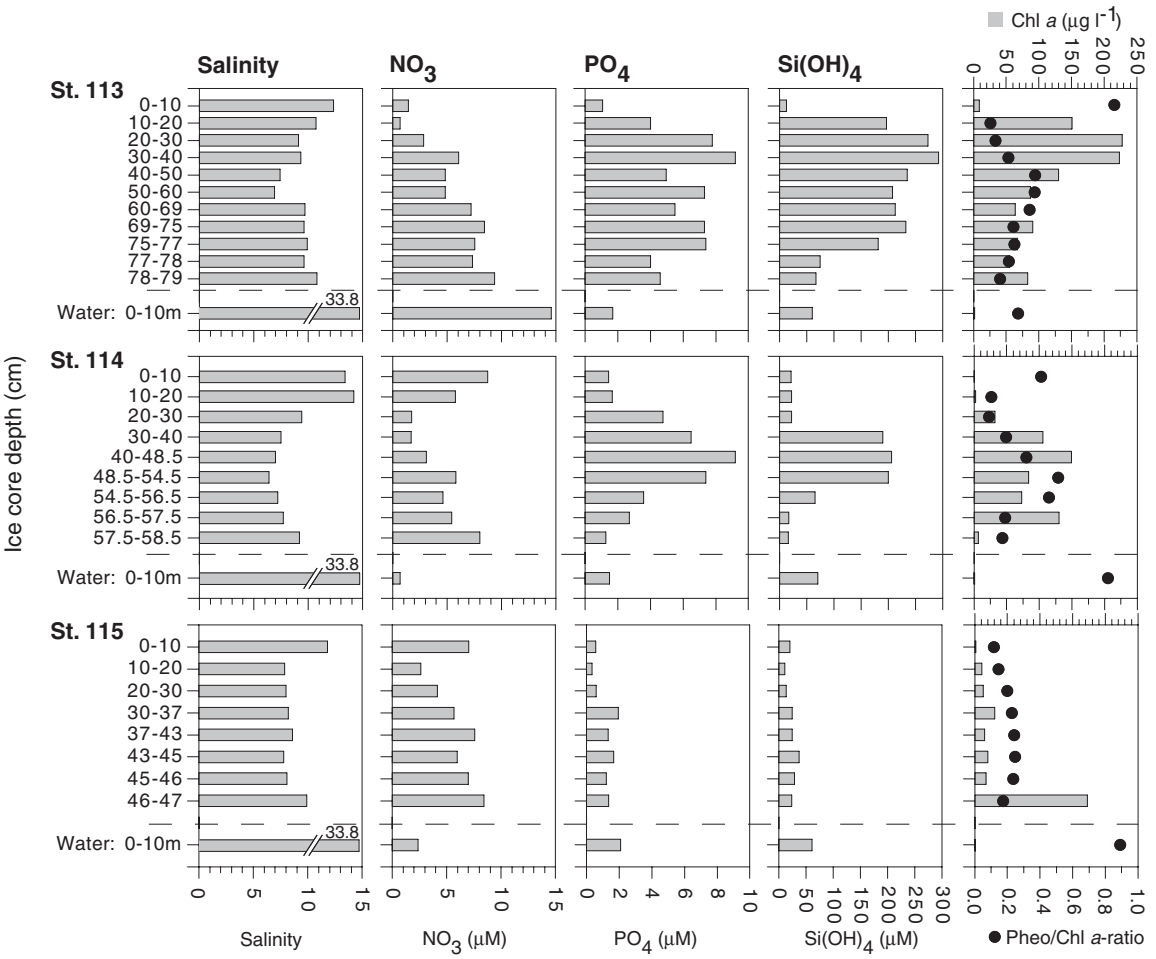

Fig. 2.3.3: Vertical distribution patterns of ice bulk salinity, NO_3, PO_4, $Si(OH)_4$, chlorophyll *a* (= Chl *a*) and the pheophytin / chlorophyll *a* ratio (= Pheo / Chl *a*-ratio) in sea ice and values for the underlying water

Chl *a* concentrations in the ice peaked in surface, interior and bottom layers (Fig. 2.3.4) and ranged between 0.2 µg l^{-1} and 228.2 µg l^{-1} (median: 65.6 µg l^{-1}). Highest chl *a* concentrations occurred in the internal porous layer of St. 113. Chl *a* concentrations in the water were much lower with a median concentration of only 0.2 µg l^{-1}. The pheo / chl *a* ratio in the ice showed maxima in top and interior layers, the ratio was very high in the water samples at stations 114 and 115 (Fig. 2.3.3). POC and PON concentrations in the ice varied between 190.8–9988.5 µg C l^{-1} (median POC: 2594.5 µg C l^{-1}) and 17.4–1568.7 µg N l^{-1} (median PON: 364.8 µg N l^{-1}), respectively (data not shown). Water concentrations were much lower with POC ranging from 39.7–355.9 µg C l^{-1} and PON from 5.4–45.9 µg N l^{-1} (median POC: 106.9 µg C l^{-1}, median PON: 13.7 µg N l^{-1}). C / N ratios in the sea ice showed values between 6.8–12.8 (median: 7.6), water values were similar at all stations with a median value of 9.0. Integrated ice POC and PON ranged between 437.3–3207.4 mg C m^{-2} (median: 2034.3 mg C m^{-2}) and 63.10–504.6 mg m^{-2} (median: 316.36 mg m^{-2}), respectively.

Algal and bacterial abundance and biomass

The results of the microscopical counts and biomass estimates for algae and bacteria are summarised in Table 2.3.1. Algal biomass peaked in the surface, interior and bottom of the ice floes (Fig. 2.3.4). The interior algal assemblages and the integrated abundance and biomass at stations 113 and 114 were dominated by centric diatoms. Dominant centric species were *Chaetoceros* spec., *Corethron* spec., *Thalassiosira* spec. and *Rhizosolenia* spec. At station 115, in contrast, pennate forms dominated the diatom assemblage. Ice-associated pennate diatoms were predominated by *Fragilariopsis* spec., *Nitzschia* spec. and *Navicula* spec.. Algal abundance and biomass was extremely low in the

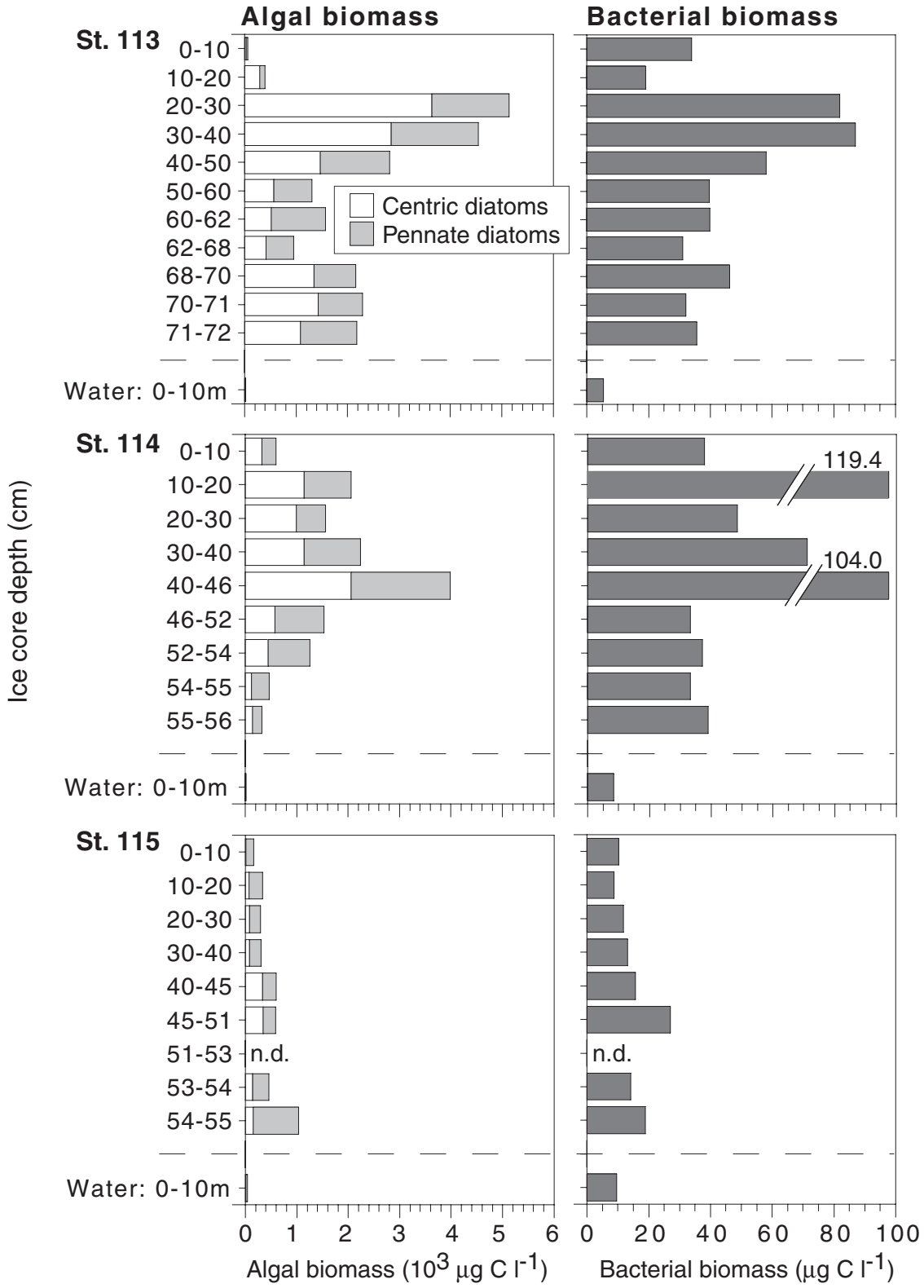

Fig. 2.3.4: Vertical distribution of the algal biomass (centric diatoms, pennate diatoms) and bacterial biomass in sea ice and underlying water. n.d. = no data

Table 2.3.1: Abundance and biomass of bacteria, pennate diatoms and centric diatoms in sea ice and underlying water (range with median values in parentheses). Integration depth for ice values = ice thickness, integration depth for water values = 10 m

	Abundance (10^6 cells l^{-1})	**(10^9 cells m^{-2})**	**Biomass (µg C l^{-1})**	**(mg C m^{-2})**
Ice				
Bacteria	544.15–4854.04 (2056.91)	320.5–1687.4 (1399.5)	8.8–119.4 (34.8)	5.6–31.5 (29.6)
Pennate diatoms	0.61–79.44 (16.22)	8.9–10.1 (9.6)	29.1–1925.2 (653.8)	111.0–511.5 (403.8)
Centric diatoms	0.18–26.88 (4.94)	0.5–6.7 (5.0)	12.8–3637.7 (433.9)	47.7–760.0 (439.1)
Water				
Bacteria	548.13–701.51 (565.91)	5481.3–7015.1 (5659.1)	5.4–9.6 (8.4)	54.0–96.0 (84.0)
Pennate diatoms	0.16–2.39 (0.21)	1.6–23.9 (2.1)	3.9–28.3 (11.0)	39.0–283.0 (111.0)
Centric diatoms	0.04–0.16 (0.06)	0.4–1.6 (0.6)	2.6–10.2 (9.1)	25.0–102.0 (91.0)

under-ice water (Table 2.3.1). No *Phaeocystis* spec. was observed in any of the samples.

High bacterial abundances and biomasses were observed throughout the entire ice thickness (Fig. 2.3.4, Fig. 2.3.5), with maximum values of bacterial biomass coinciding well with peak values of ice algal biomass. Bacterial concentrations and biomasses in the under-ice water were considerably lower (Table 2.3.1).

TEP abundance, area and size distribution

TEP were found in all ice and water samples. The concentration of TEP is reported in two ways: TEP abundance (particles l^{-1}) and TEP area (cm^2 l^{-1}). At all stations, highest concentrations of both TEP abundance and area peaked in the interior of the ice (Fig. 2.3.5). TEP abundance and area in the ice varied between 10.22–260.45 × 10^6 particles l^{-1} and 3.4–92.1 cm^2 l^{-1}, respectively. TEP abundance in the water varied between 3.04–3.64 × 10^6 particles l^{-1}, the TEP area between 0.8 and 1.1 cm^2 l^{-1}. The median concentrations in the ice (TEP abundance: 50.16 × 10^6 particles l^{-1}, TEP area: 21.3 cm^2 l^{-1}) exceeded medians in the water (TEP abundance: 3.56 × 10^6 particles l^{-1}, TEP area: 1.0 cm^2 l^{-1}) by one order of magnitude. This difference was statistically significant for both parameters (Mann-Whitney U-test: $p = 0.005$ for both TEP abundance and area).

Although TEP concentrations showed a wide variability, the general size distributions of TEP were relatively similar. TEP abundance decreased with TEP size (ESD) and this relationship could be described by powerlaw functions. The slopes in log-log regressions ($\beta+1$) in the sea-ice samples ranged between 2.5 and 3.5 and were not correlated with ice depth. $\beta+1$ of the water samples varied between 3.0 and 3.5. The relative TEP size frequencies of the pooled ice and water samples are given in Fig. 2.3.6. The slopes ($\beta+1$ values) were relatively flat in both habitats and indicate a relative large amount of larger TEP particles.

In the sea ice, a close coupling of algal and bacterial biomass and TEP was indicated by highly significant Spearman-Rank correlations. Bacterial biomass was significantly correlated to both TEP abundance ($\rho = 0.692$, $p < 0.0003$) and TEP area ($\rho = 0.703$, $p = 0.0003$). High Spearman-Correlation coefficients were also found for correlations of TEP abundance and TEP area with pennate diatom biomass (TEP abundance: $\rho = 0.699$, $p = 0.0003$, TEP area: $\rho = 0.687$, $p = 0.0004$) and centric diatom biomass (TEP abundance: $\rho = 0.729$, $p = 0.0002$, TEP area: $\rho = 0.756$, $p < 0.0001$). A close relationship was also detected for the ice data of bacterial and pennate diatom biomass ($\rho = 0.708$, $p = 0.0002$) and bacterial and centric diatom biomass ($\rho = 0.796$, $p < 0.0001$).

Bacterial colonisation of TEP

Doublestaining TEP with Alcian Blue and DAPI showed that all investigated particles were colonised by bacteria. Bacteria were observed both on the surface of and in the interior of the TEP. The colonisation was very variable, with a range of 1–220 bacteria TEP^{-1} (median: 15 bacteria TEP^{-1}) in the sea ice and 1–103

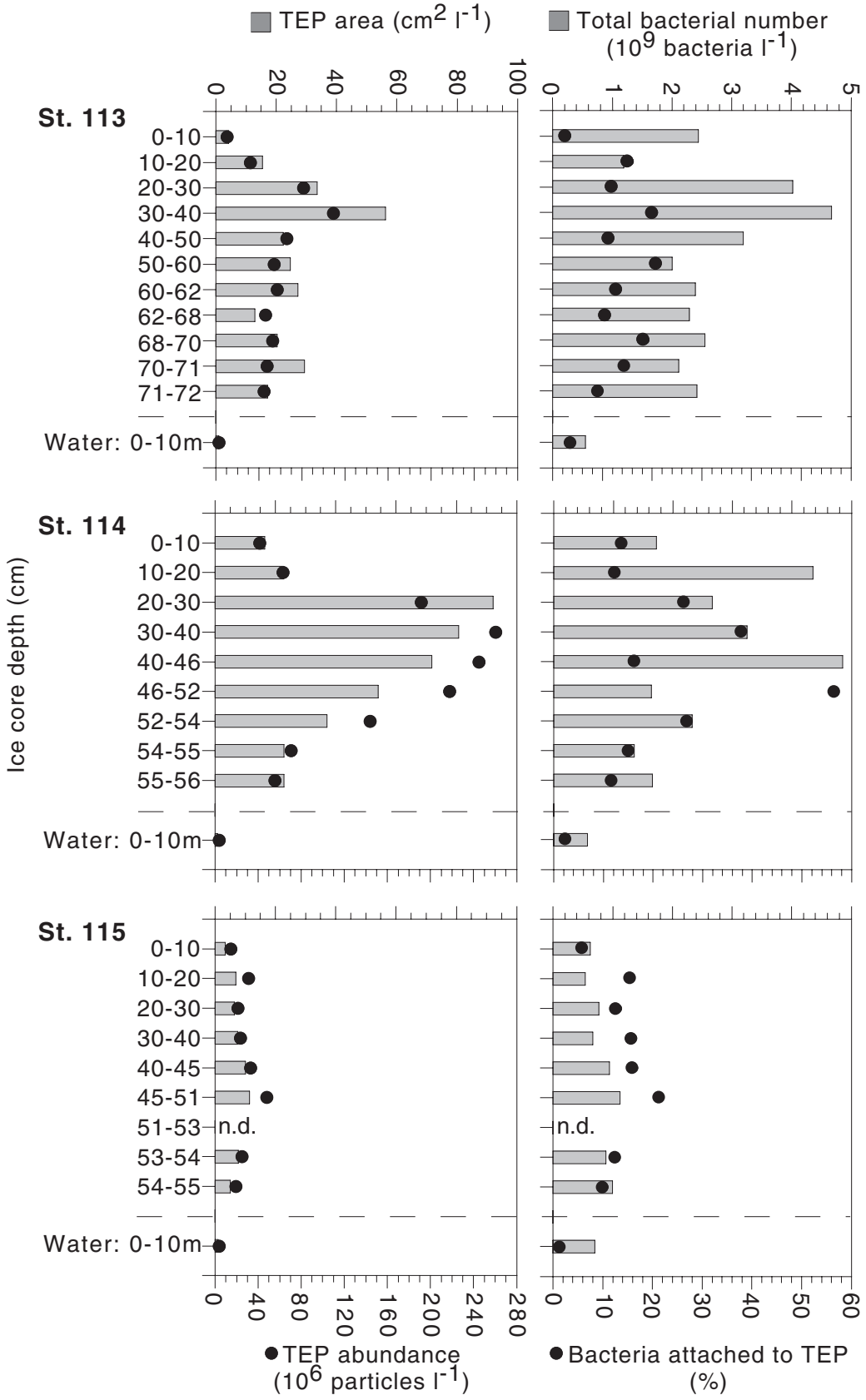

Fig. 2.3.5: Vertical distribution of TEP area, TEP abundance, total bacterial number and the relative number of bacteria attached to TEP (%) in sea ice and underlying water. n.d. = no data

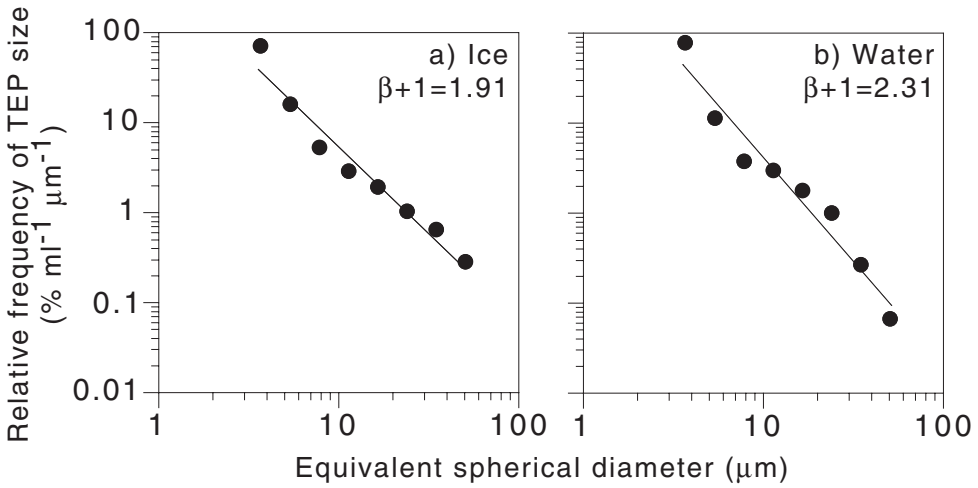

Fig. 2.3.6: Relative size frequencies of transparent exopolymer particles (TEP) for **a)** the pooled sea-ice (Ice) and **b)** water samples (Water)

bacteria TEP^{-1} (median: 13 bacteria TEP^{-1}) in the water samples. The absolute number of bacteria in both sea ice and water increased with TEP size (Fig. 2.3.7a), whereas the number of bacteria per unit TEP volume decreased with TEP size (Fig. 2.3.7b). A total range of 1.5 % to 56.5 % of the total bacterial number was attached to TEP. The median of the relative number of attached bacteria in sea ice (14.8 %) was significantly higher than the median (1.9 %) of the water samples (Mann-Whitney U-test: $p = 0.0062$). The percentage of bacteria associated with TEP in the sea ice was correlated with TEP abundance ($\rho = 0.542$, $p = 0.0048$) and TEP area ($\rho = 0.538$, $p = 0.0051$).

2.3.4 Discussion

This study gives first data on the abundance, size and bacterial colonisation of TEP in Antarctic sea ice and underlying water. High concentrations and distinct size distributions of TEP were found in all ice samples.

TEP concentration, distribution and characteristics
TEP abundances in sea ice were generally very high and comparable to or exceeding maximum concentrations reported from different marine pelagic habitats (Alldredge et al. 1993, Passow and Alldredge 1994, Mari and Kiørboe 1996, Mari and Burd 1998, Simon et al. 2002). Krembs and Engel (2001) highlighted the role of TEP in Arctic pack ice of the Laptev Sea. They reported on TEP areas between below detection and 16 $cm^2\ l^{-1}$ in Arctic pack ice, with a median of 2.9 $cm^2\ l^{-1}$. The median of the present study is approx. 10 times higher, demonstrating that Antarctic sea ice harbours large amounts of TEP.

Despite the relative close geographical vicinity of the sampled ice floes, the investigated floes are likely to have different developmental histories which might explain the distinct differences in the vertical distribution of both biomass and TEP between the stations. At all stations, maximum TEP concentrations occurred in layers coinciding with the maxima of bacterial and algal biomass. At stations 113 and 114 the TEP and biomass maxima were located in a layer of porous ice (of intermediate granular / columnar or granular texture) approximately 10 cm below the freeboard layer of the ice floes. These porous layers near sea level have been described (Ackley and Sullivan 1994) and are believed to originate by either internal melting or surface flooding and infiltration of sea water into the snow, followed by freezing (Fritsen et al. 1994). Fritsen and Sullivan (1997) proposed a conceptual model for the distribution and development of microbial communities in Antarctic pack ice and described the occurrence of biomass-rich surface and surface / internal communities for Antarctic second-year sea ice (sea ice that survived the summers melt season), whereas first-year sea ice normally shows lower biomass, often located in the interior and at the bottom of the ice floes. Therefore, despite the similar ice bulk salinities at all stations, the distinct biomass distributions suggest that stations 113 and 114 resemble older ice floes, which allowed for the accumulation of biomass and TEP to the high levels observed. Salinities > 7.8 as well as low biomass and TEP concentrations, indicate that the sea ice at Station

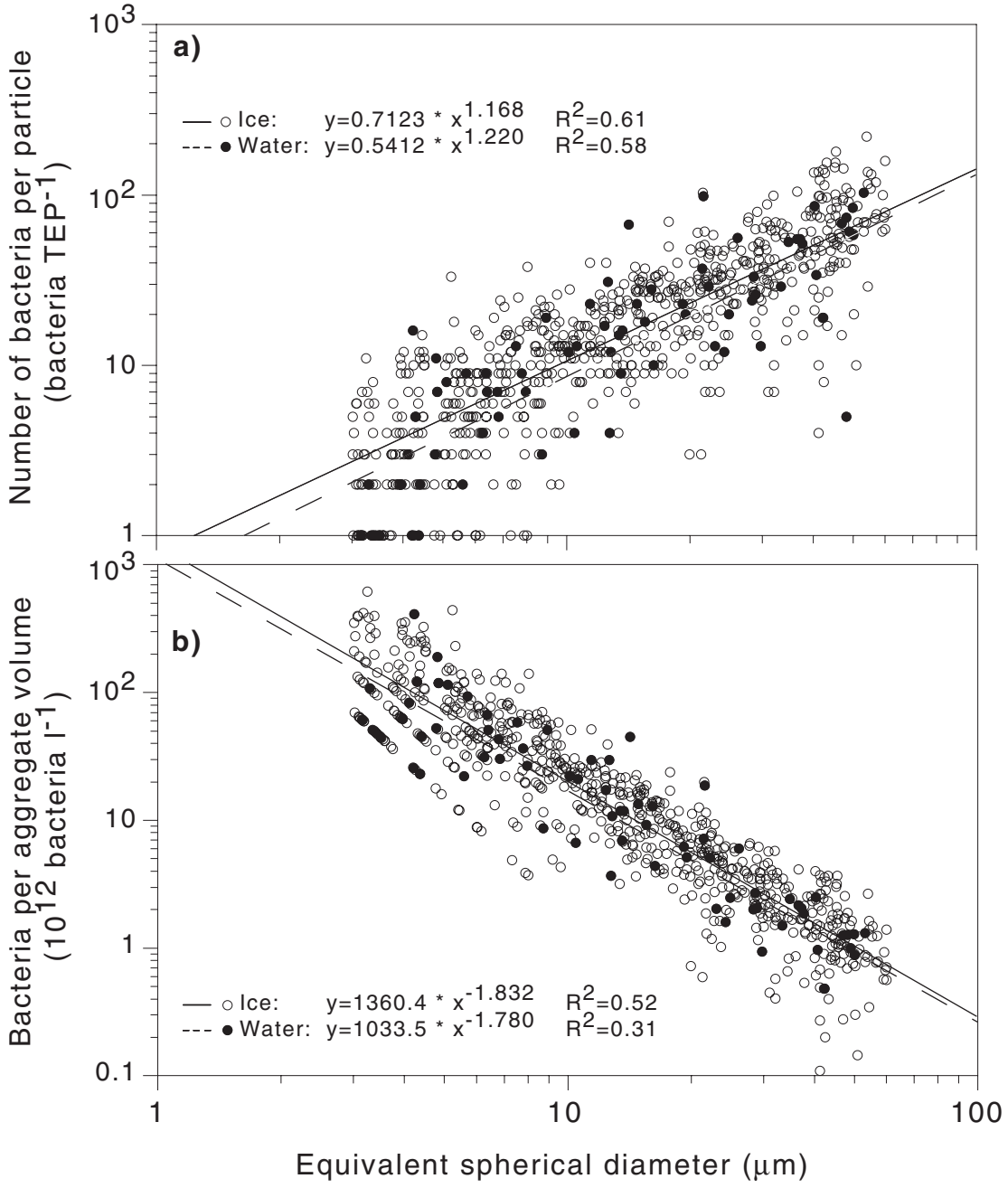

Fig. 2.3.7: a) Total number of bacteria per individual TEP versus size of the respective TEP. **b)** Bacteria per aggregate volume versus size of the respective TEP

115 was relatively young, but nevertheless already contained TEP concentrations which exceeded those found in the water by a factor of 4–13. The data suggest that TEP is an integral component of different sympagic communities of Antarctic first-year and second-year sea ice.

The number of TEP was negatively correlated with TEP size in both sea ice and under-ice water. The β+1 values of the size distributions were small and indicate a relatively large proportion of larger particles. β+1 values in this study differed from the theoretical value of β+1 = 4, consistent with steady-state size spectra of TEP being formed by shear coagulation from smaller particles (McCave 1984). The size-spectra of TEP were comparable to those reported from field studies in temperate pelagic habitats (Passow and Alldredge 1994, Mari and Kiørboe 1996) and in Arctic sea ice (Krembs and Engel 2001). A high proportion of relatively large particles has been explained by TEP formation in the form of mucus sheets, coagulation of

smaller TEP with non-TEP particles and the fractal nature of TEP (Passow and Alldredge 1994, Mari and Kiørboe 1996). The high concentrations of sympagic diatoms, potentially producing mucus in the form of sheets may serve as an explanation for the size distribution observed in the present study. However, the elevated amount of larger TEP particles can also be attributed to other characteristics in the sea ice and under-ice habitat, e.g. elevated shear or disruption of sympagic biofilms, which occurrence has been proposed by Thomas and Dieckmann (2002).

Sources and formation of TEP

The high TEP concentrations in the ice can be caused by different mechanisms: physical enrichment of TEP during ice formation, abiotic production of TEP from dissolved and / or colloidal precursors and biological production of TEP by sympagic organisms.

Physical enrichment

Different processes have been described for the physical incorporation and enrichment of sediment and organisms into newly forming and existing ice sheets (Ackley 1982, Reimnitz et al. 1990, Grossmann and Dieckmann 1994, Spindler 1994). Exceptional high accumulations have been observed in granular ice, associated with dynamic, turbulent growth conditions and high growth rates of the sea ice (Weeks and Ackley 1982, Clarke and Ackley 1984). Granular ice predominates in Antarctic pack ice with a contribution of 40–70 % (Clarke and Ackley 1984, Scott et al. 1994). Granular ice was also an important fraction in the sea ice under investigation. It is therefore assumed that TEP is already enriched in young Antarctic sea ice formed under dynamic conditions. This hypothesis is supported by the enriched TEP values observed in the relatively young sea ice at station 115.

Abiotic formation

High concentrations of dissolved organic carbon (DOC) have been reported from sea ice of both polar oceans and have been attributed to mechanical damage of organisms during the formation and consolidation of the ice, to grazing activity of sympagic proto- and metazoans, to osmotic adjustment of ice organisms and to increased algal extracellular release (Gleitz and Thomas 1993, Thomas et al. 1995, Thomas et al. 1998, Thomas et al. 2001). Herborg et al. (2001) reported on high concentrations of carbohydrates contributing up to 31 % of the DOC pool in Antarctic pack ice. DOC and especially carbohydrates are important precursors of polymers and thus for TEP (Myklestad 1995, Passow 2000). Sea-ice temperature in combination with ice bulk salinity determines the brine volume and directly controls the salinity of the brine (Assur 1958, Frankenstein and Garner 1967). During winter decreasing temperatures in sea ice, therefore increase brine salinities and concentrate DOC in decreasing brine volumes. Aggregation is a positive function of both the concentration of divalent cations (Simon et al. 2002) and precursor concentration (Chin et al. 1998). Increasing salinity and DOC concentration during cooling of the sea ice may therefore serve in concert in the abiotic formation of TEP in the sea-ice habitat.

Biotic production

A third possible explanation for the high TEP concentrations in sea ice is the direct production of polymeric substances from cell internal carbon pools, the production of extracellular polymeric substances (EPS), respectively. Especially diatoms produce copious amounts of EPS which serve the algae in adhesion, locomotion and the buffering of environmental stress (Hoagland et al. 1993, Cooksey and Wigglesworth-Cooksey 1995, Wetherbee et al. 1998). Recently protective microhabitats around diatoms in Arctic sea ice were observed with *in situ* microscopical techniques (Junge et al. 2001, Krembs pers. comm.). Increased EPS production by algae has been also described for senescent diatom blooms and as response of algae exposed to high salinities, cold temperatures, nutrient limitation and low irradiance (Aletsee and Jahnke 1992, Hoagland et al. 1993, Passow and Alldredge 1994, Mopper et al. 1995, Liu and Buskey 2000, Wolfstein and Stal 2002). These conditions are typical for Antarctic sea-ice communities during the autumn season, when irradiance levels and temperatures decrease drastically. For example, in this study ice temperatures in the internal communities with highest TEP concentrations were very low ranging between −5.9 °C and −7.7 °C. Calculated brine salinities in these layers ranged between approx. 100–120 and caused harsh osmotic stress to the inhabiting organisms. During the cooling of the sea ice, brine channels additionally become increasingly disconnected (Golden et al. 1998, Krembs et al. 2000), reducing nutrient-availability on small scales and therefore increase

nutrient stress in microhabitats, a process that can further enhance EPS production. From bulk nutrient concentrations and the theoretical derived brine volumes, the nutrient concentrations in the brine were calculated. These theoretical derived values ranged between 7.7–105.1 µM NO_3, 4.2–122.7 µM PO_4 and 77.2–3289.2 µM $Si(OH)_4$ and were much higher than half saturation constants (K_s values) reported for mixed natural phytoplankton assemblages (Sommer 1998). This suggests that the sea-ice algae were not nutrient limited during the time of investigation and that this factor was not responsible for the high observed TEP concentrations. However, nutrient limitation during Antarctic ice algal blooms has been reported (e.g. Gleitz et al. 1995, Kristiansen et al. 1998) and may have enhanced the production of TEP in the interior of the ice floes at stations 113 and 114 during spring and summer. The high TEP concentrations may therefore represent a signal of a previous situation of nutrient limitation, when algal derived refractory TEP accumulated in the ice.

Producers of TEP

Algae and especially pennate diatoms are considered as the most important producers of EPS in marine benthic and planktonic habitats (Hoagland et al. 1993, Smith and Underwood 1998, Smith and Underwood 2000, Passow 2002). However, also bacteria are capable to produce TEP, but their role in TEP production has been only recently examined and is not fully understood (Passow 2002, Simon et al. 2002). In this study TEP abundance and area showed highly significant correlations to both algal biomass and bacterial biomass. In order to estimate the importance of algal and bacterial derived TEP in the sea ice, published EPS production rates of algae and bacteria were used for the calculation of daily production rates of exopolymeric substances of these groups in the sea ice. Due to the lack of data of cold-adapted organisms, cell-specific production rates of temperate epipelic diatoms (6.31–31.46 pg glucan equivalents $cell^{-1}$ d^{-1}; Smith and Underwood (2000)) and temperate planktonic bacteria (4 amol C $cell^{-1}$ d^{-1}, Stoderegger and Herndl 1999) were used. Neglecting temperature effects, estimated EPS production of diatoms was on average 195.1 µg C l^{-1} d^{-1} (range: 6.1–581.2 µg C l^{-1} d^{-1}, the estimated bacterial EPS production averaged only 2.5 µg C l^{-1} d^{-1} (range: 0.6–5.6 µg C l^{-1} d^{-1}). The diatom EPS production / bacterial EPS production ratio averaged 102.5 (range: 2.2–507.5). Hence, the estimated algal EPS production exceeded the bacterial EPS production on average by two orders of magnitude, indicating that diatoms were the most important EPS producers in the sea-ice habitat. These estimates are consistent with results of pelagic studies from lower latitudes, which report on diatoms as the main producers of TEP in the pelagic realm (Passow et al. 1994, Passow and Alldredge 1995).

TEP carbon

To estimate the TEP carbon pool I used the formula given by Mari (1999) for laboratory-made TEP with TEP-C (µg C TEP^{-1}) = $0.25 \times 10^{-6} \times r^{2.55}$, where r is the equivalent spherical radius and 2.55 is the fractal dimension D of TEP. Integrated sea-ice TEP carbon was equivalent to 14–32 % of the integrated POC values, to 34–78 % of the integrated algal biomass (sum of pennate and centric diatoms) and to 1157–2090 % of the integrated bacterial biomass. Keeping in mind the problems in transferring characteristics (volume, carbon-content) of laboratory-made TEP to field samples, the data nevertheless indicate that TEP significantly contributes to the carbon pool in Antarctic sea ice. The estimates are similar to values from planktonic studies showing that aggregates contribute between 4–30 % to pelagic particulate organic carbon (Alldredge and Silver 1988, Alldredge and Gotschalk 1990, Riebesell 1991, Simon et al. 2002).

TEP colonisation

Different studies on Antarctic sea ice reported on the high number of epiphytic bacteria in the sea-ice habitat (e.g. Ackley and Sullivan 1994, Archer et al. 1996, Thomas et al. 1998), but no information about sympagic bacteria on aggregates has been published. In this study the first data on the bacterial colonisation of TEP in sea ice are presented.

In the pelagic realm, TEP and larger aggregates can serve bacteria as special microhabitats and have been recognised as sites of increased hydrolytic enzyme activity and nutrient remineralisation (e.g. Smith et al. 1992, Ploug et al. 1999, Ayo et al. 2001). In the present study the total number of bacteria attached to individual TEP ranged between 1–220 bacteria TEP^{-1} and was within the range reported in pelagic studies (Passow and Alldredge 1994, Mari and Kiørboe 1996, Simon et al. 2002). The high variability in the colonisation of similar sized TEP indicates differences in the

degree of colonisation and was possibly caused by the different age and chemical composition of the TEP (Passow and Alldredge 1994). The total number of attached bacteria increased with TEP size, whereas the specific number decreased with size. This relationship has also been reported for planktonic aggregates and has been attributed to the fact that porosity of aggregates increases with size (Mari and Kiørboe 1996, Ploug et al. 1999, Simon et al. 2002). By using the median brine volume (11.9 %), the total bacterial number occurring in the sea-ice brine was calculated and in turn was used for the calculation of enrichment factors (EF) = bacteria per aggregate volume (cells ml^{-1})/bacterial concentration in brine (cells ml^{-1}). EF in sea ice averaged 2950, a value consistent with high enrichment factors of bacterial colonisation of planktonic aggregates (Ploug et al. 1999, Simon et al. 2002).

The percentage of attached bacteria shows a wide range in different planktonic habitats (e.g. Alldredge and Gotschalk 1990, Turley and Stutt 2000) and depends mainly on the abundance of aggregates (Simon et al. 2002). In most pelagic environments the percentage of attached bacteria constitutes less than 10 % and often less than 5 % of the total bacterial number (Alldredge and Gotschalk 1990, Turley and Stutt 2000, Simon et al. 2002). The median percentage of bacteria attached to TEP (1.9 %) in the water samples of this study falls very well in this range. The median percentage (14.8 %) in the ice samples was relatively high, indicating favourable conditions for sympagic bacteria associated with TEP.

3 General discussion

3.1 Critical evaluation of applied methodology

Sampling

All ice samples were collected using a SIPRE-type ice corer from the upside of the sea ice. This approach can result in the destruction of the delicate skeletal layer (Weeks and Ackley 1982) at the subsurface of the ice floes and in the subsequent loss of the lowermost centimetres of the ice core. In this study only cores with an undisturbed subsurface were used for further analysis to ensure the analysis of complete ice cores.

After ice core retrieval, brine drainage causes loss of brine and sympagic biota. Fast processing of the ice cores and the generally low porosity of the sea ice under investigation ensured that brine drainage during sampling was small in this study. However, brine drainage was not quantifiable and may have affected especially measurements from ice core sections with a relatively high brine volume and porosity like e.g. bottom sections in all three regions and the porous layers in the upper parts of the Antarctic sea ice.

Melting

Melting of ice core samples drastically reduces salinity in the liquid phase of the sample causing osmotic stress for the organisms (Garrison and Buck 1986). In the present study, samples for the microscopical investigation of organisms were melted at 4 °C in the dark with addition of 0.2 µm filtered seawater to buffer osmotic stress (Spindler and Dieckmann 1986). Garrison and Buck (1986) found that this method prevents the loss of over 70 % of delicate protists (especially flagellates and ciliates) compared to direct melting of samples. During melting (ca. 4–24 h) organism abundance can be also influenced by heterotrophic growth and grazing. This can increase or reduce the abundance of organisms in the sample and may have affected estimates of *in situ* abundances in the present study. In order to minimise these factors, all samples were fixed as soon as they were completely melted.

Additional formation of TEP during melting was avoided as follows. TEP were determined in samples that were melted by addition of 0.2 µm filtered sea water (Garrison and Buck 1986, Spindler and Dieckmann 1986). Concentrations of dissolved organic carbon (DOC) in sea ice are normally considerably higher than water values (Bunch and Harland 1990, Thomas et al. 1995, Thomas et al. 1998, Herborg et al. 2001). Thus, the addition of the sterile-filtered seawater reduced not only TEP concentrations but also DOC concentrations in the meltwater. The dilution reduces encounter rates of DOC as well as TEP particles, and is therefore assumed to reduce both the abiotically formation of TEP from dissolved TEP precursors (Chin et al. 1998, Passow 2000) and coagulation of TEP into larger particles (Passow et al. 1994, Schuster and Herndl 1995, Mari and Burd 1998) during the melting process. The avoidance of osmotic stress on the organisms additionally minimised active TEP production by organisms, which can response to osmotic stress by enhanced excretion of polymeric substances (Decho 1990, Hoagland et al. 1993). Additionally, disintegration of sea-ice TEP during the ice melt can bias results. Riebesell et al. (1991) for example reported monospecific diatom aggregates on the subsurface of Antarctic sea ice, to likely have formed inside the brine channel system. This type of monospecific aggregates was not observed in any of my samples. I assume that disaggregation did not occur, since a large contribution of relatively large particles was observed in all samples. Ice melt destroys the natural structure of the sea-ice habitat and allows free interaction of particles, which before were separated by the sea-ice crystal structure. Differences between the natural and observed TEP abundances and characteristics in sea-ice samples can therefore not be excluded (Krembs and Engel 2001). To conclude, the applied methods for the determination of TEP in sea ice minimised artificial changes in the abundance and size characteristics of TEP.

TEP size and TEP volume

TEP have a high water content and can collapse and deform during and after filtration, which can greatly affect the estimates of ESD and, subsequently, calculated TEP volume (Mari and Kiørboe 1996, Berman and Viner-Mozzini 2001). In addition, the calculation of the TEP volume premises that the aggregates are spherical and solid. This assumption neglects the fractal nature of TEP, i.e. the increase of the particle porosity with particle volume (Jackson et al. 1997, Berman and Viner-Mozzini 2001, Simon et al. 2002). Therefore, my calculations of the bacterial concentrations per TEP volume should be considered only as tentative estimates.

Abundance and biomass

The microscopical count of microorganisms is subject to methodological and statistical errors (e.g. Edler 1979, Bölter et al. in press). In this study approx. 100 protists per counting unit and a minimum of 400 bacteria were enumerated per sample resulting in an average statistical counting error of ca. 10–20 % (Edler 1979). Protist biomass was calculated with a constant volume:carbon conversion factor (Baltic Marine Environment Protection Commission 1988). This method neglects that smaller organisms generally have a higher specific carbon per volume content than larger organisms (Menden-Deuer and Lessard 2000). Bacterial cell carbon was calculated using an allometric cell-volume:carbon conversion model which accounts for the condensation of carbon in smaller cells (Simon and Azam 1989, Norland 1993). In a recent study Pelegrí et al. (1999) measured carbon contents of individual cells by high temperature catalytic oxidation. The authors proposed a linear carbon:volume relationship and the use of a single carbon:volume conversion factor for bacteria and protists. In order to estimate the impact of different volume:carbon models, I used also their formula to calculate bacterial and protist biomass for the Baltic sea ice (chapter 2.1). According to the approach of Pelegrí et al. (1999) the bacterial biomass in the study on Baltic Sea ice was overestimated by ca. 250 % and the biomass of protists was underestimated by ca. 15 %.

3.2 Discussion of results

3.2.1 Structure and composition of the sympagic community in the brackish Baltic sea ice

Consistent with other studies, this work showed that Baltic sea ice is a habitat for prokaryotes, protists and metazoa (Huttunen and Niemi 1986, Norrman and Andersson 1994, Laamanen 1996, Ikävalko and Thomsen 1997, Haecky and Andersson 1999). Integrated biomass in sea ice was relatively low ranging between 2.7–45.1 mg C m^{-2}. Using the same sampling techniques and methodologies in biomass determination as in the present study, Gradinger et al. (1999) reported much higher integrated biomass values (average: 195.6 mg C m^{-2}) for Arctic pack ice in the Greenland Sea sampled in summer and autumn. In their study, bacteria contributed the largest fraction of carbon with 31 %, followed by pennate diatoms (26 %), heterotrophic flagellates (20 %), autotrophic flagellates (17 %) and meiofaunal organisms (metazoans and ciliates, 3.7 %). Total carbon in the present study, in contrast, was dominated by pennate diatoms (32.8 %), followed by centric diatoms (28.8 %), autotrophic flagellates (22.7 %), bacteria (7.7 %), heterotrophic flagellates (7.1 %) and metazoa (0.9 %). The relative contribution of autotrophic biomass in the Baltic sea ice (average: 84.3 %) exceeded that of the Arctic sea ice (ca. 42 %) by far. This, in part, reflects the different sampling seasons but can possibly also be attributed to other properties of the ice like ice structure, ice porosity and total ice thickness. These ice properties affect the nutrient availability and thus composition of interior communities. Arctic multi-year sea ice is often characterised by low nutrient concentrations, which tends to favour microbial networks (Gradinger 1999b), while in Baltic sea ice new production systems were encountered.

Metazoan biomass in Baltic sea ice was low (average: 0.05 mg C m^{-2}) compared to Arctic and Antarctic sea-ice data (including ciliates and foraminifera) which range between < 0.1–7.4 mg C m^{-2} and 0–118.2 mg C m^{-2}, respectively (Gradinger 1999a). Relative contribution of metazoa to total biomass of the Baltic sea ice was 1 %, which is similar to estimates of Gradinger et al. (1999) reporting on a small relative contribution of metazoa (< 3.7 %) to sympagic biomass in the Greenland Sea. The sympagic metazoan community in the Baltic consisted of rotifers and nauplii only, with rotifers dominating biomass at all stations. Baltic sea ice seems to lack the majority of metazoan taxa described for Arctic sea ice like acoel turbellarians, nematodes, copepods, polychaetes, gastropod and tunicate larvae and amphipods (Horner 1985a, Grainger and Hsiao 1990, Friedrich 1997, Gradinger et al. 1999, Friedrich and Hendelberg 2001, Nozais et al. 2001). Rotifers have been described as an important group in various Arctic sea-ice studies (e. g. Cross 1982, Kern and Carey 1983, Grainger et al. 1985). Benthic types dominate rotiferan abundance in Arctic fast ice (Chengalath 1985), whereas pack ice is dominated by the generally planktonic genus *Synchaeta* (Friedrich and De Smet 2000). In contrast, both Baltic Sea pack and fast ice were dominated by planktonic protist and metazoan species, and despite shallow

water depths, rather serve as additional temporal habitats for planktonic than for benthic organisms (Ikävalko and Thomsen 1997, Ikävalko 1998b). The Baltic sea ice therefore resembles ecological conditions typical for Antarctic sea ice, where the sea-ice organisms have to cope with a planktonic life-phase (Spindler 1994). In contrast, perennial Arctic sea-ice floes can serve as habitat for autochthonous organisms spending most of their life-cycle in close association with sea ice (Gulliksen and Lønne 1989, Horner et al. 1992). The seasonal ice cover and the low diversity of the brackish environment (Remane 1958, Lenz 1995) may explain the low species number of metazoans in Baltic sea ice.

3.2.2 Importance of abiotic and biotic factors for the accumulation of algae in the Baltic sea ice

The influence of temperature on the photosynthesis, respiration and growth of ice algae is still under discussion (Kirst and Wiencke 1995, Thomas and Dieckmann 2002, Gradinger 2002). Temperature affects the algal metabolism by altering reaction kinetics and membrane properties. Studies on the effect of temperature on Arctic and Antarctic ice algal growth showed that many polar species are psychrophilic (= have optimum temperatures below 15 °C) but that *in situ* temperatures are generally still suboptimal (Bunt 1968, Kottmeier and Sullivan 1987, Kirst and Wiencke 1995). There are no studies on the temperature effect on the growth of Baltic sea-ice algae. However, the findings of the Arctic and Antarctic studies in combination with the observed ice temperatures in the Baltic (−3.1 °C to −0.2 °C) suggest suboptimum growth conditions for the sea-ice algal community under investigation.

In sea ice, temperature directly controls brine salinity (Assur 1958). Maximum brine salinities measured in Baltic sea ice range between 25–30 (Ikävalko and Thomsen 1997). Brine salinities calculated in the present study were highly variable (3.6–54.2) and exceeded water column salinities by factors of 1 to 20. Sea-ice algae from the Arctic and Antarctic can grow over a wide range of salinities ranging between 5 and 90 (Grant and Horner 1976, Bartsch 1989) and can apparently cope better with decreasing than increasing salinities (Kirst and Wiencke 1995). The high brine salinity relative to the water column is assumed to limit growth of algae adapted to the low salinity regime of the northern Baltic Sea.

Reflection, backscatter and absorption of incident light in sea ice reduce irradiance below polar sea ice by a factor mostly between 50–1000 (Maykut 1985, Eicken 1992). The low ice thickness of Baltic sea ice generally allows comparatively high transmittance. However, the combined effect of ice thickness and snow cover reduced the light levels below sea ice in the Bothnian Bay by ca. 50 % (calculated after Maykut 1985). Although sea-ice algae have a high potential for photoacclimation and are able to grow at very low irradiance levels (Gleitz and Kirst 1991, Kirst and Wiencke 1995, Mock and Gradinger 1999, Gradinger 2002), I assume that the sympagic algal community in the Bothnian Bay sea ice was light limited during the time of sampling. This conclusion is in agreement with investigations on annual Arctic sea ice and a previous study on Bothnian Bay sea ice, which considered the sea-ice algal communities to be light limited during their early developmental stage (Gosselin et al. 1990, Cota et al. 1991, Haecky and Andersson 1999). I propose snow cover on the sea ice as an important factor in the onset of both the ice algal and pelagic spring bloom in the Bothnian Bay.

Both measured and potential ice algal photopigment concentrations were very low in the sea ice investigated in the northern Baltic Sea during the year 2000. This is most likely attributed to low phosphate concentrations trapped into the ice during its formation (Haecky and Andersson 1999). Nutrient availability in Baltic sea ice is also restricted due to the low brine-volumes in the brackish sea ice with a median of only 3 % (this study). Golden et al. (1998) suggest a threshold of 5 % brine volume below which sea ice is effectively impermeable for fluid transport. Low brine volumes are therefore considered an important, hitherto neglected, controlling factor for the ice algal accumulation in brackish sea ice.

Estimates of maximum potential daily ingestion rates (calculated according to Moloney and Field 1989) showed that the Baltic sea-ice metazoa consumed on average 1.5 % of the ice algal standing stock. This value is consistent with estimates for Arctic sea ice (0.9 %) given by Nozais et al. (2001) and a study by Gradinger (1999a) reporting on low meiofaunal grazing impact in Arctic and Antarctic pack ice. The pre-

sent study did not account for protozoan grazing, because protozoans were assumed to be primarily bacterivorous. However, larger ice-associated flagellates and ciliates are known to feed on sympagic diatoms (Buck et al. 1990, Ikävalko and Gradinger 1997), leading to a higher total grazing pressure. However, the concentration of larger (> 40 µm) protozoans was generally less than 100 cells l^{-1}, and thus protozoan herbivory can be neglected.

3.2.3 Distribution and size frequency of transparent exopolymer particles (TEP) in Arctic and Antarctic sea ice

This study gives first estimates for the vertical distribution of TEP in Arctic and Antarctic sea ice. Both Arctic and Antarctic sea ice showed high TEP abundances and TEP areas. In terms of abundance, maximum values in the ice were similar or exceeding water values given in various planktonic studies from lower latitudes (Table 3.2.3.1). In terms of TEP area, sea ice maximum values exceeded maximum planktonic values of various marine environments by 1–3 orders of magnitude, indicating the large size of individual sea-ice TEP. Median total TEP area in sea ice was 2–20 times higher than values reported for ice algal communities in the Arctic Laptev Sea (Krembs and Engel 2001), although diatom abundances in the studies coincided very well. The difference is most likely attributable to the examination of TEP-rich interior communities, which were neglected in the previous study. Interior communities are a typical feature of Antarctic pack ice (Horner 1985a, Horner et al. 1992, Gradinger 2002), but their importance has been recently described also for Arctic pack ice (Gradinger and Zhang 1997, Gradinger 1999b, Mock and Gradinger 1999). Interior sea-ice communities are exposed to more extreme environmental conditions than bottom communities, which might explain TEP enrichment due to the response of organisms to e.g. cold temperatures, high brine salinities and reduced nutrient availability.

First estimates of sea-ice TEP carbon (calculated according to the equation given by Mari (1999)) varied considerably between stations but demonstrate the significant contribution (14–32 %) of TEP carbon to integrated POC in Arctic and Antarctic sea ice. The results suggests TEP to be an important fraction of the carbon pool of Arctic and Antarctic sea-ice communities.

TEP size distributions in both sea ice and under-ice water were characterised by low β+1 values and were in accordance with those observed for Arctic Laptev Sea sea-ice TEP (Krembs and Engel 2001). The low β+1 values indicate a more significant contribution of larger particles compared to values typically observed in the water-column (McCave 1984, Mari and Burd 1998). I assume that the low β+1 values in the ice samples reflect the special physical conditions of the sea-ice habitat. Krembs (1998) proposed that EPS accumulates at special microsites within brine channels, characterised by high shear stress and increased advective transport, which might enhance the formation of TEP. Size spectra of TEP are also affected by other abiotic factors e.g. the concentration of TEP and non-TEP particles as well as particle stickiness. In addition, biotic factors such as the production of capsular EPS by bacteria and / or algae and grazing by metazoa have been reported to increase the relative proportion of larger TEP (Passow and Alldredge 1999, Stoderegger and Herndl 1999, Prieto et al. 2001). The latter process may also result in the disruption of sympagic biofilms whose occurrence has been proposed by Thomas and Dieckmann (2002).

The low β+1 values in the under-ice water samples suggest that the samples contained TEP from the ice interior, which may have been transported to the water column by gravity brine-drainage (Nakawo and Sinha 1981, Weeks and Ackley 1982) or Bernoulli-suction due to current flow at the ice-water boundary (Feltham et al. 2002). Larger TEP may also be formed directly in the under-ice water layer by e.g. elevated shear stress.

3.2.4 Importance of TEP for the sea-ice habitat and implications for the ice-covered ocean

Potential ecological functions

The calculations of the potential EPS production of sympagic bacteria and diatoms point towards diatoms as the dominant producers of polymeric substances in Arctic and Antarctic sea ice. This observation mirrors the situation in other porous habitats like mudflats, in which epipelic diatoms produce high amounts of EPS

Table 3.2.3.1: Abundance and area of transparent exopolymer particles (TEP) in different marine environments. n.a. = not available

Location	Environment	Depth (m)	TEP abundance (TEP l^{-1})	TEP area (cm^2 l^{-1})	Reference
Southern California Bight	Pelagial	10	2.8×10^4–4.0×10^5	n.a.	Alldredge et al. (1993)
Monterey Bay	Pelagial	5–100	1.5×10^5–4.9×10^6	n.a.	Alldredge et al. (1993)
Benguela upwelling	Pelagial	0–30	5.5×10^6–16.0×10^6	n.a.	Kiørboe et al. (1998)
Laptev Sea (Arctic)	Pelagial	sub ice	n.a.	0–2.7	Krembs and Engel (2001)
Mediterranean Sea	Pelagial	0–40	1.0×10^7–2.2×10^8	n.a.	Mari et al. (2001)
Kattegat (North Sea / Baltic Sea)	Pelagial	0–25	3.0×10^6–6.0×10^7	n.a.	Mari and Kiørboe (1996)
Kattegat (North Sea / Baltic Sea)	Pelagial	0–30	5.0×10^7–3.8×10^8	n.a.	Mari and Burd (1998)
Monterey Bay	Pelagial	5–75	2.5×10^5–5.2×10^6	0.05–0.5	Passow and Alldredge (1994)
Southern California Bight	Pelagial	10	2.5×10^4–6.3×10^5	0.25–0.65	Passow and Alldredge (1994)
Subtropical NW Atlantic	Pelagial	300–1400	2.0×10^3–6.0×10^3	< 0.01	Passow and Alldredge (1994)
Southern California Bight	Pelagial	0–20	2.0×10^4–6.1×10^5	< 0.01–1.10	Passow et al. (1994)
Northern Adriatic Sea	Pelagial	0–15	0–6.0×10^5	n.a.	Schuster and Herndl (1995)
Fram Strait (Arctic)	**Pelagial**	**0–10**	$\mathbf{4.9 \times 10^5}$–$\mathbf{8.2 \times 10^5}$	**0.2–0.9**	**This study**
Bellingshausen Sea (Antarctica)	**Pelagial**	**0–10**	$\mathbf{3.0 \times 10^6}$–$\mathbf{3.6 \times 10^6}$	**0.8–1.1**	**This study**
Laptev Sea (Arctic)	Sea ice	—	n.a.	0–16	Krembs and Engel (2001)
Fram Strait (Arctic)	**Sea ice**	**—**	$\mathbf{4.3 \times 10^5}$–$\mathbf{1.5 \times 10^7}$	**0.6–16.2**	**This study**
Bellingshausen Sea (Antarctica)	**Sea ice**	**—**	$\mathbf{1.0 \times 10^7}$–$\mathbf{2.6 \times 10^8}$	**3.4–92.1**	**This study**

(Goto et al. 1999, Smith and Underwood 2000), which serve the organisms in various function, e.g. locomotion, adhesion, protection against harsh environmental conditions and habitat stabilisation (e.g. Hoagland et al. 1993, Smith and Underwood 1998, Wetherbee et al. 1998). Sea ice has a large internal surface of about 4 m^2 kg^{-1} (Krembs et al. 2001), which the organisms use for locomotion, grazing and attachment (Ikävalko and Gradinger 1997). The potential TEP-coverage of the interior sea-ice surface, however, is low. Assuming a brine channel diameter of 200 µm (Weissenberger et al. 1992), and using the average relative brine volumes (Arctic sea ice: 8.1 % (vol / vol), Antarctic sea ice 13.2 % (vol / vol)) I calculated a crude estimate of the sea-ice interior surface, which was 1.6 m^2 l^{-1} in the Arctic and 2.4 m^2 l^{-1} in the Antarctic. Assuming that all TEP (mean TEP area: Arctic sea ice = 6.2 cm^2 l^{-1}; Antarctic sea ice = 25.6 cm^2 l^{-1}) were associated with crystal surfaces, only 0.04 % (Arctic) and 0.10 % (Antarctic) of the total interior surface of the sea ice were coated with TEP. Despite this low coverage, the development of biofilms in the ice interior is indicated by the TEP size spectra observed in the present study, but the mechanisms of the attachment of algae to ice crystal surfaces remain unknown.

Krembs (pers. comm.) observed high concentrations of Alcian-Blue stainable mucus around diatoms in winter sea ice of the Chukchi Sea. The authors propose that sympagic diatoms produce a EPS-rich "cryosphere", which serves as extracellular protection against high salinities and damage through ice-crystal. Furthermore, they observed that mucus around diatoms impacts brine-pore morphology. This is in agreement with observations by Raymond et al. (1994) who reported so-called ice-active substances (IAS) thought to be glycoproteins, influencing surface and optical properties of sea ice around diatoms.

Beside their potential role in the formation of these microhabitats, polymeric substances may also influence physical properties of sea ice on a larger scale. Elevated concentrations of polymers in sea-ice brine can reduce the brine viscosity and thus affect brine transport within the brine channel system. Reduced brine transport will result in a decreased exchange of dissolved constituents between the sea ice and the underlying water. This may affect nutrient fluxes and may also result in the retention of salt within the sea ice. This in turn influences the habitable pore space available to the organisms (Krembs 1998).

Furthermore, abiotic formation of TEP from dissolved precursors constitutes an alternative to bacterial growth and the microbial loop in converting dissolved organic matter into particulate organic matter (Mari and Burd 1998, Mari 1999, Passow 2000). Surface coating exopolymeric substances and suspended exopolymeric particles can be ingested by heterotrophic

grazers (Decho 1990, Decho 1993). The high TEP concentrations in the sea ice may therefore serve as additional carbon source for sympagic heterotrophs. Information on the ingestion of micrometre-sized particles by sea-ice organisms is limited. Laurion et al. (1995) studied the ingestion of fluorescently labeled bacteria by heterotrophic nanoflagellates in fast ice in Resolute Passage (High Canadian Arctic) and report on ingestion rates similar to those of temperate species. Scott et al. (2001) report on the large prey-size spectrum of the Antarctic sea-ice ciliate *Pseudocohnilembus* spec., which ingests fluorescent microspheres with diameters between 0.25 µm to 4.05 µm. Small-sized TEP fall well within this size range and may therefore serve as food source for sympagic protozoans channeling TEP carbon to higher trophic levels. On the other hand, the food quality of TEP is assumed to be low. Engel and Passow (2001) report on high C / N ratios of TEP (average: 26) compared to the Redfield-ratio. Protozoan grazers can distinguish between different particles (Sherr et al. 1987) and may discriminate TEP during food uptake. Nevertheless, ingestion of TEP may serve as additional food source for sympagic animals and may be especially important during the dark, polar winter when sea-ice primary production is low.

No information is available on bacterial degradation of TEP in sea ice. High rates of aggregate dissolution through enzyme hydrolysis of particulate amino acids and particulate carbon by attached bacteria have been shown for planktonic aggregates (Smith et al. 1992, Simon et al. 2002). On a volume basis, hydrolytic enzyme activities in aggregates sampled in the Southern Californian Bight exceeded those in the surrounding water by factors between 10^2 and 10^5 (Smith et al. 1992). Recent studies using microsensors and newly developed vertical flow systems allowed measurements in the microenvironments surrounding planktonic aggregates (Ploug et al. 1999, Ploug and Jørgensen 1999). These studies indicate that sinking velocity, i.e. exchange of water in the vicinity of aggregates, greatly affects aggregate dissolution rates and growth of attached bacteria. The bacterial production is up to 10-fold higher in sinking aggregates than in aggregates incubated under static conditions (Ploug and Grossart 1999, Simon et al. 2002). Thus, transfer of the results gathered on sinking planktonic aggregates to sea-ice microaggregates like TEP is difficult. Sea-ice TEP, generally occurring under relative static conditions, can therefore be assumed to degrade slowly. In addition, also the prevailing cold temperatures may reduce the activity of sea-ice bacteria and catalytic reactions and thus biodegradation of polymeric substances in sea ice. However, in a recent study, Huston et al. (2000) report on remarkably low temperature optima for extracellular enzyme activity in Arctic sea ice. Junge et al. (2002) studied the phylogenetic diversity of numerically important Arctic sea-ice bacteria and report on a significant contribution of Flavobacteriaceae of the Cytophaga-Flexibacter-Bacteroides division, which are known for their attached life style and extracellular enzymes that degrade a variety of polymeric substances (Reichenbach and Dworkin 1992), which points towards a higher potential of TEP dissolution in sea ice. The present study showed that high numbers of sea-ice bacteria are associated with TEP, which suggests that sea-ice TEP may serve as significant carbon source for sympagic bacteria. Conclusively, the proposed concepts on enzymatic degradation and bacterial utilisation of TEP components in sea ice are controversial and the assumptions remain speculative.

Sea-ice TEP may serve not only as carbon source for sympagic bacteria, but may also increase bacterial diversity in the sea-ice systems by providing microhabitats for distinct bacterial groups. Planktonic microaggregates like TEP have been proposed to provide special microenvironments in their interior, which can show elevated nutrient concentrations and depleted oxygen concentrations compared to the surrounding water (Ploug and Jørgensen 1999, Alldredge 2000). Based on 16S rDNA sequence analyses, different studies showed an increased bacterial biodiversity in Arctic and Antarctic sea ice compared to the underlying water (Bowman et al. 1997a, Bowman et al. 1997b, Brown and Bowman 2001). In contrast, also relatively low bacterial diversity has been reported for Arctic sea ice (Junge et al. 2002), but this phylogenetic analysis was restricted to isolated strains. This might have biased the results of the study (Junge et al. 2002). Most sympagic bacterial strains have been found to be cold-adapted, halotolerant with both free-living and surface-associated species (Brown and Bowman 2001, Junge et al. 2002). Petri and Imhoff (2001) showed the existence of anoxygenic phototrophic purple sulfur bacteria in the interior horizons of Baltic sea ice, indicating the occurrence of oxygen-deficient or even anoxic zones or niches in sea ice. It is assumed that high amounts of algal mucilages and TEP may provide oxygen depleted microhabitats for these distinct spe-

cies within the sea-ice habitat. Assuming incorporation of TEP into sea ice during ice-formation, TEP may also serve in the transport of distinct bacterial groups like anoxygenic and surface-associated forms from the water column into the sea ice during its formation. Junge et al. (2002) report on an isolate from Arctic sea ice related to a strain isolated from marine snow aggregates supporting this hypothesis.

Implications for the pelagic realm

TEP have been generally accepted to play an important role in biologically enhanced coagulation of planktonic algae (Alldredge et al. 1993, Passow and Alldredge 1994, Passow et al. 2001). Aggregate formation in turn regulates both the vertical flux of carbon from the upper water column to deeper layers and the retention period of algal cells in the surface layers. Riebesell et al. (1991) found large aggregates under Antarctic sea ice and noted their potential for the sedimentation of ice algae. The Arctic portion of present study was performed in the major export zone of Arctic sea ice. Approximately 10 % of the Arctic ice cover are exported each year through the Fram Strait to the Greenland Sea where the ice melts (Maykut 1985). On the southern hemisphere 60–80 % of the Antarctic sea-ice cover is melting during spring and summer (Zwally et al. 1983). Large parts of Arctic and Antarctic sea-ice carbon are therefore released to the upper water column during the spring and summer melt (e.g. Gradinger et al. 1999, Giesenhagen et al. 1999). Released ice algae can serve as an inoculum for the pelagic spring-bloom (Smith and Sakshaug 1990, Giesenhagen et al. 1999) or sink to deeper water layers and the sea floor (Carey 1987). Peinert et al. (2001) report on the high and variable vertical material flux in the marginal ice zone (MIZ) of the Greenland Sea, which they attribute to the highly patchy distribution of physical and biological settings in the upper water column of this area, which is affected by a rapidly changing ice cover. Fortier et al. (2002) report on the high interannual variability of the vertical biogenic particle flux under sea ice in the Canadian Arctic Archipelago and proposed that snow cover on the sea ice triggered sedimentation and fate of the material released from the sea ice. Assuming a low degradation of TEP in winter, large TEP concentrations are released to the water column during spring and summer, where they can mediate the formation of aggregates and subsequent sedimentation of the sea ice and planktonic carbon. TEP are therefore assumed to add to the complexity and variability of sedimentation patterns in ice-covered seas. The high TEP concentrations found in the present study indicate that sea ice derived TEP may significantly influence particle flux in ice-covered seas. The fate of sea ice derived TEP and its impact on sedimentation during ice melt are still unknown and should be addressed in future studies.

3.3 Conclusion and outlook

Based on the available data, metazoan biomass in Baltic sea ice is low and metazoa have a low grazing impact on sea-ice algae. Ice algal accumulation in the Baltic Sea seems to be controlled by abiotic factors (particularly nutrient availability as reflected by small brine volumes) rather than by metazoan grazing. Ingestion rates of sympagic metazoans have been only estimated indirectly by allometric equations (Moloney and Field 1989) derived from studies with planktonic species of temperate areas. No experimental studies on the herbivory of metazoan and protozoan grazers are available (Grossmann et al. 1996, Friedrich 1997). Autecological feeding studies under simulated *in situ* conditions are necessary i) to test if the allometric models are valid for sea-ice organisms and ii) for a better understanding of metazoan and protozoan grazing in the sea ice. Experimental set-ups should take into account the three-dimensional structure of the brine channel system and the occurrence of both suspended and attached prey particles. Further studies are needed to elucidate how ice porosity affects brine and nutrient transport and their influence on ice algal growth.

The studies in the Arctic and Antarctic showed that sea ice contains large amounts of exopolymeric substances. The estimates of TEP carbon indicate that TEP constitutes a, hitherto largely neglected, carbon fraction of Arctic and Antarctic sea ice. This might be also true for the Baltic sea ice. Sympagic biomass in this area was mainly formed by diatoms, which may produce significant amounts of TEP in the Baltic sea ice, resulting in an important contribution of TEP carbon to POC in the Baltic sea-ice habitat. However, production of TEP is species-specific and strongly depends on algal growth-rates (Corzo et al. 2000, Passow 2002) and detailed studies are needed to understand the importance of TEP in brackish sea ice.

The high concentrations of TEP in Arctic and Antarctic sea ice are most likely the result of different processes, like i) physical enrichment of TEP, ii) biological production of TEP by algae and also bacteria and iii) spontaneous accretion of dissolved organic carbon, whereby ii) and iii) are possibly enhanced due to the extreme physico-chemical conditions within the brine channel system of the sea ice during the summer-winter transition. The observed TEP particles were densely colonised by bacteria. This observation implies that sea-ice TEP may serve as important sites for the turnover of particulate organic matter in the sea-ice habitat. This hypothesis needs further support by studies in other seasons and sea areas. The observation of the annual cycle of sea-ice TEP concentration, at best combined with measurements of TEP production and TEP degradation, will be future steps for a better understanding of the importance and ecological functions of TEP for the sea-ice habitat and the ice-covered ocean. Special attention should be given to the bacterial and algal species involved in TEP production and degradation. A first step could be the characterisation of the bacterial communities colonising sea-ice TEP by means of fluorescent *in situ* hybridisation (FISH) techniques, which have been successfully applied to planktonic aggregates (Grossart and Simon 1998, Ploug et al. 1999). Sea-ice bacteria and algae species have also been considered as potentially important resources of biotechnology (Pennisi 1997, Huston et al. 2000).

The use of meso- and large-scale ice tanks (Weissenberger 1998, Giannelli et al. 2001) will allow first experiments on metazoan grazing and the production and fate of sea-ice TEP under controlled laboratory conditions. Interdisciplinary work will strengthen our understanding of the complex physical, chemical and biological influences of polymers on the sea ice and its inhabitants.

4 References

Ackley SF (1982) Ice scavenging and nucleation: Two mechanisms for incorporation of algae into newly-forming sea ice. EOS 63: 54–55

Ackley SF, Sullivan CW (1994) Physical controls on the development and characteristics of Antarctic sea ice biological communities-a review and synthesis. Deep-Sea Res I 41: 1583–1604

Aletsee L, Jahnke J (1992) Growth and productivity of the psychrophilic marine diatoms *Thalassiosira antarctica* Comber and *Nitzschia frigida* Grunow in batch cultures at temperatures below the freezing point of sea water. Polar Biol 11: 643–647

Alldredge AL (2000) Interstitial dissolved organic carbon (DOC) concentrations within sinking marine aggregates and their potential contribution to carbon flux. Limnol Oceanogr 45: 1245–1253

Alldredge AL, Gotschalk C (1990) The relative contribution of marine snow of different origin to biological processes in coastal waters. Cont Shelf Res 10: 41–58

Alldredge AL, Silver ML (1988) Characteristics, dynamics and significance of marine snow. Prog Oceanogr 20: 41–82

Alldredge A, Passow U, Logan B (1993) The abundance and significance of a class of large transparent organic particles in the ocean. Deep-Sea Res I 40: 1131–1140

Andersson A, Hajdu S, Haecky P, Kuparinen JWJ (1996) Succession and growth limitation of phytoplankton in the Gulf of Bothnia (Baltic Sea). Mar Biol 126: 791–801

Arar EJ, Collins GB (1997) Method 445.0: *In vitro* determination of chlorophyll *a* and pheophytin *a* in marine and freshwater algae by fluorescence. U.S. Environmental Protection Agency Publ 445: 1–17

Archer SD, Leakey RJG, Burkill PH, Sleigh MA, Appleby CJ (1996) Microbial ecology of sea ice at coastal Antarctic site: community composition, biomass and temporal change. Mar Ecol Prog Ser 135: 179–195

Arrigo KR, Worthen DL, Lizotte MP, Dixon P, Dieckmann G (1997) Primary production in Antarctic sea ice. Science 276: 394–397

Assur A (1958) Composition of sea ice and its tensile strength. Nat Res Counc Publ 598: 106–138

Ayo B, Unanue M, Azúa I, Gorsky G, Turley C, Iriberri J (2001) Kinetics of glucose and amino acid uptake by attached and free-living marine bacteria in oligotrophic waters. Mar Biol 138: 1071–1076

Baltic Marine Environment Protection Commission (1988) Guidelines for the Baltic Monitoring Programme for the third stage; Part D. Biological determinands. Baltic Sea Environment Proceedings 27 D: 1–161

Bartsch A (1989) Die Eisalgenflora des Weddellmeeres (Antarktis): Artenzusammensetzung und Biomasse sowie Ökophysiologie ausgewählter Arten. Ber Polarforsch 63: 1–110

Bathmann U (2002) The expedition ANTARKTIS XVIII/5b of the Research Vessel "Polarstern" in 2001. Ber Polarforsch 407: 1–98

Beers JR, Stewart GL (1970) Part IV: Numerical abundance and estimated biomass of microzooplankton. In: Strickland JDH (ed) The ecology of the plankton off La Jolla, California, in the period April through September, 1967. Bull Scripps Inst Oceanogr 17: 67–87

Berman T, Viner-Mozzini Y (2001) Abundance and characteristics of polysaccharide and proteinaceous particles in Lake Kinneret. Aquat Microb Ecol 24: 255–264

Bölter M, Bloem J, Meiners K, Möller R (in press) Enumeration and biovolume determination of microbial cells-a methodological review and recommendations for applications in ecological research. Biol Fert Soils

Bowman JP, Brown MV, Nichols DS (1997a) Biodiversity and ecophysiology of bacteria associated with Antarctic sea ice. Ant Science 9: 134–142

Bowman JP, McCammon SA, Brown MV, Nichols DS, McMeekin TA (1997b) Diversity and association of psychrophilic bacteria in Antarctic sea ice. Appl Environ Microbiol 63: 3068–3078

Brown MV, Bowman JP (2001) A molecular phylogenetic survey if sea-ice microbial communities (SIMCO). FEMS Microbiol Ecol 35: 267–275

Buck KR, Bolt PA, Garrison DL (1990) Phagotrophy and fecal pellet production by an athecat dinoflagellate in Antarctic sea ice. Mar Ecol Prog Ser 60: 75–84

Bunch JN, Harland RC (1990) Bacterial production in the bottom surface of sea ice in the Canadian subarctic. Can J Fish Aquat Sci 47: 1986–1995

Bunt JS (1968) Some characteristics of microalgae isolated from Antarctic sea ice. Antarctic Res Ser 11: 1–14

Carey AG (1987) Particle flux beneath fast ice in the shallow southwestern Beaufort Sea, Arctic Ocean. Mar Ecol Prog Ser 40: 247–257

Chengalath R (1985) The rotifera of the Canadian Arctic sea ice, with description of a new species. Can J Zool 63: 2212–2218

Chin W-C, Orellana MV, Verdugo P (1998) Spontaneous assembly of marine dissolved organic matter into polymer gels. Nature 391: 568–572

Clarke DB, Ackley SF (1984) Sea ice structure and biological activity in the Antarctic marginal ice zone. J Geophys Res 89 (C2): 2087–2095

Cooksey KE, Wigglesworth-Cooksey B (1995) Adhesion of bacteria and diatoms to surfaces in the sea: a review. Aquat Microb Ecol 9: 87–96

Corzo A, Morillo JA, Rodríguez S (2000) Production of transparent exopolymer particles (TEP) in cultures of *Chaetoceros calcitrans* under nitrogen limitation. Aquat Microb Ecol 23: 63–72

Cota GF, Legendre L, Gosselin M, Ingram RG (1991) Ecology of bottom ice algae. I. Environmental controls and variability. J Mar Syst 2: 257–277

Cota GF, Prinsenberg SJ, Bennett EB, Loder JW, Lewis MR, Anning JL, Watson NHF, Harris LR (1987) Nutrient fluxes during extended blooms of Arctic ice algae. J Geophys Res 92 (C2): 1951–1962

Cross WE (1982) Under-ice biota at the Pond Inlet ice edge and the adjacent fast ice areas during spring. Arctic 35: 13–27

Decho AW (1990) Microbial exopolymer secretions in ocean environments: Their role(s) in food webs and marine processes. Oceanogr Mar Biol Ann Rev 28: 73–153

Decho AW (1993) Methods for the observation and use in feeding experiments of microbial exopolymers. In: Kemp PF, Sherr BF, Sherr EB, Cole JJ (eds) Handbook of methods in aquatic microbial ecology. Lewis Publishers, Boca Raton, p 685–694

Dieckmann GS, Lange MA, Ackley SF, Jennings Jr JC (1991) The nutrient status in sea ice of the Weddell Sea during winter: effects of sea ice texture and algae. Polar Biol 11: 449–456

Edler L (1979) Recommendations on methods for marine biological studies in the Baltic Sea: Phytoplankton and chlorophyll. Baltic Sea Mar Biol Publ 5: 1–38

Eicken H (1992) The role of sea ice in structuring Antarctic ecosystems. Polar Biol 12: 3–13

Eicken H, Lensu M, Leppäranta M, Tucker III WB, Gow AJ, Salmela O (1995) Thickness, structure, and properties of level summer multiyear ice in the eurasian sector of the Arctic Ocean. J Geophys Res 100 (C11): 22697–22710

Engel A (2000) The role of transparent exopolymer particles (TEP) in the increase of apparent particle

stickiness (alpha) during the decline of a diatom bloom. J Plankt Res 22: 485–497

Engel A, Passow U (2001) Carbon and nitrogen content of transparent exopolymer particles (TEP) in relation to their Alcian Blue adsorption. Mar Ecol Prog Ser 219: 1–10

Engel A, Schartau M (1999) Influence of transparent exopolymer particles (TEP) on sinking velocity of *Nitzschia closterium* aggregates. Mar Ecol Prog Ser 182: 69–76

Feller RJ, Warwick RM (1988) 13. Energetics. In: Higgins RP, Thiel H (eds) Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, p 181–196

Feltham DL, Worster MG, Wettlaufer JS (2002) The influence of ocean flow on newly forming sea ice. J Geophys Res 107 (C2): 1–9

Fortier M, Fortier L, Michel C, Legendre L (2002) Climatic and biological forcing of the vertical flux of biogenic particles under seasonal Arctic sea ice. Mar Ecol Prog Ser 225: 1–16

Frankenstein G, Garner R (1967) Equations for determining the brine volume of sea ice from –0.5° to –22.9 °C. J Glaciol 6: 943–944

Freitag J (1999) Untersuchungen zur Hydrologie des arktischen Meereises – Konsequenzen für den kleinskaligen Stofftransport. Ber Polarforsch 325: 1–149

Friedrich C (1997) Ökologische Untersuchungen zur Fauna des arktischen Meereises. Ber Polarforsch 246: 1–211

Friedrich C, De Smet WH (2000) The rotifer fauna of arctic sea ice from the Barents Sea, Laptev Sea and Greenland Sea. Hydrobiologia 432: 73–89

Friedrich C, Hendelberg J (2001) On the ecology of Acoela living in the Arctic Sea ice. Belg J Zool 131: 213–216

Fritsen CH, Sullivan CW (1997) Distributions and dynamics of microbial communities in the pack ice of the western Weddell Sea, Antarctica. In: Battaglia B, Valencia J, Walton DWH (eds) Antarctic communities: species, structure and survival. Cambridge University Press, Cambridge, p 101–106

Fritsen CH, Lytle VI, Ackley SF, Sullivan CW (1994) Autumn bloom of Antarctic pack ice algae. Science 266: 782–784

Garrison DL, Buck KR (1986) Organism losses during ice melting: a serious bias in sea ice community studies. Polar Biol 6: 237–239

Garrison DL, Buck KR (1991) Surface-layer sea ice assemblages in Antarctic pack ice during the austral spring: environmental conditions, primary production and community structure. Mar Ecol Prog Ser 75: 161–172

Garrison DL, Ackley SF, Buck KR (1983) A physical mechanism for establishing algal populations in frazil ice. Nature 306: 363–365

Gasol JM, del Giorgio PA, Duarte CM (1997) Biomass distribution in marine planktonic communities. Limnol Oceanogr 42: 1353–1363

Giannelli V, Thomas DN, Haas C, Kattner G, Kennedy H, Dieckmann GS (2001) Behaviour of dissolved organic matter and inorganic nutrients during experimental sea-ice formation. Ann Glaciol 33: 317–321

Giesenhagen HC, Detmer AE, de Wall J, Weber A, Gradinger RR, Jochem FJ (1999) How are Antarctic planktonic microbial food webs and algal blooms affected by melting of sea ice? Microcosm simulations. Aquat Microb Ecol 20: 183–201

Gleitz M, Kirst GO (1991) Photosynthesis-irradiance relationship and carbon metabolism of different ice algal assemblages collected from Weddell Sea pack ice during austral spring (ESOP1). Polar Biol 11: 385–392

Gleitz M, Thomas DN (1993) Variation in phytoplankton standing stock, chemical composition

and physiology during sea-ice formation in the southeastern Weddell Sea. J Exp Mar Biol Ecol 173: 211–230

Gleitz M, Rutgers van der Loeff M, Thomas DN, Dieckmann GS, Millero FJ (1995) Comparison of summer and winter inorganic carbon, oxygen and nutrient concentrations in Antarctic sea ice brine. Mar Chem 51: 81–91

Golden KM, Ackley SF, Lytle VI (1998) The percolation phase transition in sea ice. Science 282: 2238–2241

Gosselin M, Legendre L, Therriault JC, Demers S (1990) Light and nutrient limitation of sea-ice microalgae (Hudson Bay, Canadian Arctic). J Phycol 26: 220–232

Gosselin M, Levasseur M, Wheeler PA, Horner RA, Booth BC (1997) New measurements of phytoplankton and ice algal productions in the Arctic Ocean. Deep-Sea Res II 44: 1623–1644

Goto N, Kawamura T, Mitamura O, Terrai H (1999) Importance of extracellular organic carbon production in the total primary production by tidal flat diatoms in comparison to phytoplankton. Mar Ecol Prog Ser 190: 289–295

Gradinger R (1999a) Integrated abundance and biomass of sympagic meiofauna in Arctic and Antarctic pack ice. Polar Biol 22: 169–177

Gradinger R (1999b) Vertical fine structure of the biomass and composition of algal communities in Arctic pack ice. Mar Biol 133: 745–754

Gradinger R (2002) Sea ice microorganisms. In: Bitton G (ed) The encyclopedia of environmental microbiology. Wiley, New York, p 2833–2844

Gradinger R, Ikävalko J (1998) Organism incorporation into newly forming Arctic sea ice in the Greenland Sea. J Plankt Res 20: 871–886

Gradinger R, Nürnberg D (1996) Snow algal communities on Arctic pack ice floes dominated by *Chlamydomonas nivalis* (Bauer) Wille. Proceedings NIPR Symposium Polar Biol 9: 35–43

Gradinger R, Zhang Q (1997) Vertical distribution of bacteria in Arctic sea ice from the Barents and Laptev Seas. Polar Biol 17: 448–454

Gradinger R, Friedrich C, Spindler M (1999) Abundance, biomass and composition of the sea ice biota of the Greenland Sea pack ice. Deep-Sea Res II 46: 1457–1472

Gradinger R, Spindler M, Weissenberger J (1992) On the structure and development of Arctic pack ice communities in Fram Strait: a multivariate approach. Polar Biol 12: 727–733

Grainger EH, Hsiao SIC (1990) Trophic relationships of the sea ice meiofauna in Frobisher Bay, Arctic Canada. Polar Biol 10: 283–292

Grainger EH, Mohammed AA, Lovrity JE (1985) The sea ice fauna of Frobisher Bay, Arctic Canada. Arctic 38: 23–30

Grant WS, Horner RA (1976) Growth responses to salinity variation in four arctic ice diatoms. J Phycol 12: 180–185

Grasshoff K, Ehrhardt M, Kremling K (1983) Methods of seawater analyses. Verlag Chemie, Weinheim

Grossart H-P, Simon M (1998) Bacterial colonization and microbial decomposition of limnetic organic aggregates (lake snow). Aquat Microb Ecol 15: 127–140

Grossmann S (1994) Bacterial activity in sea ice and open water of the Weddell Sea, Antarctica: a microautoradiographic study. Microb Ecol 28: 1–18

Grossmann S, Dieckmann GS (1994) Bacterial standing stock, activity, and carbon production during formation and growth of sea ice in the Weddell Sea, Antarctica. Appl Environ Microbiol 60: 2746–2753

Grossmann S, Lochte K, Scharek, R (1996) Algal and bacterial processes in platelet ice during austral summer. Polar Biol 16: 623–633

Gulliksen B, Lønne OJ (1989) Distribution, abundance, and ecological importance of marine sympagic fauna in the Arctic. Rapp P-V Reun Cons Int Explor Mer 188: 133–138

Haapala J, Leppäranta M (1997) The Baltic Sea ice season in a changing climate. Boreal Environ Res 2: 93–108

Haecky P, Andersson A (1999) Primary and bacterial production in sea ice in the northern Baltic Sea. Aquat Microb Ecol 20: 107–118

Haecky P, Jonsson S, Andersson A (1998) Influence of sea ice on the composition of the spring phytoplankton bloom in the northern Baltic Sea. Polar Biol 20: 1–8

Herborg LM, Thomas DN, Kennedy H, Haas C, Dieckmann GS (2001) Dissolved carbohydrates in Antarctic sea ice. Antarct Science 13: 119–125

Hoagland KD, Rosowski JR, Gretz MR, Roemer SC (1993) Diatom extracellular polymeric substances. Function, fine structure, chemistry, and physiology. J Phycol 29: 537–566

Hong Y, Smith Jr. WO, White A-M (1997) Studies on transparent exopolymer particles (TEP) produced in the Ross Sea (Antarctica) and by *Phaeocystis antarctica* (Prymnesiophyceae). J Phycol 33: 368–376

Horner RA (1985a) History of ice algal investigations. In: Horner RA (ed) Sea ice biota. CRC Press Inc, Boca Raton Florida, p 1–19

Horner RA (1985b) Sea Ice Biota. CRC Press Inc, Boca Raton Florida

Horner R, Ackley SF, Dieckmann GS, Gulliksen B, Hoshiai T, Legendre L, Melnikov IA, Reeburgh WS, Spindler M, Sullivan CW (1992) Ecology of sea ice biota 1. Habitat, terminology, and methodology. Polar Biol 12: 417–427

Huston AL, Krieger-Brockett BB, Deming JW (2000) Remarkably low temperature optima for extracellular enzyme activity from Arctic bacteria and sea ice. Env Microbiol 2: 383–388

Huttunen M, Niemi Å (1986) Sea-ice algae in the northern Baltic Sea. Memoranda Soc Fauna Flora Fennica 62: 58–62

Ikävalko J (1998a) Microbial communities in sea ice. Memoranda Soc Fauna Flora Fennica 74: 61–66

Ikävalko J (1998b) Further observations on flagellates within sea ice in northern Bothnian Bay, the Baltic Sea. Polar Biol 19: 323–329

Ikävalko J, Gradinger R (1997) Flagellates and heliozoans in the Greenland Sea ice studied alive using light microscopy. Polar Biol 17: 473–481

Ikävalko J, Thomsen HA (1997) The Baltic sea ice biota (March 1994): A study of the protistan community. Eur J Protistol 33: 229–243

Jackson GA, Maffione R, Costello DK, Alldredge AL, Logan BE, Dam HG (1997) Particle size spectra between 1 μm and 1 cm at Monterey Bay determined using multiple instruments. Deep Sea Research I 44: 1739–1767

Junge K, Imhoff F, Staley T, Deming JW (2002) Phylogenetic diversity of numerically important Arctic sea-ice bacteria at subzero temperature. Microb Ecol 43: 315–328

Junge K, Krembs C, Deming J, Stierle A, Eicken H (2001) A microscopic approach to investigate bacteria under *in-situ* conditions in sea-ice samples. Ann Glaciol 33: 304–310

Kaartokallio H (2001) Evidence for active microbial nitrogen transformations in sea ice (Gulf of Bothnia, Baltic Sea) in midwinter. Polar Biol 24: 21–28

Kattner G (1999) Storage of dissolved inorganic nutrients in seawater: poisoning with mercuric chloride. Mar Chem 67: 61–66

Kawamura T, Shirasawa K, Ishikawa N, Lindfors A, Granskog M, Ehn J, Leppäranta M, Martma T, Vaikmae R (2001) Time-series observations of the structure and properties of brackish ice in the Gulf of Finland. Ann Glaciol 33: 1–4

Kern JC, Carey Jr. AG (1983) The faunal assemblage inhabiting seasonal sea ice in the nearshore Arctic Ocean with emphasis on copepods. Mar Ecol Prog Ser 10: 159–167

Kiørboe T, Tiselius P, Mitchell-Innes B, Hansen JLS, Visser AW, Mari X (1998) Intensive aggregate formation with low vertical flux during an upwelling-induced diatom bloom. Limnol Oceanogr 43: 104–116

Kirst GO, Wiencke C (1995) Ecophysiology of polar algae. J Phycol 31: 181–199

Kottmeier ST, Sullivan CW (1987) Late winter primary production and bacterial production in sea ice and seawater west of the Antarctic Peninsula. Mar Ecol Prog Ser 36: 287–298

Krembs C (1998) The influence of the three-dimensional structure of sea-ice on the distribution and activity of the Arctic sea-ice communities. Dissertation. Mathematisch-Naturwissenschaftliche-Fakultät. Christian-Albrechts-Universität, Kiel, p 1–246

Krembs C, Engel A (2001) Abundance and variability of microorganisms and transparent exopolymer particles across the ice-water interface of melting first-year sea ice in the Laptev Sea (Arctic). Mar Biol 138: 173–185

Krembs C, Gradinger R, Spindler M (2000) Implications of brine channel geometry and surface area for the interaction of sympagic organisms in Arctic sea ice. J Exp Mar Biol Ecol 243: 55–80

Krembs C, Mock T, Gradinger R (2001) A mesocosm study of physical-biological interactions in artificial sea ice: effects of brine channel surface evolution and brine movement on algal biomass. Polar Biol 24: 356–364

Kristiansen S, Farbrot T, Kuosa H, Myklestad S, von Quillfeldt CH (1998) Nitrogen uptake in the infiltration community, an ice algal community in Antarctic pack-ice. Polar Biol 19: 307–315

Laamanen M (1996) Cyanoprokaryotes in the Baltic Sea ice and winter plankton. Algolog Stud 83: 423–433

Lange MA, Eicken H (1991) Textural characteristics of sea ice and the major mechanisms of ice growth in the Weddell Sea. Ann Glaciol 15: 210–215

Lange MA, Ackley SF, Wadhams P, Dieckmann GS, Eicken H (1989) Development of sea ice in the Weddell Sea. Ann Glaciol 12: 92–96

Laurion I, Demers S, Vézina AF (1995) The microbial food web associated with the ice algal assemblage: biomass and bacterivory of nanoflagellate protozoans in Resolute Passage (High Canadian Arctic). Mar Ecol Prog Ser 120: 77–87

Legendre L, Ackley SF, Dieckmann GS, Gulliksen B, Horner R, Hoshiai T, Melnikov IA, Reeburgh WS, Spindler M, Sullivan CW (1992) Ecology of sea ice biota 2. Global significance. Polar Biol 12: 429–444

Lenz J (1995) Plankton. In: Reinheimer G (ed) Meereskunde der Ostsee. Springer Verlag, Berlin, p 138–150

Leppäranta M, Manninen T (1988) The brine and gas content of sea ice with attention to low salinities and high temperatures. Finn Inst Mar Res Int Rep 2: 1–14

Leppäranta M, Tikkanen M, Shemeikka P (1998) Observations of ice and its sediments on the Baltic coast. Nordic Hydrology 29: 199–220

Leppard GG (1995) The characterization of algal and microbial mucilages and their aggregates in aquatic ecosystems. Sci Total Environ 165: 103–131

Liu H, Buskey EJ (2000) Hypersalinity enhances the production of extracellular polymeric substance

(EPS) in the Texas Brown Tide Alga, *Aureoumbra lagunensis* (Pelagophyceae). J Phycol 36: 71–77

Lizotte MP (2001) The contributions of sea ice algae to Antarctic marine primary production. Am Zool 41: 57–73

Lizotte MP, Arrigo KR (1998) Antarctic sea ice: Biological processes, interactions and variability (Antarctic Research Series 73). American Geophysical Union, Washington

Logan BE, Grossart H-P, Simon M (1994) Direct observation of phytoplankton, TEP and aggregates on polycarbonate filters using brightfield microscopy. J Plankt Res 16: 1811–1815

Mälkki P, Tamsalu R (1985) Physical features of the Baltic Sea. Finn Mar Res 252: 23–27

Mari X (1999) Carbon content and C:N ratio of transparent exopolymeric particles (TEP) produced by bubbling exudates of diatoms. Mar Ecol Prog Ser 183: 59–71

Mari X, Burd A (1998) Seasonal size spectra of transparent exopolymeric particles (TEP) in a coastal sea and comparison with those predicted using coagulation theory. Mar Ecol Prog Ser 163: 63–76

Mari X, Kiørboe T (1996) Abundance, size distribution and bacterial colonization of transparent exopolymeric particles (TEP) during spring in the Kattegat. J Plankt Res 18: 969–986

Mari X, Beauvias S, Lemée R, Pedrotti ML (2001) Non-Redfield C:N ratio of transparent exopolymer particles in the northwestern Mediterranean Sea. Limnol Oceanogr 46: 1831–1936

Maykut GA (1985) The ice environment. In: Horner RA (ed) Sea ice biota. CRC Press Inc, Boca Raton Florida, p 21–82

McCave IN (1984) Size spectra and aggregation of suspended particles in the deep ocean. Deep-Sea Res 31: 329–352

McConville MJ (1985) Chemical composition and biogeochemistry of sea ice microalgae. In: Horner RA (ed) Sea ice biota. CRC Press Inc, Boca Raton Florida, p 105–129

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

Mock T, Gradinger R (1999) Determination of Arctic ice algal production with a new *in situ* incubation technique. Mar Ecol Prog Ser 177: 15–26

Mock T, Meiners KM, Giesenhagen HC (1997) Bacteria in sea ice and underlying brackish water at 54°26'50'' N (Baltic Sea, Kiel Bight). Mar Ecol Prog Ser 158: 23–40

Moloney CL, Field JG (1989) General allometric equations for rates of nutrient uptake, ingestion, and respiration in plankton organisms. Limnol Oceanogr 34: 1290–1299

Mopper K, Zhou J, Ramana KS, Passow U, Dam HG, Drapeau DT (1995) The role of surface-active carbohydrates in the flocculation of a diatom bloom in a mesocosm. Deep-Sea Res II 42: 47–73

Myklestad SM (1995) Release of extracellular products by phytoplankton with special emphasis on polysaccharides. Sci Total Environ 165: 155–164

Nakawo M, Sinha NK (1981) Growth rate and salinity profile of first-year sea ice in the high Arctic. J Glaciol 27: 315–330

Norland S (1993) The relationship between biomass and volume of bacteria. In: Kemp PF, Sherr BF, Sherr EB, Cole JJ (eds) Handbook of methods in aquatic microbial ecology. Lewis Publishers, Boca Raton, p 303–307

Norrman B, Andersson A (1994) Development of ice biota in a temperate sea area (Gulf of Bothnia). Polar Biol 14: 531–537

Nozais C, Gosselin M, Michel C, Gugliemo T (2001) Abundance, biomass, composition and grazing im-

pact of sea-ice meiofauna in the North Water, northern Baffin Bay. Mar Ecol Prog Ser 217: 235–250

Palmisano AC, Garrison DL (1993) Microorganisms in Antarctic sea ice. In: Friedmann, EI (ed) Antarctic microbiology. Wiley, New York, p 167–218

Passow U (2000) Formation of transparent exopolymer particles, TEP, from dissolved precursor material. Mar Ecol Prog Ser 192: 1–11

Passow U (2002) Production of transparent exopolymer particles (TEP) by phyto- and bacterioplankton. Mar Ecol Prog Ser 236: 1–12

Passow U, Alldredge AL (1994) Distribution, size and bacterial colonization of transparent exopolymer particles (TEP) in the ocean. Mar Ecol Prog Ser 113: 185–198

Passow U, Alldredge AL (1995) Mass aggregation of a diatom bloom in a mesocosm: The role of TEP. Deep-Sea Res II 42: 99–109

Passow U, Alldredge AL (1999) Grazing of euphausiids on cells in the presence of transparent exopolymeric particles (TEP). J Plankt Res 21: 2203–2218

Passow U, Alldredge AL, Logan BE (1994) The role of particulate carbohydrate exudates in the flocculation of diatom blooms. Deep-Sea Res I 41: 335–337

Passow U, Shipe RF, Murray A, Pak DK, Brzezinski MA, Alldredge AL (2001) The origin of transparent exopolymer particles (TEP) and their role in sedimentation of particulate matter. Cont Shelf Res 21: 327–346

Peinert R, Bauerfeind E, Gradinger R, Haupt O, Krumbholz M, Peeken I, Werner I, Zeitzschel B (2001) Biogenic particle sources and vertical flux patterns in the seasonally ice-covered Greenland Sea. In: Schäfer P, Ritzrau W, Schlüter M, Thiede J (eds) The northern North Atlantic: A changing environment. Springer, Berlin, p 69–79

Pelegrí SP, Dolan J, Rassoulzadegan F (1999) Use of high temperature catalytic oxidation (HTCO) to measure carbon content of micoorganisms. Aquat Microb Ecol 16: 273–280

Pennisi E (1997) In industry, extremophiles begin to make their mark. Science 276: 705–706

Penny DM, Sullivan CW (1990) Bacterial distribution and activity in Weddell-Scotia Sea pack ice during austral winter. EOS 71: 79

Petri R, Imhoff JF (2001) Genetic analysis of sea-ice bacterial communities of the Western Baltic Sea using an improved double gradient method. Polar Biol 24: 252–257

Ploug H, Grossart H-P (1999) Bacterial production and respiration in suspended aggregates-a matter of the incubation method. Aquat Microb Ecol 20: 21–29

Ploug H, Jørgensen BB (1999) A net-jet flow system for mass transfer and microelectrode studies in sinking aggregates. Mar Ecol Prog Ser 176: 270–290

Ploug H, Grossart H-P, Azam F, Jørgensen BB (1999) Photosynthesis, respiration, and carbon turnover in sinking marine snow from surface waters of Southern California Bight: Implications for the carbon cycle in the ocean. Mar Ecol Prog Ser 179: 1–11

Porter KG, Feig YS (1980) The use of DAPI for identifying and counting aquatic microflora. Limnol Oceanogr 25: 943–948

Prieto L, Sommer F, Stibor H, Koeve W (2001) Effects of planktonic copepods on transparent exopolymeric particles (TEP) abundance and size spectra. J Plankt Res 23: 515–525

Rahm L, Håkansson B, Larrsson P, Fogelqvist E, Bremle G, Valderrama J (1995) Nutrient and persistent pollutant deposition on the Bothnian Bay ice and snow fields. Water, Air and Soil Pollution 84: 187–201

Raymond JA, Sullivan CW, DeVries AL (1994) Release of an ice-active substance by Antarctic sea ice diatoms. Polar Biol 14: 71–75

Redfield AC, Ketchum BH, Richards FH (1963) The influence of organisms on the composition of seawater. In: Hill MN (ed) The sea. Wiley, New York, p 26–77

Reichenbach H, Dworkin M (1992) The order Cytophagales. In: Balows A, Trueper HG, Dworkin M, Harder W, Schleifer KH (eds) The prokaryotes, vol 4. Springer-Verlag, New York, p 3631–3687

Reimnitz E, Kempema EW, Weber WS, Clayton JR, Payne JR (1990) Suspended-matter scavenging by rising frazil ice as observed in tank experiments. In: Ackley SF, Weeks WF (eds) Sea ice properties and processes. Proceedings of the W.F.Weeks sea ice symposium. U.S. Army Corps of Engineers, Hanover, p 97–100

Remane A (1958) Ökologie des Brackwassers. In: Remane A, Schlieper C (eds) Die Biologie des Brackwassers. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, p 1–216

Riebesell U (1991) Particle aggregation during a diatom bloom. II. Biological aspects. Mar Ecol Prog Ser 69: 281–291

Riebesell U, Schloss I, Smetacek V (1991) Aggregation of algae released from melting sea ice: implications for seeding and sedimentation. Polar Biol 11: 239–248

Sachs L (1984) Angewandte Statistik. Springer-Verlag, Berlin

Schauer U (2000) The expedition ARKTIS XV / 3 of the Research Vessel "Polarstern" in 1999. Ber Polarforsch 350: 1–63

Schuster S, Herndl GJ (1995) Formation and significance of transparent exopolymer particles in the northern Adriatic Sea. Mar Ecol Prog Ser 124: 227–236

Scott FJ, Davidson AT, Marchant HJ (2001) Grazing by the Antarctic sea-ice ciliate *Pseudocohnilembus*. Polar Biol 24: 127–131

Scott P, McMinn A, Hosie G (1994) Physical parameters influencing diatom community structure in eastern Antarctic sea ice. Polar Biol 14: 507–517

Shen HT, Ackermann NL (1990) Wave-induced sediment enrichment in coastal ice cover. In: Ackley SF, Weeks WF (eds) Sea ice properties and processes. Proceedings of the W.F.Weeks sea ice symposium. U.S. Army Corps of Engineers, Hanover, p 100–102

Sherr BF, Sherr EB, Fallon RD (1987) Use of monodispersed, fluorescently labeled bacteria to estimate *in situ* protozoan bacterivory. Appl Environ Microbiol 53: 958–965

Simon M, Azam F (1989) Protein content and protein synthesis rates of planktonic marine bacteria. Mar Ecol Prog Ser 51: 201–213

Simon M, Grossart H-P, Schweitzer B, Ploug H (2002) Microbial ecology of organic aggregates in aquatic ecosystems. Aquat Microb Ecol 28: 175–211

Smith DC, Simon M, Alldredge AL, Azam F (1992) Intense hydrolytic activity on marine aggregates and implications for rapid particle dissolution. Nature 359: 139–142

Smith DJ, Underwood GJC (1998) Exopolymer production by intertidal epipelic diatoms. Limnol Oceanogr 43: 1578–1591

Smith DJ, Underwood GJC (2000) The production of extracellular carbohydrates by estuarine benthic diatoms: The effects of growth phase and light and dark treatment. J Phycol 36: 321–333

Smith Jr. WO, Sakshaug E (1990) Polar phytoplankton. In: Smith Jr. WO (ed) Polar oceanography. Part B. Chemistry, biology and geology. Academic Press, San Diego, p 447–525

Sommer U (1998) Biologische Meereskunde. Springer-Verlag, Berlin

Spindler M (1990) A comparison of Arctic and Antarctic sea ice and the effects of different properties on sea ice biota. In: Bleil U, Thiede J (eds) Geological history of the polar oceans: Arctic versus Antarctic. Kluwer Academic Publishers, Dordrecht, p 173–186

Spindler M (1994) Notes on the biology of sea ice in the Arctic and Antarctic. Polar Biol 14: 319–324

Spindler M, Dieckmann GS (1986) Distribution and abundance of the planktic foraminifer *Neogloboquadrina pachyderma* in sea ice of the Weddell Sea (Antarctica). Polar Biol 5: 185–191

Staats N, Stal LJ, Mur LR (2000) Exopolysaccharide production by the epipelic diatom *Cylindrotheca closterium*: effects of nutrient conditions. J Exp Mar Biol Ecol 249: 13–27

Stoderegger KE, Herndl GJ (1999) Production of exopolymer particles by marine bacterioplankton under contrasting turbulent conditions. Mar Ecol Prog Ser 189: 9–16

Strübing K (1995) Eisverhältnisse. In: Reinheimer G (ed) Meereskunde der Ostsee. Springer Verlag, Berlin, p 81–86

Sullivan CW, Palmisano AC (1984) Sea ice microbial communities: distribution, abundance, and diversity of ice bacteria in McMurdo Sound, Antarctica, in 1980. Appl Environ Microbiol 47: 788–795

Thomas DN, Dieckmann GS (2002) Antarctic sea ice-a habitat for extremophiles. Science 295: 641–644

Thomas DN, Kattner G, Engbrodt R, Giannelli V, Kennedy H, Haas C, Dieckmann, GS (2001) Dissolved organic matter in Antarctic sea ice. Ann Glaciol 33: 297–303

Thomas DN, Lara RJ, Eicken H, Kattner G, Skoog A (1995) Dissolved organic matter in Arctic multiyear sea ice during winter: major components and relationship to ice characteristics. Polar Biol 15: 477–483

Thomas DN, Lara RJ, Haas C, Schnack-Schiel SB, Dieckmann GS, Kattner G, Nöthig E-M, Mizdalski E (1998) Biological soup within decaying summer sea ice in the Amundsen Sea, Antarctica. In: Lizotte MP, Arrigo KR (eds) Antarctic sea ice: Biological processes, interactions and variability (Antarctic Research Series 73). American Geophysical Union, Washington, p 161–171

Turley CM, Stutt ED (2000) Depth-related cell-specific bacterial leucine incorporation rates on particles and its biogechemical significance in the Nortwest Mediterranean. Limnol Oceanogr 45: 419–425

Utermöhl H (1958) Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. Mitt Int Ver Theor Angew Limnol 9: 1–38

Verardo DJ, Froelich PN, McIntyre A (1990) Determination of organic carbon and nitrogen in marine sediments using the Carlo Erba Na-1500 analyzer. Deep-Sea Res I 37: 157–167

Weeks WF, Ackley SF (1982) The growth, structure, and properties of sea ice. CRREL Monogr 82–1: 1–130

Weissenberger J (1998) Arctic sea ice biota: design and evaluation of a mesocosm experiment. Polar Biol 19: 151–159

Weissenberger J, Dieckmann G, Gradinger R, Spindler M (1992) Sea ice: a cast technique to examine and analyze brine pockets and channel structure. Limnol Oceanogr 37: 179–183

Wetherbee R, Lind JL, Burke J, Quatrano RS (1998) The first kiss: establishment and control of initial adhesion by raphid diatoms. J Phycol 34: 9–15

Wettlaufer JS (1991) Heat flux at the ice-ocean interface. J Geophys Res 96 (C4): 7215–7236

Wolfstein K, Stal LJ (2002) Production of extracellular polymeric substances (EPS) by benthic diatoms:

Effect of irradiance and temperature. Mar Ecol Prog Ser 236: 13–22

Wulff F, Ærtebjerg G, Nicolaus G, Niemi ÅCP, Schulz S, Kaiser W (1986) The changing pelagic ecosystem of the Baltic Sea. Ophelia 4: 299–319

Zhang Q, Gradinger R, Spindler M (1999) Experimental study on the effect of salinity on growth rates of Arctic-sea-ice algae from the Greenland Sea. Boreal Environ Res 4: 1–8

Zhou J, Mopper K, Passow U (1998) The role of surface-active carbohydrates in the formation of transparent exopolymer particles by bubble adsorption of seawater. Limnol Oceanogr 43: 1860–1871

Zwally HJ, Comiso JC, Parkinson CL, Campbell WJ, Carsey FD, Gloersen P (1983) Antarctic sea ice, 1973–1976: Satellite Passive-Microwave Observations. NASA SP-459, Washington

Acknowledgements

First of all I would like to thank my supervisor Prof. Dr. Michael Spindler for providing me with an excellent working place at the Institute for Polar Ecology. His support and constant interest in my work are greatly acknowledged. His comments on an earlier draft contributed significantly to this dissertation.

Special thanks go to Dr. Rolf Gradinger for his support, many fruitful discussions and his encouragement during all phases of this work.

The fieldwork of the present study was performed during cruises with the German RV *Polarstern*, the Finnish RV *Aranda* and a stay at the Tvärminne Zoological Station, Hanko in Finland. I would like to thank captains and crews of the vessels as well as the technical staff of this wonderful field station.

Many people participated and helped in the ice stations during sunny days, but also in unbearable cold Antarctic autumn storms: Special thanks to Dr. Holger Auel, Dr. André Belem, Robin Brinkmeyer, Jens Ehn, Johanna Fehling, Dr. Sebastian Gerland, Dr. Rolf Gradinger, Mats Granskog, Siri Grøttheim, Jianfeng He, Svenja Kobabe, Antti Lindfors, Annette Scheltz, Henrike Schünemann, Dr. Kirsten Tuschling and Dr. Iris Werner.

During the cruise to the Arctic many colleagues helped us doing "Polar Bear Watch" at the bridge of RV *Polarstern*. Many thanks!

Many thanks to Dr. Giuseppe Civitarese, Marina Lipizer and Bianca Rosa Guerra for performing the nutrient analyses during ARK XV-3. Tõnu Martma performed the $\delta^{18}O$ analyses and Johanna Fehling provided diatom counts of the Arctic sea-ice samples.

Matthias Steffens and Dr. Michael Schmid supported me, whenever I needed help with my computer. Matthias, loads of thanks for the layout-work and the long evenings at the IPÖ!

Thanks to all Ipö´s for enjoyable and entertaining coffee-breaks. Special thanks to Dr. Iris Werner and Henrike Schünemann for excellent co-operation in our sea-ice group.

The manuscript in its final stage was greatly improved by Dr. Bodil Bluhm, Dr. Christopher Krembs (thanks for your time and the discussions in Seattle!), Silke Lischka (the best office mate!), Janna Peters, Dr. Michael Schmid and Dr. Kirsten Tuschling.

This work was supported by the Deutsche Forschungsgemeinschaft (SP-377-1-3). Partial support for the investigations on Baltic sea ice was provided the Deutscher Akademischer Austausch Dienst (grant 313-SF-PPP-pz) and the Walter and Andreé de Nottbeck Foundation, Finland.

Thanks mom, thanks dad for your manifold support that you gave me during my academic training.

Appendix

Table A 1: Vertical profiles of the stable oxygen isotopic composition ($\delta^{18}O$) in Baltic and Antarctic sea ice. St. 67–81: Baltic sea ice, St. 113–115: Antarctic sea ice

Table A 2: Vertical profiles of temperature and brine salinity in Baltic, Antarctic and Arctic sea ice. St. 67–81: Baltic sea ice, St. 113–115: Antarctic sea ice, St. 271–280: Arctic sea ice

Table A 3: Vertical profiles of sea-ice bulk salinity and brine volume (calculated according to Frankenstein and Garner (1967) and Leppäranta and Manninen (1988)). St. 67–81: Baltic sea ice, St. 113–115: Antarctic sea ice, St. 271–280: Arctic sea ice

Table A 4: Vertical profiles for inorganic nutrient concentrations (NO_3, NO_2, PO_4, $Si(OH)_4$, NH_4) in sea ice and under-ice water values. St. 67–81: Baltic sea ice, St. 113–115: Antarctic sea ice, St. 271–280: Arctic sea ice, b.d. = below detection, n.d. = not determined

Table A 5: Vertical profiles for chlorophyll *a* concentrations and pheopigment concentrations in Baltic, Antarctic and Arctic sea ice. St. 67–81: Baltic sea ice, St. 113–115: Antarctic sea ice, St. 271–280: Arctic sea ice, n.d. = not determined

Table A 6: Vertical profiles for particulate organic carbon (POC), particulate organic nitrogen (PON) and the molar C / N ratio in Antarctic and Arctic sea ice. St. 113–115: Antarctic sea ice, St. 271–280: Arctic sea ice

Table A 7: Vertical distribution of the abundance of heterotrophic bacteria (= bacteria), cyanobacteria, autotrophic flagellates, heterotrophic flagellates, chlorophytes, pennate diatoms, centric diatoms, crustacean nauplii and rotifers in Baltic sea ice. n.d. = not determined

Table A 8: Vertical distribution of the biomass of heterotrophic bacteria (= bacteria), cyanobacteria, autotrophic flagellates, heterotrophic flagellates, chlorophytes, pennate diatoms, centric diatoms, crustacean nauplii and rotifers in Baltic sea ice. n.d. = not determined

Table A 9: Vertical distribution of heterotrophic bacteria, pennate diatoms, centric diatoms, transparent exopolymer particle (TEP) abundance, TEP area and the slopes of TEP size frequency distributions (β+1 values) in Arctic sea ice. n.d. = not determined

Table A 10: Vertical distribution of bacterial abundance, bacterial biomass, relative number of bacteria associated with transparent exopolymer particles (TEP), pennate diatom abundance, pennate diatom biomass, centric diatom abundance, centric diatom biomass, abundance of TEP, TEP area and the slopes of TEP size frequency distributions (β+1 values) in Antarctic sea ice. n.d. = not determined

Table A 1: Vertical profiles of the stable oxygen isotopic composition ($\delta^{18}O$) in Baltic and Antarctic sea ice. St. 67–81: Baltic sea ice, St. 113–115: Antarctic sea ice

	Depth (cm)	$\delta^{18}O$
St. 68		
	0–5	−12.96
	5–10	−11.55
	10–15	−8.29
	15–21	−7.42
	21–30	−7.44
St. 69		
	0–4	−9.50
	4–7	−8.07
	7–12	−7.45
	12–17	−7.53
	17–21.5	−7.60
St. 74		
	0–3.5	−9.64
	3.5–6	−9.60
	6–9	−7.53
	9–15	−6.81
	15–20	n.d.
	20–24	−6.54
St. 77		
	0–2.5	−10.37
	2.5–5	−10.19
	5–8.5	−8.31
	8.5–11	−7.07
	11–17	−6.29
	17–21.5	−6.13

	Depth (cm)	$\delta^{18}O$
St. 81		
	0–0.5	−11.43
	0.5–3	−10.74
	3–6	−9.16
	6–11	−6.75
	11–16	−5.87
	16–21	−6.07
	21–24	−6.52
	24–27.5	−6.59
St. 113		
	0–7	−0.63
	7–14	1.01
	14–19.5	1.21
	19.5–25	1.14
	25–32	1.12
	32–40	1.20
	40–49	1.29
St. 114		
	0–2.5	−0.22
	2.5–8	0.30
	8–13.5	0.22
	13.5–23.5	0.18
	23.5–33.5	0.28
	33.5–43.5	0.49
	43.5–53.5	1.10
	53.5–63	1.27
St. 115		
	0–11.5	−0.02
	11.5–23	0.91
	23–29	1.01
	29–32	0.98
	32–41.5	0.95
	41.5–51	1.41
	51–60	1.54

Table A 2: Vertical profiles of temperature and brine salinity in Baltic, Antarctic and Arctic sea ice. St. 67–81: Baltic sea ice, St. 113–115: Antarctic sea ice, St. 271–280: Arctic sea ice

	Depth (cm)	Temperature (°C)	Brine salinity
St. 67			
	5	−1.8	32.2
	10	−1.2	21.7
	15	−0.7	12.8
	20	−0.6	11.0
	25	−0.5	9.2
St. 68			
	5	−2.0	35.6
	10	−1.6	28.7
	15	−1.3	23.5
	20	−1.0	18.1
	25	−0.8	14.6
St. 69			
	5	−3.1	54.2
	10	−2.4	42.5
	15	−1.9	33.9
	20	−1.3	23.5
	24	−0.8	14.6
St. 74			
	5	−0.3	5.5
	10	−0.5	9.2
	15	−0.5	9.2
	20	−0.5	9.2
	25	−0.5	9.2
St. 77			
	5	−0.5	9.2
	10	−0.3	5.5
	15	−0.4	7.3
	20	−0.4	7.3
St. 81			
	5	−0.3	5.5
	10	−0.3	5.5
	15	−0.2	3.7
	19	−0.2	3.7

	Depth (cm)	Temperature (°C)	Brine salinity
St. 113			
	10	−6.7	110.2
	20	−5.9	98.3
	30	−5.3	89.2
	40	−2.8	49.2
	50	−3.0	52.5
	60	−2.4	42.5
	70	−2.5	44.2
St. 114			
	5	−8.8	132.8
	15	−8.1	130.2
	25	−7.3	118.9
	35	−4.9	83.0
	45	−4.7	79.9
	55	−3.3	57.5
	60	−2.8	49.2
St. 115			
	5	−5.9	98.3
	15	−5.0	84.6
	25	−4.0	68.8
	35	−3.0	52.5
	45	−2.5	44.2
St. 271			
	10	−4.3	73.6
	20	−4.3	73.6
	30	−3.8	65.6
	40	−3.5	60.8
	50	−2.8	49.2
	60	−2.3	40.8
	70	−2.0	35.6
	80	−2.0	35.6
	85	−2.0	35.6
	94	−2.1	37.4
	104	−2.1	37.4
	114	−2.1	37.4
	124	−2.1	37.4
	134	−2.1	37.4
	144	−2.1	37.4
	154	−2.1	37.4
	159	−2.1	37.4

Table A 2 (continued): Vertical profiles of temperature and brine salinity in Baltic, Antarctic and Arctic sea ice. St. 67–81: Baltic sea ice, St. 113–115: Antarctic sea ice, St. 271–280: Arctic sea ice

	Depth (cm)	Temperature (°C)	Brine salinity
St. 277-1			
	5	–6.6	108.7
	15	–5.6	93.8
	25	–4.3	73.6
	35	–2.6	45.8
St. 277-2			
	5	–4.7	79.9
St. 277-3			
	10	–5.2	87.7
	20	–3.6	62.4
	30	–4.0	68.8
	40	–3.0	52.5
	50	–2.4	42.5
	60	–2.3	40.8
	70	–2.3	40.8
	80	–2.3	40.8
	90	–2.3	40.8
	110	n.d.	n.d.
	120	–2.3	40.8

	Depth (cm)	Temperature (°C)	Brine salinity
St. 280			
	10	–7.7	124.6
	20	–8.0	128.8
	30	–7.6	123.2
	40	–7.0	114.5
	50	–6.3	104.3
	60	–5.8	96.8
	70	–5.0	84.6
	80	–4.1	70.4
	88	–3.2	55.8
	98	–2.9	50.9
	108	–2.5	44.2
	117	–2.1	37.4
	127	–1.7	30.5
	137	–1.6	28.7
	147	–1.5	27.0
	157	–1.5	27.0
	167	–1.5	27.0
	177	–1.6	28.7
	187	–1.7	30.5
	192	–1.8	32.2
	197	–2.0	35.6
	207	–1.9	33.9
	217	–2.0	35.6
	227	–2.0	35.6
	237	–2.0	35.6
	247	–2.1	37.4
	257	–2.2	39.1
	267	–2.1	37.4
	277	–2.1	37.4
	287	–2.1	37.4
	297	–2.1	37.4
	303	–2.2	39.1

Table A3: Vertical profiles of sea-ice bulk salinity and brine volume (calculated according to Frankenstein and Garner (1967) and Leppäranta and Manninen (1988)). St. 67–81: Baltic sea ice, St. 113–115: Antarctic sea ice, St. 271–280: Arctic sea ice

Depth (cm)	Salinity	Brine volume (%)
St. 67		
0–10	1.1	3.0
10–20	0.9	4.9
20–26	0.5	4.5
26–28	0.5	4.5
28–29	0.4	4.0
29–30	0.8	8.0
Water (0–10 m)	3.5	
St. 68		
0–10	1.2	2.9
10–15.5	0.4	1.3
15.5–21.5	0.5	2.2
21.5–23.5	0.4	2.0
23.5–24.5	0.1	0.6
24.5–25.5	0.5	3.2
Water (0–10 m)	3.4	
St. 69		
0–10	0.7	1.1
10–14	0.3	0.7
14–20	0.2	0.6
20–22	0.3	1.4
22–23	0.3	1.7
23–24	0.7	4.4
Water (0–10 m)	3.4	
St. 74		
0–10	0.1	1.5
10–17	0.3	3.1
17–23	0.4	4.1
23–25	0.3	3.1
25–26	0.3	3.1
26–27	0.4	4.1
Water (0–5 m)	3.2	
St. 77		
0–10	0.1	1.0
10–13	0.1	1.4
13–19	0.3	3.7
19–21	0.3	3.7
21–22	0.2	1.5
22–23	0.1	1.2
Water (0–5 m)	3.0	
St. 81		
0–10	0.1	1.6
10–13	0.1	1.6
13–19	0.4	8.0
19–21	0.6	11.9
21–22	0.5	12.4
22–23	0.5	12.4
Water (0–5 m)	2.6	

Depth (cm)	Salinity	Brine volume (%)
St. 113		
0–10	12.3	8.4
10–20	10.7	8.7
20–30	9.1	8.3
30–40	9.3	11.4
40–50	7.4	12.4
50–60	6.9	12.4
60–69	9.7	19.0
69–75	9.6	19.3
75–77	9.9	20.6
77–78	9.6	20.9
78–79	10.8	24.6
Water (0–10 m)	35.0	
St. 114		
0–10	13.4	8.3
10–20	14.2	9.4
20–30	9.4	6.7
30–40	7.5	7.7
40–48.5	7.0	7.5
48.5–54.5	6.4	8.0
54.5–56.5	7.2	10.7
56.5–57.5	7.7	13.3
57.5–58.5	9.2	21.0
Water (0–10 m)	35.0	
St. 115		
0–10	11.8	10.3
10–20	7.9	8.0
20–30	8.0	9.9
30–37	8.2	13.3
37–43	8.6	14.0
43–45	7.8	15.1
45–46	8.1	17.7
46–47	9.9	22.5
Water (0–10 m)	35.0	
St. 271		
0–20	2.3	2.7
20–40	1.5	1.9
40–60	4.3	7.3
60–80	3.9	8.9
80–100	3.5	8.3
100–120	4.1	9.3
120–140	4.1	9.3
140–160	3.3	7.5
160–170	3.1	7.1
171–177	3.9	8.9
177–179	3.8	8.7
179–180	4.2	9.6
180–181	5.7	13.0
Water (0–10 m)	32.6	

Table A 3 (continued): Vertical profiles of sea-ice bulk salinity and brine volume (calculated according to Frankenstein and Garner (1967) and Leppäranta and Manninen (1988)). St. 67–81: Baltic sea ice, St. 113–115: Antarctic sea ice, St. 271–280: Arctic sea ice

Depth (cm)	Salinity	Brine volume (%)
St. 277-1		
0–20	11.5	9.9
20–28	5.7	6.6
28–34	6.1	8.3
34–36	8.9	13.2
36–37	9.4	15.8
37–38	10.7	22.4
Water (0–10 m)	33.5	
St. 277-2		
0–10	12.3	13.2
St. 277-3		
0–20	5.6	6.4
20–40	5.0	7.0
40–60	5.9	7.6
60–80	4.0	5.9
80–100	3.9	6.8
100–120	2.5	5.2
120–133	2.0	4.2
133–139	2.4	5.0
139–141	3.2	6.7
141–142	4.2	8.8
142–143	4.9	10.2

Depth (cm)	Salinity	Brine volume (%)
St. 280		
0–20	0.1	0.1
20–40	0.6	0.4
40–60	1.7	1.4
60–80	2.0	2.0
80–100	1.9	2.7
100–120	2.0	4.1
120–140	2.2	6.5
140–160	3.3	10.8
160–180	3.1	9.8
180–200	4.0	11.1
200–220	3.9	9.6
220–240	4.1	9.8
240–260	4.5	10.0
260–280	4.2	9.6
280–294.5	4.4	10.0
294.5–300.5	4.3	9.8
300.5–302.5	4.3	9.8
302.5–303.5	4.2	9.6
303.5–304.5	4.9	10.7
Water (0–10 m)	33.5	

Table A 4: Vertical profiles for inorganic nutrient concentrations (NO_3, NO_2, PO_4, $Si(OH)_4$, NH_4) in sea ice and under-ice water values. St. 67–81: Baltic sea ice, St. 113–115: Antarctic sea ice, St. 271–280: Arctic sea ice, b.d. = below detection, n.d. = not determined

Depth (cm)	NO_3 (µM)	NO_2 (µM)	PO_4 (µM)	$Si(OH)_4$ (µM)	NH_4 (µM)
St. 67					
0–10	5.54	0.10	0.03	10.30	1.09
10–20	2.87	0.06	0.03	8.03	0.49
20–26	1.61	0.05	0.02	4.71	0.24
26–28	1.30	0.05	0.02	4.12	0.05
28–29	1.21	0.05	0.04	3.41	0.11
29–30	3.60	0.10	0.09	7.50	0.27
Water (0–10 m)	7.98	0.03	0.10	32.20	0.07
St. 68					
0–10	5.73	0.09	0.02	10.43	1.64
10–15.5	1.45	0.08	0.02	2.82	0.10
15.5–21.5	0.74	0.04	b.d.	2.81	0.06
21.5–23.5	0.78	0.03	b.d.	2.40	0.06
23.5–24.5	0.54	0.02	b.d.	1.27	0.06
24.5–25.5	1.89	0.03	0.08	5.43	0.38
Water (0–10 m)	7.88	0.05	0.40	29.84	b.d.
St. 69					
0–10	5.27	0.07	0.06	8.96	0.19
10–14	0.32	0.04	0.02	1.40	b.d.
14–20	0.41	0.05	0.02	3.60	b.d.
20–22	0.26	0.05	0.02	2.96	b.d.
22–23	0.39	0.04	0.03	3.40	0.07
23–24	2.82	0.07	0.07	6.99	0.27
Water (0–10 m)	6.97	0.06	0.05	32.44	b.d.
St. 74					
0–10	1.03	0.02	0.02	0.85	2.60
10–17	0.51	0.02	0.02	1.44	0.54
17–23	0.41	b.d.	0.02	2.92	0.41
23–25	0.14	0.02	0.02	3.06	0.43
25–26	0.12	0.02	0.05	2.41	0.44
26–27	0.23	b.d.	0.06	2.46	0.33
Water (0–5 m)	1.76	0.05	0.04	54.76	0.17
St. 77					
0–10	0.75	0.02	0.02	3.20	1.65
10–13	0.43	0.02	0.04	1.07	0.74
13–19	0.52	b.d.	0.02	1.58	0.43
19–21	0.60	b.d.	0.03	1.99	0.60
21–22	0.65	0.02	0.04	1.81	0.55
22–23	0.36	0.02	0.03	0.97	0.72
Water (0–5 m)	4.58	0.08	0.16	33.24	1.37
St. 81					
0–10	0.40	0.02	0.02	1.08	2.21
10–13	0.38	0.02	0.03	1.27	0.79
13–19	0.45	0.02	0.02	2.45	0.66
19–21	0.19	0.02	0.02	2.32	0.28
21–22	0.12	0.02	0.02	2.97	0.19
22–23	0.11	0.02	0.04	2.27	0.35
Water (0–5 m)	0.63	0.02	0.02	18.18	0.50

Table A 4 (continued): Vertical profiles for inorganic nutrient concentrations (NO_3, NO_2, PO_4, $Si(OH)_4$, NH_4) in sea ice and under-ice water values. St. 67–81: Baltic sea ice, St. 113–115: Antarctic sea ice, St. 271–280: Arctic sea ice, b.d. = below detection, n.d. = not determined

Depth (cm)	NO_3 (µM)	NO_2 (µM)	PO_4 (µM)	$Si(OH)_4$ (µM)	NH_4 (µM)
St. 113					
0–10	1.46	0.11	1.07	12.83	n.d.
10–20	0.67	0.15	4.00	196.40	n.d.
20–30	2.85	0.25	7.80	273.00	n.d.
30–40	6.06	0.31	9.20	292.00	n.d.
40–50	4.80	0.19	4.96	235.00	n.d.
50–60	4.81	0.23	7.30	207.60	n.d.
60–69	7.20	0.30	5.50	212.80	n.d.
69–75	8.42	0.39	7.30	231.60	n.d.
75–77	7.53	0.31	7.40	180.90	n.d.
77–78	7.32	0.29	4.00	74.20	n.d.
78–79	9.35	0.35	4.60	67.10	n.d.
Water (0–10 m)	14.56	0.28	1.70	60.30	n.d.
St. 114					
0–10	8.72	0.17	1.43	21.21	n.d.
10–20	5.77	0.17	1.68	22.48	n.d.
20–30	1.73	0.14	4.77	22.29	n.d.
30–40	1.70	0.20	6.50	190.00	n.d.
40–48.5	3.10	0.25	9.20	206.00	n.d.
48.5–54.5	5.79	0.18	7.40	200.40	n.d.
54.5–56.5	4.62	0.15	3.60	65.50	n.d.
56.5–57.5	5.43	0.16	2.71	17.11	n.d.
57.5–58.5	7.99	0.17	1.28	16.23	n.d.
Water (0–10 m)	0.67	0.30	1.50	70.20	n.d.
St. 115					
0–10	7.05	0.08	0.57	20.27	n.d.
10–20	2.64	0.06	0.34	11.25	n.d.
20–30	4.15	0.07	0.58	13.16	n.d.
30–37	5.69	0.06	1.94	24.25	n.d.
37–43	7.60	0.06	1.32	24.18	n.d.
43–45	5.99	0.04	1.68	37.60	n.d.
45–46	6.99	0.06	1.22	28.59	n.d.
46–47	8.43	0.08	1.35	23.98	n.d.
Water (0–10 m)	2.39	0.00	2.10	61.00	n.d.
St. 271					
0–20	0.42	0.10	0.08	0.40	n.d.
20–40	0.16	0.05	0.04	0.19	n.d.
40–60	0.22	0.06	0.05	0.32	n.d.
60–80	0.22	0.06	0.09	0.22	n.d.
80–100	0.11	0.05	0.09	0.24	n.d.
100–120	0.11	0.02	0.07	0.32	n.d.
120–140	0.10	0.06	0.07	0.51	n.d.
140–160	0.08	0.05	0.08	0.22	n.d.
160–170	0.18	0.06	0.10	0.19	n.d.
171–177	0.22	0.08	0.17	0.30	n.d.
177–179	0.59	0.08	0.17	0.24	n.d.
179–180	0.24	0.09	0.16	0.27	n.d.
180–181	0.56	0.20	0.25	0.51	n.d.
Water (0–10 m)	1.52	0.04	0.29	0.59	n.d.

Table A 4 (continued): Vertical profiles for inorganic nutrient concentrations (NO_3, NO_2, PO_4, $Si(OH)_4$, NH_4) in sea ice and under-ice water values. St. 67–81: Baltic sea ice, St. 113–115: Antarctic sea ice, St. 271–280: Arctic sea ice, b.d. = below detection, n.d. = not determined

Depth (cm)	NO_3 (µM)	NO_2 (µM)	PO_4 (µM)	$Si(OH)_4$ (µM)	NH_4 (µM)
St. 277-1					
0–20	0.37	0.09	0.15	1.05	n.d.
20–28	0.25	0.08	0.17	0.73	n.d.
28–34	0.03	0.10	0.23	1.08	n.d.
34–36	0.57	0.12	0.51	1.00	n.d.
36–37	1.01	0.07	0.39	1.59	n.d.
37–38	1.70	0.12	0.79	1.69	n.d.
Water (0–10 m)	2.96	0.07	0.32	1.92	n.d.
St. 277-2					
0–10	1.08	0.11	0.31	1.13	n.d.
St. 277-3					
0–20	0.63	0.22	0.15	1.10	n.d.
20–40	0.17	0.09	0.10	0.51	n.d.
40–60	0.22	0.15	0.23	0.62	n.d.
60–80	0.02	0.07	0.14	1.08	n.d.
80–100	0.50	0.15	0.21	1.02	n.d.
100–120	0.05	0.08	0.11	1.59	n.d.
120–133	0.05	0.02	0.18	1.13	n.d.
133–139	0.06	0.03	0.08	0.59	n.d.
139–141	0.06	0.03	0.08	0.38	n.d.
141–142	0.13	0.07	0.09	0.46	n.d.
142–143	0.05	0.04	0.12	0.56	n.d.
St. 280					
0–20	0.15	0.08	0.08	0.22	n.d.
20–40	0.09	0.04	0.05	0.24	n.d.
40–60	0.11	0.04	0.05	0.38	n.d.
60–80	0.06	0.01	0.05	0.43	n.d.
80–100	0.07	0.02	0.08	0.38	n.d.
100–120	0.08	0.04	0.09	0.65	n.d.
120–140	0.04	0.04	0.08	1.96	n.d.
140–160	0.03	0.02	0.10	4.89	n.d.
160–180	0.07	0.04	0.07	5.54	n.d.
180–200	0.00	0.11	0.17	8.63	n.d.
200–220	0.01	0.06	0.14	7.31	n.d.
220–240	0.10	0.11	0.13	4.73	n.d.
240–260	0.08	0.03	0.08	1.24	n.d.
260–280	0.06	0.04	0.12	0.89	n.d.
280–294.5	0.00	0.02	0.06	1.08	n.d.
294.5–300.5	0.07	0.02	0.06	1.05	n.d.
300.5–302.5	0.01	0.05	0.09	1.32	n.d.
302.5–303.5	0.02	0.04	0.08	0.97	n.d.
303.5–304.5	0.02	0.05	0.10	1.67	n.d.
Water (0–10 m)	2.16	0.09	0.38	0.91	n.d.

Table A 5: Vertical profiles for chlorophyll *a* concentrations and pheopigment concentrations in Baltic, Antarctic and Arctic sea ice. St. 67–81: Baltic sea ice, St. 113–115: Antarctic sea ice, St. 271–280: Arctic sea ice, n.d. = not determined

	Depth (cm)	Chlorophyll *a* (µg l^{-1})	Pheopigments (µg l^{-1})
St. 67			
	0–10	0.1	0.1
	10–16	0.1	0.1
	16–22	0.8	0.1
	22–24	0.5	0.2
	24–25	0.6	0.1
	25–26	1.7	0.1
	Water (0–10 m)	0.2	0.1
St. 68			
	0–10	0.2	0.1
	10–18	1.4	0.2
	18–24	0.6	0.1
	24–26	1.1	0.2
	26–27	0.7	0.2
	27–28	6.3	0.1
	Water (0–10 m)	0.2	0.1
St. 69			
	0–10	0.8	0.1
	10–15.5	1.5	0.3
	15.5–21.5	0.5	0.1
	21.5–23.5	0.4	0.1
	23.5–24.5	1.7	0.3
	24.5–25.5	11.3	0.4
	Water (0–10 m)	0.2	0.1
St. 74			
	0–10	0.5	0.1
	10–17	0.5	0.1
	17–23	1.7	0.3
	23–25	1.7	0.3
	25–26	15.4	1.4
	26–27	14.3	0.1
	Water (0–5 m)	4.5	1.4
St. 77			
	0–10	1.1	0.2
	10–13	2.7	0.2
	13–19	4.3	0.4
	19–21	4.4	1.1
	21–22	3.7	1.2
	22–23	1.7	0.7
	Water (0–5 m)	0.7	0.4
St. 81			
	0–10	0.6	0.3
	10–13	1.6	0.5
	13–19	1.2	0.6
	19–21	2.0	0.7
	21–22	2.3	0.8
	22–23	4.9	1.3
	Water (0–5 m)	0.6	0.5

	Depth (cm)	Chlorophyll *a* (µg l^{-1})	Pheopigments (µg l^{-1})
St. 113			
	0–10	9.0	7.3
	10–20	150.9	15.7
	20–30	228.1	30.3
	30–40	223.7	47.7
	40–50	130.2	49.0
	50–60	87.5	32.8
	60–69	63.9	21.9
	69–75	90.8	22.2
	75–77	67.4	16.8
	77–78	55.7	12.1
	78–79	83.2	13.5
	Water (0–10 m)	0.3	0.1
St. 114			
	0–10	0.2	0.1
	10–20	2.4	0.3
	20–30	32.3	2.9
	30–40	105.4	20.8
	40–48.5	149.2	47.8
	48.5–54.5	83.9	43.3
	54.5–56.5	73.5	33.8
	56.5–57.5	130.5	24.9
	57.5–58.5	6.6	1.2
	Water (0–10 m)	0.2	0.2
St. 115			
	0–10	1.9	0.2
	10–20	11.2	1.6
	20–30	12.9	2.6
	30–37	30.7	7.0
	37–43	15.4	3.7
	43–45	19.8	4.9
	45–46	17.6	4.2
	46–47	172.6	30.2
	Water (0–10 m)	0.2	0.2
St. 271			
	0–20	0.3	0.1
	20–40	0.8	0.2
	40–60	0.3	0.1
	60–80	0.7	0.1
	80–100	0.8	0.1
	100–120	0.8	0.3
	120–140	0.6	0.1
	140–160	0.7	0.2
	160–170	1.8	0.4
	171–177	2.7	0.3
	177–179	2.5	0.3
	179–180	2.7	0.4
	180–181	2.6	0.7
	Water (0–10 m)	0.4	0.2

Table A 5 (continued): Vertical profiles for chlorophyll *a* concentrations and pheopigment concentrations in Baltic, Antarctic and Arctic sea ice. St. 67–81: Baltic sea ice, St. 113–115: Antarctic sea ice, St. 271–280: Arctic sea ice, n.d. = not determined

	Depth (cm)	Chlorophyll *a* (µg l^{-1})	Pheopigments (µg l^{-1})
St. 277-1			
	0–20	1.1	0.2
	20–28	1.6	0.9
	28–34	8.6	3.6
	34–36	n.d.	n.d.
	36–37	5.4	1.9
	37–38	14.2	1.5
	Water (0–10 m)	1.2	0.3
St. 277-2			
	0–10	1.0	0.7
St. 277-3			
	0–20	1.1	0.3
	20–40	2.9	0.9
	40–60	8.0	0.9
	60–80	14.7	2.2
	80–100	29.7	1.6
	100–120	13.3	2.2
	120–133	8.9	0.7
	133–139	18.3	3.1
	139–141	5.4	0.6
	141–142	7.8	0.4
	142–143	11.6	1.3

	Depth (cm)	Chlorophyll *a* (µg l^{-1})	Pheopigments (µg l^{-1})
St. 280			
	0–20	0.1	0.1
	20–40	0.1	0.1
	40–60	0.2	0.1
	60–80	0.1	0.1
	80–100	0.3	0.1
	100–120	0.4	0.1
	120–140	0.7	0.4
	140–160	1.3	0.8
	160–180	2.7	0.4
	180–200	8.0	0.9
	200–220	6.3	0.9
	220–240	2.1	0.7
	240–260	1.0	0.3
	260–280	1.4	0.4
	280–294.5	1.4	0.6
	294.5–300.5	3.8	0.5
	300.5–302.5	7.3	0.7
	302.5–303.5	13.3	1.1
	303.5–304.5	20.3	2.7
	Water (0–10 m)	0.8	0.4

Table A 6: Vertical profiles for particulate organic carbon (POC), particulate organic nitrogen (PON) and the molar C/N ratio in Antarctic and Arctic sea ice. St. 113–115: Antarctic sea ice, St. 271–280: Arctic sea ice

Depth (cm)	POC (µg C l^{-1})	PON (µg N l^{-1})	Molar C/N ratio
St. 113			
0–10	1031.2	132.4	9.1
10–20	2635.2	364.8	8.4
20–30	9988.5	1412.2	8.3
30–40	9513.9	1568.7	7.1
40–50	5637.2	934.7	7.0
50–60	2606.7	449.9	6.8
60–68	3833.6	658.2	6.8
68–74	4268.0	710.8	7.0
74–76	4425.8	700.9	7.4
76–77	4820.9	784.5	7.2
77–78	5458.5	802.7	7.9
Water (0–10 m)	106.9	13.7	9.1
St. 114			
0–10	708.1	112.3	7.4
10–20	2110.3	341.6	7.2
20–30	2594.5	408.7	7.4
30–40	3620.8	554.1	7.6
40–50	7424.7	1126.4	7.7
50–58	5060.3	790.2	7.5
58–64	7212.8	1148.3	7.3
64–66	4151.7	679.1	7.1
66–67	2206.9	292.3	8.8
67–68	1324.2	138.2	11.2
Water (0–10 m)	39.7	5.4	8.6
St. 115			
0–10	190.8	17.4	12.8
10–20	402.0	56.9	8.2
20–30	695.9	110.4	7.4
30–40	873.0	136.9	7.4
40–50	1041.8	149.6	8.1
50–55	1462.4	214.7	7.9
55–61	743.9	109.6	7.9
61–63	923.5	117.3	9.2
63–64	1180.8	144.0	9.6
64–65	1520.8	205.0	8.7
Water (0–10 m)	355.9	45.9	9.0
St. 271			
0–20	492.3	49.1	11.7
20–40	359.4	40.6	10.3
40–60	292.9	36.6	9.3
60–80	536.7	33.6	18.6
80–100	472.4	49.4	11.1
100–120	495.6	53.1	10.9
120–140	642.8	82.1	9.1
140–160	359.1	37.2	11.3
160–170	511.1	45.3	13.2
171–177	6394.6	536.7	13.9
177–179	601.4	56.7	12.4
179–180	627.0	72.8	10.0
180–181	1331.6	155.5	10.0
Water (0–10 m)	98.7	20.0	5.7

Depth (cm)	POC (µg C l^{-1})	PON (µg N l^{-1})	Molar C/N ratio
St. 277-1			
0–20	266.5	77.1	4.0
20–28	1065.2	237.3	5.2
28–34	1342.0	157.4	9.9
34–36	1456.4	190.7	8.9
36–37	568.1	110.3	6.0
37–38	1274.5	305.2	4.9
Water (0–10 m)	280.3	47.3	6.9
St. 277-2			
0–10	388.2	42.3	10.7
St. 277-3			
0–20	512.2	30.7	19.5
20–40	780.6	52.4	17.4
40–60	935.9	73.5	14.9
60–80	n.d.	n.d.	n.d.
80–100	3098.6	273.2	13.2
100–120	2441.1	212.3	13.4
120–133	1576.6	112.1	16.4
133–139	1062.5	90.5	13.7
139–141	1359.4	94.1	16.8
141–142	248.1	45.9	6.3
142–143	1279.3	172.2	8.7
St. 280			
0–20	457.5	24.4	21.9
20–40	228.5	21.6	12.3
40–60	304.8	8.9	39.9
60–80	324.3	21.8	17.4
80–100	337.2	23.0	17.1
100–120	694.3	52.2	15.5
120–140	965.9	75.3	15.0
140–160	714.0	67.8	12.3
160–180	1063.6	90.8	13.7
180–200	2692.8	167.4	18.8
200–220	2097.4	132.8	18.4
220–240	1350.1	78.3	20.1
240–260	677.5	27.6	28.6
260–280	876.1	61.0	16.8
280–294.5	620.5	56.4	12.8
294.5–300.5	1004.7	67.9	17.3
300.5–302.5	1628.3	94.7	20.1
302.5–303.5	1352.7	31.4	50.2
303.5–304.5	5578.7	335.9	19.4
Water (0–10 m)	192.4	31.7	7.1

Table A7: Vertical distribution of the abundance of heterotrophic bacteria (= bacteria), cyanobacteria, autotrophic flagellates, heterotrophic flagellates, chlorophytes, pennate diatoms, centric diatoms, crustacean nauplii and rotifers in Baltic sea ice. n.d. = not determined

Depth (cm)	Bacteria (10^8 cells l^{-1})	Cyanobacteria (10^3 cells l^{-1})	Autotrophic flagellates (10^3 cells l^{-1})	Heterotrophic flagellates (10^3 cells l^{-1})	Chlorophyta (10^3 cells l^{-1})	Pennate diatoms (10^3 cells l^{-1})	Centric diatoms (10^3 cells l^{-1})	Crustacea (organisms l^{-1})	Rotifera (organisms l^{-1})
St. 67									
0–10	1.21	28.81	31.86	7.97	0.00	0.00	0.83	0.0	0.0
10–20	1.20	29.50	35.29	9.63	0.85	0.97	2.55	0.0	0.0
20–26	0.69	61.70	29.84	16.99	0.30	26.92	59.40	0.0	0.0
26–28	0.81	77.91	44.60	12.09	0.44	52.18	65.30	0.0	12.5
28–29	0.81	173.37	101.79	20.85	0.32	42.47	37.11	0.0	19.0
29–30	0.77	197.95	204.04	25.55	1.23	29.47	9.21	149.3	194.1
Water (0–10 m)	1.07	585.23	31.33	26.91	13.45	0.57	1.37	11.0	14.0
St. 68									
0–10	2.27	385.72	192.79	108.42	0.22	29.46	9.30	18.3	5.4
10–19	2.06	380.12	250.98	168.32	8.40	26.95	506.45	0.0	0.0
19–25	1.34	96.11	143.47	63.22	1.17	52.46	51.50	0.0	3.7
25–27	2.41	192.70	209.04	96.24	0.96	165.91	33.55	0.0	13.6
27–28	1.61	514.17	138.50	59.12	0.84	122.30	11.09	0.0	5.7
28–29	2.57	893.35	645.91	173.69	3.98	2377.58	0.00	0.0	99.5
Water (0–10 m)	2.55	1148.31	98.30	52.58	10.86	0.24	0.61	7.0	2.0
St. 69									
0–10	2.05	22.82	317.00	126.92	n.d.	116.70	69.52	0.0	3.2
10–13	2.13	85.12	261.47	114.06	9.08	23.80	160.63	0.0	0.0
13–19	1.75	130.30	277.83	79.05	1.39	47.53	0.85	0.0	0.0
19–21	2.43	535.96	414.98	217.44	1.19	38.53	11.07	0.0	7.8
21–22	1.80	1524.06	496.88	176.29	2.28	417.46	10.00	0.0	32.8
20–23	1.86	1177.34	607.90	132.25	2.08	472.40	0.00	0.0	83.4
Water (0–10 m)	2.89	1814.08	54.57	20.02	21.25	0.47	0.89	1.0	5.0

Table A7 (continued): Vertical distribution of the abundance of heterotrophic bacteria (= bacteria), cyanobacteria, autotrophic flagellates, heterotrophic flagellates, chlorophytes, pennate diatoms, centric diatoms, crustacean nauplii and rotifers in Baltic sea ice. n.d. = not determined

Depth (cm)	Bacteria (10^8 cells l^{-1})	Cyanobacteria (10^3 cells l^{-1})	Autotrophic flagellates (10^3 cells l^{-1})	Heterotrophic flagellates (10^3 cells l^{-1})	Chlorophyta (10^3 cells l^{-1})	Pennate diatoms (10^3 cells l^{-1})	Centric diatoms (10^3 cells l^{-1})	Crustacea (organisms l^{-1})	Rotifera (organisms l^{-1})
St. 74									
0–10	1.91	269.18	349.98	110.83	0.00	47.85	103.14	0.0	0.0
10–17	1.83	155.06	433.10	218.50	0.00	37.97	47.65	0.0	4.7
17–23	5.06	253.32	1295.84	538.50	0.00	209.72	25.19	0.0	3.5
23–25	3.23	103.01	507.17	545.30	0.00	1304.40	1.36	0.0	8.1
25–26	12.59	126.57	569.86	2616.32	0.00	60261.11	0.30	11.9	41.8
26–27	6.88	1102.58	971.52	639.72	0.00	4328.88	0.00	0.0	28.6
Water (0–5 m)	4.14	105.87	817.13	169.97	0.00	112.76	3979.58	8.0	32.0
St. 77									
0–10	1.76	74.71	865.33	173.07	0.00	1084.63	0.00	0.0	1.4
10–13	3.23	19.88	899.77	276.68	0.00	2871.09	0.00	0.0	1.7
13–19	5.34	166.70	584.85	255.96	0.00	0.00	420.33	0.0	1.1
19–21	17.74	50.90	1037.62	173.78	0.00	1.86	0.42	0.0	17.1
21–22	9.00	52.99	1036.40	252.35	0.00	24.58	856.87	0.0	13.4
22–23	11.31	162.96	741.34	282.39	0.00	54.24	42.19	0.0	44.6
Water (0–5 m)	8.05	94.72	221.79	53.64	0.00	0.06	2.34	8.0	9.0
St. 81									
0–10	1.63	104.63	588.76	130.23	0.00	54.45	202.05	0.0	1.6
10–13	4.70	136.98	923.69	276.52	0.00	1.68	859.85	0.0	0.0
13–19	4.45	306.72	1127.62	403.96	0.00	21.23	1411.53	0.0	0.0
19–21	1.92	202.68	564.02	120.00	0.00	96.88	518.85	0.0	0.0
21–22	3.22	329.16	678.27	229.72	0.00	289.61	469.19	0.0	7.4
22–23	2.71	188.27	969.03	297.64	0.00	879.13	966.66	0.0	0.0
Water (0–5 m)	5.12	383.25	293.63	74.20	0.00	11.04	2473.01	3.0	13.0

Table A8: Vertical distribution of the biomass of heterotrophic bacteria (= bacteria), cyanobacteria, autotrophic flagellates, heterotrophic flagellates, chlorophytes, pennate diatoms, centric diatoms, crustacean nauplii and rotifers in Baltic sea ice. n.d. = not determined

Depth (cm)	Bacteria (µg C l^{-1})	Cyanobacteria (µg C l^{-1})	Autotrophic flagellates (µg C l^{-1})	Heterotrophic flagellates (µg C l^{-1})	Chlorophyta (µg C l^{-1})	Pennate diatoms (µg C l^{-1})	Centric diatoms (µg C l^{-1})	Crustacea (µg C l^{-1})	Rotifera (µg C l^{-1})
St. 67									
0–10	1.10	0.00	0.73	0.01	0.00	0.00	0.16	0.00	0.00
10–20	1.27	0.00	0.67	0.10	0.02	0.14	0.51	0.00	0.00
20–26	0.74	0.00	1.25	0.36	0.01	2.11	11.58	0.00	0.00
26–28	0.98	0.00	5.89	0.29	0.01	4.53	12.97	0.00	0.37
28–29	1.07	0.01	16.83	0.17	0.01	4.04	7.34	0.00	0.41
29–30	0.88	0.01	57.18	0.66	0.02	2.42	1.83	6.21	0.58
Water (0–10 m)	0.93	0.04	0.58	0.23	0.24	0.04	0.26	0.89	0.44
St. 68									
0–10	2.40	0.02	3.21	2.11	0.00	4.99	1.79	0.73	0.12
10–19	2.65	0.02	3.93	3.46	0.17	3.45	98.43	0.00	0.00
19–25	1.49	0.01	2.50	1.44	0.02	5.51	10.12	0.00	0.03
25–27	3.94	0.01	12.35	1.71	0.02	15.17	6.68	0.00	0.15
27–28	1.80	0.03	16.99	1.17	0.02	9.03	2.21	0.00	0.07
28–29	5.59	0.06	136.58	2.22	0.08	166.35	0.00	0.00	1.06
Water (0–10 m)	2.59	0.07	1.62	0.62	0.22	0.03	0.08	0.80	0.04
St. 69									
0–10	3.40	0.00	14.70	11.40	n.d.	3.73	2.51	0.00	0.07
10–13	2.85	0.01	5.20	1.26	0.18	3.00	30.20	0.00	0.00
13–19	2.37	0.01	7.07	0.89	0.03	4.82	0.17	0.00	0.00
19–21	2.76	0.03	15.70	1.18	0.02	2.92	2.04	0.00	0.12
21–22	2.01	0.09	19.98	2.87	0.05	25.73	1.96	0.00	0.47
20–23	3.13	0.07	34.18	2.12	0.04	53.25	0.00	0.00	1.06
Water (0–10 m)	3.05	0.11	2.62	0.22	0.42	0.05	0.14	0.03	0.09

Table A 8 (continued): Vertical distribution of the biomass of heterotrophic bacteria (= bacteria), cyanobacteria, autotrophic flagellates, heterotrophic flagellates, chlorophytes, pennate diatoms, centric diatoms, crustacean nauplii and rotifers in Baltic sea ice. n.d. = not determined

Depth (cm)	Bacteria (µg C l^{-1})	Cyanobacteria (µg C l^{-1})	Autotrophic flagellates (µg C l^{-1})	Heterotrophic flagellates (µg C l^{-1})	Chlorophyta (µg C l^{-1})	Pennate diatoms (µg C l^{-1})	Centric diatoms (µg C l^{-1})	Crustacea (µg C l^{-1})	Rotifera (µg C l^{-1})
St. 74									
0–10	4.51	0.02	6.78	2.58	0.00	3.31	23.44	0.00	0.00
10–17	3.16	0.01	9.26	4.60	0.00	2.43	9.18	0.00	0.08
17–23	10.59	0.02	25.94	23.02	0.00	14.23	3.45	0.00	0.10
23–25	5.68	0.01	15.77	26.14	0.00	86.88	0.26	0.00	0.14
25–26	19.85	0.01	33.07	331.49	0.00	2963.45	0.08	0.75	0.85
26–27	11.47	0.07	22.64	22.32	0.00	266.24	0.00	0.00	0.92
Water (0–5 m)	4.90	0.01	19.85	7.40	0.00	7.43	733.18	1.04	1.01
St. 77									
0–10	3.45	0.00	5.77	1.31	0.00	76.28	0.00	0.00	0.02
10–13	7.55	0.00	10.48	3.15	0.00	175.18	0.00	0.00	0.03
13–19	8.55	0.01	8.42	1.96	0.00	0.00	15.26	0.00	0.02
19–21	22.74	0.00	23.11	2.55	0.00	0.13	0.08	0.00	0.31
21–22	15.48	0.00	22.11	5.71	0.00	2.62	30.82	0.00	0.30
22–23	17.19	0.01	18.18	8.08	0.00	5.77	1.52	0.00	0.86
Water (0–5 m)	5.73	0.01	1.53	0.33	0.00	0.02	0.18	4.30	0.26
St. 81									
0–10	3.70	0.01	24.82	2.52	0.00	3.76	14.04	0.00	0.02
10–13	11.44	0.01	17.73	4.91	0.00	0.21	38.22	0.00	0.00
13–19	7.86	0.02	20.82	7.34	0.00	1.46	53.73	0.00	0.00
19–21	11.62	0.01	8.63	1.53	0.00	6.69	22.30	0.00	0.00
21–22	7.27	0.02	8.26	3.94	0.00	19.35	23.31	0.00	0.05
22–23	5.24	0.01	21.76	6.19	0.00	58.97	194.34	0.00	0.00
Water (0–5 m)	4.21	0.02	3.12	0.72	0.00	0.76	453.79	0.22	0.26

Table A 9: Vertical distribution of heterotrophic bacteria, pennate diatoms, centric diatoms, transparent exopolymer particle (TEP) abundance, TEP area and the slopes of TEP size frequency distributions (β+1 values) in Arctic sea ice. n.d. = not determined

Depth (cm)	Bacteria (10^9 cells l^{-1})	Pennate diatoms (10^3 cells l^{-1})	Centric diatoms (10^3 cells l^{-1})	TEP abundance (10^6 particles l^{-1})	TEP area (cm^2 l^{-1})	TEP (β+1)
St. 271						
0–20	0.43	4.24	0.00	2.39	1.6	1.7
20–40	0.23	6.22	0.09	3.06	2.6	1.4
40–60	0.22	27.86	3.03	3.48	4.0	1.2
60–80	n.d.	68.78	0.10	2.28	2.4	1.2
80–100	0.47	113.10	0.10	5.79	8.0	1.0
100–120	0.64	214.12	3.05	4.21	7.6	0.8
120–140	0.67	147.83	0.78	4.09	4.4	1.3
140–160	0.80	73.82	0.66	8.66	12.2	1.0
160–180	0.46	78.40	1.13	3.26	6.8	0.7
180–183.5	0.41	89.30	3.56	4.83	6.2	1.1
183.5–189.5	0.29	124.79	1.39	3.53	5.2	1.0
189.5–191.5	0.48	253.89	1.59	2.87	5.1	0.8
191.5–192.5	0.25	768.25	1.02	3.74	10.2	0.6
192.5–193.5	0.49	428.17	0.92	2.97	6.6	0.7
Water (0–10 m)	0.26	4.50	4.76	0.56	0.6	1.2
St. 277-1						
0–20	0.21	40.17	29.35	3.01	4.9	1.1
20–26	0.26	52.08	46.88	1.43	2.8	0.9
26–32	1.20	140.22	2462.32	4.17	8.3	0.8
32–34	0.89	499.65	284.93	4.65	10.9	0.7
34–35	0.31	235.45	119.61	3.17	5.9	1.0
35–36	0.56	741.98	59.39	4.24	7.1	1.1
Water (0–10 m)	0.34	45.02	21.20	0.82	0.9	1.2
St. 277-2						
0–11	0.23	7.61	2.82	1.68	2.0	1.4
St. 277-3						
0–20	0.29	35.33	38.46	2.61	5.8	0.6
20–40	0.30	90.87	65.95	3.51	7.1	0.8
40–60	0.81	898.15	163.18	8.37	16.2	1.0
60–80	0.69	875.11	198.98	4.58	11.7	0.5
80–100	0.56	905.31	38.25	5.30	14.1	0.5
100–120	0.94	1323.93	41.00	5.44	5.1	1.5
120–140	0.91	1134.91	5.82	6.80	7.7	1.2
140–149.5	0.38	737.11	8.28	7.33	10.4	1.2
149.5–155.5	0.88	712.84	8.70	10.42	10.6	1.2
155.5–157.5	0.44	441.05	11.07	7.53	6.9	1.5
157.5–158.5	0.28	303.12	3.12	3.19	4.4	1.0
158.5–159.5	0.86	291.60	5.00	7.62	10.8	1.0

Table A9 (continued): Vertical distribution of heterotrophic bacteria, pennate diatoms, centric diatoms, transparent exopolymer particle (TEP) abundance, TEP area and the slopes of TEP size frequency distributions (β+1 values) in Arctic sea ice. n.d. = not determined

Depth (cm)	Bacteria (10^9 cells l^{-1})	Pennate diatoms (10^3 cells l^{-1})	Centric diatoms (10^3 cells l^{-1})	TEP abundance (10^6 particles l^{-1})	TEP area (cm^2 l^{-1})	TEP (β+1)
St. 280						
0–20	0.15	966.17	0.00	0.66	0.9	1.2
20–40	0.27	1.79	0.00	0.69	0.5	1.6
40–60	0.11	14.85	0.00	0.43	0.7	0.9
60–80	0.34	36.77	0.45	0.61	0.8	1.2
80–100	0.17	80.51	0.79	2.44	3.5	1.3
100–120	1.03	1110.65	1.29	3.55	7.2	0.9
120–140	0.49	2049.15	0.00	4.90	5.3	1.5
140–160	0.53	544.22	0.00	4.12	9.2	0.8
160–180	0.73	259.26	0.00	4.51	6.1	1.3
180–200	0.30	3.98	0.00	4.12	5.4	1.3
200–220	0.19	22.86	0.77	5.47	3.9	1.7
220–240	0.29	1295.13	0.48	5.96	3.7	1.5
240–260	0.37	486.23	0.37	8.78	8.6	1.3
260–280	0.22	74.49	0.00	7.35	6.0	1.5
280–292	1.00	155.15	2.35	6.16	4.6	1.6
292–298	0.51	1323.39	2.24	14.93	8.7	1.9
298–300	2.46	553.44	0.00	5.68	4.5	1.4
300–301	2.49	572.28	0.00	5.55	3.7	1.8
301–302	2.14	456.19	0.00	7.82	5.7	1.5
Water (0–10 m)	1.06	5.92	21.92	0.50	0.2	2.2

Table A10: Vertical distribution of bacterial abundance, bacterial biomass, relative number of bacteria associated with transparent exopolymer particles (TEP), pennate diatom abundance, pennate diatom biomass, centric diatom abundance, centric diatom biomass, abundance of TEP, TEP area and the slopes of TEP size frequency distributions (β+1 values) in Antarctic sea ice. n.d. = not determined

Depth (cm)	Bacteria (10^9 cells l^{-1})	Bacteria (µg C l^{-1})	TEP-associated bacteria (%)	Pennate diatoms (10^3 cells l^{-1})	Pennate diatoms (µg C l^{-1})	Centric diatoms (10^3 cells l^{-1})	Centric diatoms (µg C l^{-1})	TEP abundance (10^6 particles l^{-1})	TEP area (cm^2 l^{-1})	TEP (β+1)
St. 113										
0–10	2.45	33.96	2.3	605.50	29.04	245.00	30.39	10.22	4.3	2.9
10–20	1.19	19.12	15.4	3449.59	96.78	2134.38	293.56	32.01	15.4	2.7
20–30	4.02	81.97	11.6	33955.96	1502.72	25821.16	3637.68	81.36	33.5	2.9
30–40	4.68	87.06	20.3	33702.81	1684.21	26879.90	2855.79	109.27	56.2	2.7
40–50	3.20	58.16	11.4	24558.77	1343.70	16231.06	1472.97	65.77	22.3	3.0
50–60	2.00	39.71	20.7	14285.22	741.33	5753.77	564.41	53.89	24.7	2.6
60–62	2.39	39.88	12.6	15613.41	1054.13	5019.83	516.20	57.10	27.3	2.7
62–68	2.29	31.09	10.1	10105.47	537.03	4867.56	417.21	46.23	12.9	3.5
68–70	2.55	46.22	18.6	15869.34	810.12	13151.99	1350.71	52.54	20.3	2.9
70–71	2.11	32.07	14.4	12817.91	861.13	12764.95	1435.39	47.40	29.5	2.5
71–72	2.42	35.66	8.9	16568.62	1092.88	9609.80	1086.20	44.66	17.2	2.9
Water (0–10 m)	0.55	5.42	3.4	211.80	10.98	163.17	10.19	3.04	1.1	3.0
St. 114										
0–10	1.72	37.94	13.3	5474.04	277.56	3630.41	324.40	41.21	16.5	2.9
10–20	4.35	119.44	12.0	20863.29	911.53	10459.46	1148.03	63.07	22.6	2.9
20–30	2.66	48.51	26.2	13697.73	566.31	9377.48	994.05	191.21	92.1	2.7
30–40	3.25	71.21	37.8	27872.32	1098.62	14029.94	1143.75	260.45	80.7	2.9
40–46	4.85	103.99	15.8	36034.04	1925.16	23541.40	2057.33	244.99	71.9	3.1
46–52	1.64	33.31	56.5	18592.03	957.41	10265.74	579.28	217.57	54.1	3.2
52–54	2.33	37.25	26.7	15333.51	802.83	8589.61	450.55	143.97	37.1	3.3
54–55	1.35	33.24	15.1	10179.12	345.53	1878.29	120.40	70.49	22.9	2.9
55–56	1.66	38.97	11.3	7756.98	187.73	2300.48	136.50	55.75	22.9	2.6
Water (0–10 m)	0.57	8.41	1.9	162.85	3.93	40.10	2.59	3.64	0.8	3.5

Table A 10 (continued): Vertical distribution of bacterial abundance, bacterial biomass, relative number of bacteria associated with transparent exopolymer particles (TEP), pennate diatom abundance, pennate diatom biomass, centric diatom abundance, centric diatom biomass, abundance of TEP, TEP area and the slopes of TEP size frequency distributions (β+1 values) in Antarctic sea ice. n.d. = not determined

Depth (cm)	Bacteria (10^9 cells l^{-1})	Bacteria (µg C l^{-1})	TEP-associated bacteria (%)	Pennate diatoms (10^3 cells l^{-1})	Pennate diatoms (µg C l^{-1})	Centric diatoms (10^3 cells l^{-1})	Centric diatoms (µg C l^{-1})	TEP abundance (10^6 particles l^{-1})	TEP area (cm^2 l^{-1})	TEP (β+1)
St. 115										
0–10	0.62	10.24	5.7	18173.46	150.63	180.46	12.78	14.54	3.4	3.3
10–20	0.54	8.81	15.3	24132.52	262.07	770.93	73.27	31.12	6.9	3.5
20–30	0.77	11.87	13.0	20479.01	203.64	795.10	83.97	21.08	6.5	3.1
30–40	0.67	13.21	16.0	16831.63	225.00	707.99	82.23	23.38	7.5	2.9
40–45	0.95	15.70	16.2	13704.26	257.89	3846.52	335.72	32.96	10.0	2.9
45–51	1.12	26.98	21.3	10672.56	240.37	3168.97	346.68	47.78	11.5	3.4
51–53	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
53–54	0.89	14.25	12.7	20087.54	315.35	900.65	140.35	24.89	7.8	2.9
54–55	0.99	18.99	10.3	79443.94	882.59	1283.29	154.63	19.36	5.1	3.1
Water (0–10 m)	0.70	9.63	1.5	2393.10	28.31	61.05	9.14	3.56	1.0	3.1

Lebenslauf

Persönliche Daten

Name: Klaus Martin Meiners
Geboren am: 21.02.1972 in Münster
Staatsangehörigkeit: deutsch

Schulausbildung

1978–1982	Grundschule Heilig Kreuz in Münster
1982–1991	Schiller-Gymnasium in Münster
1991	Erlangung der allgemeinen Hochschulreife im Juni 1991

Studium

1992	Beginn des Biologiestudiums an der Philipps-Universität zu Marburg
1993	Studienortwechsel an die Christian-Albrechts-Universität zu Kiel und Fortsetzung des Biologiestudiums, Vordiplom in Biologie 1994
1994	Beginn des Hauptstudiums mit dem Hauptfach: Biologische Meereskunde Nebenfächer: Zoologie, Physikalische Ozeanographie
1996	Auslandssemster: Teilnahme am Arctic Studies Program der University of Lapland, Rovaniemi, Finnland
1999	Diplom an der Christian-Albrechts-Universität zu Kiel in Biologie im Februar 1999. Thema der Diplomarbeit: „Zur Dynamik des mikrobiellen Nahrungsnetzes im arktischen Meereis“

Arbeitsverträge

seit Juli 1999	Doktorand am Institut für Polarökologie, Universität Kiel. Durchführung des DFG-Projektes (SP 377/9-1-3) mit dem Thema „Aktivität und Stoffumsatz mikrobieller Nahrungsnetze im arktischen und antarktischen Meereis“

Kiel, den 23.09.2002 . . . . . .

Erklärung

Hiermit erkläre ich, dass die vorliegende Dissertation – abgesehen von der Beratung durch meine akademischen Lehrer – nach Inhalt und Form meine eigene Arbeit ist. Sie wurde keiner anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Dies ist mein erster Promotionsversuch.

Kiel, den 23.09.2002 . . . . . .