The role of copepods in cryo-pelago-benthic coupling in the Weddell Sea, Antarctica

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„Die gefährlichste aller Weltanschauungen ist die Weltanschauung derer, die die Welt nie angeschaut haben.“

“He who has never seen the world has the most dangerous vision thereof.”

Alexander von Humboldt

(1769 - 1859)

Preface

Research on Southern Ocean zooplankton and sea ice communities has provided me with the most impressive and outstanding experiences of my life. During my work in one of the most remote, and for humans most inhospitable, regions of our planet I have seen a breathtakingly beautiful world of ice and snow inhabited by fascinating and amazing organisms. There have been countless moments of unimaginably intensive happiness that have left so strong memories in my mind that I will never forget any of them for the rest of my life. It is impossible to describe these experiences in an authentic way to friends and relatives at home, and I have thus never really tried. Besides all the exciting work, it has mainly been the short private moments in between the daily working activities, which have made me fall in love with the Southern Ocean: standing at the railing of “Polarstern” and watching a stunning sunset, being alone on Antarctic sea ice beneath a most gorgeous starry sky during a winter night… Once I wrote the following to a good friend and colleague about my emotions, which I have in such situations: “It is impossible to describe these feelings of happiness. I have experienced only very few comparable situations so far. These have, for instance, included standing in Costa Rican rainforest in absolute darkness by night and letting the atmosphere impress me, or snorkelling in a blackwater lagoon within the rainforest in southern Venezuela by night while searching for turtles, and emerging under a grandiose starry sky. In such moments I feel my heart beat intensively, and I have the feeling to be in a mixture of intoxication and trance...”. In my opinion the experience of such moments in the Southern Ocean is one of the greatest and most precious privileges existing, and everybody who may experience them should conjure this up again and again and enjoy each single second as intensively as possible. I am deeply grateful for having been so privileged…

The feelings described above have been the best motivation I can imagine for the work on this dissertation. This holds true not only for the studies in the Southern Ocean but also for the work in the laboratory and the office in Bremerhaven.

The cumulative dissertation consists of six manuscripts, four of which are accepted for publication and two of which are under revision. My contributions to the related projects and the preparation of these manuscripts are described in detail in chapter 8. The layout and the citation style of the manuscripts are in accordance with the requirements of the respective journals. In each manuscript the figures and tables are numbered separately. The dissertation also comprises a general introduction to the overall research topic and the aims of the PhD study. In a synoptic discussion, the results of the single projects are comprehensively discussed in a wider context with respect to the study aims.

Summary

This thesis aimed at investigating the importance of copepods for cryo-pelagic coupling and improving the knowledge on the contribution of copepods to pelago-benthic coupling. Sampling, measurements and experiments were conducted during the two expeditions ANT XXI/2 and ANT XXII/2 with RV “Polarstern” to the shelf of the eastern Weddell Sea in late spring 2003, and to the continental slope of the western Weddell Sea in late spring 2004/2005, respectively. In the western Weddell Sea, the population dynamics and the spatial and temporal variability of (1) the metazoan fauna in the surface and sub-ice layers of a drifting ice floe, and (2) the copepod communities within the ice proper of the drifting floe and of pack ice on a transect from the ice edge to the ice drift station were studied. In the sea ice proper, the harpacticoids *Drescheriella* spp., mainly naupliar stages, were by far the most abundant species throughout the study (72 - 87 %). *Drescheriella* spp. and the calanoid *Stephos longipes* were present in all layers of the ice, whereas the occurrence of the other copepod species was restricted to the lowermost ice layer. The distribution of all species was very patchy and varied greatly between the sampling sites. The metazoan fauna within the sea ice surface layer was dominated by *Drescheriella* spp. and *S. longipes* with maximum abundances of 3830 and 1293 ind. L^{-1}, respectively. The populations were mainly comprised of adults and early naupliar stages indicating reproduction of these species within the sea ice surface layer. The copepod abundances were generally higher at the edge of the floe than in the inner part. *Drescheriella* spp. and *S. longipes* also occurred regularly in the sub-ice water layer (nauplii, copepodids and adults in *Drescheriella* spp. and mainly nauplii and adults in *S. longipes*), however, the dominant sympagic copepod species in this habitat was *Ectinosoma* sp. with a maximum abundance of 599 ind. m^{-3}. Feeding experiments were conducted with *Drescheriella* spp. females and copepodids (C) V and *S. longipes* adults, C I - V and nauplii VI, and sea ice protist communities as food. In both species high ingestion rates were measured, and no evidence for satiation feeding was found even at the highest chlorophyll *a* (Chl *a*) concentrations (up to 76.86 µg L^{-1}). Food selection by *Drescheriella* spp. and *S. longipes* was related to the size of the protists with small-sized species such as *Fragilariopsis cylindrus* and *F. curta* being preferentially ingested. At some sampling sites the estimated grazing impact of *Drescheriella* spp. and *S. longipes* on infiltration layer communities was extremely high reaching a maximum population grazing rate of 313.8 % of the ice algae stock per day.

The amount and composition of vertical particle flux at depths of 10 m and 70 m under the drifting ice floe were determined during a period of 30 days in order to investigate the influence of sea ice related biological processes on the flux. The total mass flux was dominated by diatoms, faecal material, and aggregates, and ranged from 95.28 to 197.67 mg m^{-2} d^{-1} at 10 m depth and from 51.54 to 55.34 mg m^{-2} d^{-1} at 70 m depth. A strong increase with time of the flux of chlorophyll equivalents, biogenic silica, and faecal material was recorded during the observation period, coincident with an increase in the concentration of Chl *a* in the bottom ice layer above the trap array. No copepod faecal pellets were found within the sinking faecal

material, which was dominated by krill faecal strings and contained large amounts of diatom frustule debris, as well as intact diatom frustules, mainly of the species *F. curta* and *F. cylindrus*. Low POC/PON and biogenic silica/POC ratios of the sinking particulate matter suggest that the material collected in the traps was relatively fresh.

The population dynamics of dominant calanoid copepods in the water column under the drifting ice floe in the western Weddell Sea, and on the shelf of the eastern Weddell Sea were studied during periods of about one month and three weeks, respectively. The goal was to contribute to the understanding of the importance of these copepods for carbon cycling and vertical particle flux in the pelagial. Considerable amounts of copepods were present in all investigated depth layers (down to 1000 m depth in the western Weddell Sea, and the whole water column on the eastern Weddell Sea shelf with a maximum sampling depth of 464 m). At both sites the calanoid copepod communities were characterised by the dominance of only a few species with *Microcalanus pygmaeus* being most numerous. This species contributed on average 70 % (western Weddell Sea) and 66 % (eastern Weddell Sea) of all calanoid copepods. Further dominant species at both sites were *Calanoides acutus* and *Metridia gerlachei*. Interestingly, *Ctenocalanus citer* comprised on average 13.4 % of the calanoid copepods on the eastern Weddell Sea shelf, while it occurred only in very low numbers in the western Weddell Sea. The sympagic *S. longipes* was not abundant in the water column of the western Weddell Sea. A similar situation was observed on the eastern Weddell Sea shelf for most of the study period, however, after a strong storm *S. longipes* contributed a relatively large amount (8.8 %) of the calanoid copepods present on the last sampling date. The *S. longipes* population was then strongly dominated by C I (53 %) that had probably been released from the sea ice into the under ice water layer due to ice break-up and ice melt. Although copepods were abundant in the water column, the vertical particle flux close to the sea floor on the eastern Weddell Sea shelf did not contain any copepod faecal pellets, similar to the situation observed under the ice floe in the western Weddell Sea.

The results indicate that sympagic copepods are main mediators of carbon cycling and nutrient regeneration in Antarctic sea ice, thus contributing considerably to the productivity of sea ice communities. A considerable amount of copepod faecal matter produced within the ice may be transported into the under-ice water layer and provide an important food source for pelagic grazers. In the pelagial major amounts of copepod faecal pellets do not sink to depth and are probably rapidly degraded and recycled. The direct contribution of copepods to the vertical flux of particulate organic matter in the water column is thus relatively small. However, large amounts of faecal pellets produced by sympagic and pelagic copepods might be transported to the seafloor within marine snow and serve as important food source for the benthos. Accordingly, the contribution of copepods to flux of particulate organic matter from sea ice into the water column and down to the seafloor may facilitate the coupling between the surface and the deep water layers in the Southern Ocean. Furthermore, copepods may contribute to pelago-benthic coupling due to vertical migration and as prey both for omnivorous and carnivorous organisms in deep water layers, and for benthic organisms.

Zusammenfassung

Ziel dieser Arbeit war die Untersuchung der Bedeutung von Copepoden für kryo-pelagische Kopplungsprozesse im Weddellmeer. Darüber hinaus sollte die Arbeit dazu beitragen, die Rolle der Copepoden in pelago-benthischen Kopplungs-prozessen im Weddellmeer besser zu verstehen. Die Probennahmen, Messungen und Experimente fanden im Rahmen der beiden Expeditionen ANT XXI/2 (Schelf des östlichen Weddellmeers, spätes Frühjahr 2003) und ANT XXII/2 (Kontinentalhang des westlichen Weddellmeers, spätes Frühjahr 2004/2005) mit dem Forschungsschiff „Polarstern“ statt.

Im westlichen Weddellmeer wurden die Populationsdynamik und die räumliche und zeitliche Variabilität der Metazoenfauna in verschiedenen Meereishabitaten einer driftenden Eisscholle und entlang eines Meereistransekts analysiert. Während des gesamten Untersuchungszeitraums waren die harpacticoiden *Drescheriella* spp. (vor allem Naupliusstadien) im Laugenkanalsystem des Meereises die mit Abstand häufigsten Copepodenarten (72 - 87 %). Während *Drescheriella* spp. und die calanoide Art *Stephos longipes* in allen Eisschichten vorkamen, waren die anderen Copepodenarten lediglich in der untersten Eisschicht zu finden. Das Vorkommen und die Abundanzen aller Copepodenarten wiesen eine ausgeprägte räumliche Variabilität auf.

In der Infiltrationsschicht an der Meereisoberfläche dominierten *Drescheriella* spp. und *S. longipes* mit Maximumabundanzen von 3830 beziehungsweise 1293 Individuen pro Liter die Metazoenfauna. Ihre Populationen setzten sich überwiegend aus Adulten und frühen Naupliusstadien zusammen, was darauf hinweist, dass beide Arten sich auch in diesem Habitat vermehren. Generell waren die Copepoden-Abundanzen am Rand der Eisscholle am größten. *Drescheriella* spp. und *S. longipes* kamen auch in der Untereiswasserschicht vor (Nauplien, Copepodite und Adulte von *Drescheriella* spp., und überwiegend Nauplien und Adulte von *S. longipes*). Die dominante Copepodenart in diesem Habitat war jedoch *Ectinosoma* sp. (Maximumabundanz: 599 Individuen m^{-3}).

Fraßexperimente mit *Drescheriella* spp. (Weibchen, Copepodite V) und *S. longipes* (Weibchen, Männchen, Copepodite I - V, Nauplien VI), denen Meereisprotisten als Nahrung angeboten wurden, zeigten, dass diese Copepodenarten mit sehr hohen Ingestionsraten fressen können. Die Nahrungsselektion erfolgte nach der Gröβe der Nahrungsorganismen, wobei kleine Arten wie die Diatomeen *Fragilariopsis cylindrus* und *F. curta* bevorzugt gefressen wurden. Die Ergebnisse deuten darauf hin, dass die Populationen von *Drescheriella* spp. und *S. longipes* im Meereis einen erheblichen Fraßdruck auf die Eisalgengemeinschaften ausüben können.

Um den Einfluss von mit dem Meereis assoziierten biologischen Prozessen auf den vertikalen Partikelfluss in der Wassersäule zu untersuchen, wurden unter der driftenden Eisscholle mit Hilfe von Sinkstofffallen während eines Zeitraums von 30 Tagen die Menge und die Zusammensetzung der sinkenden Partikel bestimmt. Der Gesamtpartikelfluss variierte zwischen 95,28 und 197,67 mg m^{-2} d^{-1} in 10 m Tiefe

und zwischen 51,54 und 55,34 mg m^{-2} d^{-1} in 70 m Tiefe. Diatomeen, Kotmaterial und Aggregate dominierten den Partikelfluss. Während des Untersuchungszeitraums nahm der vertikale Fluss von Chlorophyll-Äquivalenten, biogenem Silikat und Kotmaterial zu. Gleichzeitig wurde in der untersten Schicht des Meereises über den Sinkstofffallen ein Anstieg der Chlorophyll *a*-Konzentration beobachtet. Das absinkende Kotmaterial bestand überwiegend aus Kotschnüren von Krill und enthielt große Mengen zerbrochener und intakter Diatomeenschalen (vor allem von *F. curta* und *F. cylindrus*). Kotballen von Copepoden wurden nicht gefunden. Die Untersuchungen zeigten, dass ein Großteil der absinkenden Partikel aus relativ frischem organischen Material bestand.

Um zum Verständnis der Bedeutung der Copepoden für den Kohlenstoffkreislauf und den vertikalen Partikelfluss im Pelagial beizutragen, wurde in beiden Untersuchungsgebieten in der Wassersäule die Populationsdynamik dominanter calanoider Copepodenarten analysiert. Copepoden waren in allen untersuchten Wasserschichten (0 - 1000 m im westlichen Weddellmeer, und in der gesamten Wassersäule mit einer Maximumbeprobungstiefe von 464 m auf dem Schelf des östlichen Weddellmeers) abundant. In beiden Untersuchungsgebieten war die Gemeinschaft der calanoiden Copepoden durch die Dominanz weniger Arten charakterisiert, wobei *Microcalanus pygmaeus* zahlenmäßig am häufigsten vorkam und im Durchschnitt bis zu 70 % (im westlichen Weddellmeer) und 66 % (im östlichen Weddellmeer) aller Calanoida stellte. Weitere in beiden Gebieten dominante Arten waren *Calanoides acutus* und *Metridia gerlachei*. Interessant ist, dass *Ctenocalanus citer* im östlichen Weddellmeer mit einer relativen Häufigkeit von 13,4 % aller calanoiden Copepoden vorkam, während diese Art im westlichen Weddellmeer nur in geringen Individuenzahlen zu finden war. Auch *S. longipes* kam im Pelagial des westlichen Weddellmeers nur in geringen Individuenzahlen vor. Im östlichen Weddellmeer war dies über große Teile des dreiwöchigen Untersuchungszeitraums hinweg identisch. Nach einem starken Sturm wurde *S. longipes* am Ende des Untersuchungszeitraums jedoch in relativ großen Individuenzahlen und mit einer relativen Häufigkeit von 8,8 % aller Calanoida gefunden. Zu diesem Zeitpunkt bestand die Population überwiegend aus Copepoditen I (53 %), die wahrscheinlich durch das Aufbrechen und Schmelzen des Meereises in die Wassersäule gelangt waren. Obwohl Copepoden in der Wassersäule abundant waren, befanden sich in absinkendem partikulären Material, das dicht am Meeresboden auf dem Schelf des östlichen Weddellmeers gesammelt wurde, keine Kotballen von Copepoden.

Die Ergebnisse dieser Arbeit zeigen, dass Copepoden eine wichtige Rolle im Kohlenstoffkreislauf und der Nährstoffregeneration im Meereis spielen und dadurch entscheidend zur Produktivität der Meereisgemeinschaften beitragen. Es ist vorstellbar, dass größere Mengen von im Meereis produziertem Copepoden-Kotmaterial in die Untereiswasserschicht gelangen und dort eine wichtige Nahrungsquelle für pelagische Grazer darstellen. Im Pelagial sinkt jedoch ein Großteil des Copepoden-Kotmaterials nicht in die Tiefe, sondern wird relativ schnell biologisch abgebaut. Dementsprechend ist der direkte Beitrag der Copepoden zum vertikalen Partikelfluss in der Wassersäule relativ gering. Ein Teil der Copepoden-Kotballen gelangt aber in Form von schnell sinkenden Aggregaten zum Meeres-

boden und dient dort dem Benthos als Nahrung. Über diesen Prozess können Copepoden einen Beitrag zu den Kopplungsprozessen zwischen der Oberflächenschicht und tieferen Wasserschichten im Pelagial des Südpolarmeers leisten. Darüber hinaus tragen Copepoden aufgrund von Vertikalwanderungen und als Beute von omnivoren und carnivoren Organismen, die in tiefen Wasserschichten und im Benthal leben, zu pelago-benthischer Kopplung bei.

Contents

1 General introduction

1.1 The Southern Ocean

General hydrographic features

The term “Southern Ocean” often refers to the part of the World Ocean that is located south of 60° S. However, from the oceanographic point of view, pronounced meridional gradients in properties of the surface waters are considered the northern boundary of the Southern Ocean. These gradients are called Subtropical Front (STF) and separate the waters of the Southern Ocean from the warmer and saltier waters of the subtropical circulations (Fig. 1, Orsi et al. 1995 and citations therein). The largest current system in the World Ocean, referred to as Antarctic Circumpolar Current (ACC, also called West Wind Drift) is located south of the STF. An ACC water transport of 118 to 146 Sv (1 Sv = 10^6 m^3 s^{-1}) was estimated based on measurements conducted in the Drake Passage, between Cape Horn and the Antarctic Peninsula (Whitworth III 1983). The eastward-flowing ACC is driven by the world’s most powerful westerly winds (approximately between 45° and 55° S), and flows around the globe connecting all major oceans. The flow of the ACC is associated with a steep rise of isopycnals toward the south through the entire water column, and comprises fronts, which are characterised by bands of large horizontal density gradients and linked with strong surface currents (Orsi et al. 1995 and citations therein). Since the fronts are dynamic systems their location varies with time. Two major fronts, the Subantarctic Front (SAF) and the Polar Front (PF), are permanent features of the ACC (Fig. 1). Additional strong fronts may be present, e.g. the Southern Polar Front (SPF, also referred to as Southern ACC Front, Fig. 1) and the ACC-Weddell Gyre Boundary Front, observed in the Atlantic sector of the Southern Ocean (Whitworth III & Nowlin Jr 1987, Veth et al. 1997). Where the ACC is located far enough from the Antarctic continent, cyclonic cells of recirculating waters exist south of the ACC. The Weddell and Ross Gyres are the most prominent (Deacon 1979, Reid 1986). A further feature of the Southern Ocean hydrography is the Antarctic Coastal Current (also called East Wind Drift), which is driven by easterly winds and buoyancy, and flows westward along the Antarctic coastline over or near the continental slope (e.g. Tchernia 1980). The boundary between the major wind and current systems of the ACC and the Antarctic Coastal Current, the Antarctic Divergence, is characterised by major upwelling processes caused by wind-induced Ekman flow (Gordon 1988).

Three main water masses are defined in the Southern Ocean. The relatively cold and saline Antarctic Surface Water is characterised by a subsurface temperature minimum in summer. Its thermohaline structure is determined by seasonally changing air-sea interactions, advection, and formation and melting of sea ice (e.g. Gordon & Huber 1984). The major part of the water column is composed of the warmer Circumpolar Deep Water, which is transported around the Antarctic continent by the ACC and is a mixture of deep water from all oceans (Stewart 2007). The Antarctic Bottom Water is the coldest and most saline water in the Southern Ocean. It

develops on the continental shelf around Antarctica in winter, mainly in the Weddell and Ross Seas, drains from the shelf down the continental slope and spreads out along the seafloor (Stewart 2007).

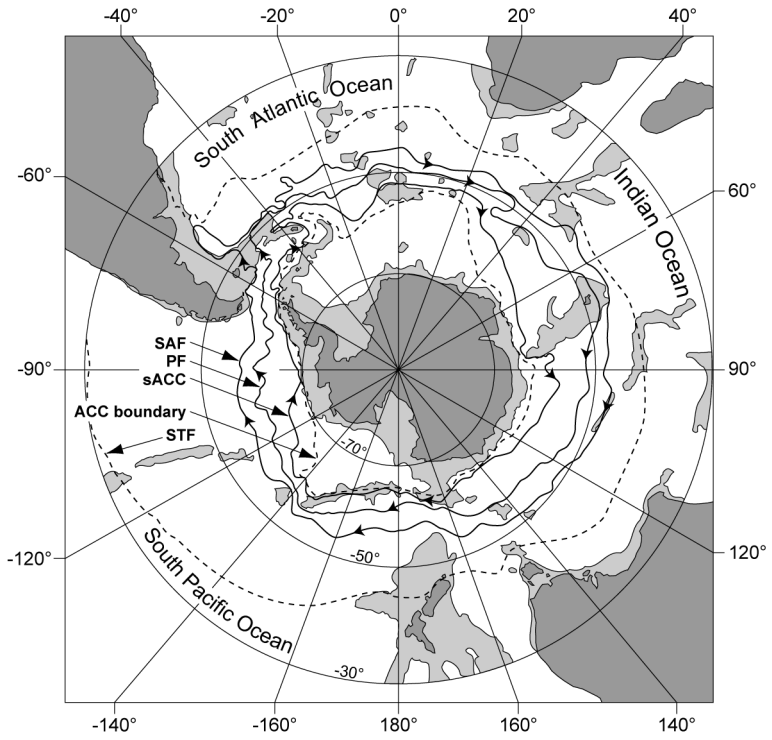

Fig. 1: Distribution of fronts around Antarctica. **STF** Subtropical Front, **SAF** Subantarctic Front, **PF** Polar Front, **ACC** Antarctic Circumpolar Current, **sACC** Southern ACC Front. Shaded areas are shallower than 3 km. Modified after Stewart (2007).

The Weddell Sea

The Weddell Sea is located in the Atlantic sector of the Southern Ocean and bordered by the Antarctic continent in the west (Antarctic Peninsula), the south (mountain ranges including the Ellsworth-Whitmore Mountains and the Shackleton Range) and the east (Coats Land, Dronning Maud Land). In the northeast, it extends to a line approximately linking the South Sandwich Islands and Cape Norvegia, while in the northwest the Scotia Ridge represents the border (Carmack & Foster 1977). One characteristic feature of the Weddell Sea, applicable to the entire Southern Ocean, is the deep shelf areas which are due to the massive ice sheet covering the Antarctic continent and pressing it down into the Earth's crust. As a result, the shelf edge is located in depths of 500 - 600 m (Carmack & Foster 1977), which is significantly deeper than at the other continents. The hydrographic properties of the

Weddell Sea are strongly determined by the Weddell Gyre and the Antarctic Coastal Current described above. Major proportions of the coastline are covered by large ice shelves such as the Ronne and Filchner ice shelves in the south and the Larsen ice shelf in the west (see Fig. 4). Along these ice shelves katabatic winds often cause the formation of polynias. The Weddell Sea is the main area of Antarctic Bottom Water formation (Carmack 1977, Orsi et al. 1999, Hellmer & Beckmann 2001), in whose processes the interactions between the ice shelves and the ocean are an important component. Ice Shelf Water (ISW), characterised by a potential temperature below the surface freezing point, is formed when dense shelf water is cooled and diluted by meltwater beneath the ice shelves. At the sill of the Filchner Depression in the Weddell Sea, for instance, ca. 10^6 m^{-3} of ISW per second leave the continental shelf and flow down the slope, subsequently mixing with the overlaying Weddell Deep Water and forming Weddell Sea Bottom Water (see Nøst & Foldvik 1994 and citations therein).

Antarctic sea ice

Besides the low temperatures and the pronounced seasonality of solar radiation, one of the prominent characteristics of polar seas is their sea ice cover. In winter, major parts of the Southern Ocean are covered by sea ice reaching extensions of about 20×10^6 km^2, and in summer, during the period of annual minimum sea ice extent, the sea ice cover still has dimensions of about 4×10^6 km^2 (Fig. 2, Zwally et al. 1983). One of the largest areas with sea ice persisting throughout the year is located in the western Weddell Sea, representing about 40 % of the total perennial ice cover of the Southern Ocean (Fig. 2, Zwally et al. 1983). It is characterised by ice concentrations higher than generally found in the seasonal pack ice (Eicken 1992 and citations therein) and large proportions of second-year ice, the latter associated with snow and ice thicknesses being among the largest recorded in the Southern Ocean (Lange & Eicken 1991).

The formation of Antarctic sea ice passes several consecutive processes described e.g. by Lange et al. (1989), Horner et al. (1992) and citations therein. Initially, seawater is cooled below the freezing point resulting in the formation of about 3 - 4 mm sized ice crystals called frazil ice. Frazil ice typically forms on the sea surface, but it may also originate in supercooled layers of the water column and ascend to the surface. The ice crystals then coagulate and form a viscous mixture referred to as grease ice. With the absence of strong wind and waves the ice crystals quickly freeze together to form pancake ice and a subsequent solid ice layer up to 10 cm thick. Ice growth then slows down, and columnar ice crystals develop on the underside of the ice, producing so called congelation ice. Frazil ice may be found between layers of congelation ice, which may be due to collisions and resulting stacking of ice floes. Since only water molecules are incorporated into the ice lattice during ice formation, the expelled seawater ions form brine, which is enclosed in long and narrow channels (between some micrometres and a few millimetres in diameter) building a network and resulting in a semi-solid ice matrix. On the ice underside, many of these

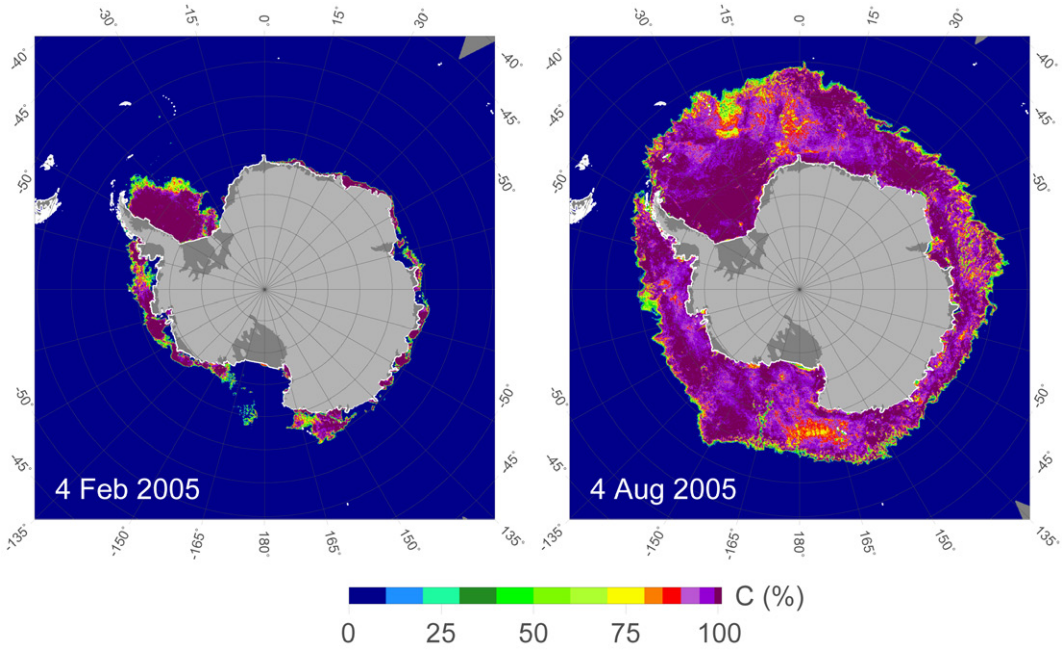

Fig. 2: Distribution and concentration of sea ice in the Southern Ocean during the periods of minimum sea ice extend in summer 2005 (left image) and maximum sea ice extend in winter 2005 (right image). Source of the satellite images: http://iup.physik.uni-bremen.de:8084/amsr/amsre.html .

brine channels are connected with the under-ice water layer (e.g. Eicken 1992, Horner et al. 1992).

Antarctic sea ice provides a habitat for a large variety of organisms including viruses, bacteria, protists, turbellarians and small crustaceans (Schnack-Schiel et al. 2001a, Thomas & Dieckmann 2002, Lizotte 2003, Schnack-Schiel 2003). Many of them are probably of pelagic origin and stick to, or are caught between, ice crystals at the beginning of ice formation, and are then trapped within the brine channels during subsequent ice growth and consolidation (Eicken 1992, Palmisano & Garrison 1993, Thomas & Dieckmann 2002). The biomass of typical sea ice protist communities is strongly dominated by diatoms, mainly pennate species, whereas dinoflagellates, auto- and heterotrophic flagellates, ciliates and bacteria only contribute minor fractions (e.g. Garrison et al. 1986). The diatoms may be present in extremely high concentrations resulting in brown colouration of the ice due to the photosynthetic pigments. Standing stocks of up to 1000 µg chlorophyll *a* (Chl *a*) per litre of melted sea ice have been measured, which is several orders of magnitude higher than the concentrations of < 0.02 to 5 µg Chl *a* L^{-1} typically measured in surface waters in the Southern Ocean (Thomas & Dieckmann 2002). Since major proportions of the brine channel system cannot be entered by larger organisms (Krembs et al. 2000), protozoan and smaller metazoan species encounter favourable conditions within sea ice, including rich food sources and the lack of larger predators. This may result in very high abundances of these sympagic (= ice-associated) organisms (Thomas & Dieckmann 2002).

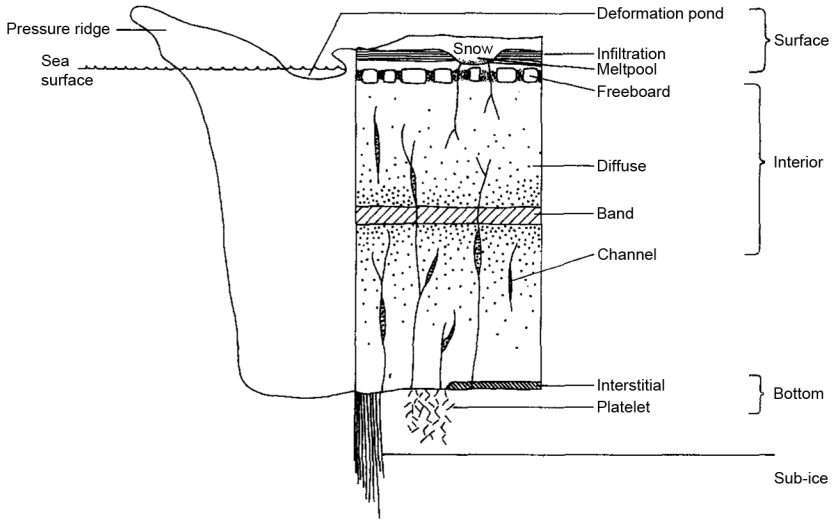

Fig. 3: Schematic representation of habitats and biological communities found in sea ice. From Horner et al. (1992).

Primary production in the Southern Ocean

The results of many studies on phytoplankton and its primary production in the Southern Ocean have represented a paradox for oceanographers. Although the major part of the Southern Ocean is characterised by high macronutrient concentrations, mainly caused by the intense upwelling processes at the Antarctic Divergence, in most open ocean waters these nutrients are underutilised, and the chlorophyll concentrations remain low throughout the year (e.g. Tréguer & Jacques 1992, Banse 1996, Moore & Abbott 2000). The Southern Ocean is thus the largest high-nutrient, low-chlorophyll region in the world (e.g. Martin 1990), and the availability of the micronutrient iron is considered to play a critical role in limiting phytoplankton growth and production (e.g. Martin et al. 1990a, b). However, large surface mixed layer depths, which can increase to over 200 m in winter and spring (Gordon et al. 1984, Nöthig et al. 1991) and are mainly caused by strong storms and thermo-haline convection due to cold brines ejected from growing sea ice (Carmack 1986), are certainly also a reason for the low primary production rates in the Southern Ocean (Mitchell & Holm-Hansen 1991). Furthermore, for areas with high zooplankton abundances grazing of phytoplankton biomass is also considered as a cause of low chlorophyll concentrations (e.g. El-Sayed 1988). While the Southern Ocean primary production estimated in several studies would theoretically not be sufficient to support the standing stocks of grazers including krill, copepods and microzooplankton, there are also results from a model suggesting four to five times higher values of primary production, which would make the concept of the “Antarctic paradox” outdated (4414 Tg C a^{-1} for the Southern Ocean south of 50° S, Arrigo et al.

1998b). Many of the different estimates have weaknesses such as the dominance of underlying data mainly obtained from productive waters, and thus further estimates from improved or new models have to be awaited.

Despite the low overall primary production of the Southern Ocean phytoplankton, some certain areas are known for relatively high productivity. One such area is the marginal ice zone (MIZ), where the formation of intense phytoplankton blooms, often induced by algae released from sea ice, is enabled and facilitated by thin and stable surface mixed layers, which result from freshwater input due to ice melt (e.g. Leventer 2003 and citations therein). These MIZ phytoplankton blooms are estimated to contribute up to 60 % of the annual primary production of the Southern Ocean (Smith Jr & Nelson 1986, Legendre et al. 1992).

The sea ice cover is also important for primary production in the Southern Ocean. It strongly reduces the amount of light available for phytoplankton in the underlying water column. However, as a habitat for dense ice algae communities, sea ice is considered to significantly contribute to the Southern Ocean productivity. In ice-covered waters, sea ice primary production is estimated to constitute up to 25 % of the calculated total annual primary production, which ranges from 141 to 383 Tg C a^{-1} (Smith Jr & Nelson 1986, Legendre et al. 1992, Arrigo et al. 1997). Ice algae communities inhabit special habitats, which are associated with the surface, the interior or the bottom layer of the ice, and the communities are named after the habitat they live in (Fig. 3, Horner et al. 1988, 1992). The highest concentrations of organisms are often found in the surface layer communities (Garrison & Buck 1989), which form due to snow pressing the upper surface of the ice below the sea level and thus causing flooding by sea water (Meguro 1962, Legendre et al. 1992). These surface layer communities contribute the majority of primary production in Antarctic sea ice (Legendre et al. 1992). Model results show that as a result of the Weddell Sea's extensive ice coverage and high rate of carbon fixation, the sea ice of this area contributes almost 50 % of the annual primary production in Antarctic pack ice, which is facilitated by a thicker snow cover than in other areas causing more extensive surface flooding and thus additional nutrient supply for the surface layer communities (Arrigo et al. 1998a).

1.2 Copepoda

Copepods inhabit an impressive variety of aquatic habitats worldwide (e.g. Huys & Boxshall 1991). They are found almost everywhere where water is available, e.g. in the oceans, in rivers, streams and lakes, in subterranean caves, in melt water puddles on glaciers and even in ephemeral waterbodies that form, for instance, in bromeliads or in leaf litter on the floor of tropical rainforests. Copepod habitats cover the entire spectrum of imaginable regions of the world including the deepest ocean trenches, high mountains, very cold polar sea ice and active hot hydrothermal vents.

The salinity regimes in these habitats range from freshwater to the hypersaline waters of salt lakes (Huys & Boxshall 1991).

The crustacean subclass Copepoda currently comprises about 11500 valid species (Humes 1994, Boxshall & Halsey 2004), which is a relatively small number compared to that of other arthropod taxa as for instance the insect group Coleoptera (currently about 350000 described species). However, copepods are arrestingly abundant, and within the metazoans they are expected to contribute the largest amount of individuals, even larger than that of insects and nematodes (Hardy 1970). As example, the largest biome on earth, the pelagic realm, is inhabited by estimated 1.37×10^{21} planktonic copepods (Boxshall & Halsey 2004). As a result of this abundance, copepods are the most numerous mesozooplankton taxon in all ocean areas worldwide, contributing 55 to 95 % of the total mesozooplankton (Longhurst 1985).

Pelagic copepods in the Southern Ocean

The dominance of copepods in the mesozooplankton is particularly pronounced in mid-latitude continental shelf areas and in polar regions. In the latter, copepods constitute about 70 % of the total mesozooplankton biomass (Longhurst 1985). Accordingly, in most regions of the Southern Ocean the mesozooplankton biomass is strongly dominated by copepods (e.g. Smith & Schnack-Schiel 1990, Conover & Huntley 1991), and in certain areas and at certain times the proportion of copepod biomass may even be larger than 90 % (e.g. Conover & Huntley 1991, Voronina et al. 1994). The presence of immense krill swarms is one of the prominent features of the total zooplankton of the Southern Ocean, and in areas with high krill abundance such as the waters around the Antarctic Peninsula the krill biomass may be an order of magnitude larger than that of the other zooplankton (Hopkins 1985). However, the mesozooplankton biomass found in the Atlantic sector of the Southern Ocean is estimated in general to be of the same order of magnitude as the krill biomass, which also holds true for main areas of krill occurrence (e.g. Boysen-Ennen et al. 1991). Even within krill swarms, the biomass of the mesozooplankton may be comparable to that of krill (Brinton & Antezana 1984).

The biomass of the pelagic copepod communities of the Weddell Sea has often been described as strongly dominated by calanoid copepods (e.g. Hopkins 1985, Boysen-Ennen et al. 1991, Voronina et al. 1994). However, studies using smaller mesh sizes have revealed that small cyclopoid species such as *Oithona similis* and *Oncaea curvata* (the latter was classified within the Poecilostomatoida, but currently it is considered to belong to the Cyclopoida, Boxshall & Halsey 2004) are also important. In terms of numbers these cyclopoid copepods may contribute major fractions of the copepod populations (e.g. Schnack et al. 1985), sometimes even of the total zooplankton populations as observed, for instance, in a study conducted at the Antarctic Peninsula where *O. curvata* constituted half of the zooplankton population (Hopkins 1985). In the eastern Weddell Sea, *O. similis* and *O. curvata* made up

about 20 % of the total copepod biomass (Schnack-Schiel et al. 1998a).

Among the calanoid copepods, a few large species including *Calanus propinquus*, *Calanoides acutus*, *Metridia gerlachei*, *Rhincalanus gigas* and *Paraeuchaeta antarctica* strongly dominate the biomass (e.g. Hopkins 1985, Boysen-Ennen et al. 1991, Voronina et al. 1994 and citations therein). However, the two small species *Microcalanus pygmaeus* and *Ctenocalanus citer* that often strongly dominate the calanoid copepods numerically (e.g. Hopkins 1985; up to 78.6 and 31.5 %, respectively, in the eastern Weddell Sea, Schnack-Schiel in press), may also contribute considerable fractions.

The largest part of the pelagic calanoid copepod communities found in the Weddell Sea consists of species, which are omnivorous or feed mainly on phytoplankton (e.g. Schnack-Schiel in press). Due to their dominance within the mesozooplankton, pelagic copepods are the main primary consumers in the Southern Ocean, thus representing important food web components and very probably key organisms for processes such as carbon cycling and nutrient regeneration in the pelagial. The high abundance of pelagic copepods leads to the assumption that copepods contribute significantly to the vertical particle flux by grazing on phytoplankton and particulate organic matter resulting in the production of large amounts of faecal pellets. However, many sediment trap studies conducted in the Southern Ocean have revealed that the sinking matter is often strongly dominated by krill faecal strings, while copepod faecal pellets make up only a small amount or are not present (e.g. Schnack 1985, von Bodungen 1986, von Bodungen et al. 1987, Wefer et al. 1988, González 1992, González et al. 1994). This is in accordance with results obtained from other ocean areas and suggests that major proportions of the copepod faecal material remain in the water column and are degraded there (Turner 2002).

Sympagic copepods in the Southern Ocean

Among the large amount of Antarctic copepod species there are two calanoid and a few harpacticoid species, which are true ice dwellers inhabiting the sea ice brine channel and pore system and there dominating the sympagic metazoan meiofauna (e.g. Hoshiai & Tanimura 1986, Dahms et al. 1990, Dahms & Schminke 1992, Kurbjeweit et al. 1993, Schnack-Schiel et al. 1995, 1998b, 2001a, b, Tanimura et al. 1996, Swadling et al. 1997a, 2000, Günther et al. 1999, Swadling 2001, Schnack-Schiel 2003). Within the Weddell Sea, the major fraction of the sea ice copepod communities is formed by the calanoid *Stephos longipes* and mainly by the harpacticoid *Drescheriella glacialis* (Dahms et al. 1990, Dahms & Schminke 1992, Kurbjeweit et al. 1993, Schnack-Schiel et al. 1995, 1998b, 2001b). *D. glacialis* is found in the ice during its complete life cycle throughout the year, and it very probably breeds and reproduces year-round within the ice matrix (Dahms et al. 1990, Schnack-Schiel et al. 1998b, Swadling 2001). In contrast, *S. longipes* spends only a part of its life cycle in the ice, reproduces mainly in the water column and is considered to overwinter in deeper water layers as copepodite stage IV (Kurbjeweit et al. 1993, Schnack-Schiel et al. 1995).

Comparable to the importance of pelagic copepods for the food web and carbon cycling within the pelagial, the dominant sympagic copepods are assumed to play a very important role as grazers on ice protists (Kurbjeweit et al. 1993) and thus for carbon cycling and nutrient regeneration within sea ice, and for export of particulate organic matter from sea ice into the underlying water column. However, a few filtration and ingestion rate data from experiments with *S. longipes* copepodids II - V fed on phytoplankton and ice algae, and the existence of pennate diatoms in guts of *S. longipes* nauplii, and in *S. longipes* faecal pellets found in sea ice and the under-ice water layer are the only published information about feeding of sympagic copepods that currently exists (Kurbjeweit et al. 1993, Schnack-Schiel et al. 1995, Swadling et al. 1997b). Furthermore, most studies on the sea ice fauna have been related to the ice proper or the platelet ice layer, and detailed investigations of vertical particle flux directly under sea ice in oceanic areas of the Southern Ocean are rare. Thus only little is known about the occurrence and importance of copepods within the very productive sea ice surface layer (see above), and the contribution of faecal pellets produced by sympagic copepods to particle flux directly under sea ice.

2 Objectives

This dissertation aimed at investigating the impact of sympagic copepods on carbon cycling processes within sea ice, and transport of particulate organic matter from sea ice into the underlying water column in the Weddell Sea. A further goal was to improve the knowledge of the population dynamics of dominant pelagic copepods in order to contribute to the understanding of the importance of these copepods for carbon cycling and vertical particle flux in the pelagial of the Weddell Sea.

The studies on the sympagic copepods were conducted in the western Weddell Sea between 14 November 2004 and 2 January 2005 (for details see next chapter). In this area ice-associated biological processes are of particular importance for the ecosystem due to the presence of large amounts of perennial sea ice. The question concerning the importance of sympagic copepods for cryo-pelagic coupling was addressed by investigating (1) the dynamics of copepod populations in the ice proper, and of the metazoan fauna in the ice surface layer and the under-ice water layer, (2) the grazing impact of the dominant copepods on ice protist communities and (3) the amount and composition of vertical particle flux under sea ice.

For the second aspect, the temporal development of abundance, composition and vertical distribution of dominant copepods was investigated both on the shelf of the eastern Weddell Sea between 9 and 28 December 2003, and on the continental slope in the western Weddell Sea between 1 December 2004 and 2 January 2005 (for details see next chapter).

Based on the results of the different sub-projects the influence of copepods on coupling processes between the Weddell Sea compartments sea ice, pelagial and benthal should be assessed.

„Überall geht ein frühes Ahnen dem späteren Wissen voraus.“

“Early intuition always precedes later knowledge.”

Alexander von Humboldt

(1769 - 1859)

3 Study areas and periods

The different sub-projects of this dissertation were part of the scientific programs of two expeditions with RV “Polarstern”. ANT XXI/2, the “Benthos Disturbance Experiment” (BENDEX), took place between 17 November 2003 and 18 January 2004. The study area was located on the shelf of the eastern Weddell Sea near Cape Norvegia. In the framework of the expedition, “Polarstern” operated in a relatively small area for several weeks allowing for regular navigation to a sampling site located at 70° 48.558' S and 10° 43.698' W (Fig. 4). In order to monitor the spring plankton development, plankton and water samples were taken at this site at frequent intervals between 9 and 28 December 2003. Due to the rapidly changing sea ice situation “Polarstern” could not always be positioned exactly on the same coordinates. However, all sampling spots were located inside a very small area of 1.5 x 0.9 km that can thus be considered a quasi-permanent station. The water depth at the sampling spots varied between 438 m and 484 m. For further details see Arntz & Brey (2005).

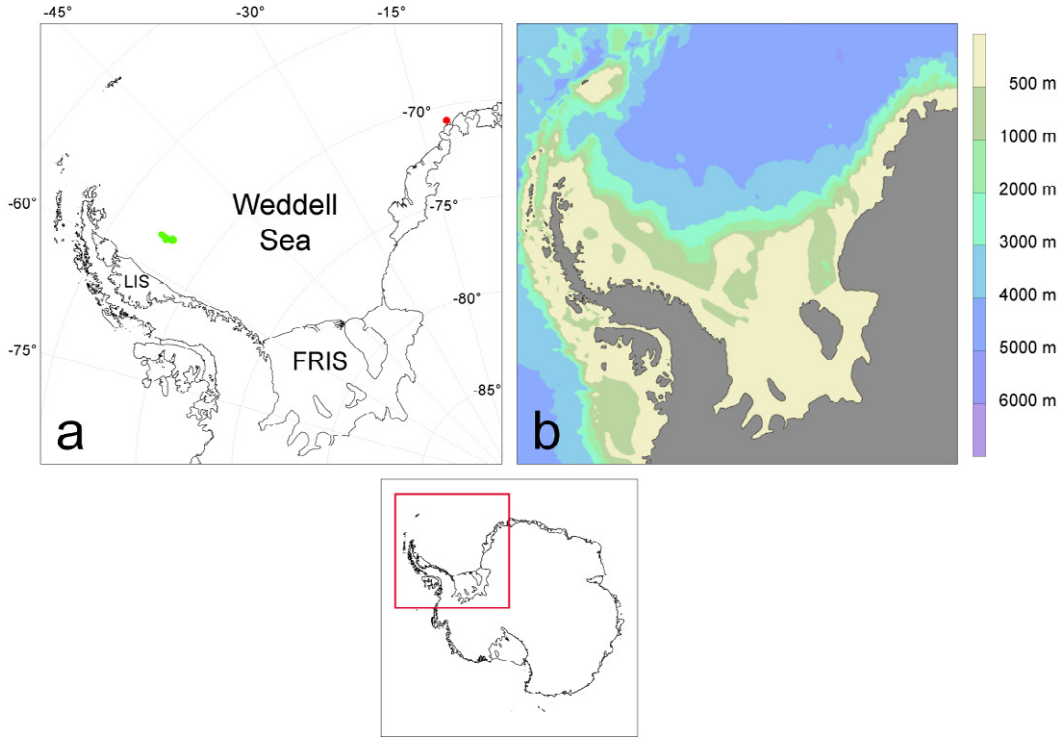

Fig. 4: a map of the Weddell Sea showing the locations of the sampling site during BENDEX (red dot) and the ice floe drift during ISPOL (green area). **b** map of the Weddell Sea bathymetry (ice shelves not shown). The areas shown in **a** and **b** correspond to the area marked with the red rectangle in the overview of Antarctica. **FRIS** Filchner-Ronne Ice Shelf, **LIS** Larsen Ice Shelf.

ANT XXII/2, the “Ice Station Polarstern” (ISPOL), was conducted between 6 November 2004 and 19 January 2005. The complete research program of this expedition had been designed as a large interdisciplinary project for studying physical and biogeochemical interactions between atmosphere, ice, and ocean within the perennial sea ice of the western Weddell Sea in spring. On 27 November 2004 “Polarstern” was anchored to an initially 10 km x 10 km sized ice floe at 68° 13.05' S and 54° 46.84' W. In the following period of 36 days the combination of ice floe and “Polarstern” served as platform for extensive atmosphere, sea ice and water column studies while drifting a total distance of 290 km. Although the main drift direction was to the north, several loops in the ice floe drift pathway resulted in a net south-north displacement of only 98 km, which was reached on 2 January 2005 when the drift station was finalised and “Polarstern” left the floe at 67° 21.16' S and 55° 24.28' W. During the drift station, the size of the floe decreased to 0.7 km x 0.8 km due to two breakup events on 2 and 24 December. The drift area was situated on the continental slope with an average distance to the shelf break of about 30 km and water depths between 1048 m and 2009 m. In addition to the work conducted during the drift station, studies on the large-scale spatial variability of different sea ice parameters and communities took place on a transect from the sea ice edge to the ISPOL floe between 14 and 24 November 2004. For further details see El Naggar et al. (2007).

4 Comprehensive discussion

This thesis has revealed new insights into the importance of copepods for biological coupling processes between the three partial systems sea ice, water column and seafloor in the Weddell Sea. In the following, the results of the sub-projects presented in chapter 8 are jointly discussed in a wider context regarding different aspects of the significance of copepods as mediators of carbon cycling within sea ice and the water column, and of transport of particulate organic matter from sea ice into the water column and from there to the seafloor.

4.1 Significance of copepods for primary production and carbon cycling within sea ice

The results of the manuscripts I - III suggest that copepods play a very important role in the turnover of organic matter in Antarctic sea ice. At single spots with maximum copepod abundances, copepod community grazing may control or even deplete the ice algae biomass of certain sea ice habitats such as the infiltration layer (manuscripts I and II). However, for Arctic sea ice a combination of measurements and experiments revealed that brine channels with diameters of ≤ 200 µm represent a spatial refuge where the grazing pressure of larger grazers is low or absent, thus resulting in abundances of microbial communities one to two magnitudes higher than in the remaining channel network; concurrently, approximately 50 % of the entire internal surface of the investigated ice were associated with brine channels having diameters of < 41 µm (Krembs et al. 2000). This suggests that larger grazers are excluded from major parts of the brine channel system, which hence provide very suitable habitats for ice protists due to the relatively low grazing risk. In contrast to the Arctic where columnar and multi-year ice prevail, Antarctic sea ice is dominated by frazil and one-year ice, in which the relative space available for organisms is larger, resulting in higher densities of organisms in Antarctic sea ice compared to its Artic counterpart (Spindler 1990). However, in a considerable proportion of the brine channel and pore system of Antarctic sea ice the potential grazing pressure on diatoms, flagellates and ciliates might also be reduced due to the limited accessibility for metazoans. In combination with the patchy distribution of the copepods and other sympagic organisms within sea ice (e.g. Spindler et al. 1990, Swadling et al. 1997a, manuscripts II and III), this very probably results in the existence of many sea ice sites characterised by a prevailing moderate copepod grazing pressure.

Under such conditions, grazing by copepods might also have a positive effect on primary production and ice algae standing stocks. Several studies have shown that, up to a specific amount, grazing may enhance the primary production, and the presence of grazers may increase the abundance of certain algae species (Porter 1972, 1973, 1976, Cooper 1973, de Mazancourt et al. 1998 and citations therein). This supports the so-called “grazing optimisation hypothesis”, which suggests that an

optimal grazing intensity may potentially increase primary production over that observed in ungrazed systems (see Briske & Heitschmidt 1991 and citations therein). Due to its influence on nutrient availability, grazing may modify the rate and pattern of energy flow in ecosystems. It affects nutrient cycling by accelerating the mineralisation rate (i.e. the rate of nutrient conversion from an organic form, e.g. amino acids and proteins, to an inorganic form, e.g. nitrate and ammonium). In systems where a large proportion of the essential nutrients is bound in organic matter, mineralisation processes are critical, since only nutrients in specific inorganic forms are available for up-take by plants (Briske & Heitschmidt 1991). Grazers retain just a small portion of the nutrients consumed, whereas the larger portion is rapidly returned to the system within metabolic end-products and faeces. In Antarctic platelet ice, for instance, the total copepod abundance was observed to be strongly correlated with high ammonium concentrations in the interstitial water between the platelets (Schnack-Schiel et al. 2004). Nutrients excreted in metabolic end-products are in the inorganic form and thus immediately available for up-take by plants (Wilkinson & Lowrey 1973). In contrast, in faecal and remaining plant material a major fraction of the nutrients is bound in organic compounds and must be mineralised by decomposers prior to up-take by plants. Consequently, a proportion of the nutrients incorporated into plant biomass during primary production becomes available for reabsorption more rapidly when transferred through the grazing food chain than when transferred directly into the decomposer compartment (Wilkinson & Lowrey 1973, Floate 1981). Estimates of higher nutrient concentrations in grazed than in ungrazed systems support the assumption of increased rates of nutrient cycling (Detling 1988).

In Antarctic sea ice containing large ice algae standing stocks algal growth is often associated with nutrient exhaustion due to the high nutrient demands (Arrigo & Thomas 2004). However, prolific diatom standing stocks have also been reported within sea ice that still contained high nutrient concentrations, which is atypical for the build up of algal biomass and indicates high rates of organic matter turnover and mineralisation within the ice (Thomas & Dieckmann 2002 and citations therein, Arrigo & Thomas 2004). These observations are in accordance with the above mentioned estimates of higher nutrient concentrations in grazed systems (Detling 1988) and suggest that grazing played an important role in the investigated sea ice systems. Modelling results indicate that grazing optimisation occurs if grazers sufficiently increase the nutrient turnover rate of the ecosystem, and if the total amount of nutrients in the ecosystem is sufficiently high (Loreau 1995). This leads to the assumption that grazing optimisation takes place in sea ice systems with relatively high concentrations of ice algae biomass and nutrients. However, an increase in the nutrient turnover rates is not sufficient to explain grazing optimisation in the long term. Modelling results have shown that grazing optimisation requires that the proportion of nutrients lost along the grazer pathway be sufficiently smaller than the proportion of nutrients lost throughout the rest of the ecosystem (de Mazancourt et al. 1998).

Copepods and turbellarians are the main metazoan grazers in Antarctic sea ice (Schnack-Schiel et al. 2001a, Schnack-Schiel 2003). The harpacticoid *Drescheriella*

glacialis and the calanoids *Stephos longipes* and *Paralabidocera antarctica* have been found to be strongly dominant, contributing up to over 90 % of the metazoan communities within the different sea ice habitats (Dahms et al. 1990, Dahms & Schminke 1992, Kurbjeweit et al. 1993, Schnack-Schiel et al. 1995, 1998b, 2001b, Swadling et al. 1997a, 2000, Günther et al. 1999, Swadling 2001, manuscripts II and III). Consequently, the bulk of ice algae grazing is probably caused by only a few copepod species, which are thus very important mediators of the above mentioned high rates of organic matter turnover and mineralisation, possibly resulting in enhanced primary production. This is emphasised by a further aspect: in the water column algae matter grazed by copepods may be further ingested by organisms from higher trophic levels due to predation; however, in contrast in sea ice the lack of copepod predators resulting from the narrow brine channels and pores leads to direct digestion of large portions of the respective algae matter, and excretion and egestion of metabolic end-products and remaining algae matter, respectively, by the copepods themselves. Accordingly, in sea ice the mineralisation pathways may be relatively short, and the related recycling processes very effective. Furthermore, nutrient losses via the grazer pathway may be considerably smaller than those during recycling of algae detritus, thus allowing for grazing optimisation (see above, de Mazancourt et al. 1998).

A further aspect is the contribution of algae matter egested within faecal pellets to algal growth of the ecosystem. Algae have been observed to survive grazing by zooplankton and to be egested in viable condition (e.g. Fowler & Fisher 1983, Jansen & Bathmann 2007). Freshly killed copepods were observed to produce considerable amounts of oxygen when exposed to light, suggesting that the conditions in the copepod gut are favourable for photosynthesis of the ingested algae (Epp & Lewis Jr. 1981). During the gut passage, the viable cells may take up nutrients from both algal remains and grazer metabolites, which may stimulate algal carbon fixation and cell division and result in enhanced algal growth after the gut passage (Porter 1976).

Due to their contribution to carbon cycling and possible facilitation of primary production in sea ice, ice inhabiting copepods play an important role in the ecosystem of the Southern Ocean. The calculated annual primary production in Antarctic sea ice (30 - 70 Tg C a^{-1}, Legendre et al. 1992, Mathot et al. 1996, Arrigo et al. 1997, 1998a) is much lower than the estimated annual primary production of Southern Ocean phytoplankton (740 - 1000 Tg C a^{-1}, Arrigo et al. 1998a and citations therein, Lizotte 2001). However, the apparently minor contribution of the former to the primary production of the entire Southern Ocean ecosystem is very significant, since ice algae provide a concentrated food source whose presence is asynchronous with the short period of primary production in the water column; furthermore, they are often virtually the only source of organic carbon for heterotrophic organisms in ice-covered waters (Thomas & Dieckmann 2002, Arrigo & Thomas 2004). Especially in winter, when other food sources are not available, ice algae sustain populations of various sea ice inhabiting proto- and metazoan grazers (Brierley & Thomas 2002, Lizotte 2003, Schnack-Schiel 2003).

Conclusions

- In Antarctic sea ice, grazing by copepods may result in short mineralisation pathways and effective recycling processes. Under such conditions grazing optimisation may take place within sea ice communities.
- Sympagic copepods are strong mediators of carbon cycling and nutrient regeneration in Antarctic sea ice, thus contributing considerably to the productivity of sea ice communities and playing an important role in the Southern Ocean ecosystem.

4.2 Copepods and cryo-pelagic coupling

Production and properties of copepod faecal matter within sea ice

When feeding on dense sea ice protist communities, copepods may have high ingestion rates and be capable of grazing large portions of the ice algae standing stocks per day (manuscript I). These high ingestion rates are very probably associated with high faecal pellet production rates, which can be assumed from a linear relationship between these rates as observed in earlier studies on copepod feeding (e.g. Besiktepe & Dam 2002). At spots with abundant protist and copepod communities, copepod grazing might thus result in considerable concentrations of faecal pellets within the sea ice brine. In fact, during ISPOL, up to over 3000 copepod faecal pellets per millilitre of melted sea ice were found in the bottom layer of some ice floe spots, and in the infiltration layer the maximum concentration discovered was 102900 faecal pellets per millilitre brine (Harri Kuosa, unpublished data). With only very few exceptions these pellets were similar in shape and size to faecal pellets obtained from feeding experiments with the sea ice associated copepod species *Stephos longipes* (Fig. 5 a). This suggests that the major part of the faecal matter in sea ice was produced by the sympagic copepod communities.

Fragilariopsis species, mainly *F. cylindrus*, were among the numerically dominant sea ice protists both in the bottom layer and the infiltration layer communities (manuscript I; Harri Kuosa, pers. comm.). This is in accordance with several earlier studies, in which *F. cylindrus* and *F. curta* have been found to be the dominant species in ice algae assemblages, and in phytoplankton collected close to the ice edge (e.g. Garrison et al. 1986, 1987, Kang & Fryxell 1992, Kurbjeweit et al. 1993, Melnikov 1995, Lizotte 2001). These diatoms thus provide an abundant food source for grazers within sea ice, and the feeding experiments revealed that they may be strongly positively selected by *Drescheriella* spp. and *S. longipes* (manuscript I).

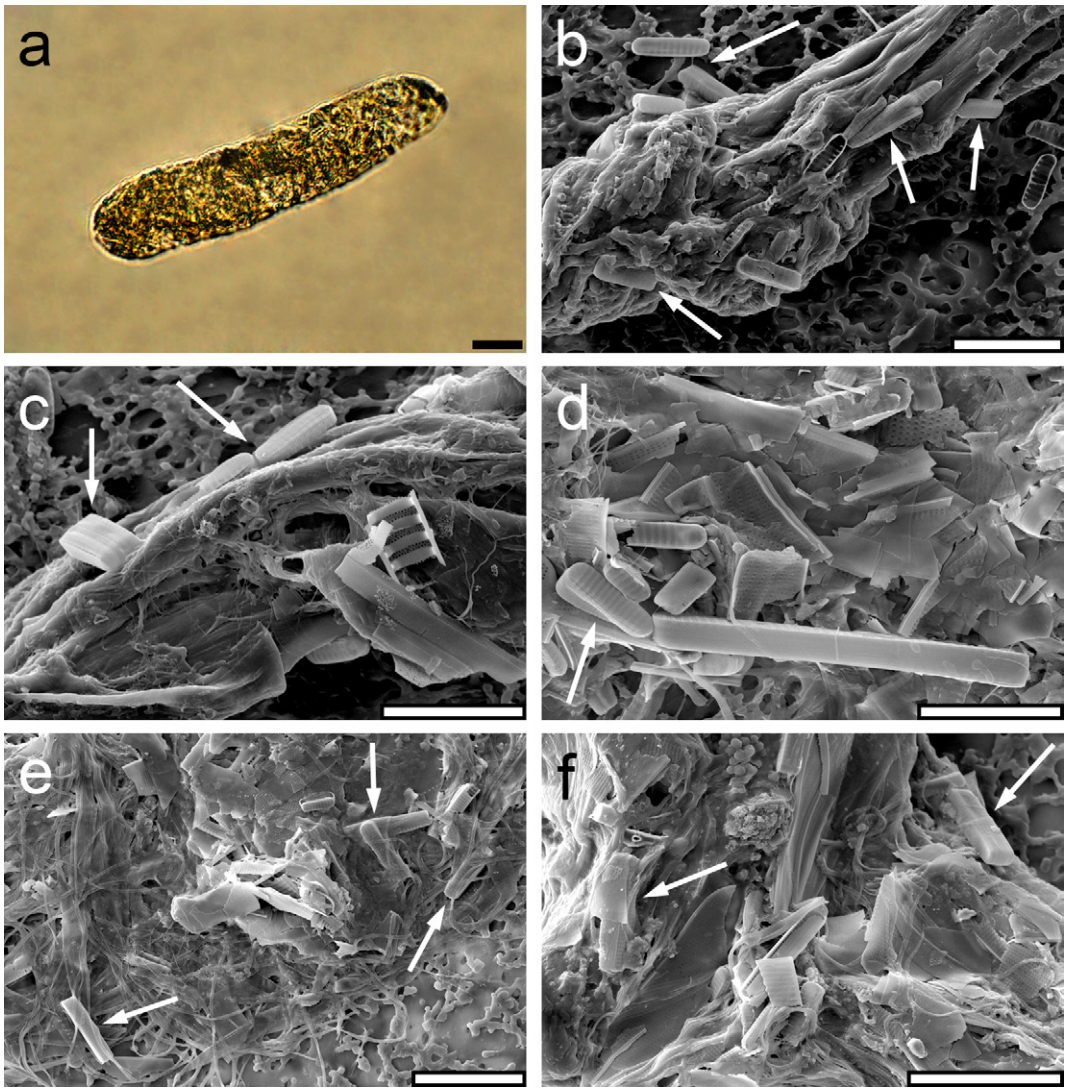

Fig. 5: Faecal pellets obtained from feeding experiments with *Stephos longipes* and *Drescheriella* spp., and sea ice protists as food. **a** light micrograph of a *S. longipes* faecal pellet. Scale bar = 20 µm (Photo: Ingo Arndt). **b** - **d** scanning electron micrographs of contents of *S. longipes* faecal pellets. Scale bars = 10 µm. **e** and **f** scanning electron micrographs of contents of *Drescheriella* spp. faecal pellets. Scale bars = 20 µm. The white arrows indicate intact small *Fragilariopsis* spp..

This agrees with results of (1) Schnack-Schiel et al. (1995) who observed *S. longipes* to feed heavily on *Nitzschia* spp. (which very probably were *Fragilariopsis* spp.), and found pennate diatoms in the guts of *S. longipes* nauplii, and in faecal pellets from sea ice samples, and (2) Kurbjeweit et al. (1993) who found only frustules of pennate diatoms such as *Nitzschia* spp. (probably *Fragilariopsis* spp., see above) within *S. longipes* faecal pellets collected in the under-ice water layer. Many of the pennate diatoms found in the guts and faecal pellets of *S. longipes* were damaged (Sigrid B. Schnack-Schiel, pers. comm.). Faecal pellets obtained from the feeding experiments

described in manuscript I also contained broken pennate diatom frustules, however, it is conspicuous that a large proportion of the small *Fragilariopsis* spp. present in these pellets were intact (unpublished results, Fig. 5 b - e). Accordingly, most of the faecal pellets found within the ice contained large amounts of intact *Fragilariopsis* spp., the major proportion still being alive (pers. observ.; Harri Kuosa, pers. comm.).

Static load tests and finite element analyses have shown that the frustules of another *Fragilariopsis* species, *F. kerguelensis*, are exceptionally stable, and that the pressure necessary to break them can probably be applied by mouthparts of large copepods only (Hamm et al. 2003). *F. cylindrus* and *F. curta* are smaller and less silicified than *F. kerguelensis*, but their frustule architectures are akin to that of the latter. In addition, the silica material properties of the three species are presumably identical, leading to the assumption that the frustules of *F. cylindrus* and *F. curta* are not easy to break by mouthparts of small copepod species. Furthermore, the morphology of the gnathobases of *S. longipes* is not suitable for crushing stable diatom frustules (Michels & Schnack-Schiel 2005). In *Drescheriella glacialis*, the tooth-like structures of the gnathobases (Fig. 6 a, see also Dahms & Dieckmann 1987) are stronger than those of *S. longipes* (Fig. 6 b), but their constitution seems not to be compact and massive enough to easily break robust diatom frustules. Consequently, in many cases the relatively small sympagic copepods are probably not able to break the frustules of *F. cylindrus* and *F. curta*.

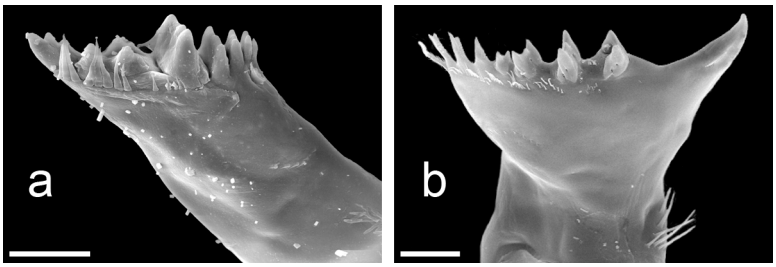

Fig. 6: scanning electron micrographs of **a** a right gnathobase of a female *Drescheriella glacialis* (shown from caudal; dorsal bristle missing) and **b** a left gnathobase of a male *Stephos longipes* (shown from caudal). Scale bars = 10 µm. **b** from Michels & Schnack-Schiel (2005).

These findings suggest that in the presence of high *F. cylindrus* and *F. curta* densities within sea ice, sympagic copepods preferentially feed on this most abundant food source, although they are probably often not able to utilise it effectively. Comparably, in several earlier studies faecal pellets from other small metazoan and protozoan grazers have been reported to contain unbroken diatom frustules, often of monospecific origin (Thomas et al. 2001, Armand & Leventer 2003 and citations therein). Such observations lead to the question how these grazers cover their energy demands when they feed mainly on diatoms many of whose

frustules they cannot break and which they therefore often cannot digest. In the case of the sympagic copepods, it is likely that they obtain the necessary energy from the digestion of other sea ice protists they also feed on, such as other small diatoms, dinoflagellates or *Phaeocystis antarctica* (manuscript I). The latter is often a dominant species in sea ice microbial communities (e.g. Garrison et al. 1986, Lizotte 2001). Although the proportion of these organisms in the copepods' diet seems to be often relatively small, it might be large enough to sustain the necessary energy supply. At high food concentrations, high ingestion rates as observed during feeding of sympagic copepods on ice protist communities (manuscript I) might enhance the amount of food digested by the copepods. The results of feeding experiments have shown that the gut passage time and the assimilation efficiency decrease with increasing food concentrations (Gaudy 1974, Landry et al. 1984, Besiktepe & Dam 2002), however, contradictory results obtained from experiments with the copepod species *Neocalanus plumchrus* revealed a constant gut passage time at chlorophyll concentrations > 4 µg L^{-1} (Dagg & Walser Jr. 1987). Furthermore, in the latter study an increase in gut content with increasing chlorophyll concentrations up to 4 µg L^{-1} and a constant gut content at higher concentrations were observed. Based on these results it is likely that sympagic copepods may digest larger amounts of food when they feed with high ingestion rates.

The composition and abundance of the sea ice microbial communities may not only influence the digestibility of the food and the amount of digestible organisms ingested by the copepods, but also the degradation rates and the size of the faecal pellets. Diatom food results in larger pellets with significantly slower degradation rates compared to pellets egested by copepods feeding on dino- or nanoflagellates (Hansen et al. 1996). In addition, at high food concentrations the faecal pellets are larger than those produced at low food concentrations (Besiktepe & Dam 2002).

From the considerations above it becomes evident that within sea ice the dominance of *F. cylindrus* and *F. curta* in microbial communities in combination with abundant sympagic copepods may result in considerable amounts of faecal material, which contains high proportions of viable diatoms and is relatively slowly degraded. This particulate organic matter may be a valuable food source for a variety of ice inhabiting proto- and metazoans, but also for organisms in the water column. The latter aspect is discussed in the following chapter.

Conclusions

- The presence of dense ice protist communities, dominated by small pennate diatoms, and abundant sympagic copepods may result in considerable amounts of relatively slowly decomposing faecal matter containing high proportions of viable diatoms.
- This faecal matter may be a valuable food source for a variety of ice inhabiting proto- and metazoans.

Copepod related export of particulate organic matter from sea ice into the underlying water column

The flux of particulate organic matter from sea ice into the water column may be facilitated by both sympagic copepods inhabiting the ice and pelagic copepods living in the water column under the ice. The former contribute to the flux due to the processes discussed in the previous chapter and as prey for pelagic predators on the ice underside, while the latter may enhance it through feeding on protist communities on the ice underside and in larger openings in the ice.

Importance of sympagic copepods

Many of the different sea ice habitats such as the infiltration and the highly porous bottom layers are directly connected with the under-ice water layer (e.g. Eicken 1992, Horner et al. 1992), and processes such as brine expulsion, gravity drainage and flushing result in exchange of fluids and particulate organic matter between sea ice and the water column (e.g. Horner et al. 1992, Hudier et al. 1995, Melnikov 1998; manuscript II: infiltration of sea water into the sea ice surface layer). This may include transport into the under-ice water layer of a considerable amount of faecal pellets produced within the ice by sympagic copepods. Since the algae concentration in the water column is often very low compared to that in sea ice (e.g. compare the results of the manuscripts I - VI), particulate organic matter originating from the ice may provide a valuable food source for pelagic grazers.

A study on the bacterial degradation of copepod faecal pellets revealed that the peritrophic membrane of pellets produced at high food concentrations may be disrupted within a few hours after pellet production (Hansen et al. 1996). Furthermore, the degradation of faecal pellets produced at high food concentrations was significantly faster than that of pellets produced at low food concentrations. Consequently, the faecal matter resulting from copepods feeding on dense ice protist communities, which are dominated by diatoms, might be relatively fragile and break to pieces during the transport into the water column. Such a process might enhance (1) the accessibility of the viable organisms inside the pellets for grazers and (2) the release of viable algae resulting in a contribution of ice algae to primary production in the water column.

Each spring and summer, when about 80 % of the 20 x 10^6 km^2 of Antarctic sea ice present in winter disintegrate (Zwally et al. 1983), immense amounts of organic matter are released into the water column. This process is most pronounced at the retreating sea ice edge, where the released ice algae often act as seed populations for intense ice edge phytoplankton blooms, which are facilitated by relatively thin and stable surface mixed layers as a result of melt water input (e.g. Smith Jr & Nelson 1985, Garrison et al. 1987, Kang et al. 2001, Leventer 2003 and citations therein). Due to these phytoplankton blooms, the marginal ice zones are major sites of primary production in the Southern Ocean, contributing large proportions of its total productivity (Smith Jr & Nelson 1986, Legendre et al. 1992, Lizotte 2001, Arrigo &

Thomas 2004). Besides the significance of released ice algae as seed populations for phytoplankton blooms and thus for the primary productivity of the water column, the enormous flux of particulate organic matter out of the melting sea ice may provide a relevant food source for pelagic grazers. Consequently, in marginal ice zones the production of faecal pellets by sympagic copepods might facilitate the coupling between the surface and the deep ocean due to its contribution to flux of particulate organic matter from sea ice into the water column.

Another contribution to the latter may be predation of sympagic copepods by pelagic organisms. Antarctic krill (*Euphausia superba*) can feed efficiently on copepods (e.g. Price et al. 1988, Atkinson & Snÿder 1997), and small calanoid copepods, similar in size to the sympagic copepods, may make up large proportions of the krill's diet (Atkinson & Snÿder 1997). Since krill feeds on ice algae by scraping them off from the surface of the underside and larger openings of sea ice (e.g. Stretch et al. 1988, Marschall 1988), it is probable that krill may also feed on sympagic copepods, which are often abundant in these habitats (Kurbjeweit et al. 1993, Schnack-Schiel et al. 1995, manuscript II). Even larger predators from higher trophic levels feed on sympagic copepods as observed in the notothenioid fish *Pagothenia borchgrevinki*, which lives in larger voids of sea ice and in the under-ice water layer. Analyses of its stomach content have shown that ice-associated copepods such as *Paralabidocera antarctica* and *Stephos longipes* may be an important food source and contribute large proportions of the diet (Hoshiai & Tanimura 1981, Hoshiai et al. 1989).

Conclusions

- A considerable amount of copepod faecal matter produced within sea ice may be transported into the under-ice water layer due to processes such as fluid exchange and ice melt.
- The released faecal matter may provide a relevant food source for pelagic grazers.
- Viable ice algae in the faecal matter may contribute to primary production in the water column.
- Feeding of predators, living in the under-ice water layer, on sympagic copepods might contribute considerably to the flux of organic carbon from sea ice into the water column.
- Within the sympagic metazoan meiofauna, copepods are key organisms for cryo-pelagic coupling. Their contribution to flux of particulate organic matter from sea ice into the water column may facilitate the linking between the surface and the deep water layers in ice covered areas of the Southern Ocean.

Importance of pelagic copepods

The under-ice water layer is inhabited by a variety of metazoan grazers including several copepod species, amphipods and krill (e.g. Menshenina & Melnikov 1995, Krapp et al. in press, manuscript II). The highly concentrated organic matter on the sea ice underside and within the ice may play an important role in the food supply of these organisms. Especially in winter, when the low light availability and large mixed layer depths often result in extremely low Chl *a* concentrations in the water column (< 0.02 µg L^{-1}, Nöthig et al. 1991, Scharek et al. 1994), whereas dense ice algae communities may be found in sea ice (e.g. up to 26.27 µg Chl *a* per litre of melted sea ice, measured in the bottom layer of sea ice in the southern Lazarev Sea in July 2006, personal observation, unpublished data), ice-associated particulate organic matter might be significant or even essential as food for many pelagic grazers living under the sea ice. Accordingly, ice algae supply from the pack ice cover over nursery grounds was found to be important for the development and growth of krill larvae during winter (Daly 1990).

Antarctic krill has been observed to feed on ice algae on the underside and in larger openings of sea ice (e.g. Hamner et al. 1983, Marschall 1988, Stretch et al. 1988, Daly 1990). A similar feeding behaviour is conceivable for some copepod species living in the water column, which very probably also benefit from particulate organic matter associated with sea ice. This can be deduced from the following observations: (1) specimens of the ice-associated copepod *Paralabidocera antarctica* collected in the under-ice water layer had mainly fed on sea ice diatoms (Hoshiai et al. 1987); (2) in winter the guts of *Ctenocalanus citer*, which is also often found directly beneath the ice (e.g. Menshenina & Melnikov 1995, manuscript II), contained large amounts of typical ice-associated diatoms of the genus *Fragilariopsis* (Pasternak & Schnack-Schiel 2007). (3) The ice-associated *S. longipes* spends certain periods of its life cycle in the under-ice water layer and may then be the most abundant metazoan species in this habitat (Kurbjeweit et al. 1993, Schnack-Schiel et al. 1995). The egg production rates of *S. longipes* were observed to be significantly higher when the copepods fed on ice algae than when they were offered planktonic diatoms (Kurbjeweit 1993). It is thus very likely that *S. longipes* is adapted to ice algae food and uses this food source preferentially, also while living in the water column beneath sea ice. It is imaginable that under-ice grazers not only feed on ice algae but also on nutritious faecal matter produced by sympagic copepods. In addition to the outflow of particulate organic matter from the interior of the ice, this direct feeding on ice-associated organic matter by pelagic grazers may considerably contribute to the organic matter flux from sea ice into the water column.

However, not only pelagic grazers, which feed directly on organic matter on the ice underside, but also grazers inhabiting the water column some meters below the ice might be relevant for cryo-pelagic coupling processes. In the ice covered waters of the western Weddell Sea, diatoms determined within gut contents of the calanoid copepods *Calanus propinquus*, *Metridia gerlachei* and *Rhincalanus gigas* corresponded to the dominant species of diatom communities contemporaneously found in the sea ice at the sampling site (Pasternak 1995, Melnikov 1998). This

suggests that pelagic copepod species which are not typically found in high abundances in the under-ice water layer may be attracted by ice-associated particulate organic matter sinking in the surface mixed layer.

Besides the winter period, feeding of pelagic grazers on particulate organic matter released from sea ice is certainly most pronounced during the main period of ice melt in spring and summer, then probably strongly contributing to the turnover and mineralisation of organic matter in the surface ocean and thus to the high productivity of marginal ice zones. In fact the marginal ice zones are often associated with the presence of large stocks of krill and other zooplankton, and with high under-ice grazing activity of these organisms (e.g. Brierley et al. 2002). Under such conditions, krill and copepods play an important role in cryo-pelagic coupling due to intensive grazing on sea ice organisms, production of large amounts of faecal matter and enhancing energy transfer to higher trophic levels as a result of increased predation.

Conclusions

- Grazing on ice algae and ice-associated particulate organic matter by pelagic copepods may be an important process facilitating the export of particulate organic matter from sea ice into the underlying water column.
- In marginal ice zones pelagic copepods may play an important role in cryo-pelagic coupling due to intensive grazing on sea ice organisms released from the ice, production of large amounts of faecal pellets within the water column and enhancing energy transfer to higher trophic levels as a result of increased predation.

4.3 Vertical flux and fate of copepod faecal matter in the water column

Traditionally, zooplankton faecal pellets were assumed to contribute a large proportion of the vertical flux of particulate matter in the ocean. However, in recent years numerous studies have shown that these pellets often constitute only a minor fraction of the total particle flux, whereas considerable proportions of this flux are due to larger aggregates (“marine snow”) and direct sinking of phytoplankton blooms (e.g. Schnack 1985, Lampitt et al. 1990, Turner 2002 and citations therein). The situations in which relatively important contributions of zooplankton faecal pellets to vertical particle flux occur are often (1) associated with short periods of high particle flux related to the season of highest productivity in the surface ocean, and (2) characterised by rapidly sinking larger macrozooplankton faecal pellets. For example, in the Southern Ocean major proportions of the vertical flux of particulate organic matter measured in spring and summer have been observed to be due to relatively large krill faecal strings (e.g. von Bodungen 1986, von Bodungen et al. 1987, Wefer et al. 1988, manuscript IV). In contrast, smaller faecal strings seem to

contribute only minor proportions of the vertical particle flux. In certain periods large proportions of the particles collected in sediment traps at 10 m depth under sea ice of the western Weddell Sea were due to krill faecal strings with diameters ≤ 100 µm, while at 70 m depth these were only found in very small amounts (manuscript IV). This is in accordance with observations made in the Scotia and Weddell Seas, where only the large krill faecal strings sank to depth, whereas the smaller ones did not leave the surface mixed layer (Cadée et al. 1992). In general, this agrees with the results of studies indicating that large particles contribute the majority of the vertical particle flux in the ocean, although the standing stock of material present in the ocean is dominated by small particles (e.g. McCave 1975, Bishop et al. 1977, Lampitt 1985).

These observations suggest that smaller macrozooplankton faecal pellets and faecal pellets of meso- and protozooplankton, including those of copepods, mainly contribute diminutive proportions of the total vertical particle flux. Under the sea ice of the western Weddell Sea, at 10 and 70 m depth, copepod faecal pellets were absent from the sinking faecal matter, although copepods were by far the most abundant taxon of the metazoan fauna in sea ice and the under-ice water layer, and also of the mesozooplankton in the water column (manuscripts I - V). Despite the relatively low ambient Chl *a* concentrations, the large pelagic copepod species produced considerable amounts of faecal pellets (up to 9 faecal pellets ind.$^{-1}$ d^{-1}, unpublished data, Fig. 7). Similar observations were made from the shelf of the eastern Weddell Sea during a spring phytoplankton bloom: pelagic copepods were abundant and distributed throughout the entire water column (manuscript VI). The large species produced up to 11 faecal pellets ind.$^{-1}$ d^{-1} at Chl *a* concentrations prevailing in the water column, and even up to 57 faecal pellets ind.$^{-1}$ d^{-1} when offered enriched phytoplankton (unpublished data, Fig. 8). However, no faecal pellets were found in sediment trap samples collected at 458 m depth (23 m above the sea floor), and the vertical flux of faecal matter was strongly dominated by cylindrical pieces of krill strings with diameters of 256 and 320 µm, and in certain periods by elliptical pellets probably of pteropod origin (Enrique Isla, unpublished data, Fig. 9). The proportion of particulate organic matter within the total mass flux (5.3 - 11.2 %, Enrique Isla, unpublished data, Fig. 10) was in the range of that measured in particle flux under sea ice in the western Weddell Sea (5.1 - 22 %, manuscript IV). The results indicate that the direct contribution of copepods to the vertical flux of particulate organic matter in both investigation areas and periods, respectively, was insignificant. Similar results were obtained by Bathmann et al. (1987) in the Norwegian Sea. Based on the observation that only 5 % of the copepod faecal pellet standing stock found in the euphotic zone sank into deeper water layers, they assumed that the bulk of these pellets remained in their production layer. Hydrographical conditions may be one of the reasons for this. It is e.g. probable that turbulent mixing often extends the residence times of copepod faecal pellets in the surface mixed layer as observed off Southern California (Alldredge et al. 1987).

As most of the copepod faecal pellets do not sink to depth, the question arises as to what is the fate of all the copepod faecal matter present in the water column. Large

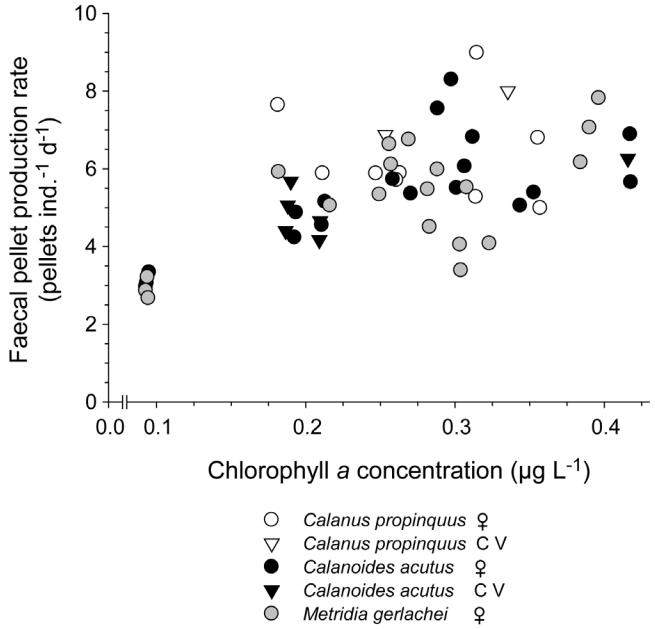

Fig. 7: Faecal pellet production rates of pelagic copepods collected in the western Weddell Sea in December 2004. The copepods were offered natural phytoplankton concentrations (unpublished data).

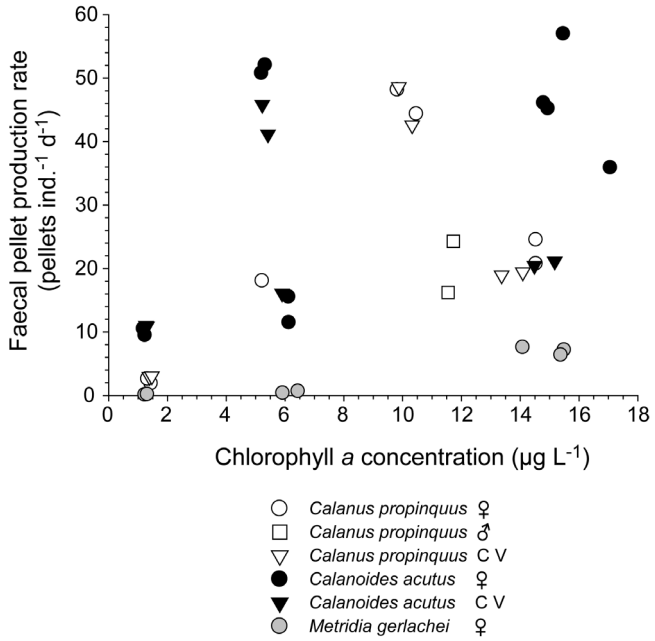

Fig. 8: Faecal pellet production rates of pelagic copepods collected on the eastern Weddell Sea shelf during a spring phytoplankton bloom in December 2003. The copepods were offered both natural phytoplankton concentrations and artificially enriched phytoplankton (unpublished data).

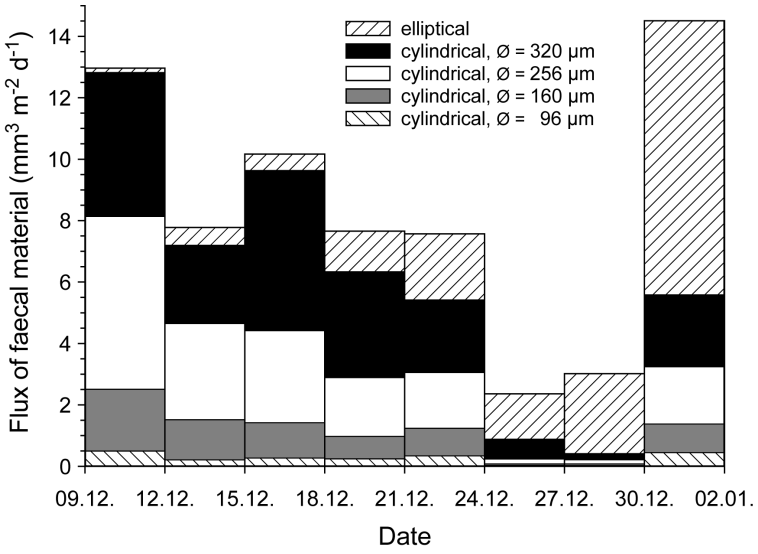

Fig. 9: Temporal development of amount and composition of vertical faecal matter flux measured 23 m above the sea floor (at 458 m depth) on the eastern Weddell Sea shelf during a spring phytoplankton bloom in December 2003/January 2004 (unpublished data from Enrique Isla).

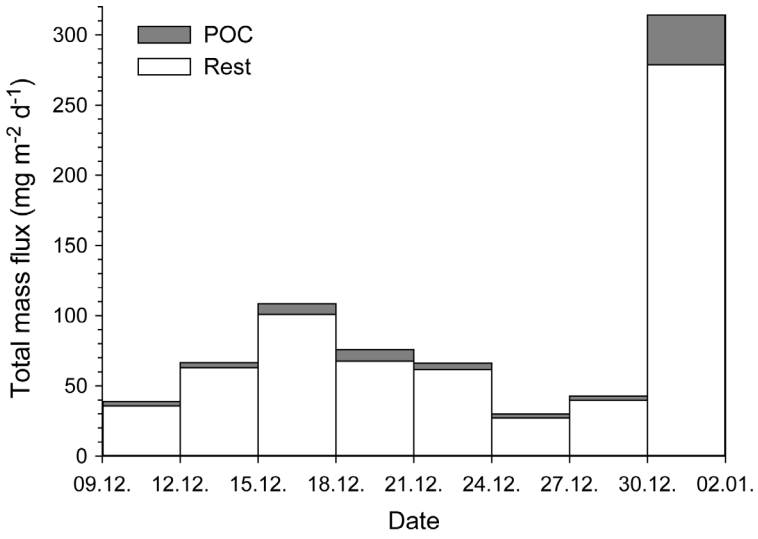

Fig. 10: Temporal development of the total vertical mass flux and the vertical flux of particulate organic carbon (POC) measured 23 m above the sea floor (at 458 m depth) on the eastern Weddell Sea shelf during a spring phytoplankton bloom in December 2003/January 2004 (unpublished data from Enrique Isla).

amounts of faecal pellets are probably rapidly degraded and recycled in the surface mixed layer, which might be a result of several processes such as bacterial degradation (Hansen et al. 1996) or leakage of dissolved organic carbon from the pellets (Jumars et al. 1989). Studies have shown that the copepods themselves probably play an important role in the degradation of faecal pellets by processes called coprophagy (ingestion of pellets), coprorhexy (fragmentation of pellets), and coprochaly (loosening of pellets) (Paffenhöfer & Strickland 1970, Lampitt et al. 1990, Noji et al. 1991). In this context, degradation of faecal pellets resulting in a retarded vertical flux of faecal matter was thought to be mainly due to coprophagy (e.g. González & Smetacek 1994). However, there is strong experimental evidence that copepods can very efficiently break their own pellets to pieces while ingesting only a small proportion of them (Lampitt et al. 1990). This is confirmed by a recent study showing that the copepods *Calanus helgolandicus* and *Pseudocalanus elongates*, two dominant species from the North Sea, ingest only a small fraction of the pellets; they immediately reject most of the pellets directly after capture thereby fragmenting them, which suggests that coprorhexy is the main process of degradation of faecal pellets caused by copepods (Iversen & Poulsen 2007). It is thus very likely that copepods mainly alter the faecal pellet standing stock by breaking the pellets into small slowly sinking pieces (Iversen & Poulsen 2007). In addition, the defaecation of some copepod species is not only in the form of densely packed pellets surrounded by a peritrophic membrane but also in form of loose faecal matter consisting of small slowly sinking pieces without a peritrophic membrane. E.g. in *Acartia tonsa* the latter were found to contribute more than 50 % of the total egested faecal matter (Olesen et al. 2005).

These results indicate that large amounts of the copepod faecal matter present in the water column consist of small particles, which are retained in the water column and can be further degraded by other organisms such as bacteria and protozooplankton. In fact, large protozooplankton, mainly heterotrophic dinoflagellates, were found to be the main degraders of faecal pellets in the strait between Denmark and Sweden, whereas mesozooplankton contributed only a small proportion of the total pellet degradation rate (Poulsen & Iversen under revision). The authors conclude that protozooplankton is the key organism group for the recycling of copepod faecal pellets within the water column.

Conclusions

- The contribution of copepods to the vertical flux of particulate organic matter in the water column is diminutive.
- Large amounts of copepod faecal pellets do not sink to depth but remain in their layer of origin where they are probably rapidly degraded and recycled.
- Coprorhexy by copepods and subsequent degradation by protozooplankton and bacteria might be the most important processes within the recycling of copepod faecal pellets in the water column.

4.4 Copepods and pelago-benthic coupling

Although the direct contribution of faecal pellets produced by sympagic and pelagic copepods to the vertical flux of particulate organic matter in the water column is often low, these copepods may be important for pelago-benthic coupling in the Weddell Sea. Under certain conditions, processes other than direct vertical flux of copepod faecal matter may considerably contribute to the transport of organic matter down to the sea floor, and thus to the energy supply of the benthos. These processes include packaging of copepod faecal pellets into larger fast-sinking aggregates, vertical migration of copepods, and predation of copepods in deep layers of the water column.

As already mentioned above, larger aggregates, referred to as marine snow (= aggregates > 500 µm in size), are considered to be major contributors of vertical particle flux in the ocean (e.g. Alldredge & Silver 1988, Turner 2002 and citations therein). Marine snow has a variety of origins and sources, including phytoplankton, faecal pellets and microaggregates composed primarily of miscellaneous organic debris and detritus (Alldredge & Silver 1988, Alldredge & Gotschalk 1990). In the presence of high abundances of copepod faecal pellets, resulting in an increased probability of pellet collision with other particles, considerable amounts of faecal material may be trapped and incorporated into large aggregates. As a result of this, copepod faecal pellets may be exported from the surface mixed layer and rapidly sink down to depth. Faecal pellets produced by sympagic copepods in the sea ice might also reach the sea floor via this pathway. In sea ice communities, aggregate formation is probably pronounced due to the often high concentrations of organic matter inside the narrow brine channels and pores. Furthermore, many ice algae species tend to form sticky and rapidly sinking aggregates suggesting that large amounts of them sink to depth after release from sea ice (e.g. Riebesell et al. 1991). Feeding of sympagic copepods might enhance the aggregate formation due to breakage of algae cells and release of substances, which cause the stickiness of the algae. Formation of aggregates consisting of ice algae and copepod faecal pellets probably takes place mainly in the periods of ice melt in spring and summer, which may result in single pronounced aggregate flux events as observed under late spring sea ice in the western Weddell Sea (manuscript IV).

Daily and seasonal vertical migration of copepods might also be important for pelago-benthic coupling. The former, observed e.g. in *Metridia gerlachei* (e.g. Rudyakov & Voronina 1974, Lopez & Huntley 1995, King & LaCasella 2003), may play a significant role in transport of fresh organic matter (e.g. algae within the guts) to depth. Seasonal vertical migration including a winter diapause in deep water layers is known from species such as *Calanoides acutus* (e.g. Schnack-Schiel & Hagen 1995, manuscript V). On the shelf of the eastern Weddell Sea, for instance, large amounts of *C. acutus* were present directly at the seafloor as revealed by epibenthic sledge catches (pers. observ., unpublished data). At the beginning of the overwintering period, when the copepods descend into deep water layers, this strategy may cause vertical transport of large amounts of algae and other organic matter into deeper water layers, where they are in part egested and contribute to the food supply of

pelagic grazers and benthos organisms. The copepods themselves may be valuable prey for predators such as copepods of the genus *Paraeuchaeta* living in deep water layers (Øresland 1991, Razouls et al. 2000). Furthermore, deep dwelling copepods may provide an important food source for omnivorous species, which are also present in these water layers. In January 1988 aggregations of Antarctic krill (*Euphausia superba*) were found close to the seafloor at depths of up to 480 m at the shelf edge of the southeastern Weddell Sea (Gutt & Siegel 1994). Since *E. superba*, as already mentioned above, has been observed to feed on copepods, it is probable that copepods constitute an important part of the food of *E. superba* during its stays at these depths. The undigested parts of the copepods may then be transported to the seafloor within the fast-sinking krill faecal strings. Feeding on copepods might be of special advantage for krill in winter, when the supply of fresh algal matter is scarce, while high abundances of small copepods (mainly early copepodite stages and nauplii) can be found in the water column (pers. observ. in the Lazarev Sea in July 2006, unpublished data).

In addition, copepods are an important food source for several fish species. The fish fauna of the high-Antarctic areas of the Southern Ocean, e.g. the Weddell Sea shelf, is dominated by notothenioid fish (e.g. Eastman 1993). Copepods such as *Calanoides acutus*, *Calanus propinquus* and *Metridia gerlachei* constitute important fractions of the food of the pelagic stages of many of these fish species (e.g. Hubold & Ekau 1990). In the notothenioid *Pleuragramma antarcticum*, the Antarctic silverfish, which is very abundant on the Weddell Sea shelf, all developmental stages occur throughout the water column (e.g. Hubold 1984, Hubold & Ekau 1987). Copepods are the main prey of the postlarvae and the juveniles, whereas in the adults euphausiids clearly dominate the food biomass although copepods may be most abundant (e.g. Hubold 1985, Dewitt et al. 1990).

Besides their importance as a food source for pelagic predators, copepods are preyed upon by benthic organisms – the most direct contribution of copepods to pelago-benthic coupling. Antarctic macro-zoobenthic communities may be dominated by so-called suspension feeders, which actively or passively capture dead organic particles or living organisms from the water column (Orejas et al. 2000 and citations therein, Gutt 2007). Copepods may constitute a major fraction of the diet of these suspension feeders (Gili & Coma 1998, Gili et al. 1999, Orejas et al. 2000). Furthermore, other benthic macrofauna organisms also feed on copepods. For instance, the guts of the echinoderm *Astrotoma agassizii* sampled from the eastern Weddell Sea shelf in late summer contained considerable proportions of *Calanoides acutus* (Dahm 1996).

Conclusions

- Considerable amounts of faecal pellets produced by sympagic and pelagic copepods might be transported to the seafloor within marine snow and serve as important food source for the benthos.
- Copepods may contribute to pelago-benthic coupling due to vertical migration and as food both for omnivorous and carnivorous organisms in deep water layers, and for benthic organisms.

5 Perspectives

The different sub-projects of this dissertation have contributed to the understanding of the role of copepods in cryo-pelagic and pelago-benthic coupling in the Weddell Sea. Several new insights have been gained, in particular with regard to the impact of sympagic copepods on carbon cycling within sea ice and on flux of particulate organic matter from sea ice into the underlying water column. However, many aspects of the life of sympagic copepods and their importance for the Southern Ocean ecosystem have still not been investigated. For instance, next to nothing is known about the influence of the strong gradients in salinity and temperature in sea ice on processes such as feeding and reproduction. Furthermore, the exact quantification of the contribution of sympagic copepods to vertical particle flux under sea ice over longer periods and during different seasons is desirable for a better estimate of the importance of copepods for cryo-pelagic coupling throughout the year. For this, the application of new methods would be necessary, e.g. the installation of cage-like constructions directly at the underside of sea ice for the purpose of collecting only particles, which originate from the ice. Several sets of measurements of under-ice particle flux, each under different conditions, could thereby be conducted. The variation of the conditions should include different combinations of the following aspects: (1) high and low concentrations of ice protists, (2) high and low concentrations of sympagic copepods within the ice, (3) presence and absence of under-ice grazers and (4) different types and thicknesses of sea ice. In this context, the recently gained knowledge of fluorescence dyes, which are incorporated in the diatom frustules during frustule formation (Shimizu et al. 2001, Leblanc & Hutchins 2005), could enable a very interesting experiment on the fate of the grazed ice diatoms. Large amounts of e.g. *Fragilariopsis cylindrus*, which is successfully kept in laboratory cultures, could be stained and then released, for instance, in infiltration layer communities containing high abundances of copepods. Subsequently, as a result of the staining the whereabouts of the diatom frustules could easily be determined on different pathways including those via grazers into faecal matter or predators and then eventually into particle flux under the ice.

For the improvement of estimations of copepod contributions to vertical particle flux within the water column, high-resolution studies on the vertical distribution of copepod faecal pellet concentrations during different seasons would be very helpful. Such measurements could be done by means of concentrating and determining the particles found within large volumes of sea water. The latter could be collected with Niskin bottles, however, the application of newly developed in-situ pumps would certainly enhance the efficiency of such studies.

These trains of thought indicate that there is still a pronounced necessity for ecological copepod research although the taxon Copepoda has already experienced extremely extensive investigation. Particularly against the background of potential climate change further studies on the importance of biological processes related to sympagic copepods, but also to whole sea ice communities, are essential in order to

assess the consequences of eventual sea ice cover decrease for the Southern Ocean ecosystem.

„Jedes Naturgesetz, das sich dem Beobachter offenbart, lässt auf ein höheres, noch unerkanntes schließen.“

“Every law of nature, which is revealed, indicates a more complex, unknown one.”

Alexander von Humboldt

(1769 - 1859)

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„Im Grunde sind es immer die Verbindungen mit Menschen,
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“Human contacts are what makes life worth living.”

Wilhelm von Humboldt

(1767 - 1835)

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8 Manuscripts

8.1 Contributions to the manuscripts

Manuscript 1

Feeding of the sympagic copepods *Drescheriella* spp. and *Stephos longipes* on protists inhabiting sea ice of the western Weddell Sea

Jan Michels, Sigrid B. Schnack-Schiel

Marine Ecology Progress Series (under revision)

I designed the research concept together with the second author. I did the sampling, conducted the experiments and measurements and processed, analysed and interpreted the data. I wrote the manuscript, which was revised by the second author.

Manuscript 2

Living conditions, abundance and composition of the metazoan fauna in surface and sub-ice layers in pack ice of the western Weddell Sea during late spring

Rainer Kiko, Jan Michels, Elke Mizdalski, Sigrid B. Schnack-Schiel, Iris Werner

Deep-Sea Research II (in press)

RK designed the research concept, collected the samples and conducted the measurements. I made major contributions to these three parts of the study. Furthermore, I contributed to the analysis of the samples and the writing of the manuscript.

Manuscript 3

Copepods in sea ice of the western Weddell Sea during austral spring 2004

Sigrid B. Schnack-Schiel, Christian Haas, Jan Michels, Elke Mizdalski, Henrike Schünemann, Matthias Steffens, David N. Thomas

Deep-Sea Research II (in press)

I helped with the copepod sampling and revised the manuscript together with the other co-authors.

Manuscript 4

Short-term biogenic particle flux under late spring sea ice in the western Weddell Sea

Jan Michels, Gerhard S. Dieckmann, David N. Thomas, Sigrid B. Schnack-Schiel, Andreas Krell, Philipp Assmy, Hilary Kennedy, Stathis Papadimitriou, Boris Cisewski

Deep-Sea Research II (in press)

I made major contributions to the development of the research concept, the sampling and the sample processing and analyses. I processed, analysed and interpreted the data. I wrote the manuscript with minor contributions by the seventh and ninth authors. The manuscript was revised by all co-authors.

Manuscript 5

Composition and community structure of zooplankton in the sea ice covered western Weddell Sea in spring 2004 – with emphasis on calanoid copepods

Sigrid B. Schnack-Schiel, Jan Michels, Elke Mizdalski, Michael P. Schodlok, Michael Schröder

Deep-Sea Research II (in press)

I contributed to the zooplankton sampling and made the chlorophyll measurements. I processed, analysed and interpreted some of the data. I revised the manuscript together with the other co-authors.

Manuscript 6

Abundance, population structure and vertical distribution of dominant calanoid copepods on the eastern Weddell Sea shelf during a spring phytoplankton bloom

Jan Michels, Sigrid B. Schnack-Schiel, Anna Pasternak, Elke Mizdalski, Enrique Isla, Dieter Gerdes

Polar Biology (positively evaluated by all three reviewers)

I designed the research concept together with the second author. The plankton sampling was carried out by me with contributions of the third author. I did the chlorophyll measurements. I processed, analysed and interpreted the data with contributions by the second author. I wrote the manuscript, which was revised by the co-authors.

8.2 Contributions to publications published during the PhD period

Publication 1

Feeding in dominant Antarctic copepods – does the morphology of the mandibular gnathobases relate to diet?

Jan Michels, Sigrid B. Schnack-Schiel

Marine Biology 146: 483-495

This publication is based on the results of my diploma thesis. I designed the research concept together with the second author. I conducted all practical work, processed, analysed and interpreted the results and wrote the manuscript, which was revised by the second author.

Publication 2

Confocal laser scanning microscopy: using cuticular autofluorescence for high resolution morphological imaging in small crustaceans

Jan Michels

Journal of Microscopy 227: 1-7

I developed the research concept, conducted the practical work, processed, analysed and interpreted the results and wrote the manuscript.

Publication 3

Depth profiles of volatile iodine and bromine-containing halocarbons in coastal Antarctic waters

Lucy J. Carpenter, David J. Wevill, Carl J. Palmer, Jan Michels

Marine Chemistry 103: 227-236

I contributed the data on the chlorophyll *a* concentrations.

Manuscript I

Feeding of the sympagic copepods *Drescheriella* spp. and *Stephos longipes* on protists inhabiting sea ice of the western Weddell Sea

ABSTRACT

Since copepods are very dominant members of the Antarctic sea ice meiofauna, knowledge of their feeding behaviour and its significance for cryo-pelagic coupling is essential for the understanding of the importance of sea ice for the ecosystem in ice covered ocean areas. In the present study, the feeding of the dominant sympagic copepods *Drescheriella* spp. and *Stephos longipes* on sea ice protist communities was investigated during the expedition ANT XXII/2 with RV “Polarstern” to the western Weddell Sea. Experiments were conducted with *Drescheriella* spp. females and copepodids (C) V and *S. longipes* adults, C I - V and nauplii (N) VI. In both species the ingestion rates of the C V and the females increased with increasing chlorophyll *a* (Chl *a*) concentrations, and the rates per unit body carbon of the C V were significantly higher than those of the females. Even at the highest Chl *a* concentrations no evidence for satiation feeding was found. The experiments with the *S. longipes* males, C I - IV and N VI could be carried out only in a small range of Chl *a* concentrations, and no clear trends in the ingestion rates with changing Chl *a* concentrations were observed. In the C IV the ingestion rates per unit body carbon were highest compared to those of all other stages at similar Chl *a* concentrations. Food selection by *Drescheriella* spp. and *S. longipes* was related to the size of the protist species. With few exceptions small-sized species such as *Fragilariopsis cylindrus*, *F. curta*, small *Chaetoceros*, *Nitzschia* and dinoflagellate species and *Phaeocystis antarctica* were positively selected, while relatively large species such as *Entomoneis* sp., *Rhizosolenia* cf. *crassa* and *Proboscia alata* were strongly negatively selected. The selection patterns suggest that the optimal food size of the sympagic copepods was in the lower size range of the naturally occurring protist species. At some sampling sites the estimated grazing impact of *Drescheriella* spp. and *S. longipes* on infiltration layer communities was extremely high reaching a maximum population grazing rate of 313.8 % of the ice algae stock per day. The results suggest that the sympagic copepods are well adapted to the food sources occurring in the sea ice brine system. The copepods’ feeding very probably strongly enhances the carbon flux within the sea ice and facilitates the export of organic matter from the sea ice into the underlying water column, thus mediating cryo-pelagic coupling in the Weddell Sea.

KEY WORDS: Sympagic copepods · Feeding · Protists · Sea ice · Infiltration layer community · Cryo-pelagic coupling · Weddell Sea

INTRODUCTION

Sea ice is one of the striking characteristics of polar oceans. In the Southern Ocean extensive areas are covered by sea ice, reaching sizes of about 4 x 10^6 km^2 in summer and 20 x 10^6 km^2 in winter (Zwally et al. 1983, Comiso 2003). During the formation of sea ice a complex brine channel system connected with the underlying water column forms within the ice (e.g. Eicken 1992, Horner et al. 1992, Fritsen et al. 1998), providing a habitat for bacteria, protists and small metazoans (Garrison 1991, Schnack-Schiel et al. 2001a, Lizotte 2003, Schnack-Schiel 2003). These organisms also inhabit the infiltration layer, which is a characteristic feature of Antarctic sea ice and is formed due to snow depressing the ice and thus enabling seawater to infiltrate the snow (Meguro 1962, Horner et al. 1992). In contrast to the brine channel system in the down part of the ice, which is often light limited, the infiltration layer is nearly always light saturated and thus a favourable ice algae habitat (e.g. Priscu et al. 1991, Kristiansen et al. 1998). Accordingly, infiltration layer communities are often the dominating ice algae communities in the sea ice of the Southern Ocean (e.g. Kristiansen et al. 1998).

The metazoan Antarctic sea ice meiofauna is dominated by copepods and turbellarians (Schnack-Schiel 2003). Among the ice inhabiting copepods geographical differences in the community composition exist: the calanoid *Paralabidocera antarctica* and the harpacticoid *Drescheriella glacialis* are the dominant species in the eastern part of the Southern Ocean (Hoshiai & Tanimura 1986, Swadling et al. 1997a, 2000, Swadling 2001), whereas in the western areas the sympagic metazoan meiofauna is dominated by the calanoid *Stephos longipes* and several harpacticoid species, *D. glacialis* being the most common (Dahms et al. 1990, Dahms & Schminke 1992, Kurbjeweit et al. 1993, Schnack-Schiel et al. 1995, 1998, 2001b, Günther et al. 1999).

The primary production associated with sea ice is estimated to be 9 - 25 % of the total annual production in the ice-covered regions of the Southern Ocean (Arrigo et al. 1997). The primary production in sea ice is very important for the entire upper layer of the ice-covered Southern Ocean since ice algae provide a concentrated food source for sympagic organisms and zooplankton (e.g. Stretch et al. 1988). The ice cover of the Weddell Sea is extensive, and large parts of it remain throughout the year (Zwally et al. 1983, Parkinson 1998). This makes the Weddell Sea a key area for sea ice primary production in the Southern Ocean, contributing about 50 % of the total annual production in sea ice of the Southern Ocean (Arrigo et al. 1997). For the assessment of the significance of sea ice primary production for the overall ecosystem of the Southern Ocean, it is thus essential to investigate the factors, which regulate ice algae growth and productivity, and processes such as carbon cycling within sea ice and carbon export from sea ice into the underlying water column.

One of the main factors regulating algal growth and productivity is grazing. The goal of the present study was to investigate the feeding behaviour of the dominant sympagic copepods in the Weddell Sea, *Drescheriella* spp. and *Stephos longipes*,

and to evaluate its impact on carbon cycling within sea ice and export of organic carbon from the ice into the water column. The experimental part of this study was conducted during the expedition ANT XXII/2 (“Ice Station Polarstern”, ISPOL) to the western Weddell Sea on board the research vessel “Polarstern” in December 2004. “Polarstern” was anchored to a drifting ice floe of an initial size of ca. 10 km x 10 km (for details see Hellmer et al. in press). This drift station provided permanent access to sea ice for several weeks and enabled regular sampling of sea ice associated copepods and food organisms.

MATERIAL AND METHODS

Sampling of copepods and food organisms

In order to collect copepods and food organisms, ice cores were taken from ice floe spots consisting of one metre thick first year ice and having a rich bottom layer community. The ice corers had internal diameters of 9 and 14 cm. The lower 10 cm thick segments of the cores were cut off and transported to the ship in clean plastic containers. There each segment was melted in two litres of filtered seawater (filtered through cellulose acetate filters with a pore size of 0.2 µm, Sartorius) at 4 °C.

Copepods and food organisms were also collected from the infiltration layer, which at certain spots contained high abundances of organisms. An area at the edge of the ice floe exhibiting a pronounced infiltration layer was chosen and regularly sampled over the period of the experimental work. For each sampling, the snow coverage and the superimposed ice (if present) were removed, and many litres of the semi-fluid infiltration layer were scooped into small plastic barrels and transported to the ship. On board the samples were melted at 4 °C, and the copepods carefully sorted out using a stereomicroscope and small glass pipettes. The water containing the naturally occurring assemblages was screened by means of a gauze with a mesh size of 200 µm in order to remove larger metazoans.

Experiments

The copepods were transferred into glass beakers (250 ml volume) containing bottom layer or infiltration layer water and acclimatised for at least two hours. The different *Drescheriella* species have a rather similar morphology, and it was not possible to determine the living specimens on board “Polarstern”. Hence, the two different *Drescheriella* species, *D. glacialis* and *D. racovitzai*, were pooled. For the experiments, the screened bottom layer or infiltration layer water was given into plastic bottles with a volume of 250 ml (NALGENE, Rochester, USA). The range of

chlorophyll *a* (Chl *a*) concentrations, which were used for the experiments, varied between the experiments with different developmental stages due to the variation in the natural Chl *a* concentrations. A wide range of concentrations (1.33 - 76.86 µg L^{-1}) could be used for experiments with *Drescheriella* spp. and *Stephos longipes* females and copepodids (C) V, whereas only a few experiments in a rather small Chl *a* concentration range (7.78 - 12.73 µg L^{-1}) could be conducted with *S. longipes* males, C I - IV and nauplii (N) VI. A determined number of acclimatised copepods (*Drescheriella* spp. females and C V: 15; *S. longipes* females, males and C V: 15; C IV: 20; C III: 40; C II: 50; C I: 60; N VI: 70) were carefully transferred into each bottle and incubated for between 10.6 and 17.6 hours. In *Drescheriella* spp. only females carrying egg sacks were used. In total 18 experiments were conducted. For each experiment and developmental stage, at least three replicates were performed (except for some cases when not enough specimens could be obtained). Control bottles (one to three per experiment) contained no copepods. During the incubation the bottles were placed on a plankton wheel rotating with a speed of one revolution per minute. The experimental set-up was kept in dimmed light and at a temperature of 0 °C. After the experiment, the copepods were removed, checked for mortality, filtered on pre-combusted (12 h, 500 °C) and pre-weighed GF/F filters (Whatman), rinsed with distilled water and stored at -20 °C for later measurements of the carbon and nitrogen contents. The concentration of Chl *a* and the abundance and composition of the food organisms were determined at the beginning and the end of each experiment. For this, different sub-samples were (1) filtered on GF/F filters and immediately kept at -20 °C for subsequent Chl *a* measurements or (2) transferred into 100 ml brown-glass bottles and fixed with Borax-buffered 37 % formalin (final formalin/seawater solution of 1.9 %) for later microscopic analyses.

Analyses

The Chl *a* concentrations were measured on board “Polarstern”, while all other analyses were performed in the laboratory in Bremerhaven. For the determination of the Chl *a* concentration, pigments were extracted using 10 ml of 90 % acetone. Extraction was triggered by ultrasonification and subsequent storage at -20 °C for two hours. The concentration of Chl *a* was determined using a Turner Designs 10-AU digital fluorometer according to Evans & O’Reilly (1983). Prior to the carbon and nitrogen measurements, the filters were dried (60 °C, 12 hours) and the dry weight of the copepods was determined using a microbalance (Sartorius MC5). Afterwards, the inorganic carbon was removed from the samples by adding two drops of saturated HCl followed by immediate rinsing with distilled water. Subsequently, the filters were re-dried, wrapped in tin foil and pressed to small globules. The carbon and nitrogen contents of the copepods were measured using a CHNSO analyser (Euro EA 3000, HEKAtech GmbH, Wegberg, Germany) with acetanilide as standard.

Growth rate, grazing coefficient, the mean Chl *a* concentration and the filtration and ingestion rates were calculated for each experiment according to Frost (1972). The

composition and concentration of food organisms were determined by means of inverted light microscopy (Axiovert 35, Zeiss, Oberkochen, Germany) applying the method of Utermöhl (1958). In order to investigate selectivity, the electivity index ε_i (Chesson 1983) was calculated for food organisms that were present in all experiments. The values of ε_i may range from -1 to 1 with negative values indicating negative selection, positive values indicating positive selection and zero indicating no selection.

Protist cell volume was calculated applying the formulae given by Hillebrand et al. (1999) and then converted to cellular carbon content via recommended carbon conversion equations (Menden-Deuer & Lessard 2000). The daily ration (percentage of body carbon uptake per day) was calculated using the carbon contents of the copepods (Table 2), the ingestion rates and the mean particulate organic carbon/Chl *a* ratio of the food organisms. The population grazing rates were estimated based on the copepod abundances and Chl *a* concentrations measured in the infiltration layer at the ice floe edges during this study (Kiko et al. in press), and on the results of the feeding experiments.

For the statistical analyses only the data sets from the experiments with females and C V were included since the number of data from the experiments with the other developmental stages was too low. The correlation between filtration and ingestion rates and the Chl *a* concentration was tested using the Spearman's rank correlation coefficient. The Mann-Whitney U test was applied to test for significant differences in the filtration and ingestion rates between developmental stages and between species. The significance level was set at 5 %. The statistical analyses were performed with the software STATISTICA (version 6.0).

RESULTS

In the bottom and infiltration layer communities 21 and 22 protist taxa were found, respectively (Table 1). Both communities were strongly dominated by diatoms. The bottom layer community was numerically dominated by *Fragilariopsis cylindrus* (40.1 %), *Pseudo-nitzschia prolongatoides* (19.5 %) and *Entomoneis* sp. (9.7 %). Dinoflagellates and ciliates accounted for 14.0 and 1.1 %, respectively. In terms of carbon biomass, the large diatom species *Entomoneis* sp. was the dominant taxon contributing an average of 75.6 % (Fig. 1). In the infiltration layer community a small *Nitzschia* sp. was numerically the most abundant species (70.1 %) followed by *F. cylindrus* (13.8 %) and *Fragilariopsis* sp. 2 (5.0 %). Dinoflagellates and ciliates contributed 3.7 and 0.8 %, respectively. The carbon biomass of the infiltration layer community was dominated by the large diatom species *Rhizosolenia* cf. *crassa* (on average 54.3 %) and *Proboscia alata* (on average 12.3 %) (Fig. 1). *Fragilariopsis* sp. 2 and the small *Nitzschia* sp. contributed on average 11.3 % and 7.4 % of the carbon biomass.

In the bottom layer community mainly *Drescheriella* spp. were found while *Stephos longipes* was very rare in this habitat. Therefore, only experiments with *Drescheriella* spp. could be conducted, however, due to the relatively low abundance of *Drescheriella* spp. the number of experiments was limited to three. In the infiltration layer community both *Drescheriella* spp. and *S. longipes* were very abundant thus permitting more experiments. The filtration rates of the *Drescheriella* spp. females and C V ranged from 0.12 to 9.72 ml [µg C]$^{-1}$ d^{-1} and from 0.61 to 5.82 ml [µg C]$^{-1}$ d^{-1}, respectively (Fig. 2). The filtration rates of the females decreased significantly with increasing Chl *a* concentrations ($p < 0.001$), while those of the C V did not have a significant correlation with the Chl *a* concentration ($p = 0.73$). The filtration rates of the females were significantly lower than those of the C V ($p < 0.01$, Fig. 4). In *Stephos longipes*, the filtration rates of the females ranged between 0.08 and 4.50 ml [µg C]$^{-1}$ d^{-1} and were also significantly lower ($p < 0.001$) than those of the C V ranging from 0.91 to 6.12 ml [µg C]$^{-1}$ d^{-1} (Figs. 3 and 4). There was a significant decrease in the filtration rates with increasing Chl *a* concentrations ($p < 0.001$) in both stages. An inter-specific comparison yielded the following results: (1) there were no significant differences between the filtration rates of both *Drescheriella* spp. and *S. longipes* females ($p = 0.82$, Fig. 4) and C V ($p = 0.31$, Fig. 4); (2) the filtration rates of the C V of both species were significantly higher than those of the females of the respective other species ($p < 0.001$, Fig. 4).

The ranges of the ingestion rates of the *Drescheriella* spp. females and C V were 2.34 - 55.20 ng Chl *a* [µg C]$^{-1}$ d^{-1} and 3.96 - 132.96 ng Chl *a* [µg C]$^{-1}$ d^{-1}, respectively (Fig. 2). In both stages the ingestion rates increased significantly with increasing Chl *a* concentrations (females: $p < 0.01$; C V: $p < 0.001$). The ingestion rates of the *Stephos longipes* females and C V ranged from 0.63 to 26.60 ng Chl *a* [µg C]$^{-1}$ d^{-1} and from 8.71 to 74.34 ng Chl *a* [µg C]$^{-1}$ d^{-1}, respectively (Fig. 3). They significantly increased with increasing Chl *a* concentrations (females: $p < 0.001$; C V: $p < 0.05$). In both *Drescheriella* spp. and *S. longipes* the ingestion rates of the C V were significantly higher than those of the respective females ($p < 0.01$ and $p < 0.001$, respectively, Fig. 4). A comparison between the species revealed the following: (1) the ingestion rates of the *Drescheriella* spp. females were significantly higher than those of the *S. longipes* females ($p < 0.001$, Fig. 4), but there was no significant difference between the ingestion rates of the *Drescheriella* spp. C V and those of the *S. longipes* C V ($p = 0.083$, Fig. 4); (2) the filtration rates of the *Drescheriella* spp. C V were significantly higher than those of the *S. longipes* females ($p < 0.001$, Fig. 4) whereas there was no significant difference between the ingestion rates of the *Drescheriella* spp. females and those of the *S. longipes* C V ($p = 0.181$, Fig. 4).

No conclusions can be drawn on trends in the filtration and ingestion rates of the *S. longipes* males, C I - IV and N VI with changing Chl *a* concentrations due to the low number of data and the small Chl *a* concentration range. The filtration (5.53 - 6.56 ml [µg C]$^{-1}$ d^{-1}) and ingestion rates (49.49 - 73.40 ng Chl *a* [µg C]$^{-1}$ d^{-1}) of the C IV were the highest compared to those of all other stages in the same Chl *a* concentration range (Figs. 3 and 5). The N VI had slightly lower rates than the C IV while the rates of the males and the C I - III were in the range of the lower part of the C V's rates and the higher part of the females' rates (Table 3, Figs. 3 and 5).

The mean carbon/Chl *a* ratio of the food from all experiments was 62.44. In combination with the measured ingestion rates and the carbon content per individual (Table 2), the application of this value yields the following daily rations: the percentage of body carbon uptake per day in the *Drescheriella* spp. females and C V was 14.6 - 344.7 % and 24.7 - 830.2 %, respectively. In *Stephos longipes* the ranges of the daily ration were 3.9 - 166.1 % in the females and 54.4 - 464.2 % in the C V. The daily rations of the C IV and the N VI ranged from 308.9 to 458.3 % and 115.2 to 380.8 %, respectively, while those of the males and the C I - III ranged from 27.3 to 306.0 %.

The population grazing rates of *Drescheriella* spp. were between 0.0 and 80.3 % of the ice algae stock per day, and 287.0 % of the ice algae stock per day at the sampling site with highest nauplii abundances (3792 individuals L^{-1}). In *S. longipes*, the population grazing was 11.5 to 61.1 % of the ice algae stock per day, and 183.5 % of the ice algae stock per day at the sampling site with the highest nauplii abundances (1280 individuals per L^{-1}). The total population grazing of the investigated copepods ranged from 13.8 to 137.8 % of the ice algae stock per day at all included sampling sites except for the two sites with the highest nauplii abundances. At the latter the total copepod grazing was 263.8 and 313.8 % of the ice algae stock per day.

In all investigated stages of both species the selection pattern was similar: with few exceptions selection was related to the size of the food organisms. The copepods positively selected small species such as *Fragilariopsis cylindrus* and *F. curta*, small *Chaetoceros* spp., small *Nitzschia* sp., small dinoflagellates and *Phaeocystis antarctica* while relatively large species such as *Entomoneis* sp., *Rhizosolenia* cf. *crassa* and *Proboscia alata* were strongly negatively selected, the latter two were hardly ever ingested (Figs. 6 - 8, Table 1). Exceptions in the bottom layer community were *Chaetoceros aequatorialis* and discoid diatoms, both of which, despite their rather small size, were strongly negatively selected, and *Fragilariopsis* sp. 1, which was not selected (Fig. 6). In the infiltration layer community the main exception were also the relatively small discoid diatoms, which were strongly negatively selected, and the negatively selected *Fragilariopsis* sp. 2 (Figs. 7 and 8). *Navicula* sp. was not selected (Figs. 7 and 8). In both communities *Pseudo-nitzschia prolongatoides* was positively selected and ciliates were strongly negatively selected (Figs. 6 - 8). In a comparison of food selection in the different developmental stages of *Stephos longipes* it is conspicuous that the earlier the stage the stronger the negative selection of the diatom species *Pinnularia quadratarea* var. *cuneata*, *Pseudo-nitzschia turgiduloides* and *Nitzschia taeniiformis* (Fig. 8).

DISCUSSION

Methodical evaluation of the feeding experiments

In the past various methods have been used to measure and determine filtration and ingestion rates of copepods. Besides the incubation method of the present study, which is common and has frequently been applied (e.g. Schnack 1983, Atkinson 1994, 1995, 1996, Atkinson & Shreeve 1995, Schnack-Schiel et al. 1995, Schultes et al. 2006, Cornils et al. 2007), methods based on radioactive tracers (e.g. DeMott 1995, Swadling et al. 1997b, Swadling & Gibson 2000), stable isotope labelling (e.g. De Troch et al. 2006, 2007) or gut fluorescence (e.g. Atkinson 1996, Bernard & Froneman 2005) have also been important. Since each of these methods has disadvantages and weaknesses, it is necessary to evaluate the method used in the context of the experimental conditions. In this study, three main aspects need to be reviewed: (1) the volume of the incubation bottles, (2) the density of copepods in the bottles and (3) the incubation of *Drescheriella* spp. in rotating bottles forcing the specimens to float in the water body.

The volume of the incubation bottles was rather small compared to that of bottles used in other studies (0.6 - 2.4 L: Schnack 1983, Atkinson 1994, 1995, 1996, Atkinson & Shreeve 1995, Cornils et al. 2007). The application of such a small volume was necessary, since the number of specimens available would not have been sufficient for an adequate number of replicates with larger bottles and appropriate copepod densities. In small-sized bottles the feeding behaviour of the copepods might be negatively influenced due to a larger probability of contacts between the copepods and the bottle wall. However, the species investigated in the present study inhabit platelet ice (Günther et al. 1999, Schnack-Schiel et al. 2004) and the brine channel system of sea ice (Dahms & Dieckmann 1987, Schnack-Schiel et al. 1995, 1998, 2001b, in press a, Swadling et al. 2000, Swadling 2001) and are thus adapted to life in small cavities and scorings under cramped conditions. Therefore, it is very unlikely that the small bottles had a negative effect on the copepods' feeding behaviour.

The abundances of adult copepods and late copepodite stages in the incubation bottles applied in this study (60 - 80 L^{-1}) are smaller than those of earlier feeding experiments with small copepods (e.g. 80 - 96 *Oithona* spp. [C IV, C V and adults] L^{-1}, Atkinson 1994, 1995, 1996; 96 *Metridia* spp. [C III and C IV] L^{-1}, Atkinson 1994; 85 - 145 *Stephos longipes* [C III - V] L^{-1}, Schnack-Schiel et al. 1995; 150 - 200 *Paralabidocera antarctica* [all stages] L^{-1}, Swadling & Gibson 2000). They are comparable to maximum densities of *Drescheriella* spp. and *S. longipes* copepodids (38 and 59 individuals L^{-1}, respectively) found in the surface layer of the ice floe during the present study (Kiko et al. in press). In the same habitat the abundance of *S. longipes* nauplii reached maximum values of 1280 individuals L^{-1} (Kiko et al. in press) being much higher than in the incubation bottles and more than twice as high as the maximum *S. longipes* nauplii abundance of 510 L^{-1} found within the annual sea ice proper in Terra Nova Bay, Antarctica (Costanzo et al. 2002). In rotten

summer sea ice of the Weddell Sea, total abundances of *Drescheriella glacialis* and *S. longipes* of up to 154 and 185 individuals L^{-1}, respectively, were found inside the lowest part of the surface ice (Schnack-Schiel et al. 2001b). Comparably, the maximum total *D. glacialis* abundance observed in a study on east Antarctic fast ice was 175 individuals L^{-1} (Swadling 2001). Taking into account that these abundance data refer to the volume of the melted sea ice, it becomes evident that the actual abundances were much higher due to the fact that the volume of the brine channel system only occupies a small part of the total volume of the sea ice. Furthermore, the abundance data given above are from single species only, whereas the total density of copepods and other meiofauna organisms is often much higher. These aspects suggest that the sympagic copepods are used to very high abundances and thus that the number of copepods in the incubation bottles of the present study did not influence their feeding behaviour.

The experimental set-up of this study included the incubation of *Drescheriella* spp. in rotating bottles. Although most of the harpacticoid copepod species have a benthic lifestyle (Huys & Boxshall 1991), swimming ability has been observed in several families (Boxshall 1979, Hicks 1988). Many benthic harpacticoid species temporarily emerge from the sediment into the water column (e.g. Walters & Bell 1986), and some species are considered to be pelagic (e.g. Boxshall 1979, Veit-Köhler & Fuentes 2007). *D. glacialis* and *D. racovitzai* have mainly been found inside sea ice (Dahms & Dieckmann 1987, Dahms et al. 1990, Dahms & Schminke 1992, Schnack-Schiel et al. 1998, 2001b, in press a, Swadling et al. 2000, Swadling 2001, Kiko et al. in press,). Their occurrence in annual pack ice far offshore above a water column of up to 5276 m makes a recolonization from coastal fast ice or the benthal unlikely and implies that these species must spend certain periods in open water (Dahms et al. 1990, Dahms & Schminke 1992). *D. glacialis* was found to be absent from the water column of the Amundsen and Bellingshausen Seas (Schnack-Schiel et al. 1998), however, during the present study *Drescheriella* spp. occurred in the sub-ice water layer and the water column (Kiko et al. in press, Schnack et al. in press b). Copepodids and adults of *D. glacialis* and *D. racovitzai* are good swimmers (Dahms et al. 1990, Dahms & Schminke 1992), and in laboratory experiments *D. glacialis* has been kept under ice-free conditions over several generations (Dahms et al. 1990, Bergmans et al. 1991). This suggests that both species are not obligate sea ice dwellers and have the ability to survive well in the pelagial. Therefore it is very likely that the necessity to swim did not influence the feeding behaviour of *Drescheriella* spp. in the experiments of the present study. In general, the results of the feeding experiments were very probably not biased by the experimental set-up and are thus reliable.

Filtration and ingestion rates

This study provides the first known detailed information on the feeding of *Drescheriella* spp. and *Stephos longipes* on sea ice inhabiting protists. To the best of

our knowledge no data on feeding of *Drescheriella* spp. have been published, while for *S. longipes* only a few filtration and ingestion rate data from experiments with C II - V fed on phytoplankton and ice algae are available (Schnack-Schiel et al. 1995, Swadling et al. 1997b). In the experiments of Schnack-Schiel et al. (1995), carried out in the eastern Weddell Sea in autumn, the Chl *a* concentration of the ice algae food ranged from about 15 to nearly 50 µg L^{-1}. The filtration rates of the C V (about 1.5 - 2.1 ml [µg dry weight]$^{-1}$ d^{-1}) were higher than those of the C V in the present study (0.37 - 1.55 ml [µg dry weight]$^{-1}$ d^{-1}) at comparable Chl *a* concentrations (13.59 - 54.20 µg L^{-1}). Similar to the results of the present study, C IV had the highest filtration rates (about 2.4 - 4.2 ml [µg dry weight]$^{-1}$ d^{-1}). Experiments with *Paracalanus*, which has a pelagic lifestyle but a size comparable to that of *S. longipes*, revealed slightly different results: the weight-specific ingestion rates increased from N IV to C III and then decreased in the subsequent stages (Paffenhöfer 1984). It is not possible to compare the filtration rates of the C III and IV of this study with those measured by Schnack-Schiel et al. (1995), since in the present study these rates were determined at lower Chl *a* concentrations only (8.84 - 11.71 µg L^{-1}). However, it seems that the rates of the present study (C IV: 1.66 - 1.97 ml [µg dry weight]$^{-1}$ d^{-1}; C III: 0.14 - 1.48 ml [µg dry weight]$^{-1}$ d^{-1}) were lower. Swadling et al. (1997b) performed their experiments at a coastal site in east Antarctica during summer and offered phytoplankton as food. Although a direct comparison of the results with those of the present study is not possible due to the different food source and since C II - V were pooled and only mean values are given, the average filtration and ingestion rates of *S. longipes* appear to have been lower (8.83 ml ind.$^{-1}$ d^{-1} and 31.87 ng Chl *a* ind.$^{-1}$ d^{-1}, respectively; range of Chl *a* concentration: about 1.5 - 17.5 µg L^{-1}).

In the framework of many experiments with copepods satiation feeding, which can be well described by an Ivlev or a rectilinear model, has been measured (e.g. Frost 1972, Mullin et al. 1975, Libourel Houde & Roman 1987, Besiktepe & Dam 2002). This feeding behaviour is characterised by linearly increasing ingestion rates with increasing food concentrations up to a critical concentration at which the gut passage rate is maximal thus limiting the ingestion rate, and by a constant ingestion rate at food concentrations higher than the critical concentration (Frost 1972, Mullin et al. 1975). However, in the present study no satiation feeding was observed. Even at very high Chl *a* concentrations the ingestion rates increased with increasing Chl *a* concentrations, and in *Drescheriella* spp. C V and females the correlation between ingestion rate and Chl *a* concentration can be described by a linear model. The maximum daily rations determined in the present study seem to have been very high. Since the mean ratio of particulate organic carbon to Chl *a* (62.44) in the offered food was in the range of ratios measured in other studies (e.g. 45.55 - 98.37, Barquero et al. 1998) and the average mass specific carbon contents of the copepods (Table 2) were within or close to a range given for polar copepods (40 - 55 %, Conover & Huntley 1991), the high daily rations are very likely not the result of measurement biases. In earlier studies comparable values have been measured (e.g. up to 481 % in N V of *Calanus helgolandicus*, Paffenhöfer [1971]; up to 660 % in adult *Acartia hudsonica*, Deason [1980]; up to 616 % in N III of *A. tonsa*, calculations of

Paffenhöfer [1988], based on results of Stoecker & Egloff [1987]). High daily rations might be a function of optimal food type for a particular developmental stage and of optimal food concentration, composition and size (Paffenhöfer 1988). The feeding behaviour observed in the present study suggests that the sympagic copepods are well adapted to the food sources found in the sea ice brine system. Sea ice organisms often have a patchy distribution (e.g. Spindler & Dieckmann 1986, Dahms et al. 1990, Swadling et al. 1997a), and the biomass of algae growing within the sea ice varies strongly (e.g. Spindler et al. 1990, Dieckmann et al. 1998). Assuming an average brine volume of 54 % measured in the infiltration layer during the present study (Kiko et al. in press) the maximum Chl *a* concentration within the brine of the infiltration layer sampled for the experiments was 142.33 µg L^{-1}. Sympagic copepods often face much higher Chl *a* concentrations, e.g. up to 2220 µg L^{-1} observed in the summer sea ice of the Weddell Sea (Spindler et al. 1990). Copepods are able to rapidly adapt their feeding behaviour to changing food conditions, which occur e.g. due to the above mentioned patchiness of food organisms (e.g. DeMott 1990, 1993). The ability to have high ingestion rates might enable sympagic copepods to cope with such a patchiness by feeding large amounts once they encounter high protist biomass concentrations, resulting in an optimal utilisation of the available food sources. Patches with high food concentrations and good food conditions attract grazers. In sea ice of the Amundsen Sea, e.g., highest abundances of foraminifers and copepods, including *S. longipes* and harpacticoid species, were in part observed to inhabit the areas of the maximum Chl *a* concentrations (up to 377 µg L^{-1}) of internal communities associated with the infiltration layer (Thomas et al. 1998). Such an aggregation results in pronounced pressure of competition for food among the copepods and between the copepods and other grazers. High ingestion rates might, thus, be an advantage making the copepods more competitive compared to other grazers within the food web of the sea ice brine system.

Selective feeding

In the present study the food selection by *Drescheriella* spp. and *Stephos longipes* was related to the size of the protist species. Earlier studies have revealed that copepods are able to feed on a large size range of food (e.g. Atkinson 1994). However, highest filtration rates have been measured in a relatively small range of optimal food size (e.g. Berggreen et al. 1988). The selection patterns of this study suggest that the optimal food size of the sympagic copepods was in the lower size range of the naturally occurring protist species. Since the optimal food size was not determined and the selectivity patterns of all investigated *S. longipes* stages were rather similar, it is not possible to make clear interpretations concerning a change of optimal food size with changing developmental stages. However, compared to the selection patterns of the late copepodids and the adults, a slightly increased negative selection of protist species with a length of 80 (*Pinnularia quadratarea* var. *cuneata*) to 127 µm (*Nitzschia taeniiformis*) was evident in the N VI and the early copepodids.

This indicates that the optimal food size of these stages was smaller than that in the later stages. Earlier studies have revealed a positive relationship between grazer size and optimal food size (e.g. Berggreen et al. 1988). In the latter study, the optimal food size of N V and VI and C I - III of *Acartia tonsa* was about 14 µm, while the subsequent stages had an optimal food size of 14 - 70 µm.

One striking result of the present study is that the N VI fed on almost the same size range of food organisms as all copepodite stages and the adults. The mouthpart morphology of nauplii is different from that of copepodids and adults (e.g. Fernández 1979, Michels & Schnack-Schiel 2005) leading to the assumption that nauplii have a different food capturing technique. Due to the smaller dimensions of nauplii one would expect that they feed on organisms smaller than those utilised by the later stages. However, the results of this study are in agreement with e.g. a study on *Acartia tonsa* revealing that the size range of food organisms ingested was similar in all stages from N IV to the adults (Berggreen et al. 1988). Similarly, in a study on calanoid copepods from the Southern Ocean, all grazers of several different sizes were able to feed on the entire measured size range of food (Atkinson 1994). In this study, the pronounced positive selection of the small protist species is in accordance with an earlier study, in which copepods and euphausids preferentially selected the nano-sized (1 - 20 µm) phytoplankton (Perissinotto 1992), and suggests that the copepods were capable of effectively capturing and ingesting these organisms. The dimension of the smallest species, *Fragilariopsis cylindrus*, is in the range of the lower size limit (1 to 4 µm) for particle capture determined for calanoid copepods with a body size close to that of *Drescheriella* spp. and *S. longipes* (Bartram 1981, Uye & Kasahara 1983, Vanderploeg et al. 1984, Berggreen et al. 1988). In contrast to the present study, in these studies the copepods' particle capture was very inefficient at the lower end of the food size spectra.

The selection patterns of this study have some conspicuous features: *Chaetoceros aequatorialis*, discoid diatoms and ciliates were strongly negatively selected, although they were among the smaller species of the bottom and infiltration layer communities, whereas *Pseudo-nitzschia prolongatoides* was positively selected despite its larger body size. In the case of *C. aequatorialis* the reasons for the negative selection might be the frequent occurrence of chains and the pronounced and very large apical and antapical setae found to have mean lengths of 514.71 and 470.00 µm, respectively. Such long and thick setae are often the cause for an inefficient consumption of diatoms of the genus *Chaetoceros* (Parsons et al. 1967, Hargrave & Geen 1970). By contrast, the much smaller *Chaetoceros* sp. 2 was only found to be solitary and did not have prominent setae, and in *Chaetoceros* sp. 1 chains occurred only rarely and the setae were not pronounced. The positive selection of *P. prolongatoides* might have been possible due to the oblong and narrow shape of the cells, which have a mean girdle width of only 2.67 µm. Such an elongation in one dimension is supposed to be no defence against grazing, while elongation in two dimensions was observed to be very useful for grazing avoidance (Vanderploeg et al. 1988). This might be an explanation for the strong negative selection of discoid diatoms and ciliates. Although the mean diameter of the discoid diatoms was relatively small they might have been difficult to handle due to the round

shape of their frustules, which might also apply to the rather broad elliptical shape of the ciliates. In earlier studies different selection patterns have been determined: copepods have been observed to feed preferentially on microzooplankton rather than diatoms (Stoecker & Egloff 1987, Stoecker & Capuzzo 1990, Atkinson 1996, Turner et al. 2001), but selection for diatoms rather than dinoflagellates, ciliates and flagellates has also been found (e.g. Koski & Wexels Riser 2006). Protozoans have a higher nutritional value than diatoms of similar size (e.g. Stoecker & Capuzzo 1990), and a diet mixture of phytoplankton and ciliates seems to be most favourable for copepod development (Kleppel 1993, Bonnet & Carlotti 2001). A study on copepod feeding in several areas and ecosystems worldwide revealed an average contribution of ciliates to the copepods' diet of 30 % (Calbet & Saiz 2005). However, the consumption of ciliates seems to depend on the trophic conditions of the habitat: in environments with low phytoplankton concentrations (< 50 µg C L^{-1}), feeding on ciliates has been found to be equivalently important as phytoplankton consumption (Atkinson 1996, Calbet & Saiz 2005), while in environments with higher phytoplankton concentrations this importance decreases (Calbet & Saiz 2005). This might be due to the copepods' ability to permute their selective feeding to the most abundant food organisms (Landry 1981, Kiørboe et al. 1996, Gismervik & Andersen 1997). It is, therefore, likely that the sympagic copepods inhabiting the sea ice brine system have adapted to the food conditions in the ice and feed mainly on small protist species, which dominate the sea ice communities.

Significance of copepod feeding for carbon cycling within sea ice and for cryo-pelagic coupling

The results of this study indicate that the feeding of sympagic copepods plays a significant role in the carbon flux within sea ice of the Weddell Sea. Besides turbellarians, copepods are the main metazoan grazers in the sea ice brine system (Schnack-Schiel et al. 2001a, Schnack-Schiel 2003). At some sites sampled during the present study the estimated grazing impact of *Drescheriella* spp. and *Stephos longipes*, which were the dominant species in the infiltration layer (Kiko et al. in press), was extremely high reaching a maximum population grazing rate of 313.8 % of the ice algae stock per day. Not much is known about the growth characteristics of ice algae inhabiting infiltration layers. However, for respective communities dominated by *Phaeocystis antarctica* and the diatoms *Chaetoceros neglectus* and *Fragilariopsis cylindrus* ice algal growth rates of 0.3 - 0.7 d^{-1} were estimated (Kristiansen et al. 1998). When applying these values to the present study, it becomes evident that the ice algae growth was not capable of compensating for the biomass losses caused by the extremely high grazing rates. Therefore, at the sampling sites with the highest copepod abundances, the ice algae community might have been rapidly grazed down by the copepods. Furthermore, at sites with lower copepod abundances the ice algae biomass was probably controlled by copepod grazing.

The high ingestion rates measured at high food concentrations in this study were very probably associated with the production of large amounts of faecal pellets. At the ice floe edge, close to the sampling sites of the present study, 1057 feacal pellets per millilitre brine were found within the infiltration layer (Harri Kuosa, unpublished data). The ingestion and faecal pellet production rates of copepods feeding on diatoms were observed to be linearly correlated (Besiktepe & Dam 2002). With increasing food concentration the assimilation efficiency decreases (Gaudy 1974, Landry et al. 1984), and a rapid decrease in gut passage time and a curvilinear increase in faecal pellet size takes place, the latter being more pronounced in relation to diatom food than in relation to other food types including auto- and heterotrophic dinoflagellates and ciliates (Besiktepe & Dam 2002). Therefore, sympagic copepods, which feed on dense ice algae communities dominated by diatoms, very probably strongly enhance the carbon flux within the sea ice due to (1) high ingestion and faecal pellet production rates, (2) rather large faecal pellets and (3) low assimilation efficiencies. These factors also mediate the export of organic material from the sea ice into the under-ice water layer, and into the water column next to ice floes and within ice floe cracks. The brine channel system of sea ice is connected with the under-ice water layer (e.g. Eicken 1992), and brine drainage is assumed to transport ice algae and particulate organic material from the sea ice into the underlying water column (Melnikov 1998). Such an export of faecal material due to fluid exchange is certainly most pronounced during ice melt when the faecal pellets are released in the water column. In addition, increased crack formation during ice melt enhances flushing of the infiltration layer with sea water, which might considerably contribute to export of faecal pellets into the water column. The small copepod faecal pellets found in the sea ice during this study contained large amounts of intact diatoms of the genus *Fragilariopsis*. Most of them had fluorescing chloroplasts indicating that the diatoms were still viable (Harri Kuosa, pers. comm.). Consequently, the faecal material produced by the sympagic copepods was a nutritious food source providing fresh and undegraded organic matter for heterotrophic organisms inhabiting the sea ice and the under-ice water layer. In conclusion, feeding of *Drescheriella* spp. and *S. longipes* was very likely an important factor facilitating cryo-pelagic coupling in the Weddell Sea.

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Tables

Table 1. Overview of the protist species found in the bottom and infiltration layer communities.

	Bottom layer community		Infiltration layer community	
	Species	Length (µm)	Species	Length (µm)
Pennate diatoms				
	Fragilariopsis sp. 1	41.69	*Fragilariopsis* sp. 2	49.00
	Fragilariopsis cylindrus	3.48	*Fragilariopsis cylindrus*	3.48
	Fragilariopsis curta	31.00	*Fragilariopsis curta*	31.00
	Pseudo-nitzschia prolongatoides	51.75	*Pseudo-nitzschia prolongatoides*	51.75
	Pseudo-nitzschia turgiduloides	99.94	*Pseudo-nitzschia turgiduloides*	99.94
	Nitzschia stellata	77.00	*Nitzschia* sp.	13.76
	Nitzschia taeniiformis	127.00	*Nitzschia taeniiformis*	127.00
	Cylindrotheca closterium	25.22	*Cylindrotheca closterium*	25.22
	Synedra sp.	80.00	*Navicula* sp.	41.72
	Entomoneis sp.	130.00	*Pinnularia quadratarea* var. *cuneata*	80.00
	Pleurosigma sp.	128.33	*Entomoneis* sp.	130.00
	Membraneis sp.	90.50	*Pleurosigma* sp.	128.33
Centric diatoms				
	Discoid diatoms	31.16	Discoid diatoms	31.16
	Chaetoceros aequatorialis	21.85	*Chaetoceros* sp. 2	5.32
	Chaetoceros sp. 1	8.90	*Rhizosolenia* cf. *crassa*	333.00
	Corethron pennatum	144.19	*Proboscia alata*	498.49
			Corethron pennatum	144.19
Dinoflagellates				
	Small dinoflagellates	7.35	Small dinoflagellates	7.35
	Prorocentrum spp.	22.79	*Prorocentrum* spp.	22.79
Flagellates				
	Phaeocystis antarctica	6.24	*Phaeocystis antarctica*	6.24
Ciliates				
	Ciliate species 1	60.00	Ciliate species 2	46.00
	Ciliate species 3	39.00	Ciliate species 3	39.00

Table 2. Dry weights and carbon and nitrogen contents of the different developmental stages of *Drescheriella* spp. and *Stephos longipes* investigated in the present study. In all cases, in which at least three measurements were conducted, the numbers and the numbers in brackets represent the mean value and the standard deviation, respectively.

	No. of measurements	Dry weight (µg ind.$^{-1}$)	Carbon content (µg ind.$^{-1}$)	Carbon content (% dry weight)	Nitrogen content (µg ind.$^{-1}$)
Drescheriella spp.					
Female with egg sack	5	7.34 (0.41)	3.18 (0.41)	43.55 (6.84)	0.70 (0.09)
Female without egg sack	5	5.57 (0.61)	2.35 (0.09)	42.39 (3.09)	0.52 (0.03)
C V	5	3.28 (0.34)	1.29 (0.13)	39.42 (3.61)	0.29 (0.10)
Stephos longipes					
Female	5	11.39 (0.36)	5.04 (0.25)	44.28 (2.20)	1.10 (0.05)
Male	5	9.91 (0.49)	3.90 (0.16)	39.49 (3.12)	0.81 (0.06)
C V	5	8.15 (0.26)	3.31 (0.25)	40.66 (4.28)	0.63 (0.07)
C IV	1	3.92 (-)	1.18 (-)	30.03 (-)	0.13 (-)
C III	1	2.83 (-)	0.94 (-)	33.20 (-)	0.10 (-)
C II	1	2.21 (-)	0.89 (-)	40.12 (-)	0.10 (-)
C I	1	1.33 (-)	0.53 (-)	39.81 (-)	0.08 (-)
N VI	4	0.82 (0.10)	0.35 (0.02)	43.34 (6.79)	0.05 (0.004)

Table 3. Filtration and ingestion rates of the *Stephos longipes* males, C I - III and N VI.

Stage	Filtration rate (ml [µg C]$^{-1}$ d^{-1})	Ingestion rate (ng Chl *a* [µg C]$^{-1}$ d^{-1})
Male	1.82 - 3.25	16.94 - 34.95
C III	0.42 - 4.45	4.37 - 49.01
C II	1.74 - 2.82	19.46 - 32.69
C I	1.36 - 3.31	14.23 - 32.12
N VI	1.84 - 5.30	18.45 - 60.99

Figures

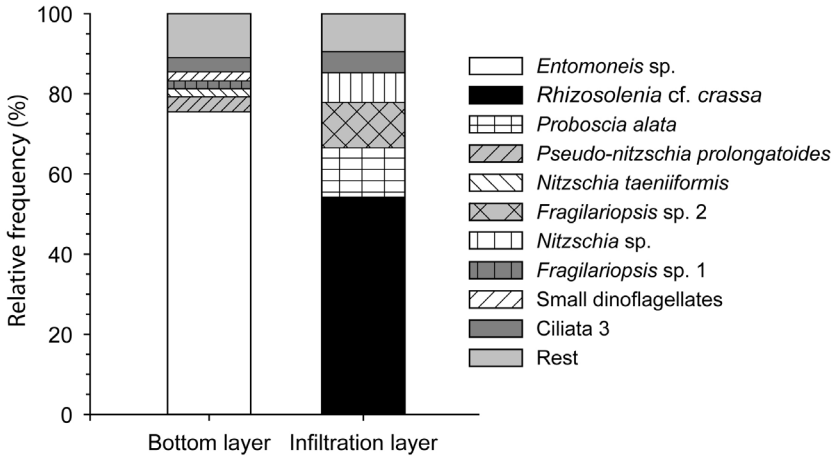

Figure 1. Relative composition of the protist communities from the bottom and infiltration layers. The calculation is based on the carbon biomass, and the values represent the means of all experiments.

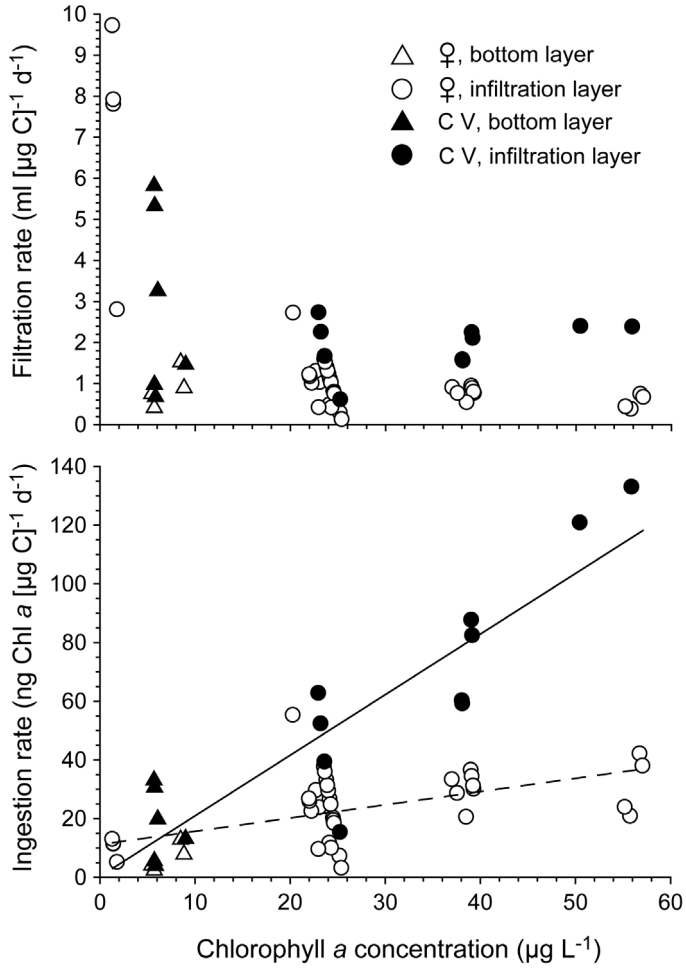

Figure 2. Filtration and ingestion rates of *Drescheriella* spp. females and C V from the bottom and infiltration layer communities. The dashed line (equation: $y = 0.4512x + 11.183$, $R^2 = 0.308$) represents the linear regression of the females' ingestion rates, the solid line (equation: $y = 2.0638x + 0.3294$, $R^2 = 0.824$) represents that of the C V's ingestion rates.

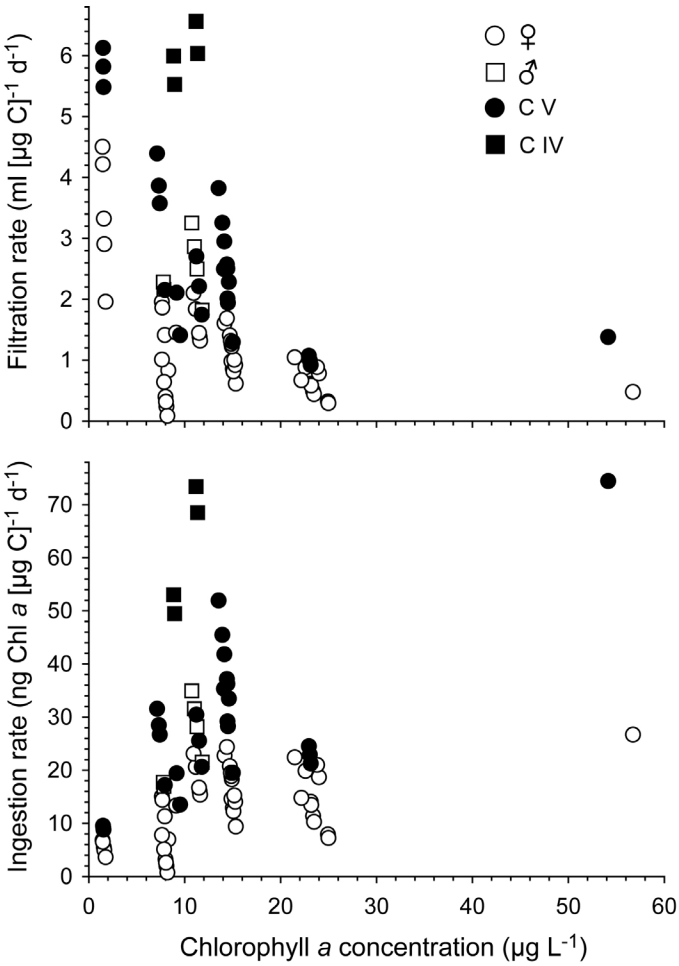

Figure 3. Filtration and ingestion rates of *Stephos longipes* females, males and C IV and V from the infiltration layer community.

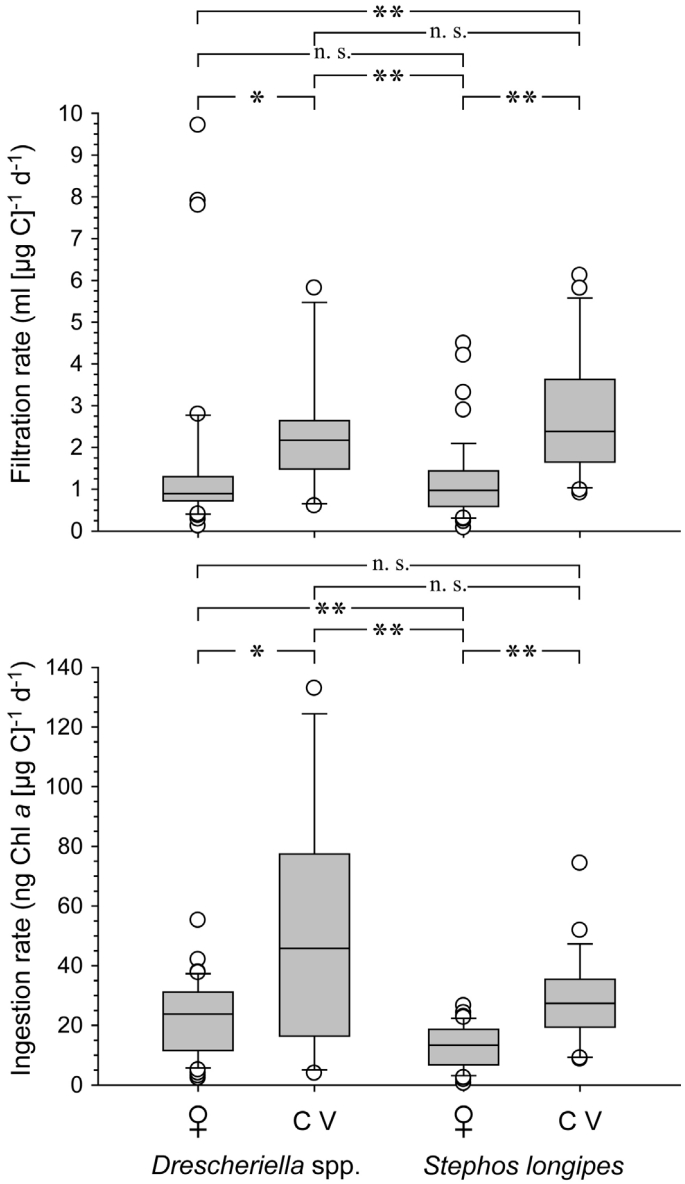

Figure 4. Box plots of the filtration and ingestion rates of *Drescheriella* spp. and *Stephos longipes* females and C V. A star indicates $p < 0.01$, two stars indicate $p < 0.001$ and n.s. indicates $p > 0.05$).

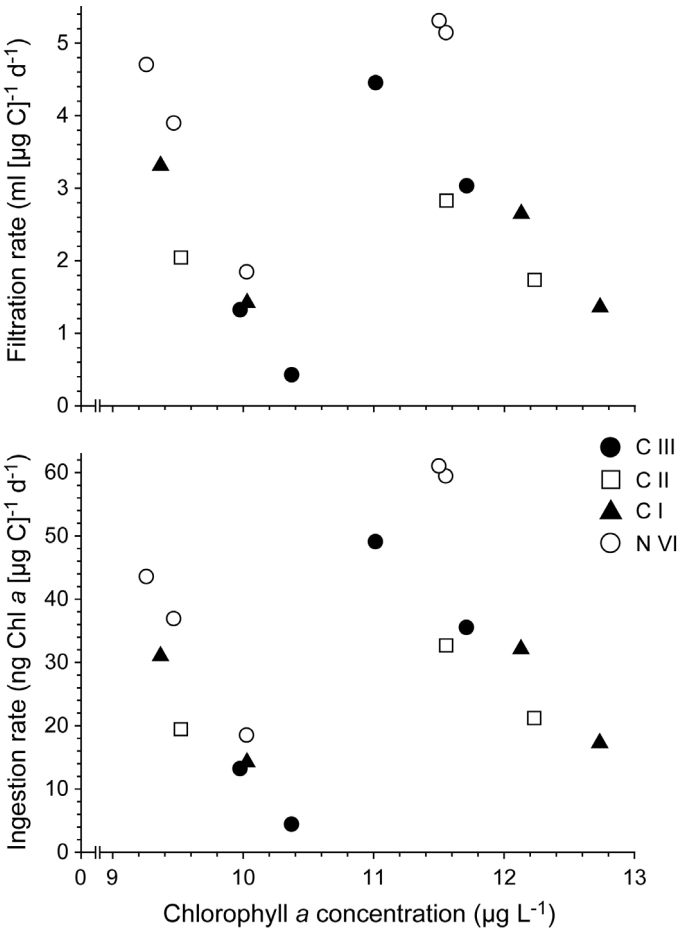

Figure 5. Filtration and ingestion rates of *Stephos longipes* C I - III and N VI from the infiltration layer community.

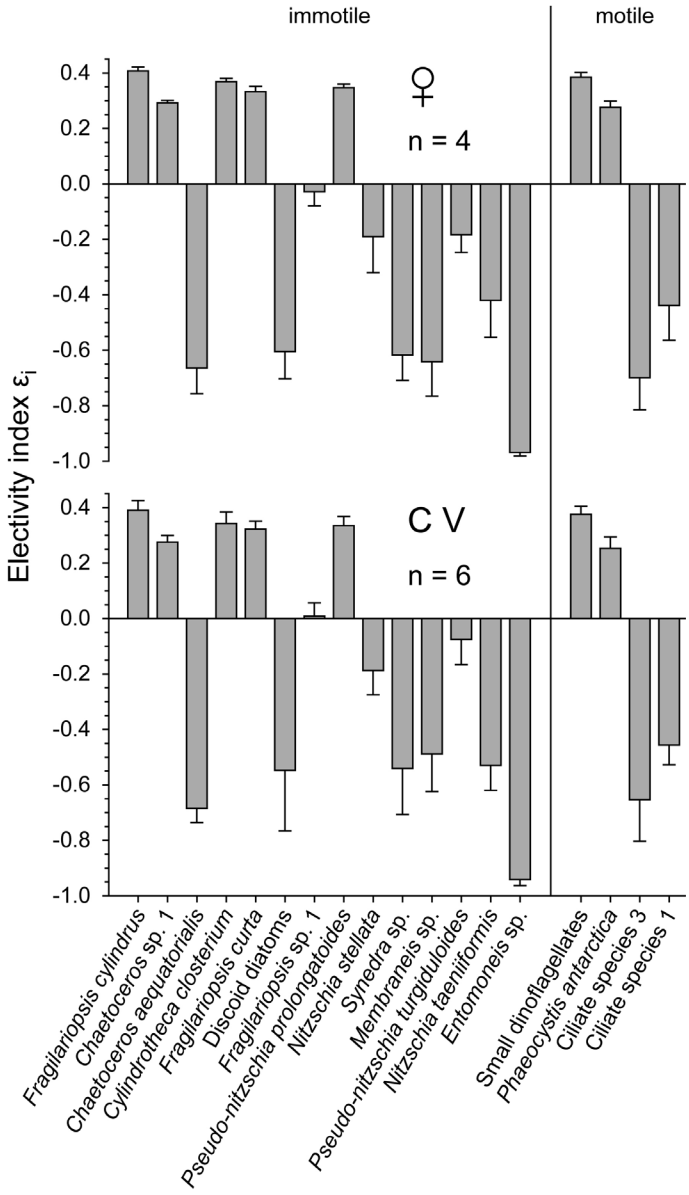

Figure 6. Mean electivity indices of the protist species of all experiments with *Drescheriella* spp. females and C V from the bottom layer. The bars indicate the standard deviation.

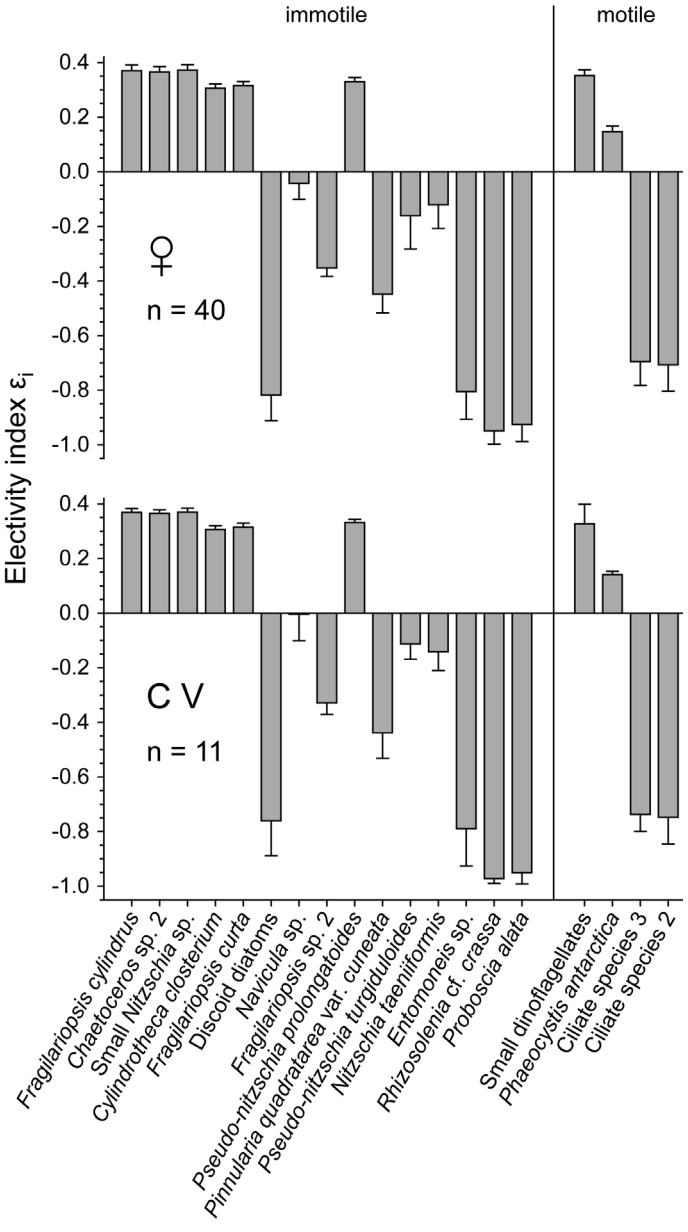

Figure 7. Mean electivity indices of the protist species of all experiments with *Drescheriella* spp. females and C V from the infiltration layer. The bars indicate the standard deviation.

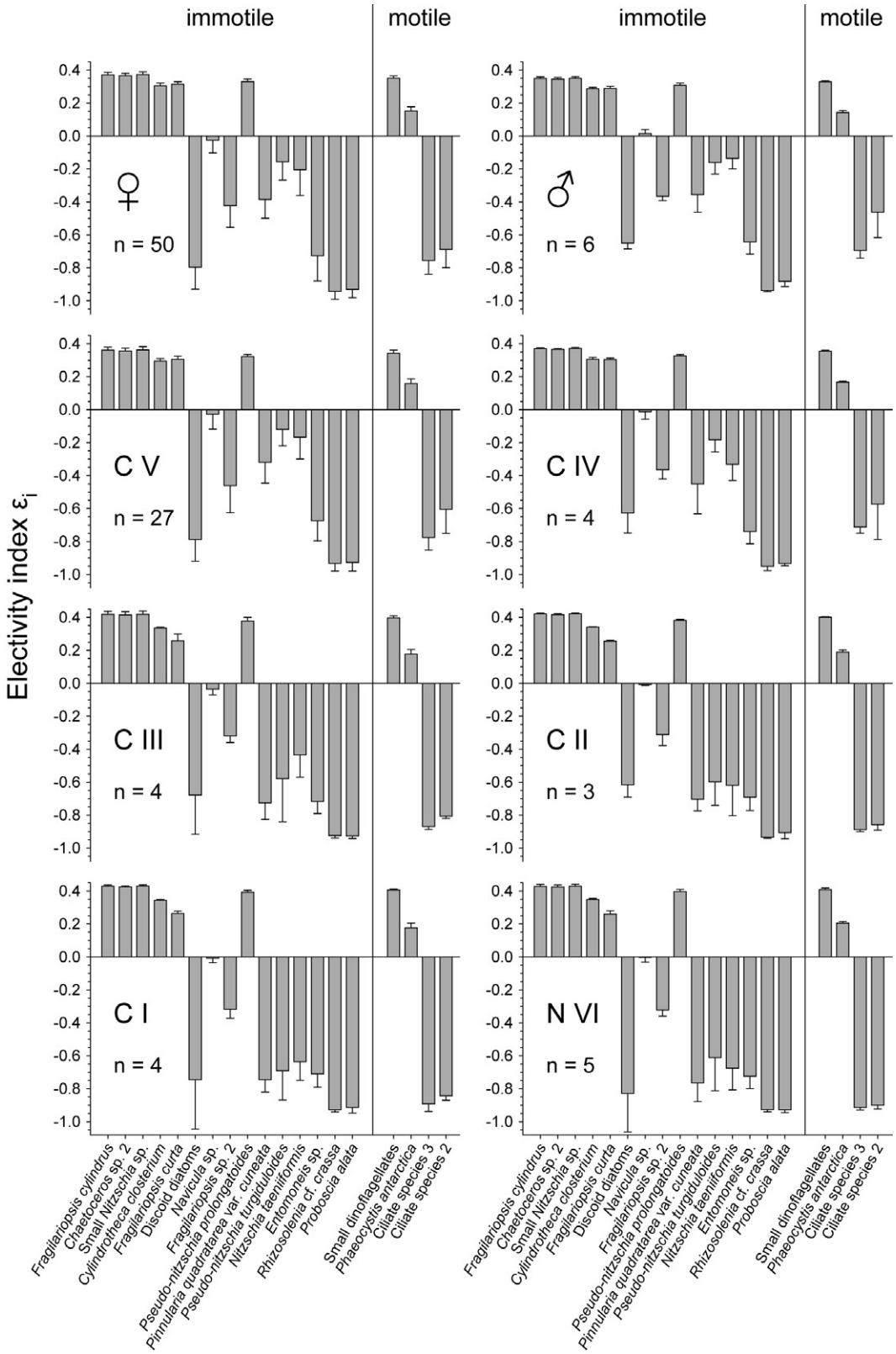

Figure 8. Mean electivity indices of the protist species of all experiments with *Stephos longipes* females, males, C I - V and N VI from the infiltration layer. The bars indicate the standard deviation.

Manuscript II

Living conditions, abundance and composition of the metazoan fauna in surface and sub-ice layers in pack ice of the western Weddell Sea during late spring

Abstract

The surface and sub-ice layer habitats and their metazoan fauna were studied on a drifting pack-ice floe in the western Weddell Sea from 29 Nov 2004 to 1 Jan 2005 during the “Ice Station POLarstern” (ISPOL). Flooding of the floe occurred at some places, and the establishment of surface layers with a brownish colour due to growing algae was observed at several sampling sites. The average surface layer temperature, brine salinity and brine volume were -1.4 °C, 25.3 and 54 %, respectively. The temperature-salinity relationship in the surface layer was seldom at equilibrium conditions. Chlorophyll *a* (Chl *a*) concentrations in the brine varied between 1.0 and 53.5 µg L^{-1}. Surface layer thickness, salinity, Chl *a* concentration and copepod abundances were generally higher at the edge of the floe than in the inner part. The sympagic copepod species *Drescheriella glacialis*/*racovitzai* and *Stephos longipes* with abundances ranging between 0 and 3830 ind. L^{-1} (median 2 ind. L^{-1}) and 0 and 1293 ind. L^{-1} (median 4 ind. L^{-1}), respectively, were the dominant members of the surface layer meiofauna. Their populations consisted mainly of adults and early naupliar stages, which points to an active reproduction of these species within the surface layer. Other taxa found in the surface layer were undetermined turbellarians, the gastropod *Tergipes antarctica,* and, for the first time, the ctenophore *Callianira antarctica*, and the amphipods *Eusirus antarcticus* and *E. tridentatus*. During the course of our study, slight melting at the ice underside took place, releasing sympagic organisms to the water column. Chl *a* concentrations in the sub-ice water layer were very low (0.1 to 0.5 µg L^{-1}), except for 25 Dec when the Chl *a* concentration at 0 m depth increased to 2.3 µg L^{-1}. The most dominant sympagic copepod species found in the sub-ice layer was *Ectinosoma* sp. with abundances ranging between 1 and 599 ind. m^{-3} (median 25 ind. m^{-3}). Other sympagic copepod species occurring regularly in this habitat were *Drescheriella glacialis*/*racovitzai*, *Diarthrodes* cf. *lilacinus*, *Idomene antarctica* and *Stephos longipes.* All of these sympagic species were generally found in higher abundances at 0 m depth underneath the ice than at 5 m depth, in contrast to pelagic copepod species which occurred more frequently at 5 m depth. Niche separation and probable life-cycle strategies of dominant sympagic metazoans are discussed.

Keywords: Sympagic copepods; Sea ice; Marine ecology; Life cycle; Distribution; ISPOL; Southern Ocean; Western Weddell Sea

1. Introduction

Sea ice harbours a highly diverse fauna and flora which play an important role in the carbon cycle of the Southern Ocean (Arrigo and Thomas, 2004). A total of 5 - 25 % of the marine primary production in the Southern Ocean are associated with sea ice (Lizotte, 2001; Arrigo, 2003 and references therein). The high ice algal standing stocks represent a potential food source for a diverse sympagic (= ice-associated) meiofauna community, but also for pelagic and benthic organisms after melting (Kurbjeweit et al., 1993; Werner et al., 2004; Lovvorn et al, 2005; Michels et al., in press). Inside Antarctic pack ice, copepods and turbellarians are the most abundant members of the sympagic meiofauna (Schnack-Schiel et al., 2001a). Three dominant species of copepods (*Stephos longipes, Paralabidocera antarctica, Drescheriella glacialis*) have been fairly well studied with respect to their life cyles (Dahms et al., 1990; Schnack-Schiel et al., 1995; Tanimura et al., 1996). However, much less is known about several other metazoan species (ctenophores, turbellarians, other copepods, nudibranchs), which have also been found in Antarctic sea ice (Pelseneer, 1903; Dahms et al., 1990; Schnack-Schiel, 2003).

According to Horner et al. (1992) four different sea-ice habitats and their respective communities can be identified in Antarctic pack ice: surface, interior, bottom and sub-ice layers and communities. Here we present studies on the environmental conditions and the metazoan meiofauna (> 50 µm) in the surface and sub-ice habitats of Antarctic pack ice. Due to different formation processes, three different surface communities can be distinguished in detail: infiltration, deformation and melt-pond communities (Horner et al., 1992). They all are found in a semi-fluid layer on top of the ice proper, in which organisms from the seawater can occur. When superimposed ice forms on top of the surface layer, the latter is sometimes called a gap layer (Kattner et al., 2004). In the following, we do not discriminate between all these varieties and speak hereafter of the surface layer only. Surface layers are a common feature of Antarctic pack ice and well known for their high primary productivity (Garrison and Buck, 1991; Kattner et al., 2004). Most studies investigating the biology of the surface layer have to date focussed on the microbial communities (Garrison and Buck, 1991; Fritsen et al., 2001; Kattner et al., 2004). Very little is known about the metazoan fauna in this habitat, from which only two species of copepods (*Drescheriella glacialis, Stephos longipes*) have as yet been described (Schnack-Schiel et al., 2001b).

The sub-ice layer directly below the ice, which is physically connected to the brine channel system and the underside of the ice, is another habitat with a special community (Tanimura et al., 1984; Kurbjeweit et al., 1993; Schnack-Schiel et al., 1998; Werner, 2006). Conditions in this habitat are governed by processes both in the overlying ice and in the underlying water column. Freezing conditions and probably scarce food supply during winter, as well as melting and enhanced release of food from the ice during summer characterize this habitat. Freshening of the sub-ice layer during summer seems to be an important factor, excluding truly pelagic, stenohaline species from this habitat (for the Arctic: Werner, 2006). Studies on the composition of the sub-ice layer around Antarctica are scarce and were performed in

areas of fast ice (Tanimura et al., 1984) or seasonal sea ice cover (Kurbjeweit et al., 1993). Only one study from an area of multiyear pack ice exists from the Bellingshausen Sea (Schnack-Schiel et al., 1998). The Antarctic krill, *Euphausia superba*, a key member of the Southern Ocean food web, exploits the sub-ice layer, and distribution and feeding activity of this species is strongly correlated with the pack-ice cover (Loeb et al., 1997). Similar to the Arctic (Werner and Auel, 2005), the ice-water interface can be inhabited by several species of amphipods, however, this is a relatively new observation for the Antarctic pack ice (Krapp et al., in press).

The goals of the present study were (i) to investigate the diversity and abundance of metazoan species in the surface and sub-ice layers in a region of perennial Antarctic pack ice, (ii) to elucidate biotic and abiotic factors influencing the species' distribution in the different habitats, and (iii) to deduce life-cycle strategies and niche separation of the species in, and between the respective habitats. Comparison of the data set presented in this publication with another data set on the abundances of copepods within the ice proper (Schnack-Schiel et al., in press) allows identification of links and differences between the ice proper, sub-ice layer and surface layer communities. It enables us to allocate and discuss life-cycle strategies of the poorly studied sympagic copepod species *Ectinosoma* sp*., Drescheriella racovitzai, Diarthrodes* cf. *lilacinus* and *Idomene antarctica* for the first time.

2. Material and Methods

2.1. Study area

This investigation of the surface and sub-ice layer habitats and their metazoan fauna took place in the western Weddell Sea during the "Ice Station POLarstern" (ISPOL, ANT XXII/2, 6 Nov 2004 - 19 Jan 2005 (Dieckmann et al., 2007)). The research vessel "Polarstern" was moored to a floe from 28 Nov 2004 until 2 Jan 2005 and drifted with this floe mainly to the north from 68° 15' S to 67° 20' S at about 55° 25' W. All investigations of the present study were performed on an initially 10 km by 10 km-sized floe, which broke up into several parts during the study period (Fig. 1). The floe consisted mainly of second-year ice (2 m thick, 0.8 m snow cover), interspersed by locally formed or advected first-year ice (0.9 and 1.8 m thick, respectively, 0.3 m snow cover). The area around the floe was covered to 9/10 by the same kind of pack ice. Flooding of the floe occurred at some places, and the establishment of surface layers with a brownish colour due to growing algae was observed at several sites. The floe composition was typical for an area of about 100 km by 500 km (north-south direction), a transition area from thick second-year ice located to the east to homogeneous first-year ice further west (C. Haas, pers. comm.). Dynamic ice conditions, which resulted in a considerable decrease of the mean floe size from 825 to 242 m^2 in the study area between 9 Dec and 1 Jan (Steer et al., press), were mirrored by a slowly progressing floe break-up, with a major break-up on 25 Dec. For further details on ice conditions see Haas et al. (in press),

Heil et al. (in press) and Steer et al. (in press). Besides shifting wind and drift directions, tidal movements, an increase in solar radiation (Bareiss and Goergen, in press) and a mean modelled heat flux of 15 W m^{-2} from the ocean into the ice (McPhee, in press) were probably responsible for the reduction of floe size. Air temperatures (measured by the ship's system) ranged between -7.0 °C and 2.7 °C with an average of -2.6 °C. For further details on atmospheric conditions see Bareiss and Goergen (in press). During the investigation period a general thinning of the snow cover of 10 to 18 cm (-0.33 to -0.64 cm d^{-1}) occurred. Snowfall was observed only twice. Between 28 Nov and 2 Dec 7 cm and on the 27 Dec 2 to 4 cm of snow accumulated on the floe (Haas et al., in press).

2.2. Sampling and processing of samples from the surface layer

Different sites on the floe, chosen by their distance to the floe edge and the timing of crack formation (Table 1, Fig. 1) were sampled. Sampling took place between 12:00 h and 19:00 h UTC (local noon was at 15:00 UTC). If possible, sampling was performed either at 1 m and 5 m distance to the floe edge or in the inner part of the floe (more than 35 m away from the floe edge). On 1 Jan a transect from the floe edge to the inner part of the floe was sampled (distances to floe edge: 1, 2, 3, 4, 5, 6, 7, 8, 15 and 30 m). This sampling took place from 22:00 h to 24:00 h UTC. At every site, snow and superimposed ice were removed carefully from above the surface layer. Thereafter, the semi-fluid layer on top of the solid ice proper was mixed with a shovel for homogeneous sampling representative of the whole layer. The thickness of this layer, the snow and the superimposed ice were measured with a ruler. A mesh was pushed inside the ice-water mixture, and temperature and salinity were measured inside the ice-free interior part of the mesh with a WTW microprocessor conductivity meter LF 196 (accuracy: T = 0.1 °C, S = 0.2). The measured salinity is regarded to be the brine salinity of the surface layer.

For the determination of chlorophyll *a* (Chl *a*) concentrations and bulk salinity, 1 L samples of the ice-water mixture were taken with a scoop, poured into acid-cleaned polyethylene-boxes and melted at 4 °C in the dark. Once melted, bulk salinity was measured with the WTW microprocessor conductivity meter LF 196. For determination of the Chl *a* concentration, melted ice samples were filtered on Whatman GF/F filters, extracted in 90 % acetone, homogenised and analysed fluorometrically with a Turner Designs 10-AU digital fluorometer according to Evans and O'Reilly (1983). Chl *a* determination on directly melted ice samples involves the risk of organism losses during ice melting (Garrison and Buck, 1986) and thus an underestimation of Chl *a* concentrations, but facilitates the determination of bulk salinity and Chl *a* concentration in the same ice sample. Furthermore, this method has already been applied in several Arctic sea ice studies (e.g. Gradinger, 1999; Mock and Gradinger, 1999; Krembs et al., 2001) and therefore allows a comparison of the results. Chl *a* concentrations are given for the melted sample (Table 1) and related to brine volume (Fig. 3).

As temperature and brine salinity in the surface layer were seldom in equilibrium (Fig. 2) brine volume was calculated as a function of bulk salinity and brine salinity according to the following formulae:

Brine volume = (bulk salinity * density of pure ice) / (brine salinity * brine density) (Cox and Weeks, 1983)

Density of pure ice = $0.917 - (1.403 * 10^{-4}) * T$ (Pounder, 1965)

Brine density = 1.0008 * brine salinity (Zubov, 1945; Cox and Weeks, 1975)

For determination of abundances and composition of the sympagic meiofauna, 1 L samples of the ice-water mixture were taken with a scoop and melted in the dark at 4 °C in a surplus of 0.2 µm-filtered seawater to avoid osmotic stress (Garrison and Buck, 1986), especially for delicate forms such as turbellarians. Once melted, the samples were concentrated over a 50 µm gauze and fixed with borax-buffered formalin in seawater (4 % final concentration). For enumeration of metazoan species and developmental stages from the surface layer, samples were sorted under a stereomicroscope (10x - 100x magnification). Samples were split into aliquots with a Folsom splitter to count small and numerous species, while large and scarce species were counted from the entire sample.

In *Drescheriella glacialis* and *D. racovitzai,* only adults were identified to species level. Their naupliar and copepodite stages were combined. With one exception (nauplii indet.), all other harpacticoid nauplii were identified to species level, whereas the nauplii of cyclopoids and calanoids (except *S. longipes*) were not further identified. Species abundances are given for the melted sample. Exuviae were also identified and counted, but data are only presented for *Diarthrodes* cf. *lilacinus*.

For dominant copepod species the mean developmental stage (MDS) was calculated, modified after Marin (1987). As nauplii were included in the calculation, a value of 1 means that all specimens found were nauplii of stage I, a value of 7 means that the copepodite stage I was the average stage found, and a value of 12 means that all animals found were adults. These indices were also calculated for nauplii and copepodids separately, if a bimodal stage distribution was obvious.

Furthermore large volumes (more than 50 L of ice-water mixture) from the surface layer were filtered first through a 1 mm sieve, which retained the ice crystals, and then through a 50 µm sieve, which retained the organisms, in order to identify species which only occurred in low numbers in the infiltration layer. These samples were taken at the sites A, B and Y (Fig. 1).

2.3. Sampling and processing of samples from the sub-ice layer

In order to document a time-series of the sub-ice fauna, sampling took place at position D, the same location as that chosen by Schnack-Schiel et al. (in press), except for two occasions (29 Nov and 14 Dec). On 29 Nov sampling took place on an area of the first-year ice near position D, which broke apart from the rest of the floe on 2 Dec. On 14 Dec sampling took place at position C (Table 1, Fig. 1). The morphology of the ice underside and the macrofauna in this habitat were recorded by a video camera lowered through a core hole (Werner and Lindemann, 1997; Werner and Gradinger, 2002). Temperature and salinity profiles in the sub-ice water layer (0 - 6 m below the ice underside) were measured in-situ with the WTW microprocessor conductivity meter LF 196 lowered through a core hole. As variations in temperature and salinity were smaller than the accuracy of the conductometer used, only the ranges found are reported in the results. Discrete water samples for the analysis of Chl *a* concentrations were collected at 0 and 5 m depth below the ice with a polyethylene tube (4 cm internal diameter) with a valve at one end. The unequipped end of the tube was lowered into the water through a core hole with the valve closed. At the sampling depth, the valve was opened and closed again and the tube with the enclosed water sample was hoisted to the surface. Determination of Chl *a* concentrations was performed as described above for the ice samples.

Organisms from the sub-ice water (0 and 5 m depth below the ice) were quantitatively sampled with an under-ice pumping system (Werner and Martínez Arbizu, 1999) equipped with a standardised water meter (accuracy 0.1 L) and inserts of plankton gauze (mesh size 50 µm) to concentrate the organisms. Between 1.4 and 3.8 m^3 of sub-ice water was pumped at each station from each depth. Samples were fixed in borax-buffered formalin in seawater (4 % final concentration). Enumeration of species and stages from the sub-ice layer and for dominant copepod species the calculation of a mean stage composition was performed as above.

3. Results

3.1. Environmental conditions in the surface layer

Surface layer thickness varied between 3 and 50 cm, with generally higher values at the edge of the floe (Table 1, Fig. 3). The daily average surface layer temperature increased from -1.9 °C (range: -1.6 to -2.0 °C) on 19 Dec to -1.2 °C (range: -0.9 to -1.6 °C) on 1 Jan. The average brine salinity decreased from 28.1 (range: 25.8 - 30.1) to 24.0 (range: 20.3 - 27.7) in the same period of time, as did the bulk salinity from 17.6 (range: 14.7 - 21.5) to 14.8 (range: 9.9 - 21.5). On most occasions, brine salinity was also higher at the edge of the floe than further inwards (Table 1, Fig. 3). Average brine volume of all samples was 54 % (38 - 83 %). The temperature-salinity relationship in the surface layer was seldom at equilibrium conditions (Fig. 2). A

change from freezing to melting conditions occurred between 19 and 25 Dec. Chl *a* concentrations in the brine varied between 1.0 and 53.5 µg L^{-1} with higher values at the edge of the floe (Fig. 3). The trends of higher surface layer thickness, bulk and brine salinities and Chl *a* concentration at the edge of the floe were clearly recognizable from the transect, sampled on 1 Jan (Fig. 3, open circles). Highest Chl *a* concentrations were found at stations with a long-established floe edge.

3.2. Metazoan fauna in the surface layer

A total of at least 12 sympagic species of metazoans were found in the surface layer (Table 3). Copepods were the most diverse group consisting of the four harpacticoid species *Drescheriella glacialis, D. racovitzai, Idomene antarctica* and *Nitocra gracilimane* and the calanoids *Stephos longipes* and *Paralabidocera antarctica.* However, only the harpacticoids *D. glacialis*/*racovitzai* and the calanoid *Stephos longipes* were abundant. Other taxa found in the surface layer were undetermined turbellarians, the gastropod *Tergipes antarctica,* and, for the first time, the ctenophore *Callianira antarctica* and the amphipods *Eusirus antarcticus* and *E. tridentatus*. The euphausid *Euphausia superba* occurred on rare occasions.

The distribution of the dominant copepod species was very variable, with highest values generally at the floe edge (Fig. 3, see especially the transect sampled on 1 Jan, open circles). Copepods were only occasionally found in samples taken at the inner part of the floe (more than 35 m away from any floe edge).

Abundances of the harpacticoids *Drescheriella* spp. ranged between 0 and 3792 ind. L^{-1} (median: 2) for nauplii, and between 0 and 38 ind. L^{-1} (median: 0) for copepodids. The maximal abundance of *Drescheriella* spp. (3830 ind. L^{-1}) which was due to the high occurrence of nauplii (3792 ind. L^{-1}) was found at a station where the floe edge had been established more than three weeks before sampling (Fig. 1, A).

Abundances of the calanoid *S. longipes* ranged between 0 and 1280 ind. L^{-1} (median: 2.5) for nauplii, and between 0 and 59 ind. L^{-1} (median: 0) for copepodids. Maximum abundance of *S. longipes* (1293 ind. L^{-1}) was found at a site, where the floe edge had been established one month before the sample was taken (Fig. 1, J). As in *Drescheriella* spp., nauplii accounted for most of the specimens found (1280 ind. L^{-1}).

A total of 5346 nauplii and 189 copepodids and adults of *Drescheriella* spp. and of 3960 nauplii and 275 copepodids and adults of *S. longipes* were found in all samples. The stage compositions of both the *Drescheriella* species and *S. longipes* were bimodal, with high numbers of nauplii and adults present. Copepodite stages I to V were found very seldom (15 of *Drescheriella* spp. and 10 of *S. longipes*). In *Drescheriella* spp. the mean developmental stage of the nauplii was 3.3, that of the copepodids 11.8. Adults of *D. glacialis* and *D. racovitzai* were encountered in similar numbers (89 and 85 individuals, respectively). 30 % of the 64 *D. glacialis* females and 47 % of the 85 *D. racovitzai* females found carried egg sacks. In *S. longipes* the mean developmental stage of the nauplii was 2.0, that of the copepodids 11.8. A total

of 113 *S. longipes* males and 134 females were found, 25 % of the females with attached spermatophores.

3.3. Environmental conditions in the sub-ice layer

The morphological appearance of the ice underside changed from a smooth, level surface on 29 Nov to a more structured surface with many small holes and depressions on 30 Dec (Table 2). Temperatures in the water column directly below the ice down to 6 m were always between -1.8 °C and -1.9 °C. On 29 Nov the salinity of the sub-ice water was between 34.2 and 34.4, thereafter the salinity always varied between 34.4 and 34.6. Chl *a* concentrations in the sub-ice water layer were very low (0.1 - 0.5 µg L^{-1}), except for 25 Dec when the Chl *a* concentration at 0 m depth was 2.3 µg L^{-1}. Chl *a* concentrations were always higher at 0 m than at 5 m depth below the ice. In general, Chl *a* concentrations in the sub-ice water layer increased slightly from the beginning of our study to the end at both depths.

3.4. Metazoan fauna in the sub-ice layer

A total of 23 species or higher taxa of sympagic and pelagic metazoans were found at the ice underside or in the sub-ice layer, 19 of which occurred directly below the ice at 0 m depth (Table 3). At five out of seven stations, amphipods (probably *Eusirus* spp.) were observed attached to, or crawling along, the ice underside, with abundances ranging from 0 to 70 ind. m^{-2}. Ctenophores (probably *Callianira antarctica*) occurred regularly at the ice-water interface, sometimes also attached to the ice, and single specimens of krill (*Euphausia superba*) were recorded at three stations below the ice. However, the dominant taxonomic group in the sub-ice layer were the copepods. All harpacticoids found in the sub-ice layer were sympagic species, whereas all but two, *Paralabidocera antarctica* and *Stephos longipes*, of the calanoids were truly pelagic species, as were the cyclopoids. The pelagic calanoid copepods occurred with more species (Table 3) and in higher numbers at 5 m than at 0 m depth below the ice. At both sampling depths, cyclopoid nauplii were the most abundant group (median: 700 ind. m^{-3}, range: 58 - 2387 ind. m^{-3}). Besides the ubiquitous *Oithona* spp. (median: 28 ind. m^{-3}, range: 5 - 233 ind. m^{-3}), *Oncaea* spp. (median: 3, range 0 - 6 ind. m^{-3}), calanoid nauplii (median: 7 ind. m^{-3}, range: 1 - 28 ind. m^{-3}), and five species of sympagic copepods were abundant in the sub-ice layer at both 0 m and 5 m depth. Within these five species, *Ectinosoma* sp. predominated in both depth layers with 69 % (0 m) and 66 % (5 m), followed by *Drescheriella glacialis*/*racovitzai* (14 and 16 %), *Idomene antarctica* (10 and 11 %), *Diarthrodes* cf. *lilacinus* (4 and 5 %) and *S. longipes* (4 and 3 %). Stage composition and abundance of each developmental stage of these six species in the course of the study period (4 - 30 Dec) are shown in detail in Fig. 4. All dominant sympagic copepods were

always more abundant just below the sea ice at 0 m than at 5 m depth. At the beginning of our study, abundances of all species of copepods were very low in the sub-ice layer and increased in the course of time. All harpacticoid species occurred in highest numbers on 19 Dec, whereas the calanoid *S. longipes* was most abundant on 14 Dec.

Ectinosoma sp.

Median abundances of *Ectinosoma* sp. over all developmental stages at 0 m and 5 m depth were 59 ind m^{-3} (range: 4 - 599 ind. m^{-3}) and 7 ind. m^{-3} (range: 1 - 118 ind. m^{-3}), respectively. Copepodids made up the largest fraction (89 %), and within the copepodids, the stages C I - C III comprised between 72 and 100 %. Copepodite stage V was found only during the last two sampling dates in low numbers, and adult specimens did not occur. Early nauplii (N I - N III) occurred only in very low numbers, whereas N V was the most abundant naupliar stage (Fig. 4 A).

Drescheriella glacialis/*racovitzai*

Median abundances of *Drescheriella glacialis*/*racovitzai* over all developmental stages at 0 m and 5 m depth were 21 ind. m^{-3} (range: 7 - 67 ind. m^{-3}) and 8 ind. m^{-3} (range: 2 - 11 ind. m^{-3}), respectively (Fig. 4 B). At 0 m depth the population consisted mainly of copepodids (50 %). Adults ranked second (36 %), and nauplii made up 14 %. At 5 m nauplii accounted for 46 %, copepodids for 39 % and adults for 15 %. Only 15 % of all adult *Drescheriella* specimens found were *D. glacialis*. 18 % of all *D. glacialis* and 53 % of all *D. racovitzai* adults were males. 9 % of all *D. glacialis* and 19 % of all *D. racovitzai* females carried egg sacks.

Idomene antarctica

Median abundances of *Idomene antarctica* over all developmental stages at 0 m and 5 m depth were 13 ind. m^{-3} (range: 3 - 58 ind. m^{-3}) and 3 ind. m^{-3} (range: 1 - 15 ind. m^{-3}), respectively. The *I. antarctica* population consisted mainly of adults which accounted for 46 % of the total. Males always outnumbered females accounting for 90 % of all adults. 25 % of the females carried egg sacks. Within the copepodids, the stages C III - C V predominated. Nauplii comprised < 2 % of the total, whereby only the stages N IV - N VI occurred (Fig. 4 C). High numbers of exuviae were found (3.5 and 1.5 exuviae m^{-3} at 0 m and 5 m depth, respectively).

Diarthrodes cf. *lilacinus*

Median abundances of *Diarthrodes* cf. *lilacinus* over all developmental stages at 0 m and 5 m depth were 5 ind. m^{-3} (range: 1 - 23 ind. m^{-3}) and 2 ind. m^{-3} (range: 0 - 5 ind. m^{-3}), respectively. Naupliar stages dominated the population (92 %). Adults,

which made up 7 %, were found only on the first three sampling days (Fig. 4 D). Females were more numerous than males (> 80 %), but no female with an egg sack was found. Regarding only the naupliar stages, the mean population stage was one stage older (4.9) on 30 Dec than on 9 Dec (3.7).

Stephos longipes

Median abundances of *Stephos longipes* over all developmental stages at 0 m depth and 5 m were 3 ind. m^{-3} (range: 1 - 26 ind. m^{-3}) and 1 ind. m^{-3} (range: < 1 - 5 ind. m^{-3}), respectively. On 14 and 19 Dec, highest abundances of adults were found when they clearly dominated the population (96 and 100 %, respectively). Highest abundances of nauplii II - IV were found on 30 Dec (accounting for 96% of the population).

4. Discussion

Several habitats associated with sea ice, which differ in their environmental conditions, are inhabited by sympagic metazoans in both polar regions (Schnack-Schiel, 2003). The present study and that of Schnack-Schiel et al. (in press) show that different species of life-stages dominate in different habitats of the same ice floe, probably depending on their respective requirements for, and adaptations to environmental factors such as temperature, salinity, space, and food resources. Gradients of mainly physical factors often control the distribution of sympagic metazoans (Swadling et al., 1997; Gradinger et al., 1999; Schnack-Schiel et al., 2001a; Werner and Gradinger, 2002), especially related to the strong seasonal variations in the sea ice ecosystem (Schnack-Schiel et al., 1995; Dieckmann et al., 1998; Gradinger, 2001; Schünemann and Werner, 2005; Werner, 2006). Organisms living within, or in close association with the ice have to survive the winter with reduced primary production, as well as freezing conditions and resulting ice growth. However, the reduction and destabilisation of the brine channel system during melting and the break-up of floes in spring and summer are probably a much larger challenge for sympagic species and their ice-associated life cycles (Werner, 2006). The present dataset provides new insights into the life-cycle strategies of different sympagic species and their respective niche separation.

4.1. Habitat and community in the surface layer

The surface layer habitat is a characteristic feature of Antarctic pack ice (Meguro, 1962; Garrison, 1991; Horner et al., 1992) formed by special processes and often characterised by high concentrations of algal biomass (Fritsen et al., 2001; Kattner et

al., 2004). One methodological constraint during sampling of the surface layer was the disturbance of its vertical structure, resulting in features such as larger liquid-filled spaces not being properly resolved. Therefore, the large brine volumes calculated from bulk and brine salinity represent an average value for slush and liquid-filled spaces. Despite the coarse sampling procedure, some interesting trends can be deduced from the data. In terms of temperature and salinity, the ice-brine system of the surface layer, which is as a whole a dynamic system, was seldom at equilibrium conditions (according to Cox and Weeks, 1983). That means that either freezing or melting occurred at any time during our sampling period. This is probably due to changes in air temperature and irradiance, which can directly influence the surface layer closely connected to the atmosphere (Eicken, 1992 and references therein). The shift from freezing to melting conditions observed in our study occurred parallel to increases in air temperature (Launiainen et al., 2007).

All physical and biological parameters in the surface layer vary primarily spatially with distance from the floe edge or crack. Largest surface layer thicknesses as well as highest salinities, Chl *a* concentrations and copepod abundances were found at the floe edges. This is in accordance with the assumption that seawater infiltrating from the floe edge is responsible for the establishment of this surface layer community (Meguro, 1962; Garrison and Buck, 1991). Chl *a* concentrations in the surface layer were in the same range (1 to 54 µg per litre brine) as found by Garrison and Buck (1991) in the western Weddell Sea one month earlier in the season, but further north. In the present study, an influence of infiltrating seawater on the different parameters (higher values of salinity, Chl *a* concentration and abundance of copepods) was clearly evident up to a distance of 8 m from the floe edge, similar to the results of an earlier study by Garrison and Buck (1991). New crack formation (break-up of large floes) therefore means the establishment of new surface layer habitats and the possibility for organisms to colonise them, making this sea ice habitat particularly dynamic.

Relatively high salinities in the inner part of the floe most probably resulted from brine expelled during freeze-up, and the surface layer here was then formed by thawing of ice and snow when air temperatures increased (Weeks and Ackley, 1986; Martin et al., 1995, Rankin et al., 2002). The absence of copepods in the surface layer of inner parts of the floe supports the interpretation that at these sites surface layer features developed independently of a direct exchange with seawater.

Physical and biological parameters secondly varied with the timing of crack formation in relation to the sampling date. Highest Chl *a* concentrations and copepod abundances were found at places, where the floe edge had been established at least one month before sampling. About three weeks after the floe had broken up at sampling site F, Chl *a* concentrations of up to 44.9 µg per litre brine were measured in the surface layer of this floe area. This can imply either a further enrichment of algal biomass by further infiltrating seawater with time, or production and growth in the newly formed habitat (Garrison and Buck, 1991; Kattner et al., 2004). Internal production with a specific growth rate of 0.2 doublings d^{-1} (Garrison and Buck, 1991), based on an initial concentration of 0.2 µg L^{-1} (as found in the sub-ice layer on 4 Dec), would have resulted in a Chl *a* concentration of 3.2 µg L^{-1} after 20 days.

Therefore, internal production based on infiltrating nutrients is not sufficient to explain the Chl *a* concentrations found. Studies on algal species composition and light and nutrient levels within the surface layer, as well as on inflow rates of seawater into the surface layer are needed for a better understanding of the process of surface layer development.

Diversity of sympagic metazoans in the surface layer was very low, with only three abundant and regularly occurring copepod species, *Drescheriella glacialis*, *D. racovitzai* and *Stephos longipes*. High abundances of adult males and females as well as of nauplii, but not of sub-adult copepodids, indicate that all three species probably use the surface layer as a breeding and nursery ground. The surface layer may be a suitable habitat, as brine volume, and thus space to colonise, is very large (in this study on average 54 %) compared with the ice proper (max. 20 %, Schnack-Schiel et al., in press). Algal biomass as a potential food source for the sympagic copepods (Hoshiai et al., 1987; Schnack-Schiel et al., 1995) can also be very high (up to 53.5 µg Chl *a* per litre brine). *D. glacialis* adults accounted for 51 % of all *Drescheriella* specimens in the surface layer, however, only for 15 % in the sub-ice layer. This enrichment points to an active immigration into the surface layer habitat and to a higher degree of specialization towards a life in the surface layer (Schnack-Schiel et al., 2001b) compared to *D. racovitzai*, which rather exploits the sub-ice habitat.

The absence or rare occurrence of pelagic or other sympagic copepod species in the surface layer, which were present in the sub-ice layer, implies that these species avoid entrainment into the surface layer. They might not be able to successfully inhabit the surface layer due to the variable and extreme environmental conditions and the consequent physiological constraints. Strong gradients and shifts in the temperature and salinity regimes as shown in the present study may set the limits, which only *S. longipes* and *D. glacialis* can cope with. This hypothesis is supported e.g. by the fact, that *D. glacialis* is able to survive salinities from 18 to 90 for 72 hours (Dahms et al., 1990) compared to the pelagic species *Metridia gerlachei* and *Calanus propinquus*, which only survive at a salinity of 35 but not at 45 (Gradinger and Schnack-Schiel, 1998). For *S. longipes* and *D. glacialis*, the ability to reproduce in a very dynamic but widespread and productive habitat is very likely a key to their dominance in the Weddell Sea pack-ice communities (Kurbjeweit et al., 1993; Schnack-Schiel et al., 1995; Schnack-Schiel et al., 1998). There are to date no investigations on the physiological mechanisms which allow *S. longipes* and *D. glacialis* to survive at low temperatures and changing salinities.

This is the second report mentioning the occurrence of the nudibranch *Tergipes antarctica* in the surface layer of Antarctic pack ice. It was first reported by Pelseneer (1903) from the Bellingshausen Sea. Due to its probably attached life style and its low abundances, the species was not observed in the sub-ice layer in our study. The retrieval of large volume samples was crucial for obtaining this comparatively rare species. More studies with a focus on large volumes will probably enlarge the number of known species from the sea ice ecosystem and enable work on their general biology.

All larger metazoan species found in the surface layer probably immigrate from the water column and profit from an ample food supply (algae and/or copepods) in a protected habitat. The large brine volumes (on average 54 %) allow for larger species and specimens, than normally found in the ice proper. *Eusirus antarcticus* and *Euphausia superba* exhibit mean lower lethal temperatures of -2.5 °C and -4.2 °C respectively, and they are osmoconformers in the salinity ranges from 26 to 40 (*E. antarcticus*) and 25 to 45 (*E. superba*) (Aarset and Torres, 1989). This allows them to survive in the dynamic surface layer habitat.

4.2. Habitat and community in the sub-ice layer

The sub-ice water layer is a habitat which is both influenced by processes related to the sea ice, e.g. freezing or melting, and by processes taking place in the water column, e.g. currents (Werner and Lindemann, 1997; Krembs et al., 2002). During the study period, slight melting occurred at the ice underside. This can be deduced from the changes in morphological appearance of the ice underside in the course of the time, showing clear melting structures (Poltermann, 1997; Werner and Lindemann, 1997). This melting probably resulted in a more or less continuous release of ice algae and sympagic copepods from the ice into the sub-ice water layer, a process which has also been described for the Arctic (Werner, 2006). The most significant melting event probably took place around 19 Dec. On 25 Dec, the Chl *a* concentrations at 0 m depth were tenfold higher than on 9 Dec. Abundances of sympagic harpacticoid copepods were also clearly elevated on 19 Dec. Due to their occurrence in the ice (Dahms et al., 1990; Schnack-Schiel et al., 1998; Schnack-Schiel et al., in press) the following harpacticoid copepod species can be defined as sympagic: *Drescheriella glacialis*, *D. racovitzai*, *Idomene antarctica*, *Diarthrodes* cf. *lilacinus*, *Nitocra gracilimana* and *Ectinosoma* sp*.. Hastigerella antarctica* is probably also a sympagic species, however, abundances were too low to allow a final conclusion about its life-cycle strategy. The decrease of abundances of all harpacticoid species after the 19 Dec to levels found before the melting event indicate that these species were either able to recolonise the ice, to colonise the surface layer, were preyed upon, or were distributed in a larger volume and/or area underneath the ice. Such a redistribution in a freshened layer underneath the ice and resulting incorporation into newly forming ice or the colonisation of older ice is probably the mode of dispersal for sympagic species. Besides sympagic species entering the sub-ice water layer from the ice, pelagic species also occur in this habitat (this study; Fukuchi et al., 1985; Kurbjeweit et al., 1993; for the Arctic: Werner and Martínez Arbizu, 1999). Very similar to observations below Arctic sea ice (Werner et al., 2002), abundances of truly pelagic species were generally higher at 5 m than at 0 m below the ice, whereas abundances of sympagic species were higher at 0 m than at 5 m below the ice. This distribution points to the respective origins and preferred habitats of the different species found in the sub-ice water

layer, and also to their adaptation capabilities e.g. to variations in salinity (Gradinger and Schnack-Schiel, 1998).

The ctenophore *Callianira antarctica* (Ju et al., 2004) and the Antarctic krill *Euphausia superba* are pelagic species, which have, however, strong relationships to the sea ice habitats at least during parts of their life cycles. It is well documented that *E. superba* uses the sub-ice layer as a crucial feeding ground during winter and spring (Loeb et al., 1997), but the function of the sea ice habitats for *C. antarctica* is not yet known. The regular occurrence of several species of amphipods at the underside of Antarctic pack ice is a new observation, possibly due to new sampling techniques such as under-ice video (this study) and scientific under-ice diving (Krapp et al., in press). Abundances in the present study were similar to those of autochthonous under-ice amphipod species below Arctic pack ice which are well known for their important role in cryo-pelagic coupling processes (Werner and Gradinger, 2002). Further studies on the ecology of Antarctic under-ice amphipods are thus necessary.

Stephos longipes occured in higher abundance at the underside of the ice on 14 Dec compared to other sampling days. Since abundances of this species inside the ice were generally low during the study period (Schnack-Schiel et al., in press), they were probably not released from the ice at our station, but rather transported laterally or from deeper waters. Part of the *S. longipes* population overwinters as C IV in the water column and develops into adults during spring (Schnack-Schiel et al., 1995). The specimens observed in the sub-ice water layer on 14 Dec were nearly all adults. The abundant nauplii II to IV, found on 30 Dec, could then have been offspring from these adults, or could have been released from the sea ice where reproduction of this species probably took place (see above). A study performed by Kurbjeweit et al. (1993) during Jan-Feb 1991 in the southeastern Weddell Sea found abundances of *S. longipes* in the sub-ice layer of up to 1100 ind. m^{-3} dominated by early copepodite stages (MDS = 8.0). Therefore, during our study reproduction of *S. longipes* in the sub-ice and sea ice habitats had probably just begun, and higher abundances in the sub-ice layer could be expected during the forthcoming summer.

In *Drescheriella* spp., all developmental stages except the naupliar stage I were found. This indicates a year-round reproduction of both *Drescheriella* species within or directly below the ice as stated by Dahms et al. (1990) for *D. glacialis*. The higher percentage (85 %) of *D. racovitzai* found underneath the ice as compared to *D. glacialis* points to a higher specialization of this species towards a life in the sub-ice water layer. The neutral buoyancy of diapausing copepodids IV and V of this species, as observed by Dahms et al. (1990), supports this interpretation.

The present study and the work by Schnack-Schiel et al. (in press) are the first published observations, which deal in further detail with the sympagic occurrence, distribution and stage composition of *Ectinosoma* sp., *Idomene antarctica* and *Diarthrodes* cf. *lilacinus*. The presence of naupliar stages of all three species implies that they reproduce in the ice proper and/or in the sub-ice layer. The generally higher abundances at 0 m depth than at 5 m depth lead to the conclusion that these species are probably truly sympagic.

The high percentage of *Ectinosoma* sp. found at 0 m depth below the ice (50 % of all copepods) in contrast to low percentages of 6 % within the ice proper (Schnack-Schiel et al., in press) and 0 % in the surface layer (this study) leads to the conclusion, that this species is mainly exploiting the ice-water interface and moves relatively freely within this confined layer. Adults and copepodite stage V of *Ectinosoma* sp. as well as naupliar stages I and II were virtually missing from the sub-ice water layer throughout the whole study. This points to an overwintering of *Ectinosoma* sp. within the ice as eggs or naupliar stages or an early reproduction of overwintering adults, which subsequently died and were not found in our samples.

Naupliar stages I to III of *Idomene antarctica* were not found during most of the sampling period, but all other stages were present. Two different strategies seem to fit to this stage distribution, either overwintering as nauplii or eggs within the ice or overwintering of adults and an early reproduction. The presence of adult females throughout the whole sampling period favours the second interpretation. The relatively high amount of exuviae found in this species also indicates active development in the sympagic habitat.

Stage distribution of *Diarthrodes* cf. *lilacinus* was bimodal at the beginning of our study with adult females and naupliar stages III to V being present. No adults were found after 19 Dec. This may indicate that *Diarthrodes* cf. *lilacinus* overwinters as adults and starts reproduction early. Further development of the nauplii within the sub-ice or the bottom-ice layer is obvious, as the mean developmental stage of nauplii increased by one stage during the study period.

4.3. Outlook for further research

The present study has shown that both, the surface layer and the sub-ice layer are important habitats for sympagic organisms in Antarctic pack ice, harbouring a special community and playing a crucial role for the life cycles of several dominant sympagic copepods. In order to further understand processes, which take place during the development of a surface layer, we propose a field experiment with an artificially produced crack in a floe with a negative freeboard which is not flooded, and subsequent sampling of the forming surface layer habitat and community at different times and distances from the crack. Such an investigation would be fundamental for the understanding of succession in the surface layer. Life cycle strategies of three dominant Antarctic sympagic copepods (*Drescheriella glacialis, Stephos longipes* and *Paralabidocera antarctica*) are comparatively well investigated in level sea ice with thicknesses of up to 3 m (Kurbjeweit et al., 1993; Schnack-Schiel et al., 1995; Schnack-Schiel et al., 1998; Swadling, 2001). However, there is a large gap of knowledge about the ecological role of pressure ridges, which can account for up to 50 % of the sea ice volume in the Antarctic (Tin and Jeffries, 2003), and thus be important for the distribution and life cycles of sympagic organisms. Furthermore, studies on the distribution of rare sympagic species within the sea ice system are needed. An inspection of already existing sample sets with a taxonomical focus on

harpacticoids would help to a better understanding of their role in the sympagic food web of the Southern Ocean.

Another open question is how sympagic meiofauna species are adapted to low temperatures and variable salinities. Physiological and molecular biological studies are needed to answer this.

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Tables

Table 1. Dates of, and environmental conditions at the different sampling sites for surface layer fauna. For positions of sampling sites A - K and of cracks on the drift-ice station see Fig. 1; sampling site J was used for a transect. B.a. = before arrival of RV "Polarstern" at the drift-ice station, / = no data, sd = standard deviation.

Sampling site	Date of sampling	Date of crack formation	Distance to floe edge (m)	Brine salinity	Bulk salinity	Temperature (°C)	Surface layer thickness (cm)	Super imposed ice (cm)	Snow thickness (cm)	Bulk Chl *a* (µg L^{-1})	Brine volume (%)
A	19 Dec 04	b.a.	1	30.1	18.3	-2	10	0	30	29.1	54
A	19 Dec 04	b.a.	4	29.1	19.6	-2	10	0	50	22.1	60
B	19 Dec 04	2 Dec 04	1	28.9	14.7	-2	50	0	30	13.6	46
B	19 Dec 04	2 Dec 04	5	29.9	19.6	-2	12	0	30	1.8	59
C	19 Dec 04	2 Dec 04	1	26.2	14.8	-1.6	5	0	10	12.2	51
C	19 Dec 04	2 Dec 04	5	25.8	16.5	-1.6	8	0	10	6.7	57
D	19 Dec 04	/	30	/	15.9	/	/	/	/	3.1	/
E	19 Dec 04	/	30	26.7	21.5	-1.8	15	0	8	0.7	72
B	25 Dec 04	2 Dec 04	1	30.5	15.3	-1.1	40	6	22	14.5	45
B	25 Dec 04	2 Dec 04	5	27.2	11.7	-1.2	25	5	25	10.8	39
F	25 Dec 04	2 Dec 04	1	29.3	23.7	-1.6	12	7	12	32.6	72
D	25 Dec 04	18 Dec 04	2	24.3	10.3	-1.1	16	10	9	2.2	38
D	25 Dec 04	/	30	23.9	14.5	-1.3	15	4	11	1.8	55
G	25 Dec 04	/	30	21.9	14	-1.2	5	4	16	1.0	58
H	25 Dec 04	/	30	19.5	13.3	-1.1	3	4	12	1.0	62
I	25 Dec 04	/	30	24.4	22.6	-1	liquid	/	/	1.6	83
J	30 Dec 04	2 Dec 04	1	31	20.2	-1.7	33	20	21	23.9	58
J	30 Dec 04	2 Dec 04	7	21.9	13.2	-1.3	12	11	33	2.0	54
K	30 Dec 04	2 Dec 04	1	27.2	10.7	-1.3	8	22	17	1.4	35
D	30 Dec 04	18 Dec 04	2	26.8	14.8	-1.2	23	8	9	4.5	50
D	30 Dec 04	/	30	26.2	12.9	-1.3	26	1	11	0.8	44
G	30 Dec 04	/	30	20.8	12.6	-1.1	17	10	8	1.0	55
H	30 Dec 04	/	30	19.4	8.4	-1.1	/	/	/	2.4	39
I	30 Dec 04	/	30	23	15.8	-1.2	20	1	5	7.6	62
J	1 Jan 05	2 Dec 04	1	26.6	15.1	-1.1	21	29	18	15.2	51
J	1 Jan 05	2 Dec 04	2	27.2	18.6	-1.2	21	37	2	9.4	61
J	1 Jan 05	2 Dec 04	3	27.7	17.6	-1.6	29	10	31	6.1	57
J	1 Jan 05	2 Dec 04	4	24.9	14.2	-1.2	15	5	28	10.1	51
J	1 Jan 05	2 Dec 04	5	24	21.5	-1.3	15	24	19	1.8	81
J	1 Jan 05	2 Dec 04	6	23.6	13.8	-1.2	12	22	23	2.4	53
J	1 Jan 05	2 Dec 04	7	20.9	11.2	-1.1	9	34	14	1.7	48
J	1 Jan 05	2 Dec 04	8	/	15.5	-1.2	7	14	32	1.1	/
J	1 Jan 05	2 Dec 04	15	20.3	10.9	-1	3	4	43	4.6	48
J	1 Jan 05	2 Dec 04	30	21.1	9.9	-0.9	4	23	25	4.4	42
mean:				25.3	15.4	-1.4	16.2	10.2	19.8	7.5	54.4
sd:				3.4	3.8	0.3	11.0	10.8	11.4	8.5	11.5

Table 2. Dates of, and environmental conditions at the different sampling sites for sub-ice layer fauna. For positions of sampling sites C and D on the drift-ice station see Fig. 1. nd = no data.

	29 Nov	4 Dec	9 Dec	14 Dec	19 Dec	26 Dec	30 Dec
Sampling site	near D	D	D	C	D	D	D
Snow thickness (cm)	35	37.3	33.3	49.6	10.6	25	35
Ice thickness (cm)	78	83	78	203	90	81	78
Freeboard (cm)	-6	-14	-14	3	4	6	nd
Bulges and depressions at the ice underside	None	Very few	Very few	Few	Many	nd	Very many

Table 3. Metazoan species found in the surface and sub-ice layers of the drift ice station. - = absent, + = present (single specimens), ++ = abundant (mostly > 1 ind. m^{-3}), +* = observed at the ice-water interface by under-ice video, but not collected by under-ice pump. * = species not quantitatively separated.

Species/Taxa	Surface layer	Sub-ice layer	
		0 m	5 m
CTENOPHORA			
Callianira antarctica (Chun 1897)	+	+*	–
PLATHELMINTHES			
Turbellaria indet	+	–	–
GASTROPODA, OPISTHOBRANCHIA			
Tergipes antarctica Pelsener 1903	+	–	–
CRUSTACEA, COPEPODA			
HARPACTICOIDA			
Diarthrodes cf. *lilacinus* Pallares 1977	–	++	++
*Drescheriella glacialis** Dahms & Dieckmann 1987	++	++	++
*Drescheriella racovitzai** Giesbrecht 1902	++	++	++
Ectinosoma sp. Giesbrecht 1902	–	++	++
Idomene antarctica Giesbrecht 1902	+	++	++
Hastigerella antarctica Dahms & Schminke 1992	–	+	+
Nitocra gracilimana Giesbrecht 1902	+	+	+
Nauplii indet	-	++	++
CALANOIDA			
Calanoides acutus (Giesbrecht 1902)	–	+	++
Calanus propinquus Brady 1883	–	+	++
Ctenocalanus citer Bowman & Heron 1971	–	–	+
Metridia gerlachei Giesbrecht 1902	–	–	+
Paraeuchaeta sp.	–	–	+
Paralabidocera antarctica (IC Thompson 1898)	+	–	+
Stephos longipes (Giesbrecht 1902)	++	++	++
Nauplii indet.	–	++	++
CYCLOPOIDA			
Oithona spp.	–	++	++
Oncaea spp.	–	++	++
Nauplii indet.	-	++	++
CRUSTACEA, AMPHIPODA			
*Eusirus antarcticus** Thomson 1880	+	+*	–
*Eusirus tridentatus** Lowry & Bullock 1976	+	+*	–
CRUSTACEA, EUPHAUSIACEA			
Euphausia superba Dana 1850	+	+*	–

Figures

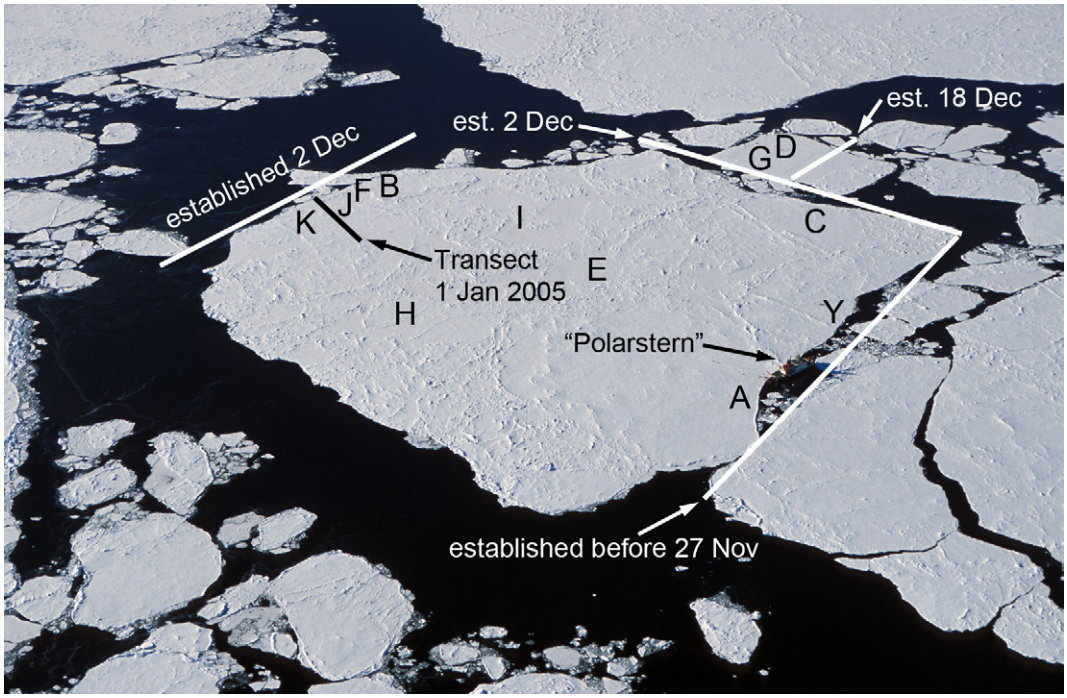

Fig. 1. Drifting sea ice station in the western Weddell Sea during the ISPOL expedition. A - K denote sites for surface layer sampling; at site J a transect was sampled from the edge to the inner part of the floe, at site Y only qualitative samples were taken, and at sites C and G the under-ice habitat and fauna were sampled; white lines show locations (and dates of establishment) of cracks. Photo: Ingo Arndt.

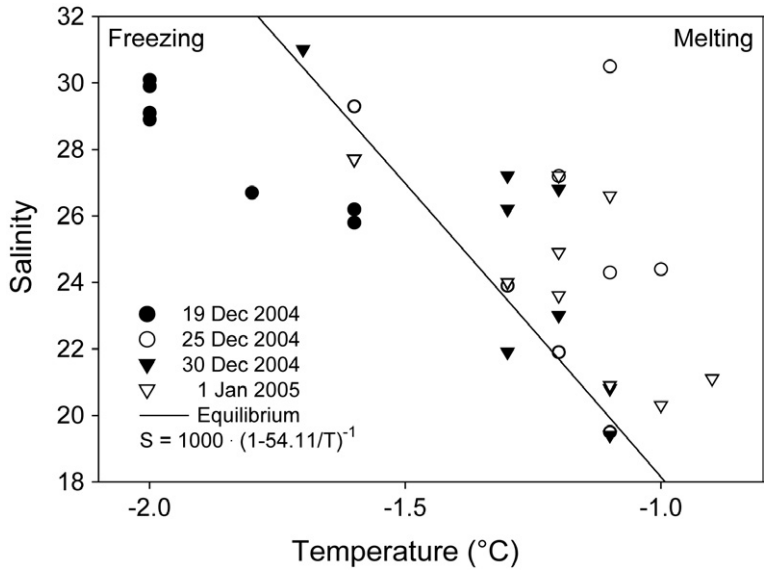

Fig. 2. Temperature and salinity in the surface layer of the drifting ice station from different sampling sites and on different sampling dates. The straight line depicts equilibrium conditions in sea ice calculated according to Cox and Weeks (1983).

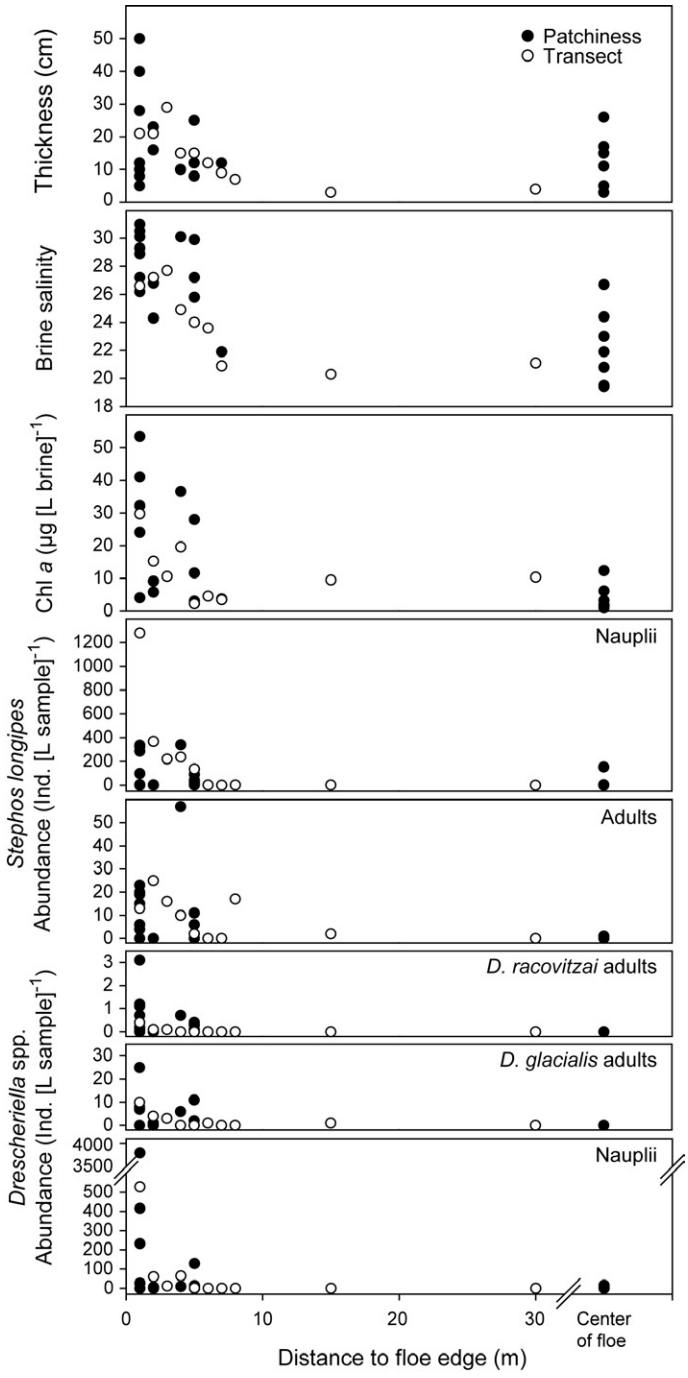

Fig. 3. Environmental parameters, algal biomass, and dominant copepod abundances in the surface layer in relation to the distance to the floe edge. Data from different sampling sites of the drifting ice station (A - K in Fig. 1, dark circles) and different sampling dates (Table 1), as well as from the transect sampled on 1 Jan (J in Fig. 1, Table 1, open circles). Data from sampling sites more than 35 m away from the floe edge are presented together at the right side of the graph, denoted by “center of floe”. Please note the high variability in salinity in the surface layer of the center part of the floe, but the comparatively low Chl *a* concentrations and low meiofauna abundances there.

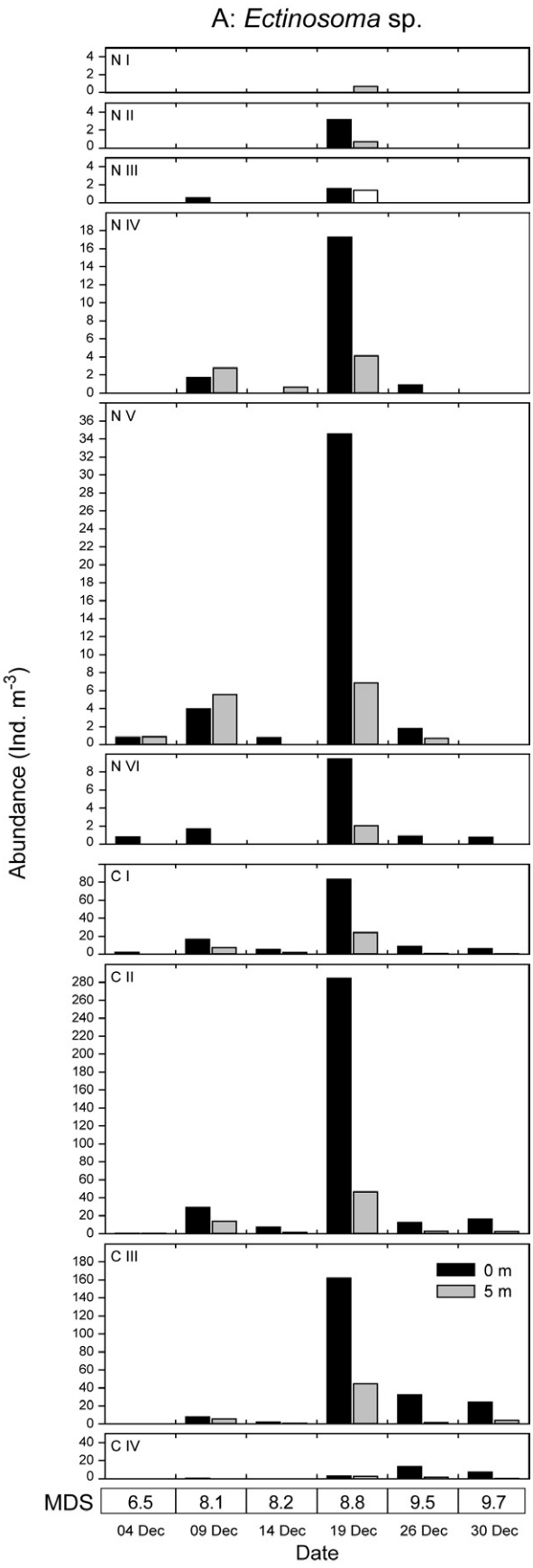

Fig. 4 A. For description see below.

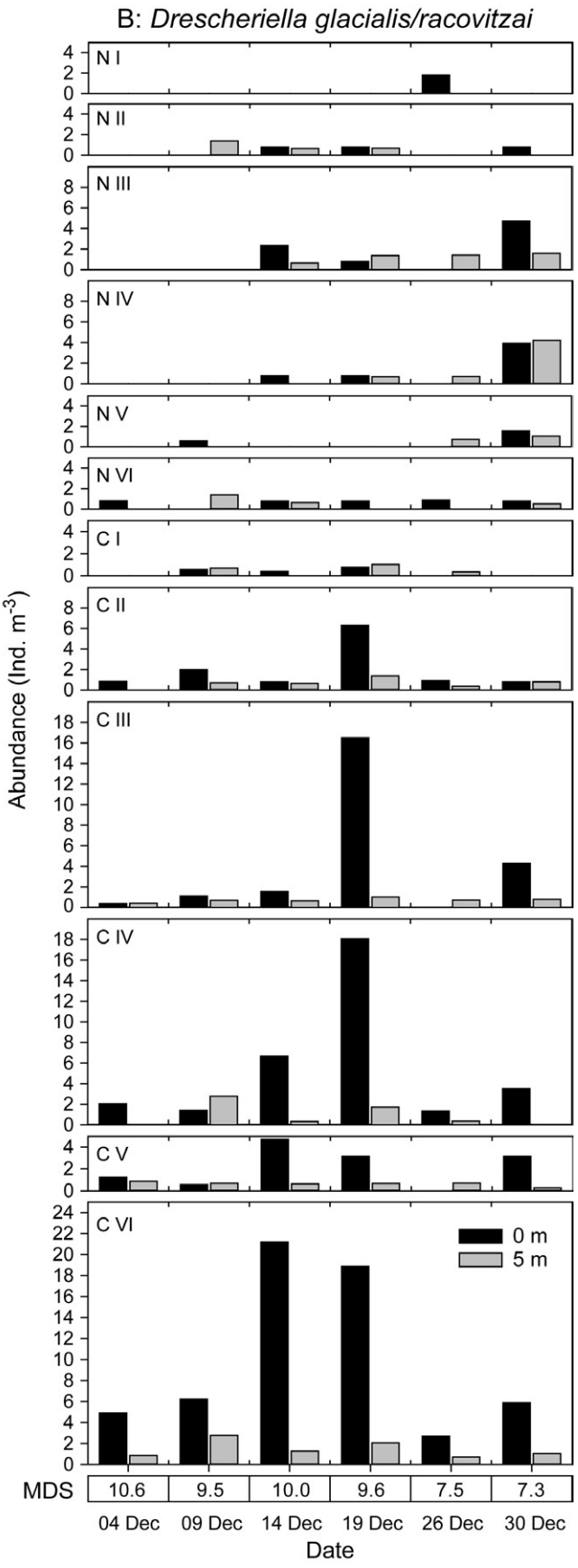

Fig. 4 B. For description see below.

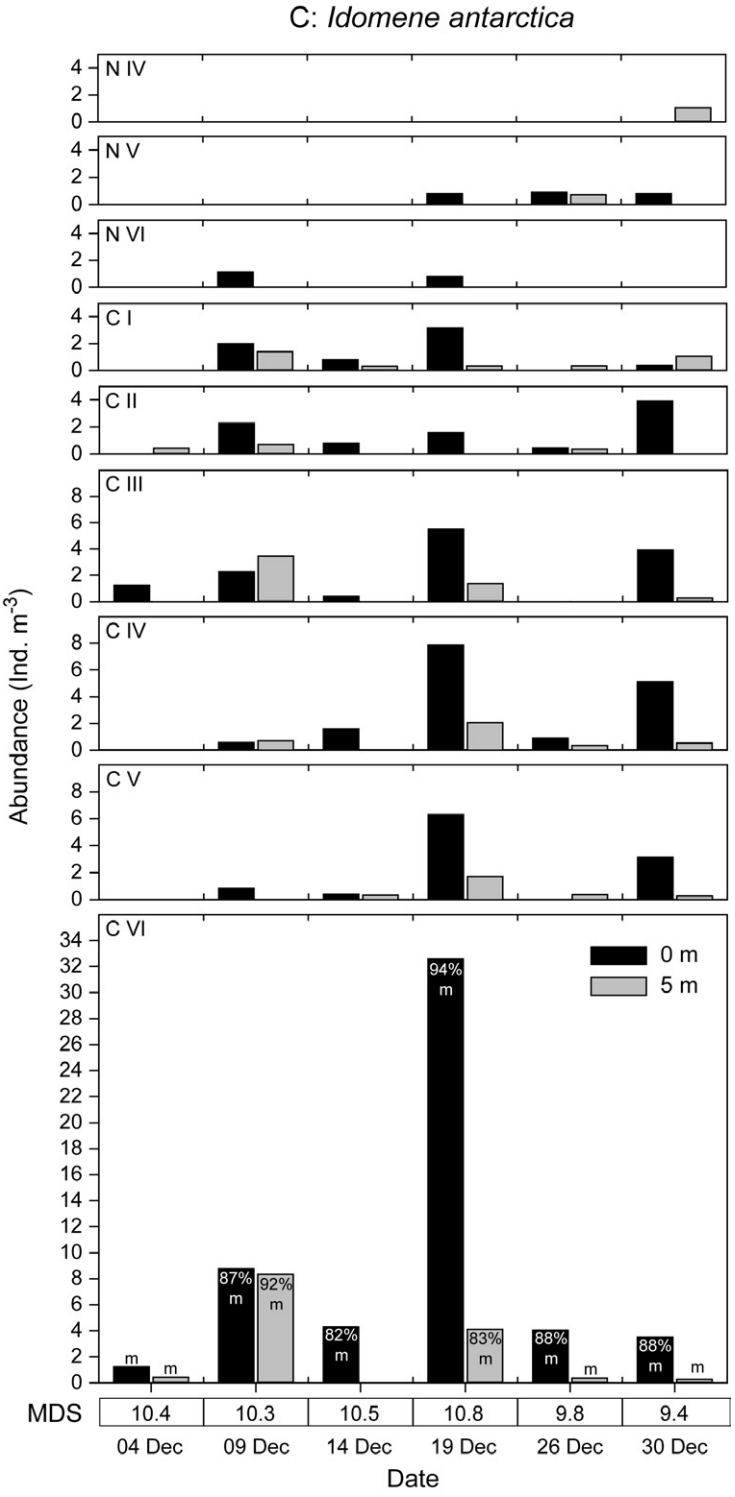

Fig. 4 C. For description see below.

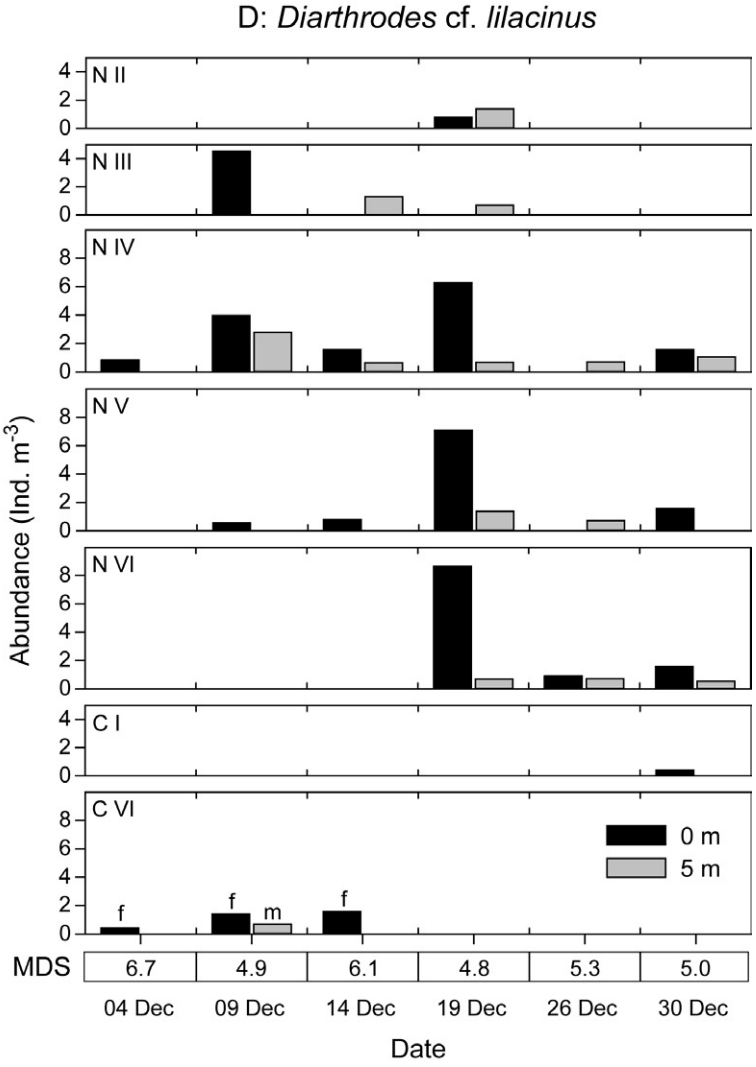

Fig. 4 D. For description see below.

Fig. 4. Stage composition and abundances of dominant copepod species at 0 m and 5 m depth under the ice over the study period. N I - N VI = naupliar stages I - IV, C I - C V = copepodite stages I - V, C VI = adults, m = males, f = females, account without percental number = 100 % of the respective sex, MDS = mean developmental stage calculated according to Marin (1987). A: *Ectinosoma* sp., B: *Drescheriella glacialis*/*racovitzai*, C: *Idomene antarctica*, D: *Diarthrodes* cf. *lilacinus*, E: *Stephos longipes*. Please note the different scale of naupliar and copepodid abundance in A: *Ectinosoma* sp..

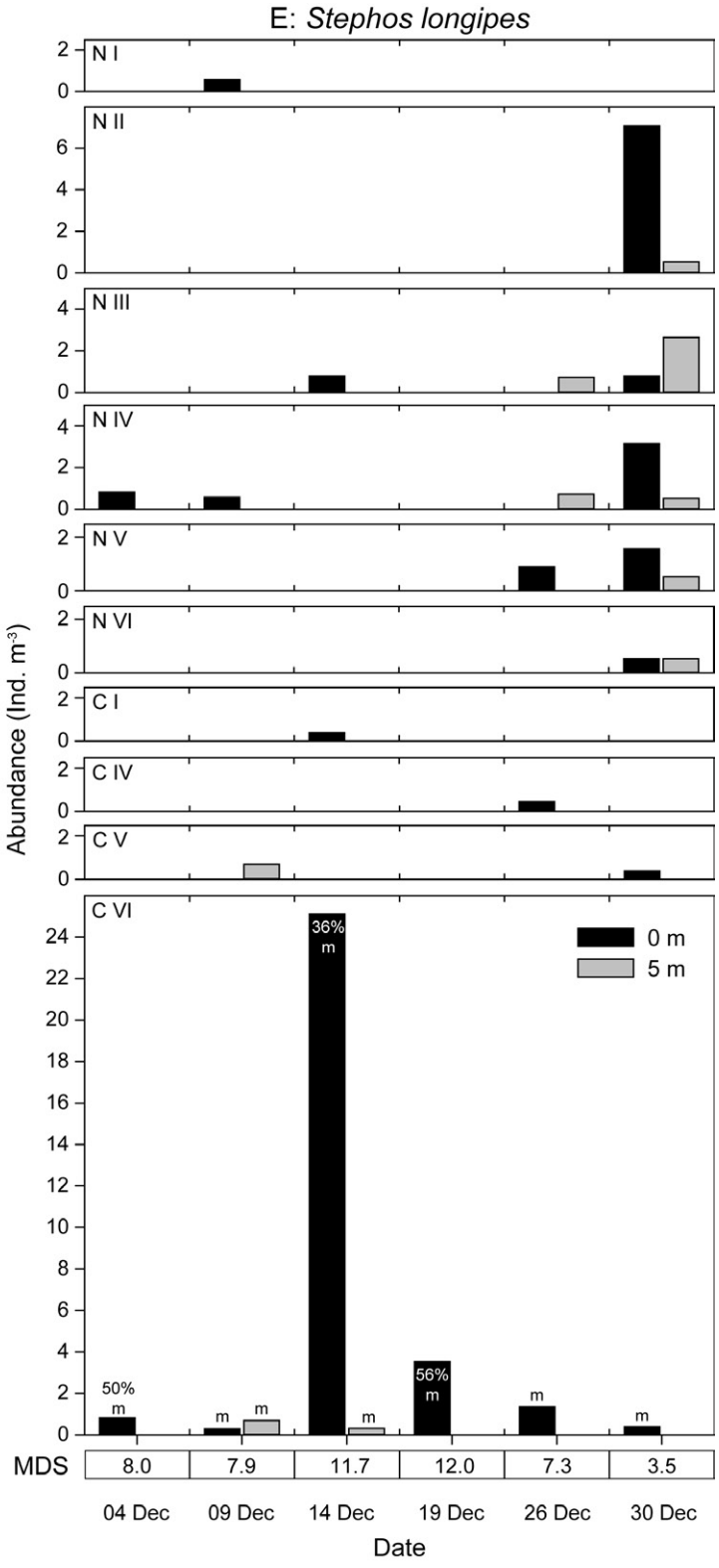

Fig. 4 E. For description see above.

Manuscript III

Copepods in sea ice of the western Weddell Sea during austral spring 2004

Abstract

In the framework of the RV “Polarstern” expedition “Ice station POLarstern” (ISPOL) spatial and temporal trends in composition, abundance and age structure of sea ice inhabiting copepods were investigated in the western Weddell Sea during the transition from the spring to the summer state. For the spatial scale, sea ice coring was performed at six locations on a transect from the ice edge to the ice drift station between 14 and 24 November 2004. The temporal changes were investigated in a time series study on a drifting sea ice floe from 29 November to 30 December 2004. A relatively large number of copepod species (15) was found in the ice with a higher number at the time station (13) than at the transect (9). *Drescheriella* spp. was by far the most abundant taxon encountered in the sea ice throughout the present study (72 - 87 %). On the transect, *Idomene antarctica* ranked second in abundance (7 %) followed by *Stephos longipes* (2 %) and *Ectinosoma* sp. (2 %). In contrast, *Diarthrode* cf. *lilacinus*, which was not found on the transect, was the second most abundant species (11 %) at the time station, followed by *I. antarctica* (9 %), *Ectinosoma* sp. (6 %) and *S. longipes* (1 %). Naupliar stages dominated the populations of *Drescheriella* spp. and *S. longipes* both on the transect and during the time series. The *Ectinosoma* sp. population was dominated by nauplii only at the stations of the transect, while copepodite stages made up the largest fraction during the time series. Copepodids always predominated the *I. antarctica* populations, and it was the only species in which adults occurred in high densities contributing significantly to the abundance. Only *Drescheriella* spp. and *Stephos longipes* occurred throughout the sea ice cores, while the occurrence of all other species was restricted to the bottom layer of the ice. The distribution of all species was very patchy and varied greatly between the sampling sites.

Keywords: Sympagic copepods; Sea ice; Spatial distribution; Temporal development; ISPOL; Southern Ocean; Western Weddell Sea

1. Introduction

Sea ice harbours a great variety of organisms and acts as a refuge, breeding and feeding ground (Lizotte, 2003), the latter due to the high standing stocks of bacteria and microalgae. Copepods are dominant members of the Antarctic sea ice assemblages, and the three most abundant species are the harpacticoid *Drecheriella glacialis* and the calanoids *Stephos longipes* and *Paralabidocera antarctica* (Schnack-Schiel, 2003). The three species differ markedly in their geographical distribution as well as in their life cycle strategies: *D. glacialis* is a dominant sympagic species in most geographical regions studied, and probably has a circum-Antarctic distribution (Dahms et al., 1990; Schnack-Schiel 1998, 2001b; Swadling et al. 2000). This species seems to spend most of its life in the sea ice (Dahms and Dieckmann, 1987; Dahms et al., 1990). *Stephos longipes* also has a circum-Antarctic distribution but with greater abundances in the Antlantic and Pacific sectors than in the Indian sector in the East (Schnack-Schiel et al. 1995, 1998; Swadling et al. 2000). Its life cycle seems to be strongly coupled to the annual growth and melt cycle of the sea ice. High abundances of *S. longipes* occur in sea ice during autumn, winter and spring but are low during the summer when this species is most abundant in the surface waters (Schnack-Schiel et al., 1995). However, in rotten summer ice containing many gaps and voids, *S. longipes* remains in the ice even during summer (Schnack-Schiel et al., 1998, 2001b; Thomas et al., 1998). *Paralabidocera antarctica* is found mostly in the Indian Ocean where it occurs in the sea ice for most of the year except in summer when it concentrates just beneath the ice (e.g. Tanimura et al., 1996). In addition to these three dominant species, several other copepods, mainly harpacticoid species, have been described from Antarctic sea ice although they have never been recorded in high numbers (Gruzov et al., 1967; Hoshiai and Tanimura, 1986; Dahms et al., 1990; Dahms and Schminke, 1992; Günther et al., 1999; Guglielmo et al., 2007).

Most of the studies on sea ice copepods in the Weddell Sea have been snapshots, and data covering longer periods of investigations are rare. From mid-November to the end of December 2004 studies on sea ice were carried out during the expedition ANT XXII/2 of RV “Polarstern” to the western Weddell Sea. The aim of this study was to investigate the temporal pattern of abundance, distribution and population structure of sea ice copepods inside a drifting pack ice floe over a period of 30 days. In addition, in order to deepen our knowledge on large-scale spatial variation of copepod distribution in ice, ice sampling was carried out on different ice floes on a transect from the open water through the ice to the drift station.

2. Methods

A detailed description of the expedition ANT XXII/2 is given by Dieckmann et al. (2007). For the investigation of large-scale spatial variation, sea ice coring was performed at six locations on a transect from the ice edge at 58° S, 15° W, to the ice

drift station at 68° S, 55° W between 14 and 24 November (Fig. 1). On each ice floe sampled, one to three sea ice cores were taken, each 0.5 m apart.

The temporal changes of the sea ice habitat regarding physical and biological properties were investigated in a five-week time series study on an ice floe at 68° S, 15° W (Fig. 1). For this purpose, an undisturbed site of thin, level first-year ice of 12 m by 12 m was sampled every 5 to 6 days in a fixed sampling design between 29 November and 30 December. All ice cores taken on the same sampling day were cored within an area of 2 m by 2 m to minimise spatial heterogeneity.

During both the transect and the drift station all ice cores were drilled with a 10 cm diameter ice auger, cut immediately into 1 - 10 cm segments and transported to the ship's laboratory. After addition of 0.2 µm pre-filtered seawater to avoid osmotic stress the ice was melted at 4 °C in the dark. After complete melting, the ice meiofauna was concentrated over a 20 µm gauze, and the copepods were collected and preserved in borax-buffered 1 - 2 % formaldehyde/seawater solution.

Ice temperature was measured immediately after drilling using a Testotherm 720 thermometer inside small holes, drilled into the core at 10 cm (transect) or 5 cm intervals (time series). After melting, bulk salinity was measured with a WTW 190 conductometer. Based on ice temperature and bulk salinity, brine salinity was calculated as a function of ice temperature, and brine volume was calculated as a function of bulk salinity and ice temperature. For the determination of the chlorophyll *a* (Chl *a*) and phaeopigment concentrations the melted ice samples were filtered onto Whatman GF/F filters, extracted in 90% acetone, homogenised and analysed fluorometrically with a Turner Designs 10-AU digital fluorometer.

Ice texture classes were classified according to Eicken and Lange (1989). For a detailed description of the sea ice core texture see Haas et al. (2007).

Copepods were removed from the entire sample, identified to species, developmental stage and sex and enumerated. The identification of the specimens was carried out according to Giesbrecht (1902), Lang (1934, 1948), Dahms (1987), Dahms and Dieckmann (1987), Dahms and Schminke (1992) and Costanzo et al. (2002). Exuviae were sorted separately, and numbers were not included in the calculation of the abundance. The mean population stage, including nauplii, copepodids and adults, was calculated after Marin (1987).

3. Results

A total of 15 copepod species was found in the ice cores: three calanoids, four cyclopoids and eight harpacticoids (Table 1). Unidentified calanoid and harpacticoid nauplii were also present. However, only *Drescheriella* spp., *Idomene antarctica, Ectinosoma* sp., *Stephos longipes* as well as the unidentified harpacticoid nauplii (which belong to one species) were abundant. The number of taxa encountered was higher during the time series (13) compared to the transect (9). Interestingly,

Diarthrode cf. *lilacinus* which occurred in high numbers in the ice cores of the time series, were not encountered within the ice at the transect locations.

3.1. Transect

3.1.1. Environmental parameters

The thickness of the floes was highly variable, ranging between 29 and 240 cm. This was due to a mixture of first-and second year ice in the outflowing branch of the Weddell Gyre (Haas et al., 2007). Ice cores consisted of 24 % orbicular granular, 25 % mixed and 48 % columnar ice, quite typical for this region of the Weddell Sea. Snow cover varied greatly between the different ice floes ranging from 4 to 61 cm. Bulk salinity of the sea ice cores ranged from 1.2 to 10.5, and temperature ranged from -1.9 to -4.1 °C. Mean salinities decreased towards the southwest, indicating an increasing amount of second year ice along the transect (Fig. 2, Haas et al., 2007). The calculated brine salinity was between 34 and 41, but reached values up to 70 in the upper parts of ice cores of > 2 m in length.

Chl *a* concentrations varied greatly among transect stations, with values ranging between 0.3 and 382.3 µg L^{-1} (median: 2.9 µg L^{-1}). While vertical distribution patterns of Chl *a* differed considerably between stations, Chl *a* concentrations generally increased towards the bottom of the ice. However, minor peaks of the Chl *a* concentration were found at the top and within the interior of the ice. Chl *a* concentrations within the upper and middle parts of the ice were mostly below 20 µg L^{-1}, and maximum concentrations were recorded in the bottom layer of ice cores taken on 22 November. Depth-integrated Chl *a* concentrations calculated for entire cores taken along the transect ranged between 0.2 and 50.3 mg Chl *a* m^{-2} (median: 9.6 mg Chl *a* m^{-2}), and pronounced variation was recorded between the various stations as well as between cores of the same station.

3.1.2. Species composition and abundance

Drescheriella spp. (two of which were identified as *D. racovitzai* and *D. glacialis*) dominated overwhelmingly and contributed numerically an average of 88 % of all sea ice copepods. These were followed by *Idomene antarctica* (7 %), *Stephos longipes* (2 %) and *Ectinosoma* sp. (2 %). Unidentified harpacticoid nauplii also occurred in relatively high numbers. All other species were found only rarely (Table 2). A considerable number of exuviae were found, especially at the location PT-1, where they accounted for about 30 % of the total, mainly due to high numbers of *Drescheriella* spp. exuviae. At all other locations of the transect, exuviae contributed between 1 and 8 % of the total (Table 3).

The number of indivduals varied greatly between sampling sites and even between replicate cores from the same sampling site. The abundance was highest at location

PT-2 varying between 485 and 1087 ind. L^{-1}. PT-5 had the lowest abundance with 1 - 5 ind. L^{-1} (Fig. 2 a). PT-2 was also characterised by a high number of taxa found (4 - 8), whereas PT-5 by the lowest (2). *Drescheriella* spp. was the most numerous copepod at all locations except at PT-6 where *I. antarctica* contributed the largest fraction (59 %, Fig. 2 b).

3.1.3. Population structure

Nauplii predominated the populations of *Drescheriella* spp., *Ectinosoma* sp. and *S. longipes* with on average 68 %, 74 % and 91 %, respectively. In *I. antarctica*, copepodids outnumbered nauplii and adults and accounted for 69 % of the total. Adults contributed 6 %, 7 % and 9 % of the total population in *I. antarctica, S. longipes* and *Drescheriella* spp., respectively. In *Harpacticus furcifer,* only females were encountered (Table 2).

The age structure of the abundant species differed greatly between the locations without clear trends (Fig. 3). N I and N II constituted the greatest proportion of the *Drescheriella* spp. population at PT-2 and PT-3. At all other locations copepodite stages and adults accounted for more than 50 % of the total. Only 4 % of all *Drescheriella* adults were *D. racovitzai*. In both *Descheriella* species males outnumbered females, and the female/male ratios were 0.5 (*D. glacialis*) and 0.3 (*D. racovitzai*). 36 % of all female *D. glacialis* and 50 % of female *D. racovitzai* carried egg sacs. 4 % of *D. glacialis* had attached spermatophores. The mean population stage [S] varied between 4.1 (PT-2) and 9.2 (PT-4).

Early copepodite stages dominated the *I. antarctica* population at the locations PT-1 to PT-4, whereas late naupliar stages were dominant at PT-5 and PT-6. Adults occurred only at PT-1 and PT-2 in low numbers accounting for 5 and 9 %, respectively. 60 % of the females carried egg sacks. N VI and C I were the most abundant developmental stages of *Ectinosoma* sp., and C III - C V and adults were absent. Nauplii dominated the *Stephos longipes* population at most stations and accounted on average for 91 % of the total. Within the nauplii, the early stages N I and N II were most abundant contributing 18 % and 65 % of all nauplii, respectively. Adults ranked second with a contribution of 7 %. Males were more numerous, and the female/male ratio was 0.5. Within the copepodids, only C IV and C V were found, and only in low numbers (Fig. 3).

3.1.4. Exuviae

Exuviae occurred in higher numbers only at the first three locations sampled (PT-1 to PT-3). At the two last locations of the transect, where the total copepod abundances were lowest, only exuviae of *Harpacticus furcifer* were found within the ice cores (Table 3).

In *Drescheriella* spp. mainly exuviae of late copepodite stages were found (C III - C V: 61 %) while the alive preserved individuals of this species were dominated by early naupliar stages (N I - N II: 40 %, Fig. 4).

3.1.5. Vertical distribution

In all cores, except PT-3, *Drescheriella* spp. and *Stephos longipes* occurred throughout the sea ice with a maximum in the upper and middle part of the ice. The occurrence of *Idomene antarctica* and *Ectinosoma* sp. was mainly restricted to the bottom layer of the ice. One exception occurred in core 2 at PT-2 where both species were found throughout the ice except in the upper 10 cm (Fig. 5). However, most individuals occurred in the lowest part of the ice. The temperature did not change significantly within the ice core at PT-2, varying only between -2.0 and -2.1°C. The bulk salinities at PT-2 were highest in the upper 30 to 50 cm attributable to secondary flooding of seawater. Chl *a* concentrations did not have a clear vertical trend in core 1 and 2 ranging from 10 to 43 µg L^{-1}. Core 3 had a minimum with 5 µg L^{-1} at 40 to 50 cm and a distinct peak with 75 µg L^{-1} at 60 to 70 cm. Peak abundance of the copepods did not coincide with highest algal biomass, which is also true for all other stations.

The nauplii of *Drescheriella* spp. had a maximum abundance in all three cores of PT-2 in the upper 10 to 40 cm. Adults occurred in highest numbers between 10 and 30 cm, whereas copepodids were most numerous in the middle part of the ice cores (Fig. 5). Most of the adult *Drescheriella* spp. were *D. glacialis*, and only 1 % were *D. racovitzai*.

3.2. Time series

3.2.1. Environmental parameters

The thickness of the ice cores ranged between 67 and 94 cm, and was representative of first year ice. On each day the ice thickness variation was generally ≤ 8 cm. The ice was made up of orbicular granular ice in the upper part of the ice cores which varied between 5 and 40 cm in thickness. The lower part was columnar ice. On 19 December, a small layer between 14 and 16 cm was a mixture of these two ice types. The snow cover varied between 6 and 30 cm. For a detailed description of the sea ice structure see Haas et al. (2007).

Ice core temperatures ranged between -2 and -2.5 °C in the first half of December, and afterwards the temperatures increased in the upper part of the cores up to -1.1 °C. In contrast, in the lowermost part, temperature remained rather constant during the study varying between -2.2 and -1.9 °C. The bulk salinities ranged between 3.3 and 11.6. Salinity gradually increased towards the bottom of the cores and reached maximum values at the lowermost section. The calculated brine salinity

was between 36 and 45 at the beginning of the study and decreased towards the end to values from 20 to 34. The calculated brine volume ranged between 10 and 20 % with a few exceptions with values up to 40 %, mainly in the bottom parts of the ice cores.

Chl *a* concentrations were one order of magnitude higher in the bottom layer than in all other parts of the ice cores, and the mean bottom values ranged from 34.6 to 38.8 µg L^{-1} with a maximum of 262 µg L^{-1} on 14 December.

3.2.2. Species composition and abundance

Harpacticoid copepods were by far the most abundant taxon (on average 98 %, Table 4): the two *Drescheriella* species, *D. glacialis* and *D. racovitzai*, dominated and contributed 72 % of all sea ice copepods. *Diarthrode* cf. *lilacinus* ranked second with 11 %, followed by *Idomene antarctica* (9 %) and *Ectinosoma* sp. (6 %). *Stephos longipes* was the most numerous calanoid species and accounted for 1 % of all. All other species occurred only sporadically in very small numbers. Exuviae occurred only rarely in the ice cores contributing < 1 % on all sampling dates. Interestingly, all *Metridia gerlachei* females found in the ice cores were dead.

There was considerable variation in abundance of copepods in all cores of the time series ranging from 40 to 236 ind. $L^{-1.}$ The occurence pattern was bimodal with highest values at the beginning and at the end of the study (Fig. 6 a). Due to the high abundance of *Drescheriella* spp., their distribution pattern reflected that of the total copepods (Fig. 6 b). The abundance of *D.* cf*. lilacinus, I. antarctica* and *Ectinosoma* sp*.* was highest in the first week of December and decreased towards late December (Fig. 6 c - e). The unknown harpacticoid nauplii were found in higher numbers only on the first two sampling dates (Fig. 6 f), and the calanoid *S. longipes* occurred in higher numbers only in one ice core in late December (Fig. 6 g). The difference in abundance between the two ice cores drilled on the same sampling day varied during the study, however, the course of abundance was similar in both cores except for *Drescherilla* spp. on the first sampling day.

3.2.3. Population structure

The dominant sympagic copepod species differed greatly in their age structure. Naupliar stages dominated the populations of *Drescheriella* spp. (76 %) and *Stephos longipes* (98 %). Copepodids made up the largest fraction in *Ectinosoma* sp*.* (85 %) and *Diarthrode* cf. *lilacinus* (61 %). In the *Idomene antarctica* populations copepodids were also predominant accounting for 42 %. However, *I. antarctica* was the only species in which adults occurred in high densities contributing significantly to the abundance (36 %).

N II made up the largest fraction of the *Drescheriella* spp. population at the beginning (75 - 89 %), while C I dominated the population in the middle (41 - 82 %) and N VI at the end of the study (50 %) (Fig. 7 a). C III - C V were very rare contributing only

≤ 2 %. Adults were also only found in low numbers accounting for < 6 %. 69 % of all adults were *D. glacialis*, and 59 % of those were males. In contrast, only female *D. racovitzai* were found in the samples.

I. antarctica nauplii were most abundant during the first half of the study, and the copepodite stages showed a bimodal occurrence pattern and were common in both early and late December. Adults had a maximum peak in mid-December when they comprised up to 85 % of the total population (Fig. 7 b). With one exception, males always outnumbered females.

Naupliar stages (N II - N VI) of *Ectinosoma* sp. were mainly found during the first week of the time series. The earliest naupliar stage (N I) was absent in all samples. Within the copepodite stages there was a shift in stage structure: C I and C II dominated during the first two days while later on C IV and C V were most abundant. Only male adults occurred, and only once (Fig. 7 c).

In *D.* cf. *lilacinus* only naupliar stages occurred during the first two sampling days, with N III and N IV contributing the largest fraction (74 to 80 %, Fig. 7 d). In mid-December, early copepodite stages (C I - C III) dominated with 83 and 94 % of the total population. Towards the end of the study the abundance of all developmental stages decreased with the exception of N VI, which comprised 84 % of the total population on 30 December. Only females were found, and only on the first sampling day.

No distinct temporal change was evident in *S. longipes*, and different naupliar stages dominated (Fig. 7 e). The latest naupliar stage (N VI), the copepodite stages II to V and males were not found in the ice cores.

The mean population stage [S] of all four dominant harpacticoid species varied greatly in the course of the investigation (Fig. 8). In all species [S] increased towards mid-December but decreased again towards the end of the study. This change was most pronounced in *Drescheriella* spp. (range: 2.3 - 7) and lowest in *Ectinosoma* sp. (range: 6.6 - 10).

3.2.4. Vertical distribution

At the beginning of the temperal study, the majority of all species was concentrated in the lower part of the ice. However, from mid-December onwards, *Drescheriella* spp. and *Stephos longipes* had a much wider distibution in the cores and also occurred in the middle and upper parts. This trend was not detected for the other species. Their occurrence remained to be restricted to the bottom layer of the ice throughout the investigation period coinciding with highest bulk salinities and Chl *a* concentrations (Fig. 9).

4. Discussion

The copepod assemblage of the sea ice in the western Weddell Sea in late spring was characterised by a relatively high species number of 15. With one exception, all species have been previously decribed in the Antarctic sea ice: the harpacticoids *Drescheriella glacialis, D. racovitzai, Harpacticus furcifer*, and the calanoid *Stephos longipes* seem truly belong to the ice fauna (Dahms and Dieckmann, 1987; Dahms et al., 1990; Dahms and Schminke, 1992; Schnack-Schiel et al., 1998, 2001b; Guglielmo et al., 2007). The harpacticoids *Ectinosoma* sp., *Idomene antarctica*, *Hastigerella antarctica* and *Nitocra gracilimana* probably also belong to the sympagic fauna since they have previously been found in different sea ice habitats (Dahms and Schminke, 1992; Günther et al., 1999; Kiko et al., in press). *I. antarctica* has been described as *Dactylopus antarcticus* by Giesbrecht (1902) from samples taken under the pack ice in the Bellingshausen Sea. It was also found together with *H. antarctica, N. gracilimana, Ectinosoma* sp. and *Drescheriella* spp. in very low numbers in plankton samples taken beneath the ice floe of the time station (Schnack-Schiel et al., in press). Six species (the calanoids *Ctenocalanus citer*, *Metridia gerlachei* and the cyclopoids *Oithona similis*, *O. frigida*, *Oncaea curvata*, *Pseudocyclopina* sp.) were represented by only a few or even just a single specimen and were probably accidentally entrapped either from the plankton or the benthos (Giesbrecht, 1902; Hoshiai and Tanimura, 1986; Menshenina and Melnikov, 1995; Swadling et al., 1997; Schnack-Schiel et al., 1998; Günther et al., 1999; Elwers et al., 2001; Guglielmo et al., 2007).

The species not previously found in the sea ice is *Diarthrodes* cf. *lilacinus*, a benthophytophile species described from Tierra del Fuego, South Argentina (Pallares, 1977). In this study, it only occurred at the time station and thus close to the shelf slope.

Drescheriella spp. was by far the most abundant taxon encountered in the sea ice throughout the present study, accounting on average for 82 % of the total copepod abundance. *Drescheriella* spp., mainly *D. glacialis*, is known as a dominant sympagic member from e.g. the Weddell Sea (Günther et al., 1999; Schnack-Schiel et al., 2001b, 2004), the Bellingshausen and Amundsen Seas (Schnack-Schiel et al., 1998), and from eastern Antarctica (Swadling et al., 2000). The second *Drescheriella* species, *D. racovitzai*, has been described for the eastern Weddell Sea (Dahms et al., 1990; Günther et al., 1999) and by Giesbrecht (1902) as *Idya racovitzai* for the Bellingshausen Sea as well as for the sea ice surface and sub-ice layers of the same ice floe of the time station (Kiko et al., in press). Since the naupliar and copepodite stages of the two *Drescheriella* species were not identified to species level, nothing can be said about their distribution within the sea ice. However, all instars together with a relatively high amount of exuviae were found in the ice indicating an active development within this habitat. Contrary to *D. glacialis,* adult *D. racovitzai* were rarely found in the upper and middle parts of the ice cores but mainly in the lowest sections of the ice. This coincides with results of Kiko et al. (in press) who found that adult *D. racovitzai* comprised 85 % of all adult *Drescheriella* spp. in the sub-ice layer. These results suggest that both *Drescheriella* spp. probably prefer different sea ice

habitats: *D. racovitzai* seems to be more adapted to life in the bottom ice layers and in the ice-water interface where an exchange with the underlying water is possible.

D. glacialis, in contrast, has a much wider distribution within the cores which is especially true in porous and rotten sea ice where brine channels are larger and hence, easier to colonise (Schnack-Schiel et al., 1998, 2001b, this study). However, in the surface layers adults of both *Drescheriella* species occurred in relatively equal numbers (Kiko et al., in press). The stage composition of *Drescheriella* spp. in the surface layers was bimodal, with high numbers of nauplii and adults but low numbers of copepodids. Kiko et al. (in press) concluded that adults migrate actively into the surface layer habitat and that they use this ice habitat as a breeding ground. In the sea ice proper, the *Drescheriella* spp. population consisted mainly of nauplii (76 %) and copepodids (23 %) while adults were only rarely found. All developmental stages occurred throughout the ice cores except in the upper 10 cm. The highest abundances were found in the middle and lower parts of the ice. It is therefore suggested that the individuals found in the sea ice originated from the ice-water interface. In contrast to previous findings (Schnack-Schiel et al., 1998, 2001b, Swadling et al., 2000) *Drescheriella* specimens (C I - C V and adults of both species) were found (with a total of 16 to 90 ind. per 100 m^3) in the upper 50 m of the water column at the time station, but without a temporal pattern (Schnack-Schiel et al., in press). According to Dahms et al. (1990) and Dahms and Schminke (1992), both *Drescheriella* species are able to survive in the water column as *D. glacialis* is a good swimmer while *D. racovitzai* has a more pronounced floating behaviour.

The harpacticoids *Idomene antarctica*, *Ectinosoma* sp. and *Diarthrodes* cf. *lilacinus*, which were found in high densities on occasions, were seldomly encountered in the middle and upper part of the ice cores but were concentrated in the bottom layers. This agrees with results of Kiko et al. (in press) who found these species in only very low numbers or absent in the surface layer. In contrast, they were abundant in the sub-ice layer, especially close to the sea ice bottom (Kiko et al., in press). Günther et al. (1999) found an unknown *Idomene* species and five unknown *Ectinosomatidae* species in the platelet layers underlying the fast ice at the Drescher Inlet in the eastern Weddell Sea. This may indicate that species of the *Ectinosomatidae* and *Thalestridae* have strong affinities to the periphery of ice floes where temperature and salinty in the brine channels are most similar to those of the underlying water.

Stephos longipes is described as an abundant member within the sympagic meiofauna of the Weddell Sea (Günther et al., 1999; Schnack-Schiel et al., 2001b), the Bellingshausen and Amundsen Seas (Schnack-Schiel et al., 1998), the Terra Nova Bay in the Ross Sea (Guglielmo et al., 2007) and eastern Antarctica (Swadling et al., 1997, 2000). In the present study *S. longipes* occurred in densities between 0 and 23 ind. L^{-1} similar to values reported in earlier sea ice studies from different geographical regions and seasons (Schnack-Schiel et al., 1995, 1998, 2001b; Swadling et al., 2000). Higher densities with up to 250 ind. L^{-1} were found especially in spring or in summer in ice-covered seas (Kurbjeweit et al., 1993; Schnack-Schiel et al., 1995; Guglielmo et al., 2007). In the present study, nauplii dominated the *S. longipes* population within the ice throughout the study period, followed by adults. Copepodite stages were hardly found. This also holds true for the surface layer from

the same ice floe of the time station (Kiko et al., in press). The concentrations in the surface layer were, however, about 30 times higher than inside the sea ice. In the sub-ice layer of the same ice floe, adults and nauplii had, on average, similar shares of the total with adults being more abundant during the first part of the study and nauplii towards the end. As in the sea ice and in the surface layers, copepodite stages occurred only sporadically (Kiko et al., in press).

The total abundance of *S. longipes* in the sub-ice layer was, in contrast to the other ice habitats, much lower and was also lower than found in earlier studies of the ice/water interface. Kiko et al. (in press) found a maximum abundance of 26 ind. m^{-3} in mid-December. In the eastern Weddell Sea, Kurbjeweit et al. (1993) and Schnack-Schiel et al. (1995) reported concentrations of about 1000 ind. m^{-3} in late winter/early spring and summer and abundances of up to 4000 ind. m^{-3} in autumn, comparable to results from the Bellingshausen and Amundsen Seas in summer (Schnack-Schiel et al., 1998). According to Schnack-Schiel et al. (1995), breeding of *S. longipes* takes place in the uppermost layers of the water column, and eggs and/or nauplii are incorporated into the ice. Due to the high abundances of nauplii and adults and the almost absence of copepodids in the surface layers, Kiko et al. (in press) concluded that the surface layers also seem to be preferential breeding habitats. Independent of the question of the breeding ground, reproduction of *S. longipes* seems to have just started during the study period reported here.

The distribution and abundance of all sea ice copepods was very patchy and varied greatly between stations coinciding with previous results (Swadling et al., 1997; Gradinger, 1999; Schnack-Schiel et al., 2001a, b). The ice floes of the transect had probably originated from the central Weddell Sea over deep waters while the ISPOL floe above the shelf slope might have been originated over the southern continental shelf. Hence, the ice regimes encountered in this study differed in age and origin, which may be partly responsible for the spatial differences.

Overriding restrictions in distribution are on one side the space available for colonisation in the ice (Krembs et al., 2000), and the ability of the organisms to adapt to the highly variable environmental conditions of the ice habitats (Eicken, 1992). Within an ice floe, most copepods occur in the lowermost (more porous) parts of the ice (Kurbjeweit et al., 1993; Schnack-Schiel et al., 1995, 2001b; Tanimura et al. 1996; Swadling et al., 2000; this study) where there is significant exchange with the surrounding seawater, and temperature and salinity in the brine channels near the ice/water interface are closer to those of the underlying water. In porous and rotten sea ice occurring from late summer to autumn, sympagic copepods spread to virtually all levels within the ice (Schnack-Schiel et al. 1998, 2001b).

During ISPOL, temperatures increased while salinities decreased in the upper parts of the cores towards the end of the study resulting in a higher sea ice porosity and hence, in an increase of space for colonisation. However, high concentrations in upper and middle layers were only found for *Drescheriella* spp. and *S. longipes* but not for all other sympagic species. This result together with the occurrence of *Drescheriella* spp. and *S. longipes* in e.g. surface and gap layers and refrozen gaps (Schnack-Schiel et al., 2001b; Kiko et al., in press) indicate that only these two

species seem to be well adapted to live in a wide range of different habitats within the sea ice.

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Tables

Table 1. Copepods found in the sea ice cores during the time series. Classification of families according to Willen (2000) and to Boxshall and Halsey (2004). - = absent, + = present (< 1 ind. L^{-1}), ++ = abundant (> 1 ind. L^{-1}).

	Transect	Time-series
Calanoida		
unidentified nauplii	+	+
Family Clausocalanidae Giesbrecht, 1892		
Ctenocalanus citer Heron & Bowman, 1971	-	+
Family Metridinidae Sars, 1902		
Metridia gerlachei Giesbrecht, 1902	-	+
Family Stephidae Sars, 1902		
Stephos longipes (Giesbrecht, 1902)	++	++
Cyclopoida		
Family Cyclopinidae Sars, 1913		
Pseudocyclopina sp.	+	-
Family Oithonidae Dana, 1853		
Oithona similis	-	+
O. frigida	+	-
Family Oncaeidae Dana, 1853		
Oncaea curvata	-	+
Harpacticoida		
unidentified nauplii	++	++
Family Ameiridae Monard, 1927		
Nitocra gracilimana (Giesbrecht, 1902)	-	+
Family Dactylopusiidae Lang, 1936		
Diarthrodes cf. *lilacinus* Pallares, 1977	-	++
Family Ectinosomatidae Sars, 1903		
Ectinosoma sp.	++	++
Hastigerella antarctica Dahms & Schminke 1992	+	-
Family Harpacticidae Dana, 1846		
Harpacticus furcifer Giesbrecht, 1902	+	+
Family Thalestridae Sars, 1905		
Idomene antarctica (Giesbrecht, 1902)	++	++
Family Tisbidae Stebbing, 1910		
Drescheriella spp. (copepodids)	++	++
D. glacialis Dahms & Dieckmann, 1987 (adults)	+	+
D. racovitzai Giesbrecht 1902 (adults)	+	+

Table 2. Copepods found in the sea ice cores on the transect (I - VI = naupliar and copepodite stages, fem = females, mal = males).

	Number of cores (total: 15)	Mean abundance (Ind. L^{-1})	Frequency (%)	Developmental/sex stage		
				Nauplii	Copepodids	Adults
unidentified calanoid nauplii	2	<1	0.1	not determined		
Stephos longipes	10	1	1.9	I-V	IV-V	fem, mal
Oithona frigida	1	<1	0.1	-	I	-
Pseudocyclopina sp.	1	<1	<0.1	-	-	fem
unidentified harpacticoid nauplii	5	1	1.7	II-VI		
Ectinosoma sp.	8	1	1.6	I-VI	I-II	-
Harpacticus furcifer	3	<1	0.3	-	-	fem
Hastigerella antarctica	2	<1	0.1	IV-VI	I-II	fem
Idomene antarctica	13	5	7.3	I-VI	I-V	fem, mal
Drescheriella spp.	15	54	86.8	I-VI	I-V	
Drescheriella glacialis (only adults)	13					fem, mal
D. racovitzai (only adults)	5					fem, mal

Table 3. Relative frequency (%) of exuviae of the total at the locations of the transect.

Sampling date	**041114**	**041116**	**041118**	**041120**	**041122**	**041124**
Location	**PT-1**	**PT-2**	**PT-3**	**PT-4**	**PT-5**	**PT-6**
Drescheriella spp.	30.3	8.3	5.4	4.0	0	0
I. antartica	0	9.5	25.0	0	0	0
Ectinosoma sp.	0	7.3	0	0	0	0
H. furcifer	100.0	0	0	0	100.0	50.0
S. longipes	15.1	0	0	0	0	0
Total	29.5	8.2	6.1	3.6	3.0	1.1

Table 4. Copepods found in the sea ice cores during the time series. (I - VI = naupliar and copepodite stages, fem = females, mal = males).

	Number of cores (total: 14)	**Mean abundance (Ind. L^{-1})**	**Frequency (%)**	**Developmental/sex stage**		
				Nauplii	**Copepodids**	**Adults**
unidentified calanoid nauplii	6	<1	0.2	not determined		
Ctenocalanus citer	1	<1	<0.1	-	I	-
Metridia gerlachei	2	<1	<0.1	-	IV	fem (dead)
Stephos longipes	8	1	1.1	I-V	I	fem
Oithona similis	6	<1	0.4	II-VI	I-IV	fem
Oncaea curvata	1	<1	<0.1	-	-	fem
unidentified harpacticoid nauplii	8	<1	0.4	II-VI		
Nitocra gracilimana	1	<1	<0.1	-	-	mal
Ectinosoma sp.	14	6	6.0	II-VI	I-V	mal
Harpacticus furcifer	1			-	-	fem (dead)
Diarthrodes cf *lilacinus*	14	11	10.9	I-V	I-V	fem
Idomene antarctica	14	9	9.1	I-VI	I-V	fem, mal
Drescheriella spp.	14	70	71.7	I-VI	I-V	
Drescheriella glacialis (only adults)	8					fem, mal
D. racovitzai (only adults)	4					fem

Figures

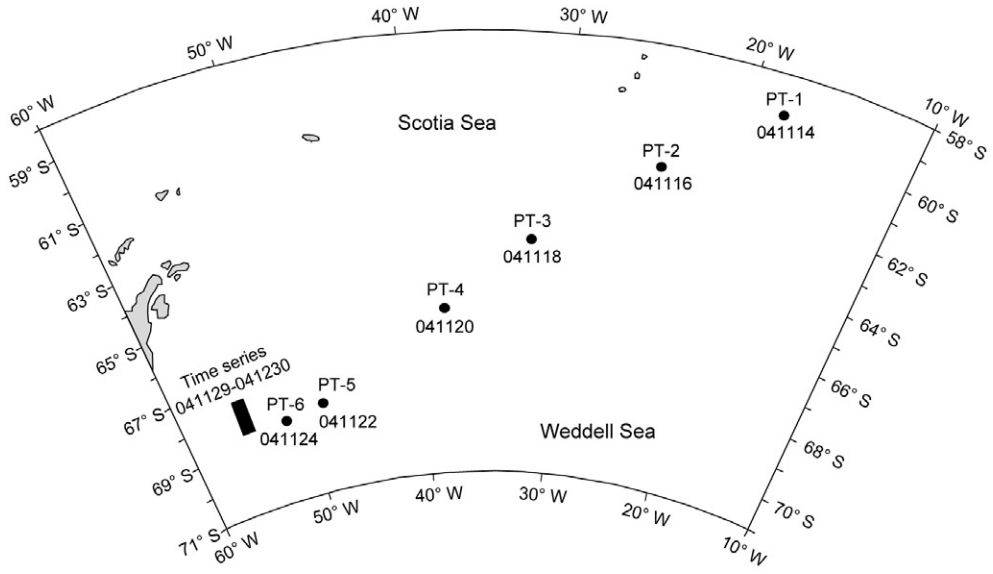

Fig. 1. Locations of the sampling sites.

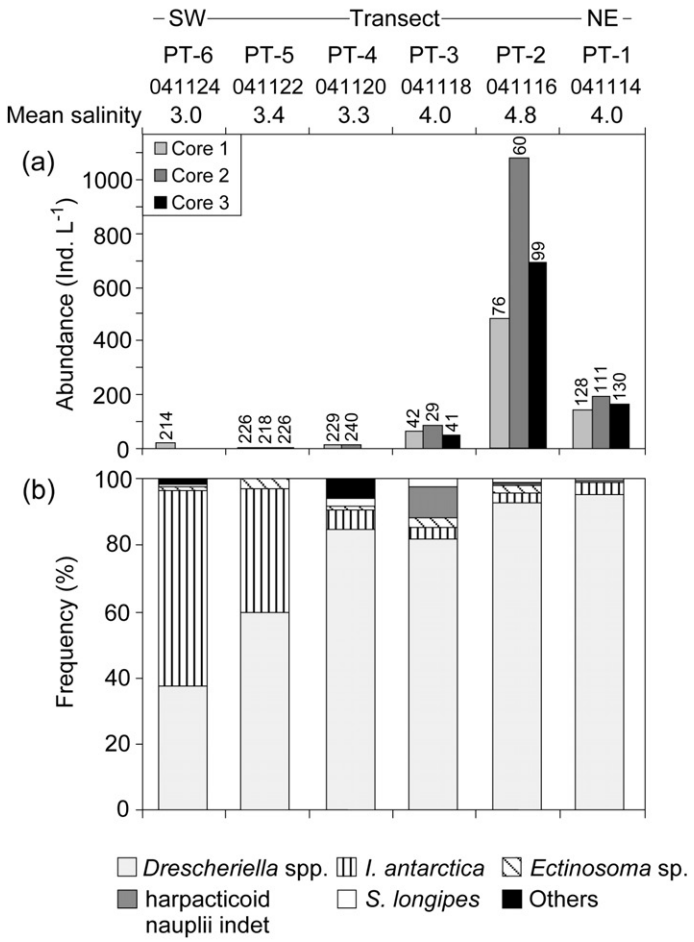

Fig. 2. Copepod abundance in the single ice cores (a) and mean relative composition (b) of the copepod species at the stations of the transect. Numbers on top of the bars denote ice thickness in cm.

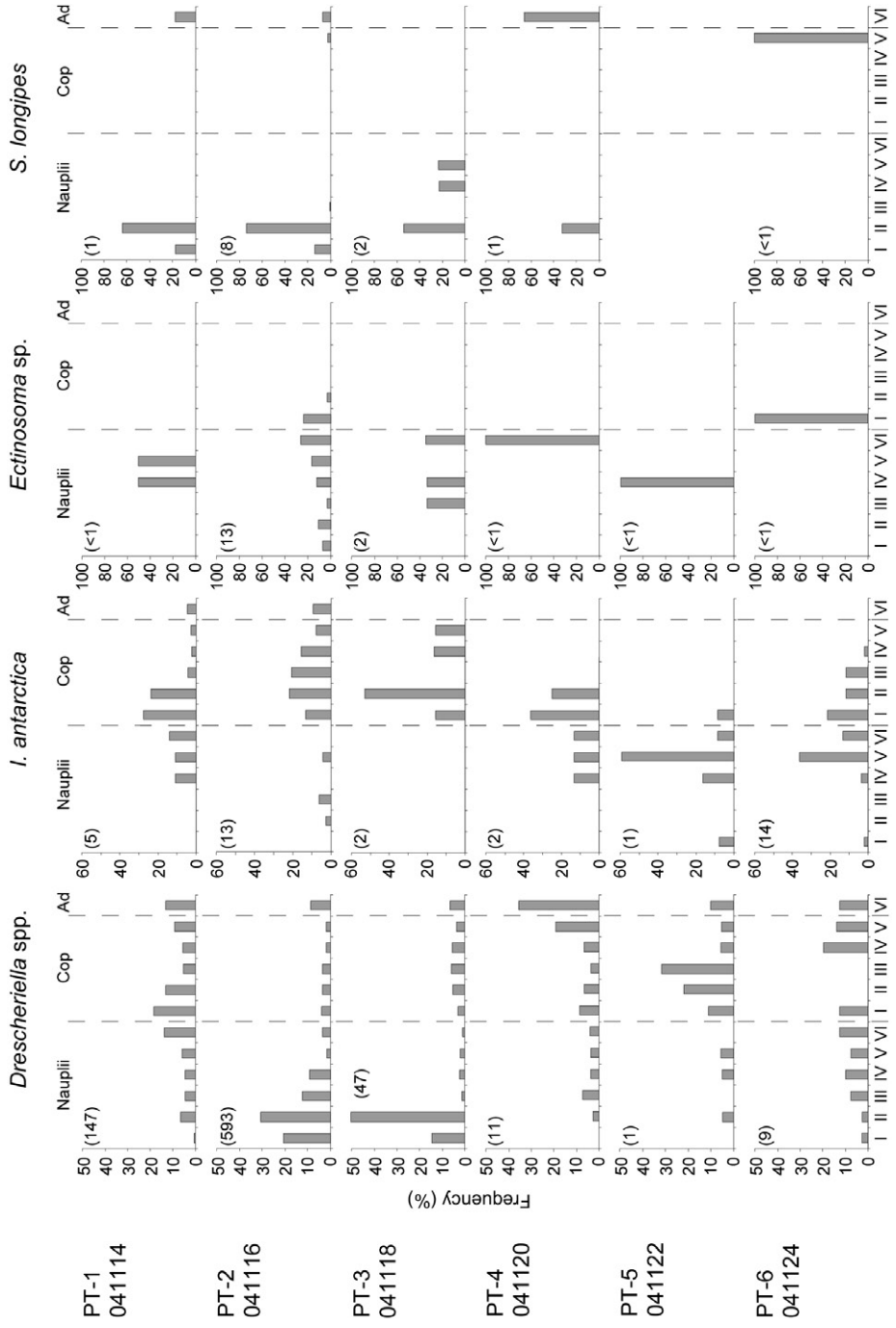

Fig. 3. Relative frequency of developmental stages of the dominant copepod species in ice cores at stations along the transect. Numbers in brackets denote numbers of individuals per litre. Cop = copepodids, Ad = adults, I - VI = developmental stages.

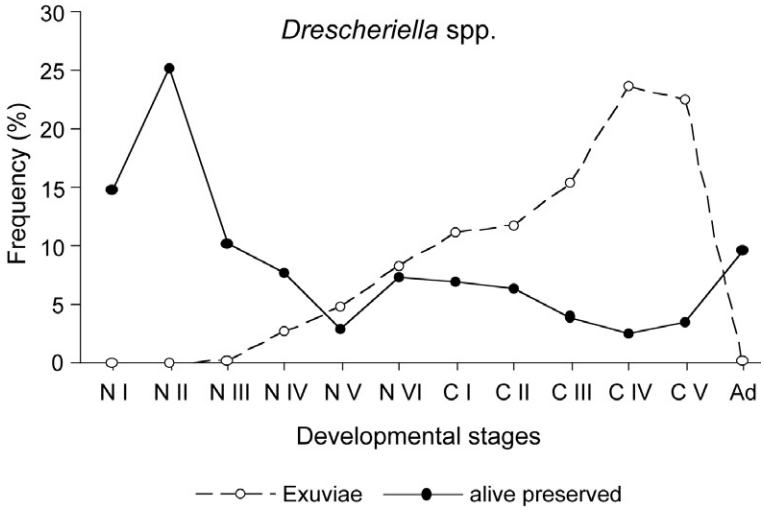

Fig. 4. Relative frequency of developmental stages of exuviae and alive individuals of *Drescheriella* spp. as mean of all transect stations. N I - N VI = naupliar stages I - VI, C I - C V = copepodite stages I - V, Ad = adults.

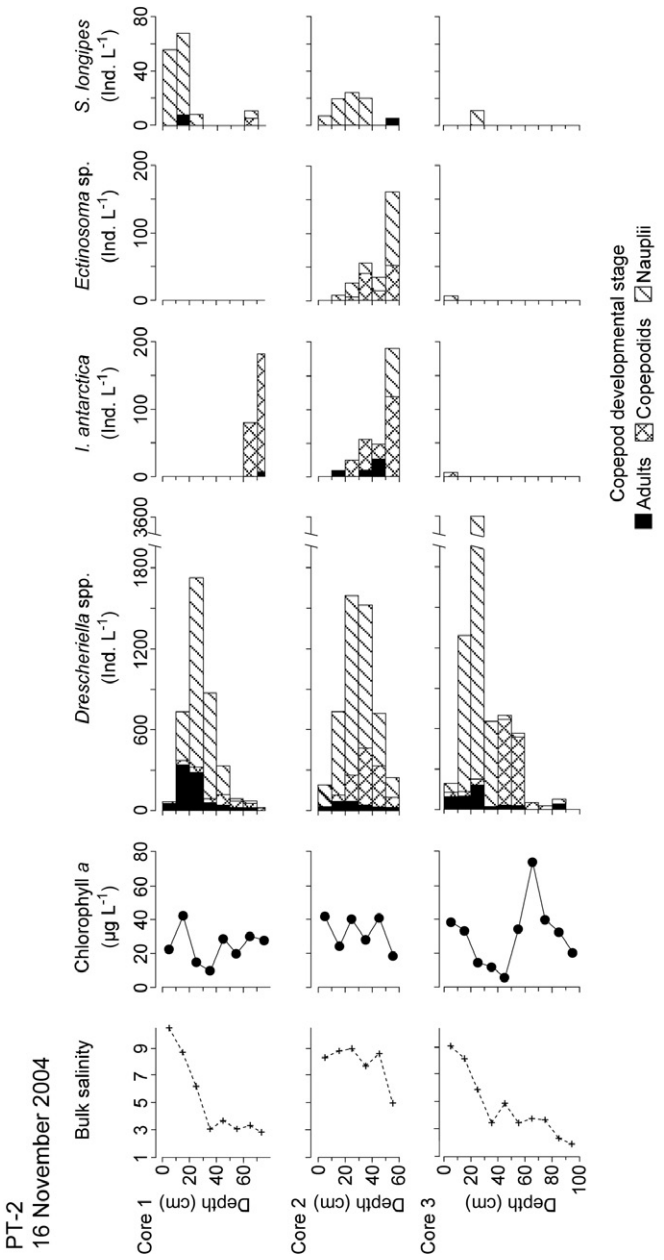

Fig. 5. Vertical distribution of bulk salinity, Chl *a* concentration and abundance of the dominant copepod species in all three ice cores of station PT-2.

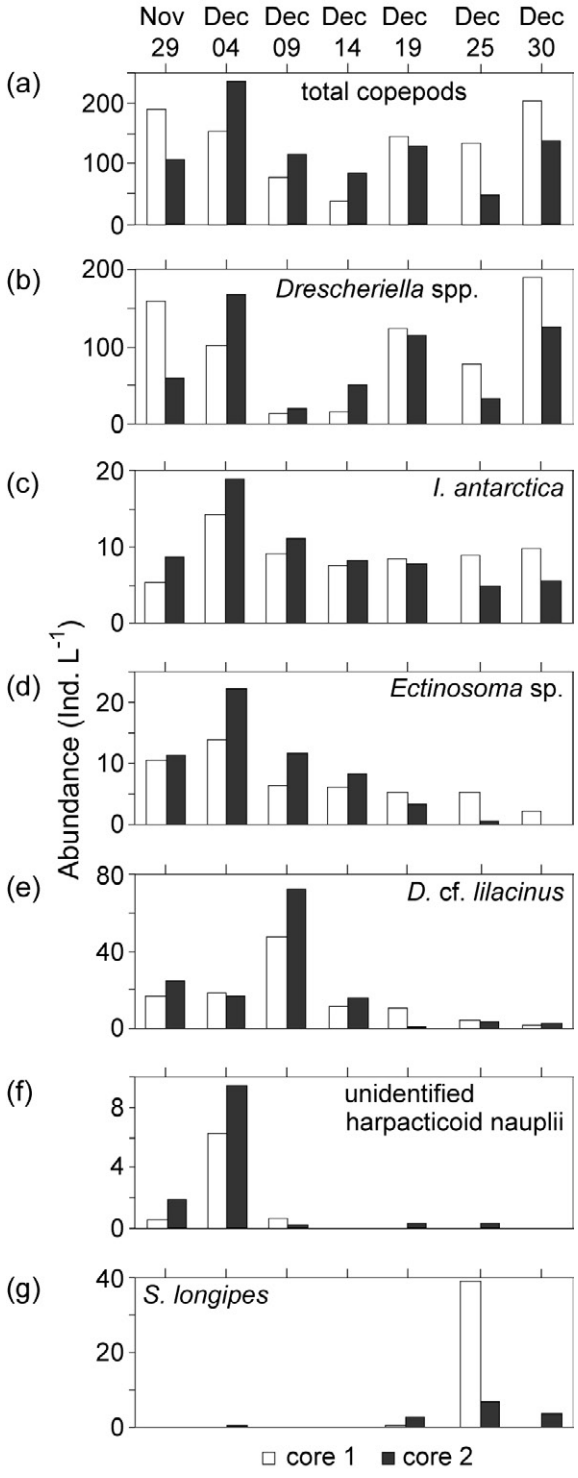

Fig. 6. Temporal change of total abundance (a), abundance of *Drescheriella* spp. (b), *Idomene antarctica* (c), *Ectinosoma* sp. (d), *Diarthrodes* cf. *lilacinus* (e), unidentified harpacticoid nauplii (f) and *Stephos longipes* (g) in both ice cores studied at the time station.

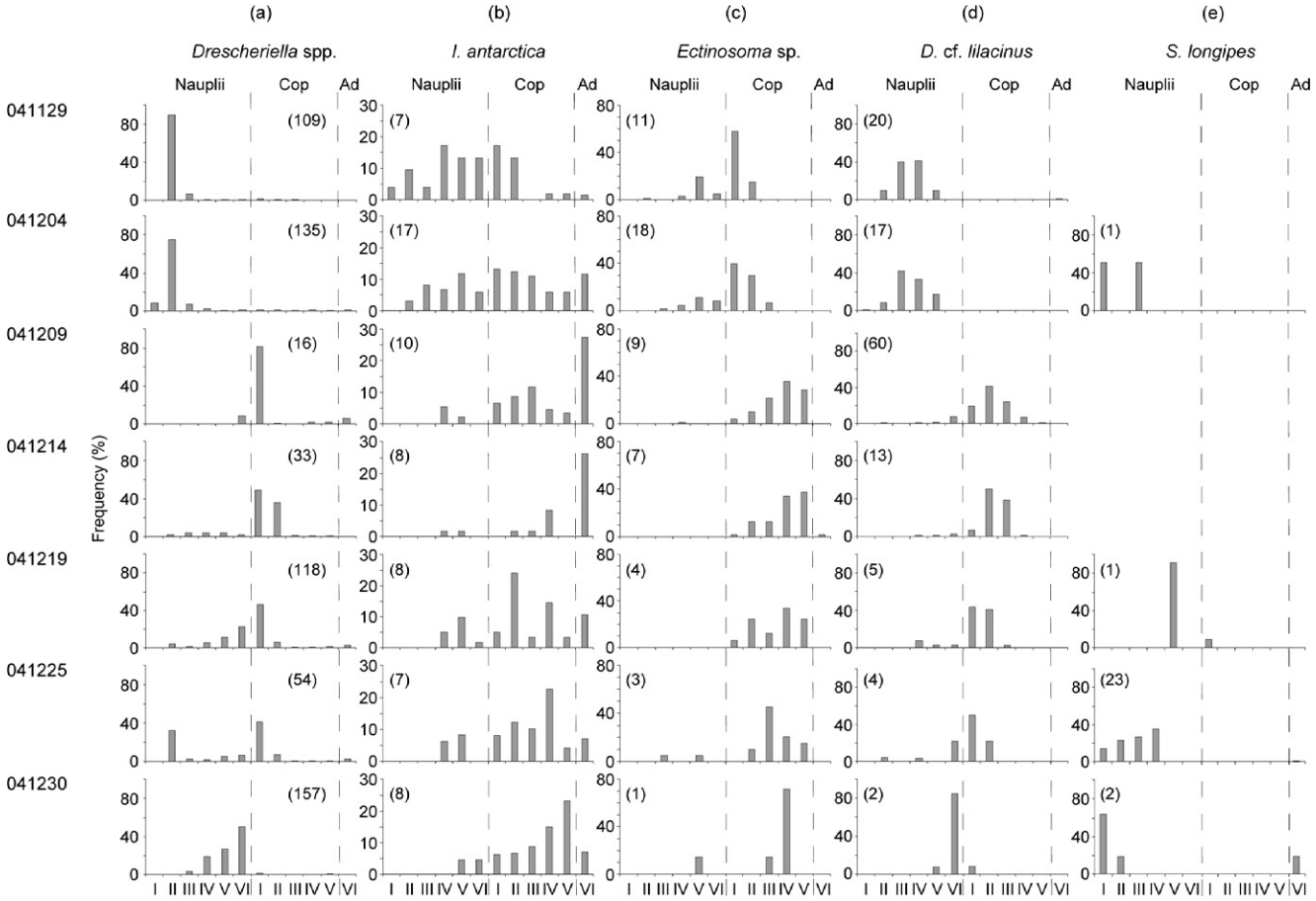

Fig. 7. Temporal change of the relative frequency of developmental stages of the dominant copepod species in ice cores of the time station. Numbers in brackets denote abundance of individuals per litre. Cop = copepodids, Ad = adults, I - VI = developmental stages.

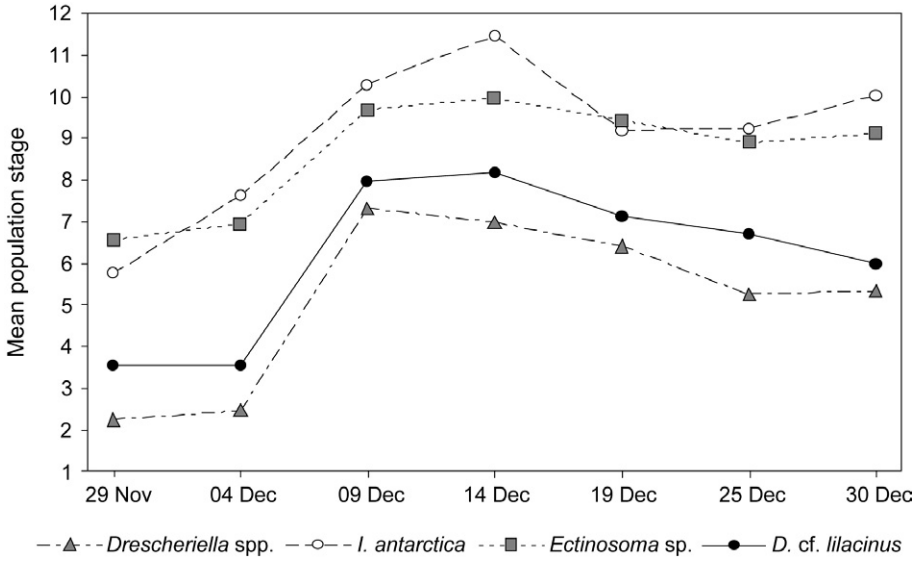

Fig. 8. Temporal change in the mean population stage of the dominant copepod species in ice cores at the time station.

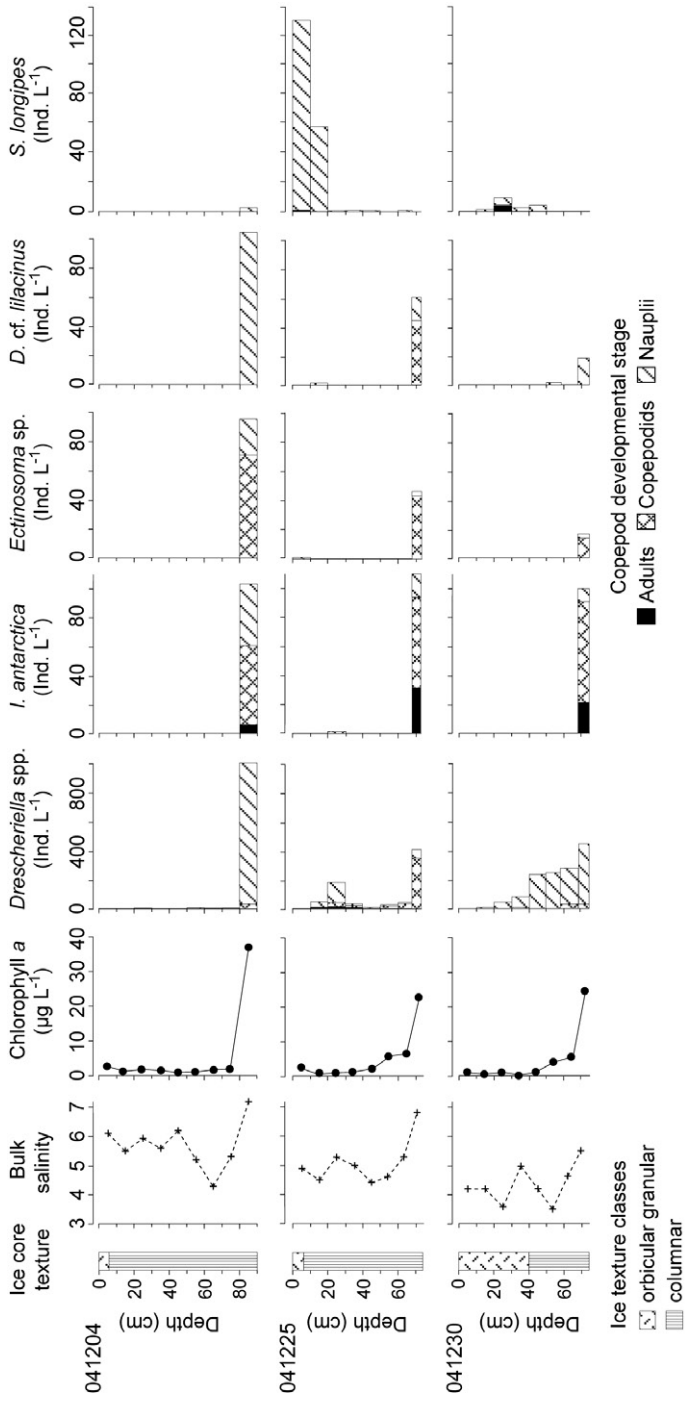

Fig. 9. Vertical distribution of ice textural classes, bulk salinity, Chl *a* concentration and abundance of the dominant copepod species at three selected stations of the time series study.

Manuscript IV

Short-term biogenic particle flux under late spring sea ice in the western Weddell Sea

Abstract

In the framework of the “Ice Station POLarstern” (ISPOL) expedition in the western Weddell Sea, two sediment traps were deployed at 10 m and 70 m water depth under a drifting ice floe in December 2004. The amount and composition of the vertical particle flux under sea ice were determined during a period of 30 days in order to investigate the influence of biological processes in sea ice and on its underside on the flux. The total mass flux was dominated by diatoms, faecal material, and aggregates, and ranged from 95.28 to 197.67 mg m^{-2} d^{-1} at 10 m depth and from 51.54 to 55.34 mg m^{-2} d^{-1} at 70 m depth. A strong increase with time of the flux of chlorophyll equivalents, biogenic silica, and faecal material was recorded during the observation period, coincident with the increase in the concentration of chlorophyll *a* in the bottom ice layer above the trap array. The latter suggests a concomitant increase in the amount of food available for grazers, such as krill, in the bottom ice layer and on the underside of the ice floe, resulting in an increased downward transport of ice algal material into the water column. The sinking faecal material was dominated by krill faecal strings and contained large amounts of diatom frustule debris, as well as intact diatom frustules, mainly of the species *Fragilariopsis curta* and *F. cylindrus*. Single pronounced flux events of *Phaeocystis antarctica* and aggregates were also observed early in the study period. Low POC/PON and biogenic silica/POC ratios of the sinking particulate matter suggest that the material collected in the traps was relatively fresh.

Keywords: Short-term vertical particle flux; Sea ice; Ice algae; Faecal strings; Krill; Western Weddell Sea; Late spring

1. Introduction

Sea ice covers vast areas of the Southern Ocean, reaching extensions of about 20×10^6 km^2 in winter and 4×10^6 km^2 in summer (Zwally et al., 1983; Comiso, 2003). The seasonal change in ice cover is associated with large seasonal variation in the vertical particle flux, characterised by a high flux during austral summer and a predominantly low flux throughout the winter. This pattern has been observed in many seasonally ice-covered areas of the Southern Ocean, such as the Bransfield Strait (Wefer et al., 1988; Kim et al., 2005), the Weddell Sea (Fischer et al., 1988), the western Pacific Ocean sector (Honjo et al., 2000), the Ross Sea (Dunbar et al. 1998; Langone et al., 2000), and the southern Indian Ocean sector (Pilskaln et al., 2004). These studies were based on collecting periods of at least one year and focused on changes in particle flux as a consequence of the seasonality of primary production in the water column due to annual changes in ice cover, light intensity and mixing depth of the surface ocean. Besides pronounced seasonal changes, the particle flux often exhibits short-term changes associated with rapid alteration of physical and biological processes, such as water mass exchange, break-up of ice cover or strong grazing on phytoplankton, the latter resulting in high faecal pellet production (Bathmann et al., 1991; Fabiano et al., 1997; Thomas et al., 2001).

In areas which are covered by sea ice throughout the year, such as the coastal fast ice regions of the Lützow-Holm Bay, the seasonal particle flux patterns observed directly under the ice were related to the annual cycle of primary production of communities living within and on the underside of the ice (Matsuda et al., 1987). Sea ice is a habitat for a large variety of organisms, including protists and invertebrates, which live within the brine channel system and on the underside of the ice (Schnack-Schiel et al., 2001; Lizotte, 2003; Schnack-Schiel, 2003). These organisms contribute in considerable amounts to the productivity and its seasonal dynamics of ice-covered regions. Sea ice, therefore, plays a key role in the overall ecosystem of the Southern Ocean (Spindler, 1994; Lizotte, 2001; Arrigo and Thomas, 2004).

Brierley et al. (2002) observed that the krill abundance under sea ice in the Weddell Sea was five times higher than in adjacent open waters, with maximum values between 1 and 13 kilometres south of the ice edge. Krill is known to feed on algae growing on the underside of sea ice (Marschall, 1988), and large krill swarms can graze down phytoplankton stocks within hours, resulting in high densities of faecal strings in the water column (Smetacek et al., 1989). Accordingly, in areas with high krill abundance, the particle flux is often dominated by faecal strings, as observed in the Bransfield Strait (von Bodungen, 1986; von Bodungen et al., 1987; Wefer et al., 1988).

During periods of ice melt, sympagic algae can also account for a large proportion of the total particle flux under sea ice. A strong tendency for ice algae to form aggregates has been experimentally observed and suggests that ice algae may be subject to rapid sinking upon release from melting sea ice (Riebesell et al., 1991).

Studies on the significance for the short-term particle flux under sea ice of processes, such as (1) grazing of ice-associated organisms on phytoplankton and ice algae,

(2) sea ice melt, and (3) onset of phytoplankton and ice algal spring blooms, are very scarce. To our knowledge, such investigations have not yet been conducted in the western Weddell Sea, which is characterised by large ice-covered regions that remain, even during the period of the annual minimum of sea ice extent (Zwally et al., 1983; Parkinson, 1998). In this type of environment, exchange of biologically derived particles between sea ice and the underlying water column has a potentially important role to play in the dynamics of the ecosystem. The present study focused on the short-term evolution of the vertical biogenic particle flux directly under sea ice in late spring. The main objectives were (1) to quantify the particle flux and its short-term changes under sea ice at two water depths during a period of 30 days, (2) to investigate the composition of the particle flux, and (3) to determine hydrographic and biological processes, which may influence the particle flux, in order to elucidate its possible sources and patterns.

2. Drift area, floe size, and sea ice thickness

This study was part of the “Ice Station POLarstern” (ISPOL), which took place in the western Weddell Sea about 30 km east of the continental shelf break (Fig. 1 a). The particle flux was measured under a drifting ice floe of 10 km by 10 km initial dimensions. During the study, the size of the floe decreased to 0.7 km by 0.8 km due to two breakup events on 2 and 24 December. The floe consisted of second-year ice of about 2 m thickness, as well as patches of first-year ice with thicknesses of 0.9 m and 1.8 m (see also Hellmer et al., in press).

3. Material and Methods

3.1. Hydrographic and meteorological conditions

The hydrographic parameters were measured on board the RV “Polarstern” by means of two Sea-Bird 911*plus* CTDs. Water samples were collected with a CTD multi-bottle rosette sampler equipped with twenty-four 12-L Niskin bottles (General Oceanics). The instruments were calibrated before and after the cruise. For in situ calibration, temperatures were measured with a digital reversing thermometer (Sea-Bird SBE35), and salinity samples were analysed with a Guildline-Autosal-8400A salinometer on board. A difference criterion was applied to predict the mixed layer depth (MLD, lower boundary of the wind-mixed surface layer) from the density field alone. The MLD was defined as that depth at which the calculated in situ density increased by $\Delta\sigma_T$ = 0.02 compared to the surface value (Cisewski et al., 2005).

The current velocities were observed continuously, using a ship-mounted 153.6 kHz RDI Ocean Surveyor acoustic doppler current profiler (ADCP). East (u) and north (v)

velocity components were averaged in 1 min ensembles in 8 m thick depth bins between 27 and 427 m depth. The transducers were located 11 m below the water line and were protected against damage from sea ice by an acoustically transparent plastic window. Heading, roll and pitch data from the gyro platforms of the ship were used to convert the ADCP velocities into Earth coordinates. The ship's velocity was calculated from position fixes obtained by the Global Positioning System (GPS) or Differential GPS when available. Standard meteorological parameters were continuously recorded and archived by the "Polarstern Data Acquisition System" (PODAS) of the ship.

3.2. Sediment trap deployment and particle sampling

Two cylindrical multiple sediment traps (MST 6, HYDRO-BIOS, Kiel, Germany) were installed under sea ice at ISPOL site 9 (see Hellmer et al., in press) between 30 November and 30 December 2004. This trap type was chosen because, compared to other geometries, the cylindrical shape was found to trap particles in the closest agreement with the sediment deposition rate (Gardner, 1980). Furthermore, cylindrical traps are considered the only traps which are able to cope with the diverse and dynamic environment of ice-influenced seas (Zajączkowski, 2002). During the drift period, the total water depth varied between 1035 and 1902 m. The sediment trap installation was secured at the surface of the ice floe, and the traps were deployed through a hole drilled in the ice and were positioned at water depths of 10 and 70 m. The collecting cylinders had opening areas of 150 cm^2 and a length of 56 cm. They were covered by a 40 mm thick plastic grid with 40 mm^2 rectangular openings. Each trap was equipped with six collecting bottles (250 ml volume) and was programmed to collect samples at intervals of six days. Since the total sampling period lasted 30 days the sixth collecting bottle remained empty. The samples were preserved with mercuric chloride made up in concentrated brine inside the collecting bottles.

After recovery of the traps, swimmers (mainly copepods) were removed from the samples under a stereomicroscope. The samples were divided using a splitter described by Kott (1953). Sub-samples for the determination of the concentrations of particulate organic carbon (POC) and particulate organic nitrogen (PON) and the carbon and nitrogen stable isotopic composition of POC and PON ($\delta^{13}C_{POC}$ and $\delta^{15}N_{PON}$) were filtered on pre-combusted (12 h, 500 °C) and pre-weighed GF/F filters (Whatman). Additional sub-samples were filtered on cellulose acetate filters (Sartorius, pore size 0.8 µm) for the analysis of biogenic silica and on untreated GF/F filters for the analysis of chlorophyll *a* (Chl *a*) and phaeopigments. The filters were stored frozen at -20 °C. For microscopic analyses sub-samples were stored in 250 ml brown-glass bottles.

3.3. Sea ice and water column sampling

Ice cores were drilled close to the ice hole of the sediment trap array using an ice corer with an internal diameter of 9 cm. The cores were cut into 10 cm thick segments, which were transported to the ship in clean plastic containers. Each segment was melted in two litres of filtered seawater (filtered through cellulose acetate filters with a pore size of 0.2 µm, Sartorius) at 4 °C. Oceanic water samples were taken at depths of 10, 25, 50, 75 and 100 m using the CTD multi-bottle rosette sampler described earlier. Sub-samples were filtered on GF/F filters and were stored at -20 °C for later analysis of Chl *a* concentrations in the onboard laboratory. Sub-samples for microscopic analyses were stored in 100 ml brown-glass bottles and were fixed with Borax-buffered 37 % formalin (final formalin/seawater solution of 1.9 %).

The concentration of Chl *a* in the water column was determined on 1, 9, 13, 17, 21, 26 and 29 December, while measurements of the Chl *a* concentration in the sea ice were conducted on 4, 11 and 18 December. The samples for microscopic analyses were taken from the water column (10 and 50 m depth) on 1 and 29 December and from the bottom segment (160 - 170 cm) of a single sea ice core on 25 December.

3.4. Sample analyses

3.4.1. Chl a *and phaeopigments*

The pigments were extracted with 10 ml of 90 % acetone. Extraction was triggered by ultrasonification and subsequent storage at -20 °C for two hours. The concentration of Chl *a* and phaeopigments was determined using a Turner Designs 10-AU digital fluorometer according to Evans and O'Reilly (1983). In order to get information on the degree of degradation of the algal material collected in the traps, the pigment degradation ratio, defined as phaeopigments/(phaeopigments + Chl *a*), was calculated for the sediment trap samples.

3.4.2. POC and PON

Prior to analysis, the filters were dried (60 °C, 12 hours) and weighed on a microbalance (Sartorius MC5) to determine the dry weight as indicator for the total mass (TM). Subsequently, two drops of saturated HCl solution were added to each sample to remove inorganic carbon, followed by distilled water rinse and oven drying. The POC and PON concentrations were measured on a CHNS analyser (Nitrogen Analyzer 1500 from Carlo Erba) with acetanilide as standard.

3.4.3. Biogenic silica (SiO_2)

The concentration of biogenic silica was determined using the wet alkaline digestion method modified after Krause et al. (1983) as described in von Bodungen et al. (1991), using silicon-tetrachloride in 14 % sodium hydroxide (Titrisol® from Merck, Darmstadt, Germany) as standard.

3.4.4. Stable isotopes ($\delta^{13}C_{POC}$ and $\delta^{15}N_{PON}$)

Samples of sediment trap material were weighed into pre-combusted (500 °C, 3 hours) silver boats, and carbonate material was removed through a combination of HCl (10 %) additions and drying at ~ 50 °C. The silver boats were loosely crimped and placed in pre-combusted (910 °C, 3 hours) quartz tubes with copper and copper oxide. The stable carbon and nitrogen isotope composition was determined on CO_2 and N_2 generated by vacuum combustion, and the gases were separated and collected by vacuum distillation from the same sample. The samples were analysed on a EUROPA-PDZ GEO 20/20 isotope ratio mass spectrometer ($\delta^{13}C$) and a VG SIRA II dual inlet isotope ratio mass spectrometer ($\delta^{15}N$). The results are reported in the δ notation as the ratio of the heavy to the light stable isotope in the material, R_{sample}, relative to that of a standard, $R_{standard}$, with standard = Vienna Pee Dee Bellemnite (VPDB) and air for carbon and nitrogen, respectively, i.e.,

$$\delta_{sample} = 1000\left(\frac{R_{sample}}{R_{std}} - 1\right)$$

Precision was better than $\pm$ 0.1 ‰ based on analyses of an internal laboratory standard run concurrently with all the samples.

3.4.5. Microscopic analyses

Faecal pellets and strings were classified and measured using a stereomicroscope (Leica MZ 16, Leica Microsystems GmbH, Wetzlar, Germany) with a calibrated graticule. For the scanning electron microscopic analysis the faecal material was placed onto cellulose acetate filters (Sartorius, pore size 0.8 µm) using a syringe and dried in a drying oven (60 °C, 12 hours). Thereafter, the preparations were coated with gold by means of an Edwards Coating System E 306A for one minute at 75 mA. Scanning electron micrographs were taken with a Philips XL 30 ESEM (equipped with cathode LaB_6).

Phytoplankton composition and concentration and aggregate concentration were determined using inverted light microscopy (Axiovert 2000, Zeiss, Oberkochen, Germany) according to the method of Utermöhl (1958). Phytoplankton cell volume was converted to cellular carbon content through recommended carbon conversion equations (Menden-Deuer and Lessard, 2000). The contribution of unarmoured

species (e.g., flagellates, ciliates and naked dinoflagellates) to the biomass of phytoplankton and ice algae was likely underestimated due to the formalin fixation method as some species tend to disintegrate when fixed with formalin.

The dimensions of the aggregates were measured using image analysis software and used to calculate the aggregate volume, which could then be converted to biomass (in terms of carbon) using the formulas given by Alldredge (1998) and Hillebrand et al. (1999).

4. Results

4.1. Hydrography, wind, and floe drift

In this study, we concentrated on the hydrographic structure of the upper 100 m of the water column since the sediment traps were deployed at 10 and 70 m water depth. Throughout this depth range, cold Winter Water (WW) was predominant (Fig. 2). The temperature was between -1.86 °C and -1.74 °C and remained constant below 50 m water depth (Fig. 2 a). Salinity freshened in the uppermost 30 m from around 10 December (Fig. 2 b). The mixed layer depth (MLD) decreased from 201 to 36 m between 30 November and 14 December (Fig. 2 c). During the following period the MLD varied only slightly between 20 and 40 m except on 21 December. The decrease of the MLD was mainly caused by the freshening of the surface layer. For further information on the hydrography see also Absy et al. (in press). The current velocities varied strongly, ranging from -34.7 to 34.6 cm s^{-1} for u (Fig. 3 a) and from -25.4 to 22.3 cm s^{-1} for v (Fig. 3 b). The resulting current speed at 67 m depth ranged between 0.7 and 23.2 cm s^{-1} (Fig. 3 c). Spectral and harmonic analysis revealed that the mean velocity field was mainly dominated by barotropic diurnal and semidiurnal tides. Accordingly, the current direction was also very variable (Fig. 3 d). The columnar pattern of the measured velocity field suggests that in the upper 27 m, where no ADCP measurements could be made, the structure of the velocity field was similar to that observed below 27 m.

The wind speed ranged from 0.4 to 11.9 m s^{-1} with an average of about 4.0 m s^{-1} (Fig. 3 e). The wind direction was stable over several periods that lasted between 2 and 7 days. Easterly, northerly and southerly winds were dominant (Fig. 3 f). During the study period, the floe drifted from 68° 3.74' S and 54° 54.55' W to 67° 28.89' S and 55° 20.62' W (Fig. 1 b), which was a net displacement in northern direction of 64.5 km (see also Hellmer et al., in press).

4.2. Concentration and composition of ice algae and phytoplankton

The distribution pattern of the Chl *a* concentration in sea ice indicates the existence of both an internal (50 - 60 cm) and a bottom algal community (140 - 164 cm) (Fig. 4). In the internal community, the Chl *a* concentration increased strongly from 4.70 to 18.88 µg L^{-1} between 4 and 18 December, while in the bottom community a very strong increase from 19.71 to 138.01 µg L^{-1} was observed between 4 and 11 December.

In the melted sea ice 138.14 µg of ice algal carbon per litre were found. The ice algae community was nearly exclusively comprised of diatoms (in terms of carbon biomass). 17 diatom taxa were found with the most abundant species, *Entomoneis* sp., *Cylindrotheca closterium,* and *Nitzschia* spp., contributing 59.9 %, 27.5 % and 7.3 % of the diatom carbon biomass, respectively (Fig. 6).

The Chl *a* concentration in the upper hundred meters of the water column was highest on 1 December, then decreased until 21 December and slightly increased again towards the end of the observation period (Fig. 5). At 10 m depth the concentration ranged from 0.05 to 0.38 µg L^{-1}, while at a depth of 100 m the range was from 0.02 to 0.16 µg L^{-1}. With a few exceptions the highest concentrations were observed in the upper 25 m.

The phytoplankton concentration, in terms of carbon biomass, was higher towards the end of the observation period (0.82 µg C L^{-1} at 10 m and 0.21 µg C L^{-1} at 50 m on 29 December) compared to that at the beginning (0.29 µg C L^{-1} at 10 m and 0.17 µg C L^{-1} at 50 m on 1 December). The phytoplankton was strongly dominated by diatoms, which contributed between 96.5 % and 98.2 % of the total phytoplankton carbon biomass. A total of 22 diatom taxa were found, however, only five species accounted for 57.5 % to 86.4 % of the diatom carbon biomass (Fig. 6). On 1 December *Proboscia alata* (54.4 %) was the most abundant diatom species at 10 m depth, while at 50 m depth *Entomoneis* sp. (35.7 %) was predominant. On 29 December the diatom carbon biomass was dominated by *Entomoneis* sp. (49.5 %) at 10 m depth and by *Corethron pennatum* (58.7 %) at 50 m depth.

4.3. Vertical particle flux and composition of trapped material

The total mass flux, expressed by dry weight, ranged from 95.28 to 197.67 mg m^{-2} d^{-1} at 10 m depth, with the highest flux measured between 24 and 30 December. At 70 m depth the total mass flux was much lower (51.54 - 55.34 mg m^{-2} d^{-1}), without a discernible temporal trend (Fig. 7).

The particulate organic carbon (POC) flux was very variable, ranging from 7.77 to 26.22 mg m^{-2} d^{-1} at 10 m and from 3.58 to 7.44 mg m^{-2} d^{-1} at 70 m (Fig. 8). Two periods of high POC flux were recorded at 10 m depth between 6 and 12 December (20.27 mg m^{-2} d^{-1}) and between 18 and 24 December (26.22 mg m^{-2} d^{-1}). In these two

periods, the contribution of POC flux to the total mass flux at 10 m depth was highest (Table 1). The PON flux showed the same pattern as the POC flux, with values of 0.80 to 5.87 mg m^{-2} d^{-1} at 10 m depth and 0.51 to 1.31 mg m^{-2} d^{-1} at 70 m (Fig. 8). No trend with time was observed in the POC/PON ratio (Table 1).

The flux of Chl *a* continuously increased from 0.83 to 11.39 µg m^{-2} d^{-1} at 10 m depth, while an increase in the phaeopigment flux (2.22 - 33.61 µg m^{-2} d^{-1}) was observed only between 30 November and 24 December. After 24 December the phaeopigment flux was lower, resulting in a smaller flux of chlorophyll equivalents (Fig. 9 a). The 70 m trap recorded a strong increase of the phaeopigment flux (6.53 - 39.86 µg m^{-2} d^{-1}) over the whole experimental period. At this depth the Chl *a* flux was relatively low (1.53 - 2.39 µg m^{-2} d^{-1}) compared to the flux at 10 m, and did not change significantly until 24 December. Between 24 and 30 December it was much higher (10.31 µg m^{-2} d^{-1}) than before and comparable in value with the flux at 10 m (Fig. 9 a). No trend with time was found in the pigment degradation ratio (Table 1).

The flux of biogenic silica strongly increased both at 10 m (4.72 - 20.71 mg m^{-2} d^{-1}) and at 70 m depth (2.83 - 26.84 mg m^{-2} d^{-1}) over the whole observation period (Fig. 9 b). At both depths the biogenic silica flux had comparably large values, and its proportion of the total mass flux increased with time (Table 1). The ratio of biogenic silica and particulate organic carbon was variable both at 10 m and at 70 m depth, with maximum values being several times higher in the last collection period than in any of the other periods at both depths (Table 1).

The flux of phytoplankton carbon biomass increased at 10 m depth during the whole observation period. At 70 m depth no trend with time was observed (Table 1). Between 30 November and 6 December a remarkably high phytoplankton flux was recorded at 70 m. This flux was 15 - 34 times higher than in the following collecting periods when the phytoplankton flux at that depth was ≤ 40 % of the phytoplankton flux at 10 m depth (Table 1), and it was very strongly dominated by flagellates, mainly *Phaeocystis antarctica*, which contributed 96.3 % to the total phytoplankton flux (Fig. 10). The relatively high proportion of flagellates in the phytoplankton flux between 6 and 12 December was dominated by unidentified species (37.2 % of the total phytoplankton flux). While diatoms were dominant between 12 and 24 December, dinoflagellates, mainly *Prorocentrum* spp. and *Polarella glacialis* (47.9 % of the total phytoplankton flux), played a major role in the last collecting period. At 10 m depth the sinking phytoplankton carbon biomass was mainly composed of diatoms making up between 50.8 and 85.9 % of the total phytoplankton flux (Fig. 10). Within the diatoms, *Rhizosolenia* cf. *crassa*, *Fragilariopsis* sp., *F. curta*, and *Entomoneis* sp. were the dominant species at both depths and throughout the whole observation period, representing 66.1 to 89.8 % of the diatom carbon biomass flux (Fig. 10). Between 18 and 30 December a strong dominance of the diatom flux by *R.* cf. *crassa* at 10 m depth was striking, whereas at 70 m depth this species contributed a much smaller amount (18 to 24 December) or was even not present (24 to 30 December). Between 6 and 12 December *R.* cf. *crassa* was not found at either 10 m or 70 m depth.

The flux of faecal material at 10 m depth increased during the observation period (0.46 - 53.69 mm^3 m^{-2} d^{-1}), while at 70 m depth, two periods without major changes were observed: one between 30 November and 12 December when the flux was much higher (13.88 - 15.21 mm^3 m^{-2} d^{-1}) than at 10 m depth, and a second until 30 December, with values from 32.28 to 36.78 mm^3 m^{-2} d^{-1}, which were also widely much higher than at 10 m depth (Fig. 11). With the exception of the period between 6 and 12 December, when oval pellets contributed 48.6 % of the flux of faecal material at 10 m depth, cylindrical strings were always the dominant type of faecal material at both depths. Between 30 November and 6 December only cylindrical strings with diameters ≤ 100 µm were found at 10 m depth. From 12 to 30 December cylindrical strings with diameters > 100 µm and ≤ 605 µm dominated the faecal material composition (60.8 - 91.6 %). Strings with diameters > 250 µm and ≤ 605 µm made up the largest amounts (31.7 - 51.4 %) in this period. Cylindrical strings with diameters > 100 µm and ≤ 605 µm were clearly dominant (80.9 - 99.2 %) at 70 m depth during the whole observation period (Fig. 11). Within this group, strings with diameters > 250 µm strongly dominated in the collecting periods between 30 November and 6 December and from 12 to 18 December. In the other periods, strings with diameters ≤ 250 µm were also important and even dominated the total flux of faecal material with a proportion of 72.7 % from 24 to 30 December. All observed faecal material contained large amounts of diatom debris (Fig. 12). Intact diatom frustules were found in many pellets and strings, mostly belonging to the species *Fragilariopsis* sp. (Fig. 12 a), *F. curta* and *F. cylindrus* (Fig. 12 b - i). No differences in the amount and composition of diatom frustules and debris found in the faecal material could be observed at 10 m and 70 m depth.

Aggregates were found in the sediment traps only within single collecting periods. Aggregate carbon flux was observed between 6 and 12 December and between 18 and 30 December at 10 m depth, while at 70 m depth aggregate carbon flux was recorded from 12 to 18 December and from 24 to 30 December (Table 1). The flux at 10 m depth was 18 - 40 times higher than the flux at 70 m depth.

The $\delta^{13}C_{POC}$ and $\delta^{15}N_{PON}$ values of the sinking material showed little variation with time of collection or depth of sediment trap (overall ranges: -28.0 to -25.1 ‰ and 4.2 to 6.6 ‰, respectively, Table 1). The mean $\delta^{13}C_{POC}$ (-26.9 ± 0.6 ‰ at 10 m depth and -26.1 ± 1.1 ‰ at 70 m depth) and $\delta^{15}N_{PON}$ values (5.5 ± 1.1 ‰ at 10 m depth and 5.8 ± 0.5 ‰ at 70 m depth) exhibited no differences between depths.

5. Discussion

The biogenic particle flux under the sea ice continuously increased during the ISPOL drift station and was dominated by diatoms, krill faecal strings and aggregates. The results are within the range of the particle flux (from < 0.001 to about 430 mg m^{-2} d^{-1}) recorded in many long-term particle flux studies conducted in the Southern Ocean at the same time of the year when the respective study sites were still ice covered

(Matsuda et al., 1987; Fischer et al., 1988; Dunbar et al., 1998; Langone et al., 2000; Accornero et al., 2003; Pilskaln et al., 2004; Kim et al., 2005). In these studies, the highest total mass flux was measured mainly in the months from January to March. The seasonal increase of particle flux often coincides with the sea ice retreat. The peak flux, however, can occur with a significant time delay, which might be caused by intensive wind mixing of the upper water column after ice break-up (Fischer et al. 1988; Dunbar et al., 1998). The particle flux in the Southern Ocean is not only seasonally but also regionally extremely variable. The lowest annual particle flux (0.37 g m^{-2} a^{-1}), and one of the lowest measured worldwide, was recorded in the Weddell Sea (Fischer et al. 1988). In all other areas studied in the Southern Ocean, the observed particle flux was several times higher (Bransfield Strait: 60 - 107.7 g m^{-2} a^{-1}; Western Pacific sector: 27.6 - 80.6 g m^{-2} a^{-1}; Ross Sea: 3.93 - 87.6 g m^{-2} a^{-1}; Leventer, 2003 and citations therein).

For the interpretation of results of particle flux studies, it is very important to take into consideration the influence of horizontal currents on the collection efficiency of the sediment traps. It has been shown that the collecting efficiency is strongly related to the velocity of horizontal currents flowing at the mouth of the trap (Butman, 1986; Baker et al., 1988). In the present study, the current velocity was mostly below the threshold of 12 cm s^{-1} of no influence on the trap efficiency regarding mass flux, as well as the distribution of size and density of collected particles (Baker et al., 1988). On a small number of occasions current velocities, only slightly higher than the threshold current velocity, were observed but each lasted no longer than a few hours. Higher current velocities with a maximum value of 23.2 cm s^{-1} were observed between 13 and 18 December and between 24 and 28 December. This maximum value is very close to a current velocity range (mean values from 1 to 22 cm s^{-1}) which was found to have no statistically significant relationship with particle flux in a study, in which several cylindrical traps were moored in different regimes of horizontal water flow velocities (Gardner et al., 1997). It is, therefore, likely that the current velocities measured in the present study did not influence the trap efficiency, and the observed flux pattern is taken to be representative of the original particle flux.

The freshening of the surface layer and the concomitant decrease of the mixed layer depth might have had an influence on the particle flux. During the first half of the observation period the trap installed at 70 m depth collected particles inside the mixed layer, while the trap was located below the seasonal pycnocline during the second half. Enhanced particle flux can occur in water layers with strong gradients in temperature or salinity. This has been observed e.g. in a study of particle flux under platelet ice in the Weddell Sea, with highest flux of particulate organic material observed either side of a thermocline (Thomas et al., 2001). However, the gradients found in the present study were rather weak and, therefore, probably did not have a significant influence on the particle flux.

The sinking faecal material under the ISPOL ice floe consisted predominantly of cylindrical strings similar in appearance to those of krill documented by von Bodungen et al. (1987) and Accornero and Gowing (2003). Such strings have often been observed to dominate the particle flux in the Southern Ocean (von Bodungen et al., 1987; Wefer et al., 1988; González, 1992a). In contrast, small round and oval

faecal pellets of protozoan origin, which have been found to be abundant in the water column (González, 1992b) and an important part of the particle flux in the Weddell Sea (Nöthig and von Bodungen, 1989; Thomas et al., 2001), were very rare in the faecal material of the present study. Furthermore, no copepod pellets were found in the traps, although the zooplankton community was strongly dominated by copepods (Schnack-Schiel et al., in press). Copepods often contribute large amounts of the zooplankton biomass of the Southern Ocean, but their pellets are rather scarce in sediment trap samples compared to krill strings or oval pellets (Schnack, 1985). This might be due to the fact that faecal pellets of small mesozooplankton, including copepods, are mostly recycled or repackaged in the water column by processes such as microbial decomposition and coprophagy (Turner, 2002).

The contribution of biogenic silica to the total particle flux observed during the present study (4 - 10 % at 10 m, 5 - 19 % and 49 % at 70 m) was much lower than in several other particle flux studies, which revealed very high amounts of biogenic silica making up the bulk of the total mass flux with values of up to 85 weight percent (Fischer et al. 1988; Wefer et al., 1988; Dunbar et al., 1998; Accornero et al., 2003). The aggregate flux at 10 m was characterised by individual and pronounced flux events that contributed a high proportion (41.1 - 46.2 %) of the recorded POC flux. Ice algae are known to show a strong tendency to form aggregates, and in cases when ice algae are released from melting sea ice, such aggregate formation can result in rapid sinking (Riebesell et al., 1991). It is possible that the observed aggregate flux events were a result of such processes. The high POC/total mass and relatively low biogenic silica/POC ratios measured during the periods of high aggregate flux indicate that the aggregates contained large amounts of non-diatom algae rather than diatoms.

A striking feature of the particle flux in this study was the extremely high amount of *Phaeocystis antarctica* cells at 70 m depth during the first collecting period. *P. antarctica* often forms large blooms in seasonal ice zones (El-Sayed et al., 1983) and can be one of the dominant algal species found in sea ice (Lizotte, 2001; Arrigo et al., 2003). *P. antarctica* colonies and aggregates were observed to dominate the material collected in sediment traps in the Ross Sea during bloom conditions (Asper and Smith Jr., 1999). In the same area evidence was found for early and rapid carbon export from *P. antarctica* blooms to deep water and sediments, which resulted from multiple episodic export events (DiTullio et al., 2000). Special photophysiological features may enable *P. antarctica* to initiate blooms at the beginning of spring when light levels are low, the mixed layer is deep, and sea ice is still widespread (Moisan and Mitchell, 1999). Though nearly no *P. antarctica* cells were found in the water column or in the investigated ice core, the recorded mass sinking of *P. antarctica* suggests that a *P. antarctica* bloom event may have occurred earlier in spring, before the onset of the present study.

No correlation was found between the composition of the algal assemblages in the water column or in sea ice and the composition of the algae collected in the traps. This may be the result of variability in the horizontal distribution of organisms in sea ice (e.g. Spindler and Dieckmann, 1986; Swadling et al., 1997) as was observed in the present study by divers in the form of patches of dense algal assemblages on the

underside of the ice floe (pers. comm., S. Brandt). Samples taken from these patches were dominated by the diatom taxon *Rhizosolenia* (pers. comm., H. Kuosa). In the trap samples this taxon was present in considerable amounts but did not play any role in the water column and sea ice samples.

The differences in the composition of the algal assemblages in the trap samples and in the samples collected from the water column and from sea ice can also be explained by advection, which often influences strongly the vertical particle flux (e.g. Bathmann et al., 1991). Although the currents observed during the present study were not very strong, it is possible that tidal water movement caused horizontal transport of organic matter under the ice floe, and the collected particulate organic matter, therefore, did not originate from the water column and the sea ice directly above the sediment trap installation. Comparably, in a study on particle flux in the Ross Sea Dunbar et al. (1998) hypothesised that advection from surface waters might have been one reason for lags between production and particle flux.

The $\delta^{13}C_{POC}$ values from this study (-28.0 to -25.1 ‰) are all within the range (-30.8 to -23.2 ‰) of other reported sediment trap studies undertaken in the Weddell Sea in open water and under sea ice or fast ice (Biggs et al., 1988; Bathmann et al., 1991; Fischer, 1991; Thomas et al., 2001). The $\delta^{15}N_{PON}$ values (4.2 to 6.6 ‰) are within the range (-2.1 to 7.8 ‰) previously reported for a sediment trap study in the Weddell Sea (Biggs et al., 1988). In the present study, the sinking material was depleted in ^{13}C but enriched in ^{15}N in comparison with the isotopic composition of carbon and nitrogen in communities within the bottom 50 cm of the overlying sea ice ($\delta^{13}C_{POC}$: -23.8 to -21.3 ‰, $\delta^{15}N_{PON}$: 1.0 to 3.1 ‰, unpublished data). The variability in location, source, and species composition during sinking events might have had a bearing on the isotopic differences between the sinking material and the communities in the overlying sea ice. Moreover, isotope fractionation of organic matter associated with zooplankton consumption and excretion might also have been involved. Faecal pellets, which were abundant in the trap samples of the present study, have been observed to be enriched in ^{13}C and ^{15}N (Checkley and Entzeroth, 1985; Fischer, 1991). But contradictory results have also been obtained, where faecal pellets have been found to be depleted in ^{15}N relative to zooplankton diet (Schmidt et al., 2003; Tamelander et al., 2006), thus underscoring the difficulties in assigning specific sources to the collected material.

The scanning electron micrographs revealed that most of the faecal material of the present study contained high amounts of diatom frustule debris and many intact frustules mainly belonging to the diatom species *Fragilariopsis curta* and *F. cylindrus*. These species have often been found to be the dominant species in ice algal assemblages (Melnikov, 1995; Leventer, 1998; Lizotte, 2001). Studies on zooplankton faecal material, including strings of euphausiids, have shown that faecal material can contain considerable amounts of living phytoplankton (Fowler and Fisher, 1983; Jansen and Bathmann, 2007). In combination with these studies, the present scanning electron microscopic findings indicate that many of the intact diatoms found inside the faecal pellets and strings of the present study had not been degraded and were still viable.

Although the pigment degradation ratios suggest that there had been significant chlorophyll degradation, the sinking organic material seems to have been fresh. This is suggested by the very low biogenic silica/POC ratios (0.26 - 4.30). In contrast, in the Bransfield Strait, the biogenic silica/POC ratios in sediment trap samples were one to two orders of magnitude higher (9.57 - 24.82) than those in the present study. The Bransfield Strait samples were strongly dominated by krill faecal strings and had low carbon contents (between 2.8 and 7.7 %, von Bodungen et al., 1987). The freshness of the sinking material of the present study is also implied by the POC/PON ratios (4.47 - 9.73), which are comparable to those (6.0 - 8.5) found during a study on particulate organic matter flux under fast ice in the Lützow-Holm Bay (East Antarctica) from December to March, when the ratios were lower than during the rest of the year (Matsuda et al., 1987). These lower ratios were attributed to fresh organic material based on the observation that POC/PON ratios of particulate material collected directly under sea ice increase with progressing decomposition (Matsuda et al., 1986).

It is striking that the flux of chlorophyll equivalents, biogenic silica and faecal material strongly increased with the simultaneous increase in Chl *a* concentration in the bottom layer community of the sea ice located above the trap array. Provided that the measured increase in Chl *a* concentration was not due to patchiness in the sea ice, this observation suggests that the ice algae biomass and consequently the amount of food available to grazers in the bottom sea ice layer and on the underside of the sea ice increased during the present study, probably indicating the onset of an ice algal spring bloom. Such a process might have favoured ice algae grazing by krill resulting in an increasing downward flux of faecal strings.

6. Conclusions

The present study has provided insights into the importance of sea ice for vertical biogenic particle flux through the surface ocean. Biological processes within and on the underside of the ice had an impact on the amount and composition of the vertical particle flux below the ice floe. The total mass flux was dominated by diatoms, faecal material and aggregates. The flux of chlorophyll equivalents, biogenic silica and faecal material increased, coincident with an increase in the concentration of Chl *a* in the bottom ice layer above the trap array. While *Phaeocystis antarctica*, ice algae and aggregates were all important components of the vertical particle flux during the first days of the collecting period, the composition of the flux changed, and faecal strings containing fresh ice algal matter became more important later during the study. This observation suggests that an increasing amount of food in the bottom ice layer and on the underside of the sea ice favoured grazing by krill. It is evident that krill grazing facilitated the export of ice algae into the water column due to rapid sinking of the faecal strings, thus contributing an important food source for zooplankton organisms inhabiting deeper water layers below the euphotic zone. However, further studies are necessary to improve the knowledge on the functioning

of biological exchange processes between sea ice and water column and their influence on the organic material sinking through the surface layer of the ice covered ocean.

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Table

Table 1. Overview of particle flux components and biochemical parameters measured on the collected sediment trap material.

Depth (m)	Date	Aggregate flux (mg C m^{-2} d^{-1})	Phytoplankton flux (mg C m^{-2} d^{-1})	POC/TM	SiO_2/TM	SiO_2/POC	POC/PON	Pigment degradation ratio	$\delta^{13}C_{POC}$ (‰)	$\delta^{15}N_{PON}$ (‰)
10	30.11. - 06.12.	0.00	0.26	0.07	0.04	0.61	9.73	0.73	-26.4	4.5
	06.12. - 12.12.	9.37	0.28	0.21	0.06	0.26	5.42	0.67	-26.7	6.6
	12.12. - 18.12.	0.00	0.42	0.07	0.05	0.73	6.55	0.78	-26.7	5.7
	18.12. - 24.12.	10.77	0.30	0.22	0.08	0.37	4.47	0.82	-26.8	6.6
	24.12. - 30.12.	6.80	0.78	0.05	0.10	2.06	6.24	0.67	-28.0	4.2
70	30.11. - 06.12.	0.00	3.73	0.11	0.05	0.46	6.10	0.75	-27.8	5.6
	06.12. - 12.12.	0.00	0.11	0.07	0.10	1.52	6.97	0.81	-25.9	no data
	12.12. - 18.12.	0.27	0.16	0.13	0.15	1.11	6.04	0.88	-25.1	6.0
	18.12. - 24.12.	0.00	0.12	0.10	0.19	1.85	7.26	0.90	-25.2	6.2
	24.12. - 30.12.	0.37	0.25	0.11	0.49	4.30	4.75	0.79	-26.3	5.2

Figures

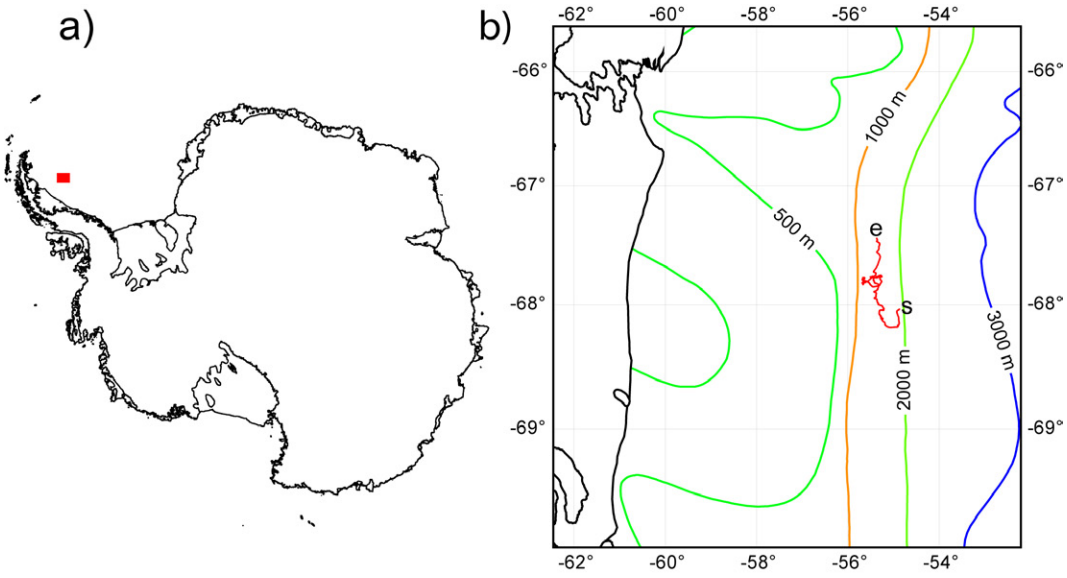

Fig. 1. (a) location of the drift area in the western Weddell Sea (stereographic projection). (b) detailed view of the drift area (Mercator projection, North at the top). The red rectangle in (a) indicates the drift area, and the red line in (b) represents the drift track of the ice floe during the particle flux study. **s** start of the drift, **e** end of the drift.

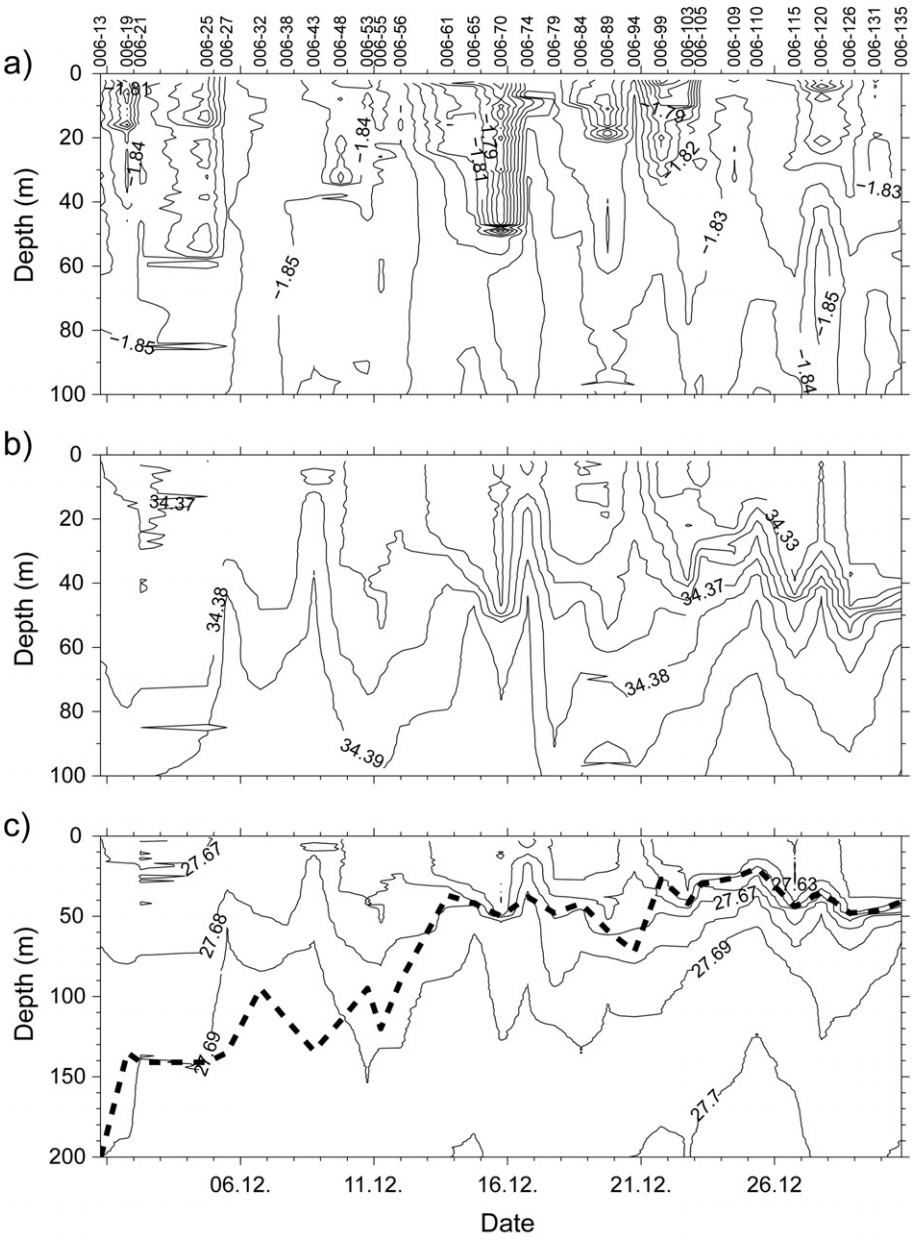

Fig. 2. Temporal development of vertical (a) temperature, (b) salinity and (c) density distribution in the upper 100 (temperature and salinity) and 200 (density) metres of the water column. The dashed line in (c) indicates the mixed layer depth, the lower boundary of the wind-mixed surface layer. The numbers on top of the figure represent the stations where the data were collected.

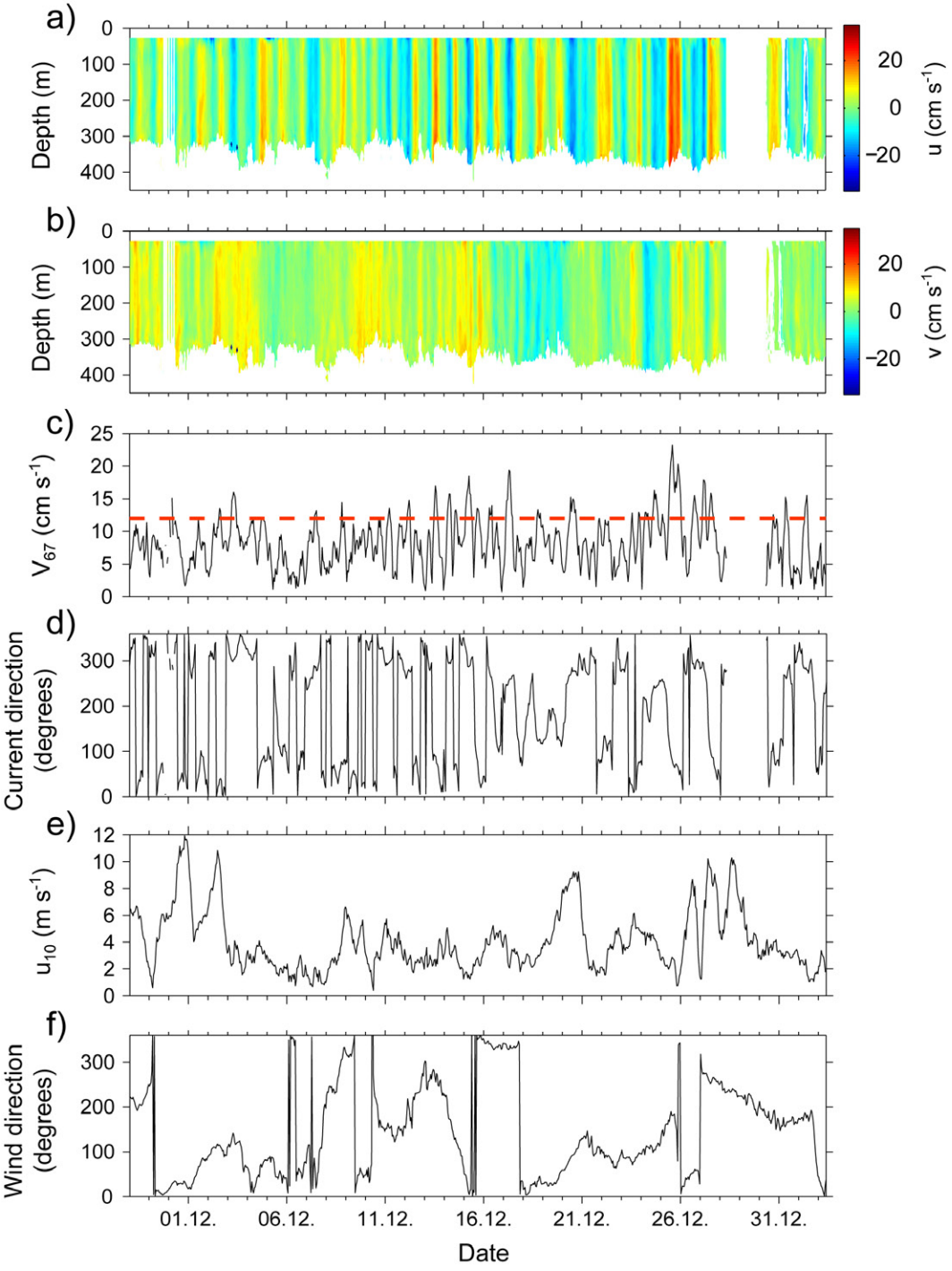

Fig. 3. Temporal development of sixty minute averages of (a - c) water current velocity (the two velocity components u and v are shown over the depth, the resulting velocity V is shown for a depth of 67 m), (d) water current direction, (e) wind velocity at 10 m height (u_{10}) and (f) wind direction. The dashed line indicates a current speed of 12 cm s^{-1}. The gaps in (a) - (d) are due to a failure in ADCP data recording between 28 December (11:09 p.m.) and 30 December (08:07 p.m.).

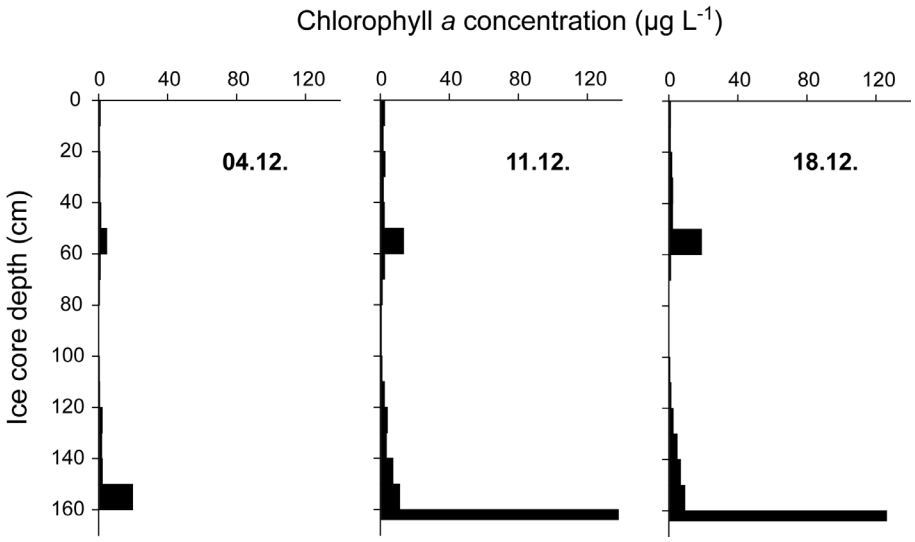

Fig. 4. Temporal development of the chlorophyll *a* concentration in the sea ice at the sediment trap site.

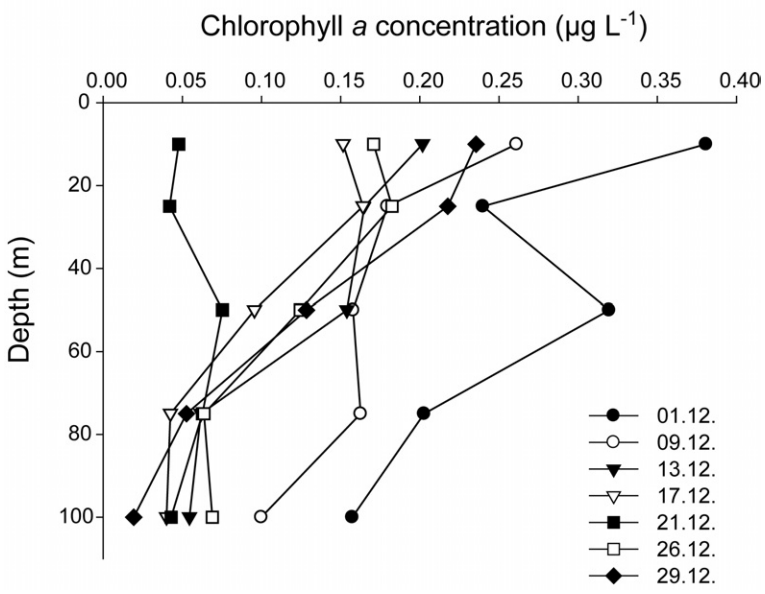

Fig. 5. Vertical distibution of the chlorophyll *a* concentration in the upper hundred metres of the water column on different dates during the collecting period.

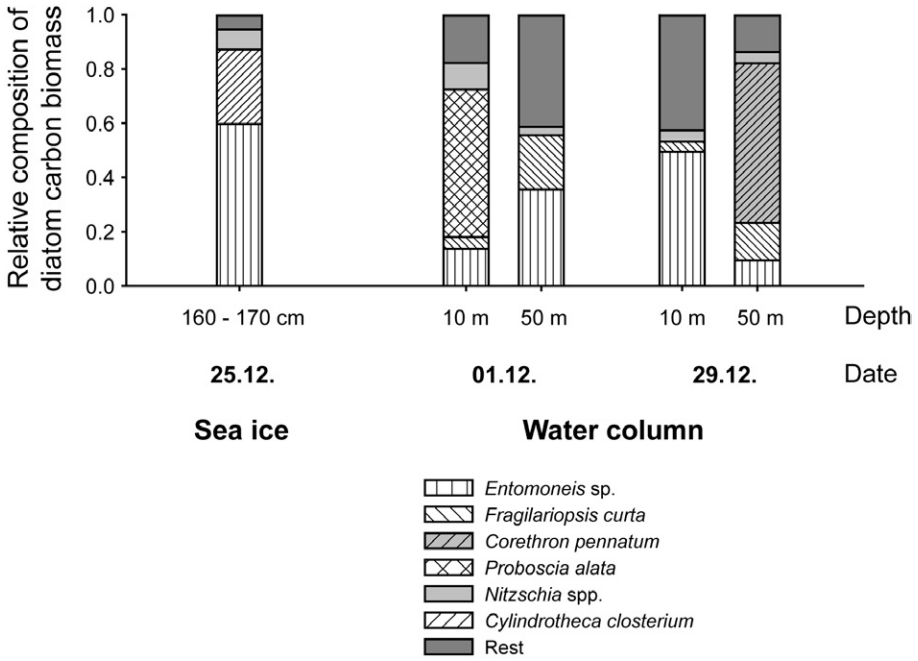

Fig. 6. Composition of the diatom carbon biomass in the water column and the sea ice at the sediment trap site on different dates during the observation period.

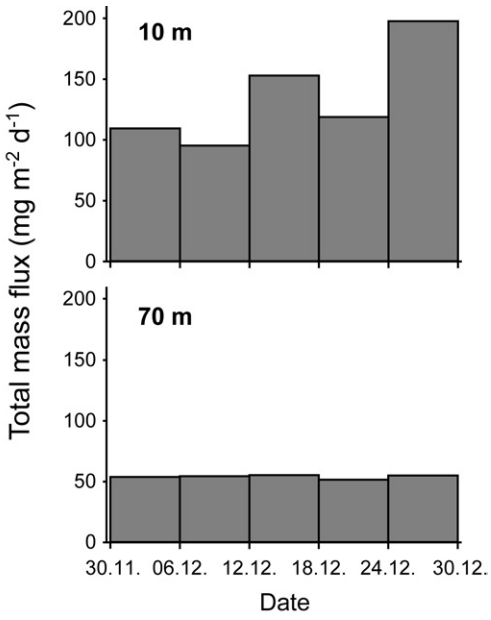

Fig. 7. Temporal development of total mass flux expressed by dry weight.

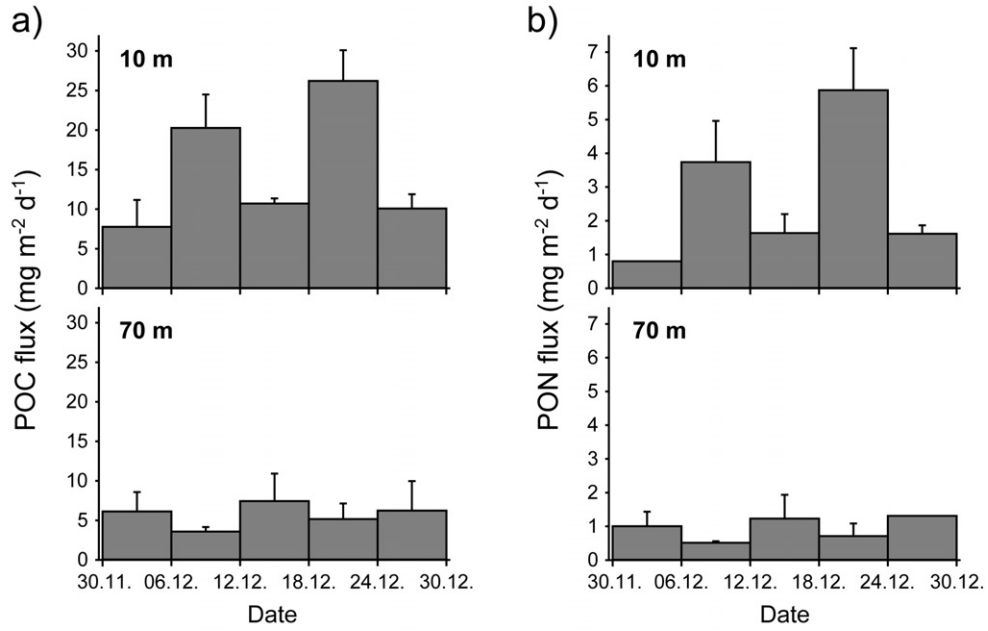

Fig. 8. Temporal development of (a) POC and (b) PON flux.

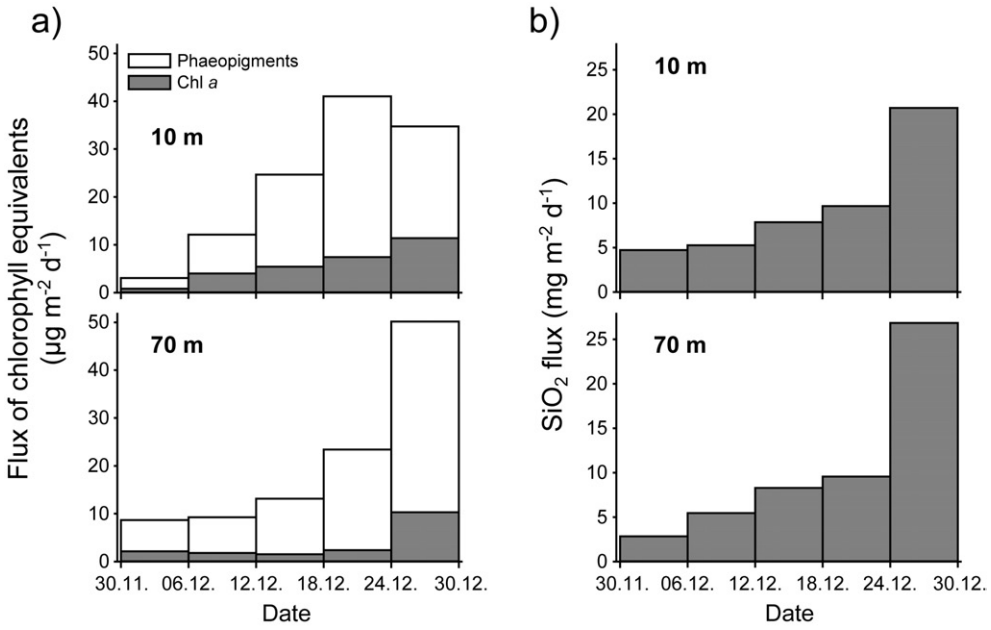

Fig. 9. Flux of (a) chlorophyll equivalents and (b) biogenic silica over the time.

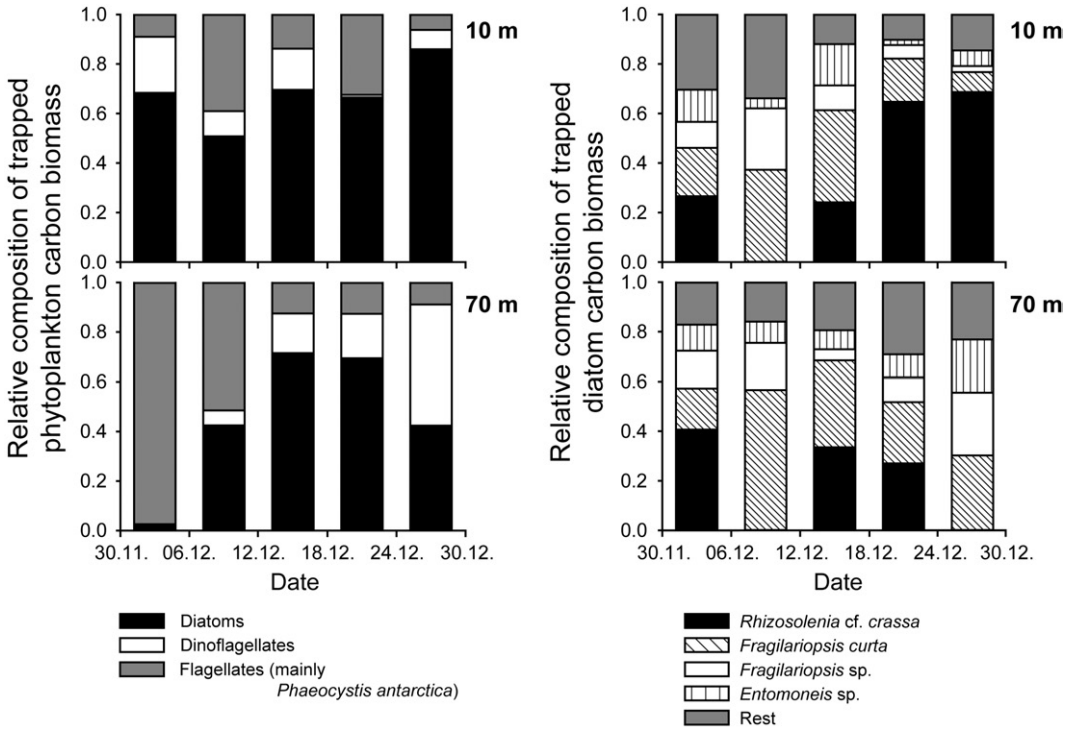

Fig. 10. Temporal development of the composition of the trapped phytoplankton carbon biomass (left) and the trapped diatom carbon biomass (right).

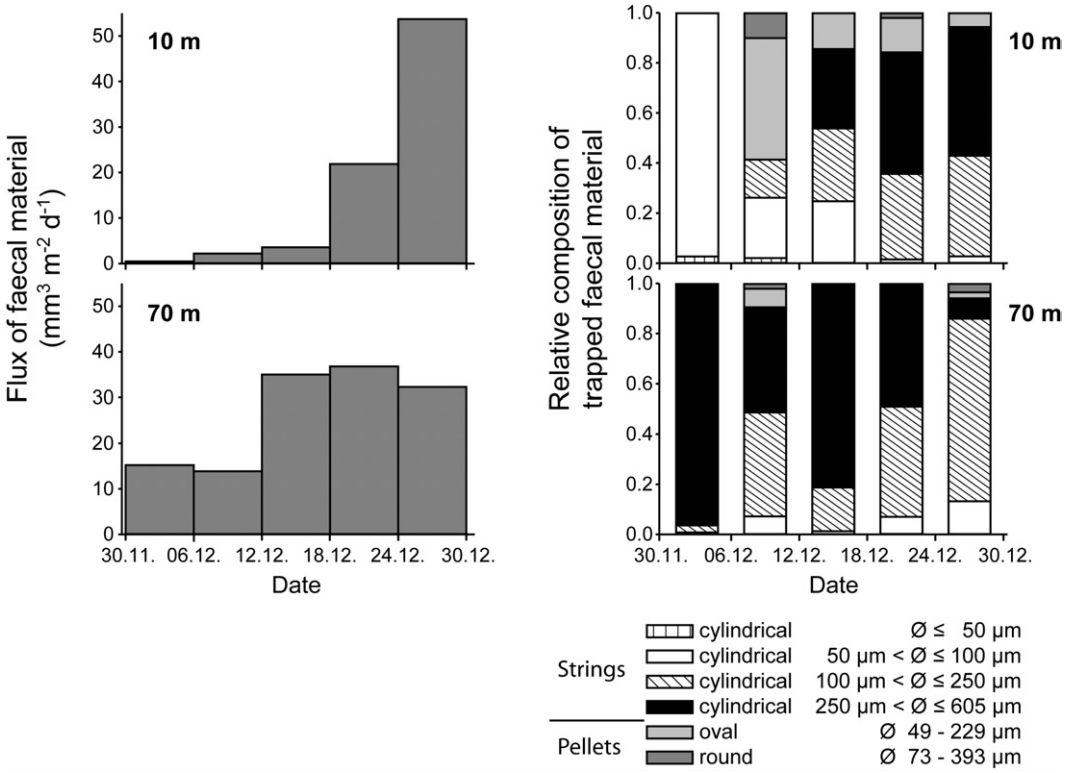

Fig. 11. Flux of faecal material (left) and composition (by volume) of the trapped faecal material (right) over time.

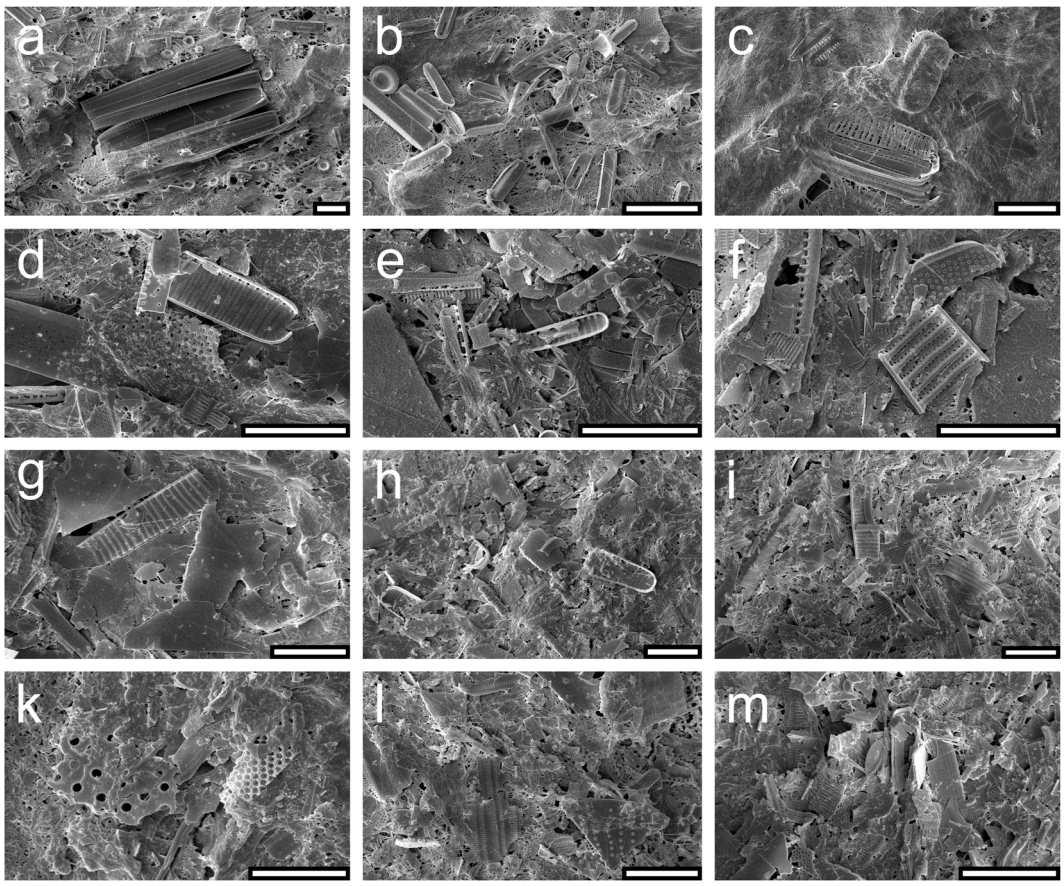

Fig. 12. Scanning electron micrographs of faecal material found in the sediment traps both at 10 m (a - c and g - i) and 70 m (d - f and k - m) depth. Scale bars = 10 µm.

Manuscript V

Composition and community structure of zooplankton in the sea ice covered western Weddell Sea in spring 2004 – with emphasis on calanoid copepods

Abstract

The mesozooplankton community, with special emphasis on calanoid copepods, was studied with respect to its species composition, abundance, vertical distribution and developmental structure during the ISPOL expedition to the ice covered western Weddell Sea. Stratified zooplankton tows were carried out nine times between 1 December 2004 and 2 January 2005 with a multiple opening-closing net between 0 and 1000 m depth. Copepods were by far the most abundant taxon contributing more than 94 % of the total mesozooplankton. Numerical dominants were cyclopoid copepods, mostly *Oncaea* spp.. A total of 66 calanoid copepod species were identified, but the calanoid copepod community was characterised by the dominance of only a few species. The most numerous species was *Microcalanus pygmaeus,* which comprised on average 70 % of all calanoids. *Calanoides acutus* and *Metridia gerlachei* represented other abundant calanoid species contributing an average of 8 and 7 %, respectively. All other species comprised less than 3 %. The temporal changes in the abundance and population structure of *M. pygmaeus* and *M. gerlachei* were small while a shift in the stage frequency distribution of *C. acutus* was observed during the study: copepodids (C) IV dominated the *C. acutus* population with 48 to 50 % during the first week of December, while C V comprised 48 % in late December. C I and C II of *C. acutus* were absent in the samples, and males occurred only in very low numbers in greater depths. In *M. gerlachei*, C I was not found, whereas all developmental stages of *M. pygmaeus* occurred throughout the study. All three species showed migratory behaviour, and they occurred in upper water layers towards the end of the investigation. This vertical ascent was most pronounced in *C. acutus* and relatively weak in the other two species. In *M. pygmaeus* and *M. gerlachei*, copepodids were responsible for the upward migration in late December, while the vertical distribution of adults did not change. In *C. acutus* all abundant developmental stages (C IV, C V and females) ascended to upper water layers. Almost exclusively (93 %) medium- and semi-ripe females of *C. acutus* and *M. gerlachei* were found, and only 3 - 4 % of the ovaries were ripe. The absence of C I and the low number of ripe females indicate that the main reproductive period had not started in *C. acutus* and *M. gerlachei* until the end of our study in early January. In contrast, the high portion of C I and C II of *M. pygmaeus* suggests that reproduction of this species had started in October-November and hence before the onset of the phytoplankton bloom in the water. The community structure did not differ between stations with one exception on 26 December, when the station was strongly influenced by the continental shelf.

Keywords: Antarctic; Ice-covered western Weddell Sea; Zooplankton; Calanoid copepods; Species composition; Abundance; Vertical distribution; Dominant species

1. Introduction

The seasonal fluctuation in sea ice growth and decay and hence in seasonal light availability is probably the most prominent feature in Polar Seas, and life is strongly affected by this distinct seasonality (e.g. Clarke, 1983). The polar zooplankton is well adapted to this changing environment in particular to the seasonal phytoplankton production, but the species have developed varying capabilities for surviving periods of food scarcity in the pelagial. It has been shown that the calanoid copepod species *Calanoides acutus* has a life cycle, which includes an ontogenetic migration coupled with a diapause at greater depth during winter. However, many Antarctic zooplankton species apparently remain active throughout the year and adjust their feeding behaviour (e.g. Atkinson, 1998; Schnack-Schiel, 2001).

Seasonal and regional studies on zooplankton living in the water beneath sea ice were carried out in various coastal and oceanic parts of the Antarctic Ocean (e.g. Fukuchi and Tanimura, 1981; Foster, 1987; Hopkins and Torres, 1988; Tucker and Burton, 1990; Atkinson and Shreeve, 1995; Schnack-Schiel and Hagen, 1995; Burghart et al., 1999). The western Weddell Sea is one of the few regions of the Antarctic Ocean, which are covered by perennial ice, and to our knowledge zooplankton was studied in that area only during the American-Russian Ice Station Weddell 1 in autumn 1992 (Voronina and Kolosova, 1999; Voronina et al., 2001).

The “Ice Station POLarstern” (ISPOL) expedition provided the opportunity to continue the investigations on zooplankton in the western Weddell Sea but in a different season, in spring 2004. The aims of the present study were the analyses of the zooplankton communities under perennial sea ice cover in the western Weddell Sea during the transition from spring to early summer with emphasis on major differences in abundance, vertical distribution and stage composition of the three dominating calanoid copepods *Microcalanus pygmaeus, C. acutus* and *Metridia gerlachei*.

2. Methods

2.1. Environmental parameters

Depending on sea ice conditions surrounding the ship and thus the flow, measurements of temperature, conductivity and depth (CTD) were carried out every 6 hours from the ship using two Sea-Bird 911*plus* CTDs. Each one was connected to a Sea-Bird caroussel with 24 x 12 L Niskin water bottles. A detailed description of the acquisition and pocessing of the data is given by Absy et al. (in press).

For the determination of the chlorophyll *a* (Chl *a*) concentration, water samples were collected at five different depth layers (10, 25, 50, 75, 100 m) using the above mentioned 12 L Niskin bottles. The samples were filtered on GF/F filters. The pigments were extracted with 10 ml 90 % acetone, ultrasonified and subsequently

kept at -20 °C for two hours. The Chl *a* concentration was determined on board using a Turner Designs 10-AU digital fluorometer according to Evans and O'Reilly (1983). For the analysis of the multinet data with respect to environmental conditions, the Chl *a* as well as the CTD data were taken from the cast immediately before the multinet haul.

2.2. Zooplankton collection

Zooplankton was sampled between 1 December 2004 and 2 January 2005. Sampling was carried out nine times, and the interval between sampling varied between three and five days depending on the sea ice conditions (Table 1). A multiple opening/closing net system (0.25 m^2 aperture) equipped with five nets of 100 µm mesh-size was used. Daytime vertical hauls were conducted at 0.5 m s^{-1} between 1000 m and the surface, covering five standard depth intervals. The filtered volume was measured for each net by a digital flow meter. The samples were preserved in 4 % borax-buffered formaldehyde/seawater solution and analysed for taxa composition, abundance, distribution and age structure. For a detailed description of the scientific programme during ISPOL see Dieckmann et al. (2007).

2.3. Analyses

According to density, samples were split into subsamples (1/2 to 1/32) using a Folsom splitter. Rare taxa and developmental stages were counted from the entire sample. With ten exceptions, calanoid and harpacticoid copepods were identified to species level, and the sex and developmental stage was also determined. Cyclopoid specimens were only identified to genus level. In the calanoid genera *Paraeuchaeta, Scaphocalanus* and *Lucicutia* and the harpactidoid *Drescheriella,* copepodite stages were not further identified to species level but combined. Mean abundance is given as geometric mean. The mean population stage was calculated according to Marin (1987), and the weighted mean depth after Bollens and Frost (1989). Female copepods of *Calanoides acutus* and *Metridia gerlachei* were sorted from preserved samples, and four different gonad developmental stages were determined according to Runge (1985): immature (stage 1), medium ripe (stage 2), semi-ripe (stage 3), ripe (stage 4).

The analysis of the community structure was carried out on all samples using Plymouth Routines in Multivariate Ecological Research (Primer) (Clarke and Warwick, 1994). Abundance (ind. m^{-3}) was fourth-root-transformed to decrease the weight of dominant taxa. Cluster anaysis was used to differentiate the temporal and vertical calanoid copepod communities based on the Bray-Curtis similarity measure and complete linkage classification. Statistical differences between the stations and

depths were tested for by means of a one-way analysis of similaritiy (ANOSIM). Species responsible for differences were identified by the similarity program SIMPER (Clarke and Warwick, 1994).

3. Results

3.1. Environment

The physical environment during the study is described in detail by Absy et al. (in press) and Haas et al. (in press), and only a brief summary is given here. As RV "Polarstern" was anchored to an ice floe during ISPOL, it drifted towards the north. While the track covered a south-north distance of about 100 km, the total drift length was almost twice as long as passing low pressure systems induced several loops resulting in a rather slow northward displacement (Hellmer et al., in press). At all stations Winter Water (WW) of about 200 m thickness showed typical winter conditions with cold temperatures (< -1.8 °C) and salinities of 34.36 - 34.42 (Fig. 1 a, b). Warm Deep Water (WDW) underlying the WW was characterised by maxima in temperature and salinity, which were higher in the eastern and lower in the western part of the cruise track due to modification from shelf water masses. Deep and bottom water masses were located below the WDW. While relatively warm bottom temperatures (> -1.1 °C) were observed in the southern part of the drift station, cold bottom water lenses (< -1.3 °C) were found in the northern part. The latter indicates the influence of continental shelf water masses descending down the slope and mixing with present water masses. During the course of the investigation, sea ice melting processes started around mid-December resulting in little freshening of the surface water layer (S < 34.33) and in releasing sea ice organisms from the sea ice into the sub-ice layer (Kiko et al., in press).

On 26 December, the station was farthest to the west. Its closer proximity to the shelf was indicated by shallower water depth (see Table 1) as well as a deeper pycnocline, which was due to the influence of denser continental shelf water masses (Fig. 2).

The Chl *a* standing stock integrated over the upper 100 m varied between 5.2 and 22.7 mg m^{-2} with the highest value on the first sampling date. Towards mid-December the standing stock decreased continuously and increased again during the second half of the study varying between 8 and 11 mg m^{-2}. The analysis of the vertical Chl *a* distribution revealed concentrations between 0.1 and 0.4 µg L^{-1} in the upper 50 m. Below 50 m the concentrations were lower, ranging from 0.02 to 0.2 µg L^{-1} (Fig. 3). Of interest are the relative high chlorophyll values throughout the upper 100 m on the first sampling date.

3.2. Mesozooplankton

The total mesozooplankton concentrations ranged between 230 and 440 ind. m^{-3}. Copepods were by far the most abundant taxon accounting for between 95 and 97 % of the total mesozooplankton. Ostracods and chaethognaths ranked second (2 %) and third (1 %), respectively. All other taxa (cnidarians, pteropods, polychaetes, euphausiids, amphipods, appendicularians, salps) made up less than 1 % each. Planktonic larvae of benthic invertebrates (e.g. anthozoans, nemertines, gastropods, polychaetes, isopods and echinoderms) occurred at all stations, however, only in low numbers, and consequently contributed only a small proportion of the mesozooplankton (< 1 %).

3.3. Copepod abundance and taxonomic composition

The abundance of copepod naupliar stages ranged between 29 and 76 ind. m^{-3}. However, as they were not sampled quantitatively due to the relatively large mesh size (100 µm), they received no further consideration. The total abundance of copepods (adults and copepodite stages) varied between 192 and 343 ind. m^{-3} with no temporal pattern. Cyclopoids contributed the largest fraction (141 - 273 ind. m^{-3}) followed by calanoids (45 - 70 ind. m^{-3}). Mormonilloids and harpacticoids, which held similar shares of the copepod population throughout the study period, reached only low densities with a mean of 69 and 25 ind. per 1000 m^3, respectively.

The copepod community was characterised by the dominance of only a few species (Table 2). Within the cyclopoids, *Oncaea* spp. was by far the most abundant genus contributing between 80 and 86 %. *Oithona* spp. ranked second, and *Lubbockia* sp. was found regularly except for 26 December, but in very low numbers. *Oithona* spp. and *Oncaea* spp. were encountered throughout the entire water column, however, with maximum densities in different depths: the bulk of *Oithona* spp. individuals occurred in the upper 100 m, whereas *Oncaea* spp. were concentrated between 200 and 500 m (Table 2). *Lubbockia* sp. and the mormonilloids occurred mainly in the deepest depth strata.

Within the calanoids, a total of 38 genera and 66 species from 18 families were identified (Fig. 4, Table 2). *Microcalanus pygmaeus* dominated overwhelmingly and attained numerically between 65 and 75 % of all calanoids, followed by *Calanoides acutus* (7 - 9 %), *Metridia gerlachei* (5 - 9 %) and *Spinocalanus longicornis* (1 - 5 %). All other species accounted for less than 1 % each (Table 2).

16 calanoid species occurred in all depth strata sampled. 21 species were encountered only in the deepest water layer**.** 16 species had their maximum concentration between 500 and 1000 m, whereas only three in the upper 50 m (Table 2).

Six harpacticoid species occurred in the samples (Table 2). *Drescheriella* spp. dominated the harpacticoids with 61 %, *Microsetella* sp. ranked second (15 %). With exception of the pelagic *Microsetella* sp. all harpacticoid species found in the present study are known to belong to the sea ice fauna (see Schnack-Schiel et al., in press). The harpacticoids were found in very small numbers in the upper 50 m of the water column except for station 112 where individuals of *Nitocra gracilimana* occurred in 100 to 200 m depth (Table 2).

3.4. The dominant calanoid copepod species Microcalanus pygmaeus*,* Calanoides acutus *and* Metridia gerlachei

Microcalanus pygmaeus occurred in densities between 33 and 50 ind. m^{-3}. The lowest values were found on 9, 21 and 26 December (33 - 39 ind. m^{-3}). On the six other sampling dates, the abundance was remarkably constant varying between 47 and 50 ind. m^{-3} (Fig. 5). All developmental stages were present, and the copepodite stages II, III and IV had very similar proportions (24 %, 20 % and 22 %, respectively). On 26 December, the population was youngest and C I - C III constituted 73 %. Adult copepods were only found in relatively small numbers (between 2 and 6 ind. m^{-3}, 5 - 13 % of all), and the female/male ratio was rather low (between 1.5 and 3.9).

The bulk of the *M. pygmaeus* population was generally concentrated in the mixed layer (Fig. 5). At the beginning of our study, the majority (65 - 81 %) was found between 100 and 500 m, and 13 - 24 % of the population occurred below 500 m in the Warm Deep Water. During the whole investigation period only a small fraction occurred in the uppermost water layer (< 5 %). On the last two sampling dates the majority of the population had ascended above 200 m, concentrating between 50 and 100 m, which was most pronounced in the earliest copepodite stages (C I - C II). Adult individuals remained in deeper waters.

Distinct differences in the weighted mean depths were observed between the developmental stages of *M. pygmaeus*: the earliest stages (C I and C II) occurred in the upper water layers and had their maximum concentrations in the transitional depth layers between 100 and 300 m. In contrast, the later stages (C IV and C V) and the adults were concentrated in the Warm Deep Water below 400 m (Fig. 5).

Calanoides acutus was generally encountered with an abundance of 4 to 6 ind. m^{-3} (Fig. 6). Late copepodite stages (C IV and C V) and females comprised > 95 % of the population, while the two earliest copepodite stages (C I and C II) were absent in all samples. C III occurred regularly but in low numbers contributing between 2 - 4 %. Males were found very rarely (< 0.5 % of the population) and only below 200 m. The stage frequency distribution shifted in dominance during the study period. Stage C IV decreased from 48 - 50 % during the first week of December to 20 - 27 % in late December/early January. Simultaneously, there was an increase of C V from 24 - 31 % in early December to 48 % later in the month. Thus, the C IV/C V ratio decreased. No temporal pattern was obvious in the abundance of females and C III.

The majority of female *C. acutus* had medium- (23 - 41 %, mean: 34 %) and semi-ripe gonads (46 - 72 %, mean: 60 %). The percentage of immature females varied between 1 and 10 % (mean: 4 %), and 0 - 6 % (mean: 3 %) carried mature oocytes. No female was spent (Fig. 6). All gonad maturity stages occurred throughout the water column, and a vertical pattern was not evident. Since females remained in the medium- and semi-ripe stages during the entire study period, maturation did not seem to progress.

The vertical distribution of *C. acutus* varied strongly during the study time. In the first week of December, 50 to 57 % of the total population was encountered below 200 m, while thereafter the population was concentrated in the upper 200 m (54 to 84 %, Fig. 6). All abundant developmental stages showed an upward migration pattern. The bulk of C IV occurred between 500 and 1000 m in early December, whereas one month later the C IV population was evenly distributed over the 1000 m water column with proportions of 13 to 24 % per sampled depth. At the same time C V and females ascended from mid-water layers to the upper 100 m. The weighted mean depths clearly separate the developmental stages of *C. acutus* according to their vertical distribution, with C V and females in upper water layers and C IV at greater depths (Fig. 6).

The overall abundance of *Metridia gerlachei* changed only slightly during the sampling period (between 4 and 6 ind. m^{-3}, Fig. 7) and without any temporal pattern. The bulk of the *M. gerlachei* population was dominated by C IV, which contributed between 34 and 60 % (mean: 43 %). Only at station 112 on 26 December did C IV fall to 23 % of the total population, and C III predominated with 41 %. On all other sampling dates, C III ranked second to C IV with 15 to 27 % (mean: 24 %), followed by C V (6 - 15 %, mean: 7 %). C II contributed only 1 - 3 % of the population, and C I was absent in all samples. Adults constituted a relatively large fraction of the population (between 18 and 36 %, mean: 25 %). Females always outnumbered males, and the female/male ratio varied between 2 and 10. The mean population stage was about 4.

As in *C. acutus*, all female gonad maturity stages, except the spent, were found during the entire study period, but females with medium-ripe (20 - 48 %, mean: 28%) and semi-ripe (46 - 76 %, mean: 65%) gonads dominated. Only 1 to 9 % (mean: 4 %) of the ovaries were ripe, and 1 to 7 % (mean: 3 %) unripe (Fig. 7). As in *C. acutus*, a development of gonad maturity during the investigated time was not evident in *M. gerlachei*.

M. gerlachei showed a bimodal depth distribution with a larger fraction in the upper 50 m (35 - 60 %) and a smaller one in the deepest water layer (18 - 30 %, Fig. 7). Towards the end of the investigation period the population was more dispersed between 200 and 1000 m, which was mainly due to a slight upward migration of C III - C V. The developmental structure differed significantly between depth, and the weighted mean depth distribution clearly demonstrates the occurrence of females in upper water layers throughout the study time, whereas the bulk of all other stages occurred in deep water layers. The majority of males were always found at a greater depth.

3.5. Community structure

The cluster analysis of the calanoid copepod community composition revealed three groupings at the 87 % similarity level (Fig. 8 a), clearly separating the station 112 sampled on 26 December (Group 3) from all other stations (Groups 1 and 2). Station 112 was at the most westerly position with the most shallow depth (see Table 1) and the deepest pycnocline (Fig. 2). It was also characterised by the lowest total calanoid copepod density. Group 1 represents hauls with high abundance and high taxa numbers (45 - 50), and stations in Group 2 had a relatively low number of taxa (38). Within Group 2 and 3, the stations had an average similarity of about 90 %. The average dissimilarity between Group 2 and 3 was 8 %.

The different depth strata sampled were separated by the cluster analysis at the 70 % similarity level, and only three samples do not fit into the clustering (Fig. 8 b). Applying the ANOSIM test to these findings revealed that the differentiation between the depth clusters is significant (R: 0.921, significance level: 0.1). Similarity exceeded 80 % within the groups below 100 m (Group 2, 3, 4), whereas the two upper depth strata (Group 5, 7) had similarities of 53 and 64 %. Thus, the calanoid assemblages were less similar above 100 m than below. Highest average dissimilarity ranging from 64 to 75 % was found between the uppermost depth layer sampled (Group 7) and all others (Table 3). The lowest average dissimilarities of 23 and 30 % occurred between Groups 3 and 4 (200 - 500 m and 100 - 200 m) and between Groups 2 and 3 (500 - 1000 m and 200 - 500 m), respectively.

The main difference between the surface layer at station 16 and those of all other stations was the absence of *Microcalanus pygmaeus* at station 16. Other distinctive features of the surface layer of station 16 were highest densities of *Metridia gerlachei* and *Calanus propinquus*, and lowest densities of *Calanoides acutus*. The particularities of the 50 - 100 m layer at station 31 were a low total abundance of calanoid copepods and again the highest and lowest abundance of *M. gerlachei* and *C. acutus,* respectively. The deepest depth stratum at station 112 was characterised by the lowest total abundance and the absence or low numbers of mid- and deep-water species such as *Gaetanus tenuispinus, Farrania frigida, Heterorhabdus farrani, Metridia curticauda, Scolecithricella cenotelis* and in particular of *Spinocalanus longicornis*, which was relatively abundant at the other stations.

The separation of station 112 sampled on 26 December coincides with the deeper pycnocline and is also reflected in our results on the dominant copepods. The weighted mean depths of all developmental stages of *M. pygmaeus* and all copepodite stages of *M. gerlachei* were greater than those either before or after. In contrast, the vertical distribution of the females and males of *M. gerlachei*, which were found almost exclusively in the uppermost and in the deepest water layer, respectively, had not changed. In *C. acutus*, only C V and females had slightly ascended, while C IV had not. A difference is also evident in the age structure at station 112. The populations of *M. pygmaeus* and *M. gerlachei* were youngest while that of *C. acutus* was oldest.

4. Discussion

4.1. Species occurrence

The overwhelming numerical dominance of copepods and in particular of cyclopoids, small calanoid species and *Metridia* spp. found during this study is similar to that previously reported for the Southern Ocean in studies using nets with small mesh sizes (≤ 200 µm, e.g. Hopkins, 1985; Schnack et al., 1985; Foster, 1987; Hopkins and Torres, 1988; Hopkins et al., 1993; Atkinson and Shreeve, 1995; Errhif et al., 1997; Fransz and Gonzalez, 1997; Atkinson and Sinclair, 2000; Mayzaud et al., 2002; Ward et al., 2006a, b). The number of calanoid species (66) was moderately high, which is in good agreement with the results of previous studies conducted in the upper 1000 m in e.g. the Croker Passage/Antarctic Peninsula and the eastern and northwestern Weddell Sea (between 55 and 70 calanoid species: Hopkins, 1985; Hopkins and Torres, 1988; Voronina and Kolosova, 1999; Schnack-Schiel, in press). All calanoid copepod species found in this study are known from the Southern Ocean, and most of them are meso-bathypelagic and have a wide distribution range (e.g. Razouls et al., 2000; Schnack-Schiel, in press). 20 species are typical for the Antarctic and sub-Antarctic (*Aetideopsis antarctica, A. minor, Calanoides acutus, Calanus propinquus, Chiridius polaris, Clausocalanus brevipes, Ctenocalanus citer, Euaugaptilus antarcticus, Metridia gerlachei, Mospicalanus schielae, Paraeucheta similis, Onchocalanus wolfendeni, Scaphocalanus antarcticus, S. vervoorti, Scolecithricella cenotelis, S. dentipes, S. schizosoma, Spinocalanus terranovae, Stephos longipes, Tharybis magna*).

Three species (*Microcalanus pygmaeus, Calanoides acutus, Metridia gerlachei*), which accounted for 86 % of all calanoids of the present study, are known to comprise a large proportion of the total calanoid copepod abundance and biomass in many parts of the Southern Ocean (e.g. Hopkins, 1985; Schnack et al., 1985; Hopkins and Torres, 1988; Hopkins et al., 1993; Carli et al., 2000; Zunini Sertorio et al., 2000; Schnack-Schiel, 2001). Voronina and Kolosova (1999), however, recorded *M. pygmaeus*, the most dominant species in our samples, only once and in low numbers in the upper 1000 m during the drift on Ice Station Weddell 1 in the western Weddell Sea in autumn. Interestingly, in accordance with our results, they also found only low abundances of *Ctenocalanus citer* and *Calanus propinquus*, which in contrast are dominant members of the calanoid copepod community in the eastern (e.g. Schnack-Schiel, 2001) and the northwestern Weddell Sea (e.g. Hopkins and Torres, 1988).

4.2. Dominant calanoid species

The three dominant calanoids *Microcalanus pygmaeus, Calanoides acutus* and *Metridia gerlachei* are described to have a seasonal pattern in abundance, vertical

distribution and population structure, but each of the three has different life cycle strategies (e.g. Zmijewska, 1993; Atkinson, 1998; Schnack-Schiel, 2001). In the present study a temporal change in vertical distribution was evident in all three species towards the end of the time studied (mid-December to early January), which was most pronounced in *C. acutus,* coinciding with observations from e.g. the eastern Weddell Sea (Schnack-Schiel, 2001), the Scotia Sea (e.g. Atkinson and Peck, 1988; Atkinson and Sinclair, 2000) and the Bellingshausen Sea (Atkinson and Shreeve, 1995).

Microcalanus pygmaeus shows only small seasonal variations (e.g. Atkinson, 1998; Schnack-Schiel, 2001). Throughout the present study, the abundance and stage frequency distribution were very similar, but a slight upward shift of mainly earlier stages was observed at the end of December. However, maximum concentrations never occurred near the surface but always deeper in or near the mixed layer. This is in agreement with previous studies from different regions and seasons (Hopkins and Torres, 1988; Kurbjeweit, 1993; Schnack-Schiel and Mizdalski, 1994; Atkinson and Sinclair, 2000; Ward et al., 2006a). All developmental stages of *M. pygmaeus* occurred during the present study. The occurrence of C I and C II (26 - 53 % of the population) in December suggests that spawning had already taken place in October/November since the development from egg to C I takes about 25 days according to Kurbjeweit (1993). This result coincides with studies by Schnack-Schiel and Mizdalski (1994) who described reproductive activities of *M. pygmaeus* in late winter in the eastern Weddell Sea.

In *Calanoides acutus* the overwintering stage, the timing of the spring ascent as well as the developmental stage, which is the main migratory stage, differ with geographical region (e.g. Atkinson et al., 1997). The overwintering stages are predominantly the latest copepodite stages (C IV and C V) and the adults (Vladimirskaya, 1978; Voronina et al., 1978; Marin, 1988; Ward, 1989; Atkinson, 1991; Bathmann et al., 1993; Zmijewska, 1993; Schnack-Schiel and Hagen, 1995; Atkinson et al., 1997; Spiridonov and Kosobokova, 1997), all of which have large amounts of depot lipids, almost exclusively wax esters (e.g. Schnack-Schiel and Hagen, 1995; Lee et al., 2006). Since C IV was the dominant copepodite stage at the beginning of our study, this stage was evidently the main overwintering stage, and the shift to C V towards the end of the study seems to indicate the end of the diapause. In contrast, Voronina et al. (2001) observed C V as most dominant stage in the western Weddell Sea at Ice Station Weddell 1 in autumn (March to May) 1992, and hence, *C. acutus* probably overwintered mainly as C V in that year. In the present study the vertical spring ascent to upper water layers was certainly fully underway in all dominant stages (C IV, C V and females). However, due to the fact that females and C V were generally concentrated above the C IV in the water column, the rise of females and C V probably preceded that of C IV. In the eastern Weddell Sea, Schnack-Schiel et al. (1991) found the spring upward migration to be primarily conducted by *C. acutus* females with semi-ripe and ripe gonads in mid-November, while C IV, which were equally abundant, remained at depth. Although our study in the western Weddell Sea was later in the season, the proportion of ripe females was very low (below 6 %) compared to the eastern Weddell Sea in mid-

November (57 %, Hagen and Schnack-Schiel, 1996). No C I and C II were found. This lack of offspring as well as the low number of mature females indicates that the main reproductive period had not yet started in early January. In contrast, offspring of *C. acutus* occurred in open waters west of the Antarctic Peninsula as early as mid-December (Huntley and Escritor, 1991).

In *Metridia gerlachei* only the copepodite stages migrated slightly upward during the course of our study. Adult males remained at depth, and females were encountered almost exclusively in the upper 50 m. This is corroborated by earlier findings describing *M. gerlachei* as a relatively weak ontogentic vertical migrator (e.g. Atkinson and Peck, 1988; Hopkins and Torres, 1988; Huntley and Escritor, 1992). The stage composition of *M. gerlachei* in our samples resembles that from previous studies in ice-covered seas in late winter and spring (Schnack-Schiel and Hagen, 1994; Atkinson and Shreeve, 1995; Burghart et al., 1999), with the exception that the earliest copepodite stage (C I) was absent in our samples. Unlike our findings, a much higher percentage of females (> 30 %) carried mature oocytes as early as October-November under pack ice in the eastern Weddell Sea, and a minute portion was already spent (Hagen and Schnack-Schiel, 1996). In the present study only 4 % of the females were ripe and no spent females were found indicating a delay in development within the ice covered western Weddell Sea similar to that observed in *C. acutus*.

4.3. Community structure

The community structure did not change greatly within the investigation period, and the stations showed a high degree of similarity. Only station 112, which was situated most westerly and hence mostly influenced by the Antarctic continental shelf, differed. This supports earlier findings showing differences in species occurrence, abundance, vertical distribution, and population and community structure depending on topographic and hence hydrologic features (e.g. Atkinson, 1989; Beaumont and Hosie, 1997; Ward et al., 2006a; Schnack-Schiel, in press). Communities were distinguished broadly associated with different depth layers, and no temporal change was evident. Differences in community structure between stations as well as between depth layers were largely determined by variation in species abundance rather than variation in species composition.

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Tables

Table 1. List of multinet stations.

Station	Date	Start	Position		Water depth
no.	2004/05	(UTC)	S	W	(m)
16	01 Dec	08:40	68° 10.41'	54° 52.74'	1897
31	06 Dec	13:55	68° 05.98'	55° 16.03'	1524
46	09 Dec	07:45	68° 02.79'	55° 12.65'	1592
58	13 Dec	07:50	67° 53.87'	55° 24.42'	1366
77	17 Dec	08:00	67° 46.24'	55° 19.18'	1473
97	21 Dec	07:40	67° 49.98'	55° 30.11'	1259
112	26 Dec	07:40	67° 46.92'	55° 39.24'	1084
129	29 Dec	07:55	67° 34.84'	55° 18.85'	1534
145	02 Jan	07:40	67° 21.37'	55° 23.41'	1419

Table 2 a. Mean abundance, dominance and depth range (depth of maximum density in brackets) of copepods found in the western Weddell Sea. Classification of families according to Huys & Boxshall (1991). (* these species were only found at one station).

Species	Abundance (Ind. per 1000 m^3)	Frequency (%)	Depth range (m)	
Calanoida Sars, 1903	**61100**	**23.51**		
Family Aetideidae Giesbrecht, 1892				
**Aetideopsis antarctica* (Wolfenden, 1908)	<1	<0.01	200-500	
A. minor (Wolfenden, 1911)	21	0.03	0-1000	(200-500)
Chiridius polaris Wolfenden, 1911	7	0.01	200-1000	(500-1000)
Euchirella rostromagna Wolfenden, 1911	1	<0.01	100-200	
**Gaetanus antarcticus* Wolfenden, 1905	<1	<0.01	500-1000	
**G. intermedius* (Wolfenden, 1905)	1	<0.01	500-1000	
G. tenuispinus (Sars, 1900)	481	0.79	0-1000	(200-500)
Pseudochirella sp.	1	<0.01	2001000	(200-500)
Family Augaptilidae Sars, 1905				
Augaptilus glacialis Sars, 1900	5	0.01	500-1000	
Euaugaptilus antarcticus (Wolfenden, 1911)	4	0.01	0-1000	(500-1000)
E. nodifrons (Sars, 1905)	2	<0.01	500-1000	
Haloptilus fons Farran, 1908	3	<0.01	500-1000	
H. ocellatus Wolfenden, 1905	16	0.03	100-1000	(100-200)
H. oxycephalus (Giesbrecht, 1889)	39	0.06	0-1000	(200-500)
Haloptilus sp.	<1	<0.01	500-1000	
**Pachyptilus pacificus* Johnson, 1936	<1	<0.01	500-1000	
Pseudoaugaptilus longiremis Sars, 1907	2	<0.01	500-1000	
Family Bathypontiidae Brodsky, 1950				
Temorites brevis Sars, 1900	17	<0.1	200-1000	(500-1000)
Family Calanidae Dana,1849				
Calanoides acutus (Giesbrecht, 1902)	4799	7.85	0-1000	(100-500)
Calanus propinquus Brady, 1883	121	0.20	0-1000	(0-50)
Family Candaciidae Giesbrecht, 1892				
Candacia sp.	4	0.01	500-1000	
Family Clausocalanidae Giesbrecht, 1892				
Clausocalanus brevipes Frost & Fleminger, 1968	2	<0.01	200-1000	(200-500)
Ctenocalanus citer Heron & Bowman, 1971	259	0.42	0-1000	(50-100)
Farrania frigida (Wolfendenm 1911)	14	0.02	200-1000	(500-1000)
Microcalanus pygmaeus (Sars, 1900)	43069	70.49	0-1000	(100-200)
Family Discoidae Gordejeva, 1975				
Disco sp.	40	0.07	0-1000	(500-1000)
Family Eucalanidae Giesbrecht, 1892				
Rhincalanus gigas Brady, 1883	116	0.19	0-1000	(200-500)
Family Euchaetidae Giesbrecht, 1892				
Paraeuchaeta spp.	2824	4.62	0-1000	(50-200)
P. antarctica (Giesbrecht, 1902) adults	31	87.37	100-1000	(500-1000)
P. rasa Farran, 1929 adults	3	9.34	100-1000	(500-1000)
P. similis (Wolfenden, 1908) adults	1	3.29	500-1000	
Family Heterorhabdidae Sars, 1902				
Heterorhabdus austrinus Giesbrecht, 1902	455	0.75	0-1000	(200-500)
H. farrani Brady, 1918	88	0.14	50-1000	(500-1000)
Heterostylitis major (F. Dahl, 1894)	4	0.01	200-1000	(200-500)
Family Lucicutiidae Sars, 1902				
Lucicutia spp.	354	0.58	0-1000	(500-1000)
L. curta Farran, 1905 adults	1	2.48	500-1000	
L. macrocera Sars, 1920 adults	6	20.47	500-1000	
L. ovalis (Giesbrecht, 1889) adults	23	75.82	500-1000	
L. wolfendeni Sewell, 1932 adults	<1	1.23	500-1000	
Family Metridinidae Sars, 1902				
Metridia curticauda Giesbrecht, 1889	271	0.44	100-1000	(500-1000)
M. gerlachei Giesbrecht, 1902	4443	7.27	0-1000	(0-50)

Table 2 b. For description see above.

Species	Abundance (Ind. per 1000 m^3)	Frequency (%)	Depth range (m)	
Calanoida Sars, 1903 (continuation from table 2 a)				
Family Phaennidae Sars, 1902				
Cephalophanes frigidus Wolfenden, 1911	1	<0.01	500-1000	
**Cornucalanus robustus* Vervoort, 1957	<1	<0.01	500-1000	
Onchocalanus wolfendeni Vervoort, 1950	3	0.01	200-1000	(500-1000)
Family Scolecitrichidae Giesbrecht, 1892				
Racovitzanus antarcticus Giesbrecht, 1902	14	0.02	100-1000	(200-500)
Scaphocalanus spp.	1142	1.87	0-1000	(500-1000)
S. antarcticus Park, 1982 adults	2	1.01	500-1000	
S. farrani Park, 1982 adults	2	1.26	200-1000	(200-500)
S. subbrevicornis (Wolfenden, 1911) adults	8	4.96	200-1000	(500-1000)
S. vervoortii Park, 1982 adults	156	91.85	50-1000	(200-500)
**Scaphocalanus* sp. adults	2	0.92	500-1000	
Scolecithricella altera (Farran, 1929)	3	<0.01	500-1000	
S. cenotelis Park, 1980	85	0.14	100-1000	(500-1000)
S. dentipes Vervoort, 1951	24	0.04	200-1000	(500-1000)
S. emarginata (Farran, 1905)	5	0.01	0-1000	(500-1000)
S. minor (Brady. 1883)	72	0.12	0-1000	(50-200)
S. schizosoma Park, 1980	4	0.01	500-1000	
**Scolecitricella* sp.	1	<0.01	500-1000	
Family Spinocalanidae Vervoort, 1951				
Mimocalanus cultifer Farran, 1908	5	0.01	500-1000	
M. nudus Farran, 1908	7	0.01	500-1000	
**Mospicalanus schielae* Schulz, 1996	2	<0.01	200-1000	(500-1000)
Spinocalanus antarcticus Wolfenden, 1906	5	0.01	500-1000	
S. longicornis Sars, 1900	2168	3.55	0-1000	(500-1000)
S. terranovae Damkaer, 1975	81	0.13	200-1000	(500-1000)
**Spinocalanus* sp.	2	<0.01	500-1000	
Teneriforma meteorae Schulz, 1989	4	0.01	500-1000	
Family Stephidae Sars, 1902				
**Stephos longipes* (Giesbrecht, 1902)	1	<0.01	0-100	(0-50)
Family Temoridae Giesbrecht, 1892				
Temoropia sp.	1	<0.01	500-1000	
Family Tharybidae Sars, 1902				
Tharybis magna Bradford, 1983	3	<0.01	500-1000	
Unidentified	3	<0.01	0-1000	
Mormonilloida Boxshall, 1979	**69**	**0.03**		
Mormonilla sp.	69	100.00	100-1000	(500-1000)
Cyclopoida Burmeister, 1834	**198716**	**76.46**		
Family Oithonidae Dana, 1853				
Oithona spp.	33081	16.65	0-1000	(0-50)
Family Oncaeidae Dana, 1853				
Oncaea spp.	165608	83.34	0-1000	(200-500)
Lubbockia spp.	26	0.01	100-1000	(500-1000)
Harpacticoida Sars, 1903	**25**	**0.01**		
Family Ameiridae Monard, 1927				
**Nitocra gracilimana* (Giesbrecht, 1902)	1	2.47	100-200	
Family Ectinosomatidae Dana, 1853				
Ectinosoma melaniceps Boeck, 1865	2	8.36	0-50	
Hastigerella antarctica Dahms & Schminke, 1992	1	5.26	0-50	
Microsetella sp.	5	18.50	0-500	(50-100)
Family Thalestridae Sars, 1905				
Idomene antarctica (Giesbrecht, 1902)	1	5.32	0-100	
Family Tisbidae Stebbing, 1910				
Drescheriella spp.	15	60.09	0-100	
Drescheriella glacialis Dahms & Dieckmann, 1987 adults	4	71.81	0-50	
D. racovitzai (Giesbrecht, 1902) adults	2	28.19	0-100	(0-50)

Table 3. Species contributions for 90 % of the average dissimilarity of the depth groups identified by cluster analysis. Average dissimilarity between groups is given in brackets. Ab = average abundance (Ind. m^{-3}), % = cumulative percentage.

Groups 2 and 3 (30.28)

	Ab2	Ab3	%
M. pygmaeus	35	57	57.04
C. acutus	3	7	66.50
Paraeuchaeta spp.	<1	4	75.94
M. gerlachei	6	3	82.42
S. longicornis	4	2	88.42
Scaphocalanus spp.	2	1	90.84

Groups 2 and 4 (45.53)

	Ab2	Ab4	%
M. pygmaeus	35	75	56.05
Paraeuchaeta spp.	<1	12	73.56
C. acutus	3	8	79.81
S. longicornis	4	<1	85.59
M. gerlachei	6	2	90.62

Groups 3 and 4 (22.86)

	Ab3	Ab4	%
M. pygmaeus	57	75	55.28
Paraeuchaeta spp.	4	12	75.94
C. acutus	7	8	81.40
S. longicornis	2	<1	85.65
M. gerlachei	3	2	89.81
Scaphocalanus spp.	1	<1	92.55

Groups 2 and 5 (59.17)

	Ab2	Ab5	%
M. pygmaeus	35	45	48.20
Paraeuchaeta spp.	<1	13	68.13
M. gerlachei	6	1	75.96
S. longicornis	4	<1	82.13
C. acutus	3	7	87.53
C. citer	<1	2	90.82

Groups 3 and 5 (52.02)

	Ab3	Ab5	%
M. pygmaeus	57	45	68.45
Paraeuchaeta spp.	4	13	81.24
C. acutus	7	7	85.32
M. gerlachei	3	1	88.92
Ctenocalanus citer	<1	2	91.87

Groups 4 and 5 (45.29)

	Ab4	Ab5	%
M. pygmaeus	75	45	84.13
Paraeuchaeta spp.	12	13	89.00
C. acutus	8	7	93.58

Groups 2 and 7 (66.20)

	Ab2	Ab7	%
M. pygmaeus	35	5	55.34
M. gerlachei	6	10	65.61
S. longicornis	4	<1	72.87
C. acutusc	3	6	79.92
Paraeuchaeta spp.	<1	2	84.07
Scaphocalanus spp.	2	<1	87.28
C. propinquus	<1	2	90.31

Groups 3 and 7 (70.00)

	Ab3	Ab7	%
M. pygmaeus	57	5	71.32
M. gerlachei	3	10	80.69
C. acutus	7	6	86.13
Paraeuchaeta spp.	4	2	88.62
S. longicornis	2	<1	90.83

Groups 4 and 7 (74.87)

	Ab4	Ab7	%
M. pygmaeus	75	5	72.62
Paraeuchaeta spp.	12	2	83.20
M. gerlachei	2	10	91.41

Groups 5 and 7 (63.82)

	Ab5	Ab7	%
M. pygmaeus	45	5	45.57
Paraeuchaeta spp.	13	2	66.44
M. gerlachei	1	10	84.54
C. acutus	7	6	93.10

Figures

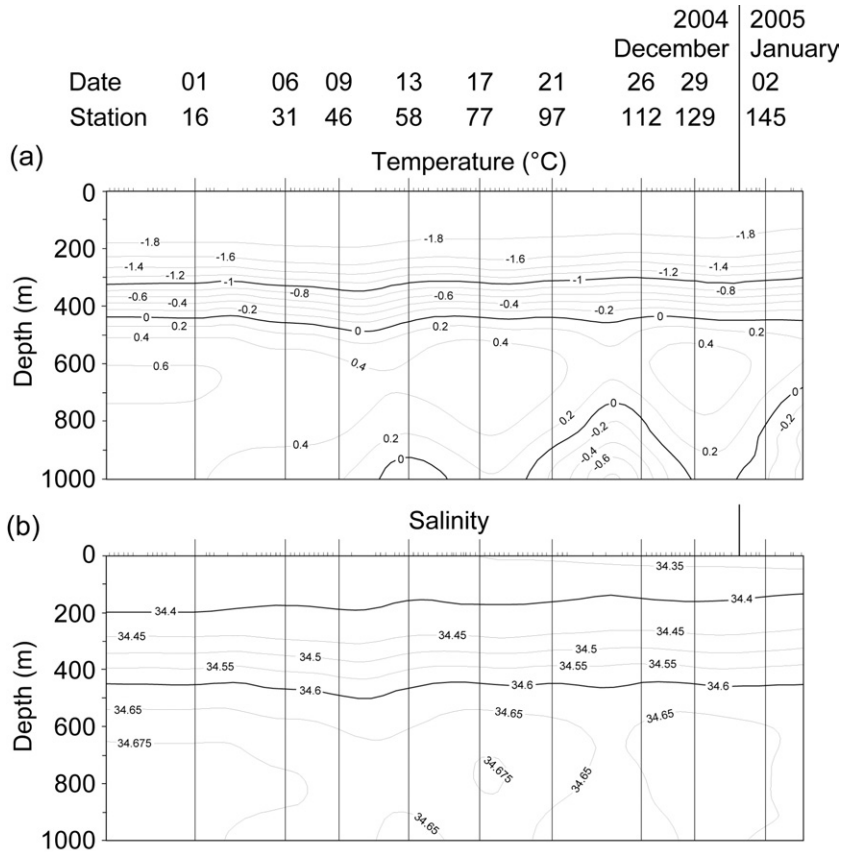

Fig. 1. Potential temperature (a) and salinity (b) within the upper 1000 m during ISPOL. Vertical lines indicate the date of zooplankton sampling.

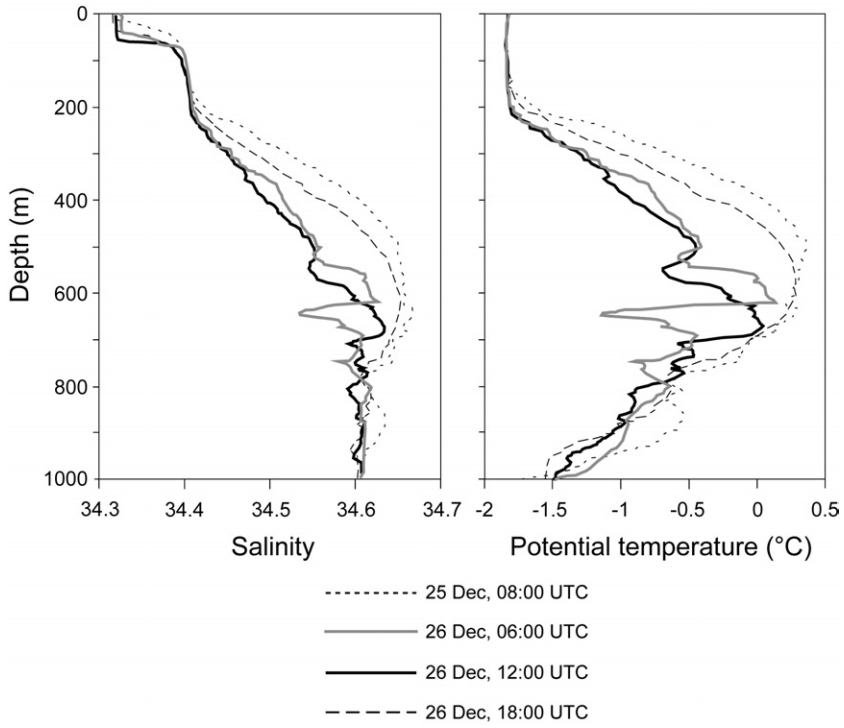

Fig. 2. Potential temperature and salinity profiles on 25 and 26 December 2004.

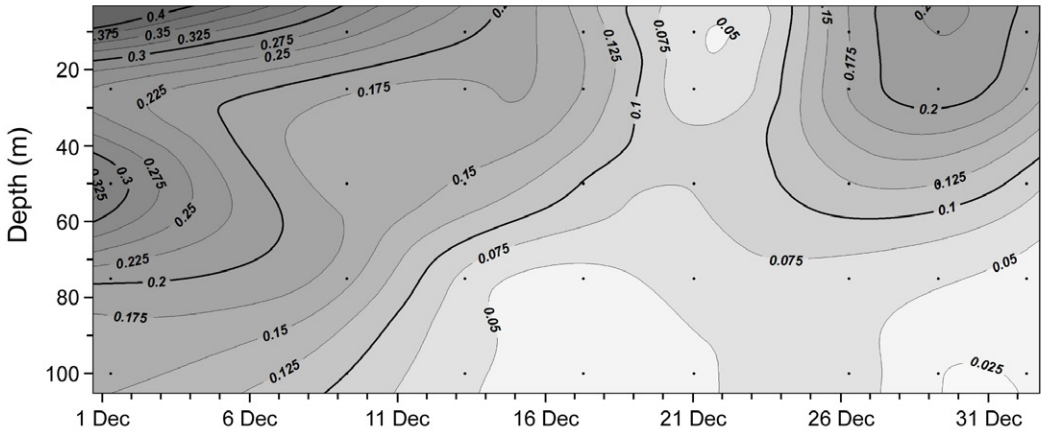

Fig. 3. Vertical distribution of the Chl *a* concentration in the upper 100 m during ISPOL. Points indicate the sampling depths. The graph was created using the software Ocean Data View (http://odv.awi.de).

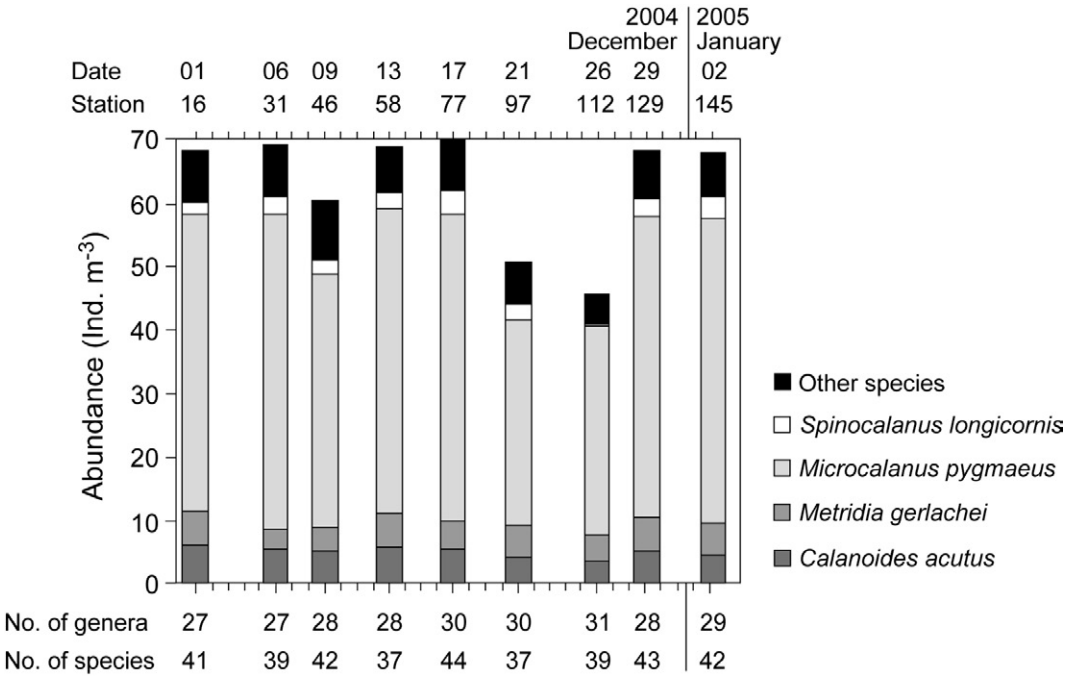

Fig. 4. Temporal change in abundance (Ind. m^{-3}) of total calanoid copepods, species composition, and number of genera and species.

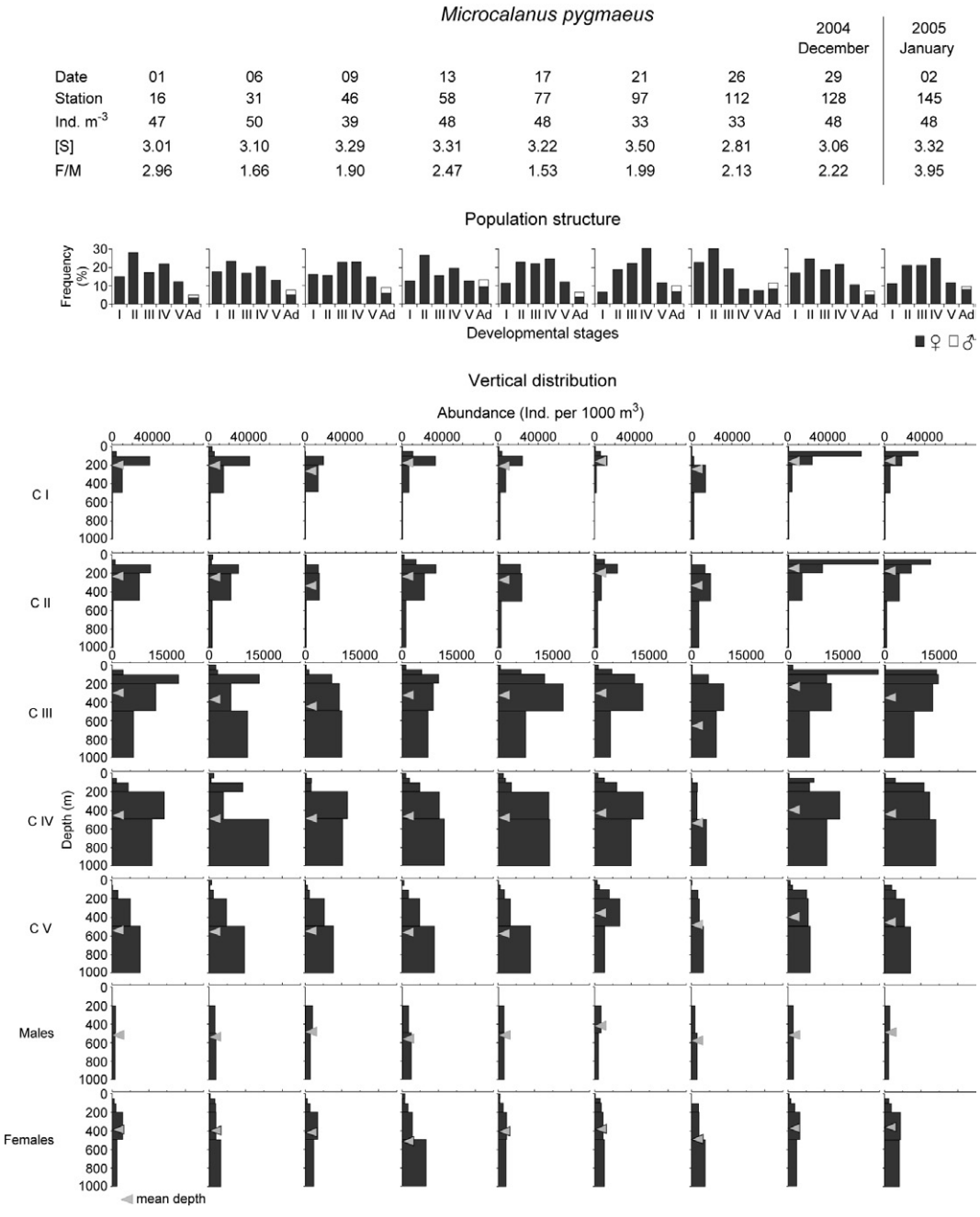

Fig. 5. Temporal change in total abundance (Ind. m^{-3}), mean population stage ([S]), sex ratio (F/M), population structure and vertical distribution of *M. pygmaeus*.

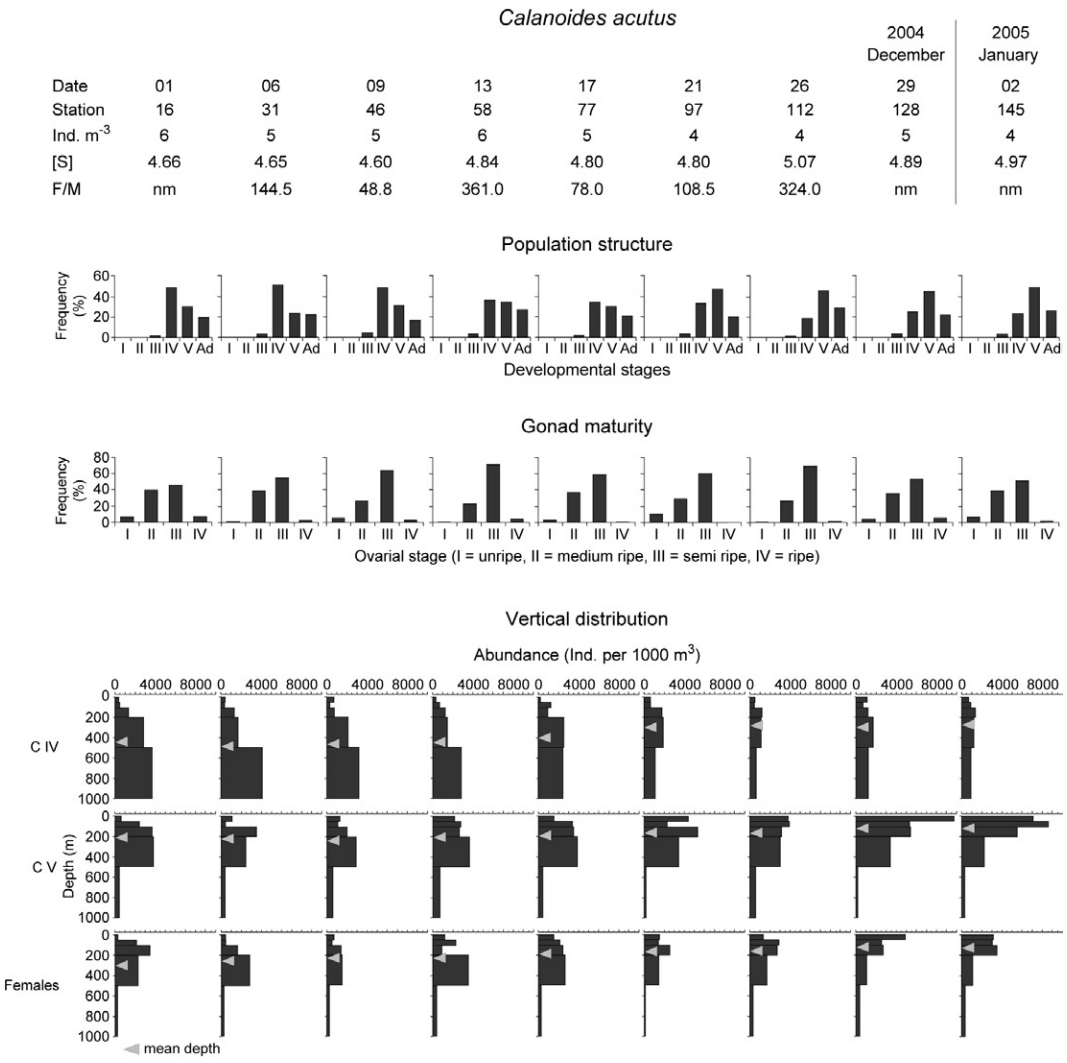

Fig. 6. Temporal change in total abundance (Ind. m^{-3}), mean population stage ([S]), sex ratio (F/M), population structure, gonad maturity and vertical distribution of *C. acutus*.

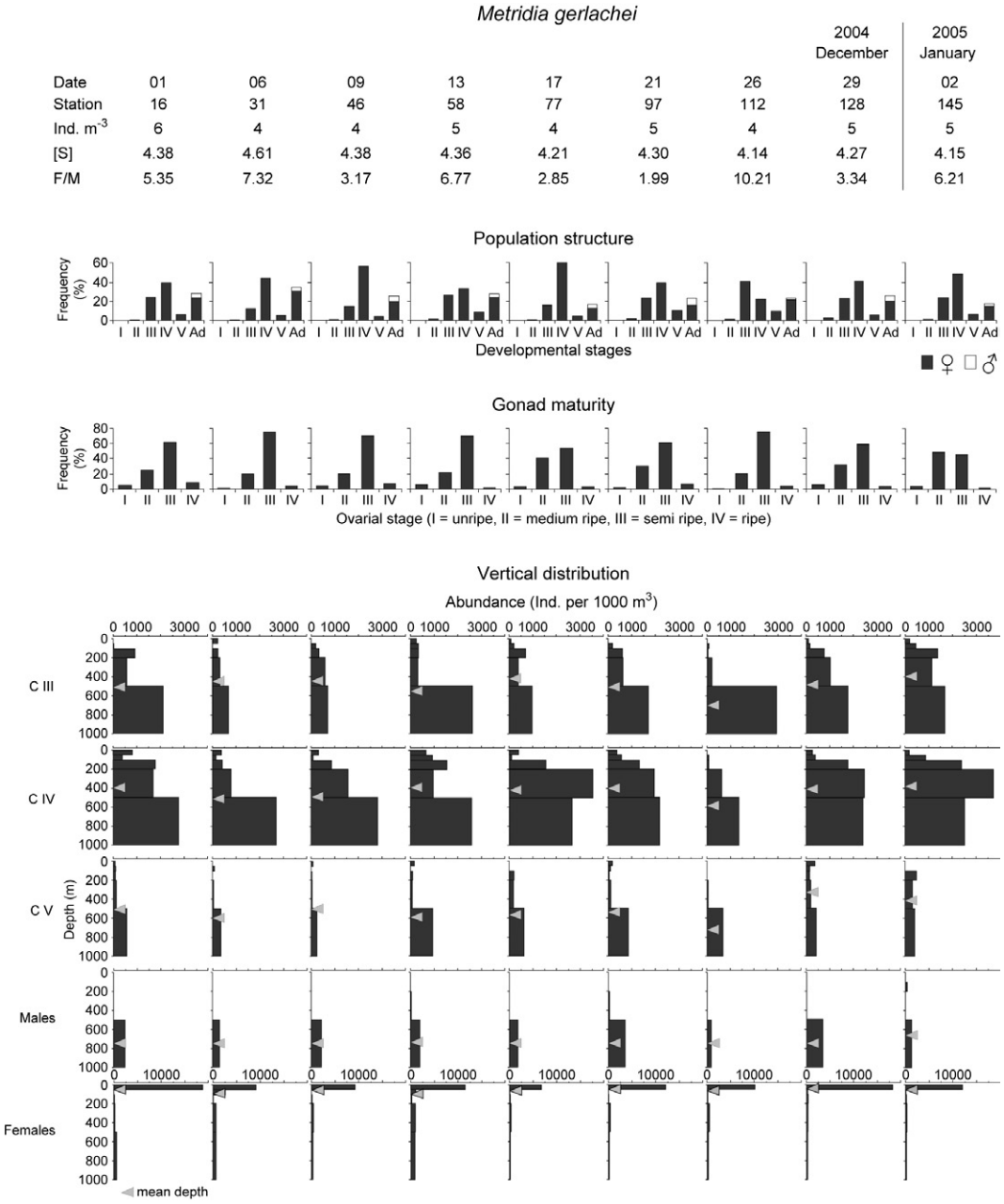

Fig. 7. Temporal change in total abundance (Ind. m^{-3}), mean population stage ([S]), sex ratio (F/M), population structure, gonad maturity and vertical distribution of *M. gerlachei*.

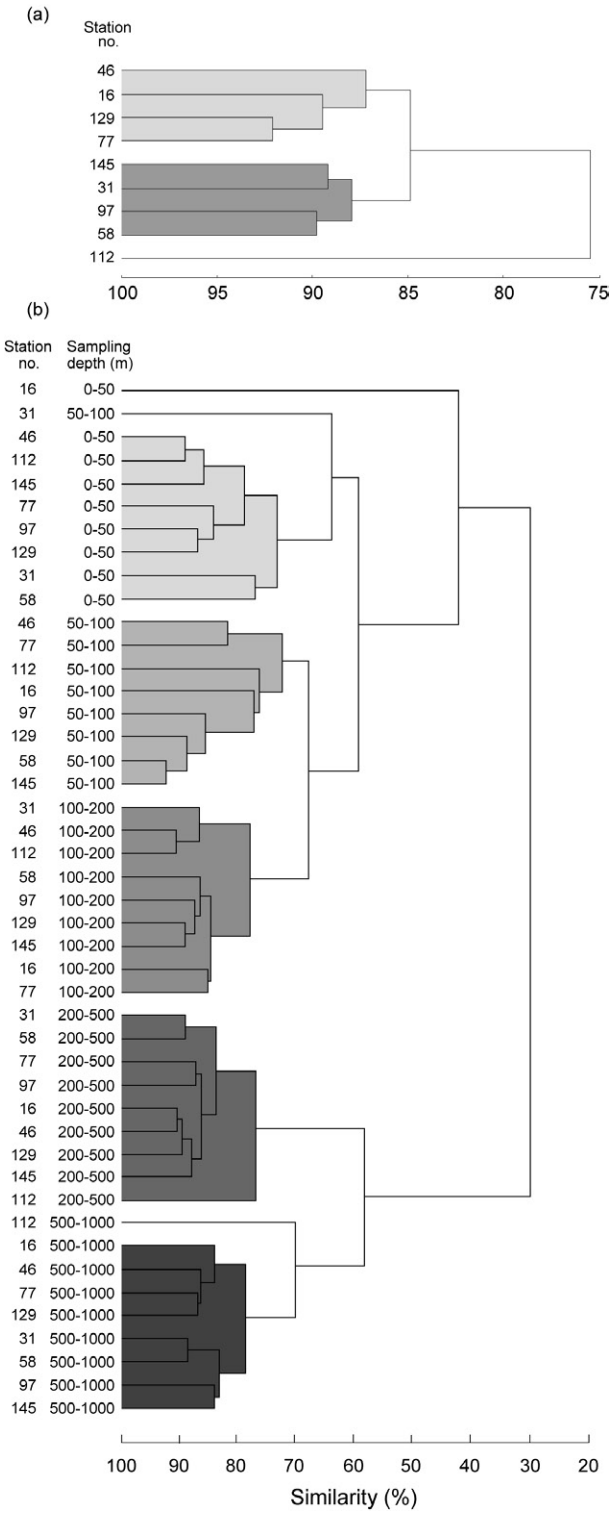

Fig. 8. Cluster analysis dendrogram of calanoid copepod species showing classification of stations (a) and depth layers (b).

Manuscript VI

Abundance, population structure and vertical distribution of dominant calanoid copepods on the eastern Weddell Sea shelf during a spring phytoplankton bloom

Abstract

The short-term development of abundance, population structure and vertical distribution of the dominant calanoid copepods *Microcalanus pygmaeus*, *Metridia gerlachei*, *Ctenocalanus citer*, *Calanoides acutus*, *Calanus propinquus* and *Stephos longipes* was investigated for almost three weeks during the expedition ANT XXI/2 to the coastal area of the eastern Weddell Sea in December 2003. A phytoplankton bloom developed during the study period. *M. pygmaeus* dominated numerically and contributed up to 75.7 % of all calanoid copepods. The population of this species was mainly found below a depth of 100 m. Copepodids (C) III were most abundant. Males contributed only a small fraction. All other developmental stages were found in comparable proportions. A rather consistent population structure and no conspicuous changes in vertical distribution and abundance were observed. The results support the suggestions of earlier studies that in *M. pygmaeus* reproduction and growth take place year-round and are not related to the spring phytoplankton bloom. In *M. gerlachei* females and C III - V dominated the population. Males were only found in deep water layers, and most of the C I stayed below a depth of 300 m at the beginning of the study. This indicates that mating and egg-laying had taken place in mid and deep water layers. Before a strong storm in the final stage of the study, the proportion of C I increased strongly from 1 to 22.5 %. On the first sampling date, the *C. citer* population consisted mainly of females and C V, whereas C I became also very dominant about one week later. In *C. acutus* the population was dominated by females and C IV and C V. C I and C II were absent. The results suggest that the diapause of this species had ended not long before the study. Most of the females had already migrated upwards into the surface layer, while the C IV and C V ascended to the surface layer in the course of the observation period. The population of *C. propinquus* was dominated by C III - V. The first C I were found in mid-December, and C II occurred one week later. At the end of the study, C I contributed a large portion (22.5 %) to the population. C I and C II were mostly located in the surface layer indicating that reproduction had taken place mainly there. The results suggest that reproduction in *M. gerlachei*, *C. citer* and *C. propinquus* had already begun some weeks before the onset of the phytoplankton bloom, while egg-laying in *C. acutus* had not started long before the beginning of the bloom. *S. longipes* was found primarily in the upper 100 m of the water column throughout the whole observation period, and its population was dominated by adults and C I. After the strong storm, the abundance increased strongly and C I contributed 53 % of the total population indicating that the early copepodids had probably been released from the sea ice into the under ice water layer due to ice break-up and ice melt.

Keywords Dominant pelagic copepod species · Population dynamics · Vertical distribution · Spring phytoplankton bloom · Weddell Sea

Introduction

The Southern Ocean is characterised by pronounced seasonal changes in light conditions, ice cover and hence primary production. In winter, the phytoplankton growth is limited due to the low availability of light and a large mixed layer depth often resulting in chlorophyll *a* (Chl *a*) concentrations as low as < 0.02 µg L^{-1} (Nöthig et al. 1991; Scharek et al. 1994). Therefore, the food supply for copepod species, which mainly feed on phytoplankton, strongly differs between seasons, and the copepods must be able to cope with long periods of food scarcity or to switch to alternate food sources. Many aspects of the life cycles and overwintering strategies of several dominant calanoid copepod species inhabiting the Southern Ocean have been studied (e.g. Atkinson 1998; Schnack-Schiel 2001). In most of the studies the information on the life cycles and the population dynamics has been composed from samples taken from large areas of the Southern Ocean. Often the plankton communities have been sampled on single dates only or in time intervals, which have been longer than a few days. Hence little information on the short-term evolution of copepod populations during the spring development is available. In spring, many copepod species face rather rapid changes in the environmental conditions in the surface layer caused by processes such as ice melt and phytoplankton blooms. Besides interannual variability in the onset of phytoplankton blooms, regional differences occur in intensity and timing of primary production (e.g. Tréguer and Jacques 1992; Laubscher et al. 1993). Consequently, the copepod species, which depend on phytoplankton blooms, have to react rapidly to changes in food availability in order to adjust the timing of the reproduction to the season of high phytoplankton supply.

During the expedition ANT XXI/2 with the research vessel “Polarstern” to the eastern Weddell Sea in December 2003, plankton samples could be collected continuously on a quasi-permanent station for almost three weeks. The station was located in the Weddell Sea coastal zone on the shelf off Austasen, an area which is characterised by the presence of fast ice for a major part of the year, polynyas and a pack-ice zone consisting of highly deformed ice (Eicken 1992). The goal of the present study was to investigate short-term changes in abundance, population structure and vertical distribution of the dominant calanoid copepods in order to assess the development of their populations during the initial phase of the spring development.

Material and Methods

Investigation area

The sampling site was located at 70° 48.558' S and 10° 43.698' W (Fig. 1). It was regularly visited by RV “Polarstern” between 9 and 28 December 2003, enabling plankton and water sampling at frequent intervals. Due to the rapidly changing sea

ice situation the vessel could not always be navigated exactly to the same coordinates, however, all sampling spots were located inside a very small area of 1.5 x 0.9 km, which can thus be considered as a quasi-permanent station. The water depth at the sampling spots varied between 438 and 484 m.

Measurements and sampling on board RV “Polarstern”

Data on wind direction and wind velocity were extracted from the “Polarstern Data Acquisition System” (PODAS), which archives the continuously recorded standard meteorological parameters. 15 CTD casts were performed regularly using a calibrated Sea-Bird 911*plus* CTD. In addition to the standard sensors the CTD was equipped with a fluorescence (Chl *a* fluorescence) and a turbidity sensor. A difference criterion described by Cisewski et al. (2005) was used to calculate the mixed layer depth (MLD) from the density field.

Water samples were collected with a CTD multi-bottle rosette sampler equipped with twenty-four 12-L Niskin bottles (General Oceanics). Sub-samples for the analysis of Chl *a* were filtered on GF/F filters (Whatman) and immediately frozen at -20 °C. For microscopic analyses sub-samples were taken from 5 m depth on all sampling dates, while sub-samples from multiple depths distributed over the entire water column were taken only on the last four sampling dates. The samples were stored in 100 ml brown-glass bottles and fixed with Borax buffered 38 % formalin (final formalin/seawater solution of 1.9 %).

Zooplankton was sampled with a multiple opening/closing net system (0.25 m^2 aperture) equipped with five nets of 100 µm mesh-size. Vertical, stratified hauls from the bottom to 300 m, 300 - 200 m, 200 - 100 m, 100 - 50 m and 50 - 0 m were sampled with a velocity of 0.5 - 1 m s^{-1}. The filtered volume was determined by a digital flow meter installed at the net system. The samples were preserved with Borax buffered 38 % formalin (final formalin/seawater solution of 3.8 %).

Sample analyses in the institute

Chlorophyll a *and phytoplankton*

To extract Chl *a*, the filters were placed in 10 ml of 90 % acetone and ultrasonified. Subsequently the Chl *a* concentrations were measured using a photometer according to the method of Jeffrey and Humphrey (1975). In total, data of 112 Chl *a* samples were used to calibrate the fluorescence sensor of the CTD. These samples had been taken in six depth layers between the surface and the seafloor regularly during the study period. No significant correlation between the Chl *a* concentrations and the fluorescence values was found. Therefore, a correlation model based on the Chl *a* data and both the turbidity and fluorescence data was established. This model showed a significant correlation justifying the calculation of Chl *a* data from the fluorescence and turbidity data.

Phytoplankton composition and concentration were determined using inverted light microscopy according to Utermöhl (1958). Phytoplankton cell volume was converted to cellular carbon content by means of carbon conversion equations recommended by Menden-Deuer and Lessard (2000).

Copepods

The copepod samples were split into sub-samples (1/2 to 1/32, depending on density) using a Folsom splitter. Rare taxa and developmental stages were counted from the entire sample. With five exceptions (*Chiridius* sp., *Euchirella* sp., *Drescheriella* spp., *Microsetella* sp. and *Ectinosoma* sp.) calanoid and harpacticoid copepods were identified to species level, while the cyclopoid copepods were only identified to genus level. Copepodite stages of the calanoid copepod genera *Lucicutia, Paraeuchaeta* and *Scaphocalanus* (except for *S. antarcticus*) were not identified to species level. Developmental stage and sex were determined within the dominant calanoid species *Microcalanus pygmaeus*, *Metridia gerlachei*, *Ctenocalanus citer*, *Calanoides acutus*, *Calanus propinquus* and *Stephos longipes*. The geometric mean was used to calculate the mean abundance. The mean population stage was calculated after Marin (1987), and the weighted mean depth (WMD) according to Bollens and Frost (1989).

Results

Environmental parameters

Based on velocity and direction, the observed wind situation can be divided in four periods with different conditions (Fig. 2): in the periods 1 (from 9 to afternoon of 15 December) and 3 (from 19 to afternoon of 24 December) the wind direction varied strongly, and fluctuation of the wind velocity was recorded. The velocity had maximum values of 13.5 and 11.9 m s^{-1} during these periods, respectively. In the first half of period 3 the wind calmed down to a maximum velocity of 2 - 2.5 m s^{-1}. During the periods 2 (between afternoon of 15 and 19 December) and 4 (between afternoon of 24 and 28 December) the wind direction changed only slightly, and wind from east was dominant. In the latter period a strong storm with a maximum wind velocity of 35.8 m s^{-1} developed rapidly and lasted more than two days. During period 2 the wind velocity was higher than in the periods 1 and 3 and reached a maximum value of 17.2 m s^{-1}.

Until the storm, the degree of sea ice cover decreased slightly from about 65 to about 60 %. After the storm the degree of ice cover had increased to about 80 %. Northeast of the study area, the degree of ice cover decreased strongly during the investigation period, and after the storm a large area was free of sea ice (Carpenter et al. 2007;

see also IRI Data Library [http://iri.ldeo.columbia.edu/]: IGOSS nmc Reyn_SmithOIv2 weekly Sea Ice Concentration). The strong easterly storm probably pressed the sea ice towards the shelf ice edge and thus caused the higher degree of ice cover at the sampling site, and the ice free area further to the northeast.

The overall ranges of temperature and salinity in the water column were -1.95 to -1.03 °C and 34.01 to 34.45, respectively (Fig. 3). The water column had a stratification characterised by a relatively warm and less saline surface layer and underlying colder and more saline water layers. The temperature of the surface layer increased until 17 December followed by slightly cooler temperatures. The surface layer reached the highest temperatures from 22 to 25 (noon) December. The salinitiy of the surface layer freshened strongly from 14 December on. This process was most pronounced during the last few days of the observation period. The MLD decreased from 81 to 17 m until the evening of 15 December, and then slightly increased to 39.5 m until the afternoon of 18 December. It subsequently strongly decreased strongly to 7.5 m until the noon of 22 December, and then rose strongly to 94 m during the intense storm.

The Chl *a* standing stock in the upper 150 m of the water column increased during the observation period (maximum value: 221.5 mg m^{-2}, Fig. 4 a). From 14 December on a maximum of the Chl *a* concentration developed rapidly in the upper 50 - 100 m (maximum concentration: 2.16 µg L^{-1}, Fig. 4 b). During and after the storm this maximum extended to greater depths. Maximum Chl *a* concentrations with values slightly above 2 µg L^{-1} occurred close to the surface between 21 and 25 December.

Phytoplankton

The phytoplankton carbon biomass varied and was dominated by diatoms and flagellates throughout the entire observation period (Figs. 5 and 6). At 5 m depth the diatom carbon biomass increased steadily until the storm and the dropped (Fig. 5).

On the days before the storm (22 and 23 December) the phytoplankton carbon biomass was concentrated in the upper 25 m, whereas after the storm (27 and 28 December) higher phytoplankton biomass concentrations were also found in deeper water layers down to the seafloor (Fig. 6). Accordingly, before the storm diatoms and *Phaeocystis* spp. were mainly found in the upper 25 m where they contributed a large part of the overall phytoplankton biomass. After the storm, they also occurred in deeper water layers down to 100 m and to the seafloor, respectively.

Composition and abundance of the copepod fauna

In total 31 copepod genera and at least 42 species were found (Table 1). Cyclopoid copepods strongly dominated the copepod community (66.5 - 84.9 %). Calanoid copepods contributed between 15 and 30.3 % of the total. Harpacticoid copepods

were found only rarely, and with the exception of *Microsetella* sp. all species found are known to inhabit the sea ice (Schnack-Schiel et al. submitted).

The abundance of the calanoid copepod fauna ranged from 66 to 112 ind. m^{-3} (Fig. 7) with a mean abundance of 81.24 ind. m^{-3}. The composition of the calanoid copepod community varied with maximum numbers of genera (20) and species (25) found on the first sampling date. The proportions of the dominant species fluctuated only slightly (Fig. 7). *Microcalanus pygmaeus* was the most dominant species contributing 50.3 - 75.7 % of the total calanoid copepods. Other dominant species were *Metridia gerlachei* (8.6 - 19.3 %) and *Ctenocalanus citer* (9.3 - 17.2 %). The large species *Calanoides acutus* and *Calanus propinquus* were also present in considerable proportions (0.5 - 4.2 and 0.8 - 1.9 %, respectively). *Stephos longipes* contributed a relatively large amount (8.8 %) only on the last sampling date (morning of 27 December).

Abundance, vertical distribution and population structure of dominant calanoid copepods

The abundance of *Microcalanus pygmaeus* varied between 3504 and 8473 ind. $(100\ m^3)^{-1}$ (Fig. 8). Males contributed only a small fraction to the population. Copepodids (C) III were the dominant developmental stage throughout the observation period, which is in accordance with the mean population stage of 3.38 - 3.62. The other copepodite stages and the females were found in comparable proportions. All developmental stages were mainly found below 100 m depth. The WMDs of the different stages varied, with few exceptions, between 200 and 300 m without any trend.

In *Metridia gerlachei* the abundance ranged from 641 to 1837 ind. $(100\ m^3)^{-1}$ and increased strongly until the storm (Fig. 9). Females and C III - V dominated the population. With the progression of the observation period the C I became also an important part of the population: until the storm their proportion increased from 1 to 22.5 %. During the entire study period C II and males were not abundant. The mean population stage of *M. gerlachei* varied from 4.04 to 4.27 between 9 and 18 December. On the two sampling dates before the storm it was lower but increased to 4.73 after the storm. The females were mainly distributed in the mid and surface water layers. The C III - V were distributed over the entire water column, however, the centre of distribution of the C III was below 200 m depth all the time. The C I were found in higher densities only below 50 m depth, and the males and the C II were absent from the upper 50 m. It is conspicuous that the C I were mainly found in deep water layers on the first two sampling dates, while their bulk was distributed in higher water layers with the progression of the observation period, and on the last sampling day C I were primarily found between 100 and 200 m depth. While the WMD of the C I decreased from 317 to 170 m, the WMDs of the other developmental stages varied without trend.

The abundance of *Ctenocalanus citer* varied between 694 and 1785 ind. (100 m^3)$^{-1}$ (Fig. 10). On the first two sampling dates the population consisted mainly of females and C V whereas later in the season C I also became very dominant. From 22 December on females and C I contributed the major part of the population. The mean population stage decreased distinctly from 4.99 to 3.03 until 22 December and was again higher on the last two sampling dates. At the beginning of the study, the females and the C II - V were mainly found in the depth layer of 100 - 200 m. Later their WMDs decreased and they were primarily distributed in the upper 100 m one day before the storm (23 December). The bulk of the males remained in mid and deep water layers below 50 m depth all the time. The C I had the highest densities in the deep water layers on the first sampling date and ascended with the progression of the observation period resulting in a decrease of the WMD from 297 to 153 m. In the other developmental stages the WMDs varied without any trend. After the storm the WMDs of the females and the C II - V had increased compared to those on the last sampling day before the storm.

The total abundance of *Calanoides acutus* varied between 43 and 293 ind. (100 m^3)$^{-1}$ (Fig. 11). The population was dominated by females and C IV and C V, while C I and C II were not found at all. In total only four males were found (below 200 m depth, on 12 and 22 December). The mean population stage varied from 4.52 to 5.33. The females were mainly found in the upper 200 m while the copepodids also occurred in deeper water layers down to the seafloor. Most striking temporal changes in the vertical distribution were observed in the C V: on 9 December the major part of the population was located below 300 m depth, whereas on 23 December C V were mainly found in the upper 100 m. In that period, the WMD of the C IV and C V decreased from 183 to 67 m and from 244 to 58 m, respectively. The WMD of the C III varied without trend. After the storm (on the last sampling date), the sub-populations of all developmental stages were located deeper in the water column indicated by the increased WMDs compared to those on the day before the storm.

In *Calanus propinquus* the abundance ranged from 68 to 155 ind. (100 m^3)$^{-1}$ (Fig. 12). The population was dominated by C III - V. C I and C II did not occurr until 15 and 22 December, respectively. On the last sampling day (27 December) C I contributed a large part (22.5 %) of the population. Males were rare (< 2.2 %) and not found in the samples of 9 and 22 December. The mean population stage varied from 3.81 to 4.12 until 23 December, whereas it was lower (3.45) on the last sampling date due to the high abundance of the C I. The late copepodids (III - V) and the adults were mainly found in the mid and deep water layers below 50 - 100 m, while the earlier copepodids (I + II) were mostly located in the surface layers.

Before the storm, the abundance of *Stephos longipes* ranged from 35 to 144 ind. (100 m^3)$^{-1}$ whereas it was 611 ind. (100 m^3)$^{-1}$ after the storm (Fig. 13). Until the storm, the population was dominated by adults and C I, and the mean population stage varied between 3 and 4.74. On the last sampling date, the population was strongly dominated by C I contributing 53 % of the total population. Accordingly, the mean population stage was much lower (2.19) than before the storm. With few exceptions, all developmental stages were found primarily in the upper 100 m of the water column throughout the observation period.

Discussion

The copepod fauna observed during this study consisted mainly of cyclopoid copepods. In the Southern Ocean, small cyclopoid copepods often dominate the copepod community in terms of numbers and contribute biomasses similar to those of the calanoid copepods (e.g. Metz 1996). In the Weddell Sea, a dominance of only a few species is characteristic for the copepod community, and often more than 95 % of all individuals and more than 80 % of the total copepod biomass are contributed by the large calanoids *Calanoides acutus*, *Calanus propinquus*, *Metridia gerlachei* and *Paraeuchaeta antarctica*, the small calanoids *Microcalanus pygmaeus* and *Ctenocalanus citer* and the small cyclopoids *Oithona* spp. and *Oncaea* spp. (Schnack-Schiel et al. 1998). As in the present study, populations of calanoid copepods are often dominated by the small clausocalanoid copepod *M. pygmaeus*, which can by far be the most abundant species attaining numerically two-thirds of all calanoids and contributing 14 % of the annual mean calanoid biomass (Schnack-Schiel 2001). In summer *S. longipes* was observed to be the dominant calanoid copepod within the upper 50 m of the water column on the continental shelf of the southeastern Weddell Sea (Kurbjeweit et al. 1993).

This study focused on the dominant calanoid copepods because of their importance in terms of biomass. The results suggest that a spring phytoplankton bloom developed during the observation period. Due to low wind speeds on the first few sampling days the mixed layer depth (MLD) strongly decreased enabling the onset of the bloom. The calm wind conditions between 19 and 22 December and the freshening and warming of the surface layer resulted in a very small MLD and a strong stratification. This facilitated the increase in the concentration of phytoplankton biomass in the surface layer. The strong storm caused an increase of the MLD and mixed the phytoplankton to greater depths. The enhanced phytoplankton biomass concentrations were probably mainly made up of diatoms, since the increase of the carbon biomass concentration in the surface layer was more pronounced in this phytoplankton group than in the others.

In *Microcalanus pygmaeus* all developmental stages were present and contributed comparable proportions to the population. Two exceptions were males and C III, which were least abundant and most dominant, respectively. Schnack-Schiel and Mizdalski (1994) observed a dominance of C II and C III in October and November (spring) whereas in January and February (summer) the dominance had shifted towards C IV. This shift was reflected by the mean population stage, which increased from about three in the spring to four in the summer. However, there was little variation in the stage frequency distribution and no obvious development of copepodite stages within a single season. Furthermore, the size of the *M. pygmaeus* population, predominantly mid-stage copepodids, was equal in spring and summer. Similarly, in the present study a consistent population structure and no conspicuous changes in vertical distribution and abundance were observed. Schnack-Schiel (2001) described low seasonal changes in abundance and the presence of all developmental stages throughout the year. These results suggest that in *M. pygmaeus* reproduction and growth occur all year-round and are not related to the

phytoplankton bloom. Kurbjeweit (1993) described year-round reproduction in *M. pygmaeus*, with stronger reproduction activities in spring and autumn. Another conspicuous result of the present study is the near absence of *M. pygmaeus* in the surface layer, which aligns with the results of a study conducted at the Antarctic Peninsula (Żmijewska et al. 1999). *M. pygmaeus* appears to prefer mid and deep water layers where phytoplankton nutrition is very scarce. In some studies on the diet composition of *M. pygmaeus* most of the determinable food items have been phytoplankton (e.g. Hopkins and Torres 1989; Pasternak and Schnack-Schiel 2001a). However, this species must have additional food sources to be able to remain active in deep water layers and in winter. An overwhelming proportion of unidentifiable mass found in guts of *M. pygmaeus* in winter (Pasternak and Schnack-Schiel 2001a) leads to the assumption that *M. pygmaeus* ingests whatever possible including a large amount of detritus and protozoans. The gnathobase morphology strongly indicates feeding on proto- and metazoans (Michels and Schnack-Schiel 2005), and Hopkins (1985) and Hopkins et al. (1993b) found pieces of metazoans in the guts of *M. pygmaeus*. It is very likely that fulfilling the energy demand via use of a broad food spectrum is one of the species' attributes which account for its numerical dominance in many areas of the Southern Ocean throughout the year.

The *Metridia gerlachei* population structure and its temporal development suggest that this species had started to reproduce some weeks before the onset of the spring bloom. In *M. gerlachei*, mating and egg-laying seems to begin before December, and more than one generation might be produced per year (Huntley and Escritor 1992). In the present study mating and egg-laying had probably taken place in mid and deep water layers since males were only found at these depths and most of the C I were found below 300 m depth at the beginning of the study. *M. gerlachei* is thought to prefer deeper water layers, and it has already been shown that the major part of the population can occur below a depth of 200 m (Huntley and Escritor 1992). The results of the present study agree with this. It is conspicuous that until the storm the proportion of C I increased strongly from 1 to 22.5 % while C II were not abundant until the end of the study. The new cohort might therefore have had relatively long moulting periods comparable to those observed by Huntley and Escritor (1992) who described a development from C I to C V of two months.

In *Ctenocalanus citer* the dominance of females and C V during the first days of this study is in accordance with observations conducted in the Croker Passage at the Antarctic Peninsula at the same time of the year (Żmijewska et al. 2000). The authors observed that females comprised 89 % of the population in the upper 400 m, the layer with the highest abundance, and the rest of the population was dominated by C V and males. In the present study the strong increase in abundance and dominance of C I from mid-December on suggests that the reproduction period had started in early spring, some time before the onset of the phytoplankton bloom. Similarly, the results of other studies revealed increased abundances of eggs, nauplii and ripe females in spring (Fransz 1988; Schnack-Schiel and Mizdalski 1994). Gonad maturity investigations indicated a partial decoupling of the reproduction from the spring phytoplankton bloom (Niehoff et al. 2002). Little is known about the life cycle of *C. citer*. Atkinson (1998) classified *C. citer* as a species with a winter

diapause. However, in the eastern Weddell Sea, Pasternak and Schnack-Schiel (2007) observed year-round feeding with highest feeding activities in winter. This suggests that the life cycle of *C. citer* does not include a resting phase. Although *C. citer* feeds mainly on phytoplankton (Hopkins and Torres 1989; Schnack-Schiel and Mizdalski 1994; Pasternak and Schnack-Schiel 2007), this species requires additional food sources during its active period in winter when phytoplankton is scarce. The observed high abundances of *C. citer* in the surface layer in winter suggest that *C. citer* feeds on ice algae during this season (Schnack-Schiel and Mizdalski 1994; Schnack-Schiel 2001). In fact, Pasternak and Schnack-Schiel (2007) found the ice-associated algae species *Fragilariopsis cylindrus, F. ritscheri* and *F. obliquecostata* in higher numbers in the guts of *C. citer* in winter. This additional food source enables *C. citer* to reproduce independently of the phytoplankton bloom in the water column.

In *Calanoides acutus* the population structure and the temporal evolution of the vertical distribution lead to the assumption that the diapause of this species had ended not long before the beginning of the observation period. The C IV and C V and the females were the dominant overwintering stages, which is in accordance with earlier observations (Marin 1988; Atkinson 1991; Bathmann et al. 1993; Schnack-Schiel and Hagen 1994; Atkinson et al. 1997; Spiridonov and Kosobokova 1997). At the beginning of the present study most of the females had already migrated upwards into the surface layer. In contrast, the major part of the C V was still below 300 m depth. During the study, the C IV and C V ascended to the surface layer. These observations corroborate the results of Atkinson et al. (1997) who described an ascent of the females before the spring bloom preceding that of the C IV and C V, and also of Schnack-Schiel et al. (1991) who observed a spring ascent of *C. acutus* females in November while C IV and C V remained at depth; later, in summer (January/February), most of the *C. acutus* were found above 200 m depth. *C. acutus* males have been observed to be present in higher numbers only in winter (Marin 1988; Atkinson 1991). Since they are mainly found below 500 m depth mating must take place in deep water layers (Marin 1988), and the spring ascent of the fertilised females to the surface layer is expected to be associated with egg-laying (Atkinson 1991). The absence of C I and C II in the present study is in accordance with the results of other studies in the Weddell Sea where no C I and C II were found in December (Atkinson et al. 1997; Schnack-Schiel et al. in press). *C. acutus* is known to feed almost exclusively on phytoplankton (e.g. Hopkins et al. 1993a) and to have a rather short reproduction period that is presumably well timed to coincide with the period of highest phytoplankton productivity (Atkinson 1998; Pasternak and Schnack-Schiel 2001b). In the absence of food, the egg production of *C. acutus* was observed to decrease strongly within a few days (Huntley and Escritor 1991). In *Calanus propinquus*, *Metridia gerlachei* and *Microcalanus pygmaeus* Kurbjeweit (1993) observed a development from the egg to the nauplius stages I and II of a few days. Assuming that the development in the later nauplius stages is similar, and that in *C. acutus* the development is comparable to that of the above mentioned species, it is likely that in the present study egg-laying in *C. acutus* had not started long before the onset of the phytoplankton bloom, even though about 80 % of the females had

ripe gonads at the beginning of the study (unpublished data). This is in accordance with an earlier study conducted in the eastern Weddell Sea: the proportion of females with ripe gonads strongly increased from mid-October on, and in mid-December more than half of the females had ripe gonads, and 15 % of the ovaries were semi-spent or spent (Hagen and Schnack-Schiel 1996).

In *Calanus propinquus* reproduction had most likely started some weeks before the onset of the phytoplankton bloom since the first C I were found in mid-December. In accordance with results of Marin (1988) who described mating of *C. propinquus* at the surface, the data indicate that reproduction had taken place mainly in the surface layer, where the occurrence of C I and C II coincided with the presence of relatively high phytoplankton biomass concentrations. Furthermore, there seems to have been strong development of the new cohort as the contribution of C I to the population increased rapidly and the first C II occurred one week after the first C I. This development rate is faster than that observed in summer, when the development from C I to C III took 3-4 weeks (Schnack-Schiel, unpublished data). Furthermore, it is much faster than the development from C I to C IV taking approximately 1.5 months, which was recorded in *Calanoides acutus* (Atkinson et al. 1997). The dominance of the population by C III and C IV at the beginning and by C IV later in this study suggests that the C III had contributed the largest part of the population in late winter whereas the dominance shifted to C IV during the spring development. Earlier studies on *C. propinquus* revealed a similar winter dominance of C III in surface waters of the central Weddell Sea (Bathmann et al. 1993) and in the coastal area of the southeastern Weddell Sea (Schnack-Schiel and Hagen 1995; Spiridonov and Kosobokova 1997). However, in other studies C V were found to be the dominant overwintering stage (Marin 1988; Marin and Schnack-Schiel 1993).

The decoupling of the reproduction period and the spring phytoplankton bloom in *Calanus propinquus* and *Metridia gerlachei* is in agreement with their life strategies. Since both species feed on phytoplankton and protozoans and also on small metazoans (Metz and Schnack-Schiel 1995), they are less dependent on phytoplankton blooms enabling them to have longer periods of feeding, growth and reproduction than *Calanoides acutus* (Atkinson 1998) and to remain active during winter (Marin 1988; Nöthig et al. 1991; Bathmann et al. 1993; Hopkins et al. 1993b; Schnack-Schiel and Hagen 1995; Pasternak and Schnack-Schiel 2001a). In accordance, the lipid composition of *C. propinquus* is dominated by triacylglycerols (Hagen et al. 1993; Kattner et al. 1994), and this lipid class also contributes a large fraction of the total lipids in *M. gerlachei* (Hagen 1988). Triacylglycerols are considered a short-term energy source and indicate continuous or frequent feeding (Hagen 1988; Hagen et al. 1993; Albers et al. 1996; Lee et al. 2006). In contrast, in *Calanoides acutus* the lipids consist mainly of wax esters, which are known to serve as long-term energy deposits and are characteristic for diapausing copepod species (Hagen et al. 1993; Kattner et al. 1994; Albers et al. 1996; Lee et al. 2006).

In *Stephos longipes* the dominance of adults and C I and the presence of all other developmental stages might suggest that intensive reproduction had started before the spring bloom. However, it is more likely that the present population consisted of two sub-populations with different origins: the adults might have been the

descendants of late copepodids, which had overwintered in deep water layers as assumed by Kurbjeweit et al. (1993) and Schnack-Schiel et al. (1995), while the early copepodids might have descended from the nauplii, which are found within the sea ice in winter (Schnack-Schiel et al. 1995) and spring (Guglielmo et al. 2007) and in rotten sea ice in summer (Schnack-Schiel et al. 1998, 2001). The present data on *S. longipes* is in agreement with results of Schnack-Schiel et al. (1995), who reported low abundances in the water column, mainly in the upper 50 m, in late winter/early spring (October - December). However, they found high abundances of *S. longipes* directly below and inside the sea ice. The population in the water column and the under ice water layer was dominated by adults whereas the sea ice was inhabited by nauplii and C I. The early copepodids found in the present study had probably been released from the sea ice into the under ice water layer due to ice break-up and ice melt. This effect was very pronounced during the storm when the freshening reached its maximum values indicating strong ice break-up and subsequent ice melt due to the wind force. These processes probably resulted in a release of early copepodids from the ice in the water column, which was so intensive that (1) the dominance of the *S. longipes* population by C I - III was particularly pronounced after the storm, (2) the abundance of *S. longipes* increased by one order of magnitude and (3) *S. longipes* contributed considerably to the whole population of calanoid copepods after the storm whereas it had not been an important contributor before.

Conclusions

During the present study the development of a spring phytoplankton bloom caused nutrition conditions favourable for copepods, in particular for species whose diet is mainly composed of phytoplankton and whose life cycle strategies are therefore related to the distinct seasonality of primary production in the Southern Ocean. Our results show that the dependence of the investigated copepod species on such spring phytoplankton blooms differs from species to species. Accordingly, differences in the population structure indicate a variation in the timing and duration of feeding, growth and reproduction periods of the different species. In *Microcalanus pygmaeus* reproduction does not depend on the phytoplankton bloom and growth and reproduction take place throughout the whole year. *Calanus propinquus*, *Metridia gerlachei* and *Ctenocalanus citer* had started their reproduction before the onset of the bloom indicating that there is no strong coupling between their reproduction period and the time of the phytoplankton bloom. *Calanoides acutus* depends strongly on phytoplankton supply. In this species egg-laying had probably not started long before the beginning of the spring phytoplankton bloom. In *Stephos longipes* the sea ice dynamics play an important role in shaping the structure of the sub-population inhabiting the water column in spring. Growth and development of nauplii and early copepodids of this species were not coupled with the spring phytoplankton bloom since ice algae can be used as an alternative food source. However, the release of *S. longipes* from the sea ice can coincide with the bloom period and therefore allow for the species' access to good nutritional conditions within the water column. The results of this study are in accordance with general patterns of abundance and

distribution of zooplankton communities reported in the published studies but at the same time provide new insights into the spring development of abundance, population structure and vertical distribution of dominant calanoid copepods on the eastern Weddell Sea shelf. However, further studies are necessary to fully understand the overwintering strategies and the factors that trigger the reproduction periods of the studied copepod species.

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Table

Table 1 a Copepod species found in the present study and data on their relative frequency and frequency of occurrence. The relative frequency data of the single species are given in relation to the abundance of the respective order. The relative frequency data of the orders are given in relation to the total abundance. F = females, M = males and C = copepodids (only determined in the calanoid copepods).

	Developmental stages	Abundance (Ind. [100 m^3]$^{-1}$)	Relative frequency (%)	Frequency of occurrence (%)
Calanoida Sars, 1903		**6624 - 11191**	**15 - 30.3**	**100**
Family Acartiidae Sars, 1903				
Paralabidocera antarctica Thompson, 1898	M	< 1	< 0.1	14
Family Aetideidae Giesbrecht, 1892				
Aetideopsis minor (Wolfenden, 1911)	F, C	0 - 2	< 0.1	14
Aetideus australis (Vervoort, 1957)	M	< 1	< 0.1	14
Chiridius sp.		< 1	< 0.1	14
Euchirella sp.	C	0 - 3	< 0.1	57
Gaidius tenuispinus (Sars, 1900)	F, C	0 - 24	< 1	71
Family Augaptilidae Sars, 1905				
Haloptilus ocellatus Wolfenden, 1905	F, M, C	< 1	< 0.1	57
H. oxycephalus (Giesbrecht, 1889)	F, C	2 - 20	< 1	100
Family Calanidae Dana,1849				
Calanoides acutus (Giesbrecht, 1902)	F, M, C	40 - 293	0.5 - 4.2	100
Calanus propinquus Brady, 1883	F, M, C	68 - 163	0.8 - 1.9	100
Family Clausocalanidae Giesbrecht, 1892				
Clausocalanus brevipes Frost & Fleminger, 1968	F	< 1	< 0.1	14
Ctenocalanus citer Heron & Bowman, 1971	F, M, C	707 - 1785	9.3 - 17.2	100
Microcalanus pygmaeus (Sars, 1900)	F, M, C	3504 - 8473	50.3 - 75.7	100
Family Eucalanidae Giesbrecht, 1892				
Rhincalanus gigas Brady, 1883	F, M, C	3 - 14	< 1	100
Family Euchaetidae Giesbrecht, 1892				
Paraeuchaeta antarctica (Giesbrecht, 1902)	F	< 1	< 0.1	14
Paraeuchaeta spp.	C	65 - 166	0.9 - 1.8	100
Family Heterorhabdidae Sars, 1902				
Heterorhabdus austrinus Giesbrecht, 1902	F, M, C	15 - 58	< 1	100
H. farrani Brady, 1918	C	0 - 7	< 0.1	71
Family Lucicutiidae Sars, 1902				
Lucicutia spp.	C	< 1	< 0.1	29
Family Metridinidae Sars, 1902				
Metridia curticauda Giesbrecht, 1889	F, C	0 - 3	< 0.1	29
M. gerlachei Giesbrecht, 1902	F, M, C	641 - 1793	8.6 - 19.3	100

Table 1 b For description see above.

	Developmental stages	Abundance (Ind. [100 m^3]$^{-1}$)	Relative frequency (%)	Frequency of occurrence (%)
Calanoida Sars, 1903 (continuation from table 1 a)				
Family Scolecitrichidae Giesbrecht, 1892				
Racovitzanus antarcticus Giesbrecht, 1902	F, M, C	2 - 14	< 1	100
Scaphocalanus antarcticus Park, 1982	C	0 - 2	< 0.1	14
S. farrani Park, 1982	F	< 1	< 0.1	14
S. vervoortii Park, 1982	F	0 - 6	< 0.1	57
Scaphocalanus spp.	C	0 - 15	< 1	86
Scolecithricella cenotelis Park, 1980	F, C	0 - 3	< 0.1	57
S. dentipes Vervoort, 1951	C	0 - 2	< 0.1	14
S. minor (Brady. 1883)	F, M, C	58 - 198	0.9 - 3	100
Family Spinocalanidae Vervoort, 1951				
Mimocalanus cultifer Farran, 1908	M	< 1	< 0.1	14
Spinocalanus abyssalis Giesbrecht, 1888	F	0 - 2	< 0.1	14
S. longicornis Sars, 1900	F, C	3 - 37	< 1	100
S. terranovae Damkaer, 1975	F, C	0 - 12	< 1	71
Teneriforma meteorae Schulz, 1989	F	< 1	< 0.1	14
Family Stephidae Sars, 1902				
Stephos longipes (Giesbrecht, 1902)	F, M, C	9 - 611	0.1 - 8.8	100
Cyclopoida Burmeister, 1834		**15207 - 37428**	**66.5 - 84.9**	**100**
Family Oithonidae Dana, 1853				
Oithona spp.		7021 - 16665	43.4 - 64	100
Family Oncaeidae Dana, 1853				
Oncaea spp.		6407 - 21169	36 - 56.6	100
Harpacticoida Sars, 1903		**25 - 120**	**0.1 - 0.5**	**100**
Family Ectinosomatidae Dana, 1853				
Ectinosoma sp.		0 - 2	0 - 3.5	29
Microsetella sp.		9 - 55	7.8 - 93.1	100
Family Harpacticidae Sars, 1904				
Harpaticus furcifer Giesbrecht, 1902		0 - 2	0 - 3.5	43
Family Thalestridae Sars, 1905				
Idomene antarctica (Giesbrecht, 1902)		0 - 9	0 -7.8	43
Family Tisbidae Stebbing, 1910				
Drescheriella spp.		0 - 75	0 - 62.5	86
Undetermined harpacticoid species		0 - 24	0 - 20.3	86

Figures

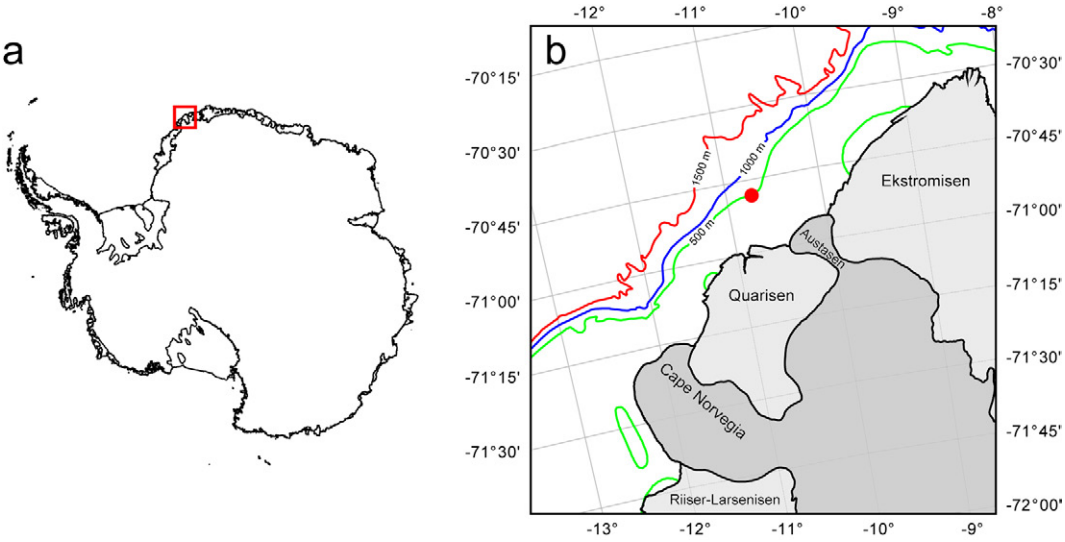

Fig. 1 (a) map of the Weddell Sea showing the location of the study area (red rectangle). **(b)** detailed map of the area marked by the red rectangle in (a) showing the location of the quasi-permanent station (red dot) on the eastern Weddell Sea shelf.

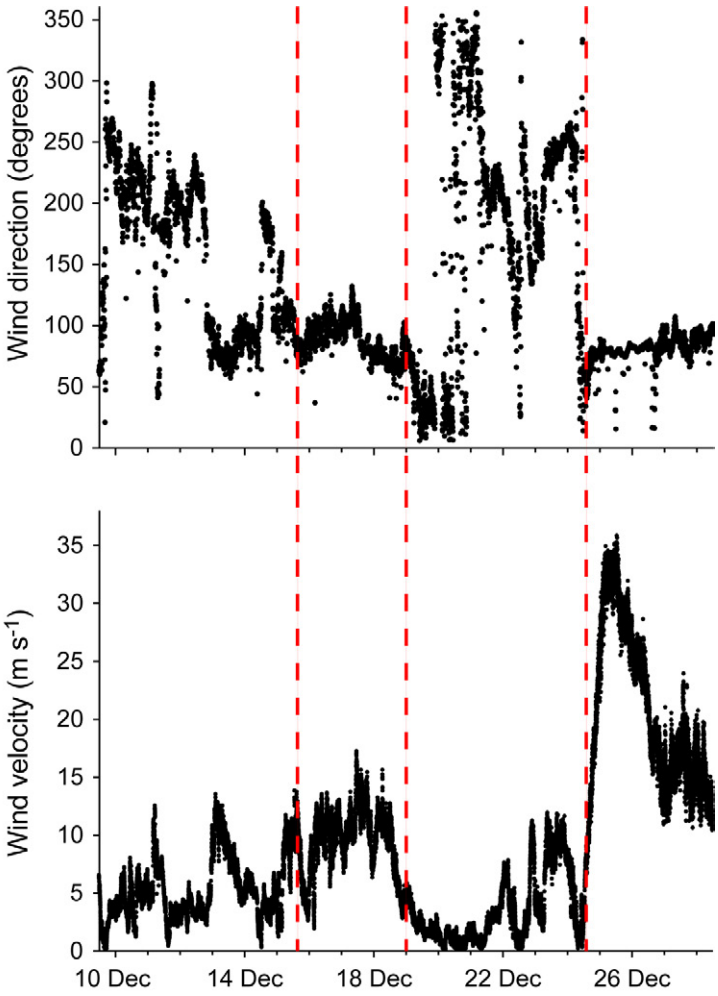

Fig. 2 Temporal development of wind direction and velocity. The dotted lines indicate the different periods described in the text.

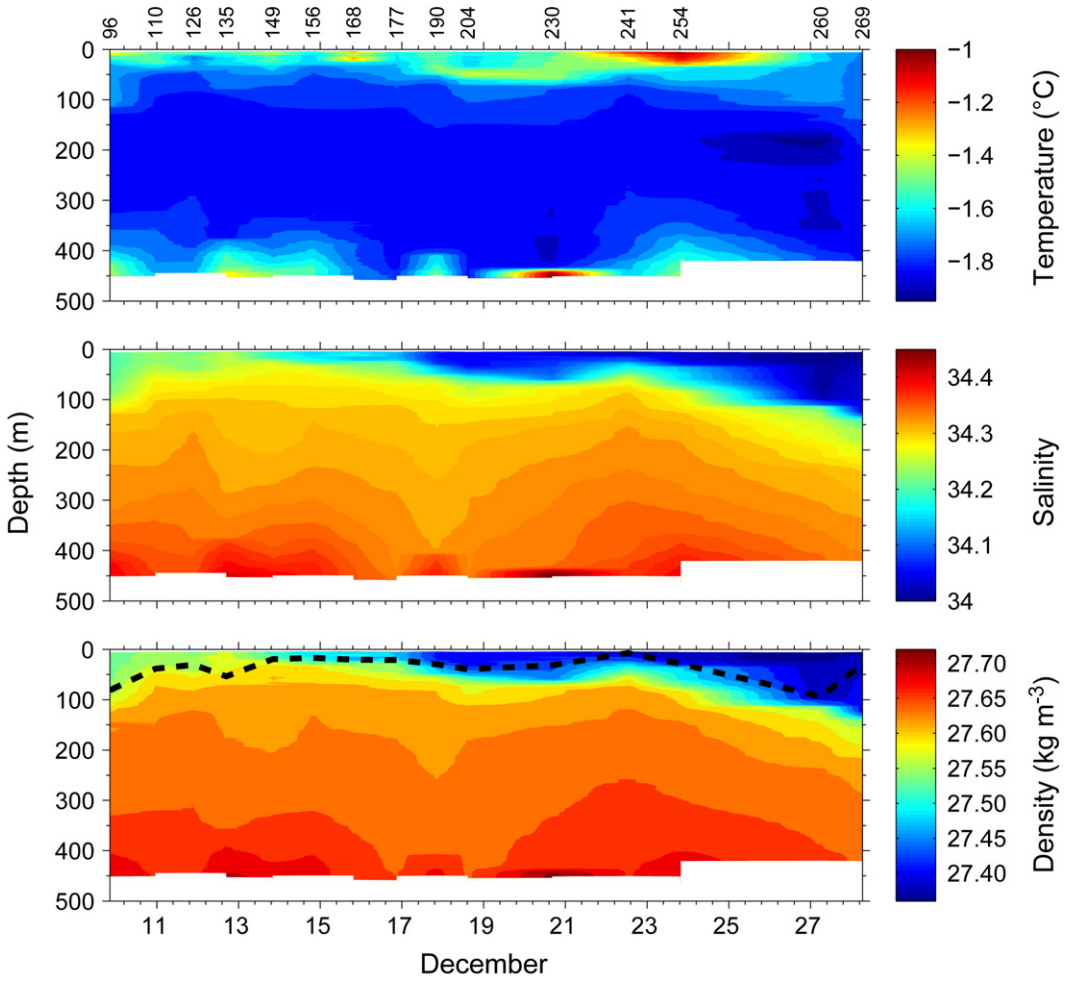

Fig. 3 Temporal development of the distribution of temperature, salinity and densitiy in the water column. The dotted line indicates the mixed layer depth. The small numbers on top of the figure represent the stations where data were collected.

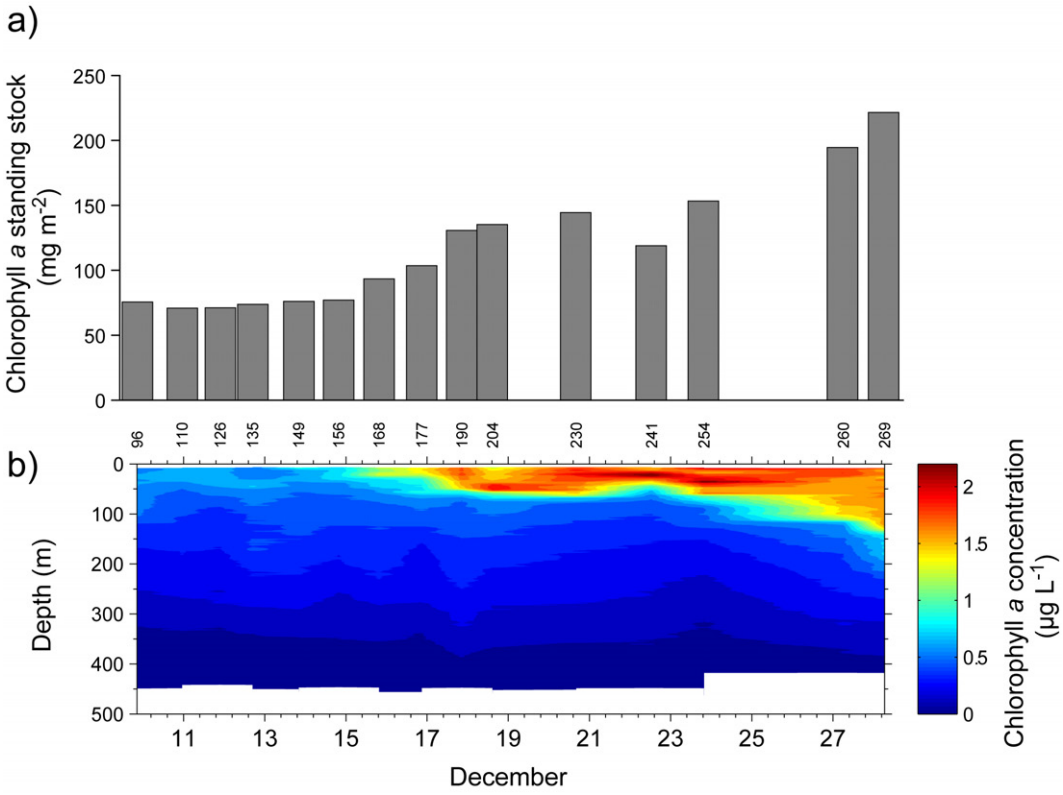

Fig. 4 (a) temporal development of the chlorophyll *a* standing stock in the upper 150 m. **(b)** distribution of chlorophyll *a* concentrations in the water column. The small numbers between the two graphics represent the stations where data were collected.

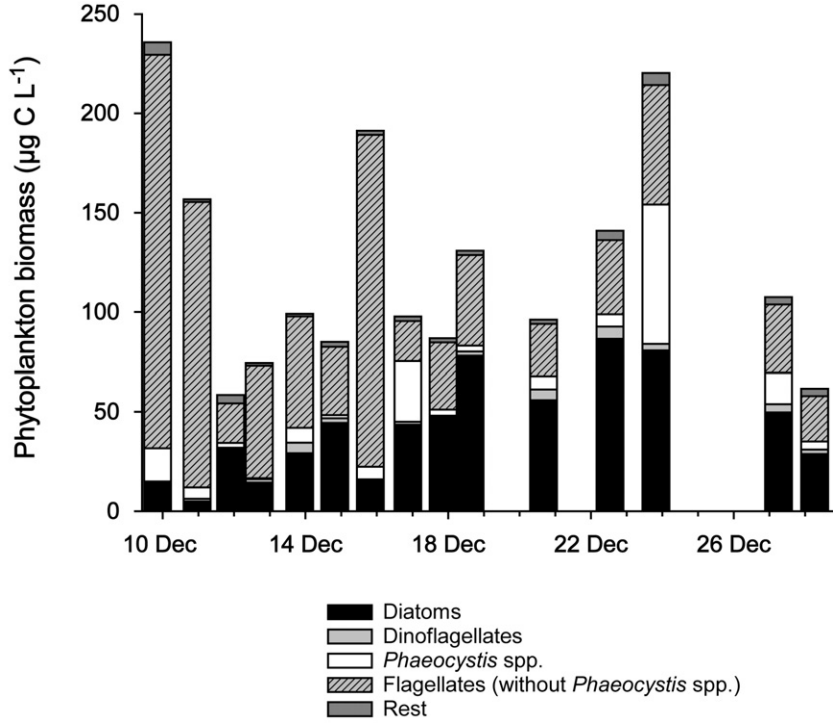

Fig. 5 Temporal development of the phytoplankton biomass concentration and composition at 5 m depth.

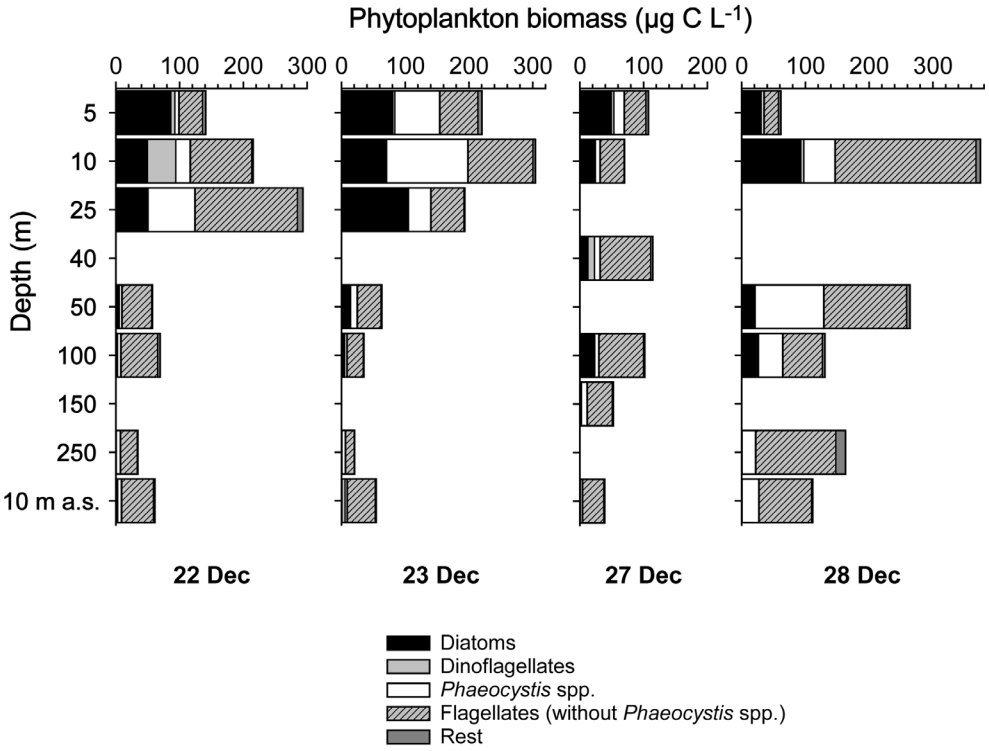

Fig. 6 Vertical distribution of concentration and composition of the phytoplankton biomass on different dates during the study. 10 m a.s. = 10 m above the seafloor.

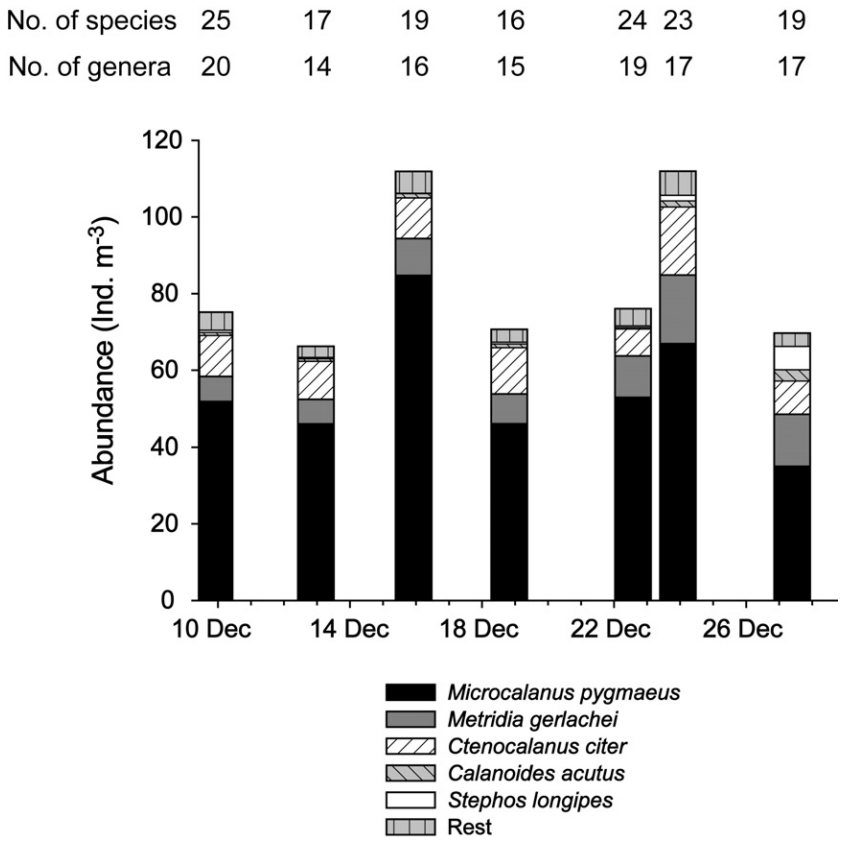

Fig. 7 Temporal development of the species and genus numbers, the abundance and the composition of the calanoid copepod population.

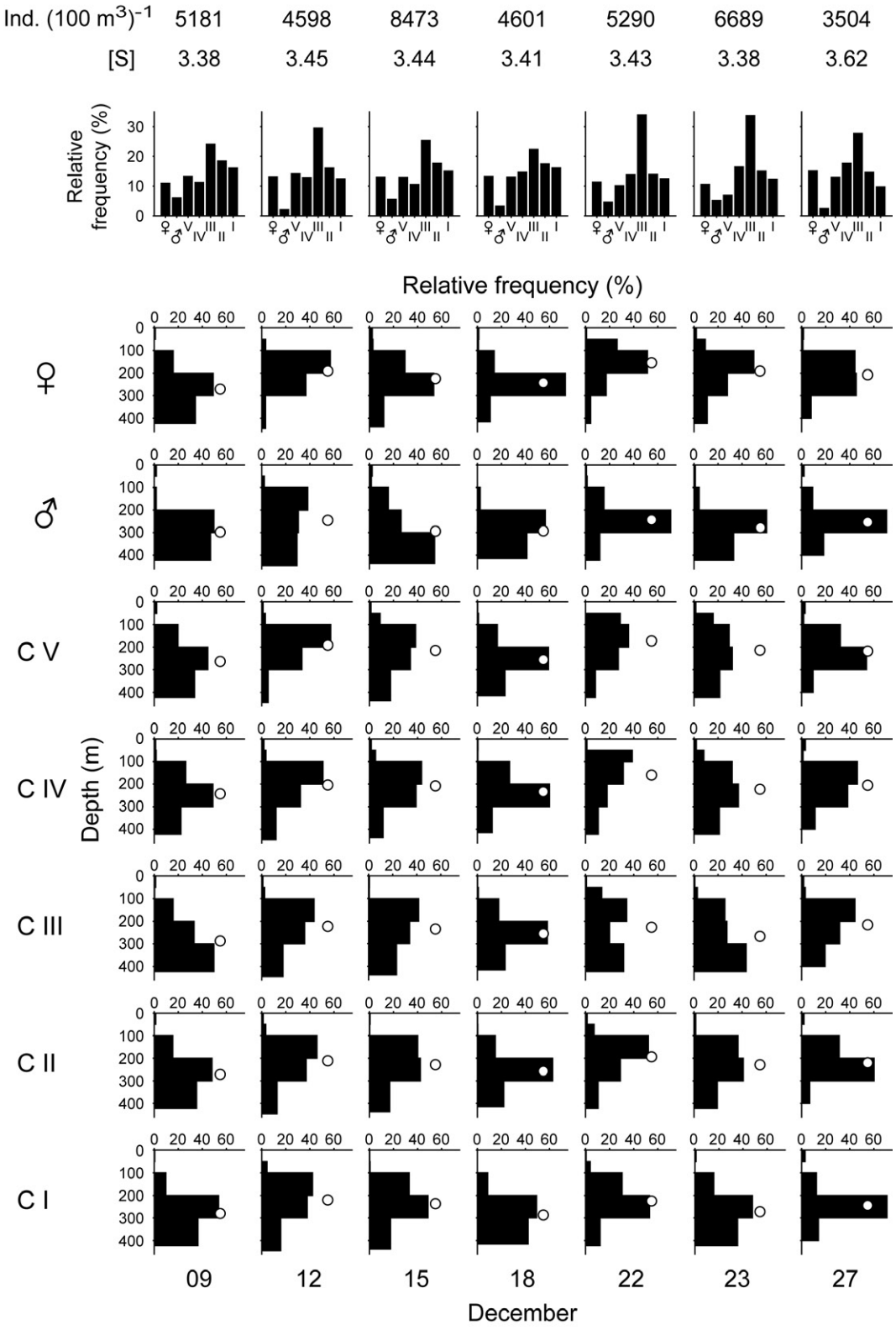

Fig. 8 Temporal development of abundance (Ind. [100 m^3]$^{-1}$), mean population stage ([S]), population structure and vertical distribution of the developmental stages of *Microcalanus pygmaeus*. The white dots represent the weighted mean depths.

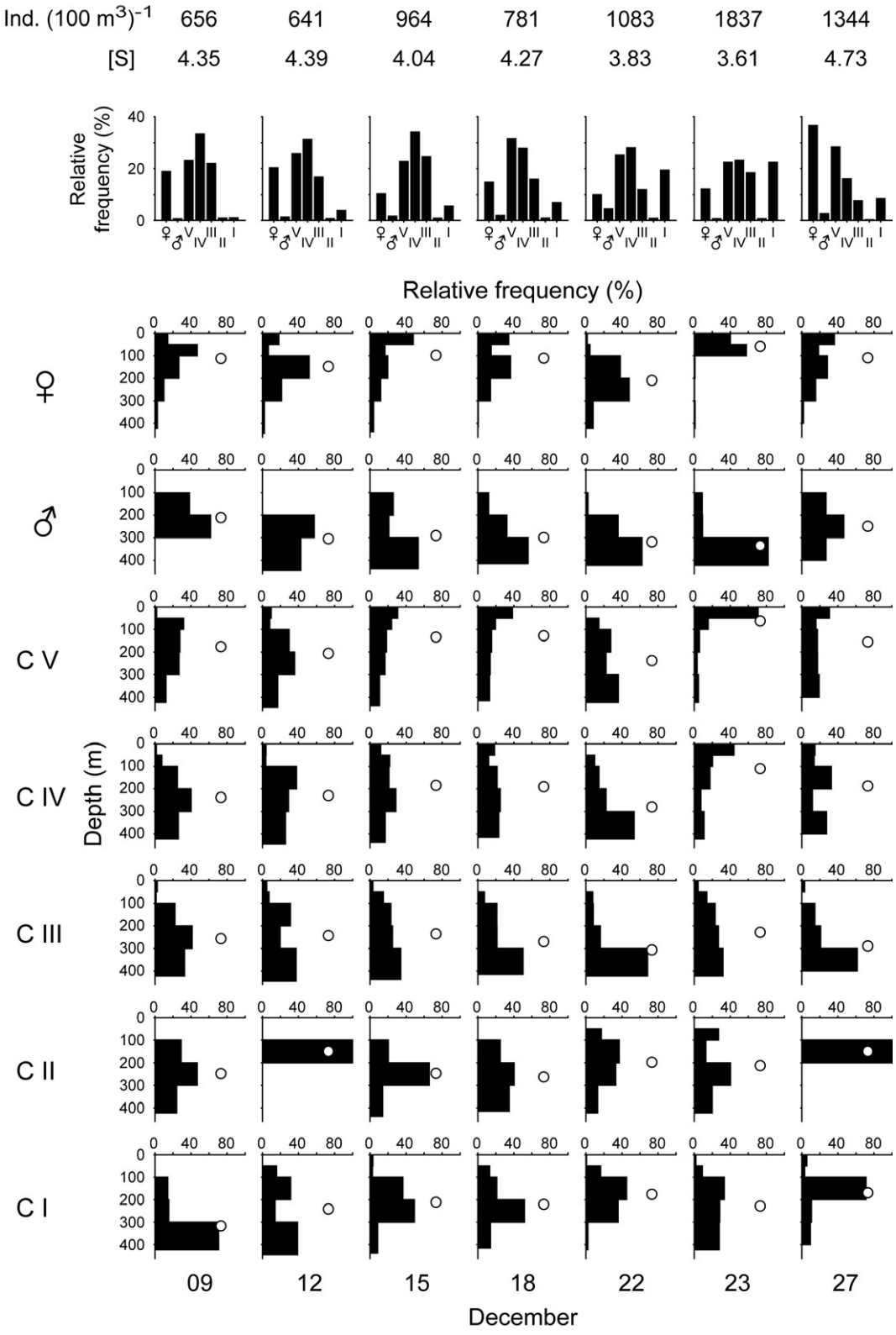

Fig. 9 Temporal development of abundance (Ind. [100 m^3]$^{-1}$), mean population stage ([S]), population structure and vertical distribution of the developmental stages of *Metridia gerlachei*. The white dots represent the weighted mean depths.

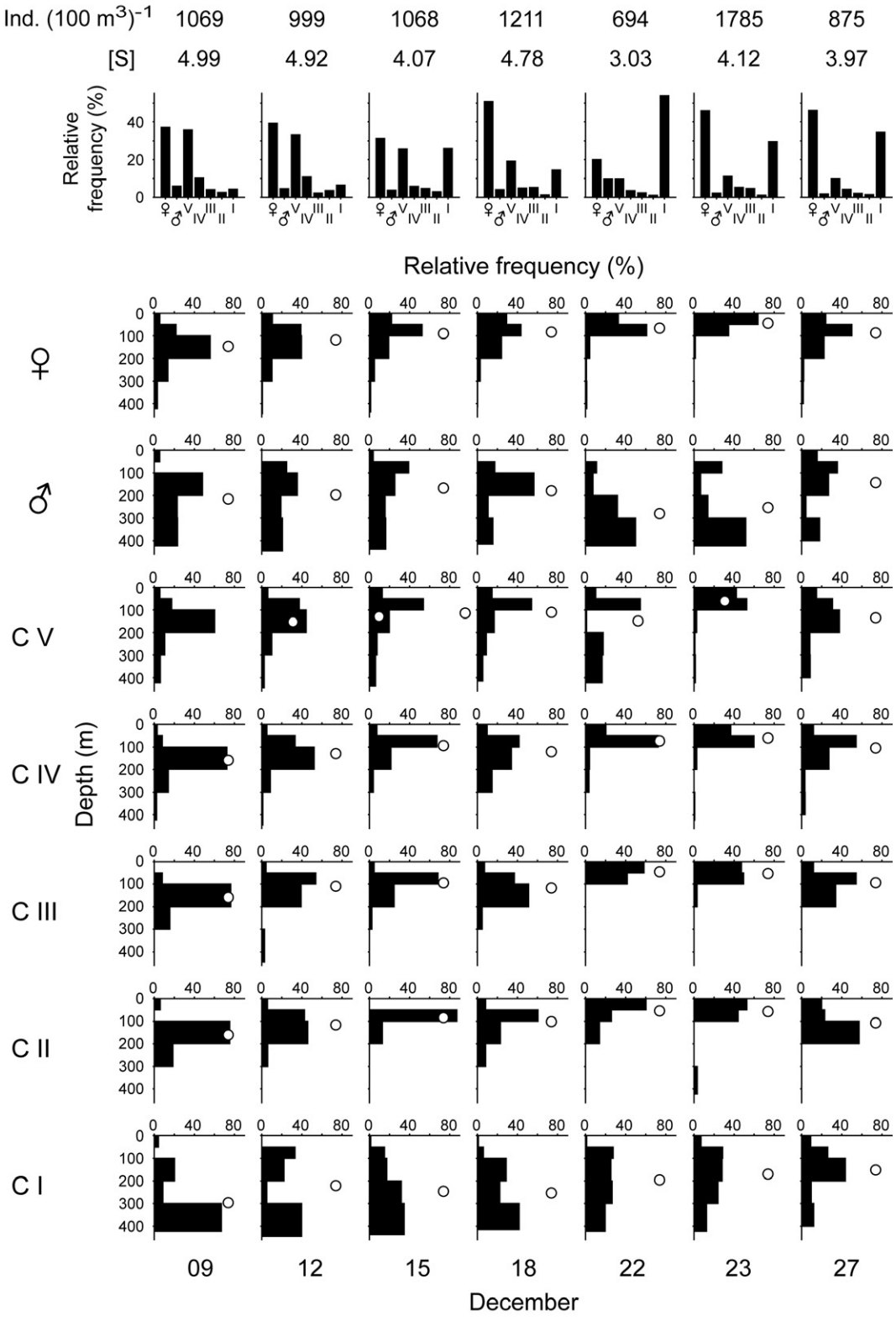

Fig. 10 Temporal development of abundance (Ind. [100 m^3]$^{-1}$), mean population stage ([S]), population structure and vertical distribution of the developmental stages of *Ctenocalanus citer*. The white dots represent the weighted mean depths.

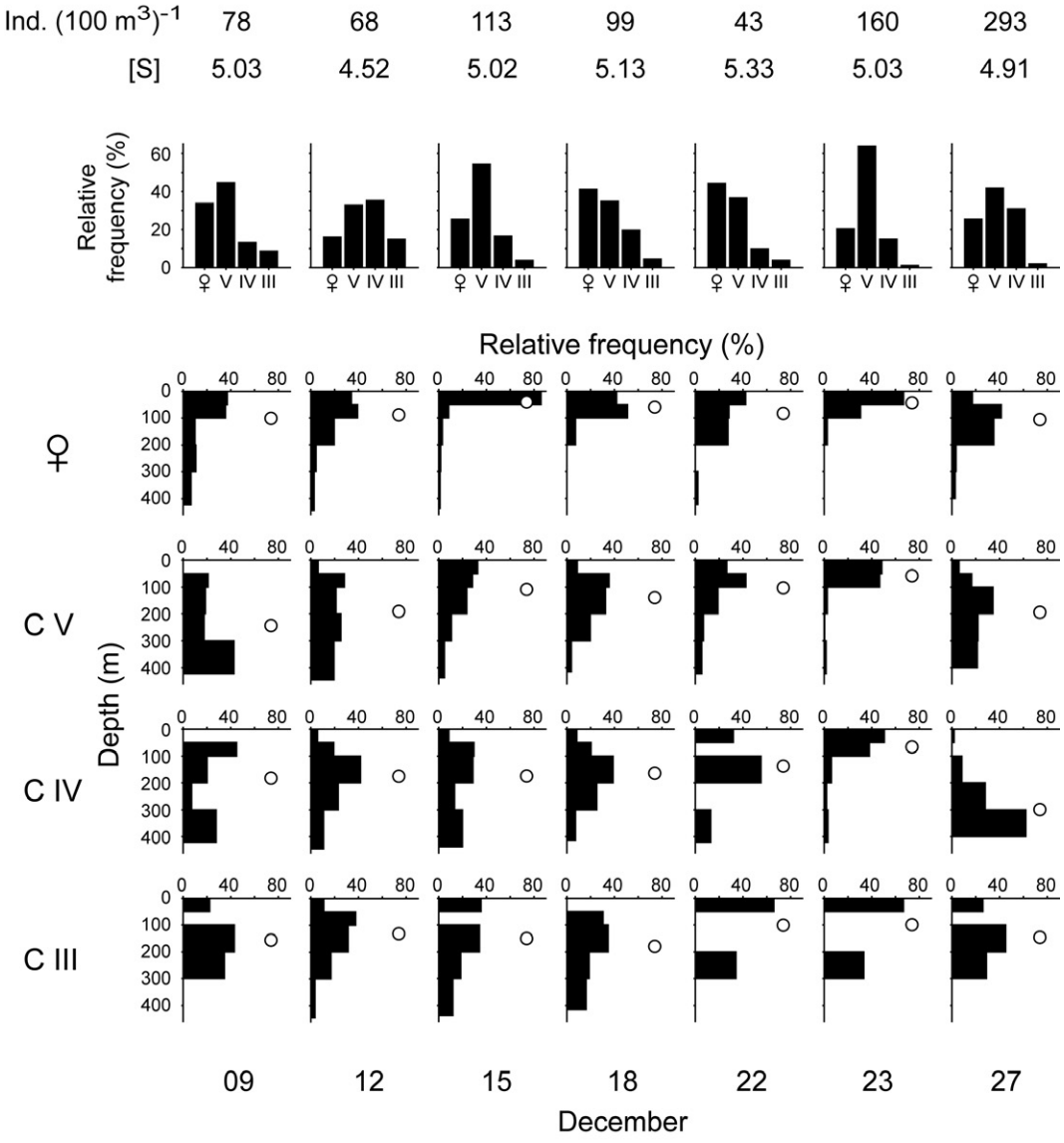

Fig. 11 Temporal development of abundance (Ind. [100 m^3]$^{-1}$), mean population stage ([S]), population structure and vertical distribution of the developmental stages of *Calanoides acutus*. The white dots represent the weighted mean depths.

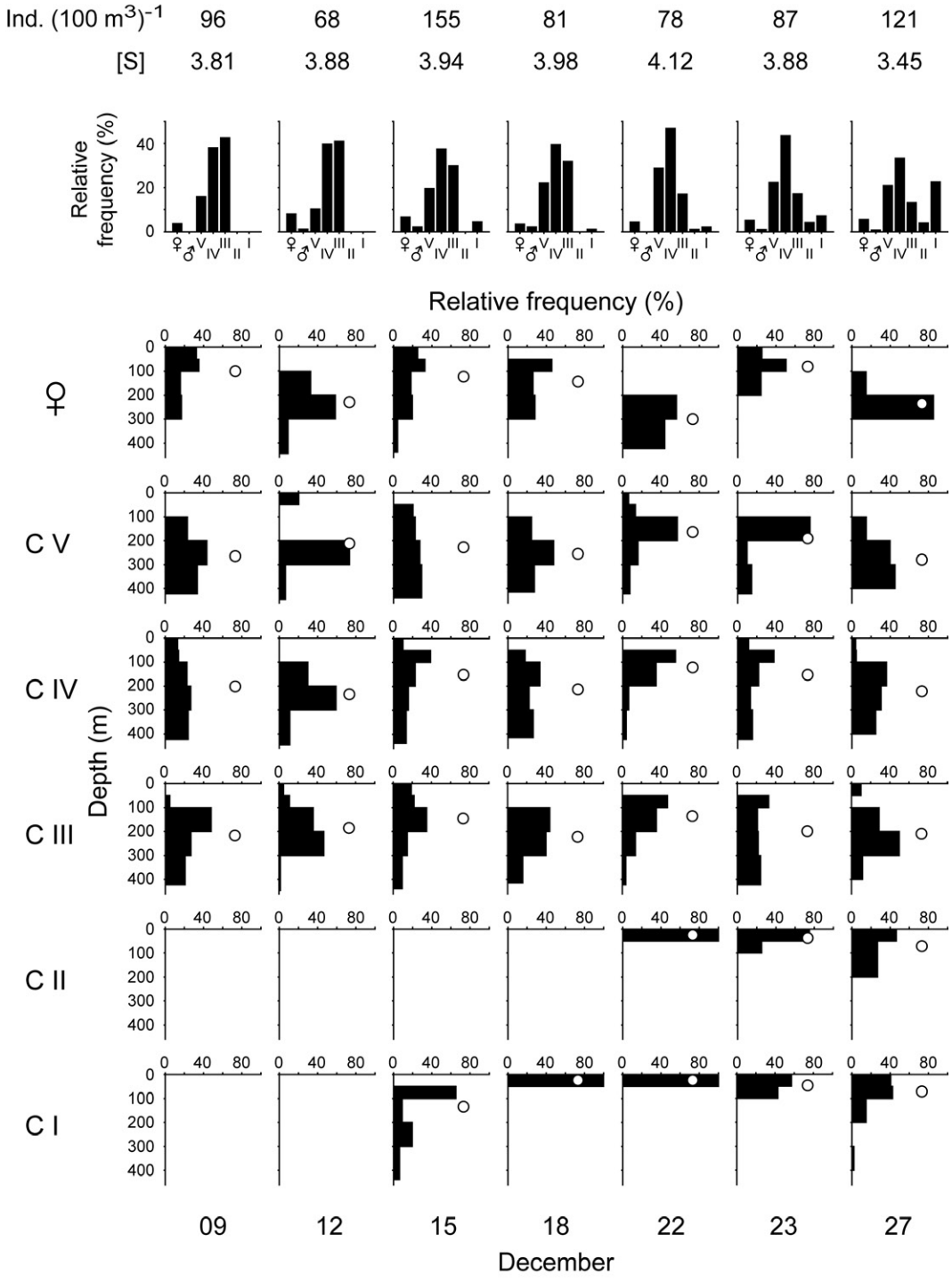

Fig. 12 Temporal development of abundance (Ind. [100 m^3]$^{-1}$), mean population stage ([S]), population structure and vertical distribution of the developmental stages of *Calanus propinquus*. The white dots represent the weighted mean depths.

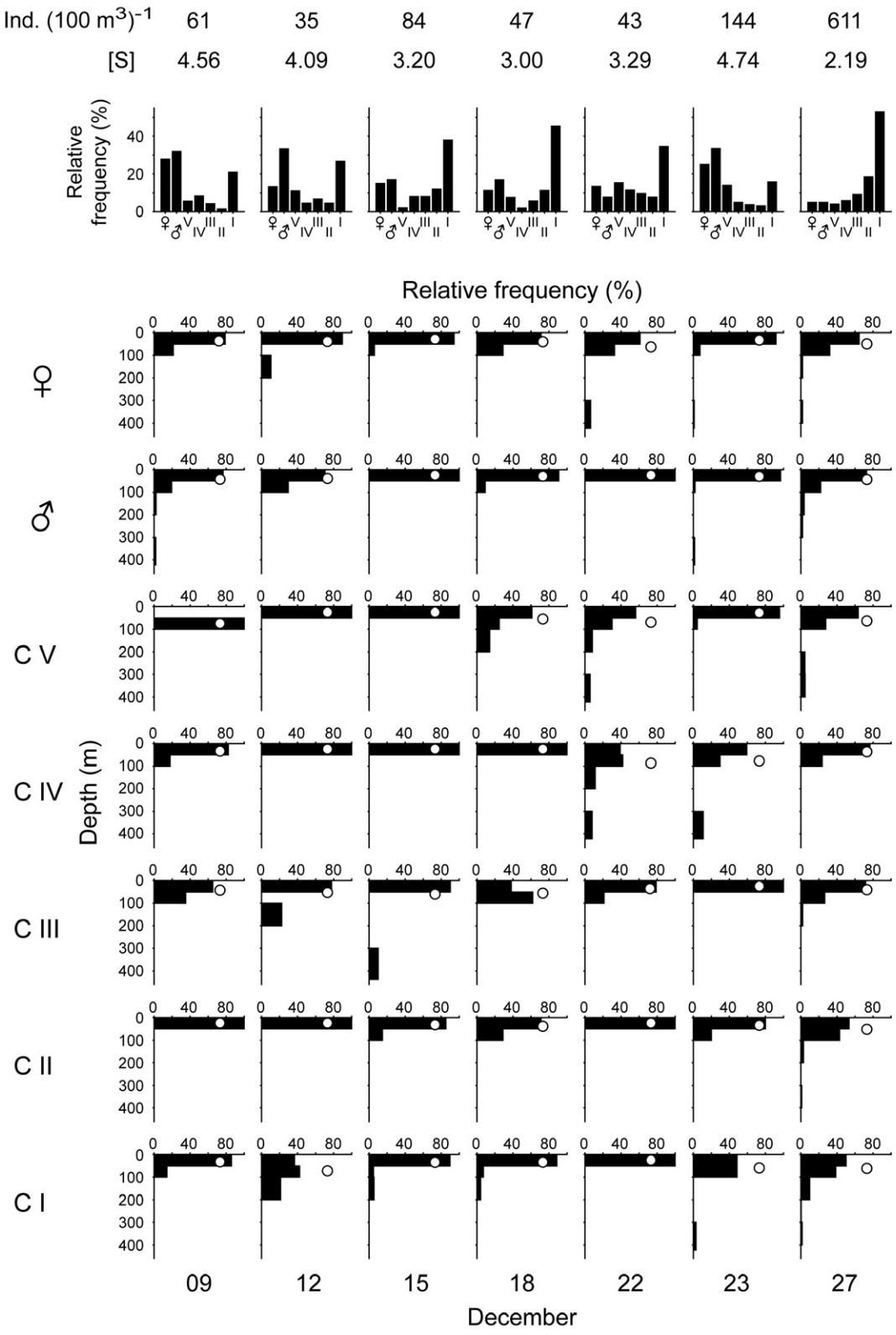

Fig. 13 Temporal development of abundance (Ind. [100 m^3]$^{-1}$), mean population stage ([S]), population structure and vertical distribution of the developmental stages of *Stephos longipes*. The white dots represent the weighted mean depths.

Lebenslauf

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Erklärung gemäß § 10 (2) Nr. 2 a - c der Promotionsordnung

Hiermit versichere ich an Eides statt, dass die vorliegende Dissertation von mir selbstständig und unter Einhaltung der Regeln guter wissenschaftlicher Praxis verfasst wurde und – abgesehen von der wissenschaftlichen Beratung durch meine Betreuerin – nach Inhalt und Form meine eigene Arbeit ist. Für ihre Erstellung wurden keine anderen als die angegebenen Hilfsmittel und Quellen verwendet. Des Weiteren erkläre ich, dass die Dissertation bis jetzt weder ganz noch in Teilen an anderer Stelle im Rahmen eines Prüfungsverfahrens vorgelegen hat.

Kiel, den 14.12.2007

_____

Jan Michels