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# The occurrence of the copepods *Stephos longipes* (Calanoida) and *Drescheriella glacialis* (Harpacticoida) in summer sea ice in the Weddell Sea, Antarctica

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**Abstract:** In January to March 1997, a RV *Polarstern* cruise that transected the Weddell Sea resulted in samples being taken in thick pack ice in the south-eastern Weddell Sea and then along the marginal ice edge towards the Antarctic Peninsula. Several ice types were thus sampled over a wide geographic area during late summer/early autumn. Common features of the first warm period was the occurrence of surface ponds, and that many floes had quasi-continuous horizontal gaps, underlying a layer of ice and metamorphic snow. With the onset of cold air temperatures in late February the gaps rapidly refroze. The calanoid copepod *Stephos longipes* occurred in all habitats encountered and showed highest numbers in the surface ice in summer, in the gap water during both seasons and in the refrozen gap water in autumn. Nauplii outnumbered copepodids in the surface ice and refrozen gap water, while in the gap water copepodids, mainly stages CI–CIII in summer and CII–CIV in autumn, comprised about 70% of the total population. The harpacticoid species *Drescheriella glacialis* did not occur in all habitats and was missing in surface ponds and new ice. Nauplii of *D. glacialis* were rarely found in gap water, but predominated in the refrozen gaps.

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**Key words:** copepods, *Drescheriella glacialis*, sea ice, seasonality, *Stephos longipes*

## Introduction

Small calanoid and harpacticoid copepods are dominant metazoans in sea ice (Gradinger 1999, Schnack-Schiel *et al.* in press). In the Weddell Sea the most abundant species are *Stephos longipes* (Giesbrecht, 1902) (Calanoida) and *Drescheriella glacialis* Dahms & Dieckmann, 1987 (Harpacticoida) (Hopkins & Torres 1988, Dahms *et al.* 1990, Kurbjeweit *et al.* 1993, Schnack-Schiel *et al.* 1995). The epibenthic species *D. glacialis* seems to spend most of its life in coastal ice, although it has also been found in annual pack ice offshore in the northern Weddell Sea (Dahms *et al.* 1990). How this species maintains a population in ice overlying deep waters is unclear. In contrast, *S. longipes* is a planktonic species, its life cycle being strongly associated with the seasonal fluctuation of sea ice cover giving a high abundance in sea ice during autumn, winter and spring but low during summer (Schnack-Schiel *et al.* 1995). However, the occurrence of *S. longipes* in porous summer sea ice has rarely been studied (Schnack-Schiel *et al.* 1998).

Clearly the ice is a refuge for the copepods, as well as a feeding ground where high algal standing stocks, primarily pennate diatoms, can be exploited. Feeding experiments, along with field observations, have shown that diatoms are a principal component of the diet of metazoans living within the ice matrix (Hoshiai *et al.* 1987, Kurbjeweit *et al.* 1993, Schnack-Schiel *et al.* 1995). Evidently this food source is an important feature in the coupling of copepod life histories with the annual cycle of sea ice formation, consolidation and subsequent melt (Schnack-Schiel *et al.* 1995, 1998).

The ecology of perennial Antarctic pack ice is still poorly understood. This is an unfortunate anomaly since it is in this sea ice type where biological activity is highest, particularly in spring and summer as a result of porous ice coupled with long day lengths, high irradiance and warmer ice temperatures (Thomas *et al.* 1998). These biological assemblages are associated with high rates of inorganic nutrient regeneration, but also with nutrient resupply via connections with the surrounding water through large pores or gaps (Haas *et al.* in press). On occasion these gaps extend to form extensive subsurface layers, with high degrees of seawater exchange possible. Many of the biogeochemical processes associated with such layers are more akin to the processes studied in detail in under-ice platelet layers. In situations where seawater supply is possible it is also quite likely that grazers, in particular small metazoans, can gain entry to the sites, and take advantage of the large algal standing stock as a food source, as well as utilizing the ice as a refuge from predators. The metazoans in these layers, sometimes present in quite remarkable numbers (Thomas *et al.* 1998, Günther *et al.* 1999), can result in a very different chemistry to that associated with more closed habitats more commonly described in pack ice studies to date.

During the summer months melting processes can result in ponds and lagoons forming on the surface of ice floes, which are at times in direct contact with the ocean below (Ackley & Sullivan 1994). Additionally, flooding of ice floe surfaces can take place, which induces further snow and ice melt. Salinities of the pond vary greatly from almost zero to undiluted seawater values, and are dependent on the dominating process causing the pond to form. Extensive surface ponds are more typically described from the Arctic, although they are not uncommon in the Antarctic pack (Ackley & Sullivan 1994).

The aim of this study was to investigate patterns of abundance, distribution and population structure of *Stephos longipes* and *Drescheriella glacialis* in porous rotten summer sea ice of the Weddell Sea, with an emphasis on individuals associated with sub-ice-surface gap layers.

## Materials and methods

In January and March 1997 studies on sea ice were carried out during the ANT XIV/3 expedition of RV *Polarstern* to the Weddell Sea (Fig. 1). During this cruise there was the opportunity to sample a wide range of ice types and features associated with late summer sea ice and early autumn freezing events.

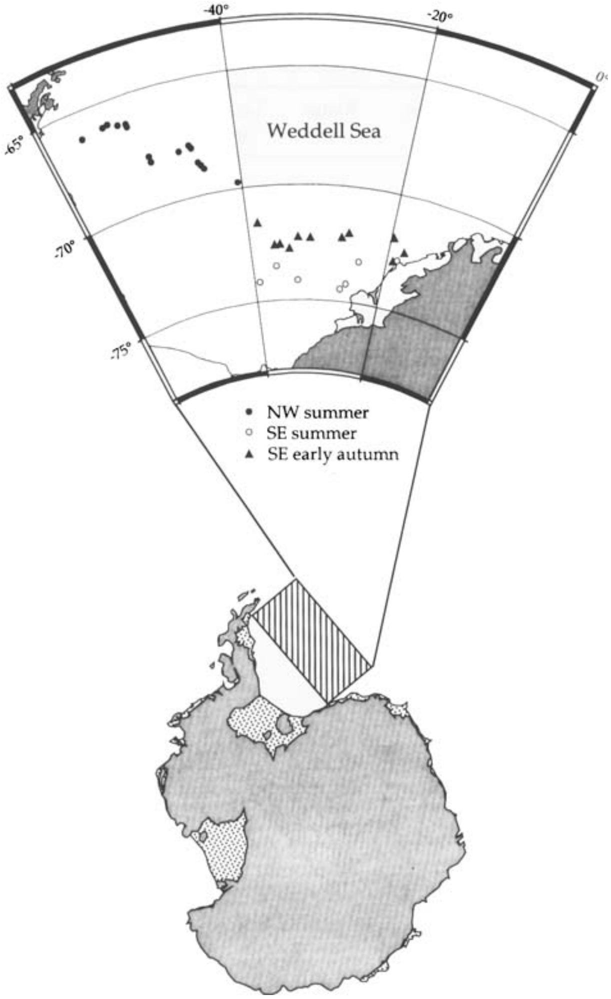

**Fig. 1.** Investigation area in the Weddell Sea.

The ship operated between the marginal ice zone (MIZ) and the inner pack ice, in ice concentrations varying between 5/10 and > 9/10 (Haas *et al.* 1998, in press). During the first two-thirds of the expedition summer conditions prevailed, with air temperatures around 0°C. Surface ponds were encountered around pressure ridges and on level ice. However, image analysis of aerial photographs indicated that these ponds covered only 3% of the total ice cover (Haas unpublished data). The surface ponds often contained high algal standing stocks, which were concentrated mainly at the ice fringe at the bottom of the pond, or at times suspended as large flocs or strands (up to 10 cm long) in the water column. Occasionally, krill were found swimming through the porous underside of the ponds.

Another characteristic was the occurrence of quasi-continuous, horizontal gaps in the ice, at or just below the water level (Haas *et al.* in press, Fig. 2). These were typically overlaid by a surface ice layer, composed mainly of low salinity ice derived from melt–freeze cycling of the snow. However, its base was often saline. The underlying ice (ice proper) was often very porous and rotten, with very large brine pockets/channels, or a skeleton of ice remaining. As in the surface ponds, krill were observed to be swimming through the ice proper into gap water layers.

After 25 February air temperatures remained below -10°C, and reached -25°C on occasions. Sub-surface gap layers and surface ponds rapidly refroze. Fields of frazil ice slicks and newly formed level nilas ice up to 18 cm thick were encountered.

### *Sample collection*

**Open water** was collected from the edges of ice floes during ice sampling, or on one occasion from a Zodiac using a bucket. Care was taken not to contaminate samples with ice brash or

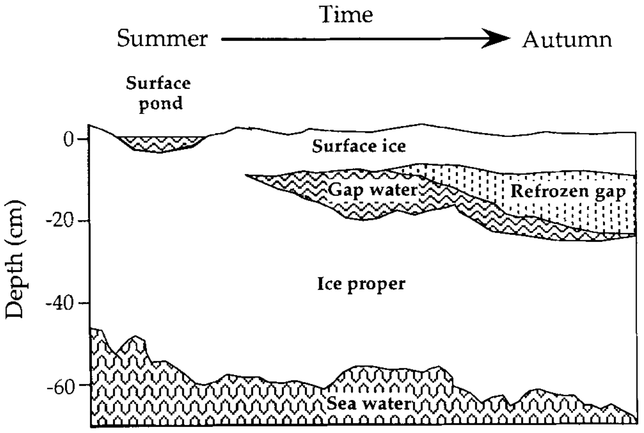

**Fig. 2.** Sketch of the ice habitats sampled indicating the nomenclature used throughout the text. Zero refers to the water level.

by taking water directly in contact with the floes.

**Ice cores** were collected with standard ice coring techniques. The thickness of the floes was highly variable, ranging between 13 and 224 cm. Cores (10 cm diameter) were immediately sectioned into < 10 cm sections and transported back to the laboratory. During coring, care was taken to avoid brine drainage, and contamination of low salinity surface ice with high salinity brine or seawater.

**Gap waters** were sampled after careful coring by hand of the overlying ice and metamorphic snow. Generally when it was determined that a floe had a gap layer, transects were made to sample the overlying ice and snow and the gap water below. Careful coring of the overlying ice (**surface ice**) meant that the gap layer was not contaminated by ice debris from the coring. The gap water was sampled by immersing bottles or 500 ml plastic containers into the gap water. On occasions it was noticed that the gap waters contained ice debris and ice slush that was clearly not associated with the coring activity. If present, this was included in the sample. As indicated above, later in the sampling period gap layers began to refreeze. These are referred to as **refrozen gaps**.

Extreme care was taken to sample the very fragile ice, often splintering ice underlying the gap layer (**ice proper**).

**Surface ponds** were sampled by bottles and 500 ml containers. Generally samples were taken from the edge of the ponds, although on occasions they were obtained from the centre. Occasionally, sampling was carried out from the top, mid and bottom of the pond.

**New ice** includes both grease ice collected from Zodiac and the edge of ice floes, and a recently formed nilas ice sheet that was 18 cm thick. The grease ice was collected using plastic containers, and the nilas ice by coring.

### *Core processing*

All ice samples, or gap waters containing ice slush/chunks, were thawed at 4°C in the dark. This procedure has been argued (Thomas *et al.* 1998) to be non-detrimental in studies focussing on diatoms and zooplankton, although it is realised that fragile organisms may be lost as a result of the procedure

**Table Ia.** Mean abundance and range (Ind. L$^{-1}$) of *Stephos longipes* in different habitats and seasons.

| | Mean | Range | Total number of samples | Number of positive samples |
|---|---|---|---|---|
| **Surface ponds** | | | | |
| summer SE | 0.3 | 0–4 | 14 | 1 |
| summer NW | 4.5 | 0–50 | 14 | 5 |
| early autumn SE | – | – | – | – |
| **Surface ice** | | | | |
| summer SE | – | – | – | – |
| summer NW | 26.3 | 0–185 | 17 | 8 |
| early autumn SE | 1.9 | 0–24 | 24 | 3 |
| **Refrozen gap** | | | | |
| summer SE | – | – | – | – |
| summer NW | – | – | – | – |
| early autumn SE | 43.0 | 0–240 | 17 | 10 |
| **Gap water** | | | | |
| summer SE | – | – | – | – |
| summer NW | 22.9 | 0–194 | 26 | 17 |
| early autumn SE | 19.0 | 0–71 | 9 | 8 |
| **Ice proper** | | | | |
| summer SE | – | – | – | – |
| summer NW | 3.8 | 0–40 | 23 | 4 |
| early autumn SE | 0 | 0 | 10 | 0 |
| **Ice cores** | | | | |
| summer SE | 1.1 | 0–21 | 20 | 1 |
| summer NW | 0 | 0 | 8 | 0 |
| early autumn SE | – | – | – | – |
| **New ice** | | | | |
| summer SE | – | – | – | – |
| summer NW | – | – | – | – |
| early autumn SE | 1.5 | 0–8 | 14 | 3 |
| **Open water** | | | | |
| summer SE | – | – | – | – |
| summer NW | 1.9 | 0–4 | 2 | 1 |
| early autumn SE | 1.8 | 0–8 | 7 | 3 |

– = no data

**Table Ib.** Mean abundance and range (Ind. L$^{-1}$) of *Drescheriella glacialis* in different habitats and seasons.

| | Mean | Range | Total number of samples | Number of positive samples |
|---|---|---|---|---|
| **Surface ponds** | | | | |
| summer SE | 0 | 0 | 14 | 0 |
| summer NW | 0 | 0 | 14 | 0 |
| early autumn SE | – | – | – | – |
| **Surface ice** | | | | |
| summer SE | – | – | – | – |
| summer NW | 33.1 | 0–154 | 17 | 9 |
| early autumn SE | 4.5 | 0–48 | 24 | 4 |
| **Refrozen gap** | | | | |
| summer SE | – | – | – | – |
| summer NW | – | – | – | – |
| early autumn SE | 20.8 | 0–111 | 17 | 11 |
| **Gap water** | | | | |
| summer SE | – | – | – | – |
| summer NW | 16.1 | 0–267 | 26 | 10 |
| early autumn SE | 2.1 | 0–8 | 9 | 4 |
| **Ice proper** | | | | |
| summer SE | – | – | – | – |
| summer NW | 15.2 | 0–107 | 23 | 11 |
| early autumn SE | 12.4 | 0–50 | 11 | 4 |
| **Ice cores** | | | | |
| summer SE | 0.3 | 0–6 | 20 | 1 |
| summer NW | 166.2 | 19–379 | 8 | 8 |
| early autumn SE | – | – | – | – |
| **New ice** | | | | |
| summer SE | – | – | – | – |
| summer NW | – | – | – | – |
| early autumn SE | 0 | 0 | 14 | 0 |
| **Open water** | | | | |
| summer SE | – | – | – | – |
| summer NW | 1.0 | 0–2 | 2 | 1 |
| early autumn SE | 0.8 | 0–4 | 7 | 2 |

– = no data

(Garrison & Buck 1986).

Salinities of all samples were measured directly on board with a conductivity salinometer (WTW, Weilheim, Germany). Subsamples (50 to 200 ml) were then filtered through glass fibre filters (Whatman GF/F) and frozen for later analyses. These were analysed fluorometrically for chlorophyll and phaeopigments (Evans *et al.* 1987).

The zooplankton in the remaining samples were collected and preserved in hexamine-buffered formalin (final concentration 0.5–1%). *Stephos longipes* was separated into sexes and developmental stages and counted, while the copepodite stages of *D. glacialis* were not distinguished and adults and copepodids were combined. A mean population stage was calculated for *S. longipes*, according to Marin (1987).

## Results

*Stephos longipes* occurred in the open water taken from the edge of the ice floes, as well as in all sea ice habitats studied (Table Ia). The greatest concentration occurred in gap water and refrozen gaps, and here *S. longipes* was encountered in 60 to 90% of the samples collected. Higher numbers were also found in the north-western Weddell Sea within surface ice, but only in summer. In all other habitats the overall abundance was low and the mean never exceeded 5 Ind. $L^{-1}$. In contrast, highest concentrations of *Drescheriella glacialis* were found in ice cores in the north-west during summer. This species did not occur in new ice and in surface ponds (Table Ib). In all habitats there was considerable variation in abundance of *S. longipes* and *D. glacialis,* as can be seen in the range given in Tables Ia & Ib.

Figure 3a shows the mean abundance and stage structure of *S. longipes* and *D. glacialis* in vertical sections typical of floes encountered in summer in the north-west Weddell Sea. *Stephos longipes* occurred in highest numbers in the surface ice and the underlying gap water. Only a few individuals were found in the surface ponds and in the ice proper. In contrast, *D. glacialis* was concentrated in surface ice, and it did not occur in the surface ponds. In the gap water and in the ice proper *D. glacialis* was found in relatively equal numbers.

In contrast, in autumn in the south-eastern Weddell Sea, the abundance of both copepod species in surface ice had decreased (Fig. 3b). Greatest concentrations were found in the refrozen gaps, which is most pronounced in *S. longipes.*

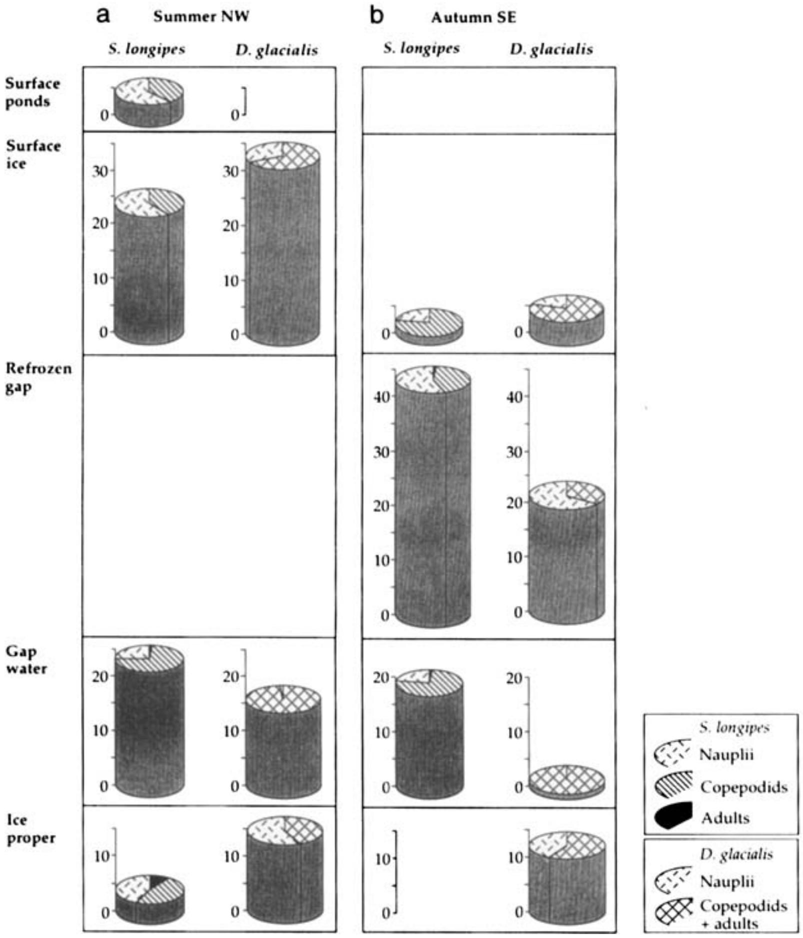

**Fig. 3.** Abundance and population structure of *Stephos longipes* and *Drescheriella glacialis*; **a.** in the north-western Weddell Sea in summer, **b.** in the south-eastern Weddell Sea in autumn.

### *Population structure*

Nauplii and copepodids of *S. longipes* were always found together, while adults occurred only sporadically and in low numbers. Nauplii dominated the population in NW summer in the surface ponds and surface ice, and in the refrozen gaps in the SE autumn (Fig. 3a & b). Nauplii of *D. glacialis* outnumbered copepodids/adults only in the ice proper in summer and in the refrozen gaps in autumn. In surface ice, copepodids/adults dominated during both seasons, independent of concentration. In the gap water nauplii were almost totally missing, and in this habitat in NW summer they comprised about 1.5% of the total population.

The age structure of *S. longipes* differed greatly between habitats and seasons. In NW summer the population got older from surface ponds to the ice proper and open water. The mean population stage was about one stage younger in the surface ponds than in the ice proper. While nauplii accounted for more than 50% of the population in the surface ponds and surface ice, their numbers decreased in the gap water and they were absent in open water (Fig. 4a). In SE autumn the age structure had changed, and the population had grown older in surface ice and gap water, and the youngest population occurred in the refrozen gaps, where nauplii dominated. A slightly similar population structure was evident in new ice samples (Fig. 4b).

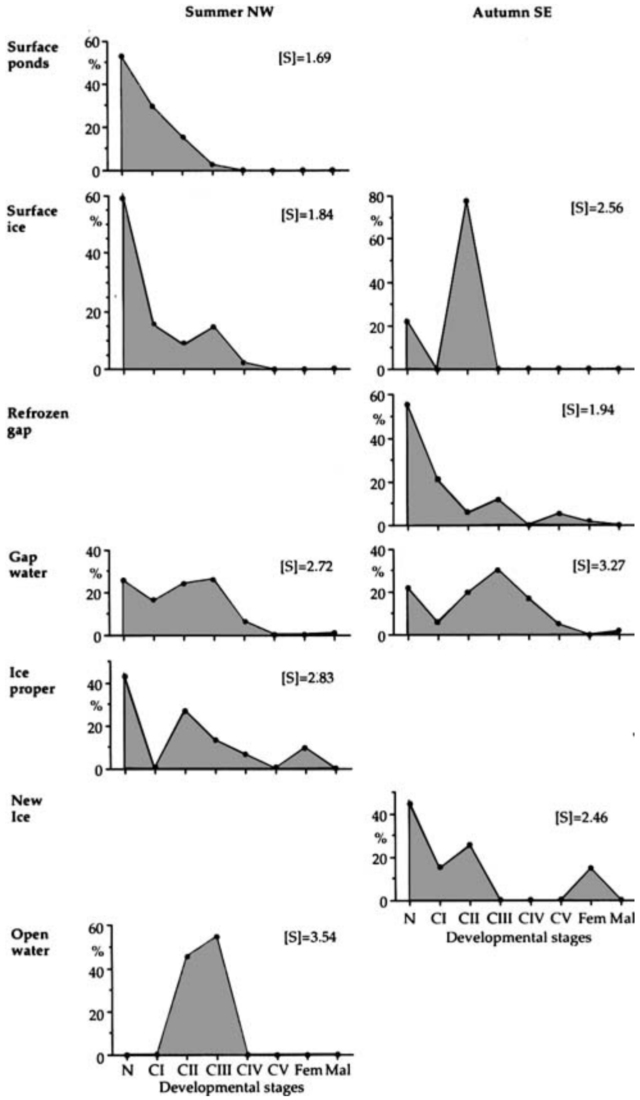

**Fig. 4.** Relative frequency of the different developmental stages and mean population stage [S] of *Stephos longipes*; **a.** in the north-western Weddell Sea in summer, **b.** in the south-eastern Weddell Sea in autumn. Nauplii are included in the calculation of the mean population stage.

### *Vertical structure*

Figure 5 shows the distribution of *S. longipes* and *D. glacialis* within an ice floe quite typical for the NW region in summer. The occurrence of *S. longipes* was restricted to the middle part of the under ice while *D. glacialis* had a much wider distribution in the core. Peak abundance of the copepods coincided with the highest concentration of chlorophyll *a* (*D. glacialis*), or with the maximum value of phaeopigments (*S. longipes*).

A typical distribution within ice for SE autumn is given in Fig. 6. Here, three ice samples were taken one metre apart. All cores were composed of surface ice, refrozen gaps and gap water. The gap layers had salinities slightly below typical sea water values, and chlorophyll concentrations were only slightly above seawater values. The highest algal biomass was found in the refrozen gap layer, where large numbers of *S. longipes* were also observed. *Drescheriella glacialis*, in contrast, occurred at much lower densities and without a clear pattern. The distribution of both species was very patchy and varied greatly between the sampling sites.

## Discussion

The distribution of *S. longipes* and *D. glacialis* differed greatly between the various habitats studied. The two copepod species had a very patchy distribution in the sea ice, both within and between ice floes, an observation also made in previous studies (Dahms *et al.* 1990, Schnack-Schiel *et al.* 1995, 1998, Swadling *et al.* 1997, 2001). Similar high densities of both copepod species are reported from rotten late summer ice in the Bellingshausen and Amundsen seas (Schnack-Schiel *et al.* 1998, Thomas *et al.* 1998). *Stephos longipes* seems to be adapted to living in all different ice habitats. However, *S. longipes* was very scarce in surface ponds, in frazil and grease ice, as well as in new, thin ice sheets less than 30 cm thick. This coincides with results from autumn in the eastern Weddell Sea (Schnack-Schiel *et al.* 1995). The highest abundances of *S. longipes* were found in gap water, refrozen gaps and in the lowest part of summer surface ice, where a young population of nauplii and first copepodite stages existed. Hence, porous and, therefore, easily accessible ice, appears to

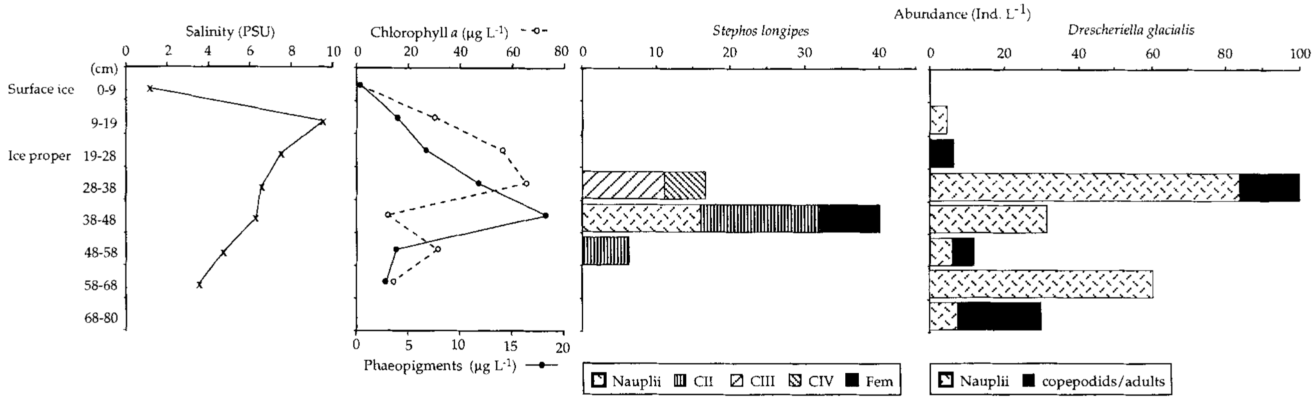

Fig. 5. Vertical distribution of salinity, chl *a*, phaeopigments and abundances of *Stephos longipes* and *Drescheriella glacialis* in the north-western Weddell Sea in summer.

be a favoured habitat, where flushing with nutrient-rich seawater, provides good conditions for algal growth, the main food source of *S. longipes*. Interestingly, nauplii predominated in the surface ice in summer as well as in the refrozen gaps during autumn, while copepodids comprised more than 70% of the population in the gap water during both seasons. We postulate that the nauplii of *S. longipes* were physically entrapped in the refrozen gaps during the freezing process, while most of the copepodids could escape, and so remained in the gap water. Alternatively, eggs may be laid onto the developing ice crystals in the gap water, resulting in a cohort of nauplii dominating this new ice.

*Drescheriella glacialis* occurred in all ice habitats except surface ponds and new ice, with maximum abundances in ice cores. In contrast to *S. longipes*, nauplii of *D. glacialis* were almost missing in gap water. According to Dahms *et al.* (1990), nauplii of *D. glacialis* are not able to swim while adults and copepodids are good swimmers, which is necessary to survive in the water column after annual melting of sea ice. Nauplii found in the refrozen gaps must therefore have immigrated from the surface ice.

As shown by data from other seasons, when ice floes had no surface ponds or gaps, brine channels were larger towards the bottom of the sea ice, with salinities similar to those of the underlying water (Weissenberger *et al.* 1992), thus permitting colonisation of larger organisms (Horner *et al.* 1992). Hence, it is not surprising that in those studies most copepods occurred in the lowest part of the ice floes, where there was an exchange

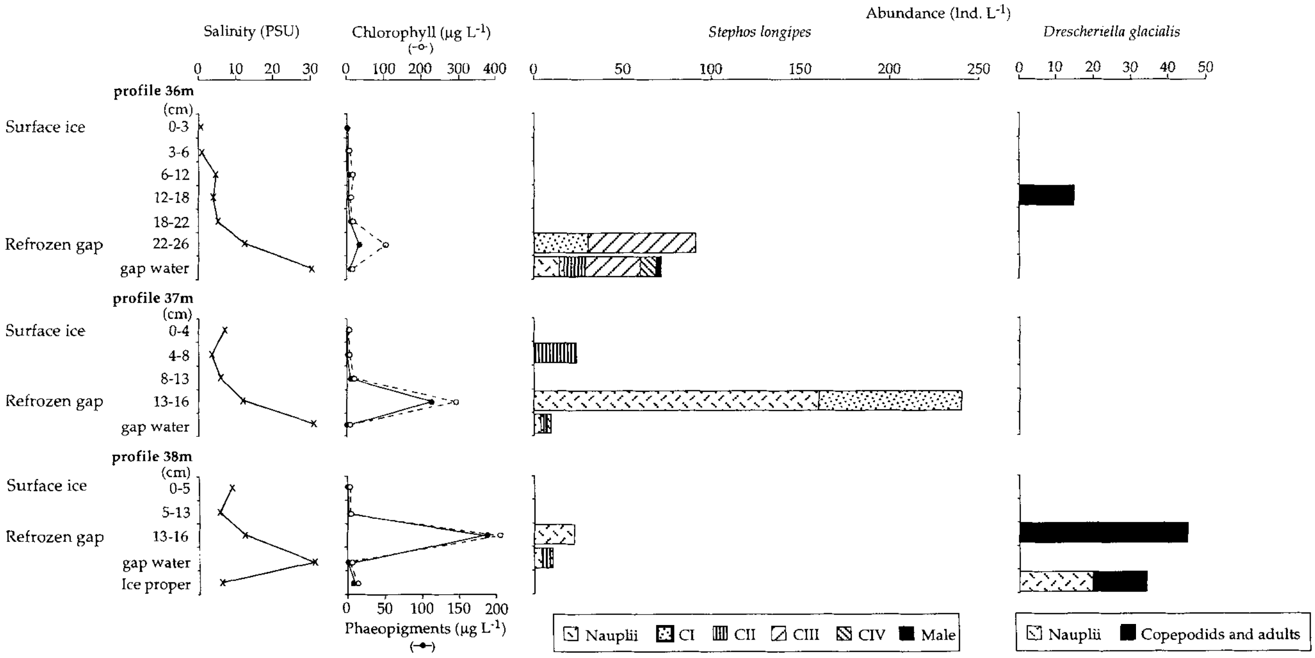

Fig. 6. Vertical distribution of salinity, chl *a*, phaeopigments and abundances of *Stephos longipes* and *Drescheriella glacialis* in the south-eastern Weddell Sea in autumn.

**Table II.** Mean abundance of both copepod species (Ind. L$^{-1}$) in the top and lowest part of surface ice and ice proper in both seasons and regions combined. Numbers in brackets denote the range.

| | *Stephos longipes* | | *Drescheriella gracialis* | |
|---|---|---|---|---|
| Surface ice | | | | |
| top part | 3.3 | (0–24) | 7.1 | (0–32) |
| lowest part | 17.9 | (0–185) | 21.4 | (0–154) |
| Ice proper | | | | |
| top part | 2.9 | (0–20) | 10.1 | (0–34) |
| lowest part | 0.9 | (0–6) | 17.4 | (0–41) |

with the surrounding seawater. Here they were associated with high chlorophyll and phaeopigment levels (Dahms & Dieckmann 1987, Kurbjeweit *et al.* 1993, Schnack-Schiel *et al.* 1995, Swadling *et al.* 2001). Therefore, if only the lowest part of the ice is taken into account for the calculation of abundances, the concentrations of *S. longipes* and *D. glacialis* should be higher compared to the upper parts. Table II gives these calculations for surface ice and ice proper during our summer study. Interestingly, the number of *S. longipes* in the upper part of the ice proper was higher than in the lowest part. One possibility is that *S. longipes*, which occurred in high abundances in the gap water just above the ice proper, swims from the gap water into the porous brine channels of the upper ice proper as well as in the lower part of the surface ice.

In this study, the maximum number of *S. longipes* and *D. glacialis* were found in the middle part of some floes (see Fig. 5 for example). This distribution pattern is in agreement with results from the Bellingshausen and Amundsen Seas as well as from the northern Weddell Sea in spring, where the ice encountered was rotten, containing slush layers that coincided with higher salinities (Schnack-Schiel *et al.* 1995, 1998, Thomas *et al.* 1998). In late spring/summer the brine channel system often has a honeycomb appearance (Horner *et al.* 1992), hence, copepods could spread to all levels. It has been shown that small copepods are not restricted to grazing at the peripheries of the ice floes but can also live deep within ice floes.

## Conclusion

The low salinities of surface ice layers would indicate that the porosity was negligible, and, therefore, we presume that any organisms associated with the surface ice were living in the lowermost portion of it. During the transition from summer to autumn there was a reduction in the concentration of *Stephos longipes* in the surface ice layers overlying ice-free gaps. This shift was associated with an increase in the relative numbers of copepodids compared to other life history stages. As space became restricted with the lowering of temperature it is possible that there was a downward migration of these copepodids into the freezing, but more porous, refrozen gap layer immediately below.

In the gap water there were few changes in the numbers and population structure between seasons. However, in the refrozen gap layer there was a significant concentration of individuals and shift to a population dominated by nauplii of *S. longipes.* A plausible explanation is that the adults in the gap waters released eggs onto the large dendritic ice crystals growing downwards into the gap water. These eggs would have hatched within three to four days (Kurbjeweit *et al.* 1993), resulting in the marked predominance of nauplii in the refrozen gap layers.

Similarly, with *Drescheriella glacialis* there was a concentration of individuals in the refrozen gaps, with reductions in the numbers in the surface ice, gap water and ice proper. Evidently, there was a migration of these harpaticoids from all regions of the ice to this porous, growing ice sheet that was supporting extensive ice algal growth.

Whereas *S. longipes* has a distinct open water phase that can partly account for large scale colonisation of pack ice, it is unclear how populations of the epibenthic *D. glacialis* are maintained in pack ice overlying deep, oceanic waters and can survive long ice-free period in the water column (Schnack-Schiel *et al.* 1998). During this study, a few individuals occurred in the open water taken just beside ice floes, and adults and copepodite stages are supposed to be good swimmers (Dahms *et al.* 1990). However, *D. glacialis* was never encountered in the water column, neither at the surface nor in deeper water layers, in the Weddell, Bellingshausen and Amundsen seas during all seasons (Schnack-Schiel *et al.* 1998, unpublished data) as well as near Vestfold Hills, eastern Antarctica (Swadling *et al.* 2001), hence this species cannot be considered to be planktonic. The dynamics of seasonal melting and refreezing within ice floes, and the effects that this has on the entrained copepods, may be fundamental for maintaining copepods within the ice in regions where recruitment from the benthos cannot take place as it does in neritic areas.

A relatively high number of *S. longipes* were found within the surface ponds. Although no refrozen ponds were sampled in autumn it is plausible that, as for the surface ice layers, these individuals would have migrated downwards into the underlying ice, thereby initiating a viable population throughout the entire ice. The absence of *D. glacialis* in the surface ponds is somewhat anomalous, although this can be explained if the introduction of the copepods into the ponds is from surrounding water rather than the underlying ice since *D. glacialis* is absent from the water column. This absence from the water column is also reflected in *D. glacialis* not being found in the new ice samples which contained *S. longipes.*

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