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Spatial distribution of copepods in fast ice of eastern Antarctica

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Abstract: The distribution and abundance of sympagic copepods in fast ice of the Australian Antarctic Territory (AAT) were investigated between October and December 1995. Copepods were collected from six sites between the northern Vestfold Hills (Murphy Rocks) and Mawson Station, a distance of approximately 650 km. Nine species of copepods were identified from the ice cores, however, of these only three were recorded regularly: *Paralabidocera antarctica*, *Drescheriella glacialis* and *Stephos longipes*. The density of copepods was highest in the bottom few cm of ice, with abundances reaching up to 147 l^{-1} . The highest concentrations of chlorophyll *a* were also found in the bottom portion of ice, suggesting that the copepods congregated in regions of high food availability. All developmental stages of *Drescheriella glacialis* were observed during this study, often from within a single core. In contrast, *Paralabidocera antarctica* occurred mainly as early copepodite stages, and *Stephos longipes* mainly as nauplii. These observations were consistent with the documented life cycles for each species. *Drescheriella glacialis* appears to reproduce and breed within the ice, *Paralabidocera antarctica* overwinters in the ice but enters a pelagic phase as late-stage copepodids, while nauplii of *Stephos longipes* are the predominant stages which associate closely with sea ice.

key words: Copepods, *Drescheriella glacialis*, eastern Antarctica, sea ice, *Paralabidocera antarctica*, *Stephos longipes*

Introduction

Sea ice is a structurally heterogeneous habitat consisting of an ice-crystal matrix interspersed with a complex array of brine channels and pockets. The annual cycle of primary productivity in sea ice is less seasonal than in the water column and a substantial biomass of algae is present throughout the year (e.g. Hoshiai, 1981; Kottmeier and Sullivan, 1987), providing a reliable food supply for small grazers that inhabit the interstitial spaces in the ice matrix. Understanding the patterns of distribution and abundance of these sympagic (ice-dwelling) meiofauna is important for an accurate assessment of their role in the south polar ecosystem. Ice algae contribute a substantial amount to annual primary production in the Southern Ocean (Legendre *et al.*, 1992), and it is likely that grazing by invertebrates removes a considerable amount of this production *in situ*. However, little is known about the consumption rates of these

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organisms and, at present, there is little data with which to assess their regional importance.

We report here the results of a study aimed at examining the spatial distribution of copepods in fast ice of the Australian Antarctic Territory (AAT). Knowledge of the biogeographical patterns of copepods associated with Antarctic sea ice is incomplete, although progress has been made recently. A previous study of sea ice near Davis Station reported abundances up to $4 \times 10^5 \text{ m}^{-2}$ of nauplii of the calanoid copepod *Paralabidocera antarctica* in autumn ice (Swadling *et al.*, 1997). Also recorded were the calanoids *Stephos longipes* and *Ctenocalanus citer*, the poecilostomatoid *Oncaea curvata*, the cyclopoid *Oithona similis*, and unidentified harpacticoids. The densities of these taxa were at least two orders of magnitude lower than those of *Paralabidocera antarctica*. A similar suite of species has been reported from the Lützow-Holm Bay region near Syowa Station (Hoshiai and Tanimura, 1986), although the presence of *Stephos longipes* was not recorded. In the Weddell Sea, the sympagic macrofauna is dominated by *Stephos longipes* and several harpacticoid copepods, the most common of which is *Drescheriella glacialis* (Dahms *et al.*, 1990; Kurbjewit *et al.*, 1993; Schnack-Schiel *et al.*, 1995). These two species recently have been found also to dominate the copepod assemblages in ice of the Bellingshausen and Amundsen Seas (Schnack-Schiel *et al.*, 1998). Other harpacticoids recorded from sea ice in the Weddell Sea include *Harpacticus furcifer*, *Drescheriella racovitzai*, *Idomene antarctica* and *Hastigerella antarctica* (Dahms and Schminke, 1992). A general pattern appears to be emerging in which *Paralabidocera antarctica* is the dominant species of copepod inhabiting sea ice on the eastern side of the continent, whereas the region near the Antarctic Peninsula is dominated by *Stephos longipes* and *Drescheriella glacialis*. However, to date, studies on the eastern side of the Antarctic continent have been restricted to quite small areas.

In this paper we present the spatial distribution of copepods inhabiting the coastal fast ice belt between the Northern Vestfold Hills and Mawson Station in late spring and early summer, 1995. Sea ice along the coast persists for approximately 11 months of each year, usually breaking out in December or January. The objectives of the present study were twofold: (i) to document the diversity of sympagic meiofauna inhabiting sea ice along this large stretch of the east Antarctic coastline, and thus to broaden knowledge of their biogeography, and (ii) to examine the vertical and horizontal distributions of the dominant species of copepods in the period just prior to ice break-out.

Materials and methods

The spatial distribution of copepods in fast ice of the AAT was investigated over a distance of approximately 650 km between October and December 1995. The sea ice was sampled near six coastal rock outcrops: (i) Mawson Station ($67^{\circ} 36' \text{S}$, $62^{\circ} 52' \text{E}$), (ii) Larsemann Hills ($69^{\circ} 24' \text{S}$, $76^{\circ} 15' \text{E}$), (iii) Rauer Islands ($68^{\circ} 51' \text{S}$, $77^{\circ} 50' \text{E}$), (iv) Murphy Rocks ($68^{\circ} 14' \text{S}$, $78^{\circ} 43' \text{E}$), and two closely situated sites offshore from Davis Station ($68^{\circ} 35' \text{S}$, $77^{\circ} 58' \text{E}$), (v) O'Gorman Rocks and (vi) Bluff Island (Fig. 1).

Ice cores were obtained using SIPRE ice augers. Five to ten cores were collected from sites (i) to (iv), along transects several kilometres in length. Each core was

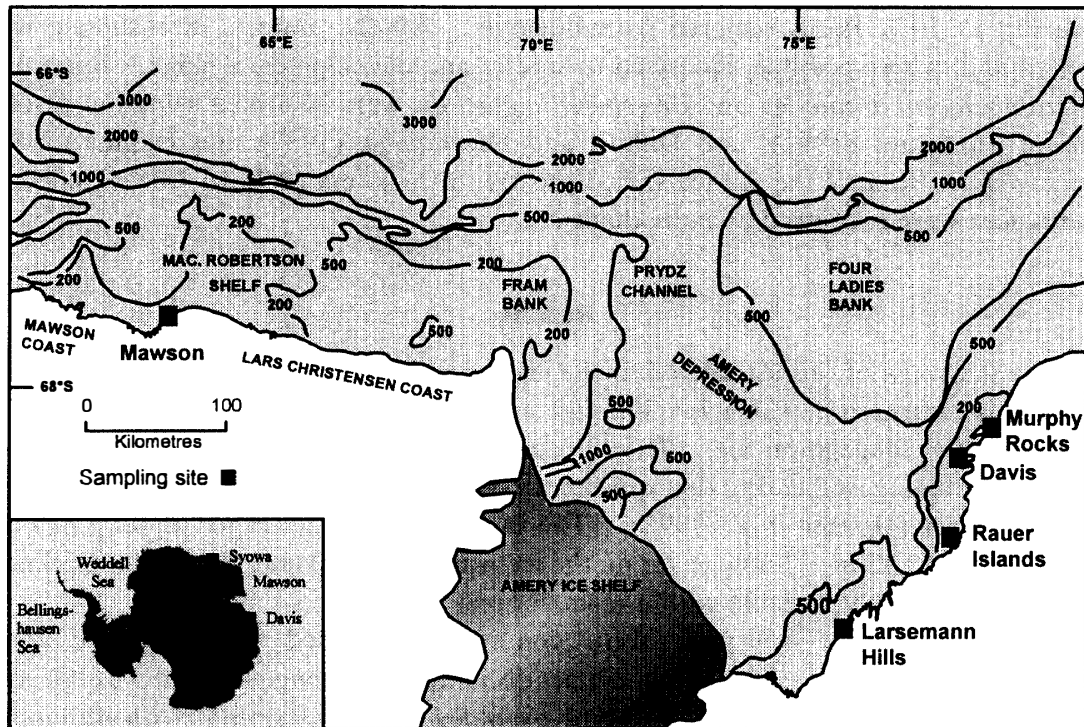


Fig. 1. Map showing locations of the sampling sites used in the study. Inset shows locations of additional sites mentioned in the text.

transferred to an opaque PVC tube which was then sealed at both ends and stored horizontally at -20°C until processing. To examine also the changes in distribution over time, the two sites near Davis Station were sampled on several occasions. On each sampling date three cores were collected within 1 to 2 m of each other. The cores were sectioned in the field and the bottom 15–20 cm returned to the laboratory. Ice thickness and the depth of the snow cover was measured at each core site.

The cores were processed soon after collection. They were sectioned into segments 10 to 20 cm in length, depending on the natural stratigraphy of the ice. Each segment was melted in 1 l of GF/F filtered seawater in covered, plastic containers that were kept in the dark at 2°C . The final dilution factor was approximately 1 : 2 ice to filtered seawater, and complete melting occurred within 24 hours. The melted core water was subsampled and a known volume (500–900 ml) filtered onto a 47 mm Whatman GF/F glass fibre filter. Chlorophyll *a* was extracted from the filters with 90% (v/v) acetone, sonicated in an ultrasonating bath for 5 min, stored overnight at -20°C , resonicated and finally centrifuged. The supernatant was transferred to a 4 cm glass cuvette and the absorbance measured at 664, 647 and 630 nm using a GBC 916 Spectrophotometer, with 90% (v/v) aqueous acetone in the reference beam. To correct for turbidity in the samples, the absorbance at 750 nm was also measured. The concentration of chlorophyll *a* was calculated using the equations given in Parsons *et al.* (1984).

Following subsampling for chlorophyll *a* measurements, the remaining melted core water was filtered through a $53\ \mu\text{m}$ mesh sieve. Metazoans collected on the sieves were

preserved in 10% Borax-buffered formaldehyde. All the animals in a sample were counted and, where possible, identified to species and developmental stage. Specimens of *Paralabidocera antarctica* and *Drescheriella glacialis* were identified using the descriptions of Tanimura (1992), and Dahms and Dieckmann (1987) and Dahms (1987), respectively. Because the sea ice varied greatly in thickness (0.78 to 1.85 m) copepod abundances were expressed as individuals l^{-1} .

Results

The thickness of the sea ice and of the snow cover at each site during the period of sampling is presented in Table 1. The fast ice sampled in this study was all first-year, predominantly congelation ice. The ice surface was generally smooth or had small amounts of ridging, indicating that quiescent conditions prevailed during the formation of the ice sheet (Horner *et al.*, 1992). The thickness of ice averaged about 1.6 m and never exceeded 1.85 m. Snow cover on the ice was between 0 and 400 mm in thickness, and was often highly variable within a small area.

Three species of copepods were commonly recorded from the ice cores: *Paralabidocera antarctica*, *Drescheriella glacialis* and *Stephos longipes*. Other copepods, including *Harpacticus furcatus*, *Mesochra pygmaea*, *Oncaea curvata*, *Oithona similis*, *Tisbe* sp. and a harpacticoid from the family Ectinosomatidae, were recorded on rare occasions. The only other metazoan species observed was the amphipod *Paramoera walkeri*. All developmental stages of *Drescheriella glacialis* were present in the ice samples, often within the same core. Adult males and females with egg sacs were noted in several cores. *Paralabidocera antarctica* occurred mainly as early copepodid stages, and adult males and females were observed only in one core at Bluff Island. *Stephos longipes* was present as adults, nauplii and early-stage copepodids.

As the variation within a site (*i.e.* along a transect) was found to be less than that between sites the cores from each site were pooled to facilitate examination of the larger scale patterns. There was considerable variation in the horizontal distribution of copepods between the six sites (Table 2). The abundance of copepods varied between cores from zero to 147 individuals l^{-1} . The highest densities were recorded at the Larsemann Hills and the lowest at Murphy Rocks.

At the Larsemann Hills, copepodids of *Paralabidocera antarctica* and nauplii of

Table 1. Mean ice and snow thickness at each site. The range (minimum to maximum) is given in parentheses. N is the number of cores.

Site	Sampling dates	Ice thickness (m)	Snow thickness (mm)	N
Mawson	2/11/95	1.28 (1.20-1.32)	32 (0-100)	10
Larsemann Hills	9-10/11/95	1.59 (1.55-1.60)	110 (0-200)	10
Rauer Islands	22/11/95	0.94 (0.92-0.97)	No snow cover	5
O'Gorman Rocks	26/10-2/12/95	1.68 (1.12-1.85)	120 (0-400)	36
Bluff Island	26/10-2/12/95	1.65 (1.10-1.80)	100 (0-350)	36
Murphy Rocks	20/11/95	0.93 (0.78-1.02)	No snow cover	5

Table 2. Mean abundance (numbers l^{-1}) of nauplii, copepodids and adults of *Paralabidocera antarctica*, *Drescheriella glacialis* and *Stephos longipes* at six sampling sites in the AAT. The mean concentration of chlorophyll *a* ($\mu g l^{-1}$), integrated for the entire ice core, is also shown for each site. The range (minimum to maximum) is given in parentheses. N is the number of cores.

	Mawson (N=10)	Larsemann Hills (N=10)	Rauer Islands (N=5)	O'Gorman Rocks (N=36)	Bluff Island (N=36)	Murphy Rocks (N=5)
<i>Paralabidocera antarctica</i>						
Nauplii	0.1 (0-0.6)	nr	nr	0.7 (0.3-3.3)	0.1 (0-0.7)	nr
Copepodids	4.7 (0-16.8)	8.1 (0-73.9)	nr	1.0 (0-6.3)	22.3 (0-90.7)	0.2 (0-1.4)
Adults	nr	nr	nr	nr	1.8 (0-9.0)	nr
<i>Drescheriella glacialis</i>						
Nauplii	nr	14.1 (0-129.1)	nr	0.3 (0-1.3)	0.4 (0-2.7)	nr
Copepodids	0.4 (0-2.8)	3.4 (0-16.2)	nr	17.5 (0.7-52.3)	2.0 (0-9.3)	1.7 (0-4.7)
Adults	0.9 (0-7.6)	0.2 (0-0.7)	nr	0.2 (0-1.3)	0.8 (0-3.3)	nr
<i>Stephos longipes</i>						
Nauplii	nr	nr	6.7 (0-18.3)	nr	nr	nr
Copepodids	0.2 (0-2)	0.1 (0-0.7)	nr	nr	nr	nr
Adults	nr	0.2 (0-1.3)	0.5 (0-1.5)	nr	nr	nr
Chlorophyll <i>a</i>	32.4 (4.2-57.9)	9.8 (1.4-26.9)	2.7 (0.9-4.5)	64.4 (1.6-114.0)	156.2 (8.2-250.0)	9.5 (28.9-91.7)

nr = not recorded at the site.

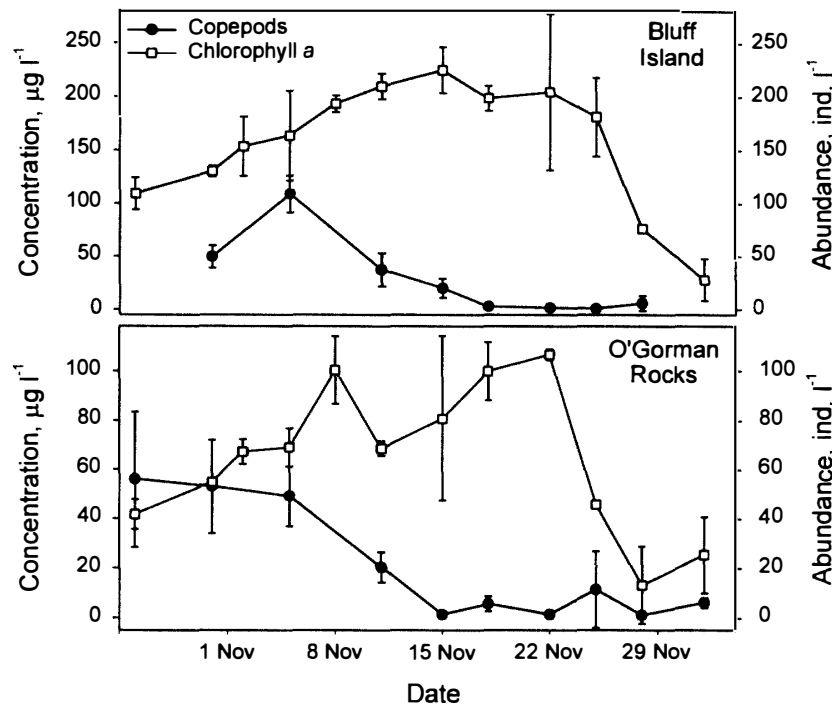


Fig. 2. Concentration of chlorophyll *a* and copepod abundance at Bluff Island and O'Gorman Rocks. Note that vertical scales are different. Some error bars were too small to be shown.

Drescheriella glacialis were the most common animals, with maximum abundances of $74 l^{-1}$ and $129 l^{-1}$, respectively. Copepodids of *Paralabidocera antarctica* and adult *Drescheriella glacialis* were more commonly reported from ice near Mawson Station. The abundance of *Stephos longipes* at those two sites was always low. At the Rauer Islands *Stephos longipes* was the only copepod recorded in the ice cores, with the nauplii reaching a maximum abundance of $18 l^{-1}$. Adults of this species were also found in the cores, however no copepodids were noted at that site. The mean abundance of copepods reached maximums of 6, 56 and $109 l^{-1}$ at Murphy Rocks, O'Gorman Rocks and Bluff Island, respectively (Fig. 2). No *Stephos longipes* were observed at those sites (Table 2). There was some variation in the distribution of species between O'Gorman Rocks and Bluff Island (Fig. 3). At Bluff Island the maximum densities of *Paralabidocera antarctica* and *Drescheriella glacialis* were $94 l^{-1}$ and $11 l^{-1}$, respectively. At O'Gorman Rocks *Paralabidocera antarctica* reached a maximum abundance of only $10 l^{-1}$, whereas that of *Drescheriella glacialis* was $55 l^{-1}$. Young copepodids of both species were the most common stages recorded.

The concentration of chlorophyll *a* in the sea ice was also very patchy. The highest mean concentration was found at Bluff Island, and the lowest at the Rauer Islands (Table 2). The concentration of chlorophyll *a* was consistently higher at Bluff Island than at O'Gorman Rocks (Fig. 2). At both sites the highest concentrations

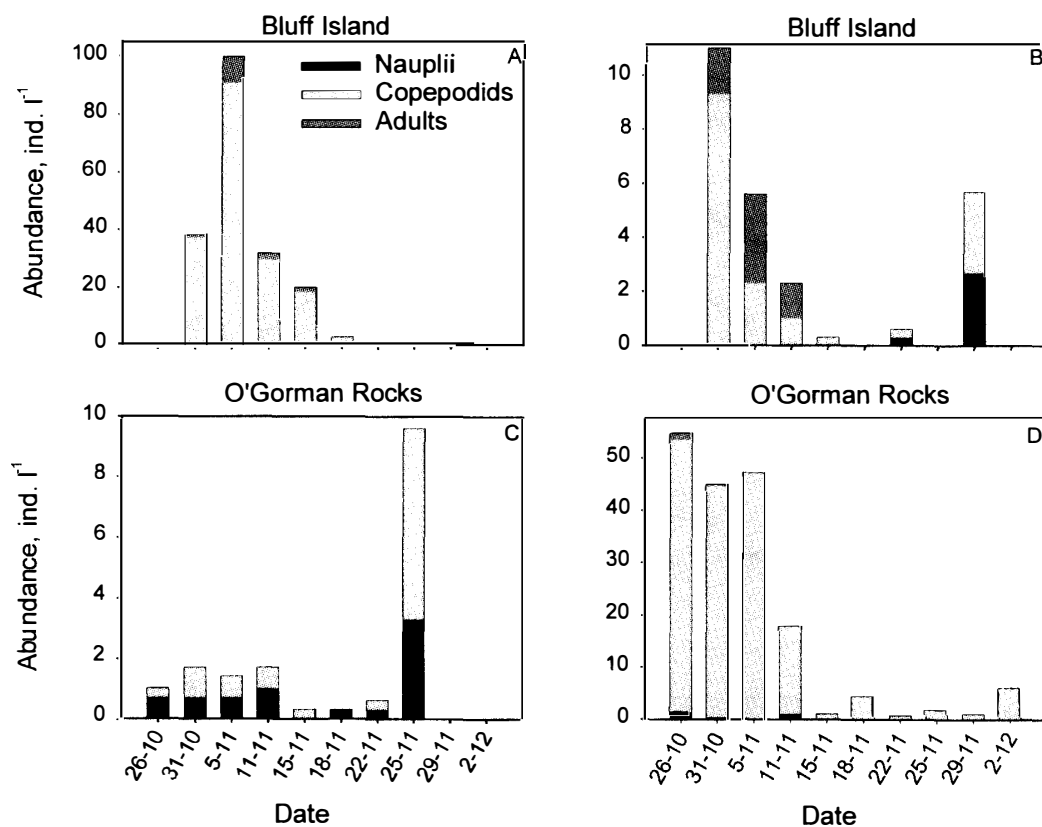


Fig. 3. Distribution of nauplii, copepodids and adults of *Paralabidocera antarctica* (A,C) and *Drescheriella glacialis* (B,D) at Bluff Island and O'Gorman Rocks. The Bluff Island site was not sampled on 26 October.

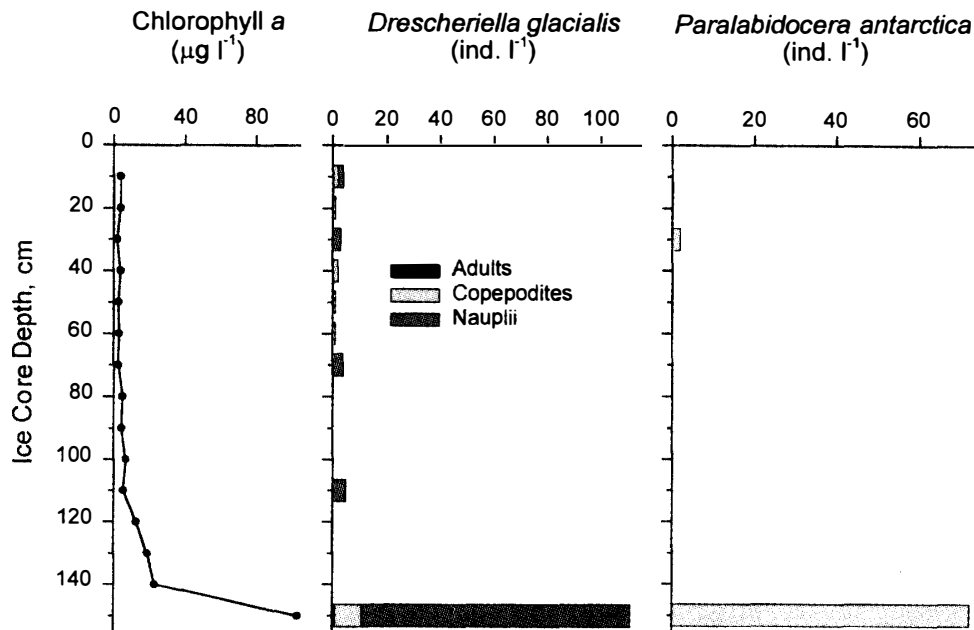


Fig. 4. Vertical profile of chlorophyll *a*, *Drescheriella glacialis* and *Paralabidocera antarctica* in an ice core collected from the Larsemann Hills.

were recorded in November, and had decreased markedly by early December.

Within the cores, the highest abundances of copepods were found in the bottom 10 cm of ice, irrespective of the species. No more than 5 copepods l^{-1} were found in other sections of the ice cores. Figure 4 presents vertical distributions of chlorophyll *a*, *Paralabidocera antarctica* and *Drescheriella glacialis* from one ice core sampled near the Larsemann Hills. Similar vertical profiles were obtained for the majority of the cores, and therefore it is unnecessary to present the data for each core. *Drescheriella glacialis* was distributed throughout the ice but was most abundant in the bottom 10 cm of the cores. *Paralabidocera antarctica* was also most abundant in the bottom 10 cm; it was rarely found in the interior of the cores. *Stephos longipes* was found only in the bottom 10 cm. The highest concentrations of chlorophyll *a* were also measured in the bottom few cm of ice, with a maximum of $373 \mu\text{g l}^{-1}$ recorded in the bottom 10 cm of a core collected at Murphy Rocks.

Discussion

The copepod assemblage of the coastal fast ice between Mawson Station and Murphy Rocks was characterised by low species richness, and high abundance of one or two dominant species. *Paralabidocera antarctica*, *Drescheriella glacialis*, and *Stephos longipes* were the commonly observed species, with other taxa recorded from one or two cores only. Low copepod diversity may be characteristic of the entire Antarctic sea ice habitat as, to date, only sixteen species have been reported from ice cores (see Schnack-Schiel *et al.*, 1998, this study). Several of those species, including *Ctenocalanus* spp., *Oithona similis* and *Oncaea curvata*, are pelagic animals that occur in high abundance in the water column and are occasionally captured near the ice water

interface. Thus, the number of truly sympagic species is possibly lower. The low number of taxa inhabiting sea ice implies that comparatively few species possess the behavioural and physiological traits necessary for successful colonisation, such as a strong salinity tolerance. Salinity of interstitial brine channels probably changes frequently as brine is either concentrated by exclusion from the ice matrix or, alternatively, diluted as the ice melts. *Drescheriella glacialis* has been shown to survive in salinities from 18 to 90 practical salinity units (psu), although it exhibited lethargic behaviour at both extremes of the range (Dahms *et al.*, 1990). *Paralabidocera antarctica* thrives in several hyposaline Antarctic lakes (10 to 20psu) (Bayly, 1978), and 100% survival rates were observed for nauplii maintained for twelve days at salinities from 35 to 50 psu (K. Swadling, unpublished data).

There was a strong degree of spatial patchiness in the horizontal distribution of the copepods, both within and between the sampling sites. Other studies of distribution have revealed similar patchiness in closely situated cores, with abundances varying by several orders of magnitude (Dahms *et al.*, 1990; Swadling *et al.*, 1997; Schnack-Schiel *et al.*, 1998). In the present study, the concentration of chlorophyll *a* also varied within and between the sampling sites, and these observations were consistent with our knowledge of small-scale heterogeneity in the physical and chemical properties of sea ice (*e.g.* Eicken *et al.*, 1991; Perovich *et al.*, 1998). Variability in the size, number and spatial arrangement of brine pockets and channels, coupled with irregularities in sea ice crystals that affect absorption and scattering of light particles, influences the growth and development of patches of ice algae. Ice algae is the most likely food source of *Paralabidocera antarctica*, *Drescheriella glacialis* and *Stephos longipes* (see Dahms and Dieckmann, 1987; Hoshiai *et al.*, 1987; Schnack-Schiel *et al.*, 1995), however the extent of their ability to detect and congregate near patches of food is unknown.

The vertical profiles of chlorophyll *a* in the sea ice were typical of those observed in other fast ice regions; *e.g.* the concentration was always highest in the bottom few cm of ice at McMurdo Sound (Palmisano and Sullivan, 1983) and near Syowa Station (Hoshiai, 1981). In the present study, copepods were also concentrated near the bottom of the ice, a feature which appears typical of sympagic biota in nearshore fast ice (Hoshiai and Tanimura, 1986). There was greater variation in the vertical distribution of chlorophyll *a* and copepods in seas near the Antarctic Peninsula (Dahms *et al.*, 1990; Schnack-Schiel *et al.*, 1995, 1998). *Stephos longipes* and *Drescheriella glacialis* penetrated well into the ice, especially in the Amundsen Sea where rotten slush layers were flooded with seawater, promoting algal growth (Schnack-Schiel *et al.*, 1998). The hardness and relatively uniform structure of fast ice along the coast of the AAT is not as conducive to the formation of these infiltration layers and so biological activity in the interior of the ice is reduced.

The three common species reported from east Antarctic fast ice differ in their relationship with the sea ice. *Paralabidocera antarctica* overwinters in the sea ice as nauplii and undergoes two main growth periods that coincide with autumn and spring blooms of ice algae. Upon entering a pelagic phase from stage CIV in late spring this species remains closely associated with the under-ice surface (Hoshiai *et al.*, 1996; Tanimura *et al.*, 1996). The life cycle described by Tanimura *et al.* (1996) for the population of *Paralabidocera antarctica* near Syowa Station was similar to that observed

for the population found in nearshore waters adjacent to the Vestfold Hills (Swadling, 1998). The development of this species is highly synchronised, so at the time of sampling it was not surprising to find predominantly early stage copepodids present in the ice cores. Adults observed in one core at Bluff Island were most likely sampled fortuitously by the corer at the ice-water interface. *Paralabidocera antarctica* is abundant in fast ice of the AAT and its low density at Murphy Rocks and the Rauer Islands is attributed to the late date of sampling; by mid-November the population had entered its pelagic phase. This change in habitat is also reflected by the drop in abundance observed at Bluff Island in mid-November.

Stephos longipes was not observed in the present study in the high abundances reported for ice near the Antarctic Peninsula (Kurbjeweit *et al.*, 1993; Schnack-Schiel *et al.*, 1995, 1998). This might be explained, in part, by the growth properties of sea ice. In the Weddell Sea frazil ice crystals form continuously at depth in supercooled water, promoting continual scavenging of particles as the crystals rise to the surface (Weeks and Ackley, 1982). It has been hypothesised that *Stephos longipes* breeds in the upper layers of the water column and attaches its sticky eggs directly onto the frazil ice crystals, facilitating their incorporation into the sea ice (Kurbjeweit *et al.*, 1993; Schnack-Schiel *et al.* 1998). Fast ice of the AAT is predominantly congelation ice which forms by the growth of large, elongated crystals perpendicular to the underside of the ice sheet (Horner *et al.*, 1992), and thus is a less efficient mechanism for concentrating copepod eggs and other particles.

Drescheriella glacialis is unusual for an Antarctic invertebrate in that it inhabits the sea ice throughout its entire life cycle, and reproduction occurs year-round in areas where ice persists (Dahms *et al.*, 1990). The presence of all developmental stages in ice cores of the present study support the hypothesis of continual reproduction by this species. *Drescheriella glacialis* occurred in high densities in coastal areas that were devoid of sea ice later in the summer, so populations inhabiting fast ice along the AAT must have a benthic or pelagic component to their life cycle. The species is found in pack ice in the Weddell Sea over water depths of 2000 to 5000 m and must be able to spend time in the open water (Dahms *et al.*, 1990). However no animals were encountered in the water column of the Amundsen and Bellingshausen Seas (Schnack-Schiel *et al.*, 1998) or in shallow waters near the Vestfold Hills (Swadling, 1998). *Drescheriella glacialis* has been found to be abundant in first-year fjord ice situated over very shallow water ($Z_{\max} = 9$ m) where turbulent mixing could be adequate to transport either nauplii or eggs from the sediment to the ice cover (Swadling, 1998). The question of whether *Drescheriella glacialis* re-colonizes sea ice from the benthos or the pelagos is not yet resolved.

The results from this study complement the general biogeographical patterns that are emerging for Antarctic sympagic copepods. *Drescheriella glacialis* is abundant in several regions and probably has a circum-Antarctic distribution. *Paralabidocera antarctica* is a dominant species along the coast from at least the Vestfold Hills to Lützow-Holm Bay and possibly throughout the east Antarctic coast. It appears to occur in lower numbers elsewhere (*e.g.* Menshenina and Melnikov, 1995). *Stephos longipes* is very abundant on the western side of the continent and, while it also occurs on the eastern side, the differences in the mechanisms of sea ice formation might

preclude it from establishing large populations. To our knowledge no studies of the pack ice macrofauna have been made in the Indian Ocean sector of the Southern Ocean, so it is not yet possible to determine whether a species assemblage similar to that in the fast ice is found further offshore.

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