

# The life cycle of *Stephos longipes* – an example for cryopelagic coupling in the Weddell Sea (Antarctica)

F. Kurbjeweit<sup>1</sup>, R. Gradinger<sup>2</sup>, J. Weissenberger<sup>1</sup>

<sup>1</sup>Alfred-Wegener-Institut für Polar- und Meeresforschung, Columbusstr., D-27568 Bremerhaven, Germany

<sup>2</sup>Institut für Polarökologie, Universität Kiel, Wischhofstr. 14, Geb. 12, D-24148 Kiel, Germany

**ABSTRACT:** Distribution, abundance and age composition of the calanoid copepod *Stephos longipes* (Giesbrecht) were studied in the southeastern Weddell Sea in January–February 1991. Samples were taken in the water column with a multiple closing net in 5 depth strata down to 1000 m. Concurrent samples were taken from drifting ice floes and from a 1 m deep layer underneath the pack ice (under ice water layer: UIWL) using a specially designed pump. *S. longipes* was the predominant calanoid copepod at most stations throughout the continental shelf area within the upper 50 m of the water column. Generally, abundances inside the pack ice floes exceeded those in the UIWL by 1 to 3 orders and the water column below by 3 to 5 orders of magnitude respectively. The mean population stage was lowest inside the ice floes followed by the UIWL and the water column. Also, nauplii and young copepodite stages (CI and CII) often outnumbered all other metazoan groups within and beneath the ice. Highest densities of *S. longipes* ( $> 90\,000\text{ m}^{-3}$ ) were observed in ice floes and UIWL samples where platelet ice was particularly frequent, probably as a result of the extreme stickiness of *S. longipes* eggs and their attachment to floating ice crystals. Fecal pellets of *S. longipes*, collected in the UIWL, were in most cases filled with sea ice algae. Our results indicate that the life cycle of *S. longipes* is closely associated with the sea ice, especially platelet ice layers, where a high algal standing crop can sustain a sufficiently high secondary production in an otherwise food limited habitat. Thus, *S. longipes* uses a completely different strategy than large calanoid copepods in the Antarctic which do not inhabit sea ice at any given time during their life cycle.

## INTRODUCTION

The sea ice cover plays an important role in structuring marine habitats of polar oceans (see Eicken 1992). It reduces the available light intensity and, thus, the productivity of the pelagic communities, but it also serves as a habitat containing a typical flora and fauna. These ice and sub-ice communities numerically consist mainly of bacteria, algae, fungi, and protozoans (e.g. Horner 1985, Garrison & Buck 1991). The few investigations focusing on the possible role of metazoans in the ice community were nearly entirely done at Arctic coastal sites.

Carey (1985) summarized the knowledge about the Arctic ice-associated fauna, where gammarid amphipods dominate the sympagic communities. Lønne & Gulliksen (1991) described the habitat selection and

behavior of 3 dominant amphipod species. Gradinger et al. (1991) demonstrated that the Arctic in-ice fauna is dominated by ciliates and acoel turbellarians, while crustaceans were of minor importance. Runge et al. (1991) recently summarized the multidisciplinary investigations on coupling processes between ice algae and metazoan zooplankton in the southeastern Hudson Bay. Here, calanoid copepods like *Calanus glacialis* and *Pseudocalanus minutus* graze on ice algae during the night time, when they actively migrate from deeper water layers to the interface between ice and water.

Andriashev (1968) developed a concept highlighting the significance of the sea ice biota for the Antarctic biosphere, where the biomass of the ice algae is comparable to the standing stock of phytoplankton blooms in some productive seas of the northern hemisphere.

He suggested that this standing crop supplies 2 major groups of animals, those that live at least temporarily inside the ice floes (in-ice fauna) or those that never directly enter the ice floes, but are to some degree trophically dependant on the ice community (sub-ice fauna). The in-ice fauna consists of amphipods (Rakusa-Suszczewski 1972, Richardson & Whitaker 1979, Hopkins & Torres 1988), copepods (Tanimura et al. 1984, Hopkins & Torres 1988, Waghorn & Knox 1988, Dahms et al. 1990), foraminifera (Lipps & Krebs 1974, Dieckmann et al. 1991), polychaetes (Andriashev 1968) and fingerlings of *Pagothenia* (= *Trematomus*) *borchgrevinki* (Andriashev 1968). The sub-ice fauna consists mainly of euphausiids like *Euphausia crystallorophias* (Andriashev 1968, Bradford 1978), *Euphausia superba* (Marr 1962, Marschall 1988), adult cryopelagic fish such as *Pagothenia borchgrevinki* (Bradford 1978, Hoshiai & Tanimura 1981) and *Dissostichus mawsoni* (Andriashev 1968) and presumably the calanoid copepod *Calanus propinquus*, that seems to live beneath the sea ice during winter (Nöthig et al. 1991).

In the present study, we examined the distribution and abundance of the ice, sub-ice (under ice water layer, UIWL) and water column fauna with special reference to the calanoid copepod *Stephos longipes* and its age composition. In all 3 habitats we observed *S. longipes* as a predominant component of the species assemblages. As a result of the abundance data and age composition analysis of *S. longipes* we established a conceptual model of its life cycle in comparison to other Antarctic copepods.

**METHODS**

In January–February 1991 plankton samples were taken from RV 'Polarstern' in the southeastern Weddell Sea, Antarctica, by means of a vertically towed multiple opening and closing net (100 µm, 0.25 m<sup>2</sup>; Weikert & John 1981) in 5 depth strata down to 1000 m chosen according to water column stratification. The volume of water filtered was calculated using a flow meter (Hydrobios, Kiel, Germany). On 3 permanent drift stations (Stns 126 to 128) and on 1 transect from close to the shelf ice to the deep ocean (Fig. 1) samples were concurrently obtained from the sea ice and an approximately 1 m deep layer underneath the sea ice (UIWL). Ice cores were taken with a modified 3" CRREL ice auger and cut into 1 to 10 cm long sections for the determination of the

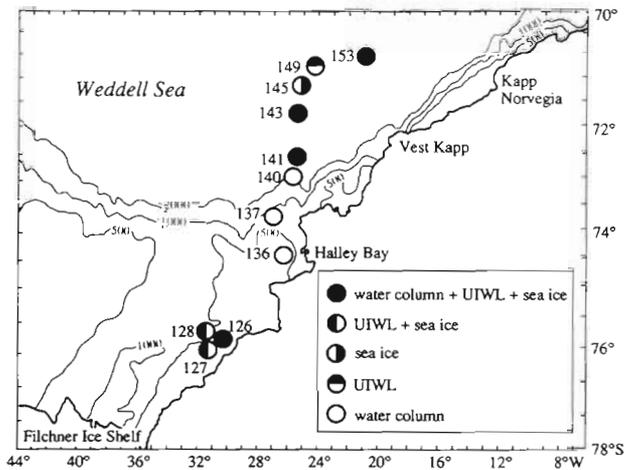


Fig. 1. Station map of the Weddell Sea with depth (m) and shelf ice (thick line) contours. Symbols indicate kind of sample taken on each station. UIWL: under ice water layer

vertical distribution of sea ice organisms (for details of ice sample treatment see Gradinger et al. 1991).

The submersible under-ice pump included a collector-tube (4 cm diameter, 190 cm length) equipped with a 20 mm gauze at the opening to prevent damage to the collected organisms by larger pieces of ice. The lower end of the tube was fixed in a rectangular position to the under-ice surface covering a sampling area of about 2.2 m<sup>2</sup>. Organisms were collected on a 60 µm gauze within a 40 l plastic container directly on the ice floe. Pumping rates were determined at the beginning and at the end of the pumping time (approximately 24 l min<sup>-1</sup>). Pumping times ranged from 30 to 120 min.

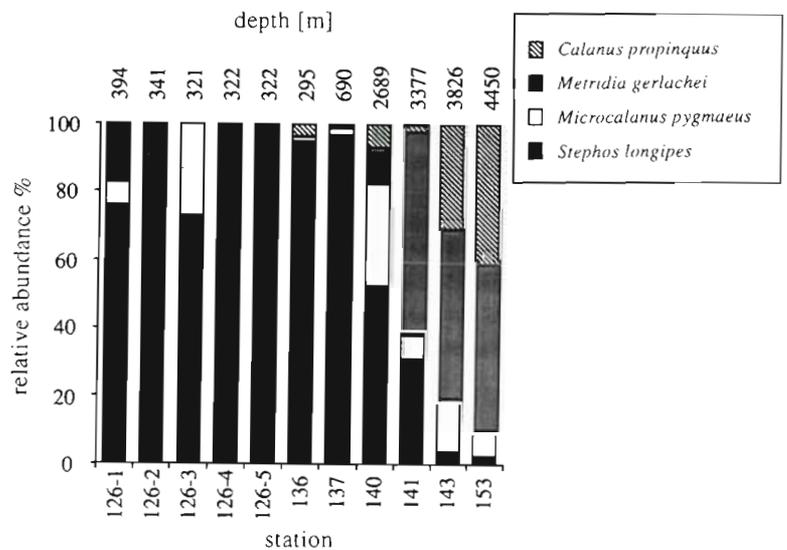


Fig. 2. Relative abundances of *Stephos longipes*, *Calanus propinquus*, *Metridia gerlachei* and *Microcalanus pygmaeus* within the upper 50 m of the water column, and depth at each station

During the drift stations, the submersible pump as well as ice cores were taken from different locations to study spatial heterogeneity in both habitats. A detailed summary of all station positions and procedures is given by Bathmann et al. (1992).

Samples were preserved in borax buffered formalin (4% final concentration). Depending on the abundance of organisms, the whole sample or at least 30 specimens per stage and species were enumerated under a dissecting microscope.

Mean population stage for *Stephos longipes* was calculated using the abundance data according to Huntley & Escritor (1991)

$$[S] = (N_{CI} + 2N_{CII} + \dots + 6N_{CVI}) / \sum N$$

where  $N_{CI}$ ,  $N_{CII}$ , ...  $N_{CVI}$  = number of specimens of copepodite stages CI, CII, ... CVI, and  $\sum N$  = the sum of all individuals.

For the determination of possible food sources of *Stephos longipes* fecal pellets from the pump samples were examined in detail using light microscopy.

## RESULTS

*Stephos longipes* constituted 2 to 100% of the total abundance of calanoid copepods in the investigation area in the upper 50 m of the water column (Fig. 2). It was the dominant species at most stations in the continental shelf area. At stations with increasing water depth the calanoid copepods *Calanus propinquus*, *Microcalanus pygmaeus* and *Metridia gerlachei* dominated in the surface layer. The vertical distribution pattern of *S. longipes* within the water column was characterized by a large decrease from the upper layers to greater water depth (e.g. Stn 126-5, Fig. 3). *S. longipes* showed an inverse distribution pattern with highest abundances in the deepest water layer just above the sea floor only at Stn 136 (Fig. 3).

The abundance of *Stephos longipes* at drift Stn 126 was  $<2$  ind.  $m^{-3}$  over the entire water column, and thus, 1 order of magnitude less than at the other shelf Stns 136 & 137 further north (Fig. 4). Along the transect (Stns 136 to 153) the abundance decreased with distance from the shelf ice and increasing water depth, respectively. High abundances of *S. longipes* were observed inside the pack ice floes and in the under ice water layer (UIWL) on most stations (Fig. 4). Generally, abundance of copepodite stages inside the ice floes exceeded those in the UIWL by 1 to 3 orders of magnitude and those in the water column by 3 to 5 orders of magnitude. The abundance of nauplii could only be determined within the sea ice and in the UIWL due to their small size and the different sampling equipments

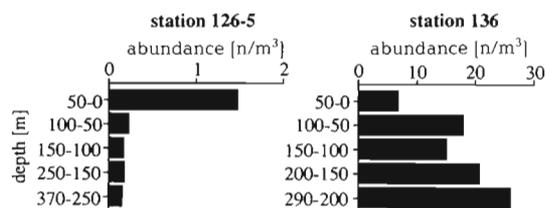


Fig. 3. *Stephos longipes*. Vertical distribution and abundance in the water column at Stns 126-5 & 136. Note different scales

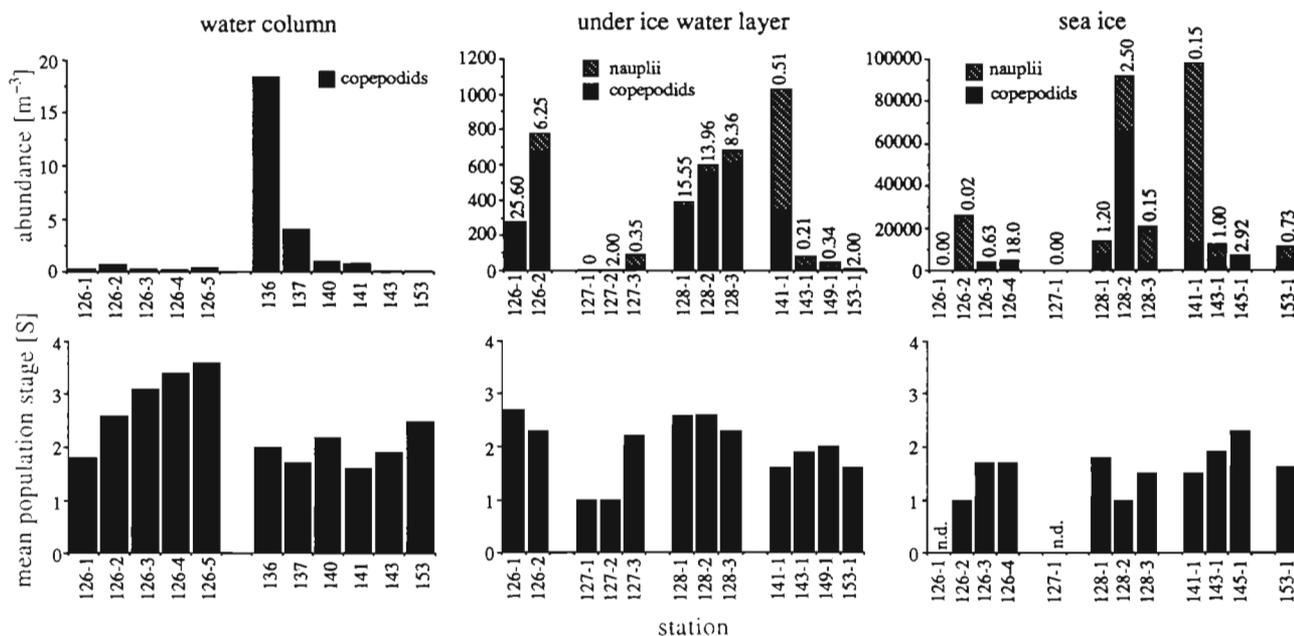


Fig. 4. *Stephos longipes*. Average abundance and mean population stage [S] in the water column, in the under ice water layer and inside the ice floes. Note different scales for abundance data. n.d.: not determined, because no copepodite stages were present. Ratios of abundance of copepodite stages vs nauplii given as numbers above bars

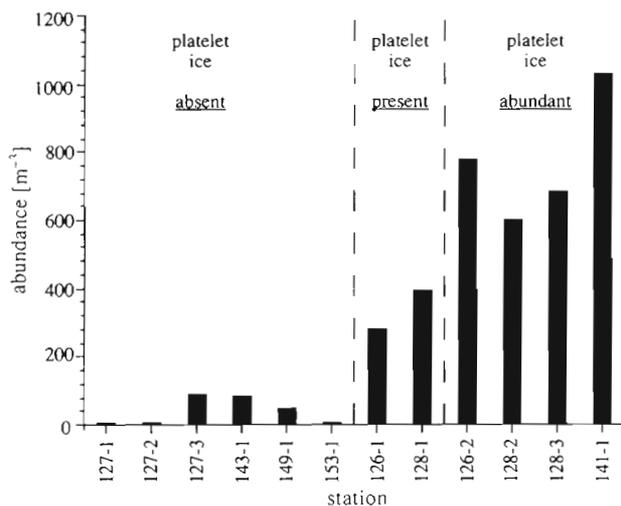


Fig. 5. Abundance of *Stephos longipes* in the UIWL in relation to the relative abundance of platelet ice

used. Inside the ice floes and in the UIWL they in almost all cases outnumbered the copepodite stages especially at the oceanic stations (Stns 141 to 153, Fig. 4).

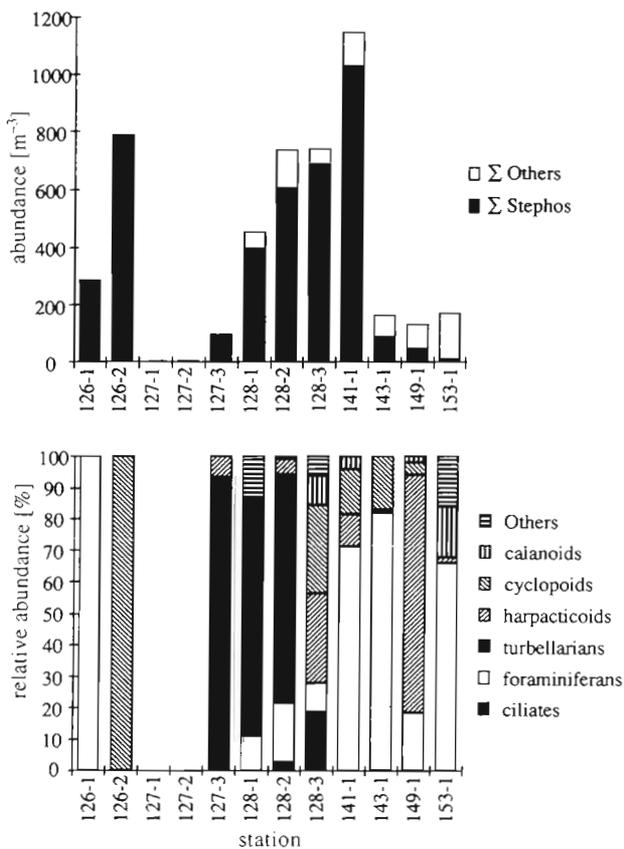


Fig. 6. Abundance of *Stephos longipes* and other groups of organisms and relative abundance of the other groups of organism without *S. longipes* in the UIWL

The mean population stage calculated for copepodite stages of *Stephos longipes* differed among the 3 habitats. The mean population stage inside ice floes ( $[S] = 1.5 \pm 0.4$ ) was significantly ( $p = 0.01$ ,  $t$ -test) lower than in the UIWL ( $[S] = 2.0 \pm 0.6$ ) and in the water column ( $[S] = 2.4 \pm 0.7$ ) (Fig. 4). The average copepodid nauplii ratio within the pack ice floes was significantly ( $p = 0.005$ ) lower than in the UIWL.

In the UIWL the abundance of *Stephos longipes* was apparently related to the occurrence of platelet ice (Fig. 5) and this species outnumbered other metazoan groups and sometimes even larger protozoans (Fig. 6). While *S. longipes* was by far the predominant species beneath the sea ice at all shelf stations, its importance decreased with distance to the shelf ice edge and increasing water depth (Fig. 6). The composition of the fauna other than *S. longipes* was heterogenous and showed no relation to the sampling sites. Protozoans like ciliates and heterotrophic flagellates were probably underestimated due to cell damage or their small size. The foraminiferan *Neogloboquadrina pachyderma* dominated the fauna at Stns 141, 143 & 153 and was the second most abundant group beside

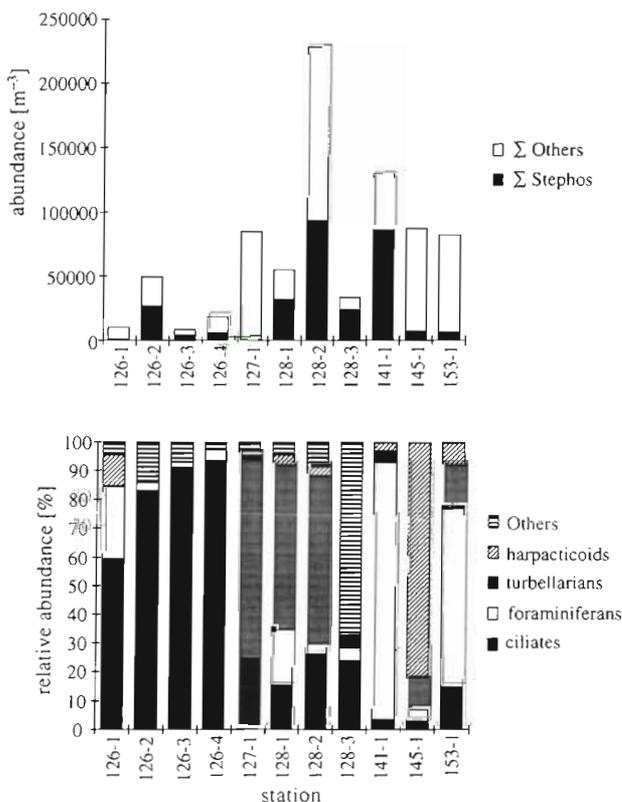


Fig. 7. Abundance of *Stephos longipes* and other groups of organisms and relative abundance of the other groups of organism without *S. longipes* inside ice floes

*S. longipes* in about thirty percent of all sub-ice samples. Studies by Berger (1971) and Brummer et al. (1986) demonstrated that over 80 % of a natural population of planktonic foraminifera are smaller than 100  $\mu\text{m}$ . Although we used a 60  $\mu\text{m}$  gauze for the concentration of the UIWL fauna a significant part of the foraminiferan population might have been lost during this process. In 3 samples, turbellarians were common and in 2 they were the second most abundant group after *S. longipes*. Other copepods were almost negligible in abundance except cyclopoids of the genera *Oithona* and *Oncaea* and a harpacticoid, belonging to the genus *Drescheriella*.

Inside the ice floes *Stephos longipes* was one of the most important species and dominated in about 45 % of all samples (Fig. 7), but, in contrast to the sub-ice samples, there was no clear distribution pattern obvious for *S. longipes* within the sea ice. Only a slight correlation between the abundances inside the ice floes and in the UIWL ( $r^2 = 0.667$ ,  $n = 9$ ) was found. The composition of the remaining fauna beside *S. longipes* showed that ciliates as well as foraminifera, acol turbellarians and harpacticoids were the most important organism groups in the sea ice. Besides *S. longipes* no

cyclopoid or calanoid copepod species was found inside the pack ice floes (Fig. 7).

No clear correlation was found between the vertical distribution of *Stephos longipes* and chlorophyll *a* inside the ice floes. In about 50 % of all ice cores highest chlorophyll *a* concentrations were found in the lowermost centimeters of the ice floes, where *S. longipes* was also most abundant (Fig. 8). Other ice core samples showed strong vertical variations of both chlorophyll *a* and abundance of *S. longipes* (Fig. 8). In all ice cores the phytoplankton stock mainly consisted of typical ice algae like *Nitzschia cylindrus*, *N. curta* and other pennate diatoms. Fecal pellets of *S. longipes*, collected from the UIWL samples, contained only frustules of pennate diatoms like *Nitzschia* spp.

## DISCUSSION

Our results show that the life cycle of the calanoid copepod *Stephos longipes* includes stages inhabiting the 2 habitats, water column and sea ice. The overall abundance of *S. longipes* increased from the water column to the sea ice. The mean population stage [S] for copepodite stages decreased from the water column to the sea ice, and its nauplii were only abundant beneath and especially inside the ice floes. Thus, *S. longipes* seems to adopt a similar strategy to *Paralabidocera antarctica* in the Indian sector of the Antarctic (Fukuchi & Tanimura 1981, Tanimura et al. 1984, 1986, Hoshiai & Tanimura 1986), in McMurdo Sound in the Pacific sector (Foster 1987) and in meromictic lakes (Bayly 1978, Bayly & Burton 1987) or as *P. grandispinosa* at White Island in McMurdo Sound (Waghorn & Knox 1988).

The first hint for a close relationship of *Stephos longipes* with sea ice was given by Schnack-Schiel (1987). In late winter/early spring she collected large numbers of late developmental stages in the UIWL using a NIPR-I net (Fukuchi et al. 1979), while it was found in the upper 100 m of the water column in comparatively low numbers. In contrast, during January–February *S. longipes* was more abundant in the upper 100 m of the water column than in the sea ice. Schnack-Schiel suggested that *S. longipes* lives and reproduces in the layer directly below the ice in late winter/early spring. After the onset of large scale melting the population is released into the water column. For the western part of the Weddell Sea, Hopkins & Torres (1988) mentioned *S. longipes* as the most common metazoan species in sea ice samples collected during March over deep water (depth > 2000 m) close to the ice edge. This is in good agreement with results of Schnack-Schiel (unpubl.), who found *S. longipes* also to be abundant within the sea ice on oceanic

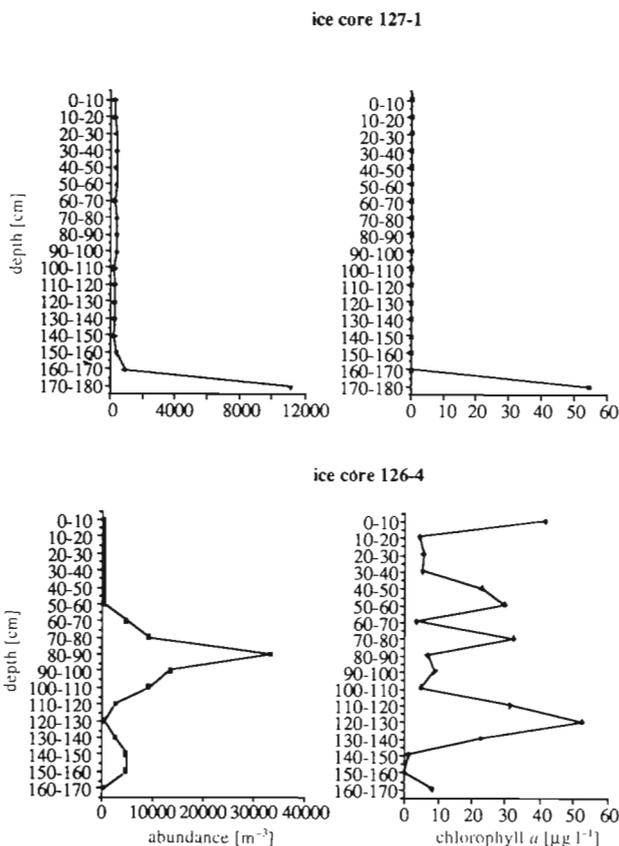


Fig. 8. Distribution patterns of *Stephos longipes* and chlorophyll *a* within sea ice cores 127-1 and 126-4

stations in the western Weddell Sea in September–October and with our results for Stn 141. In contrast, the abundance of *S. longipes* in the water column decreased drastically with distance from the shelf ice in the Weddell Sea (this study) and the Lazarev Sea (Kurbjeweit unpubl.). Therefore, the appearance of *S. longipes* in offshore areas is probably due to advection of sea ice from the shelf towards the centre of the Weddell Gyre. Our results show the significance of *S. longipes* as part of the sea ice and sub-ice community in the shelf areas.

The chlorophyll *a* concentrations within and beneath the sea ice are several orders of magnitude higher than in the underlying water column (Fig. 9). Our observations on the contents of fecal pellets demonstrated that *Stephos longipes* is mainly feeding on ice algae as Hoshiai et al. (1987) demonstrated for *Paralabidocera antarctica*. Reproduction experiments with *S. longipes* showed significantly higher egg production rates with ice algae as food than with planktonic diatoms (Kurbjeweit unpubl.). Therefore, food limitation for this species, as well as for other organism groups inhabiting the sea ice or the UIWL, seems unlikely, because, even during winter, high ice algal standing stocks have been observed in contrast to low phytoplankton stocks in the water column (Hoshiai 1977, 1981, Fukuchi et al. 1985, Spindler et al. 1990, Nöthig et al. 1991). Especially in the bottom centimeters of the pack ice floes and in the platelet ice layer (Fig. 9), conditions seem to be favourable for organisms as small as *S. longipes* or *P. antarctica*. Inside the ice brine channels of the ice floes and the platelet ice layer nauplii hatch in environments giving both enough food (Nöthig et al. 1991, Smetacek et al. 1992) and perfect protection from predation by krill (Schnack-Schiel 1987), fish (Hoshiai & Tanimura 1981, Hubold & Ekau 1990) and carnivorous zooplankton like ctenophores and amphipods (Hamner et al. 1989). Thus, the sea ice habitats serve as a 'nursery' for the larval copepods. Conclusively, *S. longipes* belongs to the group of the in-ice fauna, which lives at least temporarily in the lower part of the ice (Andriashev 1968). It was also found in intermediate layers of the sea ice, depending on the size of brine channels and pockets, whose structure have been described in detail by Weissenberger et al. (1992). The salinity of the brine is a function of the sea ice temperature and can exceed values of 120 ‰. Thus, nauplii and early copepodite stages of *S. longipes* must be able to regulate their body fluids over a wide salinity range as do other osmoconformers such as certain harpacticoids (Dahms et al. 1990).

At this stage only a preliminary picture of the life cycle of *Stephos longipes* can be drawn (see Fig. 9). Adult females and males occur in a 1:1 ratio from mid-November until mid-December just beneath the sea

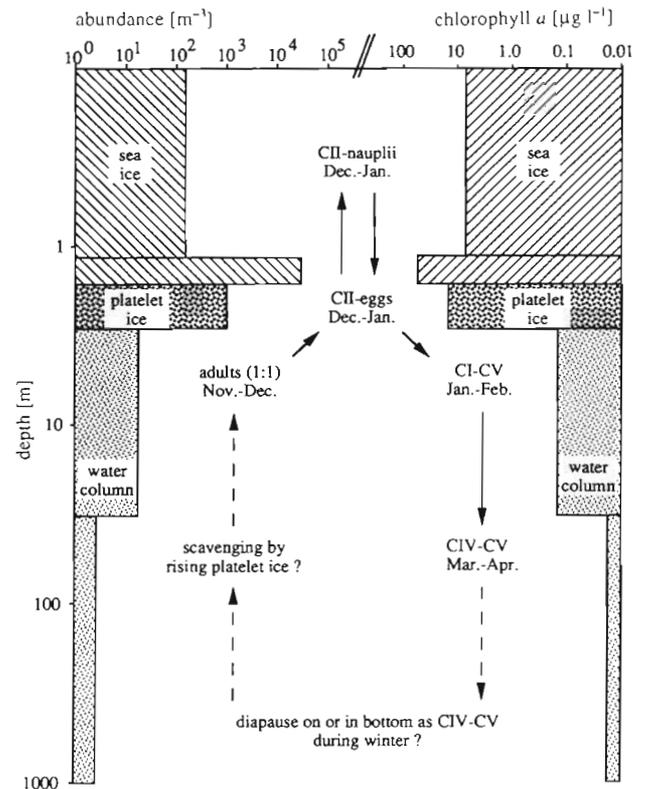


Fig. 9. Schematic representation of the abundance of different developmental stages of *Stephos longipes* and phytoplankton standing stock within and below the sea ice, and in the upper 1000 m of the water column

ice for mating on the western and eastern shelf of the Weddell Sea (Kurbjeweit unpubl.). These copepods either actively migrate to the surface or may be passively carried to the surface by dislodged anchor ice from the bottom (Dayton et al. 1969) or platelet ice formed in the water column (Dieckmann et al. 1986). Since the eggs of *S. longipes* are extremely sticky compared to those of other calanoid copepods, and females need direct contact with a substrate for egg-laying (Kurbjeweit unpubl.), they may attach their eggs directly to ice crystals or ice platelets. The harvesting of particles (sediment particles, algae, foraminifera) by drifting ice crystals, which results in a transport to the sea surface, has been demonstrated by several investigators (e.g. Ackley 1982, Reimnitz et al. 1990, Dieckmann et al. 1991). These observations may result from surface stickiness of particles which was shown for sea ice algae by Riebesell et al. (1991). At the end of December or beginning of January, young copepodite stages leave the brine channels inside the ice floes to feed in the UIWL and in the upper water column developing to CIV and CV by the end of March (Kurbjeweit unpubl.). These stages presumably migrate to greater

depths where they overwinter on or even within the bottom sediments with similar behavior to other species of the genus in tropical or boreal areas (McWilliam et al. 1981, Thain et al. 1981, Ohtsuka & Hiromi 1987, Jacoby & Greenberg unpubl.). This hypothesis is partly confirmed by Schnack-Schiel (unpubl.) who found copepodite stages CIV and CV dominating in deeper water layers and above the bottom in the eastern Weddell Sea in mid April. During this time of the year *S. longipes* was almost absent from the sea ice and the UIWL and constituted a major fraction of the sea ice community only on 1 station where platelet ice occurred. It is not yet known if CIV and CV copepodite stages feed during the winter and where they mature to adults. Due to the fact that the different developmental stages inhabit different levels within and beneath the ice and in the water column, intraspecific competition is minimal for this species and adults and juveniles may feed on different resources.

Thus, *Stephos longipes* is able to sustain a sufficiently high secondary production within and just beneath the sea ice where high algal biomass is found compared to an otherwise food limited habitat (Fig. 9). Consequently, *S. longipes* might play an important role as a grazer on ice algae and perhaps protozoans during spring and early summer within the sea ice, while its young copepodite stages may be prey for krill, fish fry and other carnivorous zooplankton later in the year in the water column. Its life cycle is therefore at least partially comparable with that of *Paralabidocera antarctica*, whose life cycle is completed within the sea ice (Hoshiai et al. unpubl.). However, it differs considerably from life histories of large copepods such as *Calanoides acutus*, which overwinters as CIV and CV in deeper water layers below 500 m (Voronina 1966, 1972, 1978, Marin 1988a, b, Schnack-Schiel et al. 1991) or *Calanus propinquus*, which seems to feed in the water column beneath the sea ice as CIII during winter (Nöthig et al. 1991). Whether *S. longipes* actively carries out ontogenetic migrations and how it differs from ecologically similar species as *Paralabidocera* spp. must be examined in more detail.

**Acknowledgements.** We are indebted to the captain and the crew of RV 'Polarstern' for their frequent assistance. We thank Richard Steinmetz and Kerstin Beyer for their support of our study. We are grateful to Dr Sigrid Schiel, Dr Michael Spindler and 3 unknown referees for helpful comments on the manuscript. This is AWI contribution Nr. 582.

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