

The life cycle strategy of the ice-associated copepod, *Paralabidocera antarctica* (Calanoida, Copepoda), at Syowa Station, Antarctica

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Abstract: The vertical distribution, abundance, population structure and life cycle of the ice-associated copepod, *Paralabidocera antarctica* was studied in the fast ice near Syowa Station (69°00'S, 39°35'E) in the eastern part of Lützow-Holm Bay in 1970, 1975 and 1982. The results indicated that *P. antarctica* inhabited the ice-seawater interface throughout the year with a one year life cycle and was actually present in the sea ice for most of the year except the summer. *P. antarctica* overwintered as naupliar stages (NIV-NV) with slow development in sea ice during winter. *P. antarctica* population then developed rapidly and attained adulthood in the water just beneath the sea ice during spring-summer. *P. antarctica* depended entirely on ice algae for food throughout its whole life-span, suggesting that the ice-seawater interface provides favourable food conditions for *P. antarctica*. The slow development in naupliar stages in sea ice and short copepodite life span in the water suggest that *P. antarctica* may adapt its growth strategy to suit the varying fast ice/water interface environment.

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Introduction

It is now generally recognized that sea ice provides one of the major habitats for microorganisms. Indeed, the ice-seawater interface (defined as the region including the bottom part of the ice and in the seawater immediately under the ice) seems to provide the special habitat supporting the richest microbial populations, such as bacteria, microalgae, heterotrophic protozoans and small metazoans (e.g. Horner *et al.* 1992). The ecological significance of these microorganisms at the ice-seawater interface has become clear in the light of the recent findings of the trophic associations between ice algae and metazoans as predators in both the Antarctic and Arctic (Richardson & Whitaker 1979, Conover *et al.* 1986, Hoshiai *et al.* 1987, Runge & Ingram 1988, 1991, Grainger & Hsiao 1990). However, as most of the studies have focused on the microalgae, the possible role of metazoans in this habitat is still poorly understood. In particular, little is known about their relationship with ice throughout their entire life-span. Possible ice-associated life cycles of metazoans have been proposed for *Paramoera walkeri* (Amphipoda) by Rakusa-Suszczewski (1972), *Drescheriella glacialis* (Copepoda) by Dahms *et al.* (1990) and *Stephos longipes* (Copepoda) by Kurbjewit *et al.* (1993) and Schnack-Schiel *et al.* (1995) from Antarctica. However, information on the winter behaviour is still insufficient.

Paralabidocera antarctica is a calanoid copepod, occurring in neritic regions along the Antarctic coast (Waghorn 1979). It is commonly found in the plankton from Antarctic coastal regions, e.g. Syowa (Tanimura *et al.* 1986), Molodezhnaya

(Zvereva 1975), Mawson (Bunt 1960), Davis (Tucker & Burton 1988) and McMurdo (Foster 1987). At Syowa Station, post naupliar stages of *P. antarctica* suddenly appear in September in the water column beneath the ice, disappearing completely in late January (Tanimura *et al.* 1986). Similar findings were also reported from Davis Station by Tucker & Burton (1988). *P. antarctica* adults are also often abundant just beneath the sea ice during the summer (Tanimura *et al.* 1984, Tucker & Burton 1988). Tucker & Burton (1988) suggested that *P. antarctica* is closely associated with sea ice and inhabits the ice-seawater interface, while Hoshiai & Tanimura (1986) demonstrated that *P. antarctica* nauplii occurred abundantly in the bottom of the sea ice during winter at Syowa Station. However, their study was limited to the population within the sea ice, and the population structure in the water was not examined in that study. Therefore the life cycle of this species is still not well known.

The aim of this study is to highlight the life cycle strategies of *P. antarctica* in relation to sea ice. We report on and compare the vertical distribution, abundance and population structure both in the water column and sea ice. The life cycle of *P. antarctica* is also compared with that of other ice-associated copepods living in the Antarctic.

Materials and methods

Sea-ice cores were collected from March to December 1970 and July to December 1975 at Stn. 1 and from September to

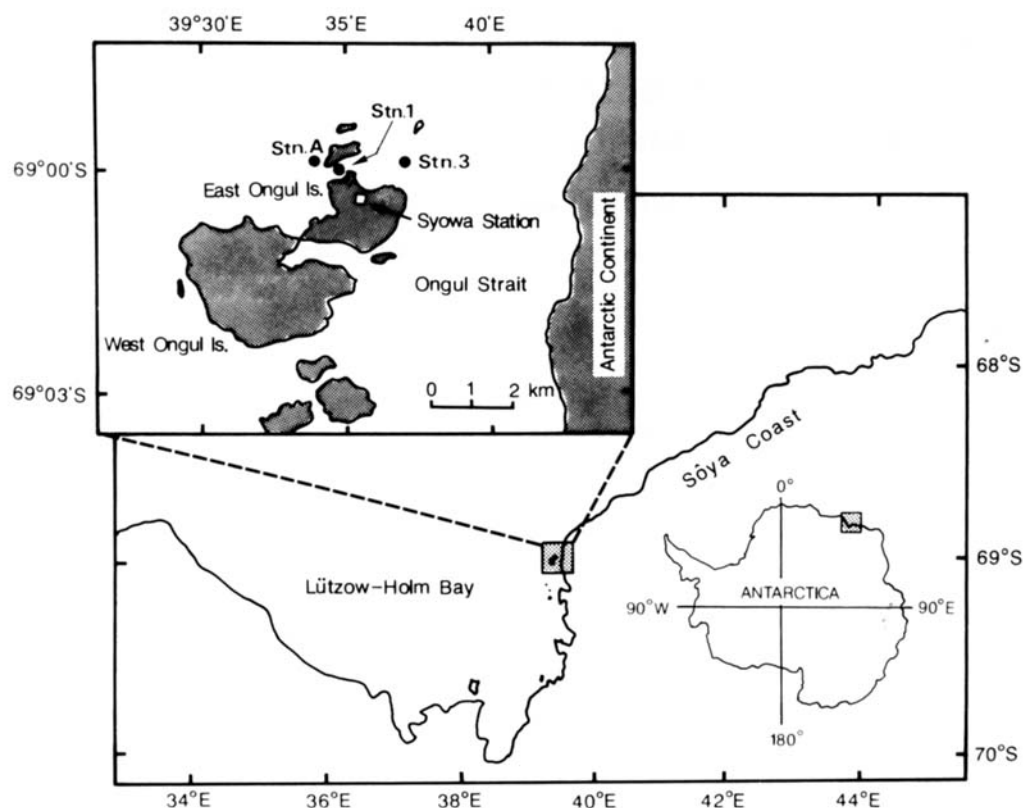


Fig. 1. Location of sampling sites.

December 1982 at Stn. A near Syowa Station (69°00'S, 39°35'E) (Fig. 1). Successive samples in each year were taken within a small area on the one-year ice. Sea ice cores were sampled with a SIPRE ice coring auger (8 cm in diameter). In 1970, each core was cut into a number of sections in the field to determine the vertical distribution of abundance and population structure of *P. antarctica*. The number of sections and length, varying between 3–15 cm, was dependent on the length of the core taken. Hence a long core had more sections cut, with several shorter sections from near the bottom of the core than from the middle and top parts of the core. In the 1975 and 1982, only the bottom 3 cm long section in each ice core was obtained and examined for population structure, because the distribution of animals was generally limited to a few centimeters at the bottom of the sea ice layer. Ice and snow depths were measured through the SIPRE core-hole on each sampling occasion. In 1970 and 1982, chlorophyll *a* concentration in the ice was fluorometrically determined (Hoshiai 1981a, 1985).

A series of plankton samples was collected every 2–3 weeks from January 1982–January 1983 at Stn. 1. Plankton samplings were carried out by vertical hauls of a Norpac net (45 cm mouth diameter, 180 cm long and 0.10 mm mesh aperture, see Motoda 1957) from near bottom of about 8 m depth to beneath the sea ice through a hole drilled into the sea ice. The net was towed at a speed of 0.5–1.0 m s⁻¹ during daytime between 08h00–11h00. The water volume passed through the net was estimated from a Rhigosha flow-meter

mounted in the mouth of each net. The abundance and the developmental stages of *P. antarctica* in the Norpac net samples were examined and compared with those in the sea ice. In addition, qualitative samples were collected every week during the reproductive season from December 1982–January 1983 at almost the same site as Stn. 1 to investigate the more exact period of *P. antarctica* reproduction. A conical plankton net (30 cm in mouth diameter, 0.10 mm mesh size) was hauled from near bottom to the surface. The vertical distribution of *P. antarctica* in the water column under the sea ice was studied by stratified sampling with a "NIPR-I" sampler modified from Fukuchi *et al.* (1979). A detailed description of the modified NIPR sampler is given by Fukuchi *et al.* (1985). It consists of a cylindrical part (mouth diameter, 20 cm; length, 80 cm) housing a propeller and an electric motor inside, and a conical plankton net (20 cm in mouth diameter, 0.10 mm mesh size). Samples were sucked into the sampler by a current caused by the rotating propeller and collected with the net attached to the posterior end of the sampler. Samples were taken from four or five selected depths from just under the sea ice to near the sea bottom during the same period as the Norpac net samplings, from January–December 1982 at Stn. 1. Three minute NIPR net sampling was performed at each layer and filtered water volume was calculated from the General Oceanics flow-meter mounted in the posterior-centre of the sampler. In addition to the NIPR samplings at Stn. 1, four series of samplings using a NIPR sampler were undertaken at Stn. 3

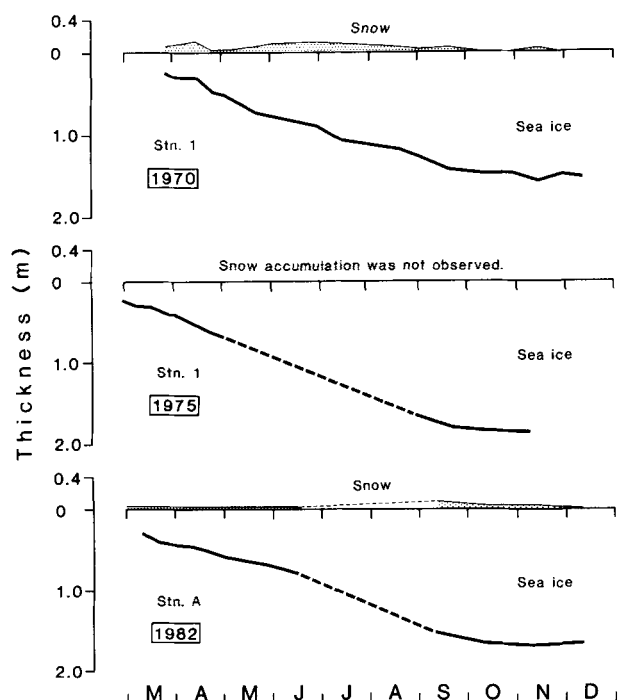


Fig. 2. Seasonal variations of sea ice thickness and snow depths at Stn. 1 in 1970 and 1975 and at Stn. A in 1982. Broken lines mean no observation.

(depth: 50 m) for determination of diel vertical migration of *P. antarctica* under the sea ice in four seasons. The sampling was made at almost 6 h intervals between 12h00 and 12h00 next day on 1–2 March (autumn), 16–17 September (spring) and 13–14 December (summer). However, the operations in winter were interrupted by bad weather, so that the samplings were carried out between 12:00 h on 10 June and 12:00 h 12 June. At each sampling site, water samples were collected for temperature, salinity and phytoplankton pigment analysis at depths from just beneath the sea ice to near bottom. Detailed data together with the methods for sampling and analysis have been published elsewhere (Fukuchi *et al.* 1985). Data on global solar radiation are cited from the results of routine meteorological observation by Japan Meteorological Agency (1984).

All ice-cores and plankton samples were brought back to the laboratory at Syowa Station and preserved in 5% buffered formalin-seawater solution for microscopic examination and enumeration in Japan. Depending on the abundance of organisms, the whole sample or an aliquot of 1/2 to 1/10 subsamples was examined. All developmental stages, excluding eggs, of *P. antarctica* were identified based on Tanimura's (1992) description and counted for each sample. The count of each developmental stage was converted to individual numbers per unit volume of water.

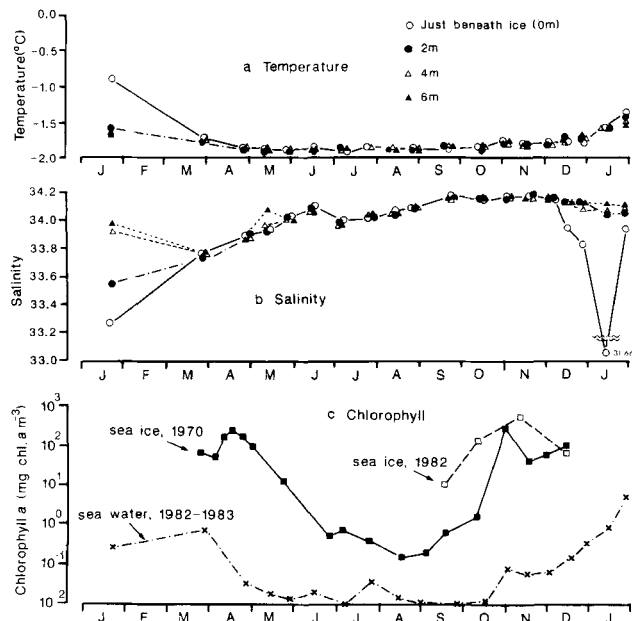


Fig. 3. Seasonal change in a. water temperature, b. salinity and c. chlorophyll *a* concentration at Syowa Station. Data on water temperature and salinity were obtained from the depth of just beneath sea ice (0 m), 2, 4 and 6 m at Stn. 1 in 1982–1983. Chlorophyll *a* concentration is expressed as an average value within bottom 10 cm of ice for sea ice (Stn. 1: 1970; Stn. A: 1982) and water column (0–8 m) for sea water (Stn. 1: 1982–1983). Data from Hoshiai (1981b) and Fukuchi *et al.* (1985).

Results

Seasonal environmental variables at Syowa Station

Figure 2 shows the seasonal changes of ice thickness at Syowa Station for three years. Sea ice generally persists through the year, although it breaks up locally in summer. In 1970 the sea ice thickness was 30 cm in late March and increased continuously to about 150 cm by early October. Thereafter it remained the same. In 1975 ice thickness was not recorded in July but reached 185 cm by September and in September to December in 1982 it was 161–169 cm in the ice core sampling periods.

Seasonal change in temperature and salinity beneath the sea ice at Stn 1 near Syowa Station are shown in Fig. 3a & b. The water temperature and salinity at each station ranged from -0.9°C to -1.87°C and from 31.66–34.18 p.s.u., respectively. They did not change much between April and November when sea ice developed and achieved the maximum thickness, while water temperature increased slightly and salinity decreased moderately just beneath the sea ice due to melting of sea ice in December and January. However, distinct thermocline and halocline were not observed throughout the year. The temperature and salinity changes

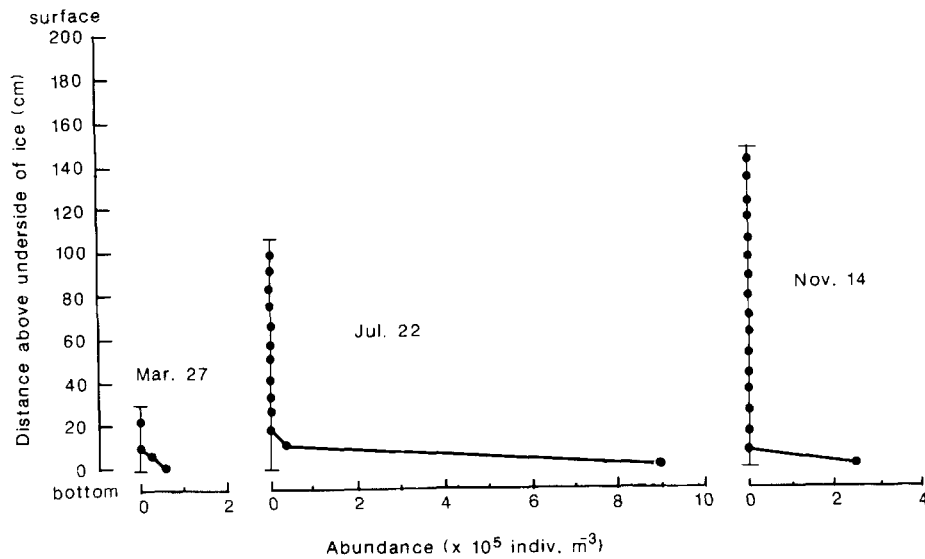


Fig. 4. Vertical distribution of *Paralabidocera antarctica* in sea ice at Stn. 1 in 1970. Distribution patterns are almost same during the period from March–November. Three typical depth profiles are selected for this period.

at Stn. 3 were similar to those at Stn. 1.

Seasonal changes of chlorophyll *a* concentrations in the water column and in the bottom 10 cm of ice are shown in Fig. 3c. Two distinctive peaks were observed in mid April (290.4 mg chl *a* m⁻³) and late October (343.3 mg chl *a* m⁻³) and the relatively high chlorophyll *a* concentrations (over 0.2 mg

chl *a* m⁻³) were maintained from May to September at the bottom part of the ice in 1970. The spring maximum value was recorded in the ice at Stn. A in early November in 1982 (844.4 mg chl *a* m⁻³). On the other hand, chlorophyll *a* concentrations in the water column at Stn. 1 in 1982 showed less than 0.1 mg m⁻³ during the period from April to November

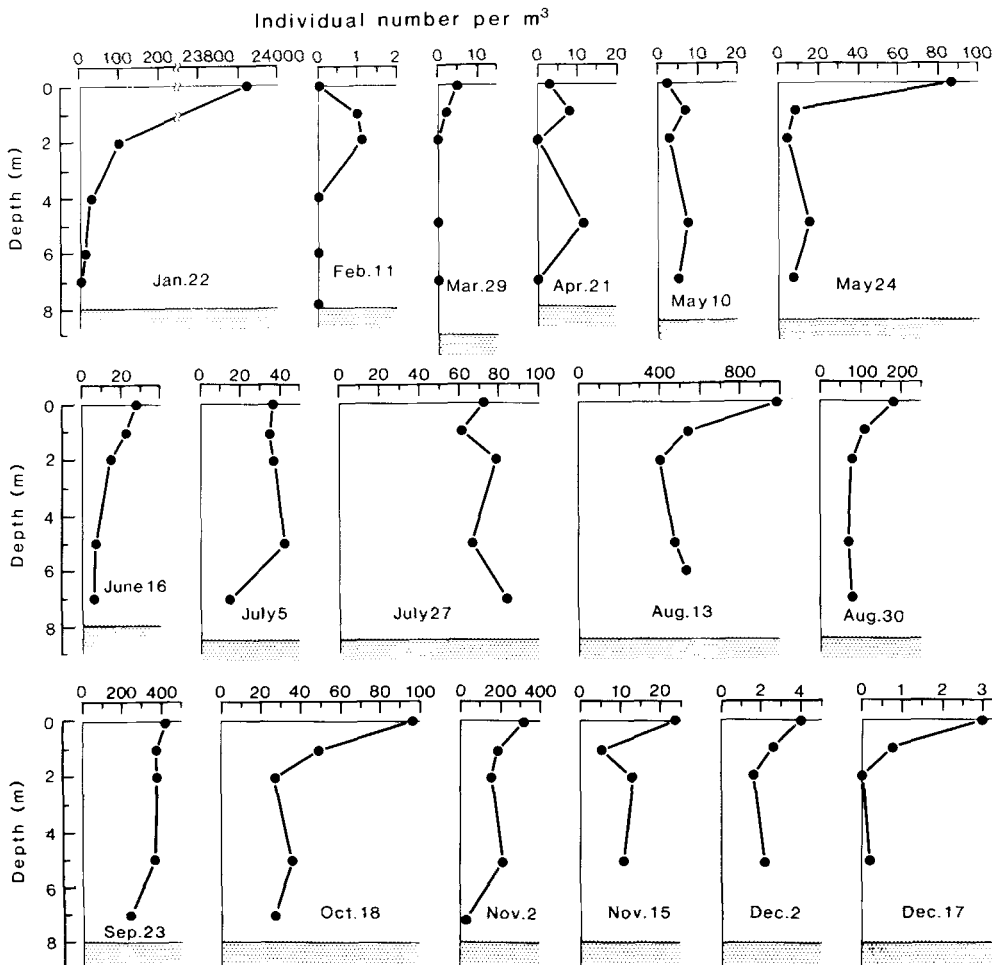


Fig. 5. Vertical distribution of *Paralabidocera antarctica* in the water column collected with NIPR sampler at Stn. 1 in 1982.

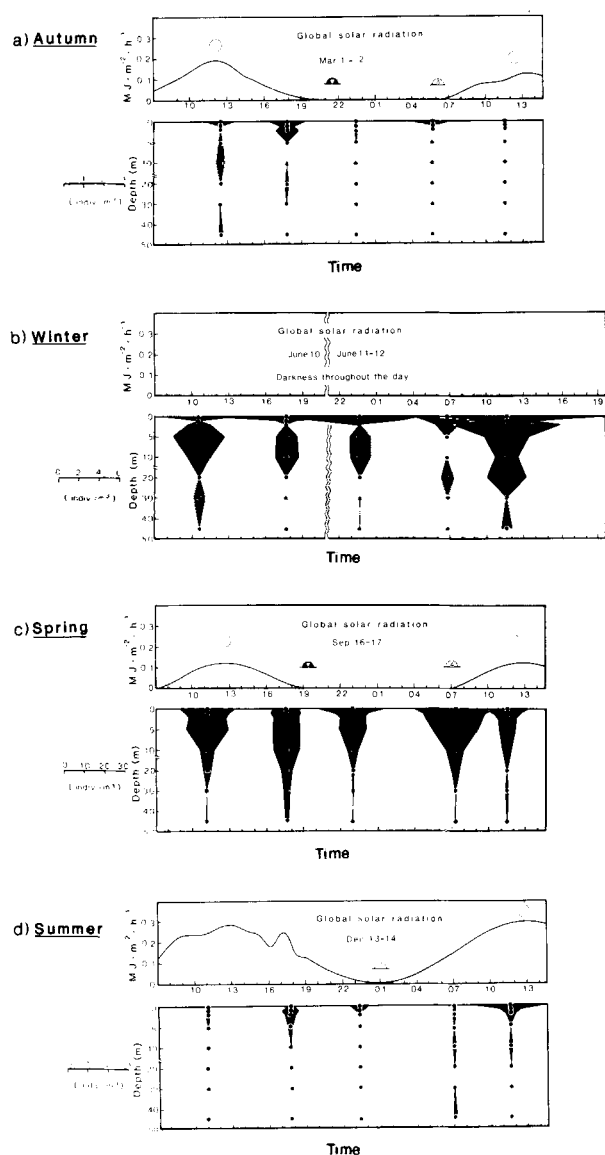


Fig. 6. Diel variation in vertical distribution of *Paralabidocera antarctica* in the water column collected with NIPR sampler in a. autumn, b. winter, c. spring and d. summer at Stn. 3 in 1982. Data on global solar radiation are cited from Japan Meteorological Agency (1984).

and the chlorophyll *a* concentration did not increase until early December. The maximum value occurred in late January ($6.2 \text{ mg chl } a \text{ m}^{-3}$).

Vertical distribution within sea ice and in the water column

Paralabidocera antarctica appeared in the sea ice in late March and disappeared by the end of November from the ice at Stn. 1 in 1970. The majority of the copepods were usually concentrated within the bottom few centimeters and were rarely distributed more than 10 cm above the bottom of the

sea ice during the period (Fig. 4). The abundance at the bottom layer ranged from 0.5×10^5 – 11×10^5 individuals m^{-3} .

P. antarctica also occupied the water column under the sea ice throughout the year. In most cases, the copepods were most abundant just beneath the sea ice and number decreased with depth (Fig. 5). However, their abundance was usually much less than that at the bottom layer of ice; fewer than 1000 individuals m^{-3} except in January.

The diurnal vertical distributions of *P. antarctica* under sea water at Stn. 3 (depth: 50 m) for four periods in 1982 are shown in Fig. 6. In early March, when the distinction between day and night was clearly distinguishable, there were few *P. antarctica*, and the bulk of the population tended to remain just beneath the sea ice during day and night. In mid-June when the sun did not rise above the horizon at all, the peak abundance of copepods was just beneath the ice throughout the diel cycle. In mid-September when there was again distinct day and night periods, the population was still concentrated beneath the ice and the distributional pattern did not vary throughout the diel cycle. Most of the *P. antarctica* population resided in the upper 5 m beneath the ice throughout the day even in mid-December when the sun did not set at all. Thus there was no apparent diel periodicity to the vertical distribution of *P. antarctica* population in the water column throughout year.

Population structure

As *P. antarctica* does not stray far from the interface between ice and sea water throughout the year, their stage composition in the water column was compared with our previous results in sea ice (Hoshiai *et al.* 1986). Figure 7b shows the results of the succession of developmental stages in the water column at Stn. 1 in 1982 which are based on vertical hauls with a Norpac net. The large population consisting of adult males and females which appeared in late January had virtually disappeared from the water column by February. The population consisting of early nauplius stages (NII and NIII) appeared in the water column in late March. However, the population in sea ice was composed entirely of nauplius stages I and II (NI and NII) in same period (Fig. 7a). The absence of NI and overall scarcity of the early naupliar stages in water column was presumably due to their passing through the 0.1 mm mesh net. This cohort was assumed to be the offspring of the previous generation.

The younger nauplius stages (NII and NIII) constituted a greater proportion of the total population in the water column during the period between May and July. In contrast, the populations in sea ice were dominated by older nauplius stages (NIV and NV) during this period (Fig. 7a). The difference in the population structure for sea water and ice during this period may be attributable to some of the practical problems of sampling this interface, such as material lost from the bottom of the ice core as it is being removed, and/or the difficulty in sampling "pelagic" copepods lurking in

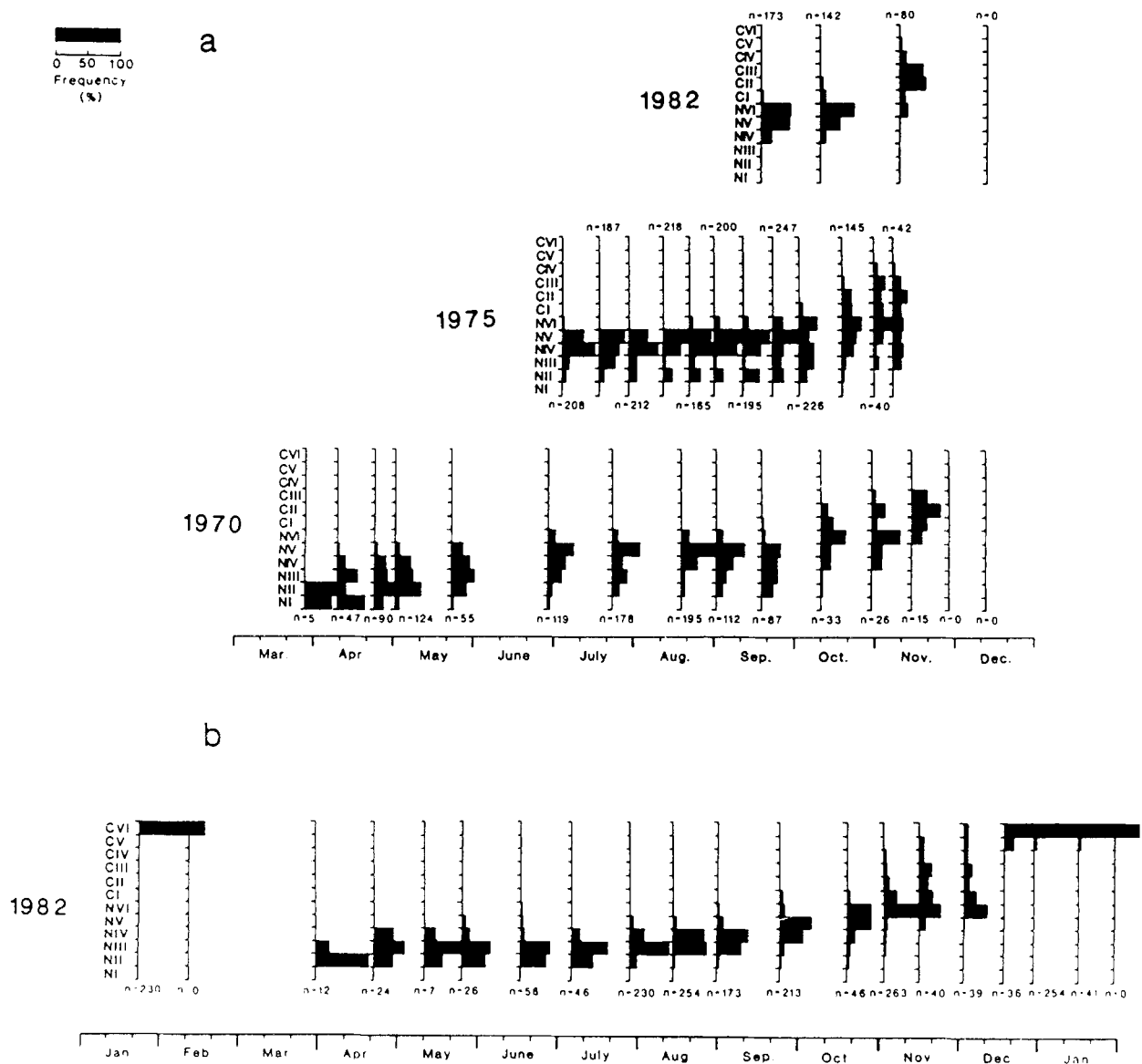


Fig. 7. Seasonal change in percentage composition of developmental stages of *Paralabidocera antarctica*. **a.** in sea ice in 1970, 1975 and 1982 (from Hoshiai *et al.* 1986) and **b.** in sea water in 1982-1983. The data for sea water are based on samples collected by Norpac net vertical hauls. *n* = numbers of individuals examined.

crevices on the underside of it.

During the period between September and November growth was more rapid and copepodite stages appeared in the sea water (Fig. 7b). At this time of year the population structure in the water column was very similar to that in the ice. There was probably an active interchange of the population between the ice and underlying water during this period. Subsequent to the disappearance of *P. antarctica* from the sea ice (Fig. 7b), most of the animals in the sea water had grown rapidly, and reached adulthood by mid-December (Fig. 7b). The adult population had disappeared again by end of January 1983.

Reproduction

Maturation of the males occurred in early December. At the beginning of the reproductive season in December males constituted about 60–100% of the adult population but this percentage showed a decreasing trend with time (Fig. 8). By contrast, maturation of the females began in late December, being nearly two weeks later than males, and the percentage of females increased in January (Fig. 8). At end of the reproductive period the male disappeared first, females being the only adults in late January.

The copulation period is indicated by the presence of males with released spermatophores and of females carrying spermatophores on their genital segments. Although all

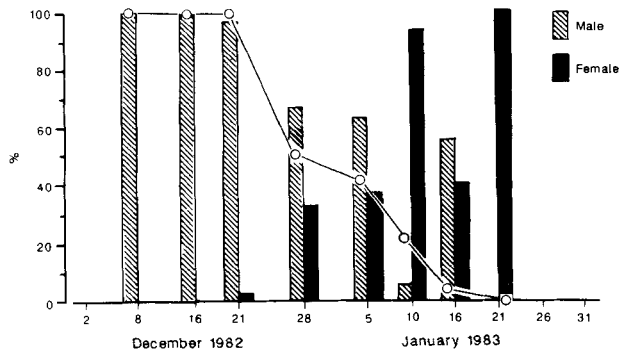


Fig. 8. Percentage of males and females to total adults numbers of *Paralabidocera antarctica*. Open circles (o) shows the percentage of males with spermatophores.

males had spermatophores in their body at the beginning of the reproductive season, the percentage of males with the spermatophores decreased with advance of the reproductive season (Fig. 8). Females with attached spermatophores were few during December, but almost all females were observed carrying spermatophores in January.

Discussion

Life cycle

Our results indicate that *Paralabidocera antarctica* has a one-year life cycle and inhabits the ice-seawater interface throughout its life span. The life cycle of *P. antarctica* is summarized in Fig. 9. Before the onset of ice growth in April the young nauplii, which are offspring of the previous generation, immediately enter the bottom part of the sea ice (possibly between growing ice crystals or brine channels). They develop to later naupliar stages of NIV and/or NV by end of May. From June through to September when the ice thickens, the population remain in the bottom part of the ice as naupliar stages. The population development recommences when ice growth stops in October. The rapid development from the later naupliar stages to early copepodites (CI to CIII) takes place in the bottom of the ice by mid-November. From November through to December the population gradually shift their habitat from the sea ice to the water immediately below the ice. Maturation and mating take place just beneath the ice as demonstrated by Tanimura *et al.* (1984) with the advance of melting of the undersurface of the ice in mid-summer. Eggs are possibly spawned at the ice-seawater interface during the late summer when the sea ice is thinnest, although spawning behaviour is not yet well known. The adults may die immediately after spawning.

Survival strategy

P. antarctica obviously overwinters as naupliar stages. It has been long believed that the nauplii of marine copepods do

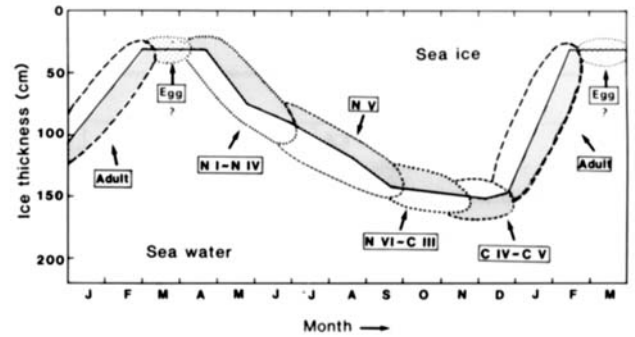


Fig. 9. Schematic diagram of *Paralabidocera antarctica* life cycle in the ice-covered area near Syowa Station. Hatched area indicates the main habitat of *P. antarctica*. Solid line denotes the seasonal change of ice thickness.

not normally overwinter because they have little resistance to food shortage and environmental extremes (Marshall & Orr 1955). Indeed, the overwintering as naupliar stages has not been reported in marine copepods so far. At Syowa Station the chlorophyll *a* concentration in the sea ice is at least one order magnitude higher than in the water column during winter especially in the bottom part of ice, where *P. antarctica* nauplii live, which provides highly concentrated chlorophyll *a* throughout the year. Winter food availability in the form of ice algae could secure the survival for *P. antarctica* naupliar population. In fact, Hoshiai *et al.* (1987) found that overwintering stages NIV, NV and NVI fed on abundant pennate diatoms, such as *Amphiprora*, *Gomphonema*, *Navicula*, *Nitzschia* and *Pleurosigma*, during winter months. These diatoms are also dominant ice algal groups in the bottom ice layer at Syowa Station (Watanabe *et al.* 1990).

Ikeda (1984) found that the first feeding stages of Antarctic krill, *Euphausia superba*, died within a few days under a starvation regime. He suggested that the survival of first feeding larvae is greatly influenced by the availability of adequate food. Similar results have also been reported for larvae of many fish species, after resorption of the yolk (Lasker *et al.* 1970, Ehrlich 1974, Houde & Schecter 1983). These results would suggest that first feeding larval stages are more susceptible to low food availability in contrast to other developmental stages. At Syowa Station proliferation of algae occurred twice in the bottom of ice, in autumn (April–June) and spring-summer (October–November) as shown in Fig. 3c is a common pattern (Hoshiai 1981b, 1985, Watanabe & Satoh 1987). *P. antarctica* start feeding at stage NIV (Hoshiai *et al.* 1987). NIV first appear in the ice in April and this coincides with the autumnal proliferation of ice algae (Fig. 7). Therefore the probable first feeding stage of *P. antarctica* takes advantage of the autumnal proliferation of ice algae for their survival. Thus, sufficient food in autumn may be an important factor enabling *P. antarctica* to overwinter.

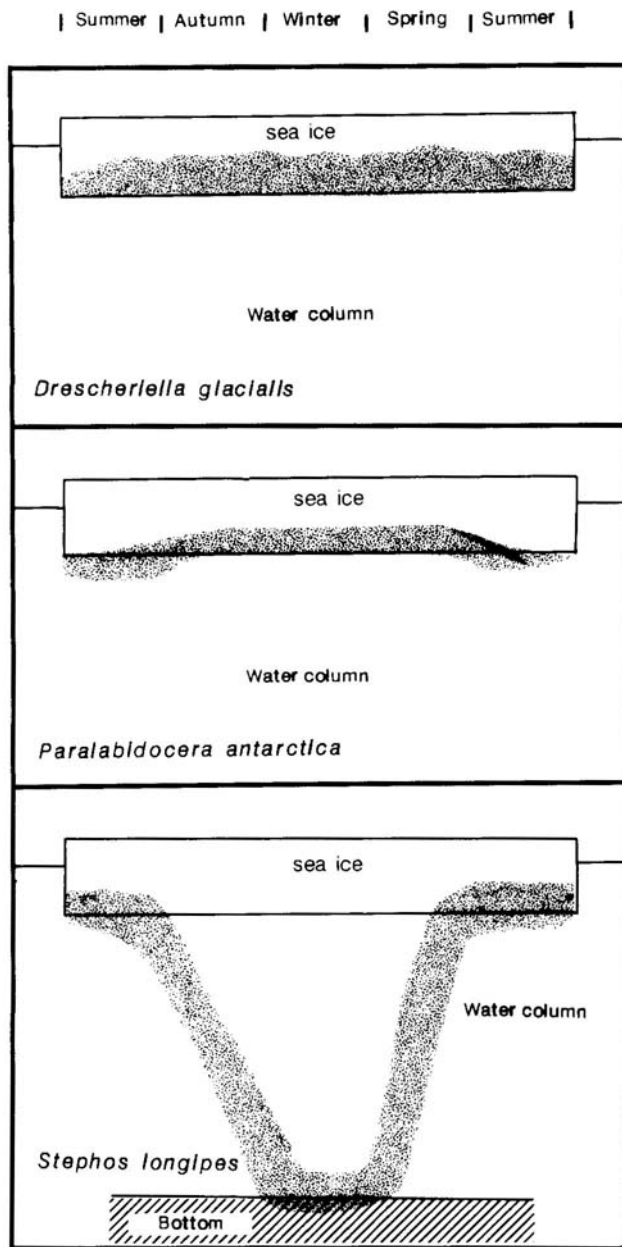


Fig. 10. Schematic comparison of the relations with sea ice among three Antarctic ice-associated copepods, *Drescheriella glacialis* (Dahms *et al.* 1989), *Paralabidocera antarctica* (present study) and *Stephos longipes* (Kurbjeweit *et al.* 1993). Stippled area indicates the main habitat throughout the life cycle in each copepod.

Winter feeding of naupliar overwintering stages suggests an active condition. Why then is the development of these overwintering stages still delayed when they are actively feeding during the winter? It is assumed that *P. antarctica* nauplii inhabit the interstitial water between ice crystals and/or in brine channels. This habitat would not only enclose niches which are often isolated from the underlying sea water (Weissenberger *et al.* 1992) but also would be highly

unstable and variable due to the various physical and chemical processes during the course of ice growth and development (Gow *et al.* 1982, Clarke & Ackley 1984, Lange *et al.* 1989). If the naupliar population developed rapidly and fed on the same resource at the same time in the sea ice, it could bring the population to a state of overcrowding and lead to deterioration of the environment by their excretions. In addition, the resource might soon become food limited under certain circumstances. It may also inevitably result in abandonment of the nursery habitat giving both adequate food and perfect protection from predation. We do not know whether the delay in the development of naupliar overwintering population is genetically or environmentally controlled in such an enclosed and unstable habitat during winter months. However, the prolongation of naupliar life allows animals to spend a great amount of time in this particular locale, extending its contact with the food resource, ensuring a more equitable population density (Coull & Dudley 1976) and minimizing predation (Smol & Heip 1974).

The *P. antarctica* naupliar population rapidly developed and attained adulthood during spring-summer months (Fig. 8). The commencement of their rapid development coincided with timing of spring ice algal bloom and change of habitat from the sea ice to the water immediately below the ice. According to Hoshiai *et al.* (1987), the food of the water dwelling copepodite stages (CIV to adult) was basically no different from that of the ice inhabitants. This indicates that *P. antarctica* may utilize the ice algae as food even during their water dwelling period. In particular, *P. antarctica* may feed on the suspended diatoms originating from ice algae, which are released from the bottom of sea ice to the underlying water by ice melting during summer. The population development and maturation were almost completed by mid-December when phytoplankton is still scarce under the ice. Therefore, it is likely that rapid development of *P. antarctica* during spring-summer is entirely dependent on ice algae.

The entire life cycle of *P. antarctica* is one year with prolonged naupliar life stages and shortened copepodite life stages. Assuming that egg laying occurs during the period between February and March, *P. antarctica* might require about 250–300 days for the development from egg to adult. The development time for copepodite stages from CI to adult is estimated as *c.* 80–90 days and takes only about 30% of total development time. Miller *et al.* (1977) have discussed an advantage of shortening the duration of copepodite life stages in unpredictable conditions. Shortening of copepodite stages would bring a shorter life cycle with the advantage of enabling rapid development during favourable conditions. Thus extreme short copepodite life stages could be a compensatory adaptation for *P. antarctica* to recover the delayed naupliar development in winter and complete the life cycle during the short summer period in Antarctica.

This study suggests that the ice algal bloom in autumn is indispensable for the survival of *P. antarctica* nauplii. The

type of autumnal ice algal bloom found at Syowa Station might also occur at other Antarctic coastal regions which have similar environmental conditions to those of Syowa (Hoshiai *et al.* 1996). If so, it is hypothesized that the distribution of *P. antarctica* is restricted to the coastal sea ice area where an autumnal ice algal bloom occurs.

Comparison with other copepods with ice-associated life cycles

In the Southern Ocean the copepods with ice-associated life cycles are *Drescheriella glacialis* (Harpacticoida, Tisbidae) (Dahms *et al.* 1990) and *Stephos longipes* (Calanoida, Stephidae) (Kurbjeweit *et al.* 1993) in addition to *P. antarctica*. Figure 10 represents schematically the habitat usage in the life cycles of *D. glacialis*, *P. antarctica* and *S. longipes*.

S. longipes and *D. glacialis* as well as *P. antarctica* depend entirely on the ice algae rather than phytoplankton in the water as food (Dahms *et al.* 1990, Kurbjeweit *et al.* 1993). However, there are differences in their relationship with sea ice through their life cycles. The relationship with sea ice is much weaker for *S. longipes* than for *P. antarctica* and *D. glacialis*. *D. glacialis* lives in the sea ice throughout its entire life cycle. The main reproductive season is winter, but reproduction goes on year-round without resting stages at least where sea ice persists (Dahms *et al.* 1990). According to Kurbjeweit *et al.* (1993), *S. longipes* is associated with sea ice only during short summer period in naupliar stages and spends the greater part of its life span in the water column away from the sea ice. They postulated that *S. longipes* spends winter as resting stages of CIV and CV on the bottom sediments. The life cycle pattern of the species described by them seems more comparable with those of the interzonal copepods as represented by *Calanoides acutus* and *Rhincalanus gigas*, although these copepods do not enter the sea ice at the surface during summer (Voronina 1972, 1978, Marin 1988, Atkinson 1991). Recently, however, Schnack-Schiel *et al.* (1995) suggested that *S. longipes* has two alternative strategies for overwintering: nauplii overwinter in sea ice and ice/water interface, while CIV remain in deep water layers or near bottom. Ice structural conditions significantly influence the biological communities in the ice as Clarke & Ackley (1984) suggest. The survival strategies of these ice-associated copepods also depend on ice formation processes and the ice structure as a consequence. Therefore, some adjustment to their sea ice phase may be necessary to ensure survival.

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