

**Seasonal and diel
changes in the vertical
distribution in relation
to the age structure of
Microcalanus pygmaeus
Sars and *Ctenocalanus*
citer Bowman & Heron,
(Pseudocalanidae,
Copepoda) from Croker
Passage (Antarctic
Peninsula)**

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Abstract

The development of two representatives of Pseudocalanidae and the nature of their population distribution in the water column were investigated on the basis of plankton samples collected over three seasons in night-day series in Croker Passage. The investigations showed that the two species begin reproducing in different seasons. Regardless of season, the growth of *M. pygmaeus* is more advanced than that of *C. citer*. Both species are characterised by a separation of their populations in the water column. The youngest copepodite stages (I–III) inhabit the upper portion of the water in which the given species occurs, while the oldest specimens, especially males, inhabit the deepest waters. Additionally, the first growth phases (CI–CIII) show a tendency to concentrate closer to the surface at night.

1. Introduction

Investigations of zooplankton in the coastal waters of Antarctica most often focus on its main components, *i.e.* krill and Copepoda. Large

Calanoida, such as *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas*, *Metridia gerlachei* and *Euphausia superba*, whose biology and ecology has been described in the greatest detail, are predominant in the area.

In the pelagic part of this area *Calanoida* and *Cyclopoida* also occur on a vast scale; however, they are much smaller in size than the species mentioned above. The *Calanoida* are representatives of the Pseudocalanidae family, widespread in the world's seas and oceans. In Antarctica this family is represented by a few species, of which *Microcalanus pygmaeus* Sars, 1900 and *Ctenocalanus citer* Bowman and Heron, 1971 are most abundant in the neritic zone (Bradford 1971, Kaczmaruk 1983, Żmijewska 1983, 1988, 1992, Hopkins 1985, Frasz 1988, Hosie & Stolp 1989, Boysen-Ennen *et al.* 1991, Menshenina & Rakusa-Suszczewski 1992, Kurbjewit 1993, Chojnacki & Węgleńska 1984, Żmijewska *et al.* in press).

Pelagic fauna research most often focuses on abundance, environmental preferences or the biomass contribution, while population issues concerning these tiny copepods are rarely addressed. The body of knowledge regarding the significance of the asynchronous reproduction processes of the dominant species of *Calanidae* in the polar environment is relatively large (Voronina 1972a,b, Voronina *et al.* 1978, Frasz 1988, Marin 1988a,b, Atkinson 1991, Conover & Huntley 1991, Żmijewska 1993). Seasonal, diel and ontogenetic migrations in the polar regions are some of the functional mechanisms which the basic components of the zooplankton are subject to, *i.e.* *Copepoda*, *Chaetognatha*, *Euphausiacea* or *Ostracoda* (Mackintosh 1937, Foxtom 1956, Marr 1962, David 1965, Vinogradov 1970, Voronina 1970, 1972a,b, Iwasa 1982, Everson 1983, Everson & Murphy 1987, Atkinson *et al.* 1992, Żmijewska & Yen 1993, Godlewska 1995, Bielecka 1996, Błachowiak-Samołyk 1996, Żmijewska *et al.* 1997). With species that occur on a mass scale, it is interesting from the point of view of the functional mechanisms of organisms in the polar regions to investigate interspecific relationships and the relevance and significance of interrelationships within the population.

The dynamics of the time-space variability of *M. pygmaeus* and *C. citer* in Croker Passage have already been described by Żmijewska *et al.* (in press). The authors confirmed a significant seasonality in the degree of concentration and the character of inhabitation in the water column. The aim of this paper is to investigate population development over time and the population distribution in the water column in relation to season and the time of day or night.

2. Materials and methods

Three seasons were spent doing fieldwork in the Antarctic Peninsula region. In December 1985, April 1988 and June 1989 zooplankton samples were collected aboard the r/v 'Polar Duke' in Croker Passage at latitude $64^{\circ}50'S$ and longitude $61^{\circ}50'W$. A single-level, opening-closing net consisting of two nets with either $500\ \mu\text{m}$ and 150 or $200\ \mu\text{m}$ sized mesh, attached side by side and with $0.5\ \text{m}^2$ square mouth openings, was used to collect zooplankton in oblique hauls. The closed net was lowered to $1000\ \text{m}$, opened and gently retrieved at a rate of $10\ \text{m}\ \text{min}^{-1}$ at a ship's speed of 1–2 knots. At $600\ \text{m}$, the net was closed and brought to the surface at $20\ \text{m}\ \text{min}^{-1}$. The collecting time from the 600 – $1000\ \text{m}$ depth with the open net was 40 to 50 minutes followed by an additional 30 minutes for net retrieval. Go-flow flow-meters were positioned in the mouths of both nets.

Two replicate day and night vertical series of samples were taken at the following discrete depth intervals: 0 – 50 , 50 – 100 , 100 – 200 , 200 – 400 , 400 – 600 , 600 – 1000 or 1200 metres. More than two days and nights were needed to obtain a complete series during the short days of winter or the short nights of summer. The replicated vertically stratified series were taken 3 times, in summer (mid-December), in late summer-autumn (mid-April), and in winter (early June). The samples were preserved immediately in sodium borate buffered formaldehyde.

In the laboratory the population structure (as percentages) was calculated as the abundance from all depth intervals of two replicate day/night series. All copepodite stages and the sex ratio of the two Pseudocalanidae species were determined.

3. Environment

Croker Passage is situated between Gerlache and Bransfield Straits, adjacent to the Antarctic Peninsula (Fig. 1). Samples were taken in the area located between $63^{\circ}52'$ – $64^{\circ}50'S$ and $63^{\circ}30'$ – $61^{\circ}50'W$, over one of the large central depressions in the passage, which is also the deepest place on the west side of the Antarctic Peninsula. The comparatively shallow depths around Croker Passage offer access to mesopelagic water from the open Southern Ocean. Croker Passage is bounded by Hoseason, Liege and Brabant Islands to the west and by Christianid and Two Hummock Islands to the east. This geographical location of Croker Passage thus makes it a very quiet area, where investigations can be carried out at practically any time. As in the southern part of Bransfield Strait, the water masses of Croker Passage are varied: the warmer waters of rather lower salinity originate

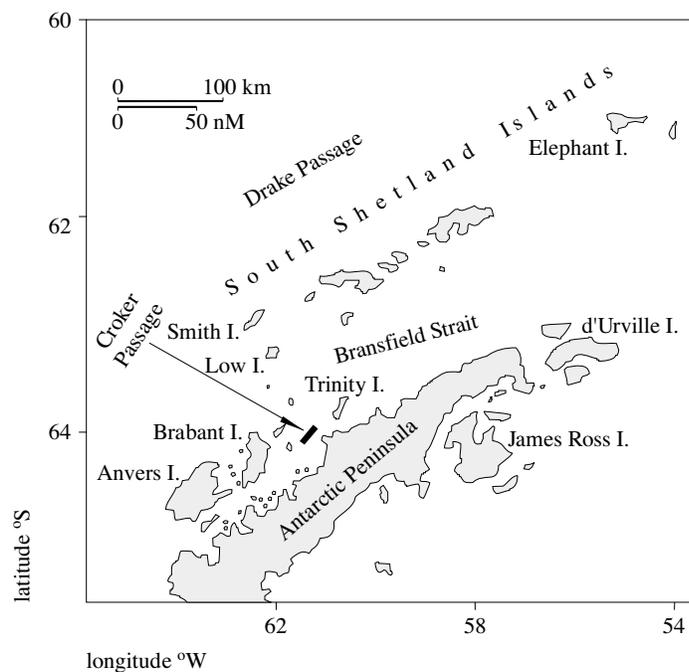


Fig. 1. Area of sampling stations in Croker Passage, Antarctic Peninsula, during three austral seasons (1985–89)

from the Bellingshausen Sea and the colder, more saline waters are similar to those of the Weddell Sea (Gordon & Nowalin 1978). The latter flow in from the Weddell Sea along the Antarctic Peninsula as far as Trinity Island, where they probably mix with waters flowing through Gerlache Strait to Bransfield Strait (Clowes 1934). In summer a narrow current flows from the Bellingshausen Sea into the western part of Bransfield Strait, but in the vicinity of the northern shores of the Antarctic Peninsula an opposite, south-western current carries Weddell Sea waters (Grelowski & Tokarczyk 1985). In winter, the influence of Weddell Sea water can be less significant than it is in summer (Eicken & Lange 1989).

4. Light cycle and temperature regime

Light-cycle and temperature profiles were measured during the three years of sampling. Changes in light intensity were recorded on a Campbell scientific data logger with a Licor quantum sensor on deck. Light intensity was determined as the percentage of the midday intensity. Temperature profiles were taken by shooting XBTs to 800 m or, by CTD profiles during winter cruises.

During the December sampling period, the period of darkness occurred between 00:00 and 03:00 local time, *i.e.* lasted for 3 hours. The surface temperature was 2°C and the temperature at 800 m was 0.2°C.

During the mid-April period, darkness was between 17:30 and 07:00 local time and lasted for 13.5 hours. The surface temperature was -0.4°C and temperature at 800 m was -1°C.

During the late-June sampling time, the night was 19 hours long, from 15:00 to 10:00 local time. The surface temperature was -1.3°C and the temperature at 800 m was -1°C.

In general, throughout the investigation period, Croker Passage was isothermal, there being little difference between the temperature near the surface and that at the bottom.

5. Results

Population structure and vertical occurrence

The analysis of the age structure of the two representatives of Pseudocalanidae revealed diversity with respect to both the time and depth preferences of the individual components.

Microcalanus pygmaeus

In the summer of December 1985, *M. pygmaeus* formed large concentrations in the upper mesopelagic layer (200–400 m), but was practically absent from surface waters (0–100 m) (Żmijewska *et al.* in press). Over 80% of the specimens were older copepodite (CIV–CV) and adult forms. Adult specimens constituted almost 50% of the population, and females 98% of these. The age structure remained unchanged with increasing depth, except in the surface layer, where a more significant presence of CI, CII and CIII copepodites (22%) was recorded, the oldest of them being dominant (Fig. 2).

In April 1988, at the end of the Antarctic summer, significant progress in the development of *M. pygmaeus* was observed. CIV–CV copepodites now made up over 50% of the population; CV was twice as abundant as CIV. At the same time, the significance of adult forms decreased. However, males occurred more often than they had in summer, and their proportion increased with depth. Females were dominant in the surface layer (100–200 m). The percentage of the youngest copepodites was much greater than in summer (Fig. 2).

In winter at the end of June 1989 significant changes in the age structure of *M. pygmaeus* occurred along with a drastic decrease in abundance. The oldest members of the population, *i.e.* adult forms (57%) with the predominance of females and CV copepods in the last stage of development

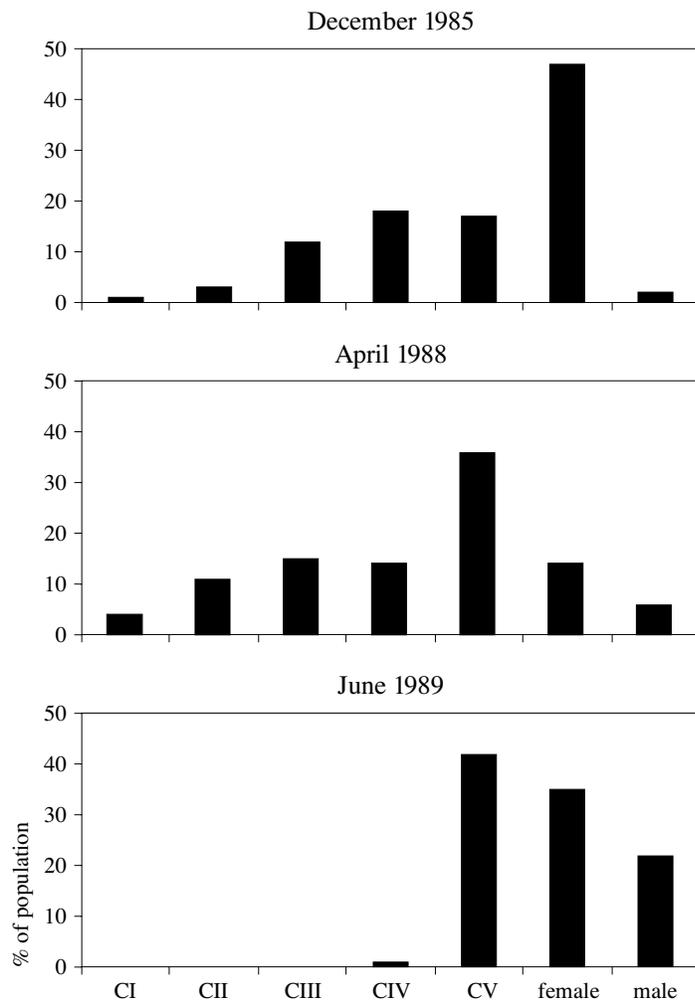


Fig. 2. Age structure of *Microcalanus pygmaeus* in Croker Passage (0–1200 m), (%)

(42%), remained in Croker Passage. The percentage of the youngest copepodites CIV was negligible (1%) (Fig. 2). Males continued to prefer deep waters: in the upper mesopelagic layer these made up 15% of the population, whereas in the deepest layer they accounted for almost 30%.

Population structure of *Ctenocalanus citer*

In summer this species was represented by the old generation. In the layer of its greatest concentration (0–400 m), 84% of the population were females, the remainder consisting of males and copepodites in stage V of development (Fig. 3).

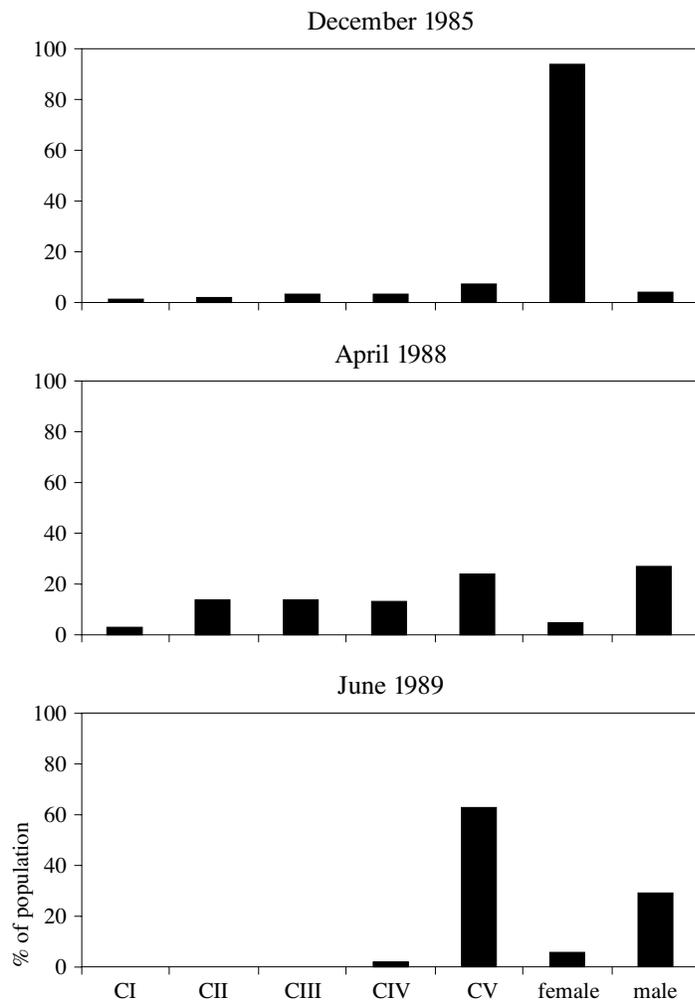


Fig. 3. Age structure of *Ctenocalanus citer* in Croker Passage (0–1200 m), (%)

At the end of the Antarctic summer, a new generation occurred in the population; however, the contribution of adult forms, mainly males, was significant. The age structure varied with depth: the youngest copepods (CI–CIII) comprised 55% of the population in the epipelagic layer, but barely 8% in the 200–400 m layer.

In winter as in summer, the population was dominated by its oldest components; however, unlike in summer, they were not females but CV copepodites, whose proportion in the population was twice as large as that of the adult forms. It is also worth noting that males outnumbered females several times (Fig. 3).

Diurnal and nocturnal migrations

The research material from all the stations was collected twice in day and night series. This allowed for the observation of the behaviour of both species throughout a 24-hour period.

In summer and in winter, by both day and night, the distribution of the *M. pygmaeus* population in the water column was quite stable. Only at the end of the Antarctic summer were significant differences in the vertical distribution of particular components of the population observed. At night, the youngest copepodite forms – CI and CII (11–19%) – inhabited the upper parts of the water column (100–200 m); their proportion in the deepest layer (1000–1200 m) was only 4%. While males concentrated in the deepest layers, females tended to congregate in the upper layers of the water column (100–200 m). Migrations occurred within the *M. pygmaeus* population during daylight. CI–CII copepodites were concentrated in the deepest layers: 23% in the 400–600 m layer, 27% in the 1000–1200 m layer; only 1% of the youngest copepods remained in the surface layer. Copepodites in older growth stages were scattered throughout the water column. With regard to the adult population, despite a high degree of segregation of the sexes, *i.e.* females usually inhabiting the upper region of the area of occurrence and males preferring the lower region, significant changes were not observed over a 24-hour period (Fig. 4).

The diel migrations of *C. citer* were of a similar character. At the end of the Antarctic summer its population, especially that of the youngest specimens, became more active. At night, 55% of CI–CIII specimens occurred in the 100–200 m layer, while only 8% were found in the next layer (200–400 m). Some specimens migrated to deeper waters during the day (Fig. 5). Like *M. pygmaeus*, *C. citer* was recorded only rarely in the surface layer (0–100 m) (Żmijewska *et al.* in press).

6. Discussion

Analysis of the age structure of two representatives of Pseudocalanidae, *M. pygmaeus* and *C. citer*, in Croker Passage revealed the individual nature of their life cycles. It must be emphasised that the material was collected in three seasons, but in different years. This may have caused certain distortions of the population picture resulting from the changes that occur in Antarctica over a period of many years. Nevertheless, the data of both the present authors and of other researchers indicate that the developmental characteristics of the two species of Pseudocalanidae described in this work are correct.

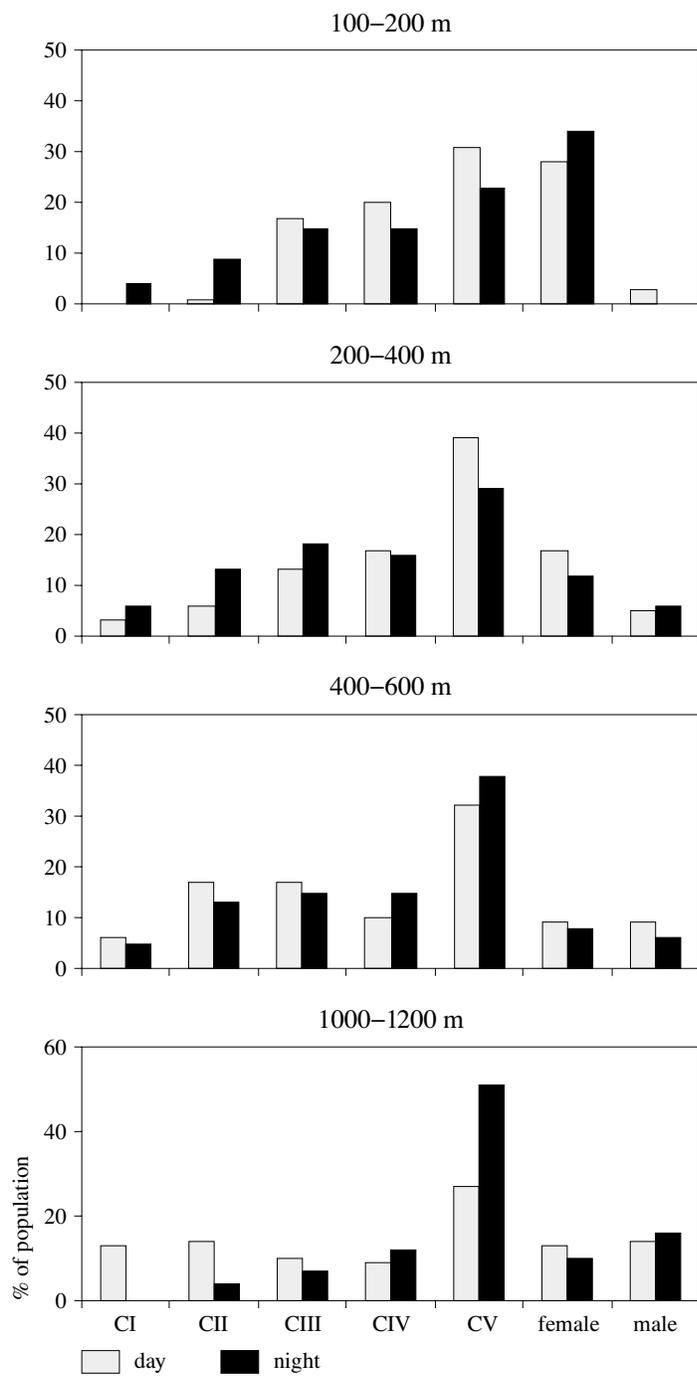


Fig. 4. Age structure of *Microcalanus pygmaeus* in the water column in Croker Passage in April 1988, (%)

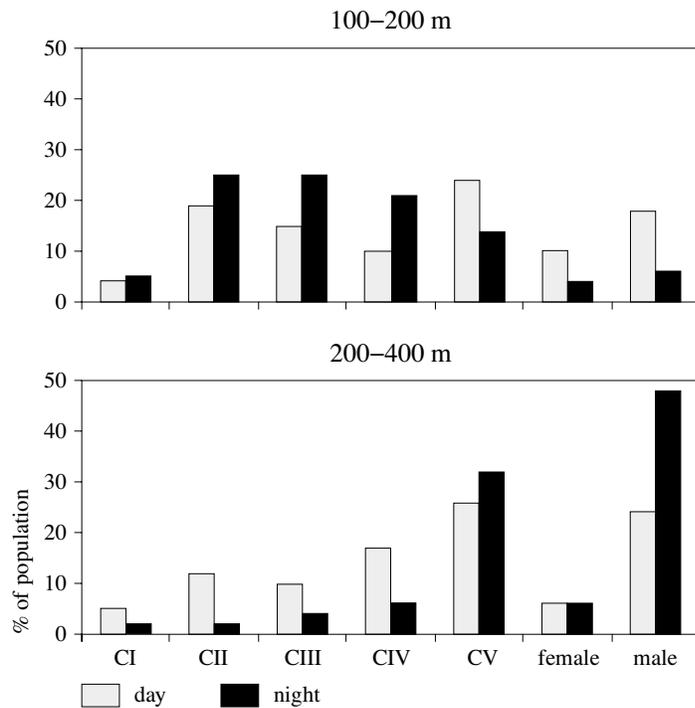


Fig. 5. Age structure of *Ctenocalanus citer* in the water column in Croker Passage in April 1988, (%)

The presence in December of the youngest *M. pygmaeus* copepods and almost exclusively adult specimens of *C. citer* indicates that the former species begins reproduction much earlier than the latter does. This seems to be justifiable since *M. pygmaeus*, owing to its variable diet, does not need to overlap the phytoplankton bloom peak (Voronina & Sukhanova 1976, Schnack 1985, Kurbjewit 1993, Żmijewska *et al.* in press). However, *C. citer* depends on phytoplankton, and in summer its population is composed largely of females of reproductive age (80%), whose fecundity depends on the phytoplankton abundance. The youngest copepods of this species, constituting one-third of the population, were observed in late summer. At this time the *M. pygmaeus* population was reaching the final stage of its development, and by the beginning of winter, half of its population had achieved reproductive maturity. Simultaneously, the *C. citer* population was dominated by copepods in the last phase of development, *i.e.* CV (62%) and adult specimens constituted slightly over 30%.

While investigating the zooplankton of the Weddell Sea, Kurbjewit (1993) also analysed the age structure of *M. pygmaeus*, but he did not mention *C. citer*. He confirmed the significant contribution of *M. pygmaeus*

specimens in the earliest stages of growth in summer and the domination of older copepodites at the end of March. However, he was not sure if this species was characterised by an annual or biannual developmental cycle (Kurbjeweit 1993).

The present data, especially those describing the degree of development of *M. pygmaeus* in winter, suggest that this species does complete its life cycle in one year.

The asynchronous reproduction and development of related phytophages is biologically very significant since it limits competition for food within the same trophic group. Population investigations of 'large' *Calanoida* occurring in vast numbers in Croker Passage showed that *C. acutus* is the first to start reproducing. It is followed by *C. propinquus* and then by *R. gigas*, the least advanced species (Żmijewska 1993, Żmijewska *et al.* 1997). Asynchronous development is also characteristic of other *Copepoda*. For example, among the *Cyclopoida*, the genus *Oncaea* develops more quickly than do animals of the genus *Oithona* (Bielecka 1996).

It is also interesting to note that in summer the adult segment of the *C. citer* population is represented almost exclusively by females, while males dominate at the end of summer and the beginning of winter. *M. pygmaeus* males also occur in the same season; however, their contribution does not exceed one-third of the adult population. It seems that the process of sex determination in this species does not occur concurrently. Males appear earlier, but they also die earlier; hence, they are non-existent in summer. However, this is not a unique phenomenon: among the *Cyclopoida* species *Oithona frigida*, males are exceedingly rare (Bielecka 1996). On the other hand, in *C. acutus*, males appear immediately prior to fertilising the females, after which they starve to death, as their mouth parts are not formed (Vervoort 1965, Bradford 1988, Żmijewska 1993).

Diel migration, one of the factors allowing organisms to adapt to polar conditions, is a phenomenon described over sixty years ago by Hardy & Gunther (1935) and Mackintosh (1937). Investigations have indicated that some species migrate to the surface at night (Andrews 1966, Atkinson & Peck 1988, Hopkins & Torres 1988, Atkinson *et al.* 1992). However, studies of zooplankton in Admiralty Bay (King George Island) by Chojnacki and Węgleńska (1984) revealed the tendency of plankton to concentrate closer to the surface during the day.

As migrators, phytophagous copepods are less active than omnivores (Żmijewska 1993). Neither of the species described here is characterised by significant changes in position in the water column over a 24-hour period. At the end of the Antarctic summer only the youngest *M. pygmaeus* and *C. citer* copepods display greater activity over a twenty-four hour period by

migrating to the surface at night. Their diet is probably plant-based. Similar day-night migrations in Croker Passage and in other areas of Antarctica have been described for *Metridia gerlachei* and *Euchaeta antarctica* (Rudyakov & Voronina 1974, Ward & Wood 1988, Żmijewska 1993, Żmijewska & Yen 1993), and also *Oithona similis* (Bielecka 1996).

The species *M. pygmaeus* and *C. citer* rely on the same adaptation mechanisms as those evolved by the 'large' *Calanoida*, which occur in vast numbers. That this is the case is demonstrated by the data obtained from a study of the time-space distributions of these two species (Żmijewska *et al.* in press) and their population distributions described in this paper.

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