

Seasonal and diel  
changes in the  
abundance and vertical  
distribution of the  
Antarctic copepod  
species *Calanoides*  
*acutus*, *Calanus*  
*propinquus*, *Rhincalanus*  
*gigas*, *Metridia gerlachei*  
and *Euchaeta antarctica*  
(Calanoida) in Croker  
Passage (Antarctic  
Peninsula)

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Antarctica  
Calanidae  
Seasonal abundance  
Diel and ontogenetic  
migration

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### Abstract

Seasonal and diel changes in the abundance and vertical distribution of 5 species of Antarctic copepods – *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas*, *Euchaeta antarctica* and *Metridia gerlachei* – have been reconstructed from analyses of sets of vertically-stratified zooplankton samples (500  $\mu\text{m}$  and 200  $\mu\text{m}$ -mesh adjacent nets) taken by day and night during 3 austral seasons (summer 1985–1986, autumn 1988 and winter 1989) from the 1200 m – deep Croker Passage, off the Antarctic Peninsula. In the laboratory, copepod counts were done of a known fraction of the total sample (1/2–1/8) from a 500  $\mu\text{m}$ -mesh net, using a Motoda box splitter (Motoda, 1959). During all investigation seasons in Croker Passage the

most abundant species is *M. gerlachei*. Seasonal ontogenetic migrations are performed by *C. acutus*, *C. propinquus* and *R. gigas*. In summer, in a 1000 m water column herbivorous species live above the *M. gerlachei* population, but in winter – below it. Both *M. gerlachei* and *E. antarctica* perform diel migrations, clearly marked in the former species, less so in the latter. *M. gerlachei* inhabits the middle part of the water column during the day, but rises nearer the surface at night. *E. antarctica* inhabits the deepest layer; at night adults, mainly females, ascend towards the surface.

## 1. Introduction

Seasonal phenomena in the pelagic waters of Polar regions are highly dynamic. Very rapid phytoplankton growth takes place only during the relatively short summer. The available data on the nutrient salts in Antarctic waters clearly show these to be in excess of phytoplankton requirements (El-Sayed, 1987). Holm-Hansen and Huntley (1984) suggested that the nutrient levels should be able to support a high phytoplankton biomass. According to Hempel (1970), Antarctic waters are four times as productive as other seas and oceans, but according to El-Sayed (1987), the rates of production in an open-ocean system are typical of oligotrophic regions and those of inshore waters are characteristic of upwelling systems. The presence of an abundant cryofauna provides sufficient food resources during the winter (Daly and Macaulay, 1988; Marshall, 1988; Schalk, 1990; Siegel *et al.*, 1990).

The Copepoda play a vital role in the Antarctic plankton (Hopkins, 1971, 1985a,b; Hempel, 1985), and make up over 70% of the biomass (Voronina, 1977). Many workers, however, are of the opinion that the *Euphausiacea* fill this leading role, comprising as they do 50% of the zooplankton biomass (Gulland, 1970; Hempel, 1970; Knox, 1970). Antarctic Copepoda are highly endemic and have a circumpolar distribution (Baker, 1954; Foxton, 1956; Vervoort, 1965).

Copepods such as *Calanoides acutus*, *Calanus propinquus* or *Rhincalanus gigas* occur in vast numbers in Antarctica and are interzonal forms, inhabiting the phytoplankton – rich surface waters in summer, and the hydrochemically stable deep waters in winter (Mackintosh, 1937; Vinogradov, 1970; Hopkins, 1971; Voronina, 1972a,b; Voronina *et al.*, 1978). Ontogenetic migrations are typical of other zooplankton species, too *e.g.* *Eukrohnia hamata*, *Sagitta gazellae* (David, 1965), *Euphausia superba* (Iwasa, 1982) or *Salpa thompsoni* (Foxton, 1966). The variation in temperature of the Southern Ocean with depth is relatively small, so it would seem unlikely that organisms can gain the energetic benefit of resting at depth which McLaren (1974) proposed as a driving force for the evolution of vertical migration. It goes without saying that the best known of the dominant plankton species of

Antarctic regions are, besides *Euphausia superba*, herbivorous copepods like *Calanoides acutus*, *Calanus propinquus*, *Calanus simillimus* or *Rhincalanus gigas*.

Investigations have been carried out in different regions of Antarctica and at various times, mainly in the summer, with the use of a wide variety of sampling equipment (Ottestad, 1932; Ommanney, 1936; Andrews, 1966; Voronina, 1972a,b, 1977; Jażdżewski *et al.*, 1982; Chojnacki and Węgleńska, 1984; Żmijewska, 1983, 1985; Atkinson, 1989a,b). Since all these studies were carried on mainly in the top 100 m or 200 m layer of water, the species inhabiting deeper waters, *e.g.* *Metridia gerlachei* or *Euchaeta antarctica*, were ignored, even though they make up a sizeable proportion of the plankton biomass (Witek *et al.*, 1985; Hopkins, 1985b).

In the last ten years interest has increasingly focused on the Antarctic high latitudes around the Antarctic Peninsula (Hopkins, 1985b; Żmijewska, 1985; Huntley and Escritor, 1991), and in particular the Weddell Sea (Kaczmaruk, 1983; Hopkins, 1985b; Boysen-Ennen and Piatkowski, 1988; Frasz, 1988; Hopkins and Torres, 1988; Siegel and Piatkowski, 1990; Schnack-Schiel *et al.*, 1991). In this region seasonality is especially striking in many aspects of the biology of marine organisms. Only a few studies in Antarctica have included a winter collection of zooplankton (Menshenina and Rakusa-Suszczewski, 1992; Żmijewska, 1992; Bathmann *et al.*, 1993; Marin and Schnack-Schiel, 1993).

The present paper seeks to show how the population dynamics and the diel and seasonal migration rhythm of several copepod species have evolved in Antarctic coastal waters in the vicinity of the Antarctic Peninsula, and to discover the spatial and temporal relationships between them. The phytophages *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas*, the omnivore *Metridia gerlachei* and the predator *Euchaeta antarctica* were selected for study.

## 2. Materials and methods

Three field seasons were spent working in the Antarctic Peninsula region. Between December 1985 and February 1986, February to April 1988, and June to August 1989, zooplankton samples were taken from the research vessel 'Polar Duke' in Croker Passage at 64°50' S, 61°50' W. A single-level opening - closing net, consisting of two nets with mesh sizes of 500  $\mu\text{m}$  and 200  $\mu\text{m}$ , attached side by side, with 0.5 m<sup>2</sup> square mouth openings, was used to collect zooplankton in oblique tows. The closed net was lowered to 1000 m, opened and retrieved at 10 m min<sup>-1</sup> at a ship's speed of 1-2 knots. At 600 m, the net was closed and brought to the surface at 20 m min<sup>-1</sup>. The collecting time from 1000-600m with the open net was 40 to 50 minutes

followed by an additional 30 minutes for net retrieval. Go-flo flowmeters were mounted in the mouths of both nets.

Two replicate day/night vertical series were taken, sampling the following discrete depth horizons: 0–50 m, 50–100 m, 100–200 m, 200–400 m, 400–600 m, 600–1000 m or 1200 m. More than two days and nights were needed to obtain a complete series during the short days of winter or short nights of summer. The replicated vertically stratified series were taken 6 times, twice in the summer (mid-December, late January), twice in the late summer – autumn (March, April), and twice in the winter (early June and late July). In addition, on 13–14 March one day/night vertical series was carried out down to 500 m, at depth intervals of 50 m (Tab. 1). These samples were preserved immediately in sodium borate-buffered formaldehyde.

**Table 1.** Station list from Croker Passage (64°50' S, 61°50' W)

Season	Date	No. of hauls		No. of samples	
		day	night		
summer	09.12.1985	1	–	7	
	17.12.1985	1	1	13	
	29.01.1986– 31.01.1986	1	1	16	
autumn	02.03.1988– 04.03.1988	2	2	25	
	13.03.1988– 14.03.1988	1	1	16	
	12.04.1988– 14.04.1988	1	1	15	
	winter	19.06.1989– 23.06.1989	1	1	15
		29.07.1989– 31.07.1989	1	1	9
	02.08.1989	1	–	1	

In the laboratory copepods counts were done of a known fraction of the total sample (1/2–1/8), using a Motoda box splitter (Motoda, 1959). To estimate total abundance, specimens were counted in the samples taken

with a 500  $\mu\text{m}$ -mesh net. When the number of specimens in the desired category was less than 1000 individuals, all of them were counted. When the number of specimens exceeded 1000 individuals, 5 replicate sub-samples (taken with a sample pipette) were counted and the results averaged. The abundance of copepods was calculated as the number of ind.  $1000\text{ m}^{-3}$  or ind.  $\text{m}^{-2}$ .

Light cycle and temperature profiles were measured parallel to the three years of sampling (Tab. 2). The change in light intensity was recorded on a Campbell scientific date logger with a Licor quantum sensor on deck. Light intensity was reported as a percentage of the midday intensity. Temperature profiles were taken by shooting XBTs down to 800 m or, during the winter cruise, by lowering CTD profiles.

**Table 2.** Light cycle and temperature regime

Sampling period	Period of darkness [h]	From local time	To local time	Surface temp. [ $^{\circ}\text{C}$ ]	Temperature at 800 m [ $^{\circ}\text{C}$ ]
12 Dec.	3	0000	0300	2	0.2
29-31 Jan.	5	2300	0400	0.2	0.3
3-6 March	10	2000	0600	0.8	-1
mid-April	13.5	1730	0700	-0.4	-1
late June	19	1500	1000	-1.3	-1
late July					
early August	15	1630	0930	-1.3	-1

In general, throughout the study period, Croker Passage was isothermal, showing little differences in temperature from near the surface right to the bottom.

### 3. Environment

Croker Passage is situated between Gerlache and Bransfield Straits adjacent to the Antarctic Peninsula (Fig. 1). Samples were taken in the area between  $63^{\circ}52' - 64^{\circ}50' \text{ S}$  and  $63^{\circ}30' - 61^{\circ}50' \text{ W}$ , over one of the large central depressions in the passage, in the deepest place off the west coast of the Antarctic Peninsula. The comparatively shallow waters around Croker Passage provide access to mesopelagic water from the open Southern Ocean. Croker Passage is surrounded by a number of islands: in the west by Hoseason I., Liege I. and Brabant I., in the east by Christianid Is. and Two Hummock I. The geographical location of Croker Passage makes it a very quiet area where investigations can be done at practically any time.

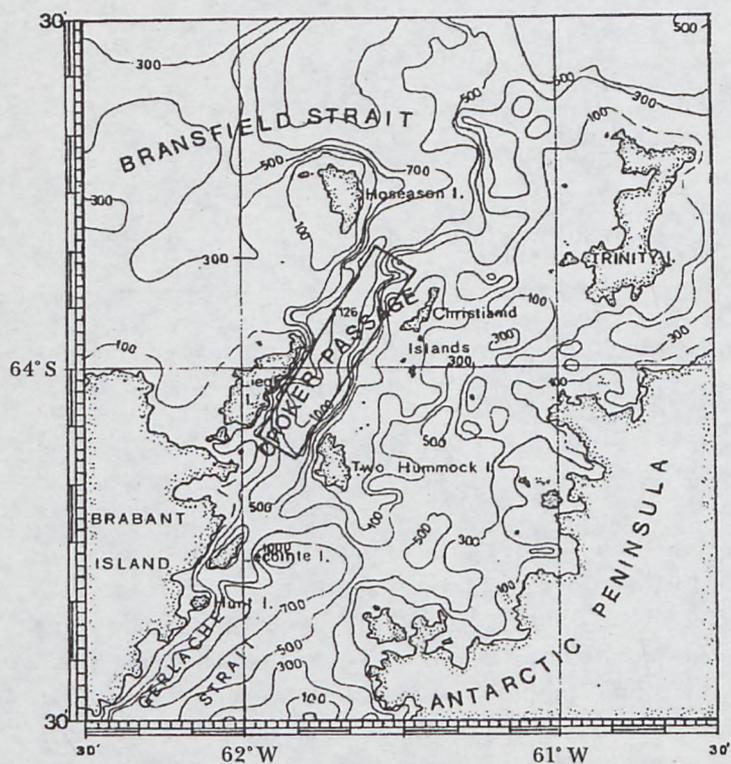
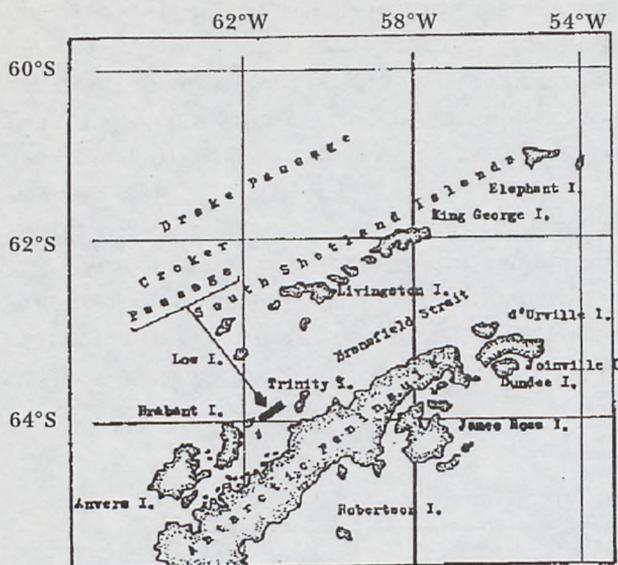


Fig. 1. Area of zooplankton sampling stations in Croker Passage, Antarctic Peninsula, during 3 austral seasons (1985–1989)

As in the southern part of Bransfield Strait the water masses of Croker Passage are varied: warmer waters of rather lower salinity originating from the Bellingshausen Sea, and colder, more saline waters with characteristics similar to those of the Weddell Sea (Gordon and Nowalin, 1978). The latter flow from the Weddell Sea along the Antarctic Peninsula as far as Trinity I., where the waters flowing through Gerlache Strait into Bransfield Strait probably mix (Clowes, 1934). In summer a narrow current flows from the Bellingshausen Sea, through the western part of Bransfield Strait, but a south-westerly current carrying waters from the Weddell Sea was recorded off the northern shores of the Antarctic Peninsula (Grelowski and Tokarczyk, 1985). In winter, the influence of Weddell Sea water can be less significant than in summer (Eicken and Lange, 1989).

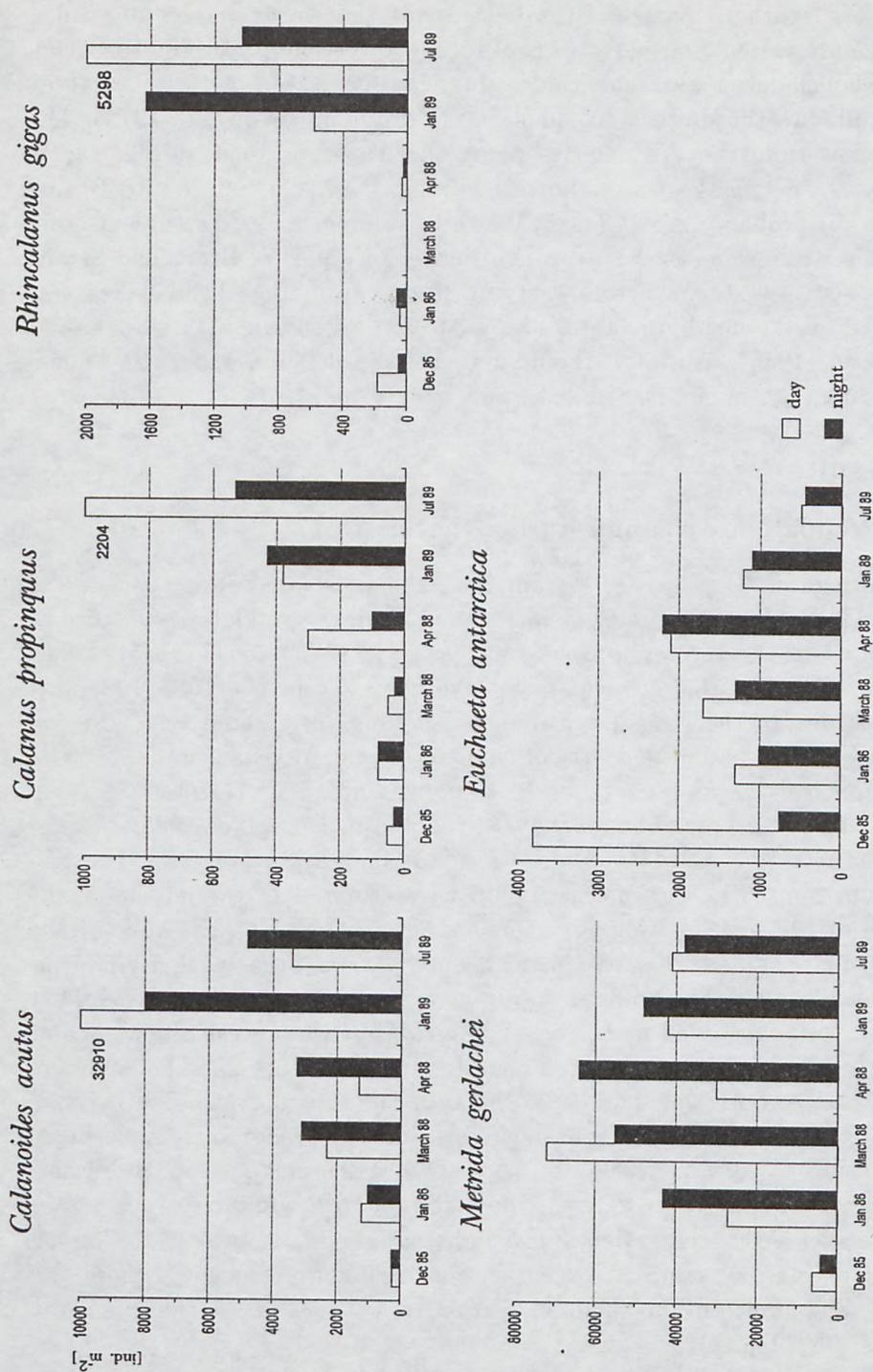
## 4. Results

### 4.1. Population dynamics during the seasons

Throughout the 3 years of sampling, the most abundant species was *M. gerlachei* (Fig. 2). A steady increase in average population abundance was noted in the three phytophagous species – *C. acutus*, *C. propinquus*, *R. gigas* (Fig. 2). Recruitment may have been low in the 1985–1986 season, but due to the lack of continuous sampling throughout one year, we can only speculate on the causes of changes in year-to-year abundance. The minimum average abundance of *R. gigas* was noted in March 1988 (Fig. 2). The lowest average abundance was reached in December 1985: *C. acutus* (205 ind. m<sup>-2</sup>) and *C. propinquus* (30 ind. m<sup>-2</sup>) (Fig. 2). The low abundance noted in the summer could be attributed to the northerly advection of the surface-dwelling juvenile stages followed by the sub-surface return of late stages which live in the deeper waters of the southerly flowing convergence layer. The minimum average aggregation of *E. antarctica* (444 ind. m<sup>-2</sup>) was recorded in July 1988 (Fig. 2) but the lowest abundance of *M. gerlachei* (5566 ind. m<sup>-2</sup>) was recorded in December 1985. The average abundances of both were highest in the autumn (March, April 1988) – 2257 ind. m<sup>-2</sup> and 65 354 ind. m<sup>-2</sup> respectively, but the predominantly herbivorous species *C. acutus* (7982 ind. m<sup>-2</sup>), *C. propinquus* (547 ind. m<sup>-2</sup>) and *R. gigas* (1747 ind. m<sup>-2</sup>) were the most abundant in winter.

The average concentration of the night samples was more or less similar to that of the day samples, except in the herbivorous species, where the average abundance of day samples was up to 5 times larger than at night (winter 1989, Fig. 2).

The relative abundance in night samples showed that *M. gerlachei* was 5–20 times more common than *C. acutus*, which in turn was 1.5 to 18 times



more abundant than *E. antarctica*. This last was up to 83 times more abundant than *R. gigas*, and up to 28 times more abundant than *C. propinquus*; the last mentioned tended to have the lowest abundance.

#### 4.2. Diel and nocturnal vertical distribution during three seasons

A three-season study of the vertical distribution of five copepods showed their population dynamics in a 1000 m water column to be distinctive, and dependent on time of day and season (Figs. 3.1-6).

In summer (December 1985 and January 1986) phytophages concentrated mainly in the upper layer. *C. acutus* was present in the 50-100 m layer, although night-time hauls were more abundant than day-time ones. From December to January maximum numbers rose by several orders of magnitude - from 391 to 134 552 ind.  $1000\text{ m}^{-3}$  in day-time hauls and from 4674 to 15 095 ind.  $1000\text{ m}^{-3}$  in night-time hauls.

During the same season *C. propinquus* occurred at greater depths than did *C. acutus*. In December it was found in the top 200 m layer, whereas a month later, its numbers peaked again, but this time in the 200-400 m layer. At the same time, maximum numbers of *C. propinquus* were found in the 0-100 m layer, and tripled from 200 ind.  $\text{m}^{-3}$  in December to 600 ind.  $1000\text{ m}^{-3}$  in January.

During the same period the vertical distribution of *R. gigas* was similar to that of *C. propinquus*. In December *R. gigas* was far more numerous than *C. propinquus*, but in January its numbers decreased almost threefold, and the entire population was even more widely dispersed in the 1000 m water column than *C. propinquus*.

In autumn, (early March 1988) *C. acutus* was still concentrated in the top 100 m layer, although some individuals were found in the whole water column. At this time *C. propinquus* was concentrated solely in the top 200 m, while very small numbers of *R. gigas* were caught only in the 150-200 m layer. However, two weeks later, the vertical distribution of these phytophages in the top 500 m had altered conspicuously: only *C. propinquus* remained in the surface layer (Fig. 3.6). Maximum concentrations of *C. acutus* were now recorded in the 150-300 m layer; *C. propinquus* was found in the top 100 m by night but in the 100-300 m layer by day. Least numerous of these herbivores, *R. gigas* was only to be found in the 100-250 m layer.

During the following two weeks, in April, *C. acutus* sank to below 400 m; less than 8.5% of its total population remained in the top 100 m. Maximum concentrations (2100 ind.  $1000\text{ m}^{-3}$  in day-time hauls and 6027 ind.  $1000\text{ m}^{-3}$  at night) were at depths of 1000-1200 m. The bulk of *C. propinquus* remained in the top 50 m layer - 47.5% of the population by day,

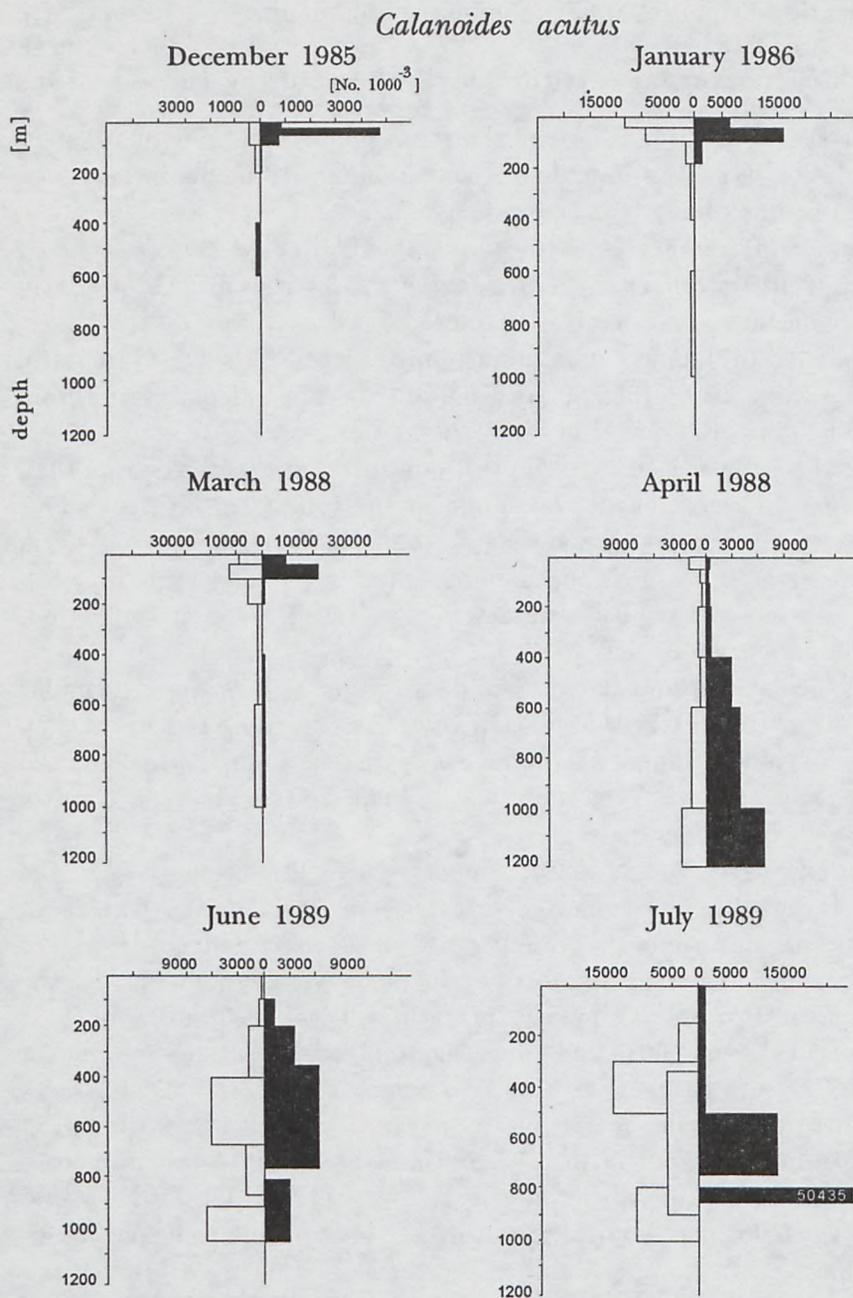


Fig. 3.1 Diel changes in vertical distribution of *Calanoides acutus* in Croker Passage during 3 austral seasons (ind. 1000 m<sup>-3</sup>)

*Calanus propinquus*

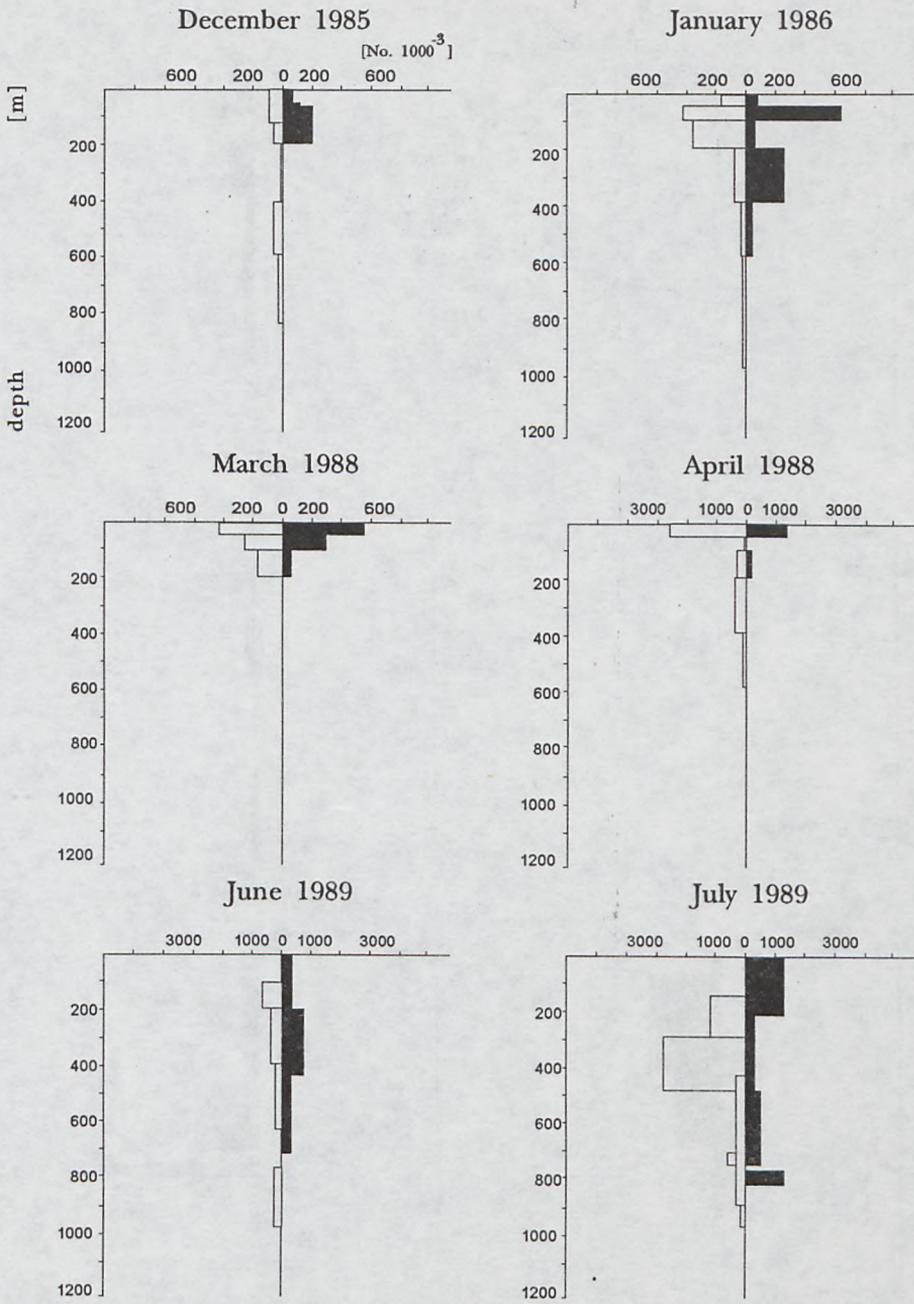


Fig. 3.2 Diel changes in vertical distribution of *Calanus propinquus* in Croker Passage during 3 austral seasons (ind.  $1000\text{ m}^{-3}$ )

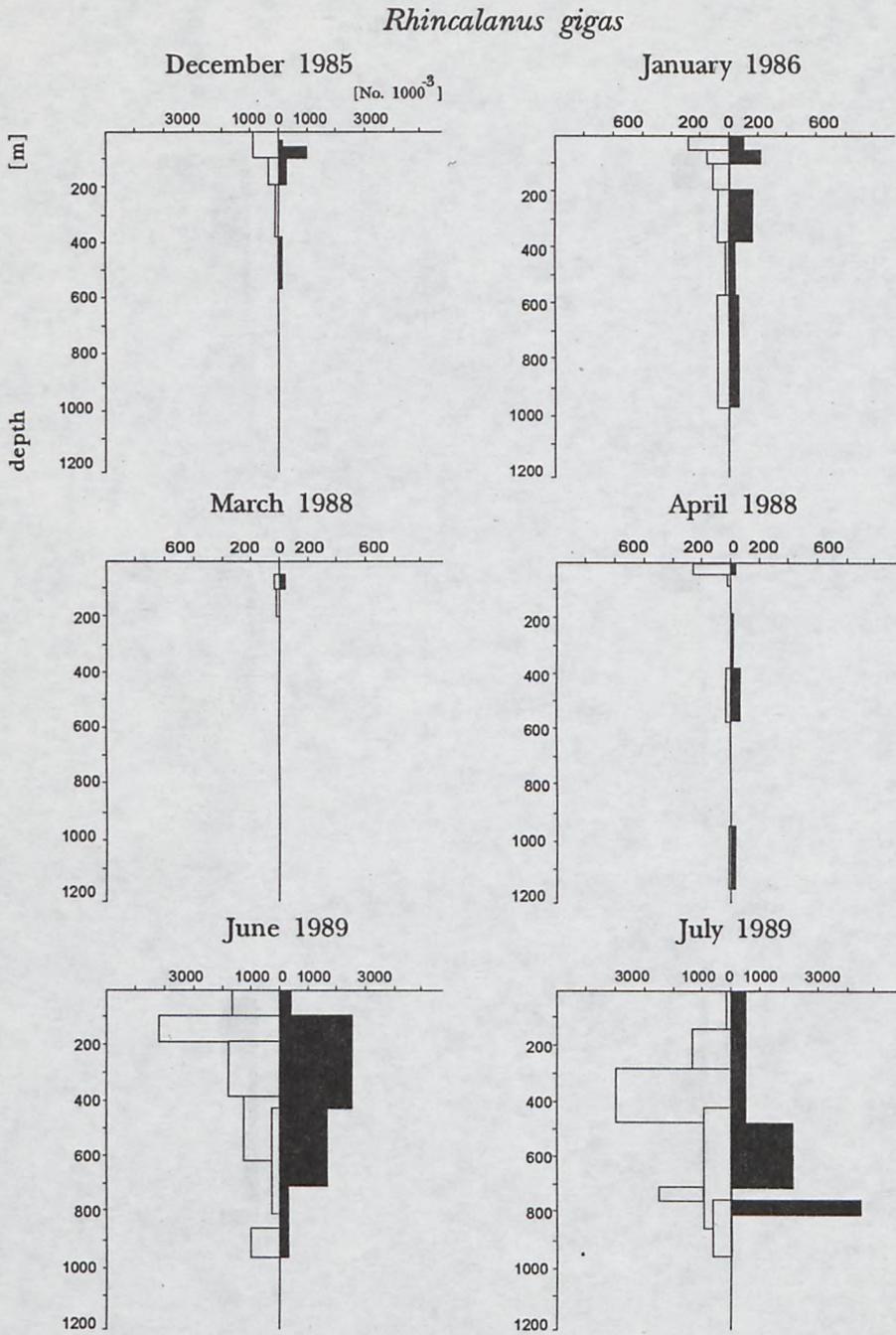


Fig. 3.3 Diel changes in vertical distribution of *Rhincalanus gigas* in Croker Passage during 3 austral seasons (ind.  $1000\text{m}^{-3}$ )

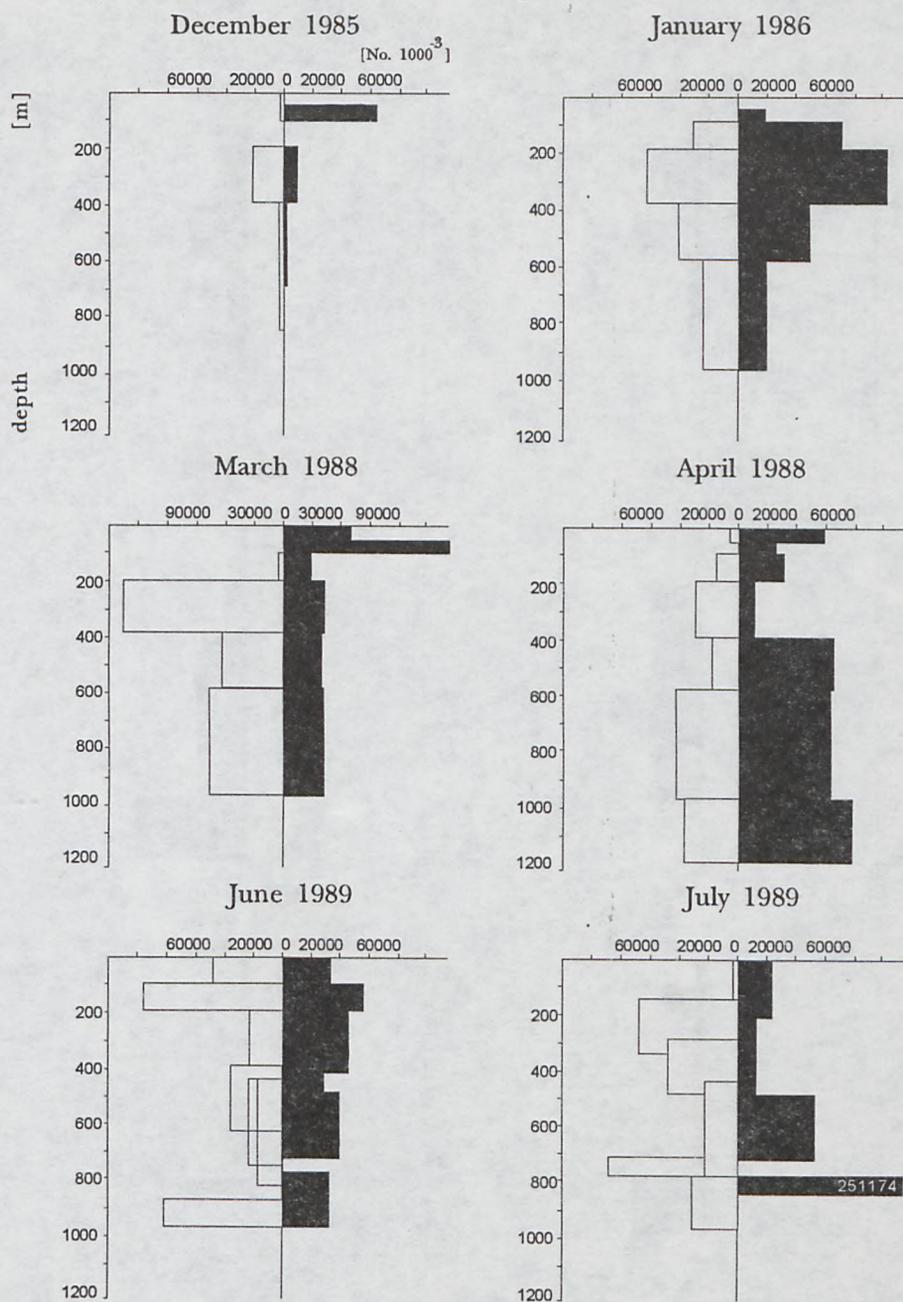
*Metridia gerlachei*

Fig. 3.4 Diel changes in vertical distribution of *Metridia gerlachei* in Croker Passage during 3 austral seasons (ind.  $1000\text{m}^{-3}$ )

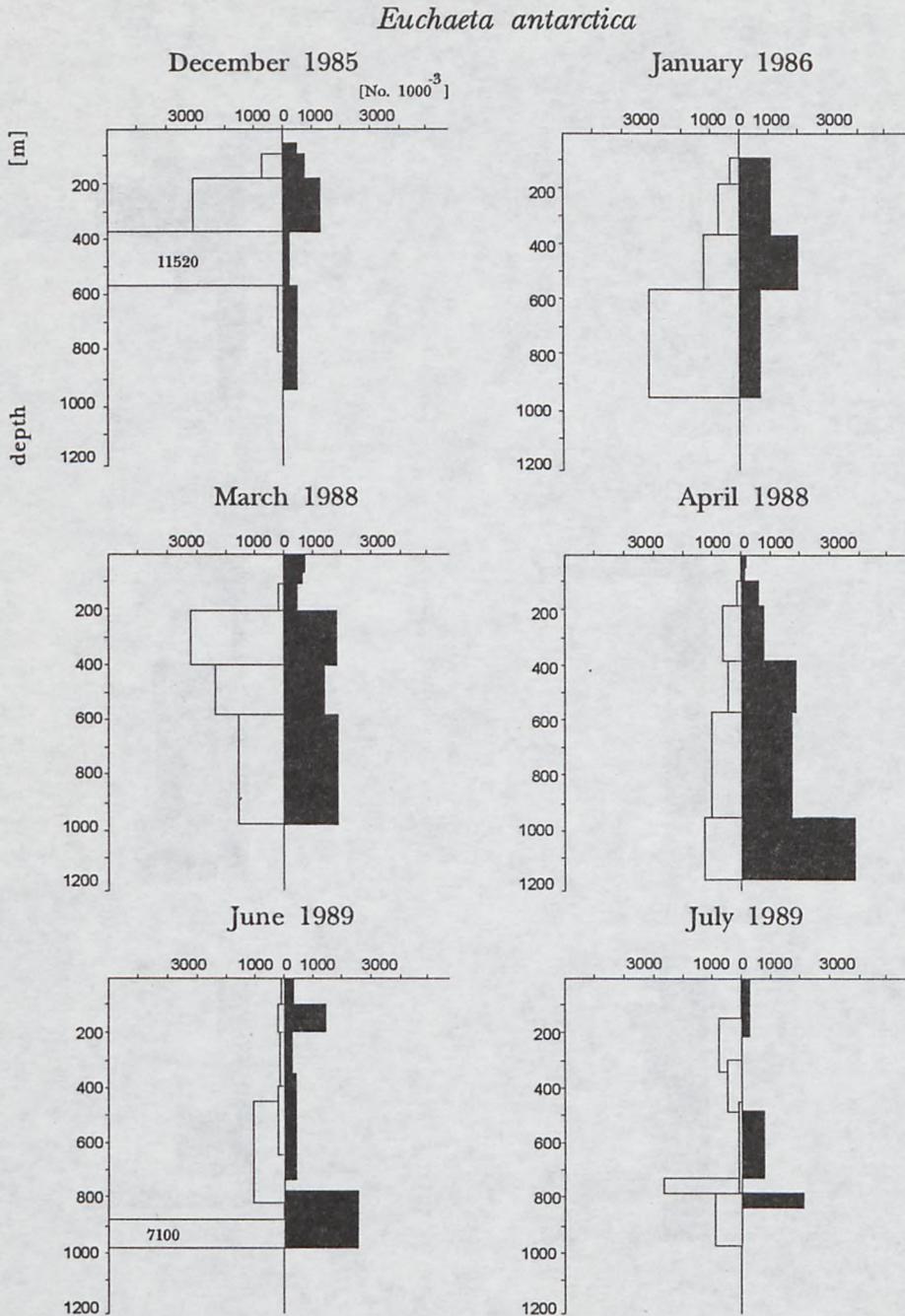


Fig. 3.5 Diel changes in vertical distribution of *Euchaeta antarctica* in Croker Passage during 3 austral seasons (ind. 1000 m<sup>-3</sup>)

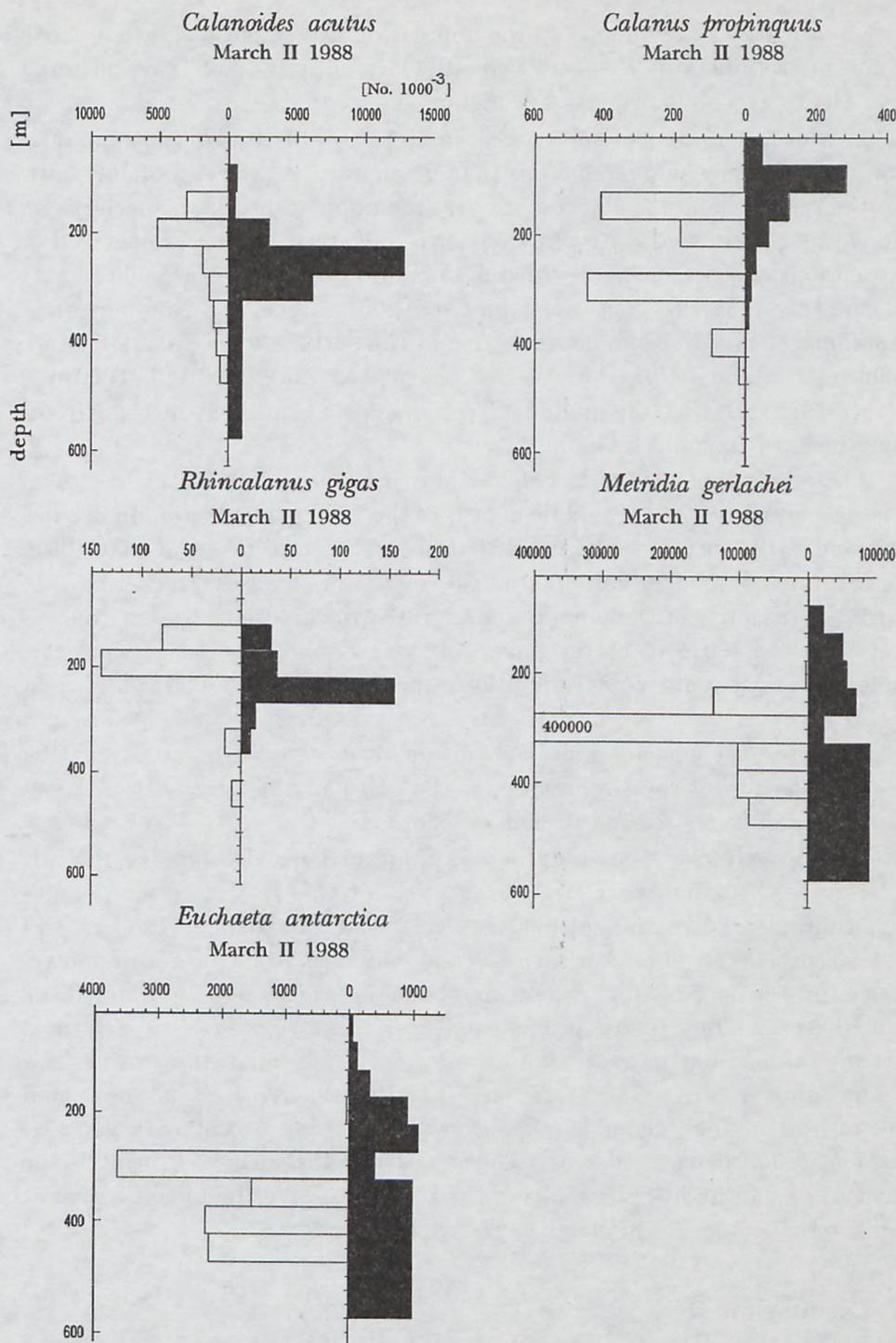


Fig. 3.6 Diel changes in vertical distribution of 5 copepod species in Croker Passage on 13-14 March 1988 (ind. 1000 m<sup>-3</sup>)

81% by night. The remainder of the population was found down to a depth of 600 m. Numbers of *R. gigas* were still very low: by day they clustered near the surface, but dispersed at night.

In winter, numbers of herbivores are high; notably the *R. gigas* population is many times more numerous than in summer. At the end of July, during the second half of the winter studies, the populations of all species were increasing progressively. Absent from surface waters, *C. acutus* occurred in the mesopelagic water layer with the maximum of 50436 ind.  $1000\text{ m}^{-3}$  at 800 m (July 1989). *R. gigas* was found 100–200 m higher up. Numbers of *C. propinquus* peaked at two depths – one in the surface layer (max 2084 ind.  $1000\text{ m}^{-3}$  – June 1989), the other at 300–500 m (max 2990 ind.  $1000\text{ m}^{-3}$  – July 1989). During this period *C. propinquus* was present in the surface layer both by day and by night.

The omnivorous *M. gerlachei*, the most numerous inhabitant of Croker Passage, was found at the middle depths of the 1000 m water column in summer and early autumn. The largest concentrations occurred at 200–400 m (max numbers 400 000 ind.  $1000\text{ m}^{-3}$  – night time haul – March 1988). In April the majority of the population migrated to the deeper water, concentrating in the 400 m to bottom layer. In summer and autumn *M. gerlachei* underwent very regular diel migrations, moving some 150–200 m higher at night.

In winter, the whole population split up, as it were, with one population peak at the top of the water column, the other in the near-bottom layer, and diel migrations seemed to be less vigorous.

Like *M. gerlachei*, the predatory *E. antarctica*, usually avoided the surface layers. In summer, a large proportion of the *E. antarctica* population concentrated in the top 600 m layer (max 11 520 ind.  $1000\text{ m}^{-3}$  at 400–600 m). In autumn (April) these copepods sank to below 600 m and remained in the near-bottom zone throughout the winter (max numbers 7100 ind.  $1000\text{ m}^{-3}$  – July 1989). Again, like *M. gerlachei*, *E. antarctica* performed diel migrations, but in contrast to the former, these migrations intensified as the summer progressed. They were particularly dynamic in the second half of March 1988 (samples taken every 50 m, from 0 to 500 m), when at night *E. antarctica* moved nearly 250 m closer to the surface. In winter, the relatively small numbers inhabiting the top 200 m layer remained active at night, moving 100–150 m closer to the surface.

## 5. Discussion

The results of our studies have revealed that the life styles of copepods vary within the same and different trophic groups.

### 5.1. Population dynamics during the seasons

The mean numbers of the phytophages *C. acutus*, *C. propinquus* and *R. gigas* displayed a pronounced seasonal variability; however, in *M. gerlachei* and *E. antarctica* this variability was much less. *M. gerlachei* was the dominant species in Croker Passage and was the most numerous at all times during the study. *E. antarctica* was also ever present, but in much smaller numbers. The evident fluctuations in numbers of herbivores could, on the one hand, be due to long term changes (our studies covered only three seasons in separate years), but on the other could be evidence of a variety of life styles in copepods with differing trophic requirements.

It is striking that the population of phytophages is so much larger in winter than in summer. Atkinson and Ward (1988) found that in the waters of South Georgia the winter copepod biomass was 77% of its summer level. Hopkins (1971) showed that in the Indian Ocean sector, the winter plankton biomass in the 0–250 m layer was under 10% of the summer level. During winter in our study area, vast numbers of phytophages (though not *C. propinquus*) were present in the deep layers.

*C. acutus* was one of the most abundant phytophages in Croker Passage. It is a species typical of the area to the south of the Polar Front and, depending on the time of year, is present in various layers of the water column (Mackintosh, 1934, 1937; Hardy and Gunther, 1935; Andrews, 1966; Voronina, 1972a,b; Voronina, 1984). In summer it inhabits the top 100 m, and fluctuations in numbers are considerable even in the same season or region, e.g. the high Antarctic. In December the mean numbers of *C. acutus* in Croker Passage hovered around the 200 ind. m<sup>-2</sup> mark; but 40 days later this figure had increased fivefold. In the late summer or early autumn (first days of March) this figure was only 2.5 times as high. In December, Huntley and Escritor (1991) counted an average of 413 ind. m<sup>-2</sup> in the top 200 m layer of Gerlache Strait, not far from our study area; one month later they found this figure to have increased tenfold, but from February to March they recorded first a gradual, than a very abrupt drop in numbers. Schnack *et al.* (1991), conducting their investigations in the Weddell Sea from October to February, reported a similar abundance of *C. acutus* until the end of January; in February, however, this increased almost fourfold. At a similar latitude in Olaf Prydz Bay in the Indian Ocean sector, the highest numbers of *C. acutus* (over 20 000 ind. m<sup>-2</sup>) were recorded in February (Żmijewska, 1983). Together with our own results, these data show that in high latitudes, *C. acutus* concentrations peak later than, for example, in areas closer to the Polar Front (Voronina *et al.*, 1978; Voronina, 1984).

Two other species *C. propinquus* and *R. gigas* – occur quite frequently in the vicinity of Antarctica, but their numbers are nowhere near those

of *C. acutus* (Jażdżewski *et al.*, 1982; Chojnacki and Węgleńska, 1984; Żmijewska, 1985; Boysen-Ennen and Piatkowski, 1988; Park and Wormuth, 1993). *C. propinquus* is a species generally found together with *C. acutus*, but it has a much more extensive range both north and south of the Polar Front (Vervoort, 1965); it can be the dominant species, *e.g.* in the South Georgia region (Marin, 1987). In Croker Passage *C. propinquus* was caught with great regularity throughout the study period, but its numbers were only 1/10 the average numbers of *C. acutus*. It was also less frequent than the latter in the Weddell Sea (Fransz, 1988; Schnack *et al.*, 1991; Bathmann *et al.*, 1993) and in Olaf Prydz Bay (Żmijewska, 1983). Boysen-Ennen and Piatkowski (1988) found that in the Weddell Sea these two species made up as much as 61% of the plankton biomass. In high latitudes, however, *C. propinquus* appears to have a much more restricted range than *C. acutus* (Żmijewska, 1985, 1987). By contrast, the winter studies of Bathmann *et al.* (1993) in the Weddell Sea suggest that *C. propinquus* will live in colder waters than *C. acutus*.

Even more opportunistic as regards occurrence is the largest of the Antarctic copepods, *R. gigas*. In summer it was ever – present in the zooplankton of our study area: in autumn it practically disappeared, only to reappear in winter in numbers far in excess of the summer level. Hopkins (1985b) did not record even a single specimen of *R. gigas* in Croker Passage in March. At the same time of year it was absent from the Davis Sea, too (Żmijewska, 1979). This suggests that *R. gigas* leaves Antarctic coastal waters in March and drifts away with the surface currents in a south-easterly direction, and returns in winter with deep-water currents flowing in from the north.

The populations of *C. acutus*, *C. propinquus* and *R. gigas* may well be swelled by recruitment from the north, a fact which would explain their numbers in the winter months. On the other hand, it is well to remember that our research material comes from various years and the figures we obtained could be evidence of long-term changes.

The most typical species of high latitudes is *M. gerlachei* (Kaczmaruk, 1983; Hopkins, 1985b; Humbold and Hempel, 1987; Żmijewska, 1987; Men-shenina and Rakusa-Suszczewski, 1992). In Croker Passage its mean numbers did not vary conspicuously, although they did decline slightly in early summer. From their three-year summer study around Elephant Island, Park and Wormuth (1993) report that the zooplankton was alternately dominated by *M. gerlachei* and *Salpa thompsoni*. In early spring, Hosie and Stolp (1989) recorded only very small numbers of *M. gerlachei* in Olaf Prydz Bay, as did Fransz (1988) in the Weddell Sea. The small proportion of *M. gerlachei* in the plankton reported by some workers could be due to the fact that an

insufficiently deep layer was trawled (0–100 m or 0–200 m). According to Vervoort (1965), *M. gerlachei* is found mostly in the 100–250 m layer; Bradford (1971), however, considers that the range of *M. gerlachei* is connected with the  $-1^{\circ}\text{C}$  isotherm. In his assessment of the zooplankton biomass of Croker Passage, Hopkins (1985b) stated that 74% of it consisted of *M. gerlachei*, *C. acutus* and *E. antarctica*; the numbers of *C. propinquus* were insignificant.

Like *M. gerlachei*, *E. antarctica* is less commonly recorded, owing to the fact that it is a meso- and bathypelagic species (Vervoort, 1965; Park, 1978), although in shelf waters it also occurs in the top 250 m (Ward and Wood, 1988). In summer, its mean numbers in Croker Passage are three times as high as in spring between King George I. and Elephant I. (Żmijewska, 1988). In summer, Ward and Wood (1988) caught a maximum of 138 ind.  $\text{m}^{-2}$  around South Georgia, and in winter half as many. In our study area, *E. antarctica*, like *M. gerlachei*, was always present though not as numerously. It made only sporadic appearances in the upper layers of open waters (Żmijewska, 1988). Clearly, then, *E. antarctica* displays a preference for the water of high latitudes.

## 5.2. Diel and nocturnal vertical distribution during three seasons

Several Antarctic copepods are typical interzonal forms, among them the three phytophages discussed here. Ontogenetic migrations of zooplankton in the polar regions of both hemispheres are a well-known phenomenon (Mackintosh, 1937; Ostvedt, 1955; Foxtton, 1956; Vinogradov, 1970; Dawson, 1978). In the austral summer of 1985/86 in Croker Passage, *C. acutus*, *C. propinquus* and *R. gigas* were to be found in the top 100 m in Croker Passage; in view of the fact that only a fraction of their populations were inhabiting deeper waters, the spring migration must practically have come to an end. Andrews (1966) is of the opinion that *C. acutus* begins to migrate in October. In Croker Passage we found that *C. acutus* remained in the 0–100 m layer until the beginning of March. A fortnight later the population was already below 200 m at night and 50 m higher by day. This could have been the beginning of the winter migration, because in the course of the next 14 days these copepods descended a further 200 m; in winter they concentrated in mesopelagic waters.

Another of the herbivores, *C. propinquus*, had not yet completed its spring migration in December; a large part of the population was still below 200 m. In autumn, the winter migration began two weeks after that of *C. acutus*. Unlike the latter, which clearly avoids the upper parts of the water column in autumn and winter, *C. propinquus* disperses throughout the

water column for the winter. Hopkins and Torres (1988) found *C. propinquus* below 150 m in the Weddell Sea in March while at the same time *C. acutus* was occurring in the mesopelagic layer. In her description of these ontogenetic migrations, Voronina (1972a, 1984) stated that *C. propinquus* spends the winter in deep waters, in the same way as *C. acutus* and *R. gigas* do.

Schnack-Schiel *et al.* (1991) see the cause of the winter activity of *C. propinquus* in the chemical composition of the lipids accumulated in the copepods' oil sac during the growing season. They found that whereas *C. acutus* achieves maximum lipid concentrations already in January, *C. propinquus* doubles its quantity from January to March. The former species accumulates lipids in the form of wax esters, the presence of which are indicative of starvation processes, but the latter stores energy in the form of triacylglycerols, which stimulate feeding (Sargent *et al.*, 1981; Sargent and Falk-Petersen, 1988).

In summer *R. gigas* was much more widely dispersed than either *C. acutus* or *C. propinquus*, but did tend to concentrate in the upper layers of the water column. In autumn *R. gigas* was practically absent from the species composition of zooplankton, but reappeared in winter in numbers 20–30 times greater than the summer population. In lower latitudes, *e.g.* off South Georgia, early – summer numbers of *R. gigas* were very low (Marin, 1988). According to Voronina (1975), the abundance of *R. gigas* in Antarctica is seasonally dependent. In the Antarctic she recorded the highest concentrations of this species in early spring, and in the Subantarctic in summer; this was because numbers had been swelled by the very abundant new generation. Ommanney (1936) considers the range of *R. gigas* to be contiguous with that of the Antarctic Circumpolar Current, but Voronina (1984) is of the opinion that its range is greater. In Atkinson's (1991) view, *R. gigas* displays a preference for the Subantarctic region. Our results show that this species is not a permanent constituent of the pelagic fauna of high latitudes.

Our data on the depths of occurrence of *C. acutus*, *C. propinquus* and *R. gigas* within the water column in Croker Passage show that, depending on season, migrations vary greatly as to their rate and time of inception. They confirm Voronina's (1970, 1972a; Voronina *et al.*, 1978) theory of asynchronous life cycles in the very abundant species of Antarctic copepods. During her studies of the horizontal and vertical distribution of these Antarctic phytophages, she found *C. acutus* was the first to begin the spring migration and was followed by *C. propinquus* and *R. gigas*, and that these species started their winter migrations in the same order. *C. propinquus* does not fit very well into this scheme of things; in autumn it tends to descend to deeper

waters, but the majority of its population remains in the surface layer even in winter.

In view of the fact that *M. gerlachei* clearly prefers the middle depths both in summer and in autumn, it is interesting to note that its population ascends towards the surface in winter. This upward winter expansion could be due to the departure of the phytophages from the surface layers in autumn, which leaves this niche to be occupied by the now-active *M. gerlachei* (diel migrations).

*E. antarctica* migrates in the opposite direction: in autumn it begins to descend to deeper water and overwinters in the near-bottom layer. The tendency of *M. gerlachei* and *E. antarctica* to undertake seasonal migrations could be specific to our study area; in lower Antarctic latitudes, these species do not do so. Neither Ward and Wood (1988) nor Atkinson and Peck (1988), investigating the waters of South Georgia, found any evidence for ontogenetic migration in either of these species.

In Croker Passage we were also able to study diel migrations. In general, opinions on the subject of the diel migrations of phytophages are divided. The diel migrations of *C. acutus* have been described by Andrews (1966); Huntley and Escritor (1991), however, do not confirm their existence, although Chojnacki and Węgleńska (1984) and Atkinson *et al.* (1992) report a tendency in this species to congregate nearer the surface during the day. The best documented diel migrations are those of *C. propinquus* (Mackintosh, 1937; Hopkins and Torres, 1988). Our findings are that this copepod tends to gather nearer the surface at night. Drits *et al.* (1990) state that the position of *C. propinquus* in the water is dependent on the available food resources: if these are sufficiently abundant, the copepods feed without changing depth, regardless of their developmental stage. Atkinson *et al.* (1992) found that species undergoing migrations are capable of feeding no matter which direction they are moving in.

The differences in depth of occurrence of *C. acutus* during a 24-h period, which we recorded in early March, do not appear to be adequate evidence for the existence of diel migrations. They are more probably due to the error inherent in every haul and were not recorded at other periods of our studies. The same applies to *R. gigas*.

By contrast, diel migrations are a distinctive aspect of the biology of *M. gerlachei* and suggest a high degree of environmental adaptation in this species. This phenomenon was first reported by Hardy and Gunther (1935) and thereafter confirmed to varying degrees (Mackintosh, 1937; Hopkins, 1985a; Hopkins and Torres, 1988; Atkinson and Peck, 1988). The reasons why these copepods move from one depth to another during a 24-h period are many: complex behavioural forms, reproduction orientation, or feeding,

to mention but three. Our data, obtained during three seasons, clearly indicate that the *M. gerlachei* population is concentrated in the upper layers of the water column at night. These copepods are very active, capable of moving up to 200 m in 24 h. Rudyakov and Voronina (1974) found their amplitude of migration to be 160 m; and considered the migration mechanism to involve both active and passive movements.

Unlike the three previously mentioned species, *M. gerlachei* did not undertake ontogenetic migrations. In summer and autumn this population was conspicuous by its absence from the upper 100 m layer; in winter, however, it was present there, inhabiting the niche previously occupied by phytophages. This state of affairs no doubt continues until the interzonal copepods start their spring migration. In spring *M. gerlachei* congregated in the middle depths of the open waters between King George I. and Elephant I.; it also inhabited the surface waters of shelf seas (Żmijewska, 1988). They may well have been able to feed on algae released by the melting ice. In summer numbers of *M. gerlachei* increased with depth both in Bransfield Strait and in Croker Passage (Żmijewska, 1987). It seems probable that the winter migration of *M. gerlachei* towards the surface is connected with feeding. In autumn in the Weddell Sea, Hopkins and Torres (1989) found considerable quantities of minute Protozoa in its gut. Yen and Hosset (unpubl. data) report that in winter, unlike most phytophages and even predators, *M. gerlachei* is very active, displaying a relatively high level of respiration and a high thermal tolerance.

During the entire study period *E. antarctica* was found to exhibit a rather lower level of diel activity than *M. gerlachei*, even though both species ascended to shallower depths at night. Both species are good migrators, a fact that concurs with the findings of other studies in various regions of the Southern Ocean (Hardy and Gunther, 1935; Mackintosh, 1937; Rudyakov and Voronina, 1974; Chojnacki and Węgleńska, 1984).

## 6. Conclusions

The relative abundance (night hauls) showed that *M. gerlachei* was 5–20 times more common than *C. acutus*, which in turn was 1.5 to 18 times more abundant than *E. antarctica*. This last was up to 83 times more abundant than *R. gigas*, and up to 28 times more abundant than *C. propinquus*; the last one tended to have the lowest abundance.

The large variation in the population of phytophagous copepods suggests a deep-water recruitment from north to south. The lack of any large variation in the populations of *M. gerlachei* and *E. antarctica* indicate that these constituted stationary coastal populations.

Seasonal and ontogenetic migrations were performed by all five copepod species. They contrast strongly in details and differ in vertical distribution, timing of inception and duration.

No diel migratory behaviour of planktonivorous copepods was observed, except in *C. propinquus*, which appeared to be a weak migrator. *M. gerlachei* and *E. antarctica* exhibited significant nocturnal ascents. We conclude that the ontogenetic and diel migrations are an important adaptation to survival in the high polar environment.

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