Seasonal and spatial variations in the population structure and life histories of the Antarctic copepod species *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas*, *Metridia gerlachei* and *Euchaeta antarctica* (Calanoida) in Croker Passage (Antarctic Peninsula)

OCEANOLOGIA, No. 35
pp. 73–100, 1993.
PL ISSN 0078-3234

Antarctica
Calanidae
Migrations
Age structure

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Manuscript received February 17, 1994, in final form May 5, 1994.

Abstract

Seasonal and spatial variations in the population structure and life cycles of 5 Antarctic copepod species – *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas*, *Metridia gerlachei* and *Euchaeta antarctica* – have been reconstructed from analyses of sets of vertically-stratified zooplankton samples taken with a 200 μ-mesh net by day and by night during 3 austral seasons (summer, 1985–1986, autumn 1988 and winter 1989) from the 1200 m deep Croker Passage off the *Antarctic Peninsula*. Developmental stages from C1 to adults were enumerated. Sex ratios were determined in *M. gerlachei* from C5 to adults, in *E. antarctica* from C4 to adults, and in other species in adults only.

Seasonal changes in the relative depth distribution and abundance of the various stages were used to compare the population dynamics of these 5 copepods. The life span of *C. acutus* is less than one year while *C. propinquus* can live for even more than a year. The population of *R. gigas* shows the occurrence of 2 generations per year. Multiple generations are noted for *M. gerlachei*, while *E. antarctica* shows a single reproductive peak in the winter followed by the growth of a single generation. The seasonal portioning of vertical space in the water column is very important for copepods with different food requirements. The spatial separation eliminates competition not only between species but among their developmental stages as well. These population characteristics are related to other aspects of the ecology of polar zooplankton.

1. Introduction

The pronounced seasonality of such physical phenomena as the intensity of ice processes, low temperatures, pressure systems, and almost total darkness for several months of the year is a factor affecting, among other things, the nature of the water masses and current systems in polar regions, and in turn is a primary determinant of life processes in the pelagic waters of these regions (Conover and Huntley, 1991). In the Antarctic ecosystem, the zooplankton consists principally of phytophages whose biology is determined by the abundance and frequency of phytoplankton blooms (Voronina and Sukhanova, 1976; Schnack, 1985; Schnack *et al.*, 1985; Voronina, 1984). Because of the severity of the environment, plankton studies in the Southern Ocean are usually carried out in the austral summer. Research stations are located mainly in open waters and are equipped to study the surface, the top 100 m or the 200–300 m layers of water dominated by phytophages such as *Calanoides acutus*, *Calanus propinquus*, *Calanus simillimus* or *Rhincalanus gigas* (Hardy and Gunther, 1935; Mackintosh, 1934, 1937; Ottestad, 1932; Ommanney, 1936; Foxton, 1956; Andrews, 1966; Nakamura and Kadota, 1982). The nature of the horizontal and vertical distribution of copepods, their frequency of occurrence and numbers reflect the structure of the water masses, the abundance of food resources, and hence, the age structure of the populations (Voronina, 1972a,b; Jażdżewski *et al.*, 1982; Żmijewska, 1987, 1988; Marin, 1987; Menshenina and Rakusa-Suszczewski, 1992; Bathmann *et al.*, 1993). There are undoubtedly many other factors affecting the rate of individual growth and the number of generations per year, *e.g.* local environmental conditions or intensity of competiton for food.

In recent years fresh hypotheses on the life cycles of *Calanoides acutus*, *Calanus propinquus*, *Calanus simillimus* or *Rhincalanus gigas* have been put forward in the world literature (Marin, 1988a,b; Fransz, 1988; Atkinson, 1991; Huntley and Escritor, 1991), which depart to varying degrees from the model of asynchronic development of Antarctic phytophages elaborated by Voronina (1972a,b, 1984). The adaptive mechanisms of copepods with other trophic requirements or living in deeper waters, of predators, or even of omnivores not directly dependent on the extent of phytoplankton growth, will differ from those of the phytophages. Our knowledge of the biology and ecology of species such as *Metridia gerlachei* or *Euchaeta antarctica* appears to be incomplete; both of them make up a sizeable proportion of the zooplankton biomass, particularly in the high Antarctic (Hopkins, 1985a,b; Witek *et al.*, 1985).

It is the aim of this paper to explore the life cycles of the very abundant *Copepoda* and to assess the extent of inter– and intraspecific interactions. To do this, 5 copepod species with different feeding requirements were chosen: three are phytophages – *Calanoides acutus*, *Calanus propinquus* and *Rhincalanus gigas*, one is omnivorous – *Metridia gerlachei*, and the fifth is the predatory *Euchaeta antarctica*. The research material comprised plankton samples taken in summer, autumn and winter in Croker Passage, which is situated on the west coast of the Antarctic Peninsula, in the Pacific Ocean sector.

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 by the research vessel 'Polar Duke' in Croker Passage (64°50′ S, 61°50′ W). A single-level opening-closing net, consisting of two nets with mesh sizes of 500 μm and 200 μm attached side by side, with square mouth openings of $0.5\,\mathrm{m}^2$, was used to collect zooplankton in oblique hauls. The closed net was lowered to 1000 m, opened and retrieved at $10\,\mathrm{m\,min}^{-1}$ at a ship's speed of 1–2 knots. At 600 m, the net was closed and brought to the surface at $20\,\mathrm{m\,min}^{-1}$. The collecting time from 1000–600 m with the open net was 40 to 50 minutes followed by an additional 30 minutes for the net retrieval. Go-flo flowmeters were positioned 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. In order to obtain a complete series during the short days of winter or short nights of summer, more than two days and nights were needed. 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) (Tab. 1). These samples were preserved immediately in sodium borate-buffered formaldehyde.

In the laboratory copepod counts were done of a known fraction of the total sample (1/2–1/64) using a Motoda box splitter (Motoda, 1959). For the stage composition, specimens were counted in samples taken with the finer-mesh net (either 150 μm or 250 μm). The population structure (%) was calculated as the average of the total abundance from all depth intervals of two replicate day/night series. All copepodite stages of *M. gerlachei*, *E. antarctica*, *C. acutus*, *C. propinquus* and *R. gigas* were counted as well as

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

Season	Date	No. of hauls day	No. of hauls night	No. of samples
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

Table 2. Light cycle and temperature regime

Sampling period	Period of darkness [h]	From local time	To local time	Surface temp. [°C]	Temperature at 800 m [°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

the nauplii of the last species. The sex ratio was determined in *Metridia gerlachei* from C5 to adults, in *Euchaeta antarctica* from C4 to adults, and in the other species in adults only. The population structure of the 5 copepod species is given as a relative figure (%). Diel changes in stage-abundance distribution were calculated in ind. 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.

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°52′ - 64°50′ S and 63°30′ - 61°50′ 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 the 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. 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 waters 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).

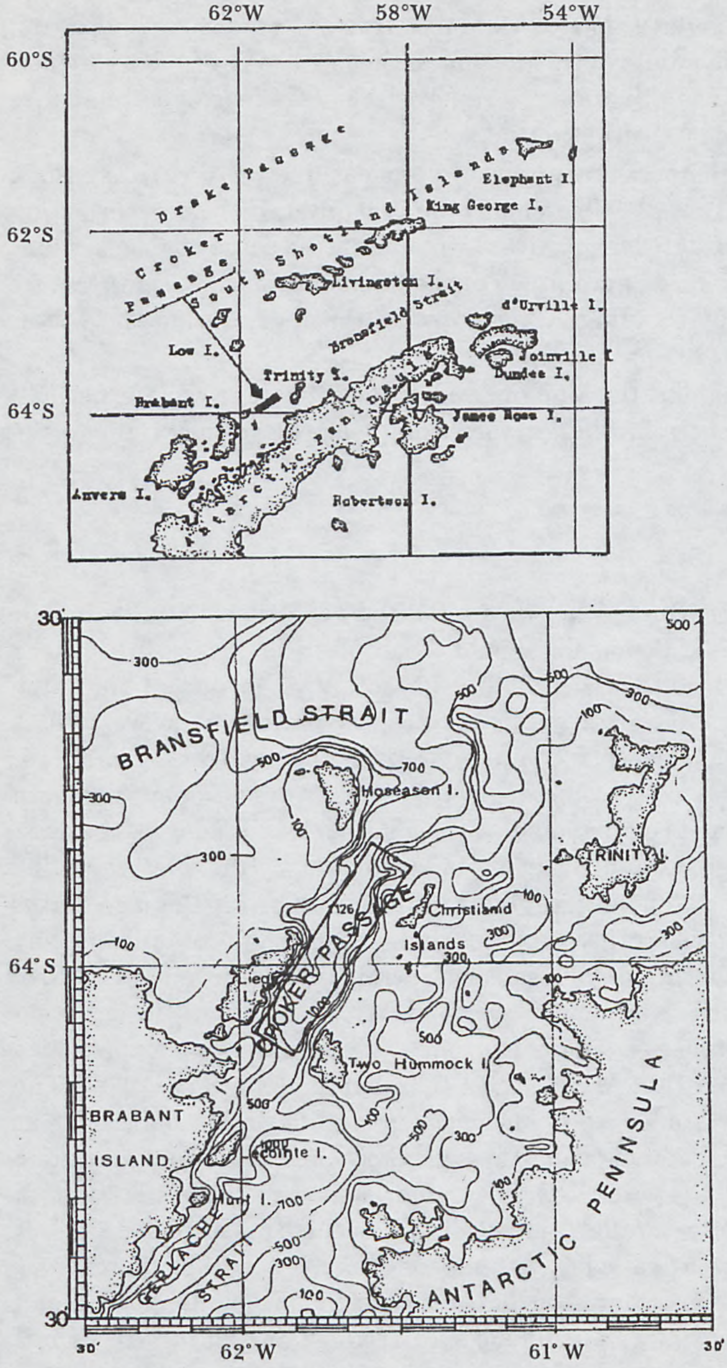


Fig. 1. Area of zooplankton sampling stations in Croker Passage, Antarctic Peninsula, during 3 austral seasons (1985–1989)

4. Results

4.1. Seasonal changes in population structure

High or low abundance is usually a reflection of population dynamics in copepods. Figs. 2.1–5 show the population structure of the 5 copepods studied. The proportions of each stage during 6 months were calculated from averages taken from the day/night estimates of population abundance.

By mid-December (the first season sampled), very early juveniles (C1) were present in the *C. acutus* population. This was dominated by C2 (51.9%); C4 was absent. About 20% of the population comprised late juveniles (C5) and adults. The early juveniles represented the new generation of this year while the older stages in the population represented the residual overwintering generation. By January, the older stages ($< 20\%$) had practically disappeared, while the new generation was represented by an equal number of 3 copepodite stages – C2, C3, C4 ($> 80\%$). In autumn (March, April), about 90% of the population consisted of C4 and C5. In winter (June, July) the young stages were practically absent, while the late copepodite stages were dominant: C4 made up nearly 30%, C5 over 45% and C6 20% of the total population. Later in winter, the abundance of adults decreased. Possible reasons for this could include mortality or advection.

C. propinquus exhibited a similar age structure to that of *C. acutus* but the latter was more advanced by one copepodite stage. In summer, early juveniles of *C. propinquus* were dominant, while adults constituted less than 20% in December and 3% in January. Later in the season, the dominance shifted to the older copepodite stages and adults representing the new generation. In contrast to *C. acutus* adults, which disappeared in mid-summer, *C. propinquus* adults were found throughout the whole sampling period. Furthermore, the continuous presence of early juveniles, (C2 and C3 during June made up 15% of the total population) suggested that the developmental time per stage is longer in *C. propinquus* than in *C. acutus*, but on the other hand *C. propinquus* may begin its reproductive cycle later than *C. acutus*. During winter, late stages were dominant: the total population included about 58% of C5 in June, and of C5 62% in July; adults were increasing in number.

In December, the population of the *R. gigas* was dominated by C5 (35%) and adults (28%); less than 5% of the population consisted of early juveniles (nauplii, C1, C2). But a month later, in January, the population was dominated by nauplii (40%) and the youngest copepodite stages (C1, C2), although adults were still present (more than 10%).

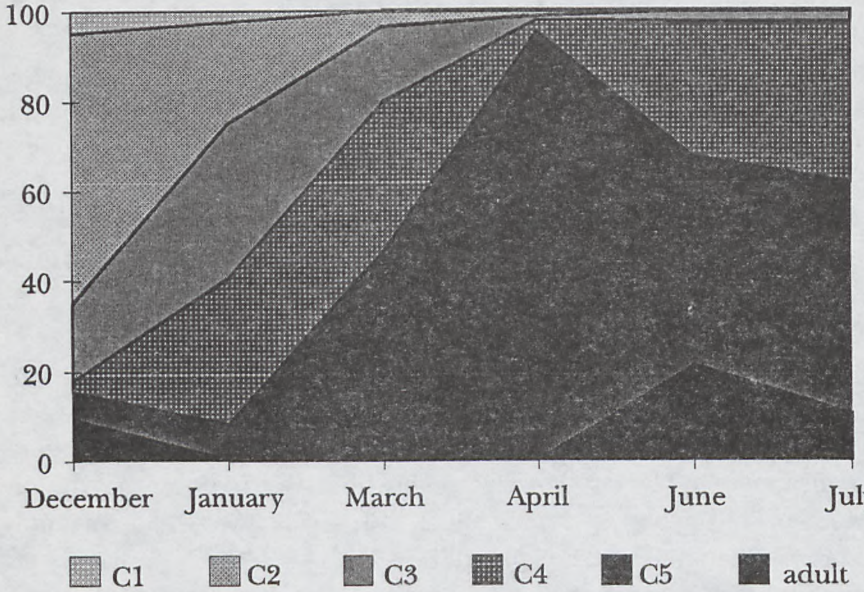


Fig. 2.1 *Calanoides acutus* population structure (%) in Croker Passage during 3 austral seasons

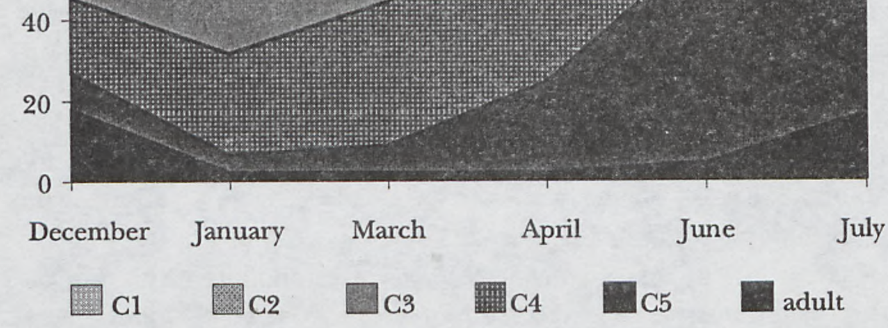


Fig. 2.2 *Calanus propinquus* population structure (%) in Croker Passage during 3 austral seasons

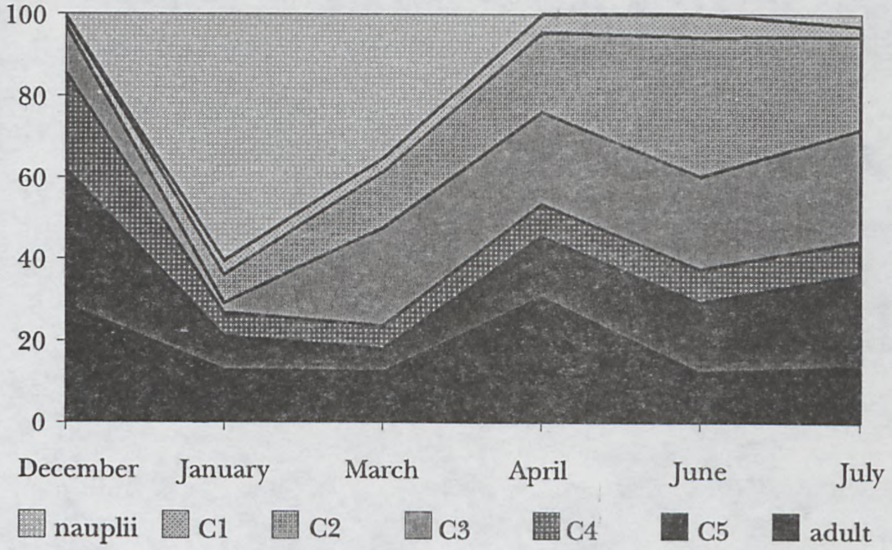


Fig. 2.3 *Rhincalanus gigas* population structure (%) in Croker Passage during 3 austral seasons

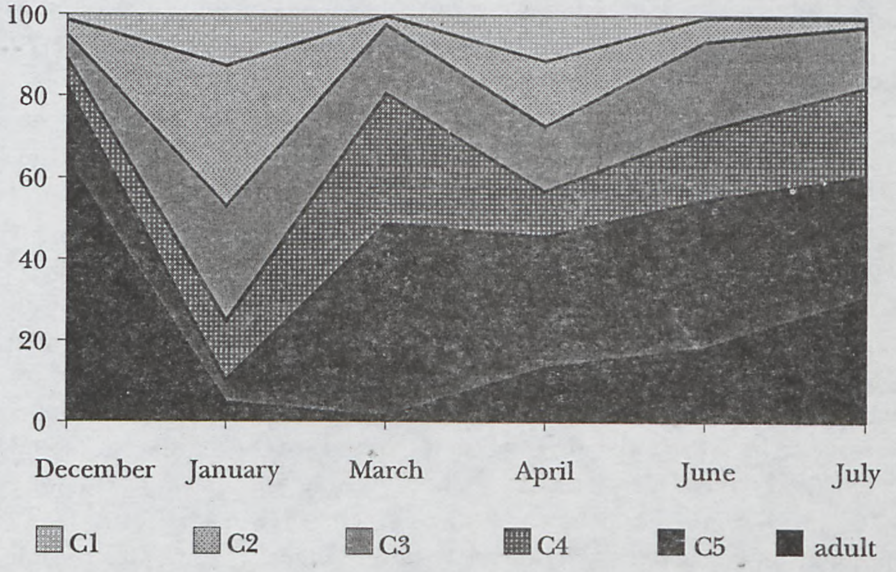


Fig. 2.4 *Metridia gerlachei* population structure (%) in Croker Passage during 3 austral seasons

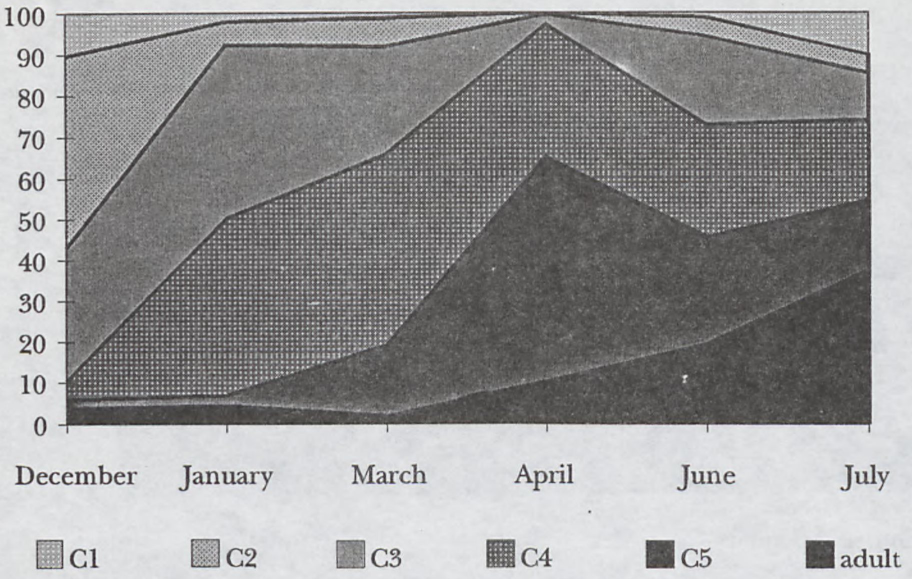


Fig. 2.5 *Euchaeta antarctica* population structure (%) in Croker Passage during 3 austral seasons

By early autumn, in March, the new generation had increased to such an extent that C2 and C3 (40%) were now dominant. Adults of *R. gigas* were present during the whole sampling period in numbers greater even than those of *C. propinquus.*

In winter, the population of *R. gigas* was represented by the new generation – nauplii (< 3%) and C1–C3 (*ca.* 65%); the overwintering generation was in the minority. By July C3, C5 and adults had increased in number.

The research of 3 sampling seasons proved that the population of *M. gerlachei* consisted of two generations. In mid-December the bulk of this population was dominated by older stages, mainly adults (62%). By the end of January, the older copepodite stages had practically been replaced by juveniles of the new generation (C1 – 11%, C2 – 47%, C3 – 28%). In autumn (March, April), similar changes in the population structure of *M. gerlachei* were observed. In April, the proportion of older stages (mainly C5 and adults) and early ones were the same (both 45%). Spermatophores were only noted in December and at the end of April. In winter the majority of the population consisted of significantly older stages. During this period the numbers of adults increased with the input from the growth of younger stages. There were two peaks of C1 abundance – in January and April, which was evidence of a multiple spawning period.

In contrast to *M. gerlachei*, the population structure of *E. antarctica* has only one generation. Almost 95% of the summer population was represented by the new generation (C1–C3) with C2, C3 predominant in December and C3, C4 in late January. In autumn (March 1988) the age structure was dominated by C4 (45%), in mid-April, 6 weeks later, by C5 (54%). At the beginning of the winter sampling, in June, the older stages (mainly C4, C5 and adults) made up more than 70% of the population. By July, not only had the relative abundance of C4, C5 and adults changed slightly, and the density of adults increased significantly (almost twofold), but the youngest copepodite stages (mainly C1) of the new generation were appearing as well.

5. Diel vertical stage distribution

The seasonal diel vertical migrations of all stages of these 5 copepod species are shown in Figs. 3.1–5.

In summer (December) the day/night distribution of the early stages of *C. acutus* were similar. They were concentrated close to the surface. However, the day/night distribution of the older stages was different. C5 and females (<10 ind. m^{-2}), found at greater depths at night, appeared to migrate during the day. C1–C3 occurred in the upper 100 m, very few adults were still below 400 m. In April no early stages were present except for a few C3, 83% of them in the 0–50 m layer. The dominant stage was C5, with more than 1000 ind. m^{-2} in the deepest layer. Abundance increased logarithmically from the surface to its greatest level near the bottom. The first appearance of adult females was noted below 500 m. In winter, as in late autumn, no C1 or C2 were present, and C3 and C4 were found higher up than C5 and adults. The number of C3 was below 100 ind. m^{-2}. The density of C4, C5 and females was about 1000 ind. m^{-2}, while that of males was much less, about 10 ind. m^{-2}. C3 and C4 exhibited slight daytime upward migration; C5 and adults were less active.

The pattern of day/night stage distribution in *C. propinquus* was similar to that of *C. acutus*, but in summer (December), in contrast to the latter, the population of *C. propinquus* lay deeper at night. Males and females of *C. propinquus* were also present in the upper 100 m layer. Abundance of all stages and at all depths were very low (<10 ind. m^{-2}). In autumn (April), the abundance of *C. propinquus*, especially of C2–C4, increased tenfold, and the population remained above 300 m both by day and by night; females, however, were found below 500 m. C5 and C6 stages were still at a very low abundance (*ca.* 10 ind. m^{-2}). From autumn to winter dominance within the population shifted from C4 to C5, the density of females increased tenfold and males appeared. In June, by day, the *C. propinquus* population remained close to the surface, while at night all stages avoided the 0–50 m layer.

The age structure and the day/night stage distribution of *R. gigas* seemed to be more variable than that of *C. acutus* or *C. propinquus* (Figs. 3.1–3). In December *R. gigas* was dominated by the overwintering stages – C4, C5 and adults, which ascended to the surface layer by day like *C. propinquus*, but the majority of C4 and C5 remained at middle depths. Spawning took place in the upper 200 m layer, where the youngest stages, females and a few males occurred. In autumn, all stages except females (<10 ind. m^{-2}) were present in very low numbers, *ca.* 10 ind. m^{-2}. The early copepodites (C1–C3) were found at shallower depths than the oldest (C5 and females). In winter, the age structure seemed especially variable. Two generations were present. The new one, with dominant C2 and C3, was located above 500 m, preferring the euphotic zone by day; the old generation avoided the surface and occurred mostly below 450 m.

The seasonal diel vertical migration of all stages of *M. gerlachei* is illustrated in Fig. 3.4. In December, all stages were present, but at a relatively low abundance. No significant differences in day/night distribution of early copepodites were noted but the oldest, with the exception of males, appeared to be close to the surface at night. At the end of January, by day, the youngest stages – C1–C3 (72%) as well as C4, C5 and adults occupied the 200–500 m layer. At night all stages, including the males, ascended to the upper layer, while by day, all stages except C5 avoided the layers above 100 m. In March, a small fraction of the main cohort (C3–C5) and females ascended 100 m higher at night than by day, unlike C1 and C2 . In April, no evident differences were observed in the dispersion of juveniles and adults, but the whole population lay closer to the surface than in the previous month and C1, C2 seemed to be more active than in March, moving up to the surface at night. In winter the whole population, including males, rose to the top layer, but a few of the youngest stages remained near the surface. None of the stages exhibited any distinct daily migratory movements. During the 3 study seasons males always stayed deeper than females and their abundance increased with depth.

The age structure of *E. antarctica* differed from that of the other species. In summer its population was almost exclusively represented by the new generation, occurring below 100 m. Diel migrations were not observed. At the beginning of March, late juveniles evidently migrated, unlike the youngest copepodites, which remained in the same position by day and by night. In April the daily migrations seemed to be less pronounced. The abundance of the later stages increased with depth, except for a few C1, C2 (< 100 ind. m^{-2}) which were found mostly above 300 m. Spawning began during this month, the abundance of males and females was very high: there were

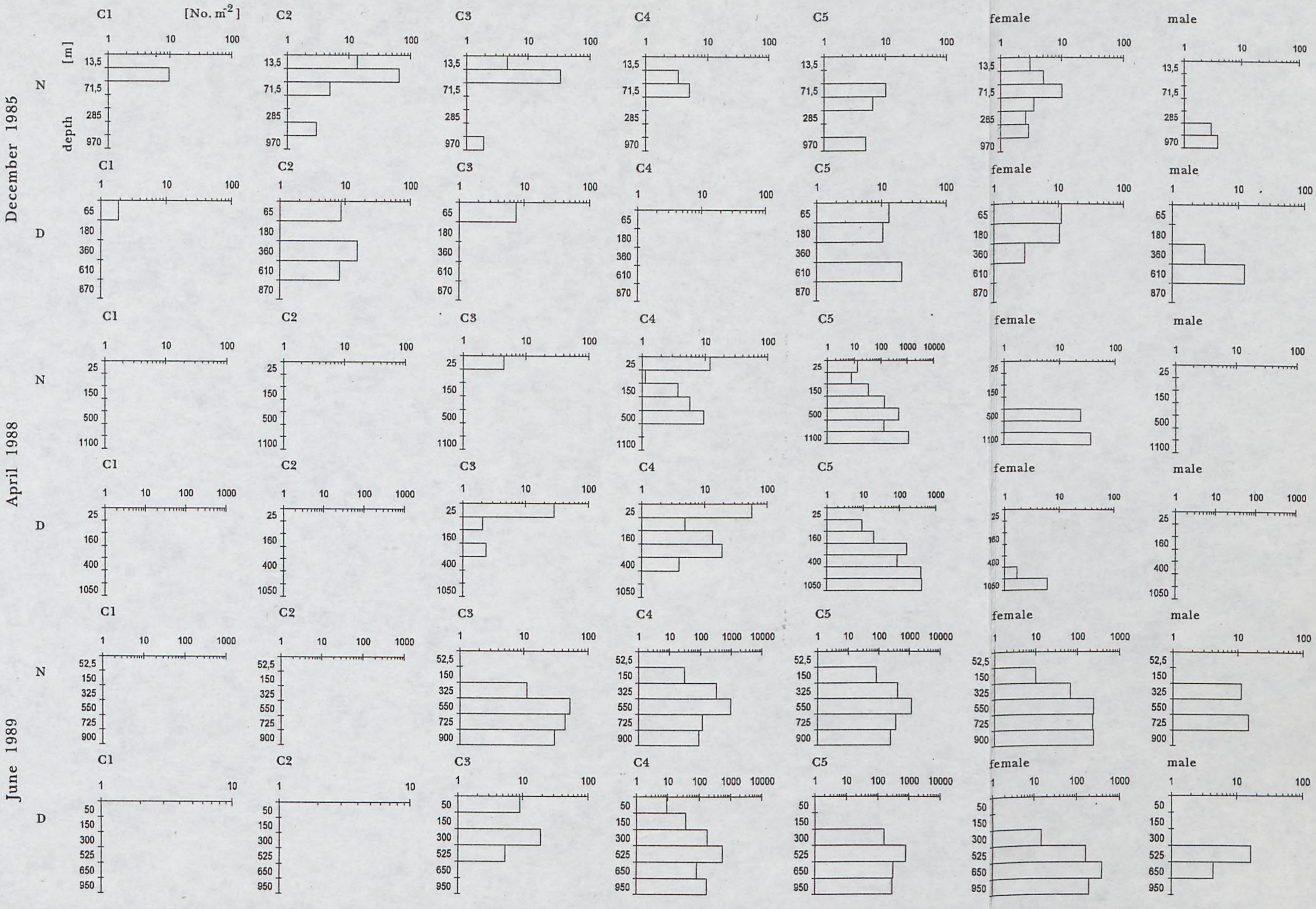


Fig. 3.1 Diel changes in stage-abundance distribution (ind. m^{-2}) of *Calanoides acutus* in Croker Passage during 3 austral season (N = night; D = day)

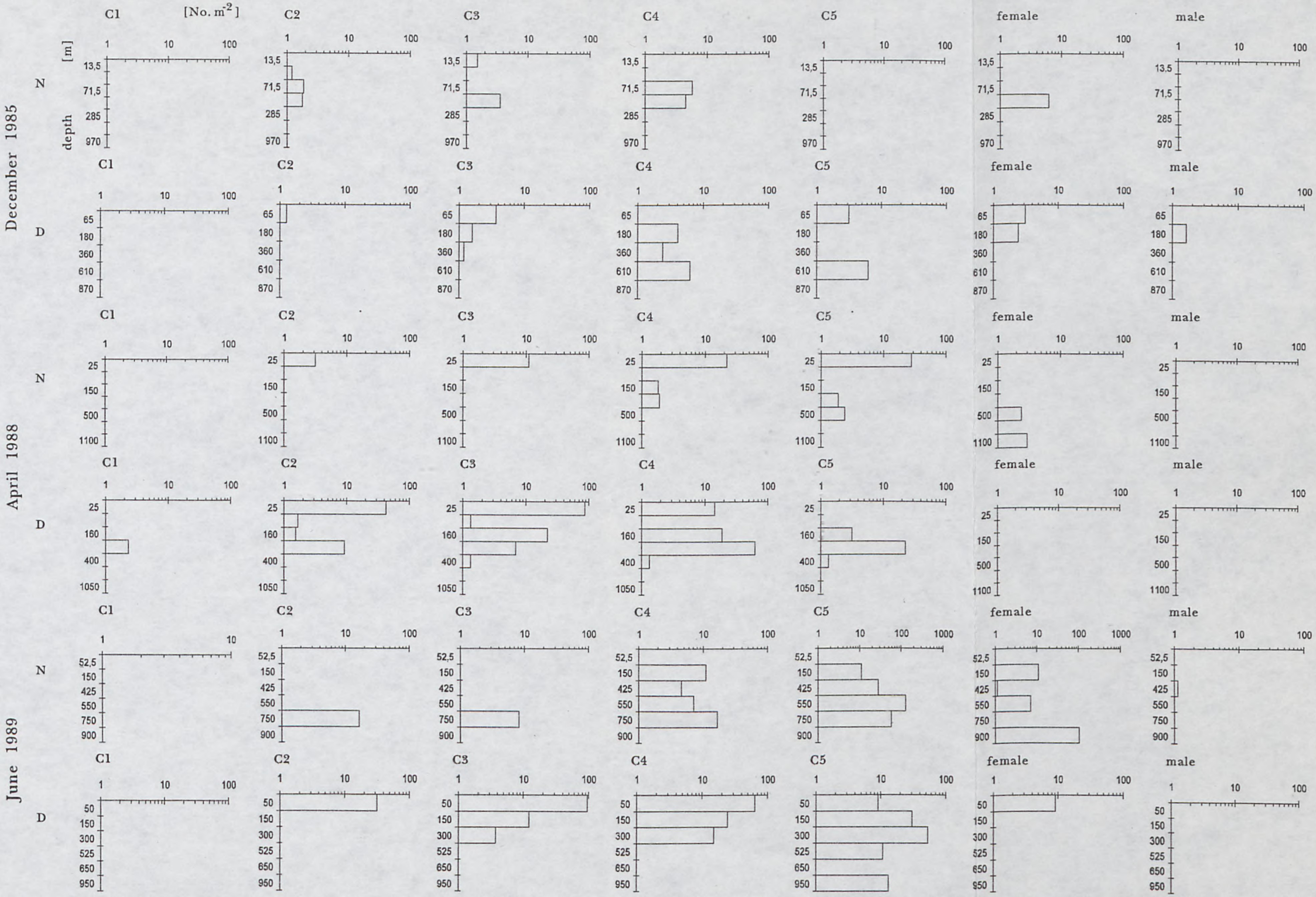


Fig. 3.2 Diel changes in stage-abundance distribution (ind. m^{-2}) of *Calanus propinquus* in Croker Passage during 3 austral season (N = night; D = day)

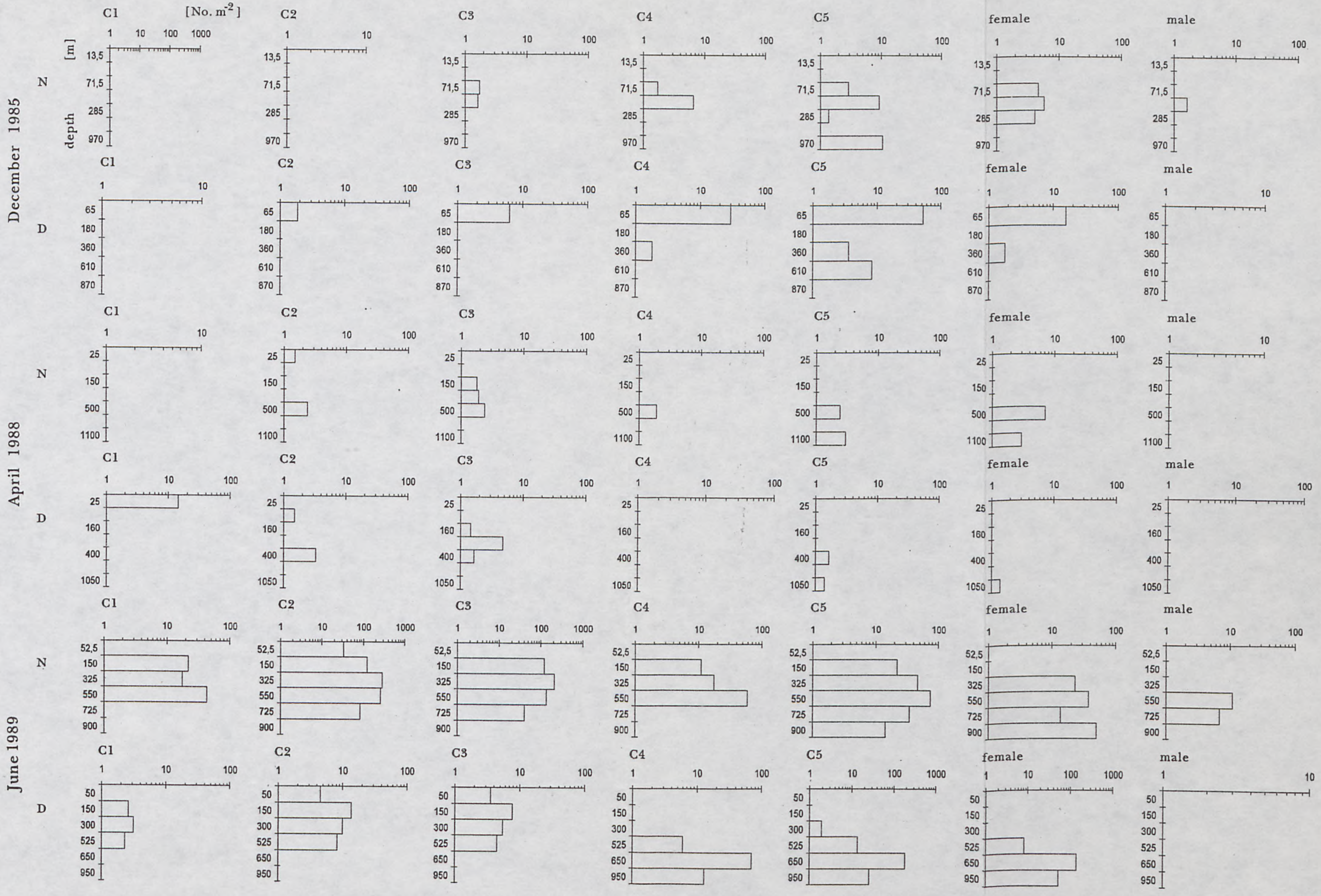
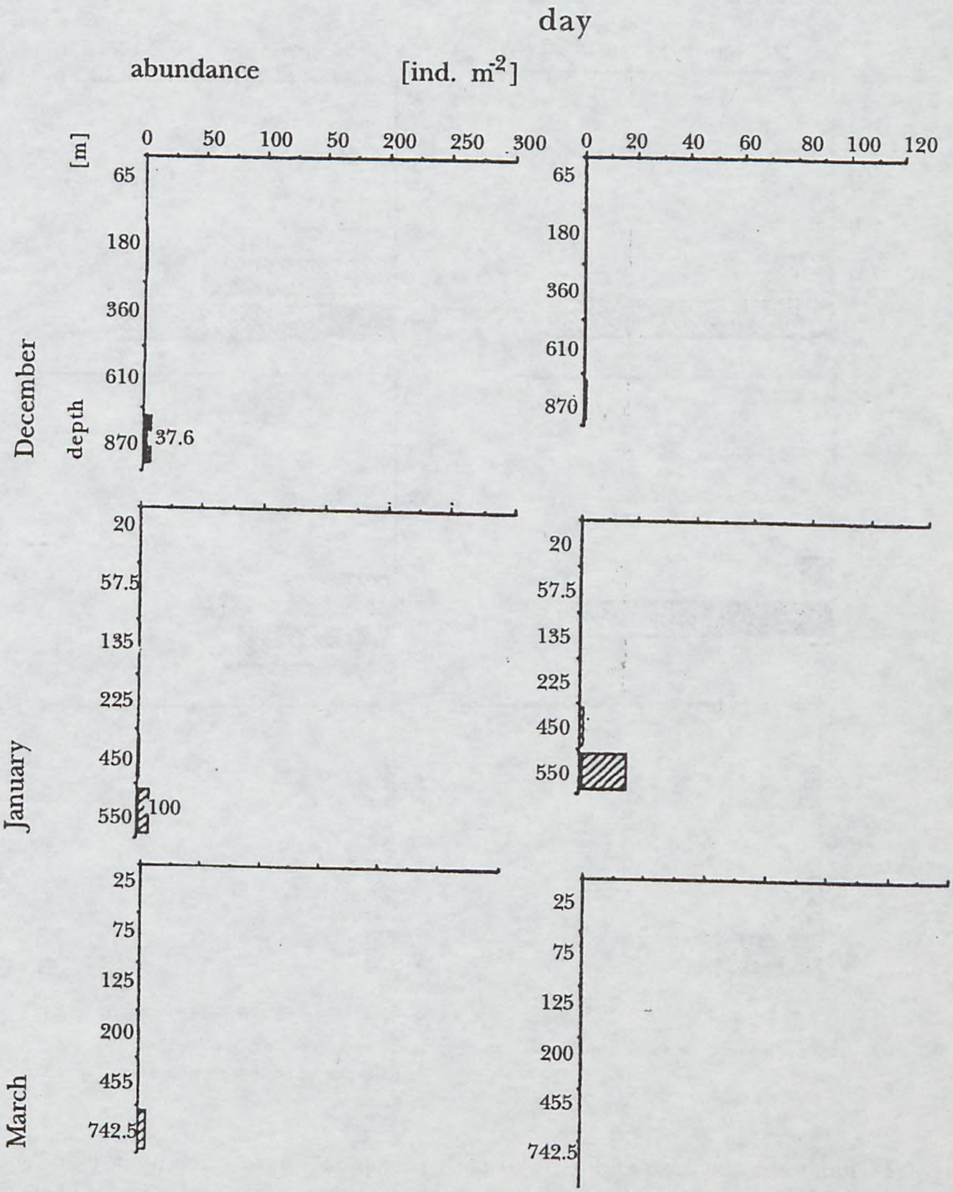


Fig. 3.3 Diel changes in stage-abundance distribution (ind. m^{-2}) of *Rhincalanus gigas* in Croker Passage during 3 austral season (N = night; D = day)

Fig. 3.4 Diel changes in stage-abundance distribution (ind. m^{-2}) of *Metridia gerlachei* in Croker Passage during 3 austral seasons (N = night; D = day)

Fig. 3.5 Diel changes in stage-abundance distribution (ind. m^{-2}) of *Euchaeta antarctica* in Croker Passage during 3 austral seasons (N = night; D = day)


day
abundance
[ind. m-2]
depth [m]
0
50
100
50
200
250
300
0
20
40
60
80
100
120
December
65
180
360
610
870
37.6
65
180
360
610
870
January
20
57.5
135
225
450
550
100
20
57.5
135
225
450
550
March
25
75
125
200
455
742.5
25
75
125
200
455
742.5

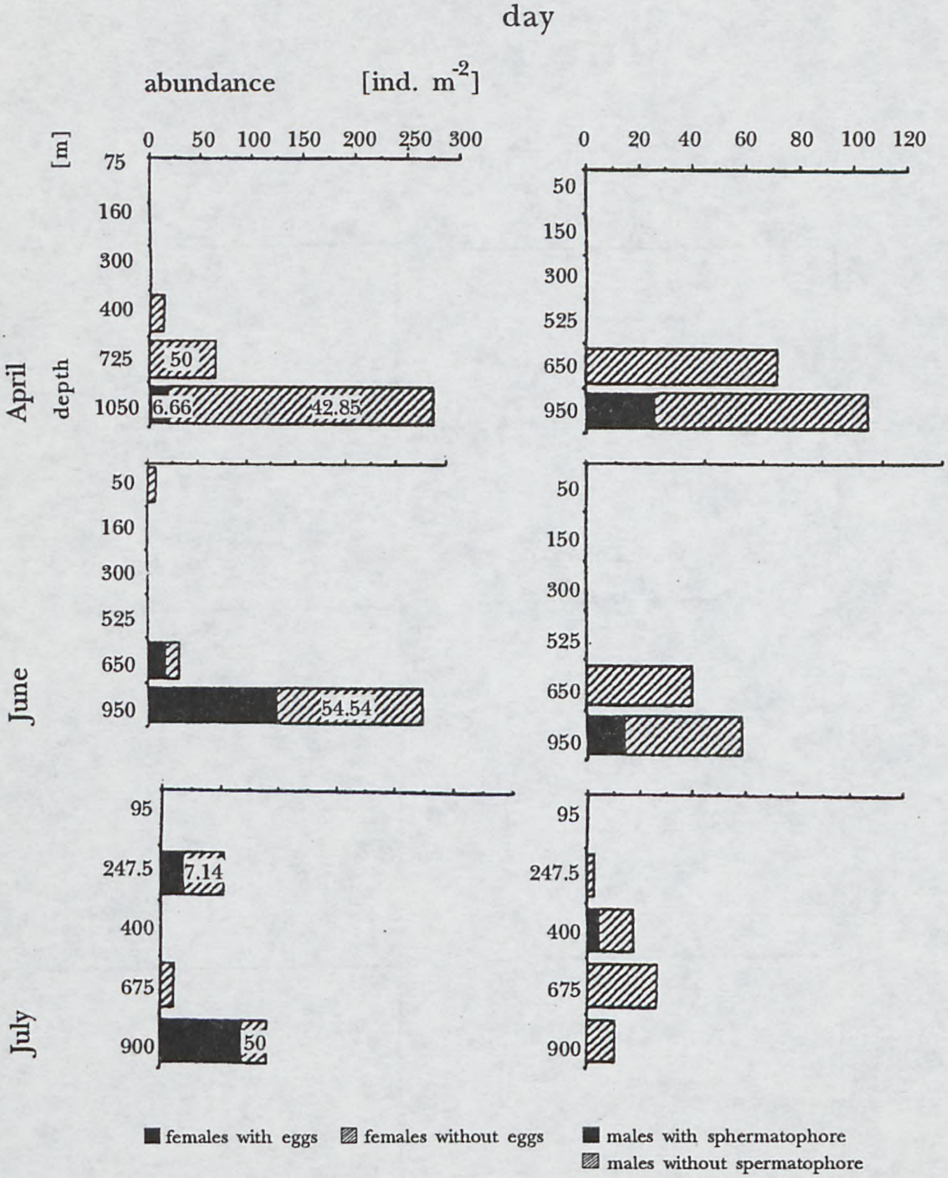
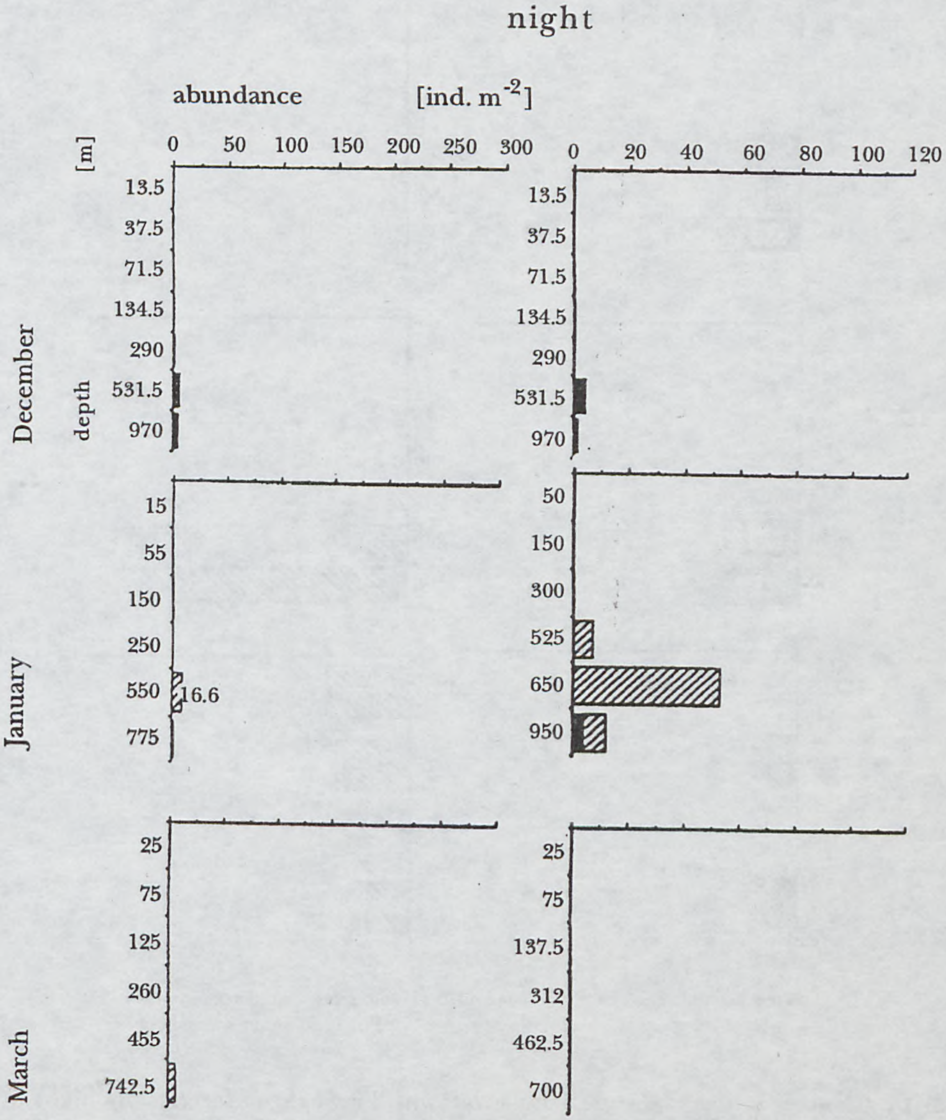


Fig. 4.1 Changes in the male and female ratio of *Euchaeta antarctica* by day in Croker Passage during 3 austral seasons (ind. m^{-2}; numbers (%) of spermatophores)


night
abundance [ind. m^{-2}]
0 50 100 150 200 250 300
0 20 40 60 80 100 120
depth [m]
December
13.5
37.5
71.5
134.5
290
531.5
970
January
15
55
150
250
550
775
16.6
50
150
300
525
650
950
March
25
75
125
260
455
742.5
25
75
137.5
312
462.5
700

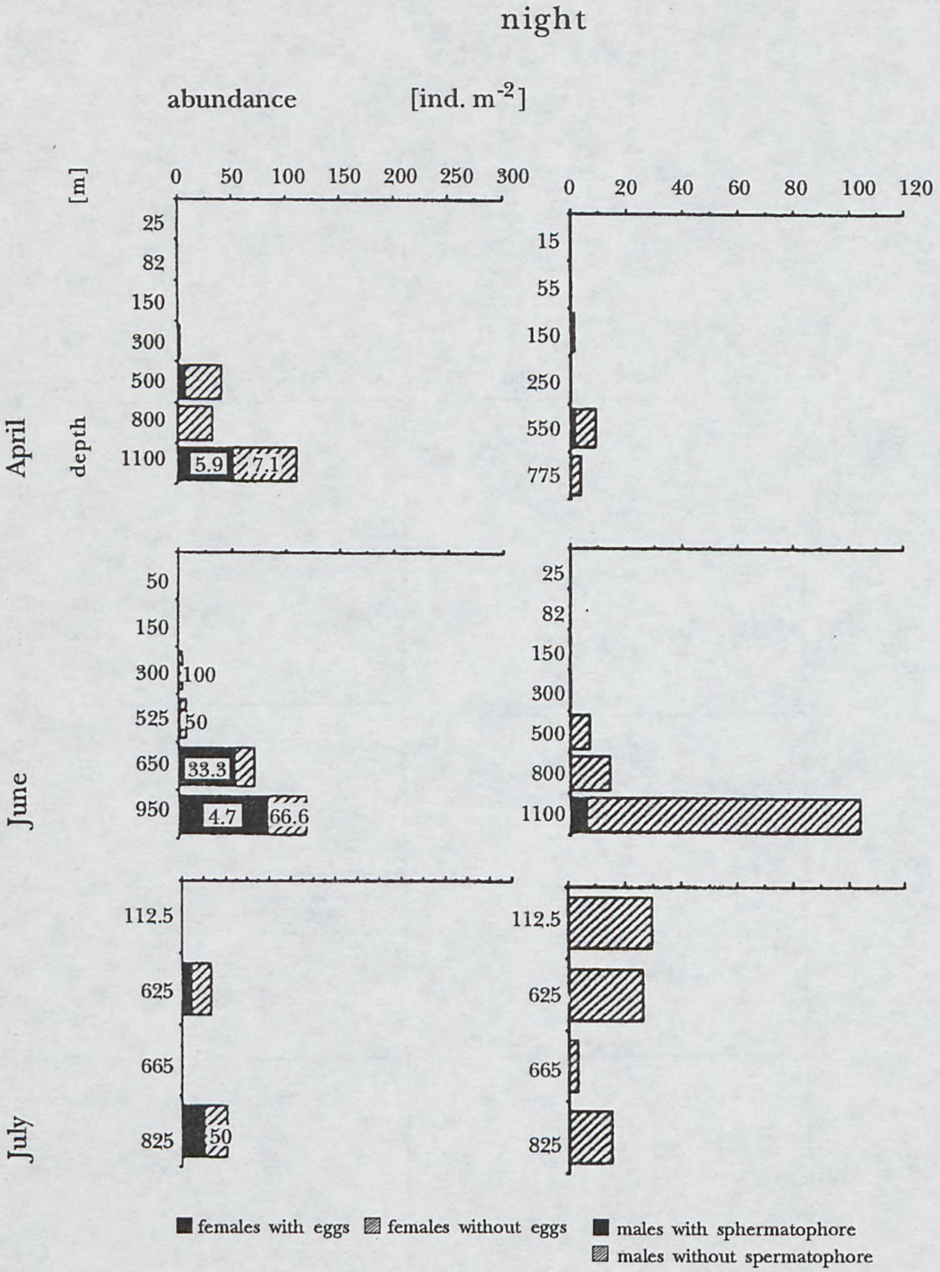


Fig. 4.2 Changes in the male and female ratio of *Euchaeta antarctica* by night in Croker Passage during 3 austral seasons (ind. m^{-2}; numbers (%) of spermatophores)

ca. 150 male ind. m^{-2} and twice as many females. 50% of females were found with eggs and 25–33% of the males had spermatophores (Figs. 4.1–2). At the beginning of winter, more than 50% of females were found with egg sacs and spermatophores, 33% of the females were carrying spermatophores, and more than 50% of males had spermatophores. At this time the early stages were located at shallower depths than the later ones and displayed a tendency to migrate to the upper zone at night, while the deepest layer was occupied by males and females. It should be added that males, usually living in the deepest water, spread into the whole water column at the end of July (Fig. 3.5). During the following winter sampling period the number of females with egg sacs decreased significantly and only one male with spermatophores was found (Figs. 4.1–2).

6. Discussion

The vertical and horizontal distribution of these copepods is a reflection of their population structure. The spatially and temporally varying numbers and age structures of *C. acutus*, *C. propinquus*, *R. gigas*, *M. gerlachei* and *E. antarctica* in Croker Passage point not only to interspecific differences but also to intrapopulational variations.

The most numerous of the phytophages, *C. acutus* (Żmijewska and Yen, 1993), was distinctive in that its individual development reached a relatively advanced stage.

In early summer, *i.e.* the first 10 days of December, the *C. acutus* population was concentrated in the top 100 m layer and was bimodal. The abundance of phytoplankton at this time (my own observations) must have provided excellent feeding for the females, as less than two weeks later the population was dominated by the youngest copepodites (C2) of the new generation. The relatively small proportion of C1 in the population, not only of *C. acutus* but of the other species too, could have been due to the net mesh being too large (150 or 200 μm) to retain the smallest developmental stage. The remnants of the winter population, represented by the oldest copepodite stage and adults, stayed in deeper waters. In December a significant proportion of males (2.26–1.84%) were found to be concentrated below 300 m, although some were netted in surface waters, as happened during a similar period in Bransfield Strait (Żmijewska, 1985). The literature only sporadically records the presence of *C. acutus* males; even Andrews (1966) makes no mention of them in his extensive monograph. The male of *C. acutus* was first described by Vervoort (1965); the presence of males was subsequently reported by Vladimirskaya (1978) in the Scotia Sea. More reports of males have appeared recently. At the end of winter, Marin (1988b) recorded over 60% males in deep hauls from some stations around

South Georgia. Schnack *et al.* (1991) have also recorded males in the Weddell Sea: they were concentrated in the 500–1000 m layer, but were found in very early spring. In Croker Passage males had disappeared by the end of January, the significance of the dominant C1 and C2 fell by 1/3 in favour of C3 and the development rate from C2 to C3 was 0.9% of the hemipopulation per 24 h. Adult mortality was estimated at 0.2%. In early autumn the *C. acutus* population was polymodal with a predominance of C4 and C5 copepodite stages, and at this time the most advanced developmental stages were beginning to leave the surface waters. By April, when surface water temperatures had fallen to below zero, 95% of the population consisted of C4 and C5 stages and the C4–C5 development rate peaked at 1.5% per 24 h. The overwintering population inhabited meso- and bathypelagic waters; females comprised, an average, *ca.* 10% and males *ca.* 1.5% of the population. The C5 – adult development rate was estimated at *ca.* 0.3% per 24 h.

These data suggest that *C. acutus* has a one-year life cycle. The presence of males and females in the winter population and the first signs of their death, observed by me in late July, appear to indicate that fertilization begins already in winter in warm, deep waters, and that it is a protracted process – the presence of males and females until the end of January is evidence of this. Marin (1988a) and Schnack-Schiel *et al.* (1991) express the view that fertilization in *C. acutus* must take place in winter, during a very short period of time, since the males, which do not possess any mouthparts (Vervoort, 1951; Bradford, 1988), cannot live very long. In winter, the first fertilized females produced eggs, which remain in a dormant state until the spring. The egg dormancy phenomenon has been described by Zilloux and Gonzalez (1972) in Arctic species. Huntley and Escritor (1991) are of the opinion that spawning of *C. acutus* in the vicinity of the Antarctic Peninsula must occur earlier than Andrews (1966) believed, *i.e.* in November.

The present results from Croker Passage, as well as earlier ones (Voronina *et al.*, 1978), indicate that in winter individual development continues, whereas Schnack *et al.* (1991) consider that it goes into a diapause, as is the case with Arctic copepods of the genera *Calanus* or *Neocalanus* (Conover, 1988).

The population dynamics of the second phytophage species, *C. propinquus*, are more varied. In summer it was more widely dispersed in the 1000 m water column than *C. acutus*. While C2 stages were dominant in both populations, the proportion of adults remained high, twice as high as *C. acutus*, in fact; moreover, males and females were recorded in early autumn. With the elapse of time, the developmental stages ceased to be synchronic: *C. propinquus* fell behind in its development by a whole copepodite stage. Unlike

C. acutus, it remained in surface waters in autumn. In winter, much of the *C. propinquus* population descended to deeper waters but a part remained in the upper layers. The development rate from C5 to adult, estimated at 0.83% of the hemipopulation per 24 h, was much higher than during the analogous period for *C. acutus*.

According to Voronina (1975, 1977, 1984), interzonal species overwinter at depths below 500 m, and the females are fertilized there. The winter distribution of *C. propinquus*, in Croker Passage was not so unequivocal: there were two population peaks in the water columns. Marin (1988a,b) observed that in winter *C. propinquus* tends to inhabit the entire water column and thus questioned whether this species undergoes any ontogenetic migrations at all. Vladimirskaya's (1978) winter studies revealed concentrations of this species in the 500–1000 m layer, but a few individuals were found near the surface. A similar vertical distribution in winter was described for *Calanus* species from the northern hemisphere (Hirche, 1983; Flaminger, 1985).

The summer population of *C. propinquus* is bimodal to a greater degree than that of *C. acutus*. The fact that adults were present for a longer time and exhibit no particular depth preference indicates that fertilization can also take place in the surface layer (Marin, 1988a,b; Atkinson, 1991).

At the same time, I believe that, like *C. acutus*, its life cycle is completed within the space of one year, even though the reproductive process begins later. This could continue right into early autumn, which would explain the presence of the large number of C3 stages in winter. On the other hand, it must be remembered that the relatively small numbers of *C. propinquus* require caution to be exercised in the interpretation of these results.

The largest of the copepods under discussion here, *R. gigas*, has a life cycle very different from those of the two species just described. In summer (December) more than 60% of the population is represented by the overwintering generation (C5, adult); the older generation inhabited deeper waters than the first copepodites of the young one, which made up no more than 5% of the total population. At the end of January the population underwent an abrupt transformation: it was dominated by the new generation, over 40% of which were nauplii. Adult mortality was high at roughly 1% per 24 h. Beyond any doubt, spawning took place in the upper layers, as it was here that the nauplii and the youngest copepodite stages were caught.

In autumn the *R. gigas* population left the Croker Passage, although the fact that a very small percentage of the population remained signifies its bimodal population structure, C3 stages being in the ascendancy.

In winter the population structure of this species was quite different. Initially, at the end of June, nearly 40% of the population comprised the youngest copepodite stages of the new generation, congregating above and below the 300 m isobath. C5 stages and adults of the overwintering generation made up nearly 30%, and in comparison with the summer population picture, the proportion of nauplii was small. The following month saw the entire population make evident progress in its development. Atkinson *et al.* (1992) noted representatives of the new generation in the upper parts of the water column and individuals of the preceding generation in the deeper water. In the region of the Antarctic Peninsula the proportion of the new generation was considerable already in May (Marin and Schnack-Schiel, 1993).

Winter spawning of *R. gigas* was first described by Ommanney (1936). Although Voronina (1970) questioned his results, later winter investigations in the Scotia Sea were to endorse them entirely (Voronina, *et al.*, 1978). The existence of two spawning periods in *R. gigas* was also suggested by Bradford (1971), who was of the opinion that summer spawning occurred in surface waters, whereas winter spawning took place in the deep waters once the summer generation had reached maturity. Marin (1988a,b) thinks it is highly unlikly that *R. gigas* has two generations in one growing season, and on the basis of his own researches postulates a biannual life cycle.

In summer, nauplii and the youngest copepodite stages were found in Drake Passage a month earlier (Żmijewska, 1985), in the Scotia Sea numbers of nauplii peaked in late November-early December (Atkinson, 1991), and in the Weddell Sea they were found in September and October (Bathmann *et al.*, 1993).

These data could be evidence for twice-yearly spawning in *R. gigas*, in summer and in winter. Wheather this applies to the same population cannot be answered unequivocally, because my studies were carried out in three separate years. A further aspect blurring the picture of the life cycle of *R. gigas* is the fact that it leaves the waters of high latitudes in autumn and returns there in winter. There is much to suggest that *R. gigas* is a very flexible species, and depending on the conditions in the two environments, mainly the abundance of food, may well spawn in summer and in winter; its readiness to spawn is usually demonstrated by the broad age spectrum of its populations. The following scheme of things seems possible: copepods of the summer generation spawn the following summer, those of the winter generation spawn the next winter. This hypothesis could be confirmed by studies at the genetic level.

This scenario for the life history of the three phytophages is based mainly on the food resources available in summer. In polar regions, the survival of every animal, not only as an individual but also as a species, regardless of its position in the trophic web, must exhibit a high degree of vitality, low mortality and a constantly high level of reproduction in the overwintering population.

My three-year studies in Croker Passage, as well as those of Jażdżewski *et al.*, 1982; Chojnacki and Węgleńska (1994), Menshenina and Rakusa-Suszczewski (1992), and Żmijewska and Yen (1993), have shown that *M. gerlachei* is one of the most numerous copepod species, and that it is present all the year round. The relatively insignificant temporal fluctuations in numbers indicate that this is a genuinely Antarctic species. The question arises how it is that *M. gerlachei* is able to maintain such large numbers, practically independently of the time of year. Could the factor determining the high numbers be diet and a high growth rate? Marin (1988b) believes that physical environmental factors play the deciding role, and that the availability or lack of food cannot be a factor limiting the numbers of copepods. It seems, however, that the types of food available must be a crucial factor in the life strategies of polar animals. *M. gerlachei* can survive on a very catholic diet. Being omnivorous, it finds sufficient nourishment in summer, when it feeds on phytoplankton (Schnack, 1985; Schnack *et al.*, 1985), in early spring, when it takes copepod eggs (Fransz, personal comm.), and in winter, when it turns to other animals, chiefly *Metazoa* (Hopkins, 1985a).

The following factors suggest that the life cycle of *M. gerlachei* differs from that of other copepods in Croker Passage: its vast numbers, the fact that throughout the study period the age structure of the population remained highly differentiated, and that the population was dispersed to varying degrees in the entire water column. The oldest individuals, especially the adults, concentrated in the deepest leyers, males occurring at greater depths than females. This is where fertilization must take place. Evidence for this are single female specimens with attached spermatophores – females in this state have never been caught in the surface layers. The youngest stages of the new generation were found in the middle depths. Females were the most active migrators. By contrast, it was the males that performed the longest diel migrations in winter. The separation of the various constituents of the *M. gerlachei* population, as in the other copepod species, is of great biological significance: it reduces competition for food, and at the same time indicates that their diets are different.

It may be inferred from the data obtained that at least two generations – a summer one and an autumn one – must exist at any one time. According to Vervoort (1965), *M. gerlachei* repreduces at the end of summer. Żmijewska observed spawning in Bransfield Strait in summer and in Admiralty Bay on King George I. (Żmijewska, 1987) at the end of winter (Żmijewska, 1992). In spring, it was mostly the middle copepodite stage (C3) that was most often caught in the eastern Bransfield Strait (Żmijewska, 1988). Kaczmaruk

(1983) reports a high proportion of the youngest stages (C1–C3) in the Weddell Sea in January and February.

These data incline one towards the conclusion that *M. gerlachei* is capable of continual reproduction, and hence its very large population.

Though not one of the most numerous of the Antarctic copepods, *E. antarctica* is, apart from *M. gerlachei* and *C. acutus*, significant constituent of the plankton biomass (Hopkins, 1985a,b) if only because of its size; the only larger species is *R. gigas*. *E. antarctica* prefers deeper water – our study confirmed this. As mentioned earlier, it is the surface layers in Antarctica that were most frequently trawled, where the highest concentrations of pelagic species are to be found. Smaller numbers of meso- and bathypelagic copepods must have been caught, and therefore underestimated.

My studies of seasonal changes in the dynamics of the distribution, migration and population structure of *Euchaeta antarctica* in Croker Passage indicate that this species has a unique life cycle. Population structure analysis shows it to have a single generation per year. Spawning must take place in winter in warm near-bottom waters, as is evidenced by the high proportion of males and females caught there, even though the first signs of reproductive readiness can be observed already in late autumn. In winter, adults were dominant at first, mainly females with egg sacs. Every third female had both eggs sacs and spermatophores (as many as 4–5), and males with spermatophores were also present. At the same time, the first copepodite stages of the new generation were being recorded. Later, at the end of July, the proportion of females with spermatophores declined, even though the overall proportion of adults continued to increase. By early summer (December) the population was dominated by the new generation with C2 prevalent, and by the end of January C3 and C4 were predominant. In autumn (March) C4 made up over 50% of the population, and a month later more than 60% of the population were C5. The rate of moulting was very high and the population was bimodal.

In the region of South Georgia, Ward and Robins (1987) found two generations of *E. antarctica*; the temperature there, 5° C higher than off the Antarctic Peninsula, may have been the cause. In lower latitudes spring begins earlier and the summer lasts longer; the metabolic rate increases logarithmically together with the abundance of food. In summer, when various kinds of food are present in abundance, metabolic processes proceed rapidly, but in winter, they slow down to a very low rate (Bamstedt and Tande, 1988).

In summer both adults and the youngest copepodites behave like typical predators: females feed on the copepodites of, *e.g. M. gerlachei*, the preferred size being 1200 μm. The younger developmental stages feed on smaller organisms, *e.g. Microcalanus pygmaeus* (Yen and Hosset, personal comm.). In autumn in Croker Passage, Hopkins (1985a) found *Oncaea* spp., *M. gerlachei* and remains of *Pelagobia longicirrata* in the diet of *E. antarctica.* In spring, in the southern Scotia Sea, Hopkins *et al.* (1993) reported finding mainly copepods in the gut of *E. antarctica.* In winter *E. antarctica* does not feed (Yen, personal comm.) At this time potential victims could be the final copepodite stages of *e.g. C. acutus* or *C. propinquus*, which as Halleberg and Hirche (1980) state, are not very mobile.

Like *M. gerlachei*, *E. antarctica* tended to perform seasonal migrations. The species generally displayed a preference for deeper waters. Older copepodite stages and adults became increasingly common with depth, with adults occupying the deepest layers; the youngest copepods were found in the highest layers of its depth range. Off South Georgia, Ward and Wood (1988) were unable to confirm that *E. antarctica* undergoes ontogenenetic migrations. A characteristic element of the behaviour of this species are its diel migrations (Hardy and Gunther, 1935; Mackintosh, 1937; Chojnacki and Węgleńska, 1984; Hopkins, 1985b). In Croker Passage these copepods swam up to higher layers at night, although this vertical migration was not as intense as in *M. gerlachei.* The most active forms were the adults, the youngest stages less so, while the intermediate stages did not change their position in the water column to any extent. In winter, these diel migrations ceased, which suggest that this predator is then much less active. For its egg production *E. antarctica* makes use of wax ester lipids, but to produce its blue coloration triacylglycerides are essential (Yen and Hosset, personal comm.), the same ones that the winter-active *C. propinquus* stores (Schnack-Schiel *et al.*, 1991). Even though its life activities in winter are less intensive, *E. antarctica*, like the other species discussed in this paper, does not go into diapause or an arrested development phase; evidence for this is its continuing development during this time.

7. Conclusions

The life span of *C. acutus* is less than one year while *C. propinquus* can live for more than a year. The population structure of *R. gigas* shows that this species has two generations per year. Multiple generations are noted for *M. gerlachei*, while *E. antarctica* has a single reproductive peak.

The life cycles of the herbivorous copepods are staggered. *C. acutus* is the first to reproduce; it is followed by *C. propinquus* and *R. gigas.* The time difference separating the copepodite stages of the various species is maintained throughout their life cycles, *e.g.* when *C. acutus* is at stage C5, *C. propinquus* is at stage C4.

The life histories of the five copepods analysed seem to be closely connected with food resources. Potential competition for food resources among these species is minimized by differences in diel and seasonal migration, and by occupancy of different depths not only by the species as a whole but also by their copepodite stages.

In early summer the phytophages inhabit mainly the top 100 m layer. The new generation of all three species resides just below the surface; the overwintering generation occurs below them: first the final copepodite stages and adult females, and deepest of all, the males (not *C. propinquus*). The oldest copepodite stages of *C. acutus* are the first to begin the autumn migrations, and they are followed by *C. propinquus*. *R. gigas* leaves the coastal waters of the Antarctic Peninsula altogether. In winter *C. propinquus* inhabits the surface water, especially during the day, and *C. acutus* occurs below it. The new generation of *R. gigas* also occurs in the surface water; the previous generation of this species occupies deeper water.

The youngest stages of *M. gerlachei* reside in the middle depths; the oldest individuals, especially the adults, concentrate in deeper layers, with males occurring at greater depths than females; this is where fertilization must take place.

E. antarctica displays a preference for bathypelagic waters: the older stages and adults occupy the deepest layers, while the youngest copepodites occur in the highest layers of its depth range.

Continuous progression through the lifestages indicated that these copepods did not go into diapause during the winter.

Acknowledgments

I thank the officers and crew of r/v ‘Polar Duke’ and Dr. R. P. Hassett and J. Finn for their willing help at sea. I also thank the personnel at Palmer Station for providing good working conditions. My special thanks are extended to Dr. J. Yen for her patience in assisting me in my work and for her very useful advice and comments. I am very grateful to Professor S. Rakusa-Suszczewski for his comments on the manuscript.

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