

Winter distribution and overwintering strategies of the Antarctic copepod species *Calanoides acutus*, *Rhincalanus gigas* and *Calanus propinquus* (Crustacea, Calanoida) in the Weddell Sea

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Abstract. During the Winter Weddell Gyre Study in September–October 1989, the horizontal and vertical distribution, stage composition and feeding condition of the three antarctic copepod species *Calanoides acutus*, *Rhincalanus gigas* and *Calanus propinquus* were studied. The data indicate that *C. acutus* and *R. gigas* have the bases of their distributional ranges (sensu Makarov et al. 1982) in the Antarctic Circumpolar Current (ACC) and in the Warm Deep Water (WDW) entering the Weddell Gyre (WG). *C. propinquus* lived mainly in the cold WG south of the ACC. *C. acutus* overwintered mainly in the WG as stage IV copepodites (C). The species mainly inhabited the layers below the T_{\max}° stratum and down to 2000 m, but C V and females occurred slightly higher than C III and IV. Males prevailed over females and were confined to a rather narrow layer between 500 and 1000 m. Feeding experiments suggested all deep-living stages to be resting. However, if this species spawns in late autumn the younger C I–II can stay in the Winter Water (WW). *R. gigas* inhabited mainly the T_{\max}° stratum. In the eastern part of the WG, *R. gigas* breed in the WDW in autumn and hibernate as C I–III and C V–VI in the first and second winter, respectively. In the ACC zone, however, its life cycle is different and winter breeding of overwintered adults occurs. Most of the *C. propinquus* population overwintered in the WG as C III–V, inhabiting the WW. In the upper water layers in the interior of the WG, C III dominated with upto 18,000 individuals $1,000\text{ m}^3$. Shallow living *C. propinquus* were in the active, feeding state. Persistence of active feeding zooplankton populations in the WW of the WG can be an important factor influencing processes of phytoplankton development and the particle flux.

in their stage compositions when sampled in the spring to autumn seasons. These differences are subject to conflicting interpretations; they result either as an asynchronism of principally similar life cycles (Voronina 1970, 1984) or as a result of quite different life cycles (Marin 1988a). Apart from this, the stage compositions vary considerably in different types of Antarctic waters (Vladimirskaya et al. 1988; Marin 1987; Makarov et al. 1990; Schiel 1991). The overwintering strategy is a key factor in the life cycle of a polar zooplankton species which should be understood before the models of life cycles are suggested and tested. However, observations on Antarctic copepod populations under winter sea-ice are limited. Some were confined to coastal areas (Fukuchi and Sasaki 1981), and in those made in the oceanic waters (Fransz 1988; Hosie and Stolp 1989; Schnack-Schiel et al. 1991) the depth of sampling rarely exceeded 1000 m which could be insufficient for covering the whole vertical range of interzonal copepod species.

The international project Winter Weddell Gyre Study (WWGS) 1989 (Augstein et al. 1991) provided an opportunity to obtain large-scale data on the winter distribution and population composition of the common Antarctic calanoid species. These data and the results of feeding experiments performed during this project allows us to reappraise the overwintering strategy of *Calanoides acutus*, *Calanus propinquus* and *Rhincalanus gigas* in the Weddell Gyre. Furthermore, WWGS'89 was the beginning of a 4 year program to study water mass transformation based on salinity-temperature-depth (CTD) sections across the Weddell Sea (Fig. 1) and moored current meter measurements. These data provide hydrographical information with longer time periods than those collected during the WWGS'89 cruise (Bathmann et al. 1992).

The antarctic species of Calanidae (e.g. *Calanoides acutus* Giesbrecht and *Calanus propinquus* Brady) and Eucalanidae (*Rhincalanus gigas* Brady) which commonly form the bulk of mesozooplankton biomass (Voronina 1984) differ

Materials and methods

Zooplankton sampling

The Plankton samples were collected on board RV *Polarstern* and *Akademik Fedorov* in September–October 1989 (Augstein et al.

1991). Zooplankton sampling was carried out along two transects by RV *Polarstern* (northwest-southeast PF-1 transect across the Weddell Gyre; south-north PF-2 transect between the Georg-von-Neumayer station and South Africa) and three transects by RV *Akademik Fedorov* (AF-1 from South America to 68°S 20°W; AF-2 from 68°S 20°W to about 66°S 0°W and AF-3 from there to 59°S 15°W). The positions of stations and exact dates for particular transects are shown in Fig. 1.

Multinet and Bongo net (both 0.25 m² mouth opening, 100 µm mesh size) were towed vertically on board RV *Polarstern*. Five strata, chosen according to the vertical structure of the water column, were hauled in the case of Multinet tows. The maximum depth of the tows varied from 1000 to 3000 m (Augstein et al. 1991). Vertical tows of Bongo net (0.25 m² mouth opening, 300 µm mesh size) and sometimes of Juday net (0.1 m² mouth opening, 170 µm mesh size) were performed on board RV *Akademik Fedorov* down to 500 or 1000 m depth. In the samples collected, all copepodite stages of *C. acutus*, *C. propinquus*, *R. gigas* were counted as well as the nauplii of the latter species.

Experiments for net comparison were made (Spiridonov, unpublished). Six stations (Sta. PS 151, 154, 156, 158, 161, 171) were used for comparing Multinet and Bongo net on board *Polarstern*. When 9 paired *t*-test was performed, comparing stages in a species, mostly non-significant differences in log-transformed numbers of all 3 species were observed (*t* values in a range of 0.03–2.67). Significant differences were found for *C. propinquus* in Sta. 151 (*t* = 3.22, *P* 0.05), Sta. 156 (*t* = 3.95, *P* 0.05) and Sta. 161 (*t* = 5.97, *P* 0.01) and in the latter station also for *C. acutus* (*t* = 2.92, *P* 0.05). The comparison of Bongo and Juday nets on board *Akademik Fedorov* (three pairs of the consequent tows) showed that the catching efficiency of the latter is smaller, approximately by a factor of 1.1–1.5; however, the proportions of different copepodite stages in the catches of both nets did not differ significantly. One series of parallel tows for intercomparison of the *Polarstern* and *Fedorov* Bongo nets was made (St. PS204 and AF194). The numbers of copepodites were somewhat lower in the case of the *Fedorov* tows, but the percentages of stages in all species were similar. Thus, the nets used for this study were suitable to obtain a general picture of the horizontal distribution and stage composition of the calanoid species investigated in the Weddell Gyre in winter 1989.

Feeding experiments

For feeding experiments, copepods from the upper 100 m water column were captured with a Ring net (200 µm mesh size) with an opening area of 1 m² and a closed cod end (5 l volume) to reduce filtering stress for the animals. The animals were immediately transferred into a 10 l carboy and brought to a cool container (1°C). Only active swimming copepods were used for experiments; these were sorted and identified to species level and copepodite stage under cold-light by means of a stereo-microscope as described in Bathmann et al. (1990).

Two sets of experiments were conducted in 5 l glass bottles according to the two main copepod species present. In a given experiment, only copepodites of *C. acutus* and *C. propinquus* of the same stage were used with CV and VI in experiment II and I, respectively. Each bottle was filled with seawater enriched by a factor of 1.5 to 5 with natural phytoplankton 1 day prior to the experiments. Each set of experiments contained two controls and parallel sets with up to 16 copepods. The water in the experiments was continually mixed by means of a peristaltic pump with a flow rate of about 100 ml min. As the inlet of the tubing was placed very close to the bottom of the bottles, this procedure was suitable to maintain the algae in suspension without sucking copepods into the tubes or into the pump. From all experimental bottles, subsamples for the determination of chlorophyll *a* (Evans et al. 1987) were taken daily. Grazing rates were calculated according to Omori and Ikeda (1984) and Paffenhöfer (1971).

Hydrography

The open Weddell Sea comprises four basic water masses. The cold and fresh surface mixed layer in winter forms the Winter Water (WW; Gordon and Huber 1984, 1990). Below, a layer with relatively warm water, the Warm Deep Water (WDW), is found with potential temperatures between 0 and 0.8°C and salinities between 34.64 and 34.72 (Foster and Carmack 1976). It derives from the Circumpolar Deep Water (CDW) which circulates in the Antarctic Circumpolar Current (ACC; Bagriantsev et al. 1989). The colder and less saline

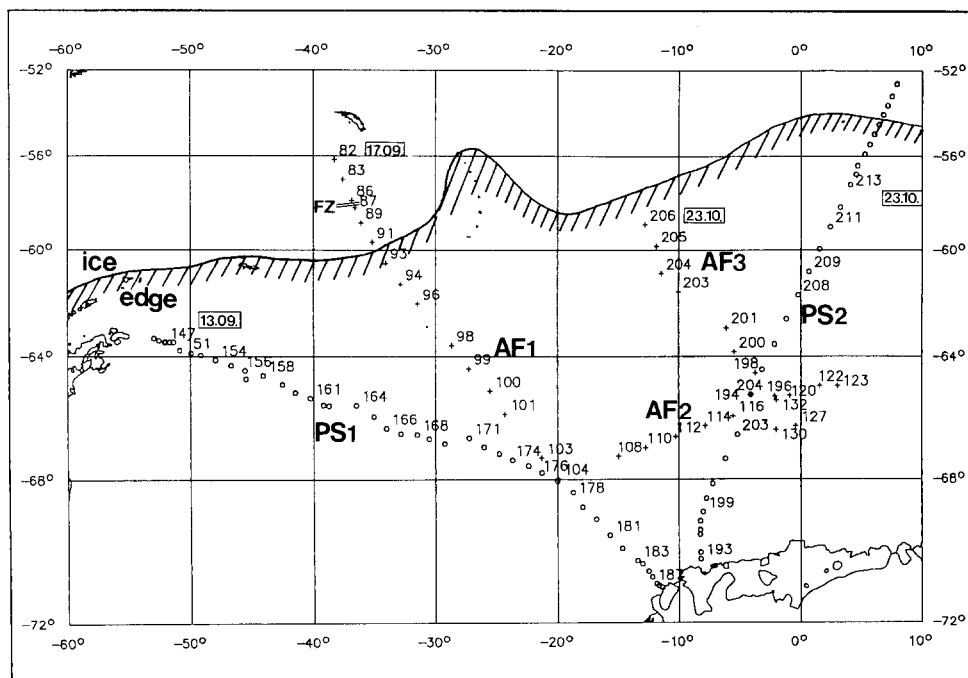


Fig. 1. Positions of the oceanographic transects and zooplankton stations (indicated by numbers) of RV *Polarstern* (PS; white circles) and *Akademik Fedorov* (AF; crosses) during Winter Weddell Gyre Study 1989 (Black circle – joint Sta. PS204/AF194). Dates of the first and the last stations, average position of the ice edge (September–October; from Augstein et al. 1991) and the position of the ice edge (September–October; from Augstein et al. 1991) and the position of the frontal zone (FZ) between the Antarctic Circumpolar Current and the Weddell Gyre Waters (at the transect AF1) are indicated

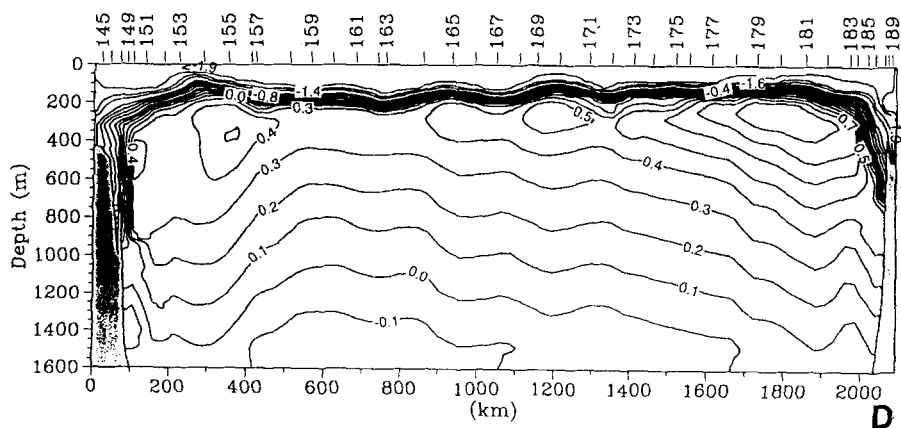
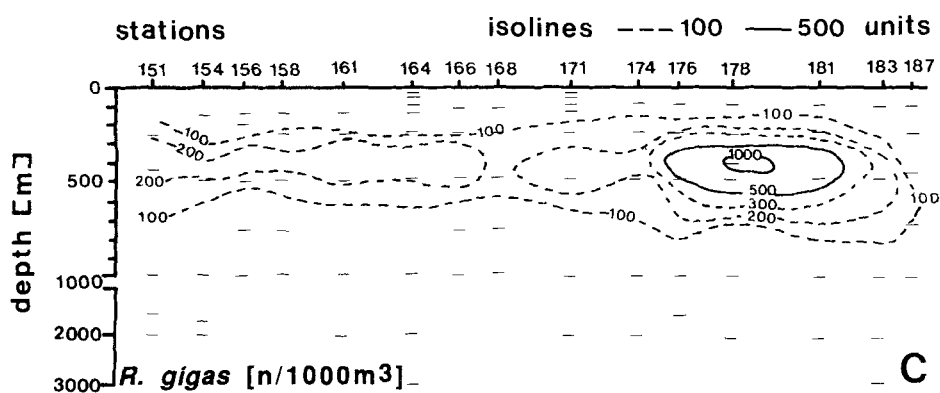
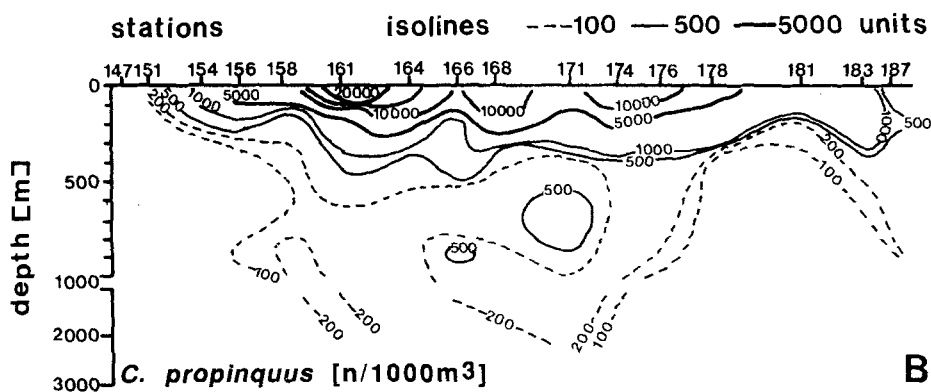
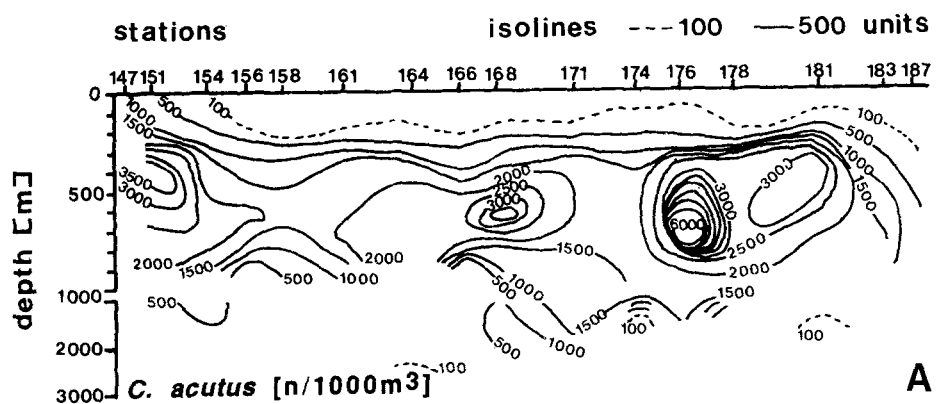


Fig. 2A-D Distributions of *Calanoides acutus* (A), *Calanus propinquus* (B), *Rhincalanus gigas* (C) and the potential temperature (D) along the transect PS 1 (Antarctic Peninsula – Kapp Norvegia) 12 September–8 October 1989. Small horizontal dashes in C indicate sampling intervals for the nets; vertical dashes close to the station numbers in D indicate sampling positions for the continuous vertical salinity/temperature/depth (CTD) measurements

water masses below belong to the Antarctic Bottom Water (AABW) and the Weddell Sea Bottom Water (WSBW).

The current system in the Weddell Sea is determined by the cyclonic Weddell Gyre (WG) which extends from the Antarctic Peninsula to approximately 30°E (Klepikov 1963; Comiso and Gordon 1987; Gouretski and Danilov 1992). The structure of the gyre was obvious in the vertical section of potential temperature from the northern tip of the Antarctic peninsula to Kapp Norvegia (Fig. 2D). At the eastern side, the temperature in the WDW was

significantly higher than in the west with $T_{max} \approx 0.7^\circ\text{C}$ at Sta. 181 and $T_{max} \approx 0.4^\circ\text{C}$ at Sta. 151–155. The temperature decrease reflected that WDW was entering the southern part of the WG in the east and was cooled by mixing with the adjacent water masses during its path through the southern Weddell Sea (Fahrbach et al. 1991). The Antarctic Coastal Current was associated with the horizontal pressure gradient due to the descending isotherms over the upper continental slope (Fahrbach et al. 1992). Inshore of that gradient, cold and fresh water was found to a depth of 1000 m.

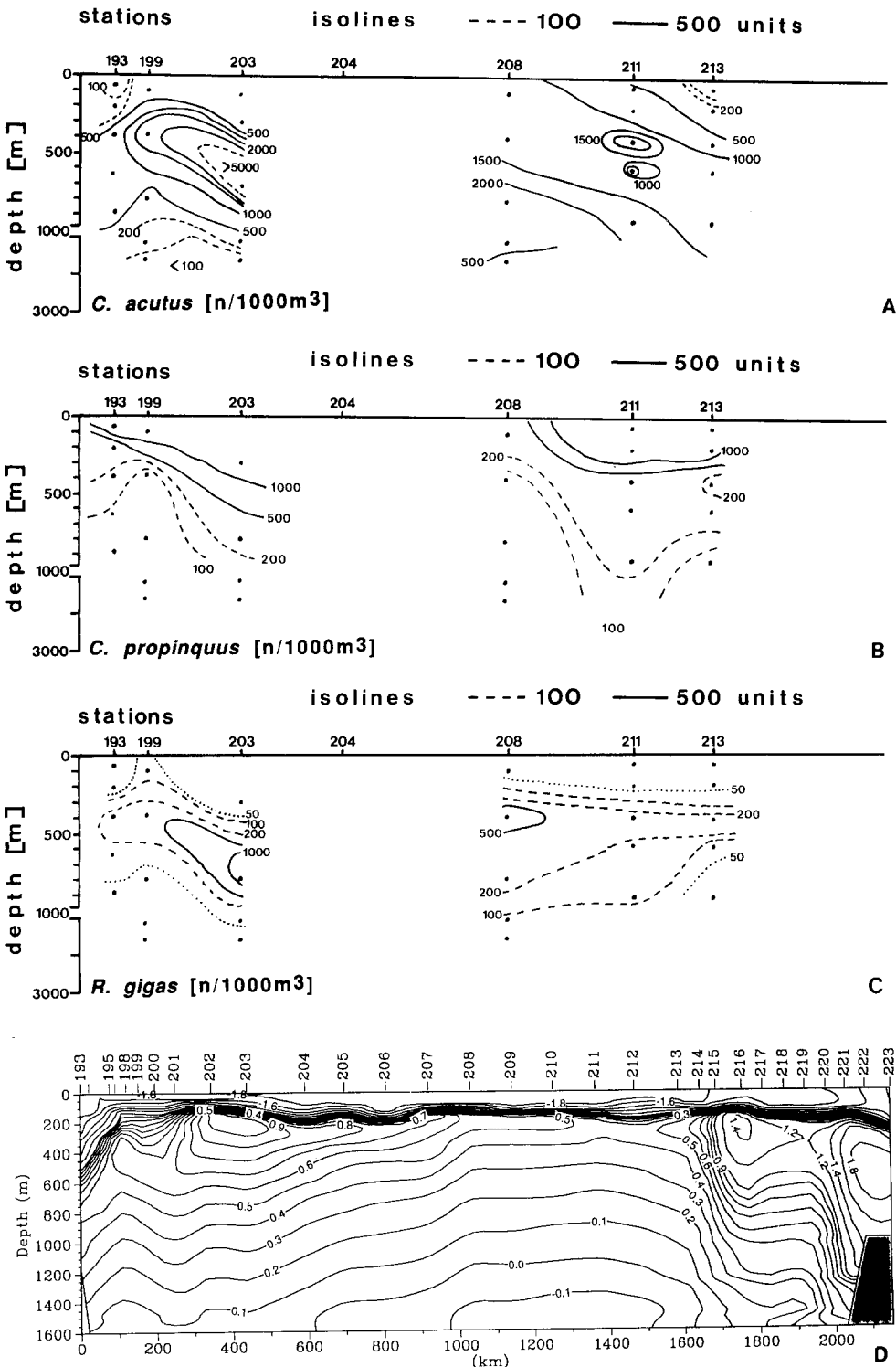


Fig. 3A–D. Distribution of *Calanoides acutus* (A), *Calanus propinquus* (B), *Rhincalanus gigas* (C) and the potential temperature (D) along the transect PS2 (G.v. Neumayer – Cape Town) 12–25 October 1989. Dots in A–C indicate sampling intervals for the nets; vertical dashes close to the station numbers in D indicate sampling positions for the continuous vertical CTD measurements

The long AF1 transect in the north covered the ACC waters distinctly separated from the WG by a frontal zone between Sta. AF 86 and 87 (Fig. 1). In the WG portion, the water mass composition principally resembled that in the PS1 transect described above (Augstein et al. 1991).

In the eastern northward transect (Fig. 3D), the structure of the gyre is not so obvious as further south, because the vertical temperature maximum of the WDW is strongly reduced. Therefore the eastward return flow does not show up as a horizontal maximum, but as a minimum between the warm core of the ACC and the inflowing WDW in the south. The frontal zone between the ACC and the WG at Sta. 213 is obvious (Fig. 3D). The inflow of WDW to the gyre is evident by the warm core at Sta. 202 and 203. Due to the topographic effect of Maud Rise (location between 64°30' and 66°S; 0° to 2°E) the inflow pattern is rather complex.

The records of moorings recovered in November and December 1990 which were deployed in 1989 confirm the circulation patterns obvious from the temperature section PS1. The annual mean velocities reach maximum speeds in the boundary currents and low speeds in the interior (Bathmann et al. 1992; Fahrbach et al. 1993). The repetition of the temperature section during the same cruise displayed only a little change in the deeper levels which indicates the stability of the observed patterns.

Ice conditions reflected to some extent the hydrography. The position of the ice-edge is shown in Fig. 1. A mixture of the floes of the first and second year ice with heavy snow cover was encountered in the northern periphery of the WG. To the south, 1-year pack-ice predominated. The greatest number of leads and the weakest ice were found in the Maud Rise area, where in some previous years the Weddell Polynia was formed (Bagriantsev and Sarukhanian 1984; Gordon and Comiso 1988).

Results

Horizontal distribution and stage composition of the calanoid species in the upper 1000 m water layer.

Calanoides acutus. This species exhibited rather regular distributions with abundances of 2,000–4,000 individuals/1,000 m³ (Fig. 4). The highest abundance was observed in the ice-free ACC waters (Sta. AF82; 7,500 ind/1,000 m³). Its abundance increased south-west of the Maud Rise (Fig. 4C), where the T_{max}^o layer was thick (down to 600 m) and warm (up to 1.1°C; Augstein et al. 1991). Minimum abundances (below 1,000 ind/1,000 m³) were observed in Sta. AF89-96, which corresponded to the northern part of the WG (Fig. 4B). A decrease of species abundance was observed also in the eastern part of the area, to the north-north-west of Maud Rise (Fig. 4D,E).

The species was represented mainly by stage III–VI copepodites (C III–VI); a few C I–II were observed only in Sta. PS208-213 (Fig. 4E). Adult specimens (females mostly; see Table 1) distinctly predominated in the ACC waters in the north (Sta. AF82-89). In the northern part of the WG abundances decreased, with C V and VI dominant (Sta. PS147-161, AF93-99; Fig. 4A,B). C IV were the most abundant stage in the WG in general, but at some stations in the eastern part of the WG (Sta. PS208-213) C III prevailed (Fig. 4E). Some changes in the population structure occurred also near the Antarctic continent: C V and VI dominated over younger stages (Sta. PS183-199; Fig. 4A,E). It is important to note that most of the adults in the WG were males; in the west part of the area (unlike in the east) they were roughly twice as abundant as females (Table 1).

Table 1. Absolute and relative abundance of the males and females of *Calanoides acutus*

Transect ^a	AF1 ^b ACC	AF1 ^b WG	PS1 ^c north	PS1 ^c central	PS1 ^c south	PS ^d coastal	PS2	AF2 ^e	AF3 ^f
Mean abundance of ♀ + ♂ in the water column ind/1000 m ³ (SD)	4222 (1301)	563 (328)	304 (238)	371 (135)	588 (170)	188–252	268 (140)	419 (67)	197 (72)
Mean percent. of adults of total populations % (SD)	80.4 (2.9)	28.1 (15.6)	51.5 (8.0)	30.8 (3.2)	29.9 (6.8)	40.5–53.8	13.1 (9.9)	12.0 (3.9)	19.9 (11.8)
Mean male/female ratio (SD)*	0.08 (0.03)	2.69 (2.38)	0.91 (0.50)	2.80 (0.78)	1.90 (0.86)	0.74–0.80	0.51 (0.43)	1.17 (0.26)	0.8 (0.42)
Number of stations	3	6	5	6	4	2	6	4	7
Dates	17.09	19.09–25.09	13.09–20.09	22.09–02.10	04.10–06.10	08.10–12.10	16.10–23.10	28.09–04.10	19.10–22.10

PS, *Polarstern*; AF, *Akademik Fedorov*; WG, Weddell Gyre; ACC, Antarctic Circumpolar Current

^a Except for stations in the Antarctic Circumpolar Current only tows down to 1000 m depth were used for calculations

^b AF1 transect was subdivided into ACC and Weddell Gyre parts according to the position of the frontal zone indicated in Fig. 1; ACC part: Sta. AF83-89, 500-0 m depth; WG part: Sta. AF94-104

^c PS1 transect was subdivided into northern, central and southern parts according to Nöthig et al. (1991); Northern part: Sta. PS147-158; central part: Sta. PS161-174; southern part: Sta. PS176-183

^d Sta. PS187, 193

^e Sta. AF108, 122, 127, 130

^f Sta. AF196-205; Juday net samples only

* Male to female ratios with standard deviation in brackets

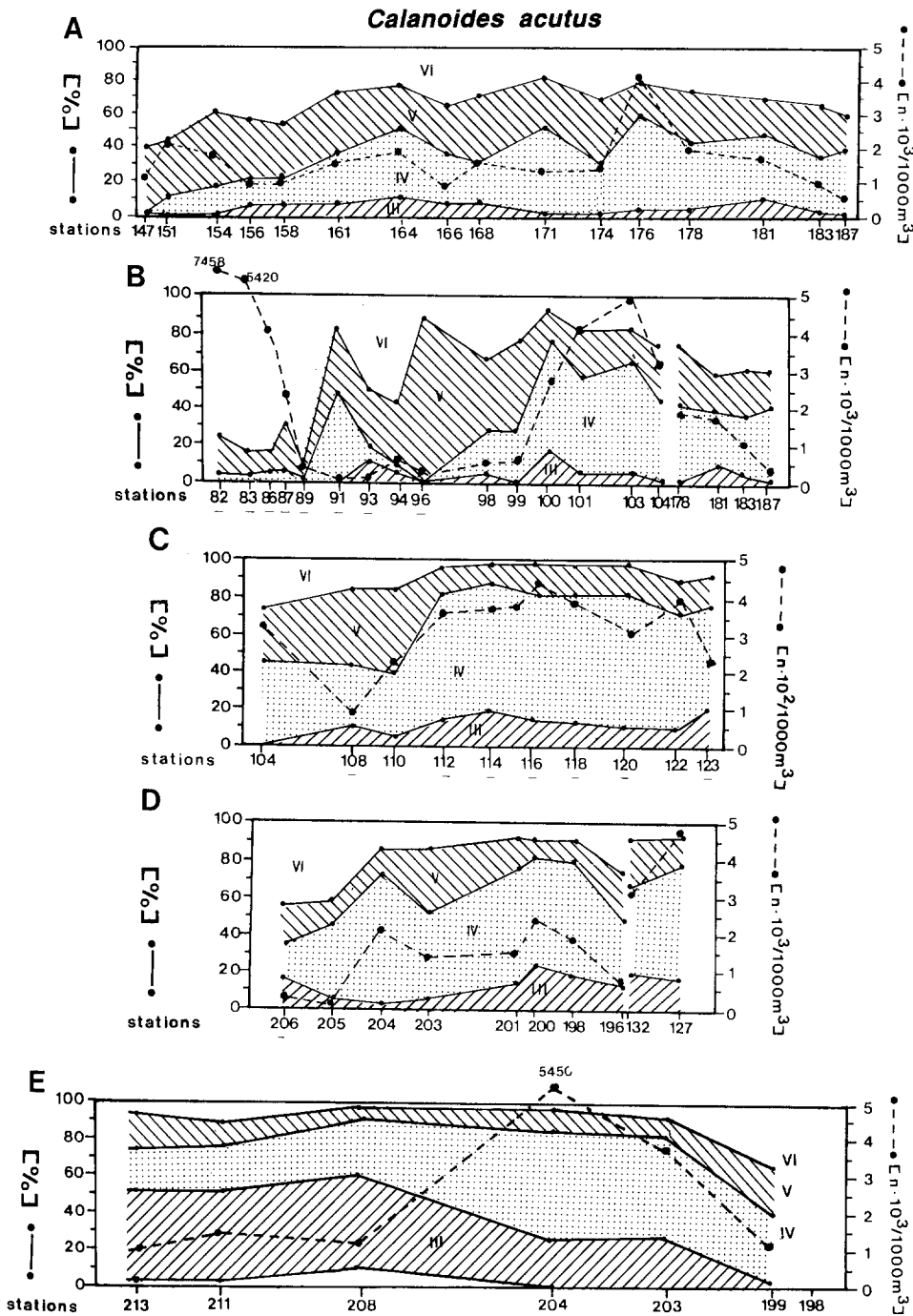


Fig. 4A-E. Abundance (broken line) and stage composition (solid lines, shaded areas) of *Calanoides acutus* in the upper 1,000 m or in the upper 500 m (underlined; only AF stations). A PS 1 transect B AF1 transect (Stations PS181-187 are added to comparison). C AF2 transect D AF3 transect E PS2 transect

Calanus propinquus. Minimum abundances of this species (less than 500 ind/1,000 m³) were observed in the north-western part of the area studied (e.g. in the ACC waters and the north part of the WG; Fig. 5A,B). Abundance increased by almost an order of magnitude (up to 5,000 ind/1,000 m³) in the central part of the WG, but it was again low in the vicinity of the continent (Fig. 5A,B). A variation of abundance by an order of magnitude was observed in the Maud Rise area (Fig. 5C-E).

C V and VI predominated in the ACC and in the northernmost areas of the WG (Fig. 5A-D). There, males reached up to 23% of the stage VI specimens (or up to

10% of total population). In the other part of the area studied, the percentage of adults was low (normally less than 10%); females predominated. In the narrow zone in the northern WG (Sta. AF89-91), C IV were dominant (Fig. 5B). In all other parts of the WG (except some places in the south, where C V dominated; e.g. Sta. PS183, 203, AF127) C III predominated (Fig. 5).

Rhincalanus gigas. Generally, the abundance of copepodite stages of this species was lower by an order of magnitude compared to the Calanidae considered above. *R. gigas* reached maximum abundances (up to 300 ind/1,000 m³) in the ACC (Fig. 6B). In that area also,

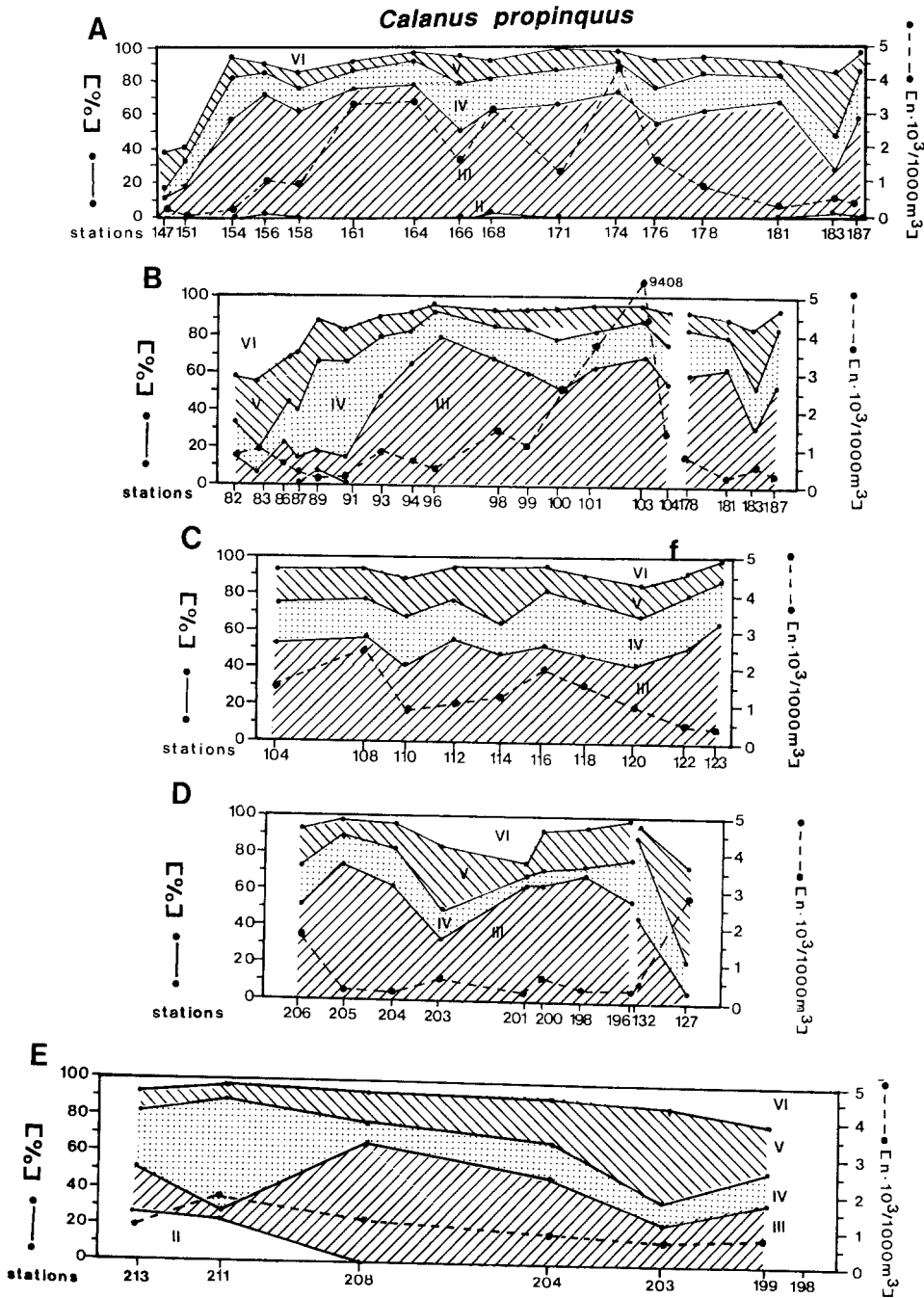


Fig. 5A–E. Abundance (broken line) and stage composition (solid lines, shaded areas) of *Calanus propinquus* in the upper 1,000 m or in the upper 500 m (underlined; only AF stations). A PS1 transect B AF1 transect (Stations PS181–187 are added for comparison). C AF2 transect D AF3 transect. E PS2 transect

nauplii of this species were recorded; at Sta. AF82–83 their abundance exceeded 2,000 ind/1,000 m³, but was lower by one order of magnitude at Sta. AF86–87; to the south of these stations the nauplii were absent. This species occurred with low-to-moderate abundance over the west portion of the WG (about 100 ind/1,000 m³) and to the southwest of the Maud Rise (Fig. 6A,C), but only a few specimens were found in the west and east part of the WG (Fig. 6B,D).

All copepodite stages of *R. gigas* (CI–VI) occurred in the ACC (Sta. AF82–87). The older stages (CIV–VI) dominated in the western part of the WG and near the continent (Fig. 6A,B). Wherever adults were recorded, the

percentage of males within C VI was below 16%; C III were common in the south-west of the area (Fig. 6A,B). C II were found in inflowing WDW; their percentage increased along the transect directed to the Maud Rise (Fig. 6C). Around Maud Rise, the distribution of copepodite stages was distinctly bimodal, with C II and C V–VI predominating (Fig. 6C,D).

Vertical distribution

C. acutus. The density maximum of this species was associated with the centre of the WDW located within the

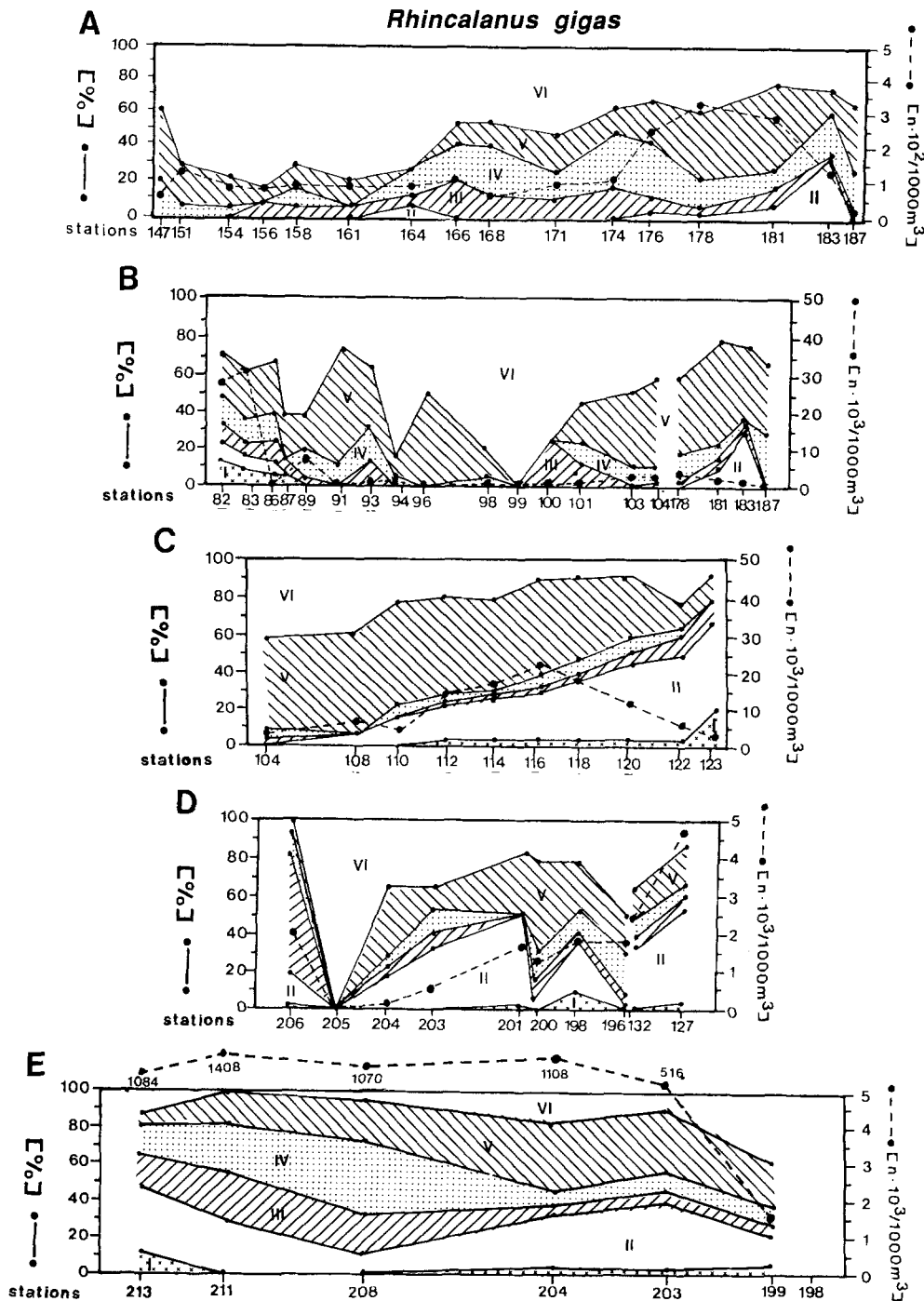


Fig. 6A-E. Abundance (broken line) and stage composition (solid lines, shaded areas) of *Rhincalanus gigas* in the upper 1,000 m or in the upper 500 m (underlined; only AF stations). **A** PS1 transect **B** AF1 transect **C** AF2 transect **D** AF3 transect **E** PS2 transect

depth range 400–1,000 m (below the T_{\max}°). Considerable numbers of specimens were observed below 1,000 m, some even below 2,000 m, but few copepods inhabited the WW (Figs. 2B, 3B, 7A–E, 8). The youngest stages, when present in the east part of the area, lived mostly above 500 m (Fig. 7A). C III were found over the whole of the water column examined; the highest abundances were between 500 and 1000 m (Fig. 7A–E). The C IV stage was found mostly below 500 m; generally it occurred deeper than other stages (Fig. 7A–E). The C V stage also sometimes occurred below 1,000 m, but it was much more abundant

in the 300–1000 m layers. Adult copepods rarely occurred below 1,000 m; they lived somewhat higher than C IV–V but generally below the T_{\max}° stratum (Fig. 7C–D). Males were more restricted in their depth range than females, mostly inhabiting the 500–1000 m layer (Fig. 7A–E).

C. propinquus. This species had its maximum abundance in the very cold surface layer of the WW with 18,000 ind/1,000 m³ (St. 174). Concentrations decreased rapidly with depth and few specimens were found below the T_{\max}° layer (Figs. 2C, 3C, 7F–I). Also, along the AF1-transect, subsequent tows in the layers of 0–100 m and 0–1000 m

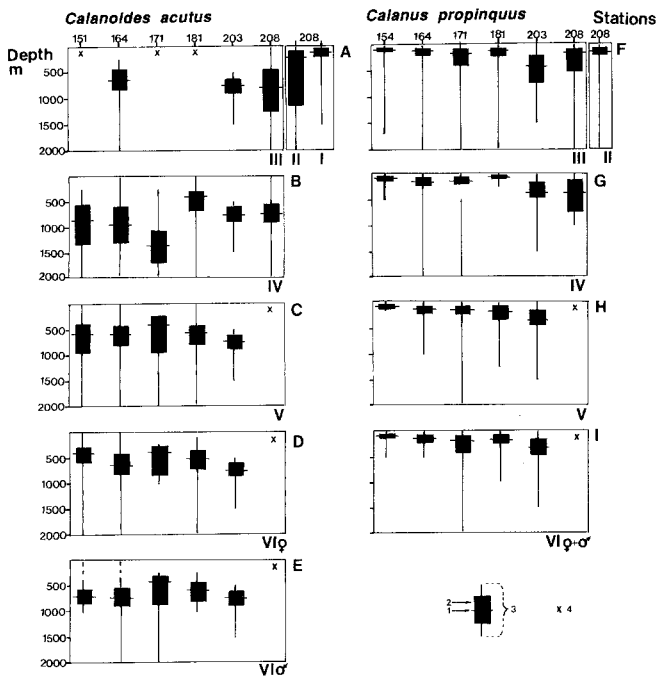


Fig. 7A–I. Vertical distribution of copepodite stages of *Calanoides acutus* (Stage I–III, IV, V, VI females and VI males; A–E) and *Calanus propinquus* (stages II–III, IV, V, VI; F–I) at the selected stations of RV *Polarstern*. Conventions: 1, median depth; 2, vertical limits where 50% of a hemipopulation grouped around the median depth are concentrated; 3, overall vertical range of a stage; 4, a stage is scarce or absent

showed that most of the population (up to 80%) were concentrated in the surface layers. However, in the WG, C III were abundant and sometimes occurred in depths down to 2,000 m.

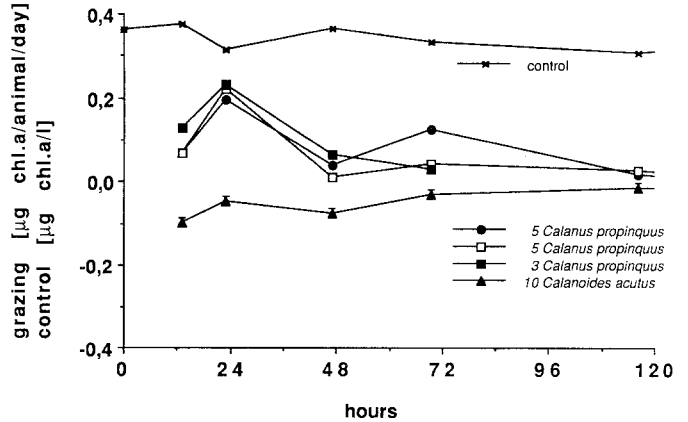
Sampling of the WW (0–250 m) with high depth resolution was performed at eight stations. Bimodal vertical distribution was observed at six of these stations. The first density maximum was located in the 0–50 m stratum, the second at about 100 m.

R. gigas. This species was confined to the top 1,000 m layer. The highest abundances were observed in the T_{\max}° stratum (in the core of the WDW; Figs. 2D, 3D). Practically no differences were found in the vertical distributions of different copepodite stages in the area studied.

Feeding

In all feeding experiments, grazing rates of the copepods did not exceed $0.85 \mu\text{g chl } a \text{ animal}^{-1} \text{ day}^{-1}$ (Fig. 8). Assuming a constant grazing rate, this would translate to $0.0354 \mu\text{g chl } a \text{ animal}^{-1} \text{ h}^{-1}$. This corresponds to a filtration rate of about $5.6 \text{ ml copepod}^{-1} \text{ h}^{-1}$ (calculated after Paffenhöfer 1971; Omori and Ikeda 1984). Among species and experiments, however, grazing rates varied considerably. In experiment I where food concentration was low (mean of $0.443 \mu\text{g chl } a \text{ l}^{-1}$) and comparable to field values, *C. propinquus* showed constant grazing of

A) EXPERIMENT I



B) EXPERIMENT II

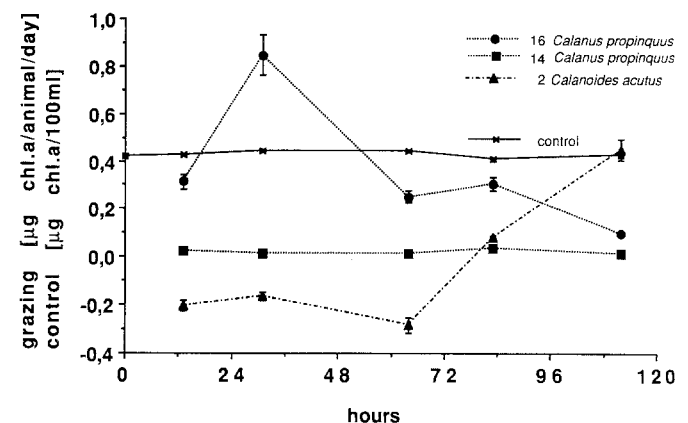


Fig. 8A, B. Results of feeding experiments with *Calanoides acutus* and *Calanus propinquus* with indicated numbers of individuals. A Grazing experiment I at low food concentrations ($0.4 \mu\text{g chl } a \text{ l}^{-1}$). B Grazing experiment II at high food concentrations ($4.3 \mu\text{g chl } a \text{ l}^{-1}$)

about $0.1 \mu\text{g chl } a \text{ animal}^{-1} \text{ day}^{-1}$ in all flasks (Fig. 8A). In contrast, *C. acutus* did not graze at all.

In experiment II (Fig. 8B) with food concentrations one order of magnitude higher (mean of $4.28 \mu\text{g chl } a \text{ l}^{-1}$), grazing rates in one set of experiments (16 *C. propinquus*) were increased ($0.36 \mu\text{g chl } a \text{ animal}^{-1} \text{ day}^{-1}$). In the second set, however, the same species showed rather little grazing ($0.2 \mu\text{g chl } a \text{ animal}^{-1} \text{ day}^{-1}$). Again, *C. acutus* did not graze during the first 60 h of the experiment; thereafter its grazing rates increased to levels similar or even higher than those of the *C. propinquus*.

Discussion

Regional distribution

The abundances of the common calanoid species differed in the subdivisions of the Weddell Gyre (WG) and the Antarctic Coastal Current (ACC). In the ACC waters, *C. acutus* and *R. gigas* were abundant, whilst the abundance of *C. propinquus* was lower by one order of magnitude. Similar proportions (regardless of the season) were

observed in the Scotia Sea (or the ACC waters east of Scotia Sea) by other workers (Voronina 1975; Voronina et al. 1978; Vladimirskaya 1978; Marin 1987; Bondarenko and Polonsky 1990; Atkinson 1991).

The south-eastern area influenced by the Warm Deep Water (WDW) and the ACC was characterized by moderate-to-high abundances of the species studied. More than 50% of their joint abundance was represented by *C. acutus* with the two other species sharing approximately equal percentages (however, *R. gigas* was rare in the vicinity of the continent). Vladimirskaya et al. (1988) found that *C. propinquus* was the most abundant species in the Maud Rise area in March, but its abundance was approximately the same as that of *C. acutus* (although sometimes slightly lower) in the Coastal Current zone. This was confirmed for the late winter to summer season by Schnack-Schiel et al. (1991). Boysen-Ennen and Piatkowski (1988) also concluded that both species dominated in the North-Eastern shelf community of the Weddell Sea. Comparing the life cycles and storage lipids of *C. propinquus* and *C. acutus* in the southeastern Weddell Sea, Schnack-Schiel et al. (1991) concluded that because *C. acutus* accumulated wax-esters it overwintered in resting stage in deeper waters. *C. propinquus*, with triacyl-glycerol as storage product, may feed and reproduce over a more extended period.

In the interior of the WG, the most abundant species in winter 1989 was *C. propinquus*. *C. acutus* was less abundant and only a few specimens of *R. gigas* were found. The northernmost zone of the interior area was very poor in all species studied. To our knowledge, no other literature data are available for the winter situation. In contrast, in summers 1983 (Boysen-Ennen 1987), 1987 (Bondarenko and Polonsky 1990) and 1988 (Makarov and Solyankin 1990), equal abundances of *C. acutus* and *C. propinquus* were observed in the central WG with *R. gigas* being scarce; no nauplii of the latter species were found. No further information about copepod abundances are available for the central WG.

The data presented here indicate different biogeographic distributions of the common Antarctic calanoid species or, in other words, different structures of their distributional ranges (to use the terms introduced by Beklemishev 1969). *C. acutus* inhabit all types of Antarctic waters and reproduce there (Andrews 1966; Voronina 1984; Vladimirskaya et al. 1988). However, they are scarce in the northern part of the WG interior (at least in the west cell). The presence of only C V and VI at some stations in that area (when the younger stages occur to the north and south) suggests them to be expatriates.

R. gigas is a species of the ACC, inhabiting also its subantarctic extension (Voronina 1975, 1984). In the present study, the species had two cores of abundance. The northern core corresponded with the ACC whilst the south-eastern one was associated with the WDW. The considerable abundance of young copepodite stages in the Maud Rise area indicates successful spawning some time before sampling. Vladimirskaya et al. (1988) showed that in early autumn C I were restricted to the waters adjacent to Maud Rise. Thus, the eastern WDM and especially the area of active eddy generation around Maud Rise (Bagriantsev et al. 1989) may be considered an extension of the

distributional range i.e. those areas or water masses in which populations maintain themselves over at least several life cycles (Beklemishev 1969). The central waters in the WG and the waters adjacent to the continent are the zones of expatriation as Ommaney (1936) suggested for the western WG.

The basis of the distributional range of *C. propinquus* seemed to be similar to that of *C. acutus* (Voronina 1984). However, the pattern of horizontal distribution of *C. propinquus* differs considerably from those of *C. acutus* and *R. gigas*. *C. propinquus* is apparently adapted for living in the cold central area of the WG. It inhabits also the eastern WDW, the coastal area (Schnack-Schiel et al. 1991) and pre-continental area, but the conditions of the ACC are less favourable for it. Naumov (1973) demonstrated that generally *C. propinquus* was associated with colder water in contrast to *C. acutus* and *R. gigas*. However, he has not related these differences to certain macro-scale patterns of water circulation.

Voronina (1984) suggested a model for the structure of distributional ranges of Antarctic plankton species. She postulated the gyres south of the ACC as a base for many species. The ACC would then be an area of expatriation. This model may describe the distribution of *C. propinquus*, but not *C. acutus* and *R. gigas*. The base for these species is likely to be the ACC and its derived water masses. The central WG may be an area of expatriation for *R. gigas* (which does not reproduce there) and *C. acutus* (which remains fertile).

Vertical distribution in winter

Voronina (1972, 1984) described seasonal vertical distributions of the interzonal species. She assumed that the cores of sub-populations (or hemi-populations, as she called them) of all stages are confined to the surface waters in summer (Type I). During autumn, the stages shift to greater depths with increasing age (Type II). This scheme postulates that all three species overwinter in deep waters. When upward seasonal migration begins, density maxima occur with older stages being closer to the sea surface (Type III).

The vertical distribution of *C. acutus* corresponds well to the winter situation with a slight upward shift of the older stages (a transition from Voronina's Type II to the Type III). A similar pattern was found in late winter in the south-eastern Weddell Sea (Schnack-Schiel et al. 1991). At the only station where C I–II were present (Sta. PS208), they inhabited the WW. Since this station was in the centre of the eastern part of the WG where seasonal planktonic development may be delayed (Makarov et al. 1990), these youngest copepodites were likely to be the latest recruits of the previous season. They did not descend to greater depth during winter, remaining mostly in the upper layers and probably even feeding there since the concentration of chlorophyll was notably pronounced for winter – above 0.13 µg/l (E.-M. Nöthig, personal communication).

Our data on the vertical distribution of *R. gigas* could be interpreted as their overwintering pattern, since the population inhabited mostly the WDW, but did not

descend to greater depths as *C. acutus* did. This is generally in agreement with the data of Voronina (1975) and Voronina et al. (1978). However, Hosie and Stolp (1989) noted that *R. gigas* was more abundant in the top 200 m than in the underlying 200–1000 m layer in Prydz Bay area in October. The authors suppose that this deviation from the expected situation was due to spatial variations in the onset of ascending migration, likely linked with food availability.

The vertical distribution of *C. propinquus* appeared to be quite dissimilar to those described above. Most of the population was concentrated in the WW, in some cases close to the surface. Our observations are not unique. Hosie and Stolp (1989) found a dense aggregation of *C. propinquus* in the small polynya at a depth of 45–55 m in October. Marin (1988b) noted that the species was equally abundant at surface and in deep layers in August–September south of South Georgia. Schnack-Schiel et al. (1991) also reported that part of the population stayed in surface layers in late winter in the south-eastern Weddell Sea, although many specimens were between 200 and 500 m. Voronina's (1972) data on the transect along 20°E (i.e. in the eastern WG) in early autumn indicate the submergence of *C. propinquus* copepodites to the T_{\max}° layer (200–500 m). Vladimirskaya et al. (1988) reported 26% of the total population of the species to be found below 500 m between the Maud Rise and the Lasarev Shelf in March. Our material demonstrates that a small portion of the population was at considerable depth. Thus, some part of the population of *C. propinquus* can undergo seasonal vertical migration but in the WG during the winter 1989, the main part of that population remained in the surface waters.

Hosie and Stolp (1989) explained the presence of interzonal copepods in the upper layers in winter with food availability, which also could be valid for *C. propinquus* in the present case. Different parts of the WG differed in the chlorophyll *a* concentrations and the richest area was in the south-east (Nöthig et al. 1991). However, *C. propinquus* was even more abundant in the WW of the WG interior where very little chlorophyll was found. Thus, within its specific overwintering mode, other sources of food (e.g. microzooplankton) should be considered.

Overwintering strategies

Grazing experiments demonstrated that *C. acutus* were generally inactive and did not feed on phytoplankton when they were taken out of natural conditions. A pronounced decrease of its grazing rates in the south-east of the Weddell Gyre was noted in March (Bathmann 1992). In the WG, the main part of the summer generation attained C IV stage, which survive winter in the diapausing state generally below the T_{\max}° stratum. This is in agreement with the data of Andrews (1966) and Voronina (1984) for the high-latitude part of the species population. However, in the ACC, the main overwintering stage was C V (Fig. 4B; see also Voronina 1975, 1984; Atkinson 1991). In the WG, a slight upward shift of the older stages

sometimes takes place in September and females occur slightly above C V, as our data also indicate. Marin (1988b) believes that only adult females can complete the seasonal ascent. We found a lot of males in the restricted depth range of 500–1,000 m. As Marin (1988a,b), Schnack-Schiel et al. (1991) and Atkinson (1991) have stated, mating of *C. acutus* takes place in late winter at depths, probably when females pass the layers inhabited by males. The energy requirements of this species in the overwintering state was probably covered by lipid reserves accumulated in the previous summer-autumn period which consist mostly of wax-esters (Schnack-Schiel et al. 1991).

It was shown, however, for oceanic (but not coastal) high-latitude populations of *C. acutus*, that spawning can be delayed until February–March; the population consisted mainly of C V and remained at depths (Makarov et al. 1987; Vladimirskaya et al. 1988). If spawning occurs in autumn, young copepodites seem to overwinter in the WW, as was observed by us in the east cell of the WG. Voronina (1984) supposed that some proportion of adult copepods do not breed when the conditions (e.g. seasonal food supply) are unfavourable and come to a resting stage again. We believe that C V and VI in the interior of the WG were such secondary overwinterers. For the exceptions mentioned above, the overwintering strategy of *C. acutus* in the WG is similar to that in the ACC.

R. gigas reproduces only in the eastern WDW, in particular in the waters adjacent to the Maud Rise. Breeding of this species in that area is very late (Vladimirskaya et al. 1988; Makarov and Solyankin 1990). The late offspring then forms the sub-population of young copepodites which we observed in winter. On a transect along 10°E in early summer after ice had retreated, such a bimodal distribution was observed (Bondarenko and Polonsky 1990). Thus, young copepodites overwinter in the lower layers of the WW and in the upper layers of the WDW. It is likely that they also hibernate. This generation apparently does not reach maturity during the short vegetation season in the WG, but survives a second winter forming the second maximum in a stage distribution (C V and VI) and submerges again to the depths. It is possible that they penetrate with the WDW into the central part of the WG and overwinter a third time before they die. Thus, only the high-latitude population of *R. gigas* is characterized by a prolonged 2 year life cycle, as Marin (1988a,b) proposed for the species as a whole. Similar prolongation of the life cycle is described, in particular, for *Calanus hyperboreus* Kröyer in the Arctic Basin (Pavschtiks 1977; Conover 1988).

The overwintering of *R. gigas* in its "native" habitat, the ACC, appears to be quite distinct from the overwintering strategy just described. Ommaney (1936) postulated additional breeding of this species in the depths in winter; which could be due to mis-interpretation, Voronina et al. (1978) confirmed these results. Our findings – a lot of nauplii and young copepodites – also suggest this hypothesis to be true. Such winter reproduction is known also for some large boreal *Neocalanus* spp. and the arctic *C. hyperboreus* (Conover 1988). Thus, *R. gigas* has a 1-year life cycle in the ACC. It is unknown, however, if this species survives winter in this area in hibernation and utilizes its

lipid reserves during spawning in spring, or if it actively feeds during winter. At the time we sampled the area (17–18 September), there was an intensive diatom bloom in the ACC providing food for reproducing copepods and their offspring. However, Arashkevich (1978) found that *R. gigas* effectively feeds not only on the phytoplankton but also on detritus and zooplankton. Thus, it is likely that late winter breeding of *R. gigas* in the ACC is also fueled by this type of food.

The most interesting overwintering pattern we observed was in *C. propinquus*. In the WG this species overwinters mainly as the C III, in the ACC the main overwintering stage was C V. The latter is in agreement with Marin (1988b). Hence, the differences in duration of the vegetation seasons in these two types of water produce sharp differences in the stage which the species can attain before overwintering. However, at some of our stations in the south, both C III and V also predominated in late winter 1986 (Schnack-Schiel et al. 1991). This could be due to the accelerated seasonal development of plankton communities in some coastal areas (Makarov et al. 1982) where *C. propinquus* is capable of reaching an older developmental stage (C V) in summer-autumn. Mixing of such local populations with C III populations which normally occurred in the area might occur. These C V can then moult to C VI and even spawn under ice in late winter – early spring, as the data of Fransz (1988) for the southern Weddell Sea indicate.

Our results demonstrate that generally the overwintering stages of *C. propinquus* were not resting but feeding on phytoplankton with grazing rates comparable to summer values reported by Drits et al. (1992). However, feeding exclusively on phytoplankton would not be sufficient to cover the metabolic costs of the animals as a simple calculation (suggested by Dr. M. Huntley) demonstrates: The ingestion rates from our experiments of $0.2\text{--}0.36 \mu\text{g chl.}a \text{ animal}^{-1} \text{ day}^{-1}$ translate to $12\text{--}21.6 \mu\text{g C animal}^{-1} \text{ day}^{-1}$ when a C:chl ratio of 60:1 is assumed. This means that an adult *C. propinquus* would have consumed only 2.4 to 4.3% of its body carbon per day which is hardly enough to cover metabolic costs (Dr. M. Huntley, personal communication). Thus, other food sources must have been present, such as protozooplankton and detritus, which were not quantitatively measured during the experiments. This was investigated during a cruise of RV *Polarstern* in the central Weddell Sea in early austral spring 1992 (Dubischar and Bathmann, unpublished data). Such a feeding behaviour may be reflected also in the composition of the body lipids. These are mostly tri-acylglycerols, like in the Antarctic krill, *Euphausia superba* Dana, and suggest year-round feeding (Schnack-Schiel et al. 1991). Under-ice feeding of *E. superba* on ice-algae is well known (Spiridonov et al. 1985; O'Brien 1987; Marschall 1988; Bergstrom et al. 1990). Krill live in close contact with ice when overwintering in the oceanic areas of the Southern Ocean. Considerable parts of the population of *C. propinquus* occupy depths well below the under-ice layer, so we speculate that *C. propinquus* avoids close contact with *E. superba* by feeding on the rather low phytoplankton stocks (chlorophyll concentration less than 40 ng/l) at 10 to 50 m water depths. Marin (1988b) found diatom frustules in the

guts of *C. propinquus* collected in the surface waters in June. Additional food sources of this species might be microheterotrophs (Hopkins and Torres 1989) which were rather abundant in the WG (Nöthig et al. 1991; Nöthig and Gowing 1991).

However, many individuals of *C. propinquus* were also found to the sea surface. Hosie and Stolp (1989) give evidence of formation of swarms of this species in leads and polynias; the copepods are attracted to the leads, reacting to increased light intensity as described for the arctic copepod *Calanus glacialis* Yashnov (Melnikov 1984). We observed the Antarctic petrel, *Thalassoica antarctica* feeding in the leads on some organisms – possibly on *C. propinquus* – even in the central area of the WG when krill was absent (Spiridonov 1992). Probably, in the absence of krill, *C. propinquus* can also feed in the under-ice layer or in leads on ice diatoms mechanically released by rafting within the “pancake ice cycle” (Lange et al. 1989) or on algae melted off the ice in early spring.

Since some part of the population is in the Deep Water in autumn-winter and the lipid content of deep living animals has been found to be higher than in the surface waters (Drits et al. in press), *C. propinquus* probably uses different overwintering strategies even in the same habitat: active winter feeding at or close to the sea surface or diapause at depths beyond 200 m. A similar situation was found in *C. finmarchicus* (Gunnerus) in the Norwegian Sea and some fjords, where two populations overwintered – one resting in the depths and one actively feeding in the subsurface layers (Hirche 1983; Bathmann et al. 1990). The proportions in which the population of *C. propinquus* overwinters as resting or non-resting specimens probably vary with different water masses (e.g. the ACC, the WG, the Coastal Current) and, possibly, with different years. The various sets of data of the stage frequencies and their depth distributions can lead to rather controversial views on the life cycle of *C. propinquus* (Voronina 1984; Marin 1988b; Drits et al., in press.). They should be re-evaluated in the light of the winter data presented here.

Finally, it is evident that the overwintering strategies of *C. acutus*, *R. gigas* and *C. propinquus* differ in relation to the main developmental stages surviving winter, their physiological state (resting or not) and their ascending stages when overwintering takes place in the depths. This probably reflects their different histories of evolutionary adaptation. Particularly important is the fact that winter diapause is not a necessary condition for a large herbivorous copepod species in polar seas. *C. propinquus* in the Weddell Gyre demonstrates an active way of surviving winter in the upper layers. As it was shown for the North Atlantic (Bathmann et al. 1990), such overwintering modes can affect spring phytoplankton development, that, in turn, seriously modifies processes associated with vertical particle flux in different polar waters.

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