

Seasonal comparison of *Calanoides acutus* and *Calanus propinquus* (Copepoda: Calanoida) in the southeastern Weddell Sea, Antarctica

Sigrid B. Schnack-Schiel, Wilhelm Hagen*, Elke Mizdalski

Alfred-Wegener-Institut für Polar- und Meeresforschung, W-2850 Bremerhaven, Germany

ABSTRACT: The herbivorous Antarctic copepods *Calanoides acutus* and *Calanus propinquus* were studied for seasonal differences in life cycles in the southeastern Weddell Sea in January/February 1985 and in October/November 1986. During late winter/early spring older stages of *C. acutus* were concentrated below 500 m. Males had reduced mouthparts and were only found in October/November in deep waters where mating occurred. Females with semiripe and ripe gonads migrated to the surface in November to spawn. Their ascent coincided with an increase in swimming and respiration activity. In summer the majority of *C. acutus* occurred above 200 m and the density increased dramatically as the new cohort hatched. Copepodite stage CV and females in the surface layers had large lipid depots by the end of January, mainly wax esters. They seem to start their descent by mid February. *C. propinquus* also occurred in deeper waters in late winter/early spring, but above 500 m. Males had well-developed mouthparts and were found in small numbers throughout both investigated periods. No great changes in activity were observed from late winter to summer. The summer population was concentrated in the upper 100 m. As for *C. acutus* there was a dramatic increase in abundance of *C. propinquus* from January to February. The lipid content of CV stages and females doubled from January to February and reached similar maximum values at least 3 wk later in the season than *C. acutus*. The lipids of *C. propinquus* consisted mainly of triacylglycerol, a very unusual storage lipid class in polar calanoid copepods. *C. acutus* and *C. propinquus* seem to represent different life histories: the wax-ester-accumulating *C. acutus* overwinters in a resting stage in deeper waters while the triacylglycerol-storing *C. propinquus* may feed and reproduce over a more extended period than *C. acutus*.

INTRODUCTION

Calanoides acutus and *Calanus propinquus* are dominant large copepods in Antarctic waters (e.g. Ottestad 1932), with a circumpolar distribution ranging from the Antarctic continent to the Antarctic Convergence (Ottestad 1936, Andrews 1966). Both species perform ontogenetic vertical migrations, and inhabit deeper water layers during winter and surface waters during summer (e.g. Voronina 1972, Voronina et al. 1978). These migrational patterns are related to the pronounced seasonality of the Southern Ocean. During the short summer the phytoplankton bloom supplies plenty of food for herbivorous copepods in epipelagic waters, and they can rapidly accumulate large lipid depots in their oil sacs (Lee et al. 1971, Sargent &

Henderson 1986, Hagen 1988). These energy reserves may then be utilized during winter when food is scarce and for reproduction, as reviewed by Båmstedt (1986).

According to Voronina's asynchrony hypothesis (1978) late copepodite stages (CIV and CV) of both species successively migrate to the surface in spring, moult to adulthood and mate in the upper 200 m. The offspring (copepodite stages CI and CII) remain at the surface during the feeding and growth period. At the end of summer, stages CIII and CIV start to descend below 500 m to overwinter. Marin (1988) opposed this asynchrony hypothesis and suggested independent life cycles for *Calanoides acutus* and *Calanus propinquus*. He proposed that *C. acutus* mates in deep water layers and the fertilized females migrate to the surface to spawn in spring. *Calanus propinquus*, however, ascends as copepodite stage V and mating occurs in surface layers. Marin (1988) postulated that part of the *C. propinquus* population remains in surface waters during winter.

* Present address: Institut für Polarökologie, Universität Kiel, W-2300 Kiel, Germany

There are only sporadic studies on copepods from high Antarctic waters like the Weddell Sea and the Ross Sea (e.g. Kaczmaruk 1983, Hopkins 1987, Boysen-Ennen & Piatkowski 1988, Franz 1988), and especially data on seasonal variability are scarce (Hubold & Hempel 1987). Our studies were carried out during 2 Antarctic expeditions in January/February 1985 (summer) and in October/November 1986 (late winter/early spring). One main objective was to highlight major seasonal differences in abundance, vertical structure and age composition of *Calanoides acutus* and *Calanus propinquus* in the eastern Weddell Sea. In addition, feeding experiments, respiration measurements and lipid analyses were carried out to obtain information on the physiological state of the investigated species.

METHODS

During 2 expeditions with RV 'Polarstern' zooplankton was sampled in the southeastern Weddell Sea using a multiple opening/closing net (Weikert & John 1981) with 100 μm mesh size. The net was towed vertically at 0.5 to 1.0 m s^{-1} and sampled 5 successive depth layers from near the bottom or 1000 m depth to the surface. At one station in February 1985 (# 334) zooplankton sampling was carried out down to 2500 m depth. In this paper only offshore stations (water depth > 1000 m) with 1000 m sampling depth are considered (Table 1, Fig. 1). The filtered volume was calculated by multiplying the vertical distance of the tow with the

Table 1. List of multinet stations (D: day; N: night; DA: dawn; DU: dusk)

Stn no.	Date	Depth (m)	Time of day	Start (h; UTC)
512	17 Oct 1986	3575	N	00:20
513	18 Oct 1986	4211	D	10:40
514	18 Oct 1986	3050	DU	21:40
516	19 Oct 1986	1675	D	13:55
562	03 Nov 1986	1114	D	17:40
565	04 Nov 1986	3125	DA	03:50
570	05 Nov 1986	3220	DA	02:35
604	17 Nov 1986	3253	DU	21:05
607	18 Nov 1986	1732	D	09:30
611	20 Nov 1986	2891	D	11:55
614	21 Nov 1986	3079	DA	01:55
618	22 Nov 1986	1133	D	16:15
623	24 Nov 1986	1538	DU	23:22
278	29 Jan 1985	1976	D	14:30
279	29 Jan 1985	2783	D	18:15
332	15 Feb 1985	1965	D	14:10
333	15 Feb 1985	2782	D	17:19
334	15 Feb 1985	3427	DU	20:20

multinet's mouth area (0.25 m^2), assuming 100 % filtering efficiency. The samples were preserved in 4 % buffered formalin. For detailed descriptions of the biological and oceanographic programme of the 2 'Polarstern' cruises see Hempel (1985) and Schnack-Schiel (1987).

Abundance was normally calculated from the entire

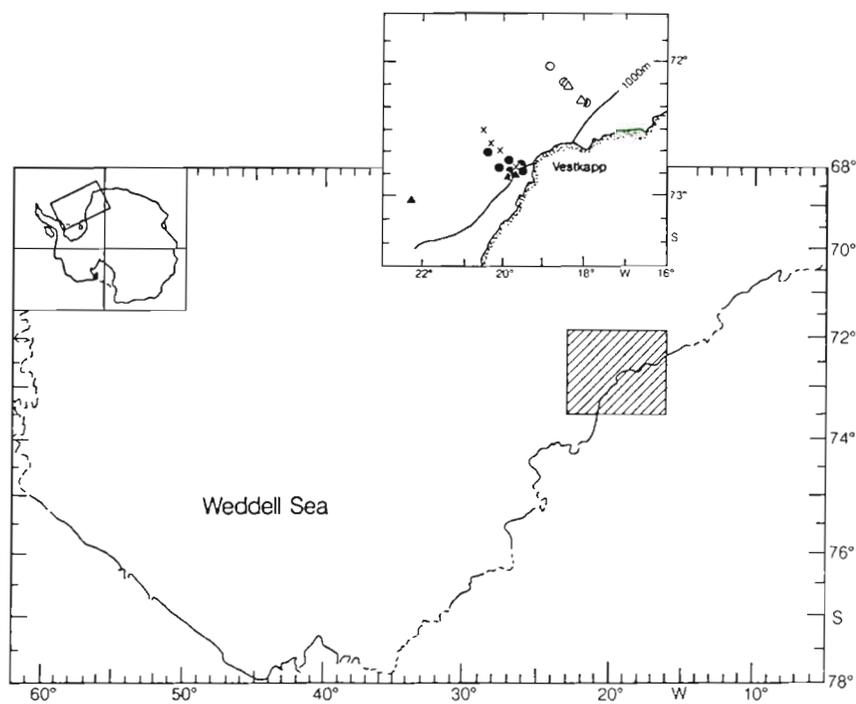


Fig. 1. Sampling area in the southeastern Weddell Sea and position of zooplankton stations. (Δ) 29 Jan, (\circ) 15 Feb 1985; (\times) 17 to 19 Oct, (\blacktriangle) 4 to 5 Nov, (\bullet) 17 to 24 Nov 1986

sample. In a few cases the abundance of each stage was evaluated by counting a minimum of 30 individuals per stage from a subsample (1/2 to 1/10) using a Kott whirling apparatus. Geometric means of abundance data from offshore stations were used to compare between sampling periods. Following Huntley & Escritor (in press) the mean population stage [S] was calculated as:

$$[S] = \frac{N_{CI} + 2 N_{CII} + \dots + 6 N_{CVI}}{\Sigma N}$$

where N_{CI} , N_{CII} . . . N_{CVI} are the number of specimens of copepodite stages CI, CII . . . CVI; and ΣN = the sum of all individuals.

For experimental work copepods were sampled from the upper 300 m (summer) or 500 m (winter/spring) with a Nansen net. All experiments were carried out in a cooling container at 0 °C at dim light for 10 to 24 h (feeding) or for 6 to 10 h (respiration). Each experiment comprised 2 replicates and 2 controls without copepods. For feeding experiments, seawater was collected by membrane pump from 5 m depth (summer) or with Niskin bottles in the upper 100 m (winter/spring). The natural phytoplankton suspension was transferred into experimental 5 l glass flasks to which actively swimming copepods were added. Copepod densities ranged between 10 and 94 specimens per flask depending on stage. Chlorophyll a concentration was analyzed spectrophotometrically at the beginning and at the end of each feeding experiment. Filtration rates were calculated after Frost (1972). For respiration experiments, 5 individuals were pipetted into 100 ml bottles containing 0.2 µm filtered, oxygen-saturated seawater. Respiration was measured by the Winkler method and rates calculated as the difference between dissolved oxygen in the control and experimental bottles before and after the experiment. During sorting under the microscope we noticed differences in swimming activity of *Calanoides acutus* females. Therefore, respiration measurements were carried out with females separated according to the activity levels 'non-active', 'active' and 'very active'.

For dry weight (DW) and lipid analyses copepods were carefully collected by Bongo net. Immediately after sampling, live copepods were sorted in a cooling container at 4 °C. For a single sample 45 to 240 specimens of one species/stage were sorted and stored under nitrogen at -80 °C. After determination of dry weight (lyophilized), total lipid content was measured gravimetrically (after Folch et al. 1957). Lipid class composition was analyzed according to Fraser et al. (1985) by thin-layer chromatography-flame ionization detection with an IATROSCAN. Different standard mixtures were prepared for calibration that approximated the lipid class composition of the analyzed

samples. The wax ester fraction also includes sterol esters. For details see Hagen (1988). For summer samples the dry weight data of the above lyophilized samples were used. Dry weights of smaller copepodite stages were extrapolated from older stages using log-transformed length-weight relationships (after Boysen-Ennen pers. comm.). Winter samples were dried at 60 °C for 24 h.

RESULTS

Population structure

Calanoides acutus was generally more abundant than *Calanus propinquus*. The abundance of each species did not vary significantly (*H*-test, 95 % level) between October, November and January, but in February the abundance of both species was by far higher compared with 2 to 3 wk earlier at the end of January (Fig. 2).

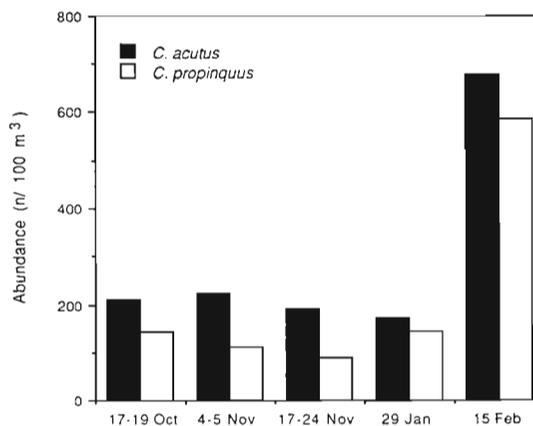


Fig. 2. *Calanoides acutus* and *Calanus propinquus*. Mean abundance of total populations (1000 to 0 m depth)

Older stages (mainly CIV and adults) dominated the *Calanoides acutus* population in October/November, while early stages (CI and CII) were absent in all samples. The bulk of the *Calanus propinquus* population was dominated by copepodite stages CIII, CV and females and only the first stage (CI) was not present in late winter/early spring (Fig. 3). At the end of January the population of *C. acutus* showed a bimodal stage structure in the upper 1000 m: CV specimens (44 %) were present from the previous year's generation, as well as offspring of the current year (CI 27 % and CII 22 %). In mid-February, 2 to 3 wk later, older copepodite stages and adults were practically replaced by juveniles of the new generation (CI 56 %, CII 24 %, CV 11 %). A similar change in population structure is obvious for *C. propinquus* (Fig. 3).

The vertical distribution differed greatly between

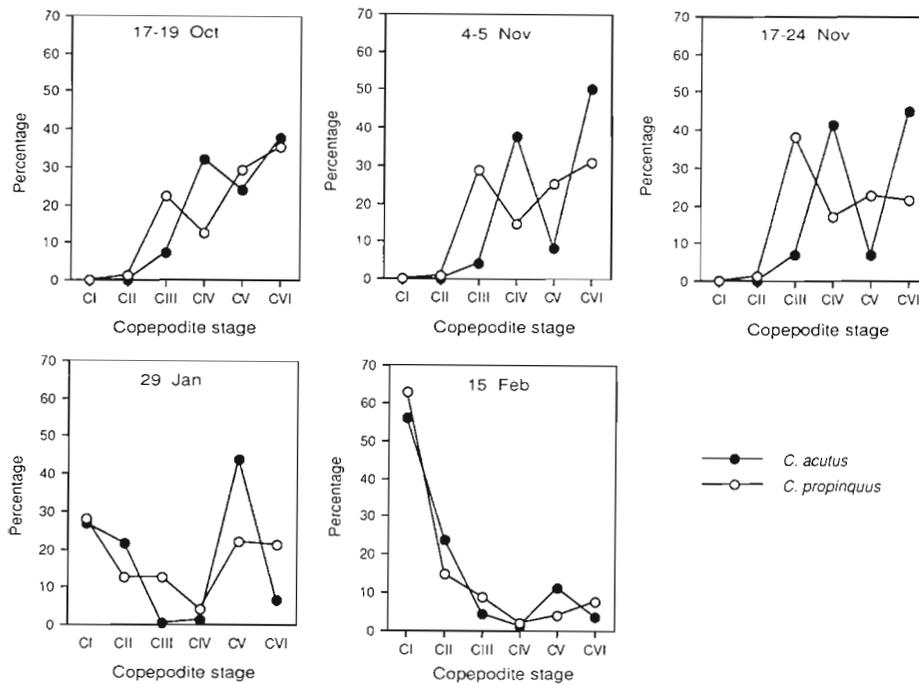


Fig. 3. *Calanoides acutus* and *Calanus propinquus*. Relative composition of developmental stages in the top 1000 m

species and developmental stages. During October/November the major part of the *Calanoides acutus* population was concentrated below 500 m, except for females in mid-November (Fig. 4): from 17 to 21 November the majority of females were encountered between 500 and 200 m; from 21 to 24 November they were found in the upper water layers (Fig. 5). Hence, only females seemed to have migrated upward during this period. Microscopic observations of the gonads showed that the state of maturity of most females was semiripe or ripe (after Runge 1985). In contrast to adults, the vertical distribution of CIV stages did not change during this time and the bulk remained below 500 m (Fig. 5). Males were found in higher numbers only between 1000 and 500 m depth and only in October/November.

In summer the majority of the *Calanoides acutus* population had ascended above 300 m (Fig. 4). At the end of January CV specimens that had overwintered were concentrated below 50 m, whereas the offspring of the current year (CI and CII) were found above 50 m. In February copepodite stages CI to CIII were highly concentrated in the uppermost 50 m (Fig. 4). There is a slight tendency for CV and females to descend. Very few specimens occurred at the only deep station between 2500 and 1000 m: 1 female, 5 CV, 4 CIV and 1 CI. No males were present in any of the summer samples.

The bulk of the *Calanus propinquus* population was found between 500 and 100 m in October/November (Fig. 6). No upward migration of *C. propinquus* was

detected during this period. In summer the early stages CI and CII comprised a large proportion of the population, which was almost entirely concentrated in the upper 50 m. Males were found in very low numbers (< 1 to 4 % of the total population) throughout the water column during the investigated period. The low abundance of males and the high abundance of females in January was in contrast with observations for *Calanoides acutus* (Figs. 3 & 6). At the only deep station in February 1985 no *C. propinquus* individual occurred between 1000 and 2500 m.

In October and the beginning of November the *Calanoides acutus* population consisted of significantly older stages than the *Calanus propinquus* population (*U*-test, 95 % level) (Fig. 7). During this period, and integrated over the top 1000 m, *C. acutus* had a significantly different mean population stage [S] of 5.0, as compared to *C. propinquus* with 4.5 (*U*-test, 95 % level). This difference was most pronounced in mid-November due to the beginning ascent of *C. acutus* females, while *C. propinquus* females did not show such an upward migration. In summer both species had a similarly young mean population stage in the upper 50 m, where the bulk of both populations was concentrated. This young mean population stage reflects the dominance of the early copepodite stages of the new generation. Between 50 and 1000 m the mean population stage of *C. acutus* was significantly more advanced than in *C. propinquus* (*U*-test, 95 % level).

Females of both species occurred in higher numbers than males (Table 2) except for *Calanoides acutus* in

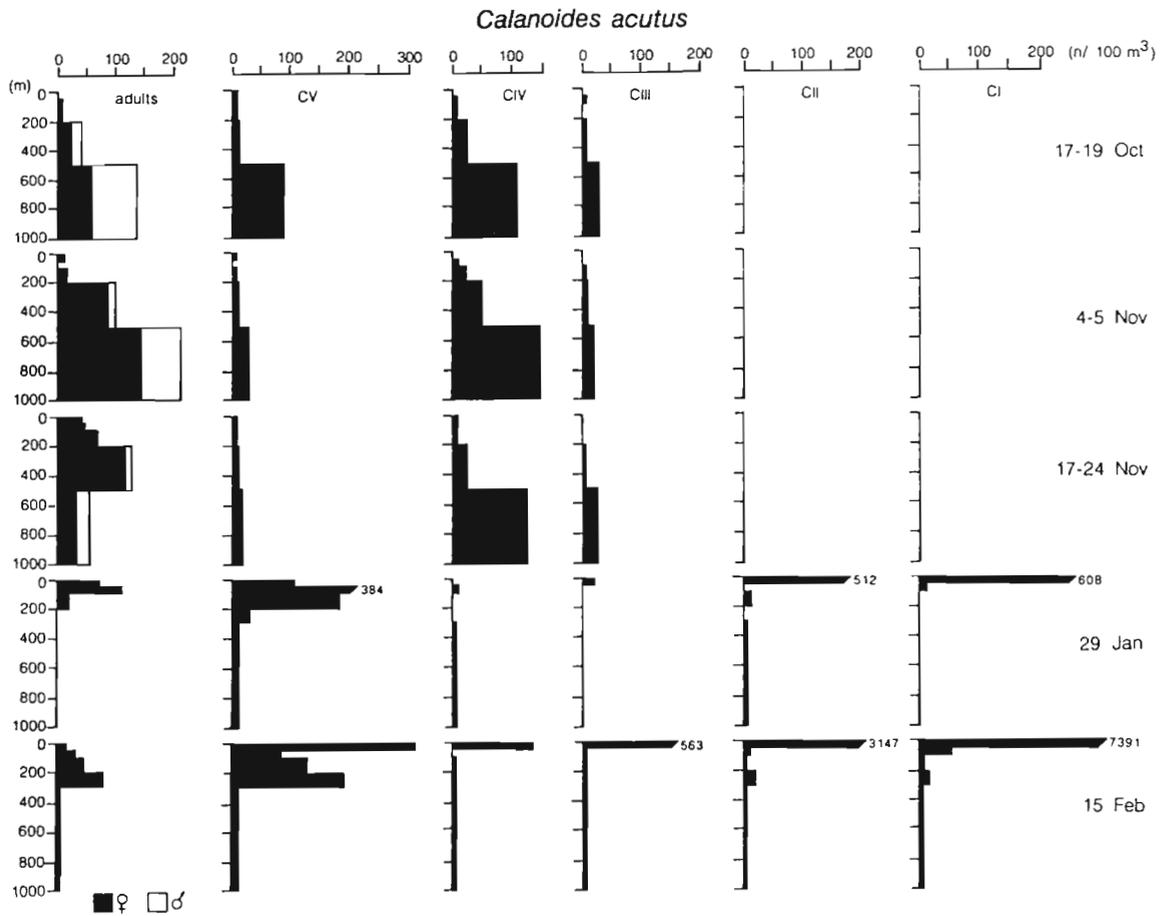


Fig. 4. *Calanoides acutus*. Seasonal vertical distribution pattern of copepodite stages I to V and adults

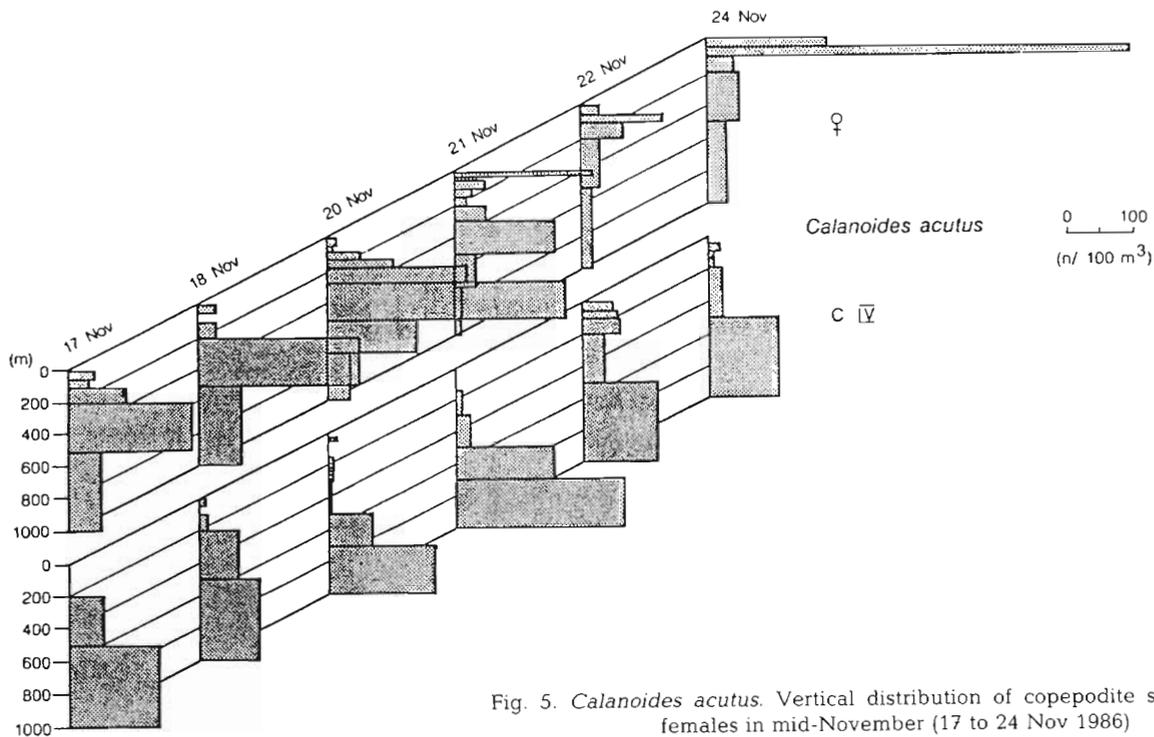


Fig. 5. *Calanoides acutus*. Vertical distribution of copepodite stage CIV and females in mid-November (17 to 24 Nov 1986)

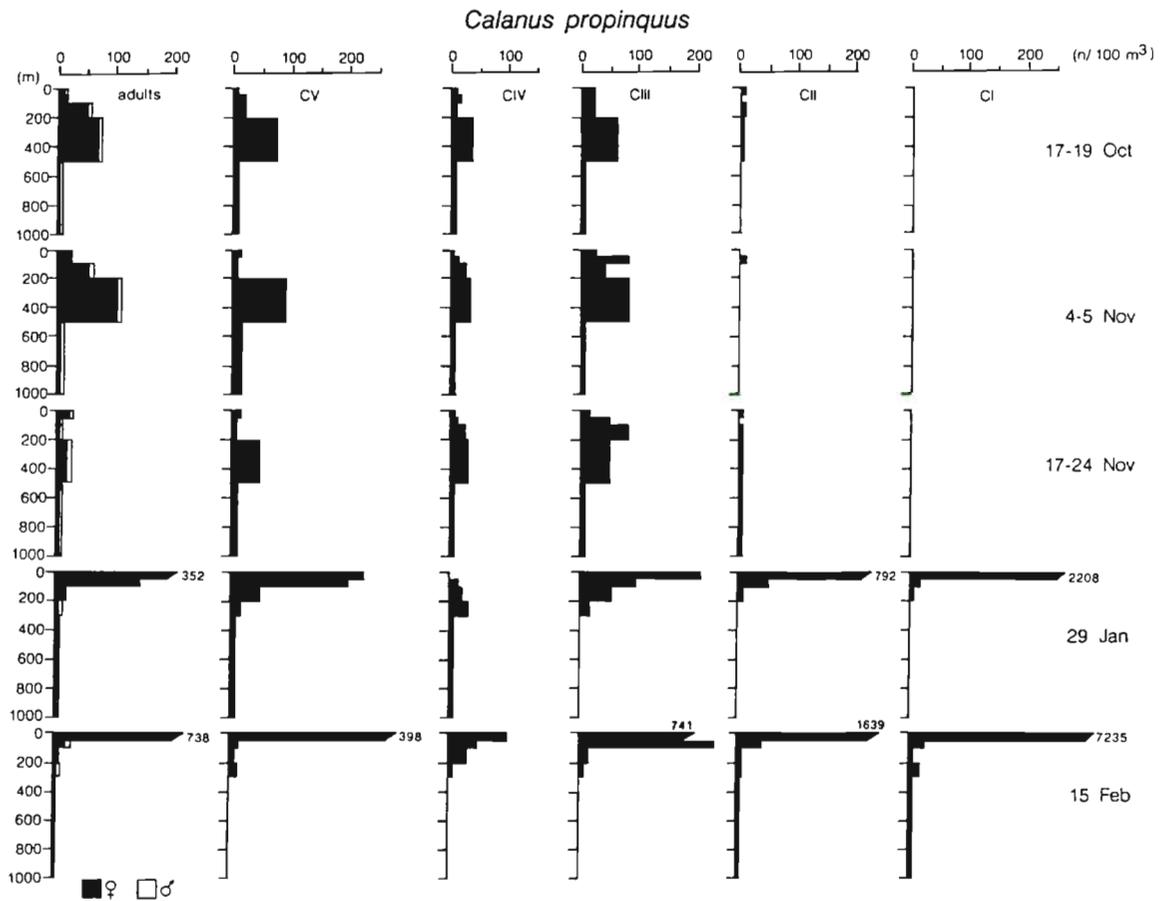


Fig. 6. *Calanus propinquus*. Seasonal vertical distribution pattern of copepodite stages CI-V and adults

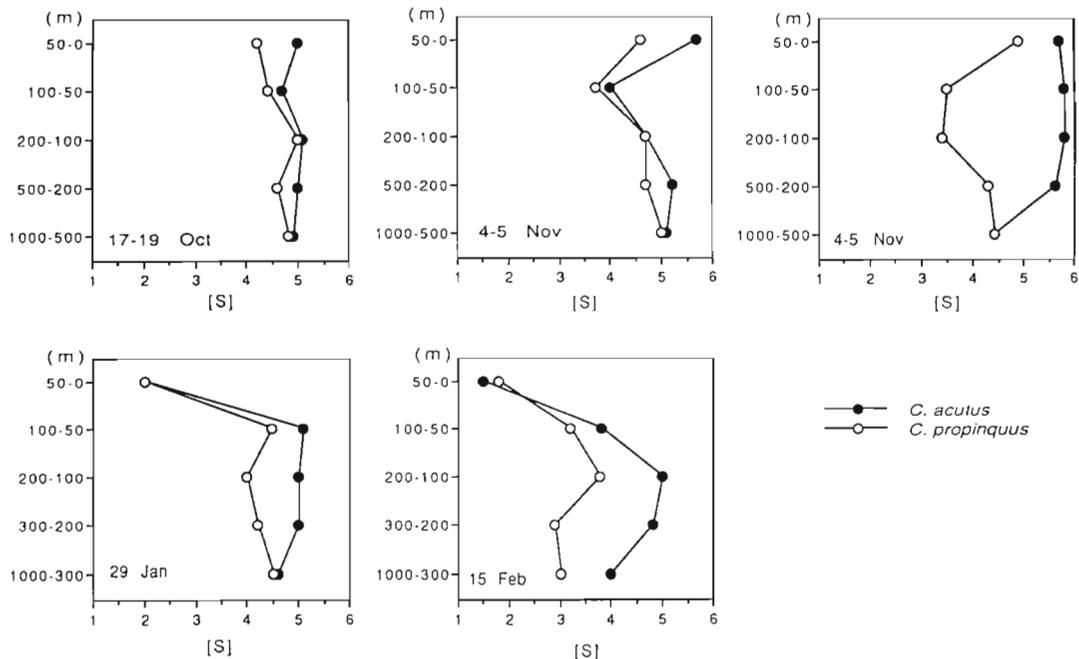


Fig. 7. *Calanoides acutus* and *Calanus propinquus*. Mean population stage [S] at different sampling times

Table 2. *Calanoides acutus* and *Calanus propinquus*. Female/male ratios in the top 1000 m. R: ratio; Σ : sum of adults; nm: no males

Depth (m)	17–19 Oct		4–5 Nov		17–24 Nov		Depth (m)	29 Jan		15 Feb	
	R	Σ	R	Σ	R	Σ		R	Σ	R	Σ
<i>Calanoides acutus</i>											
0–50	–	0	nm	8	nm	41	0–50	nm	72	nm	3
50–100	1.0	4	–	0	nm	45	50–100	nm	112	nm	76
100–200	nm	3	nm	13	22.0	69	100–200	nm	20	nm	45
200–500	2.6	32	31.3	97	60.0	122	200–300	–	0	nm	29
500–1000	0.9	127	2.2	207	2.1	52	300–1000	nm	2	nm	15
<i>Calanus propinquus</i>											
0–50	6.0	14	nm	25	13.5	29	0–50	nm	352	105.3	744
50–100	nm	16	nm	23	6.0	7	50–100	nm	144	1.9	29
100–200	53.0	54	19.7	62	2.0	6	100–200	nm	12	3.0	8
200–500	11.8	77	18.3	116	7.0	24	200–300	1.0	8	1.0	4
500–1000	4.0	5	1.5	10	0.8	7	300–1000	2.0	3	1.0	2

October in the 1000 to 500 m depth layer (female/male ratio: 0.9). Between 500 and 200 m in mid-October and between 1000 and 500 m in November the female/male ratio of *C. acutus* was also rather low (2.1 to 2.6).

Feeding and respiration experiments

In October and the beginning of November no feeding was detected in females and copepodite stage CV of both species at naturally occurring phytoplankton concentrations ($< 1 \mu\text{g chl } a \text{ l}^{-1}$). Feeding experiments with specimens collected later in the season (28 November) and with enriched food supplies (10 to $40 \mu\text{g chl } a \text{ l}^{-1}$) – as can be found in the under-ice water layer on the shelf south of 74°S (Scharek 1990) – showed that both species were actively feeding on phytoplankton (Fig. 8). Large amounts of eggs were

detected under the microscope, produced by each of the 2 species at chlorophyll *a* concentrations exceeding $15 \mu\text{g l}^{-1}$.

Calanoides acutus females could be divided into 3 categories according to swimming behaviour and thus, oxygen consumption: non-active (the majority in mid-October), active (the majority in early November) and very active (the majority in mid-November) (Table 3). From October towards November their respiration rates were increasing. A slight increase was also found for the respiration rates of *Calanus propinquus*, although in this species no differences in swimming activity of females were observed.

At the end of January both species were feeding on ambient phytoplankton concentrations below $1 \mu\text{g chl } a \text{ l}^{-1}$. Only small differences in clearance rates (expressed as $\text{ml mg}^{-1} \text{ DW}$) were found between developmental stages of *Calanus propinquus*. There was, how-

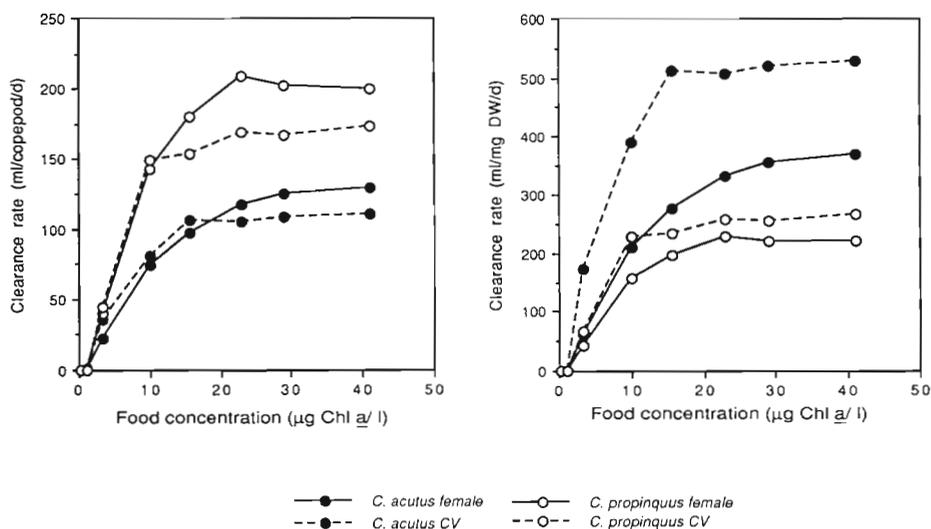


Fig. 8. *Calanoides acutus* and *Calanus propinquus*. Clearance rates of copepodite stage CV and females at different chlorophyll *a* concentrations in late winter/early spring 1986

Table 3. *Calanoides acutus* and *Calanus propinquus*. Respiration rates in late winter/early spring

	Dry weight (mg cop. ⁻¹)	$\mu\text{l O}_2 \text{ cop.}^{-1} \text{ h}^{-1}$			$\mu\text{l O}_2 \text{ mg}^{-1} \text{ DW h}^{-1}$		
		21 Oct	2 Nov	26 Nov	21 Oct	2 Nov	26 Nov
<i>Calanoides acutus</i>							
CV	0.21	–	–	0.38	–	–	1.81
Fem. (non-active)	0.49	0.10	–	–	0.20	–	–
Fem. (active)	0.49	0.34	0.40	0.43	0.69	0.82	0.88
Fem. (very active)	0.49	–	0.63	0.65	–	1.29	1.33
<i>Calanus propinquus</i>							
CV	0.69	–	0.47	0.78	–	0.68	1.13
Fem.	1.07	–	1.00	1.05	–	0.93	0.98

ever, a pronounced decrease in feeding activity with increasing development in *Calanoides acutus* CIII to CV (Table 4).

Lipid content and composition

No significant differences in the lipid content of copepodite stage CV of *Calanoides acutus* were found

between January and February (Fig. 9). The analyzed specimens had high lipid depots at the end of January as well as in February (> 42 % DW). The lipids consisted mainly of wax esters (92 % of total lipid; Fig. 9). At the end of January copepodite stage CV and females of *Calanus propinquus* had only medium lipid contents of about 25 % DW. Within 2 to 3 wk these values rose to 47 % (CV) and 43 % (females). Early

Table 4. *Calanoides acutus* and *Calanus propinquus*. Clearance rates of different copepodite stages in late January at ambient chlorophyll concentrations (0.54 to 0.98 $\mu\text{l chl a l}^{-1}$)

	Dry weight (mg cop. ⁻¹)	<i>Calanoides acutus</i>		Dry weight (mg cop. ⁻¹)	<i>Calanus propinquus</i>	
		ml cop. ⁻¹ d ⁻¹	ml mg ⁻¹ DW d ⁻¹		ml cop. ⁻¹ d ⁻¹	ml mg ⁻¹ DW d ⁻¹
CIII	0.20 ^a	74.1	370.5	0.24	67.2	275.4
CIV	0.40 ^a	101.5	255.0	0.49 ^a	122.5	250.0
CV	0.85	65.3	76.8	0.95	282.4	298.2
Fem.	1.06	109.2	103.1	1.60	337.0	211.0
Male	–	–	–	1.02	188.2	184.5

^a Calculated after Boysen-Ennen (pers. comm.)

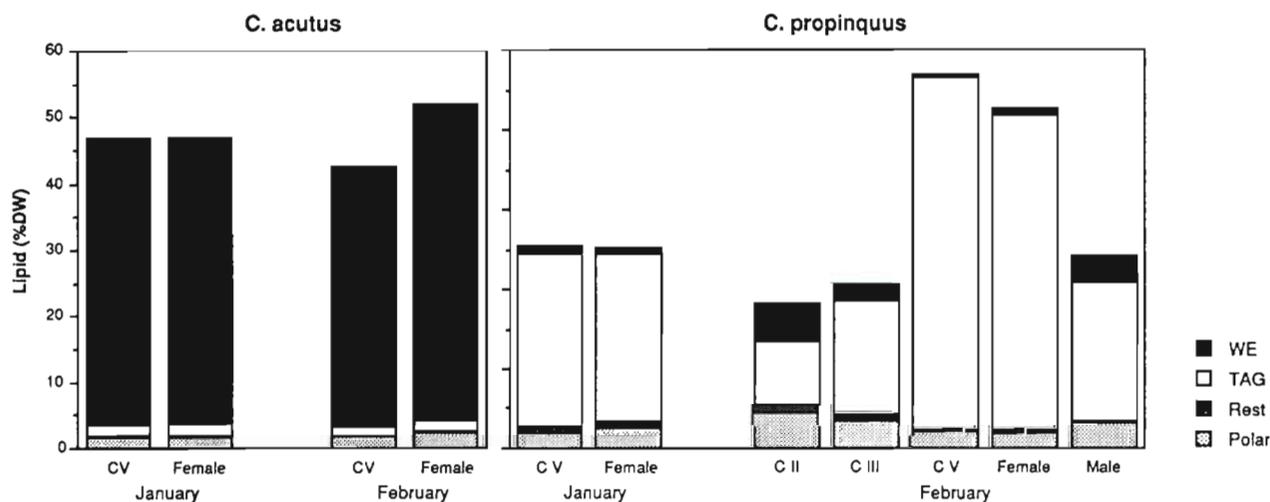


Fig. 9. *Calanoides acutus* and *Calanus propinquus*. Lipid content and composition in summer 1985. WE: wax esters; TAG: triacylglycerols; Polar: polar lipids

stages CII and CIII and males contained relatively little lipid in February: 18, 21 and 24 %, respectively. All stages stored predominantly triacylglycerols (Fig. 9).

DISCUSSION

Our results from the southeastern Weddell Sea clearly demonstrate that *Calanoides acutus* and *Calanus propinquus* – mainly early copepodite stages – are concentrated in the surface layers (50 to 0 m) in summer, whereas older stages inhabit deeper water layers (1000 to 500 m: *C. acutus*; 500 to 100 m: *C. propinquus*) in winter/spring. This is in agreement with previous descriptions (e.g. Ottestad 1932, 1936, Andrews 1966, Voronina 1972). According to Andrews (1966) the ascent of *C. acutus* in circumpolar waters starts in October, and the population began to appear in deep water layers in February/March. In the Drake Passage the descent of *C. acutus* overwintering stages occurred by late March (Huntley & Escritor in press). In the northern Weddell Sea Hopkins & Torres (1988) found the *C. propinquus* population in March in the upper 150 m, whereas most of the *C. acutus* population was located below 300 m. This indicates that winter descent had already started. Our data suggest that the upward migration was delayed in high Antarctic waters by about 1 mo to mid-November, whereas the descent of *C. acutus* in mid-February did not show a delay as compared to the more northerly regions.

According to Voronina (1972, 1978), *Calanoides acutus* first ascends to the surface in spring and descends again to deeper water layers in autumn. *Calanus propinquus* is thought to follow the same pattern a little later in season. Consequently, in the same water masses the *C. acutus* population should be more advanced than the *C. propinquus* population (Vladimirovskaya 1978, 1979, Voronina 1978, Nakamura et al. 1982, Chojnacki & Weglenska 1984). In the southeastern Weddell Sea in late winter/early spring the *C. acutus* population consisted of older developmental stages than the *C. propinquus* population, especially in mid-November. In summer this was also true below 50 m depth, but no difference in the mean population stage could be observed in the top 50 m of the water column where the bulk of the population was concentrated, dominated by the new generation.

No *Calanoides acutus* males were found in January and February, but in late winter/early spring males made up 5 to 18 % of the whole population. Their occurrence was almost exclusively confined to the layer between 1000 and 500 m, which is in agreement with Vladimirovskaya (1978, 1979) and Marin (1988). These males have reduced mouthparts (Vervoort 1951, Brad-

ford 1988, Schnack-Schiel unpubl.) indicating their short life span. Hence, males may occur in deep water layers only for a short period of time during winter/early spring when mating and fertilization takes place. This is supported by the ascent of fertilized females in mid-November in the Weddell Sea and confirms the results found by Marin (1988). On the other hand, males of *Calanus propinquus* were not restricted to the deeper water layers and occurred at all seasons investigated. Their mouthparts were well-developed. This indicates a more extended longevity and thus a prolonged fertilization period. This is in agreement with Franz (1988) who found *C. propinquus* from eggs to adults in October/November in the upper 200 m, whereas eggs and nauplii of *C. acutus* were not present before the end of November.

In October/early November there was practically no phytoplankton in the water column (Gieskes et al. 1987), but the ascent of *Calanoides acutus* females in mid-November coincided with the onset of sea-ice melting and a subsequent slight increase of chlorophyll *a* in the water column (0.01–0.02 to 0.1–0.2 $\mu\text{g l}^{-1}$; Scharek 1990).

These distributional differences are supplemented by our experimental and biochemical data, which also indicate physiological differences. In early spring (October) older stages of both species did not feed on the ambient phytoplankton concentrations of the water column ($< 1 \mu\text{g chl a l}^{-1}$), although at the end of January feeding occurred below these concentrations. However, clearance rates in the Weddell Sea were about 3 to 4 times lower than in November/December 1980 in the Drake Passage at similar chlorophyll concentrations (Schnack et al. 1985). In the high Antarctic Ross Sea in February gut content analyses showed that both species were still feeding (Hopkins 1985). Near the Antarctic Peninsula in March/April *Calanoides acutus* had ceased feeding, whereas half of the *Calanus propinquus* population had food in their guts (Hopkins 1987). In the Antarctic Peninsula region there were no great differences in feeding behaviour of *C. acutus* and *C. propinquus* in November/December 1980 and February 1982 apart from one station close to the ice edge, where *C. acutus* seemed to be in overwintering condition with relatively low feeding activities (Schnack 1985). At open-water stations in the northern Weddell Sea in March, *C. acutus* and *C. propinquus* had mainly phytoplankton in their guts. Within the pack ice, however, *C. propinquus* had ingested a significantly larger proportion of metazoans (mainly cyclopoid copepods), whereas *C. acutus*, which only occurred below 200 m, had empty guts (Hopkins & Torres 1989).

In the Weddell Sea both species increased their respiration rate during spring and *Calanoides acutus*

changed from non-active to very active swimming behaviour within weeks, as expected when awakening from diapause. *Calanus propinquus* was active throughout this period. The oxygen consumption values determined in this study fit well into the range of previous data (Ikeda & Mitchell 1982, Schnack et al. 1985). Extremely low oxygen consumption rates were published by Hirche (1984) for *C. acutus* CV ($0.086 \mu\text{l O}_2 \text{ mg}^{-1} \text{ DW h}^{-1}$) from the northwestern Weddell Sea in February, probably due to overwintering conditions (diapause) of the specimens.

Furthermore, there are striking differences in the lipid data. The lipid stores of older stages of *Calanoides acutus* (CV, females) had already reached maximum lipid contents in January, whereas *Calanus propinquus* CV stages and females almost doubled their lipid depots from January to February. Hence, they reached similar maximum lipid values at least 3 wk later than *C. acutus*. Lipids in *C. acutus* were accumulated as wax esters, whereas *C. propinquus* stored their energy as triacylglycerols. Previously, calanoid copepods from high latitudes were known to store wax esters as energy resource (Lee et al. 1973). *C. propinquus* is one exception from polar regions deviating from this pattern (Hagen 1988). Based on their investigations on Arctic copepods and euphausiids Sargent et al. (1981) proposed that triacylglycerols are indicators for continuous feeding, whereas wax esters suggest long periods of starvation (Lee & Hirota 1971, Sargent et al. 1981, Sargent & Henderson 1986). Like *C. propinquus*, the Antarctic krill *Euphausia superba* is rich in triacylglycerols but wax-ester-deficient (Clarke 1984, Hagen 1988) and underwater observations revealed *E. superba* living in pack ice crevices during winter/early spring and feeding extensively on ice algae (Daly & Macaulay 1988, Marschall 1988, Stretch et al. 1988). It is unknown whether *C. propinquus* can also utilize this food source. Hopkins' & Torres' (1989) data from the northern Weddell Sea indicate feeding of *C. propinquus* and *E. superba* in March on metazoans.

In summary, our data suggest that both copepod species follow different modes of life ('strategies') as adaptations to the pronounced Antarctic seasonality. *Calanoides acutus* seems to descend to deeper water layers, cease feeding and overwinter in a resting stage (diapause) to save energy during the starvation period. In spring it is the first species to ascend and the females make use of their remaining wax ester reserves to produce offspring. *Calanus propinquus* also descends to mesopelagic waters, but not as deep as *C. acutus* and may overwinter without diapause period. Their spawning period is not restricted to the spring season and small numbers of young stages (CII) are also present when food is scarce. During

these periods *C. propinquus* can utilize their large triacylglycerol reserves or may switch to carnivorous feeding.

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