

Calanoides acutus in Gerlache Strait, Antarctica.

I. Distribution of late copepodite stages and reproduction during spring

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ABSTRACT: *Calanoides acutus* (Giesbrecht) in 0 to 290 m stratified samples collected repetitively at 23 stations in Gerlache Strait, Antarctica, in November 1989 consisted of stage III to VI copepodites (CIII to CVI). All stages except CV decreased in abundance through the 3.5 wk sampling period. Vertical distributions of all copepodite stages remained consistent, with no evidence of diel vertical migration. Centers of mass were as follows: female CVI, 44 m; CV, 66 m; CIV, 127 m; male CVI, 189 m. Progressive ovarian maturation in adult females was not correlated with ambient chlorophyll *a* concentrations. Mean daily egg production at 16 stations over a 3 d period in late November was a hyperbolic function of 0 to 150 m integrated chlorophyll *a* concentrations.

INTRODUCTION

The life history of the Antarctic copepod *Calanoides acutus* (Giesbrecht) has been outlined by Andrews (1966) on the basis of samples taken throughout the Southern Ocean. In general, this species occupies the upper 250 m of the water column in spring and summer. The single generation spawned in spring undergoes diapause as late-stage juveniles in deeper waters through fall and winter, and has been suggested to return to the surface as stage IV copepodites (CIV) (Voronina 1978). On the other hand, because adult males appear to occur only in deep water and have very short life spans, Marin (1988) inferred that mating must occur at depth, and that the ontogenetic ascent must be undertaken by fertilized females. Whichever stage does return to surface waters, overwintered juveniles mature later in the year at higher latitudes, with a corresponding delay in the onset of the spawning season (Voronina 1972, Vladimirovskaya 1978, Schnack-Schiel et al. 1991). This trend may be obscured by mesoscale variations in ice conditions and

water-mass characteristics (e.g. Vladimirovskaya 1980, Marin 1986, 1987).

In the western Bransfield Strait and Palmer Archipelago region, Antarctica, during December 1986 to March 1987, Huntley & Escritor (1991) found no spatial differences in the development rate of juvenile *Calanoides acutus*. However, abundance in the upper 200 m was greater, and the overwintered generation seemed to have spawned and disappeared earlier, in Gerlache Strait than in Bransfield Strait and Drake Passage to the north. Of these areas, Gerlache Strait had the warmest, most vertically stratified waters (Niiler et al. 1990), associated with the highest microbial and phytoplankton standing stocks and productivity (Taylor & Haberstroh 1988, Bailiff & Karl 1991, Holm-Hansen & Mitchell 1991, Karl et al. 1991, Leventer 1991, Mitchell & Holm-Hansen 1991).

Sampling at a finer scale was conducted in Gerlache Strait and the southern reaches of Bransfield Strait in November 1989 to examine the environmental correlates of events in the life history of *Calanoides acutus*. In this paper, we describe the vertical distribution and reproductive maturation of late-copepodite stages of *C. acutus* in Gerlache Strait. These are then discussed in relation to various hypotheses regarding ontogenetic migration of the species.

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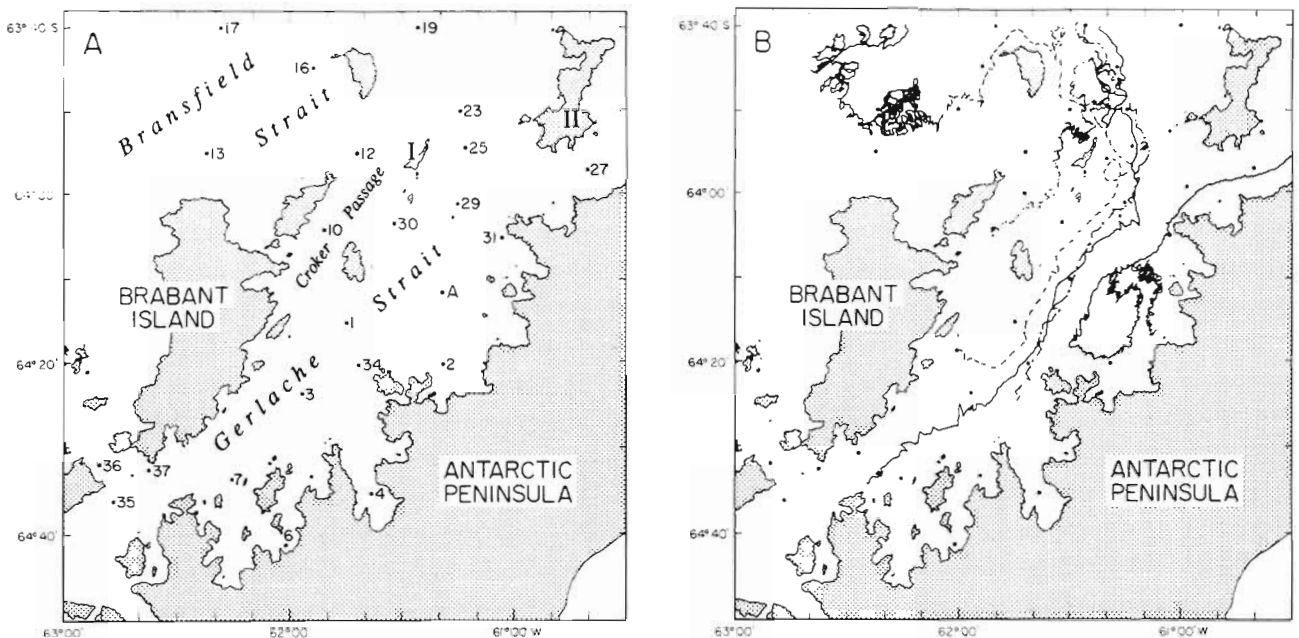


Fig. 1 (A) Gerlache Strait and environs, showing zooplankton sampling stations occupied during RACER, November 1989. I. Intercurrence Island, II. Trinity Island. (B) Tracks of 5 Tristar drifters at 40 m launched November 1989 in Gerlache Strait, showing the jet as it flowed to the northeast, and the eddies flanking it. Data courtesy of P. P. Niiler

MATERIALS AND METHODS

Zooplankton sample collection. Four cruises were conducted in a 4000 km² grid in Gerlache Strait from 30 October through 23 November 1989 (Fig. 1; Table 1). Each cruise began with approximately 3 sampling days at a time-series station (A), followed by sampling at the remaining stations over an additional 3 d. When sea state permitted, zooplankton were collected with oblique tows of a Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS, Wiebe et al. 1976, 1985) with a 1 m² mouth opening. Although 14 of the 23 stations were in areas with soundings >300 m, the net was taken to a standard depth of 290 m to avoid the bottom in the highly variable bathymetry; a single tow was made to 520 m. Tows at 2 to 3 knots at 23 stations were generally completed within 45 min. The entire 290 m column was sampled with a 180 µm mesh net during descent. During ascent, 330 µm mesh nets sampled fixed depth intervals with the following lower limits: 5, 15, 50, 90, 130, 170, 210, 250 and 290 m. At stations where the bottom was shallower, samples were taken only to the standard depth closest to the bottom (250 m: Stns 6, 23, 31 & 36; 210 m: Stns 17 & 13, 170 m: Stns 29 & 30; 130 m: Stn 16). An average of 100 m³ was filtered per net. Filtering efficiency of the nets was assumed to be 100% (Wiebe et al. 1985). Catches were preserved in borate-buffered 10% formalin.

A study of diel vertical migration was conducted at Stn A (bottom depth 325 m) from 02:30 h, 19 November, through 23:30 h, 21 November. MOCNESS tows beginning at the station and heading southeast were made approximately every 90 min. Simultaneous measurements of photosynthetically available radiation (PAR) at the surface were taken with a 2π irradiance meter (Biospherical Instruments, Inc., QSR-230).

Sample analysis and other biological measurements. Copepodite stages of *Calanoides acutus* from the stratified tows were generally enumerated in entire samples. In samples which included more than 500 individuals of a single stage, that stage was enumerated from $\frac{1}{2}$ or $\frac{1}{4}$ of the sample. Depth of the center of mass for each developmental stage at each station was calculated according to the equation:

$$\frac{\left[a_1 \times \frac{H_1}{2} \right] + \left[a_2 \times \left(H_1 + \frac{H_2}{2} \right) \right] + \dots + \left[a_n \times \left(H_1 + H_2 + \dots + \frac{H_n}{2} \right) \right]}{(a_1 + a_2 + \dots + a_n)}$$

where a_n is the abundance (number m⁻²) in layer H_n (Vinogradov 1970).

Reproductive maturity was determined microscopically at a magnification of 200× in unstained, formalin-preserved adult females. We distinguished 6 maturity stages (Table 2) similar to those described in *Calanus finmarchicus* by Marshall & Orr (1955). Ovarian development of *Calanoides acutus* females

Table 1. RACER cruise schedule, 1989

Cruise	Date
FA	14:00 h, 30 Oct – 14:00 h, 5 Nov
FB	20:20 h, 9 Nov – 22:45 h, 12 Nov
FC	04:00 h, 16 Nov – 07:00 h, 19 Nov
FD	01:10 h, 21 Nov – 14:00 h, 23 Nov

was compared across stations using 100 to 120 females from the integrated 0 to 290 m samples. Reproductive maturity in relation to depth within stations was evaluated in all available females (or a maximum of 60 when they were more abundant) from each depth interval.

Egg production of *Calanoides acutus* was determined at Stn A in early November, and at 16 stations from 22 to 24 November. Within 0.5 h after a MOCNESS tow at each station, zooplankton were collected with 0 to 100 m oblique hauls of a 1 m diameter, 330 μ m mesh net equipped with a large-volume (15 l) cod end (Reeve 1981). Adult females were immediately sorted from the catch and stocked in groups of 10 (Stn A) or individually (other stations) in the inner compartment of egg production chambers. Each chamber consisted of a 250 ml polyethylene beaker with a 500 μ m mesh bottom, which was immersed in a 500 ml polyethylene jar containing surface seawater from the same station where the females were collected. An average of 51 females from each station were incubated in the dark for approximately 1 d (range: 0.8 to 1.4 d) at $0.5 \pm 0.5^\circ\text{C}$. Per capita egg production rates were normalized to 24 h. Chlorophyll *a* in water samples taken from a General Oceanics 12 \times 10 l bottle rosette sampler was measured using methods described by Holm-Hansen & Vernet (1990).

Physical environment. Lagrangian flow of surface waters was measured using ARGOS satellite-linked Tristar drifters released at various locations in Gerlache Strait at depths of 15 and 40 m. Drifters were monitored for periods up to 90 d. At each station, temperature and salinity were measured from the surface to the bottom with a Seabird SBE-9 CTD with a high-speed ducted pumping system. Geostrophic calculations resolved a rapid southwest-to-northeast axial current flanked by 2 mesoscale eddies within Gerlache Strait (Amos et al. 1990, Niiler et al. 1990). The axial current accelerated from 15 cm s^{-1} in the south, to a jet of 40 to 60 cm s^{-1} in the region between Stns 3 & 29 (Fig. 1), caused by shoaling of the bottom toward the northeast. The 10 km wide jet persisted in the center of Gerlache Strait throughout the study period, as indicated by drifter tracks (Fig. 1) and hydrographic measurements (Amos et al. 1990, Hu et al. 1991). Water exited Gerlache Strait between Intercurrence and Trinity Islands into Bransfield Strait; however, an intrusion of Bransfield Strait water into Croker Passage was apparent in early November (Amos et al. 1990). Transit times of surface drifters ranged from approximately 5 d when deployed in the central axis of the Strait, to >75 d when deployed in the coastal eddy at Stn A (Niiler et al. 1990).

Although several surface water masses were distinguishable in Gerlache Strait at any given time, Gerlache Strait was generally warmer and more strongly stratified than Bransfield Strait (J.-H. Hu unpubl. data). The upper 50 m of the water column in Gerlache Strait was characterized by temperatures $>0^\circ\text{C}$ and steep salinity gradients, especially in coastal bays of the Antarctic Peninsula. Stronger winds in Bransfield Strait resulted in deeper mixing, and surface temperatures $<0^\circ\text{C}$. During the 3.5 wk

Table 2. Reproductive stages of adult *Calanoides acutus*. Nomenclature given by Marshall & Orr (1955) for corresponding stages in *Calanus finmarchicus* are in parentheses

Stage 1 (immature)	Ovary small. Oviducts and dorsal and ventral channels of anterior diverticulae contain a single row of transparent oocytes. (In some female CV with well-differentiated reproductive systems, oocytes were developed to the same degree within the oviducts. Thus, it is probable that stage 1 females were recently molted.)
Stage 2 (medium)	Ovary larger and more elongated. Oocytes in dorsal channel of diverticulae larger. More than 1 row of transparent oocytes in oviducts.
Stage 3 (semiripe)	Oocytes larger and opaque, light pink, larger in ventral than in dorsal channel of the diverticulae. Ventral, most mature row of oocytes in oviducts still closely pressed against each other and appear polygonal, with margins sometimes indistinct. In some females yellow, granular material envelops oviducts although eggs are visible when exoskeleton is pressed against the ducts.
Stage 4 (ripe)	Ventral row of eggs in oviducts rounded, larger than in stage 3, closely packed. Oviducts do not develop lateral pouches.
Stage 5	As in stage 4, but with empty spaces in the oviducts, suggesting recent expulsion of eggs.
Stage 6 (spent)	Ovaries shrunken. Diverticulae and oviducts empty, the latter appearing as thin lateral bands running to genital segment. Lysing eggs sometimes present at posterior end.

Table 3. *Calanoides acutus*. Depth of center of mass of copepodites in the RACER study area, November 1989. N: number of MOCNESS tows

Location	N	Stage	Mean depth (m)	Stations where mean depth < 90 m (% of total)
Gerlache Strait	73	CIII	80	61
		CIV	127	12
		CV	66	93
		CVI female	44	99
		CVI male	189	4
Coastal bays	9	CIII	68	50
		CIV	150	17
		CV	80	34
		CVI female	66	50
		CVI male	230	0
Bransfield Strait	10	CIII	118	10
		CIV	144	0
		CV	120	10
		CVI female	127	10
		CVI male	197	0

RESULTS

Vertical distribution of copepodite stages

Only copepodite stages III to VI occurred during November; all were assumed to have been quantitatively sampled, given a mean cephalothorax width of 0.55 mm for CIII (Andrews 1966). Late copepodites were distributed at characteristic depth intervals, which varied according to geographic location. Three regions were distinguishable: Bransfield Strait (Stns 12 to 19), coastal bays of the Antarctic Peninsula (Stns 4, 6, 35 & 36), and Gerlache Strait proper. Stages CIV to CVI in Gerlache Strait tended to occupy shallower depths than those in Bransfield Strait and in the coastal bays of

sampling period, insolation and meltwater from continental ice enhanced stratification in both straits. Salinity and temperature ranges below 100 m in both straits were similar (A. Amos, J.-H. Hu & P. Niiler unpubl. data).

the Antarctic Peninsula (Table 3). In all 3 regions, the relative depth distributions of *Calanoides acutus* copepodites were as follows, in order of increasing depth: female CVI, CV, CIV, and male CVI. The relative position of CIII could not be gauged accurately because it

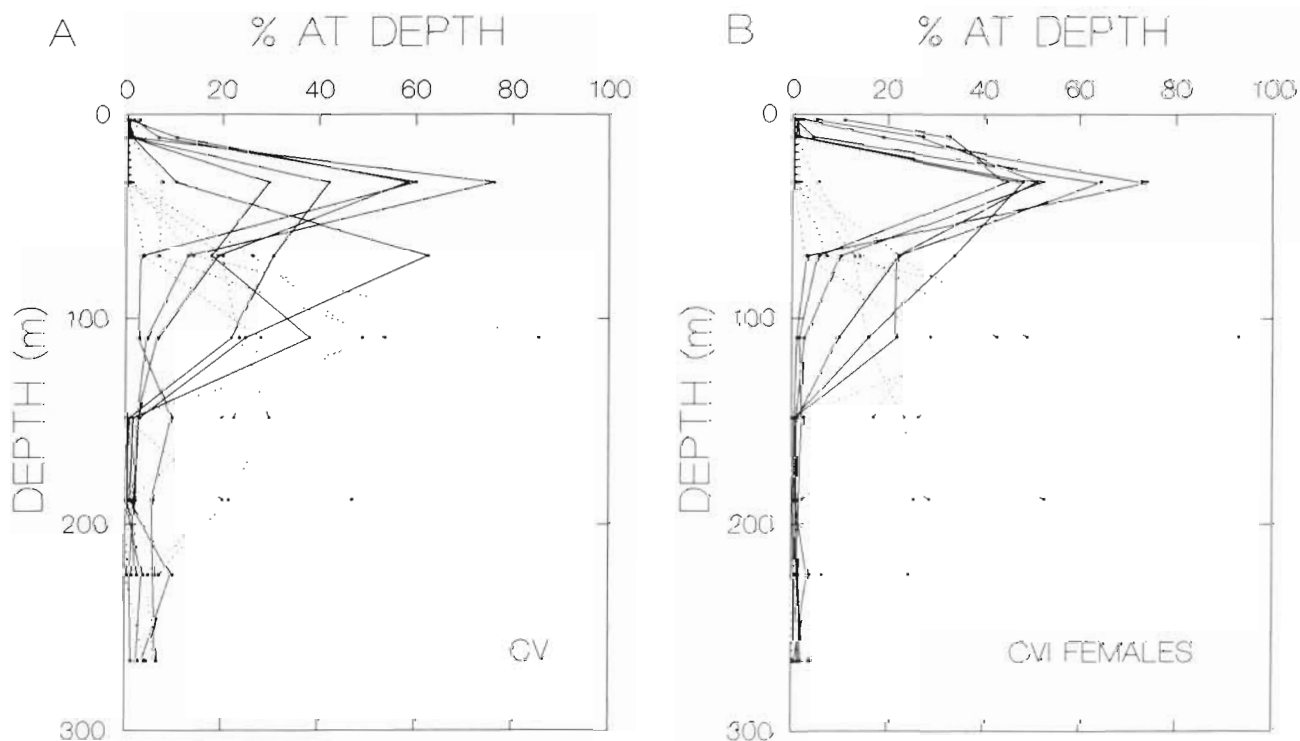


Fig. 2. *Calanoides acutus*. Vertical distributions of (A) copepodite stages CV and (B) female CVI as % of total numbers at 0 to 290 m at all stations in Bransfield Strait (· · · · ·) and Gerlache Strait (—) during Cruise FC. Truncated profiles are for stations < 290 m deep

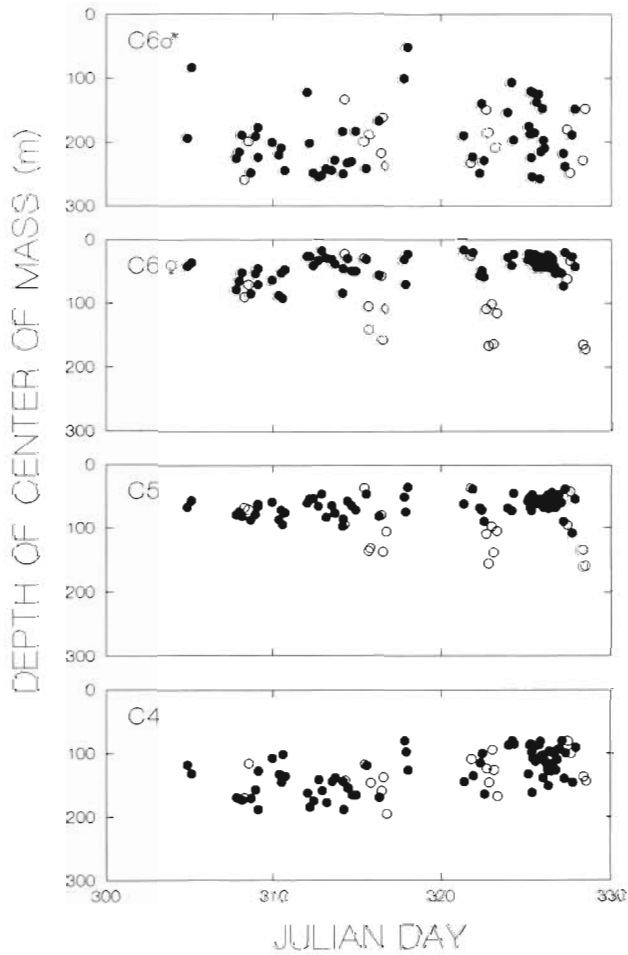


Fig. 3. *Calanoides acutus*. Centers of mass of copepodite stages versus Julian day. (○) Bransfield Strait stations. (●) Gerlache Strait stations

was rare, but it tended to occur near female CVI and CV, and above CIV copepodites. The same relative distribution of copepodites was found in the single 520 m haul. As in the shallower stations, abundance was greatest in the upper 100 m; CIV copepodites comprised a minor abundance peak below 250 m.

Aggregation and regional differences in vertical distribution were more distinct for CV and female CVI than for CIII, CIV or CVI males. During Cruise FC, when areal coverage was greatest, >40% of all CV were found in the 15 to 50 m interval at most Gerlache Strait stations, whereas they occurred mainly at 90 to 170 m in Bransfield Strait (Fig. 2A). Approximately 20% of adult females in Gerlache Strait were found in the upper 15 m, and an additional 43 to 76% occurred between 15 and 50 m. At Bransfield Strait stations, >80% of adult females occurred at depths below 50 m, with the highest abundances observed in the 90 to 130 m interval (Fig. 2B). The total abundance of all

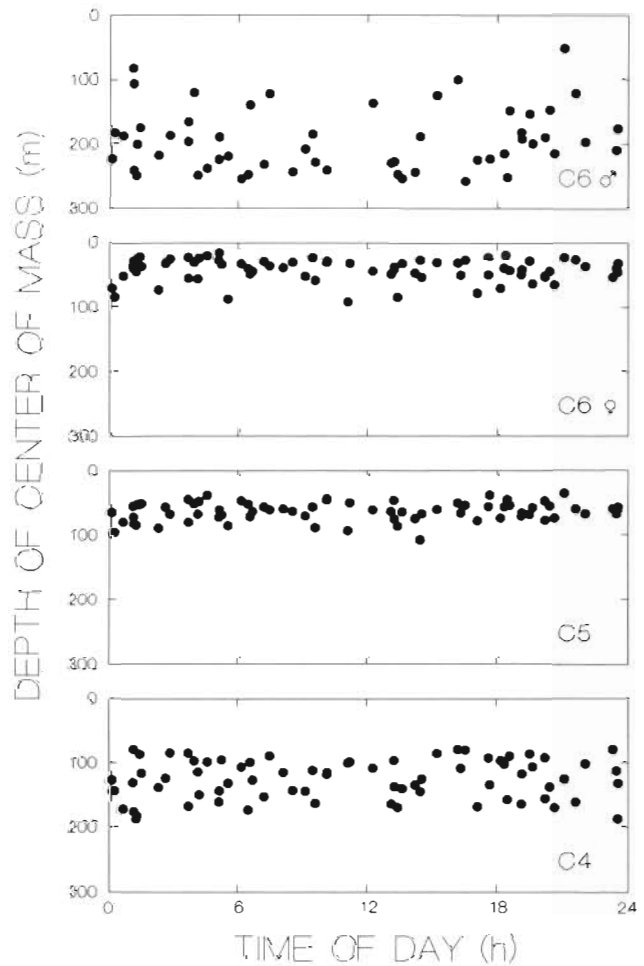


Fig. 4. *Calanoides acutus*. Centers of mass of copepodite stages in Gerlache Strait population versus time of day. (Values for samples from Bransfield Strait, which were collected mainly during daytime, are not shown)

stages in the upper 290 m was approximately the same in both straits.

There was no systematic change in the depth of the center of mass of each stage with respect to sampling date over the 3.5 wk sampling period, although CV and CVI were deeper in Bransfield Strait (Fig. 3). There was no evidence of change in the vertical position of any copepodite stage in Gerlache Strait with respect to time of day (Fig. 4).

Combining data from many stations over an extended period could obscure the existence of diel vertical migration behavior at a single locality. To address this concern, we analyzed the depth distributions of late-copepodite stages at Stn A with respect to time of day, surface light intensity and chlorophyll *a* concentration, from a set of 32 MOCNESS tows taken over a period of 44 h. There was no evidence of diel vertical migration at Stn A (Fig. 5). Through 2 diel

cycles, 67 to 88% of all copepodite stages between 0 and 290 m remained within the upper 90 m. Absolute abundances of all stages decreased in concert by a factor of approximately 3 only on the morning of the second day, and increased again in the late afternoon and evening. The variation in abundance appeared unrelated to the diel cycle. Most adult females occurred just below the surface chlorophyll maximum of $\sim 10 \text{ mg}^{-3}$, whereas greatest abundances of CIV and CV copepodites occurred at greater depth ($< 1 \text{ mg chl a m}^{-3}$).

Reproductive stages

The proportion of adult females with immature ovaries (Stages 1 & 2) decreased from about 30% in early November to less than 10% within 3 wk; those with developing gonads (Stages 3 to 5) increased from 60 to 90% in the same time period (Fig. 6). At Stn A, the percentage of females with Stage 3 to 5 ovaries increased from 50 to 90%, with no apparent diel cycle in ovarian maturation (Fig. 7). The majority of females, most of which had ripe and seminripe ovaries, were found in the upper 90 m; spent females were few and tended to occur below 90 m (Lopez 1991). Station-to-station variation in ovarian development was not related to ambient chlorophyll *a* concentrations (Fig. 8). Over a range of 50 to 600 mg chl a m^{-2} , about 20% of female CVI were in reproductive Stages 1 & 2, while approximately 80% were in Stages 3 to 5.

Spawning females were observed throughout the study area in late November. During Cruise FD, the percentage of ripe and semi-ripe females (Stages 3 to 4) in preserved samples was positively correlated with the percentage of females which spawned over 1 d incubation periods. The regression equation for arcsine-transformed percentages was

$$\% \text{ spawned} = 24.3 + 0.65 \times \%(\text{Stages 3+4})$$

$$(r^2 = 0.401, p < 0.05)$$

The average number of eggs per spawning female was related to 0 to 100 m integrated chlorophyll *a* as follows:

$$\text{Eggs spawned d}^{-1} = \frac{43.2 (\text{CHL} + 14.7)}{75.7 + (\text{CHL} + 14.7)}$$

where CHL is in mg chl a m^{-2} (Fig. 9). Frequency dis-

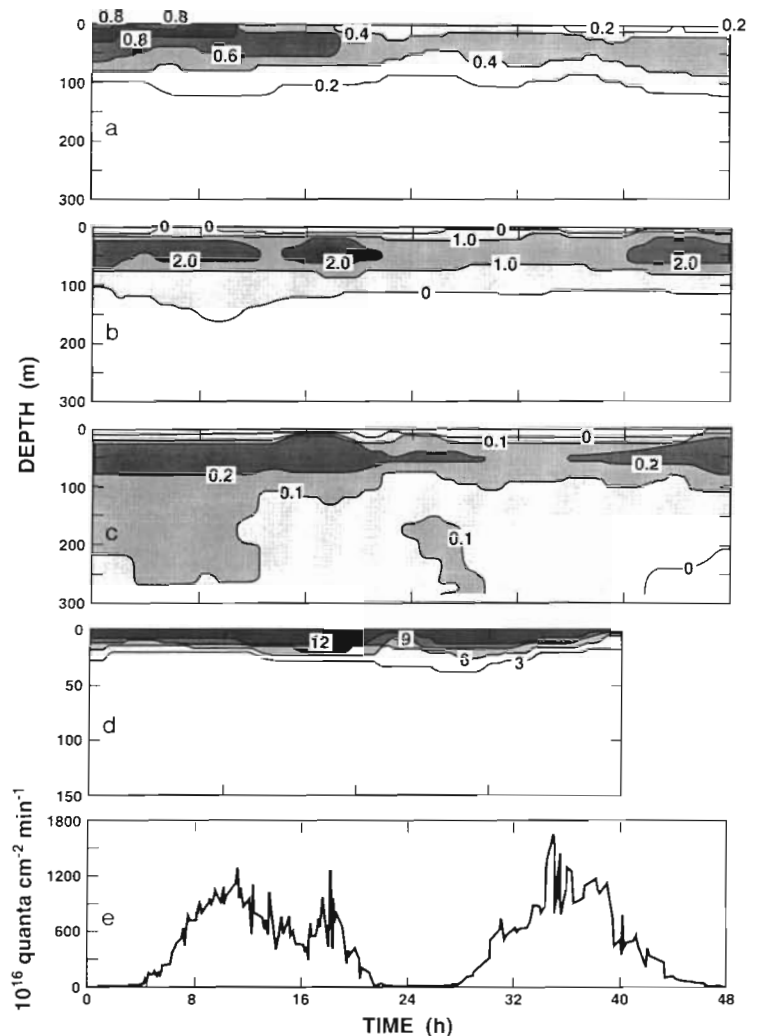


Fig. 5. *Calanoides acutus*. Contours of vertical distribution of copepodite population at Stn A through a 44 h period, 20 to 21 November. (a) CVI females; (b) CV; (c) CIV; (d) chlorophyll *a*; (e) PAR at sea surface. Values are copepodite numbers m^{-3} in panels a to c, and mg chl a m^{-3} in panel d. Chlorophyll and PAR data courtesy of O. Holm-Hansen and M. Vernet

tributions of per capita egg production were bimodal (Fig. 10). As integrated chlorophyll *a* concentrations increased, the mode of 1 to 10 eggs d^{-1} decreased in importance while the second mode shifted toward larger classes. Mean egg production ranged from 4 to 37 eggs $\text{female}^{-1} \text{ d}^{-1}$ (Table 4). The highest daily production by a single female was 118 eggs. This exceeds the number of ripe eggs counted in large preserved females with full oviducts (range: 54 to 72 eggs; $n = 10$), suggesting that spawning cycles may take less than 24 h when food is abundant.

Calanoides acutus eggs observed within 24 h of being spawned were enclosed in a spiny outer membrane. The time required for the spines to develop

after spawning was not determined. Formalin-preserved eggs had an inner diameter of 148 μm (SD = 4 μm) and an outer diameter of 210 μm (SD = 8.5 μm), excluding the spines ($n = 20$). Applying these dimensions to the carbon:volume relationship determined by Huntley & Lopez (1992), egg carbon content would be between 0.24 and 0.68 μg .

Assuming a mean weight of 135 $\mu\text{g C female}^{-1}$ (Schnack et al. 1985), and a minimum of 0.24 $\mu\text{g C egg}^{-1}$, egg production of adult females at the 16 FD stations would have been at least 1.1 to 6.9% body carbon d^{-1} (Table 4). Further assuming that gross efficiency of egg production is 0.33 (H.-J. Hirche & U. Meyer pers. comm.), the minimum daily carbon ration of spawning female *Calanoides acutus* would have ranged from 3.3 to 20.7% d^{-1} (mean = 12.8, SD = 5.04).

DISCUSSION

Vertical distribution

The tendency of *Calanoides acutus* copepodites to remain in the upper 90 m in Gerlache Strait while occupying deeper strata in Bransfield Strait is consistent with observations made over a larger area in the same region by Huntley & Escritor (1991). This variation was not correlated with the vertical distribution of either phytoplankton or total microbial biomass, both of which were most abundant in the upper 50 m of the 2 straits (Taylor & Haberstroh 1988, Holm-Hansen & Vernet 1990, Tien et al. 1990, Bailiff & Karl 1991, Holm-Hansen & Mitchell 1991, Karl et al. 1991, Leventer 1991, Mitchell & Holm-Hansen 1991). The greater depth of the mixed layer in Bransfield Strait may have influenced regional differences in centers of mass of CV and female CVI. Centers of mass of CIV, which were well below the mixed layer, were similar in both straits.

We found no consistent relationships between depth distributions of copepodite stages and physical characteristics of the water column, except that CIV tended to occur at salinities in the range 34.4 to 34.5‰. In general, all stages appeared to avoid regions of strong temperature gradients ($\sim 0.02^\circ\text{C m}^{-1}$), whether near the surface or at depth. However, our data set includes frequent exceptions: abundance maxima were sometimes found where temperature gradients were $> 0.3^\circ\text{C m}^{-1}$, but order-of-magnitude changes in abundance also occurred at gradients $< 0.01^\circ\text{C m}^{-1}$. A rigorous test of the association is difficult because spatial resolution for copepod abundance was much coarser (40 m intervals) than that for temperature measurements. There was no clear avoid-

ance of any specific temperature range. Depth of the water column was also not a factor: at some shallow stations in Bransfield Strait high abundances occurred in the deepest sampling interval, but this was not observed at shallow stations in Gerlache Strait. We cannot say why late-stage copepodites occurred at greater depth in Bransfield Strait than in Gerlache Strait, but we suspect that the phenomenon is a behavioral response to the local environment.

Any single vertical profile of copepodite stage abundances in the water column during spring would also reflect the effects of ontogenetic migration behavior. Voronina (1978) suggested that the spring ascent is undertaken by CIV copepodites, while Marin (1986) proposed that it takes place after molting into CVI. In our samples, CV centers of mass were generally within the photic zone, supporting a post-diapausal ascent prior to adulthood. On the other

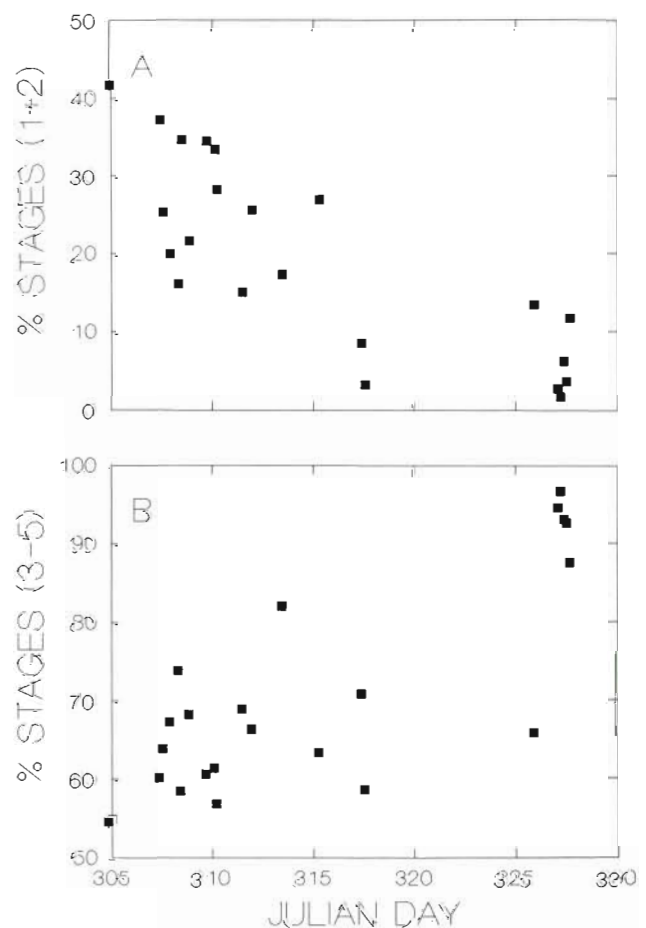


Fig. 6. *Calanoides acutus*. Percentages of reproductive stages of adult females during the study period from early through late November. (A) Percentage immature and medium (Stages 1 & 2) females; (B) percentage semiripe, ripe and spawning (Stages 3 to 5) females

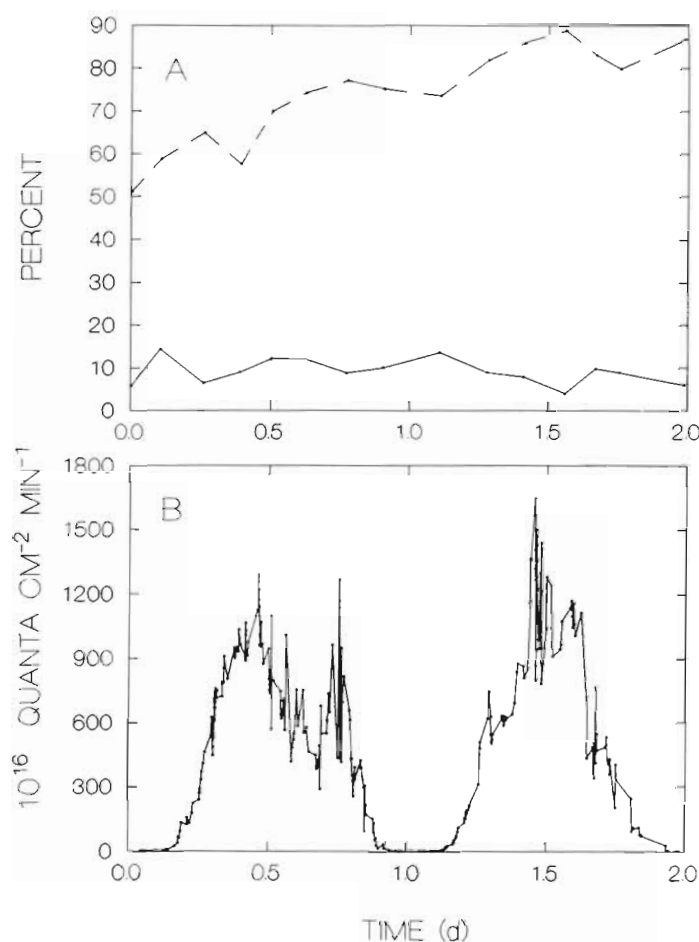


Fig. 7 *Calanoides acutus*. (A) Percentages of reproductive stages of adult females over a 44 h period at Stn A, 20 to 21 November, showing combined Stages 1 & 2 (—) and Stages 3 to 5 (---). (B) PAR during the same period

hand, Schnack-Schiel et al. (1991) showed migration primarily by adult females from deep water in the Weddell Sea. Thus both proposed migration scenarios do occur. In general, variation in the vertical distribution of *Calanoides acutus* copepodite stages sampled at different locations at the same time of year is common (e.g. Vladimirovskaya 1978, 1980, Voronina 1978, Marin 1986). On occasion, *C. acutus* is more abundant in the upper 100 m than in deeper water even during winter (e.g. Ward 1989, Marin & Schnack-Schiel 1993). The developmental stage which returns to the surface would depend on development rate, which would be influenced by water temperature, and probably by the amount of lipid reserves in diapausing copepodites, as well as food availability in deep water. Water column depth may be a contributory factor because maturation is more likely to be completed before attaining the surface where water is sufficiently deep.

Diel and ontogenetic vertical migration

No diel changes were evident in the vertical distributions of CIV to CVI copepodites in the composite data set or in the 2 d sample series at Stn A. Previous studies addressing vertical migration by *Calanoides acutus* compared day and night samples collected from different areas at different times of year. These yielded conflicting conclusions because diel migrations could not be distinguished clearly from larger-scale variations in vertical distribution. For example, in analyzing samples from the Discovery Collection, Andrews (1966) concluded that *C. acutus* undergoes diel migrations in the summer, while Hardy & Gunther (1935) found no discernible migrations using only samples from South Georgia obtained during the same expedition. Huntley & Escritor (1991) were also unable to find diel changes in the vertical distribution of *C. acutus* copepodites.

In our data set, differences in the centers of mass of each copepodite stage were unrelated to the diel light cycle. This does not preclude diel cycles in active swimming in response to tidal shifts in order to remain within the surface layer, as suggested by Bogorov (1946). This possibility cannot be addressed using our samples which integrate abundances over depth intervals greater than the tidal amplitude. Using a Longhurst Hardy Plankton Recorder near South Georgia, Atkinson et al. (1992) showed that CIV to CVI *Calanoides acutus* migrate from a median depth of 70 m during the day to 20 m at night. They pointed out that the use of median rather than modal depths can lead to different conclusions about changes in vertical distributions. Had *C. acutus* in Gerlache Strait been vertically migrating between 20 and 70 m, our sampling procedure would have detected it.

The depths of centers of mass of different copepodite stages in Gerlache Strait suggest that CIV had undergone diapause at depth, whereas molting from CV into CVI occurred mainly in the upper 100 m. The rare occurrence of adult males in surface waters and the reduction of their feeding appendages would imply a brief mating season and a short male life-span restricted to deep water (Vervoort 1951, Vladimirovskaya 1978, 1980, Zmijewska 1985). Thus, Marin (1988) suggested that the spring migration must be undertaken by fertilized females. Vertical profiles of *Calanoides acutus* abundance in the Weddell Sea clearly show that only adult females ascended en masse (Schnack-Schiel et al. 1991). On the other hand, the present data demonstrate that postdia-

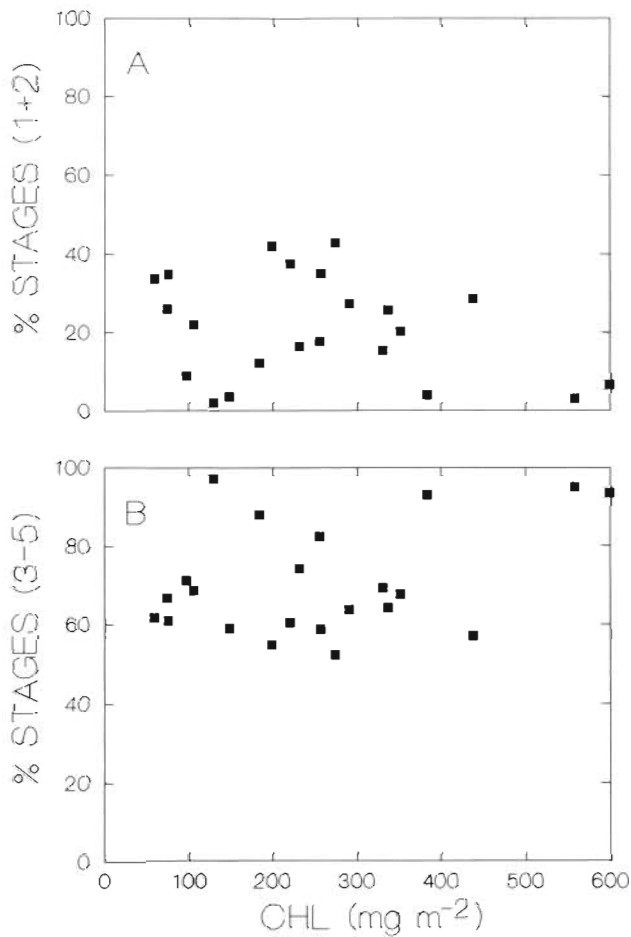


Fig. 8. *Calanoides acutus*. Relationship between reproductive stages of adult females and chlorophyll *a* (mg m⁻²) at Gerlache Strait stations. (A) Percentage of Stage 1 & 2 females. (B) Percentage of Stages 3 to 5 females

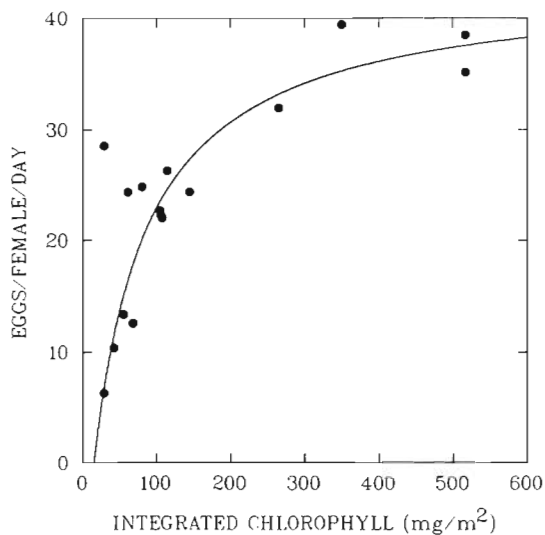


Fig. 9. *Calanoides acutus*. Mean eggs female⁻¹ d⁻¹ within Gerlache Strait versus 150 m integrated chlorophyll *a* concentration, 21 to 23 November 1989

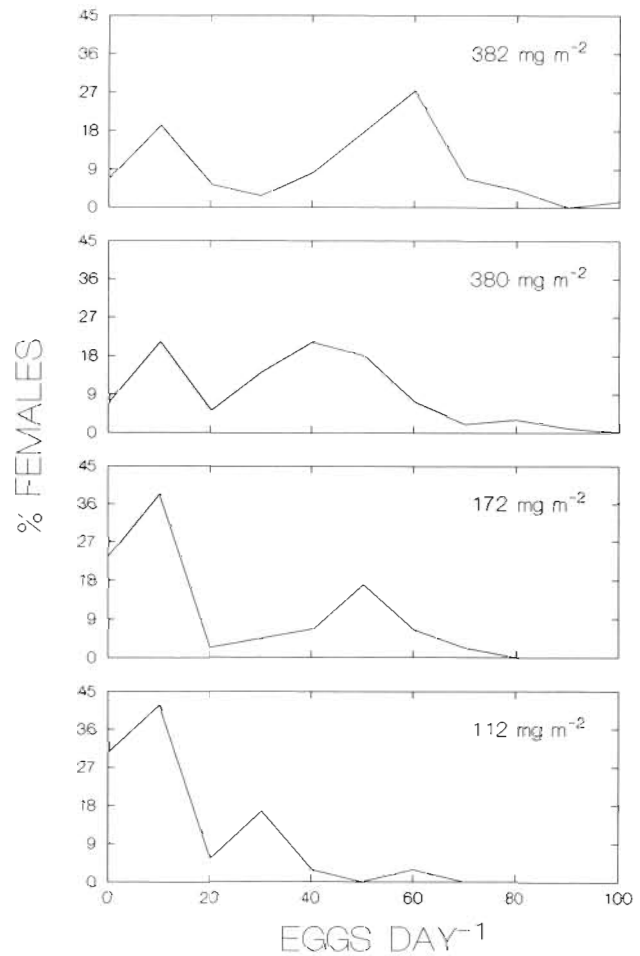


Fig. 10. *Calanoides acutus*. Frequency distributions of per capita egg production normalized to 24 h at 4 stations differing in standing stock of chlorophyll *a* (mg m⁻², 0 to 150 m)

pausal juveniles as well as adult males can attain the upper 200 m when water depth is less than 500 m. There may have been an advective component to the ontogenetic ascent of *C. acutus* in Gerlache Strait, from localized jet-induced mesoscale upwelling (Woods 1988).

Mass migration by CV copepodites to the deep water column was not detectable, and therefore the presence of adult males in the upper 100 m of Gerlache Strait is to be expected. It is perhaps more surprising that males were not found in greater numbers, even at stations where the entire water column was sampled. We found male:female ratios ranging from 0.0003 to 0.02 in the upper 290 m. The highest ratio (0.1) was for the 520 m water column sampled at Stn 35. In 0 to 1000 m samples, male:female ratios for adult *Calanoides acutus* range from 8.5–29.8 for the entire water column in late winter (Marin 1988) to 0.02–1.1 at different depths in early spring (Schnack-

Table 4. *Calanoides acutus*. Daily egg production in Gerlache Strait, 21 to 23 November. N: number of individual females in experiment; Int. chl: 0 to 50 m integrated chlorophyll a concentration

Stn	N	% Spawned	Eggs female ⁻¹ d ⁻¹		% Female body carbon	Int. chl (mg m ⁻²)
			Mean	Range		
1	66	89	20	0.7–57	3.9	160
3	77	88	22	0.8–96	4.3	182
4	29	76	17	0.8–58	4.0	128
6	50	100	35	0.8–58	6.2	549
7	73	93	37	0.9–99	6.9	382
12	8	93	4	0.7–24	1.1	56
16	10	60	6	1.1–54	1.8	65
19	37	68	9	0.7–53	2.2	112
23	46	76	10	0.8–80	2.4	85
25	16	81	20	0.9–46	4.3	117
27	55	91	26	0.9–71	3.9	172
29	47	77	17	0.9–66	3.9	172
30	49	86	23	1.1–81	4.7	162
31	21	90	22	1.2–71	4.4	100
33	21	70	22	1.2–118	5.6	282
A1 ^a	69	93	36	8–95	6.8	557
A2a ^a	32 ^b	–	20	8–33	–	329
A2b ^a	13 ^b	–	15	1–29	–	73
A4a	99	93	29	0.8–81	5.5	380
A4b	62	94	30	0.9–68	5.7	421
A4c	99	92	12	0.8–64	2.4	231

^aExperiments conducted in the first week of November. ^bNumber of replicates, 10 females per replicate

Schiel et al. 1991). It might be argued that males had already died off in Gerlache Strait during our study. This would imply that the remaining CV copepodites would produce only females, which would then have extremely low chances of reproducing. Alternatively, maturation might occur in discrete pulses (i.e. adult recruitment is not continuous), such that the adults we sampled were senescing remnants of an earlier pulse, with the remaining CV copepodites then giving rise to an entirely new set of adults, male and female, in the following weeks.

The present observations are not the only exceptions to generalizations regarding the timing of ontogenetic migration and the stages which do so in *Calanoides acutus*. Marin (1987) noted that mesoscale variations in the stage composition of *C. acutus* populations are probably related to water-mass distributions and mixing processes, via their effect on food accessibility, and thus on breeding schedules and development rates. To begin with, some populations may go into diapause primarily as CIV, although development frequently advances to CV prior to overwintering (Table 2 in Andrews 1966; Marin 1987, Huntley & Escritor 1991, Marin & Schnack-Schiel 1993). It follows that variations in timing of the subsequent return to the surface and in the developmental stages involved might also be expected (Vladimirovskaya 1978, Marin 1986, Atkinson 1989).

Female reproductive condition and spawning

The copepodites we collected belonged to the overwintered generation. Because *Calanoides acutus* was the dominant copepod in the study area, it is likely that large stage IV and V calanoid nauplii in our 180 µm net catches in mid-November represented the new generation of this species. Our analysis of the population dynamics of overwintered copepodites suggests that most spawning probably took place in early October, when female CVI were more abundant (Huntley et al. in press). Huntley & Escritor (1991) found a well-developed summer generation dominated by stage CII in Gerlache Strait in mid-December. They predicted that *C. acutus* should have been mainly at CI in late November, if development is isochronal. However, laboratory observations of an Arctic copepod, *Calanus hyperboreus*, suggest that, like lower-latitude species, younger stages of polar species have shorter stage durations (Conover 1967). This would support our view that the main spawning event must have occurred in October. The abundance of overwintered juveniles in early October, as projected by our population dynamics model (Huntley et al. in press), was an order of magnitude greater than we observed during November. Thus, even if the juveniles we found in November eventually molted and reproduced, the resulting progeny would have been a small fraction of those produced in October.

From a large number of circumpolar samples, Andrews (1966) concluded that significant spawning by *Calanoides acutus* does not occur until November, with peaks in December and January. Our observations indicate that spawning in Gerlache Strait had been in progress from at least early November, and probably early October, since we found spent females as well as late-stage nauplii presumably belonging to this species in mid-November. This corroborates a previous observation that development and maturation occurred earlier in Gerlache Strait than in the northern Bransfield Strait and Drake Passage (Huntley & Escritor 1991). In the absence of diel migration below 100 m, adult females may remain in the surface layer through most of their reproductive lives. Immature and medium (Stages 1 & 2) females in deep water may have been reascending, assuming that copepods sink during the quiescence associated with molting (A. Fleminger pers. comm.). Semiripe and ripe (Stages 3 & 4) females found below 100 m could have been senescent and sinking prior to the final spawning episode. It is also possible that such females had molted at depth and were still en route to the surface, but had been able to feed sufficiently, despite the low average microbial biomass below 50 m (Tien et al. 1990). Mature females have been found below 500 m in September, prior to the spring migration (Table 12 in Andrews 1966).

The progressive reproductive maturation of *Calanoides acutus* females in Gerlache Strait was unrelated to ambient chlorophyll *a* concentrations (Fig. 7). Because the gonadal cycles of temperate copepods are usually shorter than 1 d, their reproductive condition reflects ambient food availability reasonably well (e.g. Runge 1985, Williamson & Butler 1987). However, spawning intervals in Arctic species such as *Calanus finmarchicus* and *Calanus glacialis* are typically 2 to 3 d (Hirche & Bohrer 1987, Hirche 1990). Over such periods, large fluctuations in chlorophyll *a* concentration can occur within the same location within Gerlache Strait (Holm-Hansen & Vernet 1990), accounting for the absence of a correlation between reproductive maturation of *C. acutus* and their food supply.

The long-term trends in Fig. 6 may instead reflect the slower maturation rate preceding initial spawning by young females. The ontogenetic ascent of *Calanoides acutus* continues for several months (Andrews 1966), during which molting from CV to CVI occurs. Newly molted females may require approximately 10 d of feeding before starting to spawn (Huntley & Lopez 1990). In other copepod species, the period between the final molt and initial spawning may be several multiples of subsequent spawning intervals (e.g. Conover 1967, Paffenhöfer 1970, Runge 1984). If females sampled in early November had indeed just molted, and if

the attrition in numbers through the remainder of the month was due to senescence, the implication is that physiological death of adult females occurs within a few weeks of the last molt.

Egg production

The best-fit Michaelis-Menten function relating average egg production to ambient chlorophyll suggests a threshold concentration of 14.7 mg chl *a* m⁻². Thus, chlorophyll concentrations in early October (Holm-Hansen & Vernet 1990) would have been insufficient to support egg production by *Calanoides acutus*. This narrows our estimate for the onset of spawning to the latter half of October (cf. Huntley et al. in press). With the preceding assumptions about egg and female carbon content and gross efficiency of egg production, weight-specific egg production rates by *C. acutus* at the highest *in situ* chlorophyll *a* concentrations are similar to estimates for other large, high-latitude copepods fed in excess (5.5 to 9.6%: Hirche & Bohrer 1987, Peterson 1988, Hirche 1990). The range of egg production and ingestion estimates in terms of carbon closely overlap the growth and feeding rates directly measured in *C. acutus* females by Schnack et al. (1985).

Population dynamics

Those aspects of the life cycle of *Calanoides acutus* examined in this paper – the vertical distribution of maturing copepodites and their subsequent reproduction – do not provide sufficient information to describe the dynamics of the overwintered population. The first requirement for conducting an analysis of population dynamics is to identify the population itself in space and time. There are no indications in the data presented here to suggest that *C. acutus* occurring in the Gerlache Strait belonged to more than a single population. We observed strong similarity of vertical distributions, presumably related to ontogenesis, and regional coherence in ovarian development. A demographic analysis of this presumptive population which considers the effects of physical and biological factors on its abundance is detailed in Huntley et al. (in press).

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