

Diel feeding behaviour of krill in the Gerlache Strait, Antarctica

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ABSTRACT: Abundance, gut fluorescence and gut content of juvenile krill *Euphausia superba* (15 to 20 mm) were measured during a diel cycle in the Gerlache Strait (Antarctic Peninsula). Krill remained in the upper layers (0 to 100 m) during the day and migrated downward below this depth during the night, coinciding with the vertical ascent of the copepod *Metridia gerlachei* to shallower layers. Krill fed on phytoplankton during the day (as deduced from gut fluorescence measurements), whereas they switched to carnivory during the night (as deduced from gut contents). The vertical migration and the feeding behaviour of krill agree with different observations in the literature and gives an additional explanation to the observed inverse relationship between krill and non-krill zooplankton. The fact that krill is able to prey on mesozooplankton suggests that euphausiids can exert a top-down effect which structures the plankton community of Antarctic waters.

KEY WORDS: Feeding · Vertical distribution · Zooplankton · Antarctica

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INTRODUCTION

An important milestone of bio-oceanographic research in polar waters is the study of the structure and dynamics of plankton communities as the basis to understand its economy (i.e. energy flux) and how changes in environmental conditions can affect population dynamics. In Antarctic waters, *Euphausia superba* (hereafter 'krill') have an important role in the presence/absence and on the development of many species of birds and mammals. However, little is known about the cues for aggregation, swarm formation, vertical migration, distribution and behaviour of these crustaceans.

Historically, euphausiids have been considered as efficient grazers and most of the studies of their energy budget have been focused on their impact on the phytoplankton crop and primary production (e.g. Que-

tin et al. 1994, Pakhomov et al. 1997, among others). However, krill are able to prey upon other zooplanktonic organisms such as copepods (Price et al. 1988, Hopkins & Torres 1989, Granéli et al. 1993, Nishino & Kawamura 1996, Atkinson & Snýder 1997) as well as to be cannibalistic (Nishino & Kawamura 1994). On the basis of energetic requirements, it has been suggested that *E. superba* has to consume a much larger proportion of heterotrophic carbon than previously supposed (Perissinotto et al. 1997). Cripps et al. (1999) also observed krill surviving on low algal biomass areas in the South Georgia region, suggesting that they probably resorted to carnivory on copepods rich in polyunsaturated fatty acids (PUFA). During the same cruise, it was found that protozoans and copepods supplied most of their carbon intake (Atkinson & Snýder 1997). The latter authors also found that krill preyed upon copepods in the range of 1 to 3 mm (the most common size of large copepods in Antarctic waters) at the fastest rates. Moreover, Perissinotto et al. (2000)

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observed that the heterotrophic component of the mass gut content accounted for an average value of 79%.

It has been shown that krill can switch from algal to animal food and that there is a positive electivity on copepods when they are exposed to both kinds of food (Granéli et al. 1993). Recently, Atkinson et al. (1999) showed that areas of persistently high krill abundance were characterised by exceptionally few copepods. Copepods also appeared to live deeper and to make more extensive vertical migrations when krill were present. Therefore, based on experimentally obtained predation rates on copepods and on krill biomass, they suggested that copepod numbers can be controlled by a combination of competition and predation by krill.

During 2 surveys in December 1991 and February 1993, very low values of zooplankton (<14 mm) biomass were found around the Antarctic Peninsula (Hernández-León et al. 1999, 2000) and most of the large copepod abundance was found to be the strong diel vertical migrant *Metridia gerlachei* (see Lopez & Huntley 1995). To study the vertical distribution of krill *Euphausia superba* and the migratory pattern of *M. gerlachei*, we sampled the abundance of those organisms in the upper 600 m. We also analysed animals for gut content in order to investigate their feeding behaviour. The results presented below indicate that krill can play an important role in structuring the plankton communities in Antarctic waters as deduced from their switch to carnivory and the long-term changes in krill and copepods in these waters.

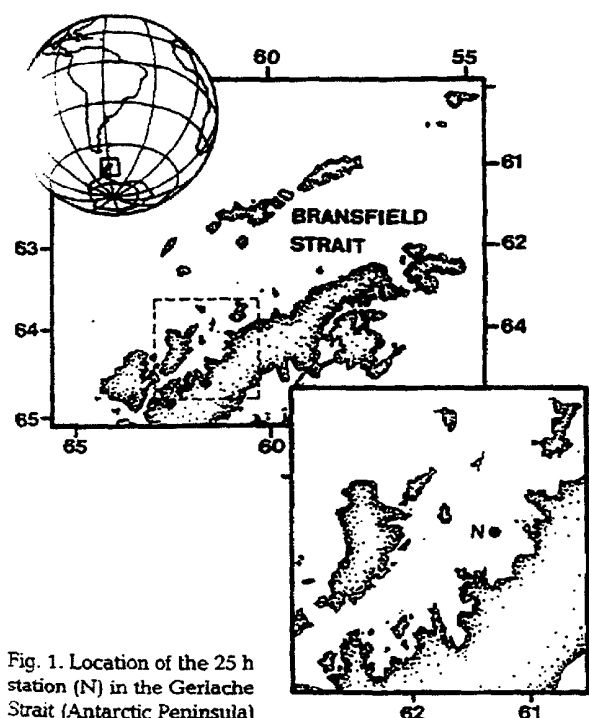


Fig. 1. Location of the 25 h station (N) in the Gerlache Strait (Antarctic Peninsula)

MATERIALS AND METHODS

Zooplankton abundance was sampled from 9 to 10 February 1993, in the waters between the Gerlache and Bransfield Straits (Fig. 1) during a 25 h station. Samples were obtained by means of a 1 m² BIONESS net (Sameoto et al. 1980) equipped with 10 nets of 200 µm mesh size. The net was deployed every 2 h (except at 19:00 h on the first day, where the interval was 3 h) in order to sample the 0 to 20, 20 to 50, 50 to 100, 100 to 200, 200 to 400 and 400 to 600 m layers. The net filtered between 86 and 437 m³ of seawater in the upper layer and between 610 and 916 m³ in the lower layer. Temperature and salinity were obtained by using a CTD sensor, and samples for chlorophyll were obtained with Niskin bottles.

To study the feeding behaviour of euphausiids and copepods, we measured the gut fluorescence (Mackas & Bohrer 1976) and stomach contents of krill during a diel cycle at the different depths. Both measurements might have been affected in animals trapped on the cod-end of the net. Atkinson et al. (1992a) found that samples taken at different depths in a Longhurst-Hardy Plankton Recorder (LHPR) did not introduce errors other than those described in the literature, i.e. pigment degradation and partial gut evacuation. The BIONESS net do not preserve the animals motionless as in the LHPR net. Therefore, the possibility of ingestion during the catch exists, although it must affect gut fluorescence and stomach content in all the samples. However, although krill were caught by day and night in the upper layers, the gut fluorescence appeared higher only during the day (see below). The inverse can be said of the stomach content. Thus, the variability found should be related to feeding prior to the capture.

Between 5 and 15 adults or CV-stages of *Metridia gerlachei*, and 1 to 5 specimens of the most abundant size class (15 to 20 mm) of krill were immediately sorted after the net arrived on board for gut content analysis. Gut fluorescence was determined using the procedure described by Morales et al. (1990). Individuals were placed in a test tube with 10 ml of 90% acetone and stored at -20°C (for 24 h) for gut pigment analysis. Fluorescence of the samples was measured before and after acidification with 2 drops of 10% HCl in a fluorometer (Model 10, Turner Designs, Sunnyvale, CA) previously calibrated with pure chlorophyll (Yentsch & Menzel 1963). Pigments were calculated with the equations given by Strickland & Parsons (1972) slightly modified to:

$$\text{Chlorophyll} = k(F_0 - F_a)/N$$

$$\text{Pheopigments} = k(RF_a - F_0)/N$$

where k is the machine calibration constant, F_0 and F_a are the fluorescence readings before and after acidification, and R is the acidification coefficient and N is the number of individuals. Gut pigment concentration in this study refers to the addition of chlorophyll and pheopigments. Because no attempt was made to calculate grazing rate, no correction was made for background fluorescence and for pigment loss.

In the laboratory, *Euphausia superba* and *Metridia gerlachei* were sorted and counted; the former were also measured and grouped in 1 mm intervals. The stomach content of *E. superba* was analysed by microscopic examination of the suspended gut content on slide preparations. The hindgut of these organisms (15 to 20 mm) was too small and no attempt was made in order to analyse its content. Items were examined at magnification of $\times 40$ to $\times 600$ depending on their sizes. Counts were made of all the crustacean fragments (mainly appendages) within the whole preparation.

RESULTS

Temperature and salinity showed low variability during the diel cycle studied and chlorophyll was $>1 \text{ mg m}^{-3}$ in the upper 10 m layer (Fig. 2). The vertical distribution study of *Metridia gerlachei* showed high abundance at the 400 to 600 m layer during the day, with the population ascending during the night to shallower layers where their gut fluorescence increased

(Fig. 3) as the result of feeding in the surface chlorophyll-rich layer. This higher gut content also remained during their downward migration at dawn, decreasing at the end of the cycle studied. Numbers of other large copepods such as *Calanoides acutus* and *Rhincalanus gigas* were very low, and the only pattern observed was the higher gut pigment content at night (not shown).

The euphausiids sampled by the BIONESS net were measured (3380 individuals, Fig. 4) and 3 size classes with a normal distribution were obtained (7 to 13, 15 to 25 and 26 to 36 mm). Higher abundance was found during night, probably as a consequence of net escapement during daylight hours (Holm-Hansen & Huntley 1984, Mathew 1988, Nordhausen 1994). The vertical distribution of the 15 to 25 mm size class and of all euphausiids during the study (Fig. 5) showed that they stayed in the 20 to 100 m layer during the day, but they dispersed during the night, appearing in the 200 to 400 and 400 to 600 m depths, and at the surface at the end of the night. The gut fullness of those organisms was rather low, probably due to degradation to non-fluorescent products which have been estimated in the range of 67 to 90% of the total pigment ingested (Perissinotto et al. 1997). However, they showed a higher pigment content during daylight hours at the shallower layers (0 to 100 m, filled symbols in Fig. 6A) and a sharp decrease during the night in all depths.

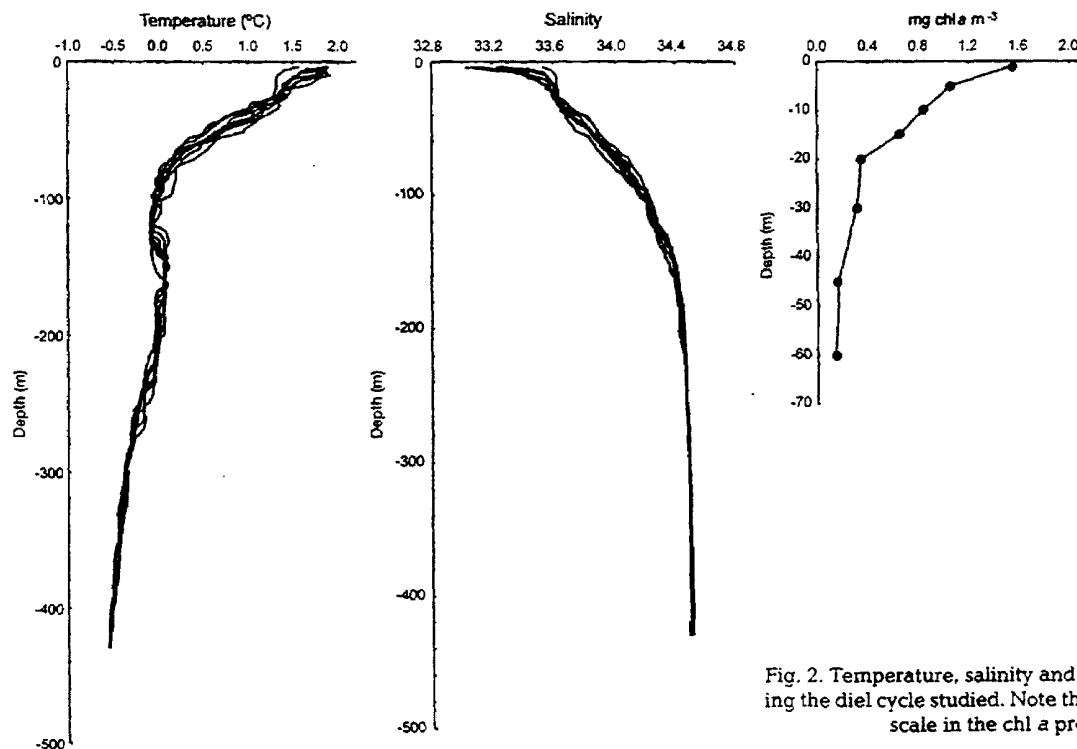


Fig. 2. Temperature, salinity and chl a values during the diel cycle studied. Note the different depth scale in the chl a profile

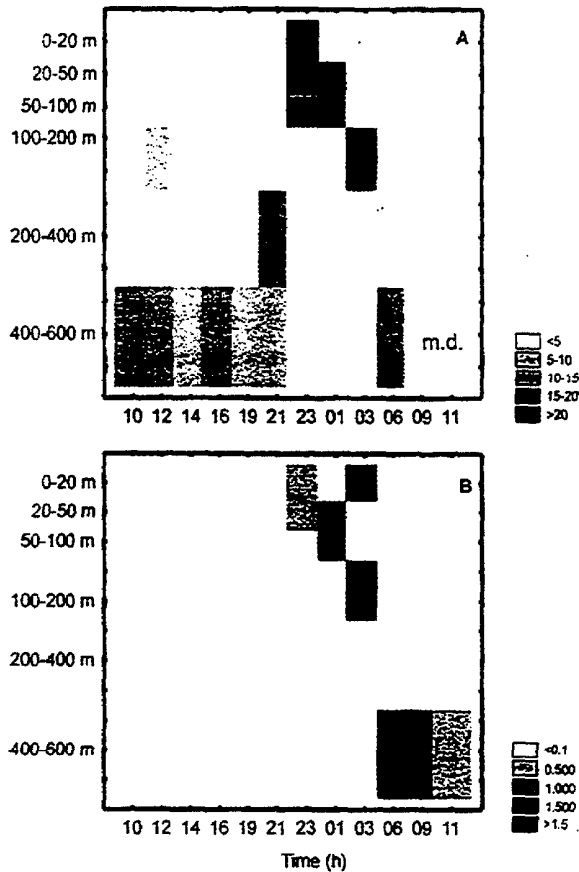


Fig. 3. *Metridia gerlachei*. (A) Abundance (ind. m⁻³) and (B) gut pigment content (ng ind.⁻¹). Data were obtained in all the layers sampled and the absence of shading indicates low values, except at the deeper layer in the 2 last samplings in (A) in which copepods were not counted because of preservation failure (md stands for missing data). Observe their vertical migration and the increase in gut pigment content during twilight and night (complete dark from 23:00 to 03:00 h) at the shallower layers and the presence of high gut pigment levels during the morning at the deeper layer

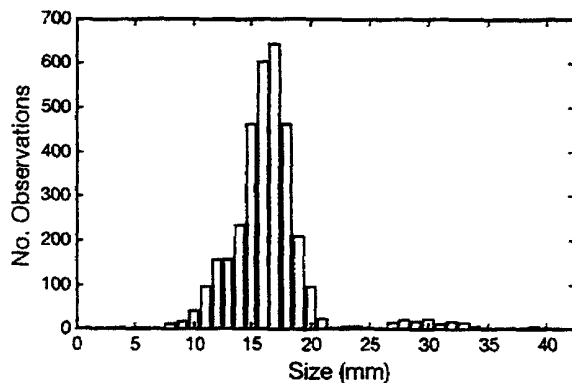


Fig. 4. Size distribution of *Euphausia superba* captured during the diel cycle

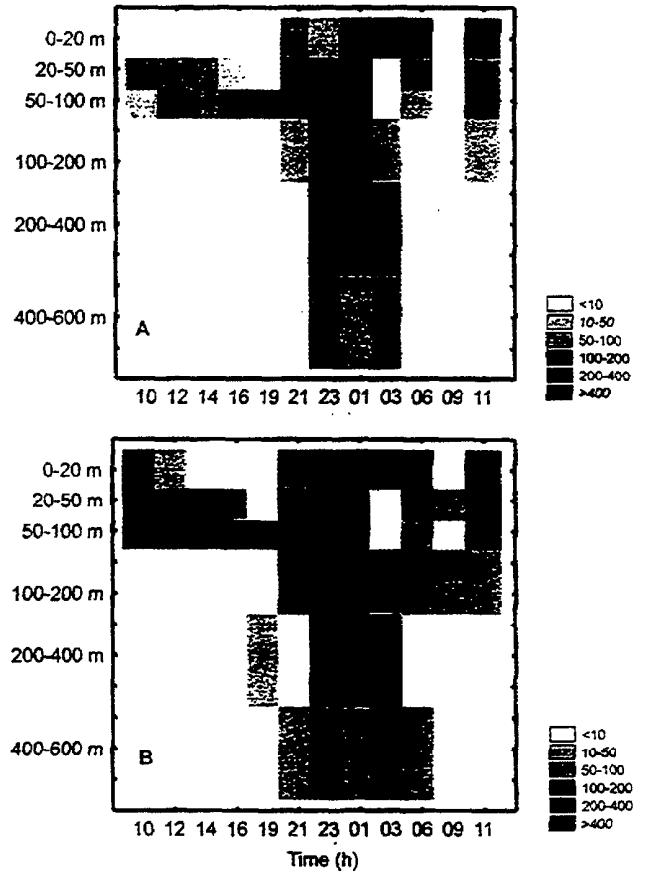


Fig. 5. *Euphausia superba*. Vertical distribution (ind. m⁻³) of (A) the 15 to 25 mm class and (B) of all specimens. Data were obtained in all the layers sampled and the absence of shading indicates low values. Observe the deeper distribution of organisms during the night

The gut content analysis of krill also revealed a significant (ANOVA, $p < 0.05$) higher number of crustacean fragments during the night (Fig. 6B) coinciding with the decrease in gut fluorescence at all depths during that time.

DISCUSSION

The vertical distribution of euphausiids and copepods as well as their nocturnal movements observed during the study are consistent with previous research in the area. Acoustic techniques have revealed the presence of 2 layers in Antarctic waters (Pakhomov et al. 1994, Weeks et al. 1995). A surface layer corresponding to large organisms such as euphausiids and a deeper one of smaller organisms below 200 m, appeared as an homogeneous and diffuse scattering layer. The latter layer has been observed to follow the

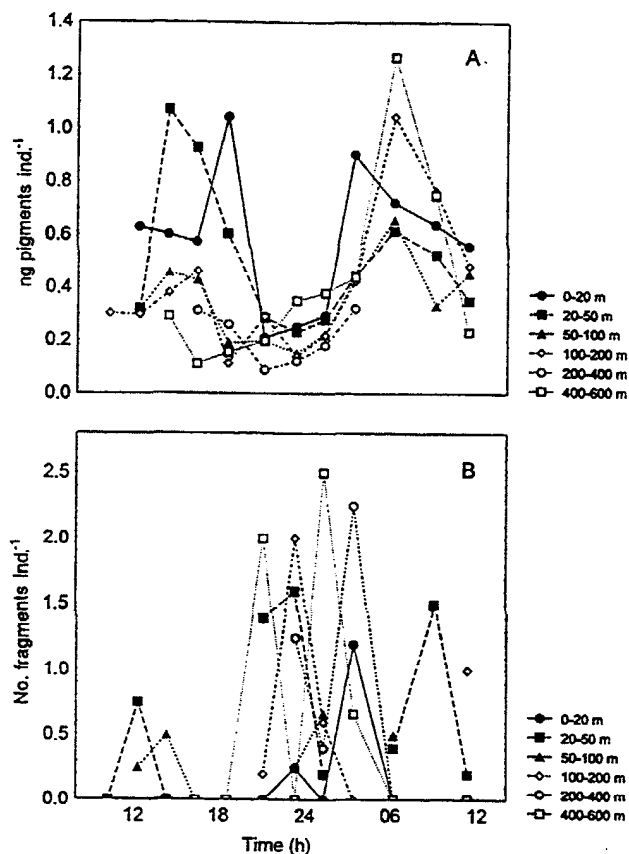


Fig. 6. *Euphausia superba*. (A) Gut pigment content and (B) crustacean fragments in the gut of juveniles. Observe the lower values of gut pigment during the twilight and dark hours coinciding with an increase in crustacean fragments

distribution of illumination (Weeks et al. 1995), ascending during night (Pakhomov et al. 1994). At this time, both layers were less evident and appeared uniformly distributed in the water column (Pakhomov et al. 1994). This pattern agrees with observations that the number of krill swarms is higher during daylight hours than during the dark period (Everson 1982, Siegel 1988, Demer & Hewitt 1995). There is also evidence from direct observations with nets of a decrease in the number of krill during night in the 0 to 200 m layer, increasing in the 200 to 400 m layer (Piatkowski et al. 1994). The ascent of the copepod *Metridia gerlachei* to surface layers at night has been shown recently (Lopez & Huntley 1995) as well as vertical movements of copepods at night, increasing the gut pigment during dark and twilight hours (Atkinson et al. 1992a,b). The latter authors did not sample below 180 m, but high abundances of adult specimens of the dominant copepods of Antarctic waters below 200 m have been observed (Ward et al. 1995). This pattern of diel vertical migration (downward and upward movements during the night for krill and copepods, respectively) has also

been observed in stratified sampling in the water column by Park & Wormuth (1993), although no explanation was given to this pattern. A tentative explanation for the absence of downward diurnal migration of krill could be related to the presence of mesopelagic fishes which feed largely on krill (Lancraft et al. 1989, 1991, Rowedder 1979a,b) and are found by day below 200 m (Torres & Somero 1988, Williams & Duhamel 1994, Duhamel et al. 2000) or at 150 to 300 m depth as observed from the gut content of king penguins (Pütz & Bost 1994).

The feeding behaviour of euphausiids and copepods is also consistent with this pattern of vertical distribution and migration. Our observation of a decrease in gut pigment content and an increase in crustacean appendages in the gut of euphausiids coinciding with the twilight and dark hours suggests a switch from plant-based to animal food in those organisms. The switch to animal food agrees with the observation of predatory feeding by krill (Price et al. 1988, Atkinson & Snýder 1997) and with the preference of those organisms for animal food in the presence of both phytoplankton and mesozooplankton (Granéli et al. 1993). In fact, it has been observed that the heterotrophic component of diet accounted for an average 79 % of the mass of the gut contents (Perissinotto et al. 2000). Krill is also able to prey on the most common size of large copepods at the fastest rates (Atkinson & Snýder 1997). The feeding behaviour studied is also consistent with the observation that during the day almost all the krill faeces were concentrated near the surface while during night they were found deeper (González 1992). Although sinking of large faeces has been postulated to explain this nocturnal distribution (González 1992), the possibility that they could be produced deeper during night-time cannot be ruled out.

This pattern of feeding and vertical migration of both euphausiids and copepods supports the observations that high krill abundance areas are characterised by exceptionally few copepods, and those appeared to live deeper and to make more extensive vertical migrations (Atkinson et al. 1999). The former observation has precedents in the literature. Brinton & Antezana (1984) found a scarcity of mesozooplankton in areas of high krill densities, and Rakusa-Suszczewski (1982), Hosie (1994) and Voronina et al. (1994) observed an inverse relationship between krill and non-krill organisms in Antarctic waters. Moreover, measurements of mesozooplankton biomass in Antarctic waters reported by Hernández-León et al. (1999) during December 1991, Robins et al. (1995) during November and early December 1992, and Hernández-León et al. (2000) during January 1993 revealed values corresponding to the lowest observed in the literature for Antarctic waters despite the rather high chl *a* concentrations at

the same oceanographic stations (Aristegui & Montero 1995, Robins et al. 1995, Aristegui et al. 1996). Mesozooplankton should not be food limited because a high proportion of primary production is not consumed (see Atkinson & Shreeve 1995, Dubischar & Bathmann 1997, Swadling et al. 1997, Hernández-León et al. 1999, among others) and organisms were actively growing as deduced from indices of growth (Hernández-León et al. 2000). Moreover, the energy budget of krill based on autotrophic material during laboratory incubations shows that ingestion rates are generally insufficient to meet their daily requirements (Antezana et al. 1982, Holm-Hansen & Huntley 1984, Perissinotto et al. 1997, among others). In which case, the explanation for the low biomass of mesozooplankton (especially large copepods) around the Antarctic Peninsula should be related to predation. It is known that the Bransfield Strait and surrounding waters are areas of high krill densities (Everson & Miller 1994, Siegel & Kalinowski 1994); therefore, the potential to diminish the mesozooplankton biomass by predation is also high. This would explain the decrease in mesozooplankton biomass normally observed as we approached the coastal waters from the Polar Front (Foxton 1956, Boysen-Ennen et al. 1991). In fact, a tendency of the copepod biomass to decrease and that of euphausiids to increase southward has been observed (Voronina et al. 1994). This behaviour of krill, which suggests a predation pressure on large copepods and on mesopelagic vertical migrants, would also explain the migration of major parts of the krill stock from under the ice-cover towards open (deeper) waters during the spring-summer months (Siegel 1988, Sprong & Schalk 1992).

Krill is heavily dependent on the formation and melting of the pack-ice. The inter-annual variability of ice concentration determines the dynamics of krill populations as there is an effect on its spawning and recruitment (Siegel & Loeb 1995). Ice concentration will determine the development of plankton dynamics and consequent food web effects (bottom-up control) as it influences the stability of the water column as well as the release of ice-algae. However, krill would impose a predatory impact down food webs (top-down control), the effects of which are at present quite unknown. The predatory effect of krill could explain the scarcity sometimes observed of dominant species of copepods in certain areas of the Southern Ocean. Evidence of a top-down control, such as that reported above and also in the literature, is accumulating and shows the importance of predation in relation to the standard bottom-up paradigm in biological oceanography. In this context, the tentative suggestion by Kawamura (1986) that the zooplankton composition of Antarctic waters may have changed over the last half century could be con-

troversial because his samples were obtained from widely separate regions and could also be affected by the inverse relationship between krill and non-krill zooplankton (Hosie 1994). However, he observed that while zooplankton biomass remained unchanged over the past several decades, during the BIOMASS-SIBEX I cruises (1983–84) herbivorous copepods (*Calanus propinquus*, *Calanoides acutus* and *Rhincalanus gigas*) were only 1 to 10% as numerous as during the 'Discovery' investigations 60 years ago. The predatory behaviour of a supposed increased population of krill could produce the decrease in abundance of those copepods (see also Atkinson et al. 1999) and would explain the sometimes observed dominance of the copepod *Metridia gerlachei*, an active vertical migrator (hence better adapted to avoid predation) in locations around the Bransfield Strait (see Park & Wormuth 1993). It is also suggested that future investigations should study the effect of 'superswarms', which are high densities of krill extending over 2.8 to 21.6 km (Cram et al. 1979, Mathisen & Macaulay 1983, Macaulay et al. 1984, Shulenberger et al. 1984, Higginbottom & Hosie 1989, Siegel & Kalinowski 1994, Murray et al. 1995, among others), and should also focus on the top-down effect described above because it could produce important changes in the structure of plankton communities in the Southern Ocean.

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