



PERGAMON

Deep-Sea Research II 49 (2002) 3169–3187

DEEP-SEA RESEARCH  
PART II

www.elsevier.com/locate/dsr2

# Carbon intake by zooplankton. Importance and role of zooplankton grazing in the Indian sector of the Southern Ocean

P. Mayzaud<sup>a,\*</sup>, V. Tirelli<sup>a,1</sup>, A. Errhif<sup>a</sup>, J.P. Labat<sup>a</sup>, S. Razouls<sup>b</sup>, R. Perissinotto<sup>c</sup>

<sup>a</sup> *Océanographie Biochimique et Ecologie, LOBEPM, ESA-CNRS 7076, Observatoire Océanologique, P.O. Box 28, 06230 Villefranche sur mer, France*

<sup>b</sup> *Laboratoire Arago, Observatoire Océanologique, BP 44, 66651 Banyuls sur mer, France*

<sup>c</sup> *School of Life & Environmental Sciences, University of Natal, Durban 4041, South Africa*

Accepted 2 July 2001

## Abstract

Ingestion by mesozooplankton and micronekton was monitored during two of the ANTARES cruises in the Indian sector of the Southern Ocean in spring and summer. The composition of the mesozooplankton populations varied in space and with season. Copepods always dominated in number and biomass, but salps and pteropods were present in the northern part of the transect in summer. Five species of large copepod (*Calanus simillimus*, *Calanoides acutus*, *Rhincalanus gigas*, *Calanus propinquus* and *Metridia gerlachei*) dominated the biomass with a North–South gradient. Smaller species (*Oithona* spp., *Ctenocalanus citer*, *Clausocalanus laticeps*) were also present. Biomass showed a definite trend with highest levels towards the polar front zone and permanent open-ocean area. Feeding activity was monitored either for the total population (summer) or specific individuals (spring). In summer, depending on the area considered, grazing rates by mesozooplankton appeared to have a significant impact on phytoplankton primary production. In the northern part of the transect (polar front zone or PFZ), salps and to a minor extent pteropods and copepods contributed mostly to the feeding pressure. Maximum intensity was observed in the Coastal Antarctic Zone (CCSZ) where *Euphausia superba* (adults and calyptopis larvae) could ingest more than 100% of the daily primary production. In spring, the impact of copepods dominated the zooplankton community. Small calanoids and young stages of large species of copepods rather than adult stages were the dominant contributors to grazing pressure. In summer, respiration rates of the dominant copepod species showed that energy expenditure exceeded by far chlorophyll ingestion. This is generally interpreted as the consequence of ingestion of alternate non-chlorophyll food source. The inverse correlation between the biomass of microzooplankton and the area of maximum difference between grazing and respiration confirmed that in summer the protozoans are strongly controlled by the copepod community. © 2002 Elsevier Science Ltd. All rights reserved.

## Zusammenfassung

La consommation de carbone particulaire par le zooplancton et le micronekton a été étudié pendant deux des campagnes ANTARES dans le secteur sud-Indien de l'océan Antarctique au printemps et en été. La composition des

\*Corresponding author. Tel.: +33-4-93-76-38-28; fax: +33-4-93-76-38-48.

E-mail address: mayzaud@ccrv.obs-vlfr.fr (P. Mayzaud).

<sup>1</sup> Present address: University of Trieste, Department of Biology, via Weiss 2, 34127 Trieste, Italy.

communautés du mesozooplankton varie dans le temps et l'espace: les copépodes dominent généralement en nombre et biomasse mais les salpes et ptéropodes sont présents dans la partie Nord de la zone d'étude en été. Cinq espèces de grands copépodes calanoides (*Calanus simillimus*, *Calanoides acutus*, *Rhincalanus gigas*, *Calanus propinquus* et *Metridia gerlachei*) dominent la biomasse avec un fort gradient Nord-Sud. Les petites espèces (*Oithona* spp., *Ctenocalanus citer*, *Clausocalanus laticeps*) sont aussi présentes. La biomasse totale montrent des valeurs plus élevées au voisinage du Front Polaire et dans le Zone Océanique sans Glace.

L'intensité du broutage a été quantifiée soit sur la population totale (Eté) soit au niveau de l'espèce (printemps). En été, l'activité nutritionnelle montre un impact significatif sur la production primaire. Dans la région Nord (Front Polaire), les salpes et, dans une moindre mesure, les ptéropodes et les copépodes assurent l'essentiel de la pression de broutage. Dans la région côtière et du plateau continental Antarctique, l'essentiel de la consommation est faite par l'euphausiacé *Euphausia superba* (adultes et larves calyptopis) dont la pression de broutage atteint 100% de la production primaire journalière. Au printemps, les petits calanoides et les jeunes stades des grandes espèces de copépodes assurent l'essentiel de la prédation sur le phytoplankton. En été, les niveaux de dépenses énergétiques (respiration) des principales espèces de copépodes montrent un net excédent par rapport à l'assimilation du carbone phytoplanktonique. Ce déficit est généralement interprété comme la conséquence d'une nutrition à partir d'organismes non-chlorophylliens. La corrélation inverse entre biomasse de microzooplankton et les régions de maximums de déficit métabolique confirme qu'en été les populations de protozoaires sont fortement contrôlées par la communauté des copépodes.

---

## 1. Introduction

Various studies have suggested a relatively minor role on the influence of oceanic mesozooplankton grazing on phytoplankton (Atkinson et al., 1996; Dam et al., 1993; Morales et al., 1991, 1993; Tsuda and Sugisaki, 1994; Ward et al., 1995). In the Antarctic communities, the per cent of primary production consumed daily varies with season, location, population structure and abundance, but most of the time remains below 5% (Atkinson and Shreeve, 1995; Atkinson et al., 1996; Hopkins, 1987; Swadling et al., 1997), though higher values ranging from 25% to 80% have been reported (Perissinotto, 1992; Ward et al., 1995).

The general consensus on low-grazing impact is largely based on feeding rate data obtained on copepod populations using the recommended gut pigment technique (gut content and transit time) or differential chlorophyll-based assays or incubation techniques followed by microscope enumeration of the grazed and non-grazed particles. Because these methodologies focus on live phytoplankton, they do not account for feeding mode on protozoan cells (Atkinson, 1994; Gifford, 1993; Stoecker and Egloff, 1987; Turner and Graneli, 1992; Waidyana and Rassoulzadegan, 1989) or

small zooplankters (Landry, 1981; Metz and Schnack-Schiel, 1995) or on detrital carbon (Poulet, 1976), providing a source of nutrition for the animal not detected by any of the chlorophyll-based techniques. Moreover, they only consider copepods as the acting grazers in the zooplankton communities.

Measurement of natural grazing rate for oceanic mesozooplankton remains a major challenge, and we need information on the various sources of carbon ingested to ascertain the actual role of the communities. During the ANTARES programme in the Indian sector of the Antarctic Ocean, a survey of the zooplankton population and feeding activity was carried out at three seasons (spring, summer and early fall) and from the subantarctic front to the Antarctic coastal waters.

In the present paper, we review the data obtained for the different zooplankton communities and individual species sampled during two cruises. We also attempt to relate them to separate evaluations of energy expenditure to derive more appropriate feeding rates. Such comparison should help in understanding the influence of zooplankton metabolism in the biological pump of carbon and ascertain its role in a specific province of the Antarctic Ocean.

2. Methods

2.1. Zooplankton abundance and biomass

ANTARES 2 and 3 cruises took place along 62°E at two different periods. The first one took place in summer (February–March 1994) between 50°S and 68°S, and the second one in spring (October–November 1995) between 49°S and 58°S at the ice edge (Fig. 1). Additional data came from the ANTARES 4 cruise, which took place in

summer in the frontal zone North-West of the Kerguelen archipelago between 44°S and 46°S and between 62°E and 65°E.

The abundance and biomass of mesozooplankton were estimated from vertical tows using a triple WP II net (200 µm mesh size). Hauls were made from 200 m to the surface. The contents of the first net, which was used for population structure analysis, were preserved in formalin. The second net, used for total biomass measurement, was filtered on pre-weighed 200-µm sieves,

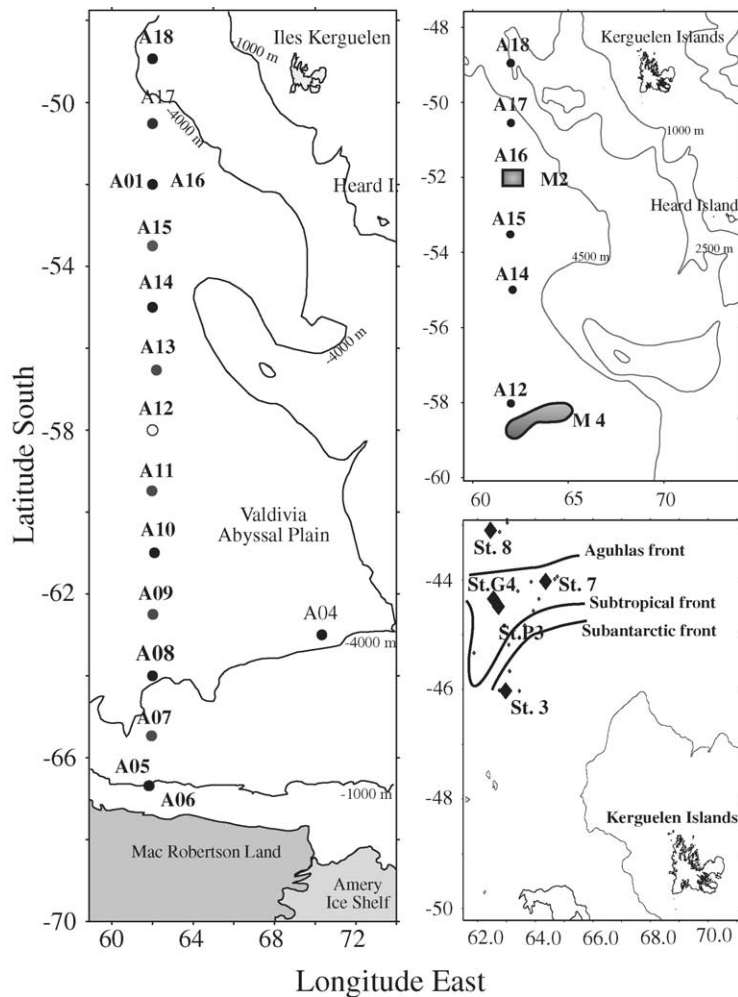


Fig. 1. Investigated zones and locations of sampling stations during the three *Marion-Dufresne* cruises: left, ANTARES 2 (February–March 1994); top right, ANTARES 3 (September–October 1995) and bottom right, ANTARES 4 (January–February 1999).

rinsed with ammonium formate, and dried at 60°C until constant weight. The content of the third net was immediately diluted with surface water in a 40-l cooler and used for experiments on live animals.

### 2.2. Copepod feeding rates measured by gut fluorescence method

Ingestion rates on phytoplankton were measured using the gut pigment analysis method described by Dagg and Walser (1987). During ANTARES 2, the zooplankton from night tows was fractionated according to size on 2000, 1000, 500 and 200 µm mesh. Each fraction was frozen on Sharkskin filter paper and immediately deep-frozen (−80°C). In the laboratory, the animals were picked while frozen under dim cold light and extracted in 90% acetone. Fluorescence was measured before and after acidification with a Turner 10 fluorometer. During ANTARES 3 and 4, a more specific approach was used, and dominant species collected at mid-night and mid-day were sorted live under dim cold light and extracted immediately in 90% acetone. However, the feeding budget considered solely night results. In addition, experimental determination of gut transit times and pigment destruction efficiency were made. Detailed protocols can be found in Tirelli and Mayzaud (1999) and Perissinotto et al. (2001).

### 2.3. Respiration

Individuals from the diluted tow were placed in a cold room adjusted at seawater temperature (2–4°C in the Antarctic waters and 6–8°C in the subantarctic area sampled during ANTARES 4). Animals from night collection were sorted to species, copepodite stage, and sex under a binocular microscope (for the larger form directly by eye) and placed in 1-l beakers filled with filtered seawater (0.45 µm) for 1–2 h. The animals were then placed in experimental chambers filled with filtered seawater saturated in oxygen. The volume of the chambers varied from 2 to 150 ml depending on the size and the number of individuals (ind) used. The animal density was kept around 400 ind/

l for the smaller species (*Oithona* or *Ctenocalanus*) and 20–40 ind/l (3–6/150 ml) for larger copepod species (*Calanus propinquus* or *Rhincalanus gigas*). Control chambers without animals were used to monitor possible oxygen changes. Incubations were made under darkness at seawater temperature for periods varying around 15–24 h at 2–4°C and 12 h at 6–8°C.

Oxygen concentration was monitored using a Strathkelvin oxygen meter equipped with a Clark-type electrode. Oxygen consumption was computed by difference between beginning and end of the incubation, corrected for a possible change in the control bottles. Experimental animals were usually preserved for length or weight measurements. All measurements were normalised per unit dry weight. Values of individual biomass of each species were obtained from direct measurement and or literature data (see Conover and Huntley, 1991). When specific dry weights were not available, values were computed from the relationship between size and weight for that species (Uye, 1982; Cohen and Lough, 1981; Kubjeweit, 1993; Webber and Roff, 1995).

A total of 13 different species were studied (*Calanoides acutus*, *C. propinquus*, *Calanus simillimus*, *Candacia maxima*, *Clausocalanus laticeps*, *Ctenocalanus citer*, *Euchirella rostrata*, *Metridia lucens*, *Oncea antarctica*, *Pareuchaeta antarctica*, *Pareuchaeta* sp., *Pleuromamma robusta*, *Rhincalanus gigas*). Usually three different copepodite stages were considered (C4 to adult). Measurements were made in triplicate. Mean values for all species and stages were used to compute the regression between dry weight and respiratory rates. The resulting relationship is:  $\log \text{Resp}(\mu\text{l O}_2/\text{ind d}) = 0.78(\pm 0.018)\log \text{Dw} + 1.28(\pm 0.016)$  ( $R^2 = 0.988$ ).

### 2.4. Egg production

Copepods egg production experiments were performed at different stations along the transect 48°59'S (A18)–58°16'S (M04), with main surveys at the two long-term stations M02 and M04. Night collections of copepods were immediately diluted and stored in a cold room at the temperature near that of in situ water, i.e. 5°C in the north and 1°C

in the south. Females were sorted by eye according to the apparent dark colour of their gonads, and isolated individually in vials filled with 30 ml of natural seawater from the field. They were then incubated under controlled conditions (cold-room temperature, dim light). Vials were inspected every day, eggs were counted, and the females transferred into new natural water. Experiments were carried out on the five most abundant species of copepods,

### 2.5. Contribution of copepodite stages to population density

For each large species (*C. acutus*, *C. propinquus*, *C. simillimus*, *R. gigas*, *M. lucens*), the actual copepodite stage composition was used to calculate their contribution to the total copepod community of each zone. This contribution is a weighted average taking into account the relative frequencies of copepodite stages. The small species (*Oithona*, *Oncaea*, *Clausocalanus*, *Ctenocalanus*, *Scolecithricella*) were only partially sampled by the 200- $\mu$ m mesh net and were mainly represented by their adult and C5 stages. Thus, their contribution was computed considering these two stages only. Full account of the composition of the copepod population can be found in Errhif (1998).

## 3. Results

### 3.1. Biomass distribution and population structure

Zooplankton biomass, in terms of dry weight, was integrated over the 200-m water column sampled. The values varied with the time of the day, the season, and the location (Fig. 2). The dry weight ranged from 2.4 to 16 g/m<sup>2</sup> in summer, with dominance of late copepodite and adult stages (ANTARES 2), and from 0.6 to 16 g/m<sup>2</sup> in spring, with a dominance of young copepodite stages (ANTARES 3). This seasonal variability was associated with a strong and variable spatial heterogeneity. In summer, maximum values were observed in the permanent open-ocean zone (POOZ, station A14) and to a lesser extent on the polar front zone (PFZ, station A17) while

minimum values were recorded in the seasonal ice zone (SIZ) and the continental shelf zone (CCSZ). In spring, biomass was maximum in the SIZ (station A12), intermediate in the POOZ and low in the PFZ. In the subantarctic–subtropical area (ANTARES 4) biomass was on average lower, with values ranging from 0.3 to 13 g/m<sup>2</sup>, with maximum values in the PFZ and minimum ones in the subtropical areas. Day-time biomass was generally lower than at night, confirming diurnal vertical migration of part of the population.

Abundance in number of individuals per cubic metre confirmed the dominance of copepods in the community regardless of the station or the season considered (Table 1). In summer, the salps (*Salpa thomsoni*) and the pteropods (mostly *Limacina* spp.) were limited to the northern part of the transect (POOZ), while euphausiid larvae were located in the Antarctic shelf area (CCSZ). In spring, salps were low in number and found only in the SIZ area (Table 1). Pteropods and euphausiid larvae showed the same North–South gradient observed in summer, but with lower densities. Detailed species composition of the copepod group can be found in Errhif (1998) as well as distribution of the copepodite stages for the four dominant species of large copepod. A summary is presented in Table 2, which shows the dominance of the cyclopid species in numbers at all seasons and locations, followed by *C. citer* in the POOZ and SIZ areas at both seasons, and *Oncaea* spp. in the CCSZ. Larger copepod species such as *C. simillimus* were mostly located in the POOZ at both seasons, while *R. gigas* and *C. acutus* were evenly distributed in POOZ and SIZ, with higher densities in spring. *C. propinquus* was present mostly in the SIZ in summer. *M. lucens* was recorded in both POOZ and SIZ, while *M. gerlachei* was to a large extent restricted to the CCSZ. Using the index defined by Marin (1987) and Huntley and Escritor (1991), copepodite stages dominated at all times, with younger stages in spring for *C. propinquus* ([S]=3.1–3.6 versus 2.4), similar stage distributions at both seasons for *Rhincalanus gigas* ([S]=2.8–4.3), and a younger stage in summer for *C. acutus* ([S]=3.4–4.1 versus 5.3–5.8) and *C. simillimus* ([S]=4.3–5 versus 5–5.2).

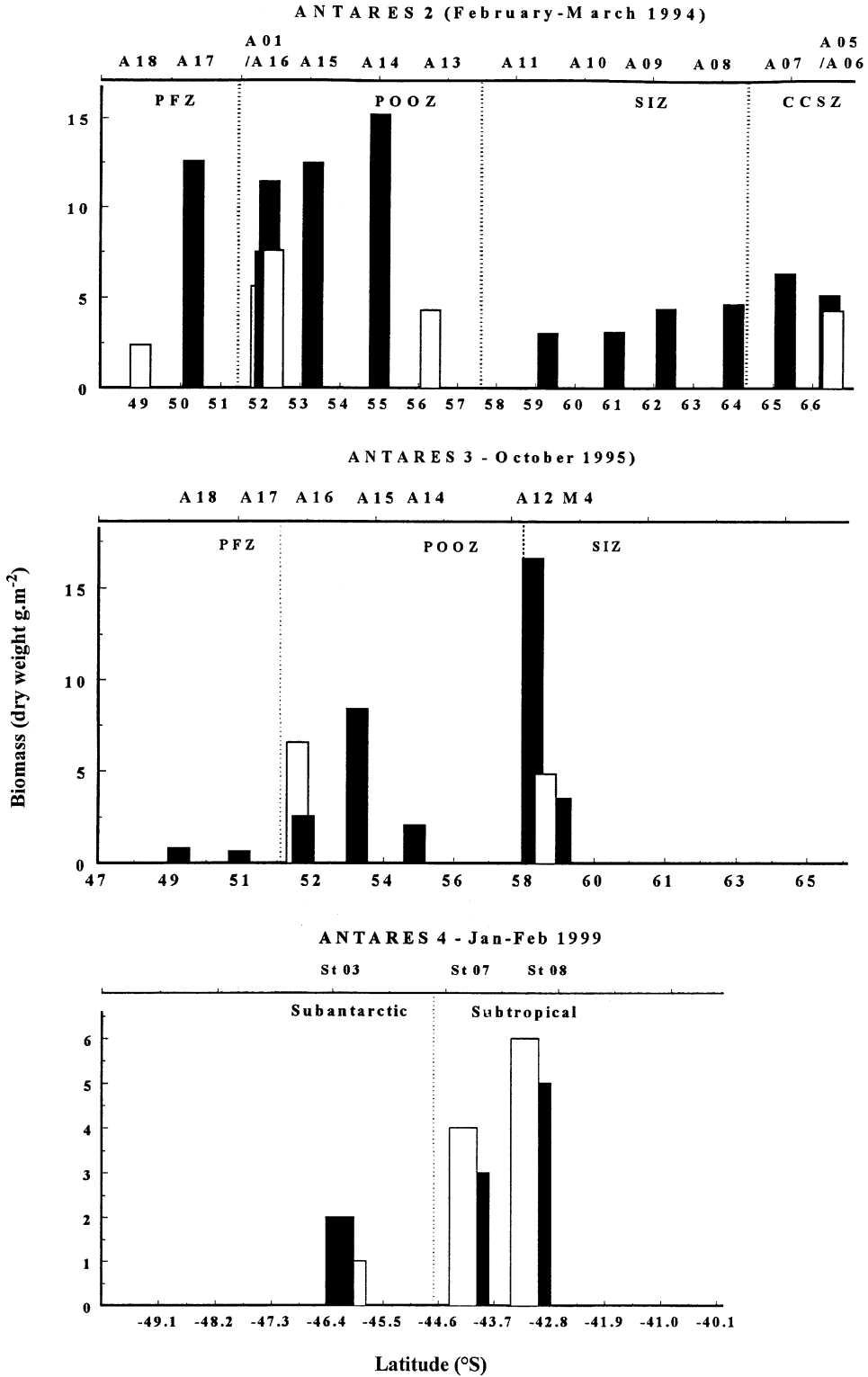


Table 1

Abundance estimates (number/m<sup>3</sup>) of the main taxa of the mesozooplankton community during the two cruises

	ANTARES 2 (summer)			ANTARES 3 (spring)		
	POOZ	SIZ	CCSZ	PFZ	POOZ	SIZ
Copepods	320	114	293	299	198	591
Euphausiid larvae	7.5	2.0	104	1.6	3.2	14.4
Pteropods	1.4	0.1	0.5	0.6	0.9	0.3
Salps	3.4	0	0	0	0	0.1

Table 2

Composition of the copepod populations in the different oceanic provinces of the Indian sector of the Antarctic Ocean in spring (ANTARES 3) and summer (ANTARES 2)

Copepod species	ANTARES 2			ANTARES 3	
	POOZ (%)	SIZ (%)	CCSZ (%)	POOZ (%)	SIZ (%)
<i>O. similis</i>	25.2	52.4	57.2	21.0	40.5
<i>Oithona frigida</i>	25.1	11.9	0.4	12.5	14.0
<i>C. citer</i>	22.3	21.9	7.0	37.4	23.9
<i>C. simillimus</i>	20.5	0.2	—	13.3	0.7
% females in spring				(34.1)	(11.1)
<i>R. gigas</i>	0.4	0.6	—	7.3	3.6
% females in spring				(2.2)	(12.6)
<i>C. acutus</i>	0.3	0.9	0.4	1.2	3.4
% females in spring				(83.9)	(25.2)
<i>C. propinquus</i>	0.1	1.3	0.8	0.04	0.7
% females in spring				(80)	(13.4)
<i>Paraeuchaeta copepodites</i>	0.1	0.2	—	0.5	0.3
<i>Oncea</i> spp.	—	2.4	24.5	1.1	7.6
<i>M. lucens</i>	0.5	1.8	—	2.2	1.1
<i>M. gerlachei</i>	—	0.7	3.4	—	—
Total	94.5	94.3	93.7	96.5	95.8

Data are expressed as % in number/m<sup>2</sup> for the total population. (—): absent.

### 3.2. Gut pigment content

Pigment gut content was analysed in two different ways throughout the cruises. A global approach was used during ANTARES 2, and analyses were made on the zooplankton population fractionated into three size categories. The smaller size (200–500 µm) consisted mostly of the

copepods *Oithona* spp., *Oncaea* spp. and *C. citer*, the medium size (500–1000 µm) included most species of medium size copepod, (e.g., *C. simillimus* in the PFZ and POOZ, *C. acutus* in the POOZ and SIZ and calyptopis stages of *E. superba* in the CCSZ), the 1000–2000 µm size range comprised mostly large species of copepods (*C. propinquus*, *M. gerlachei*, and *R. gigas*). As anticipated,

Fig. 2. Distribution of the mesozooplankton dry mass along the transect surveyed during the three cruises ANTARES 2, 3 and 4. White bars: day-time and black bars: night-time.

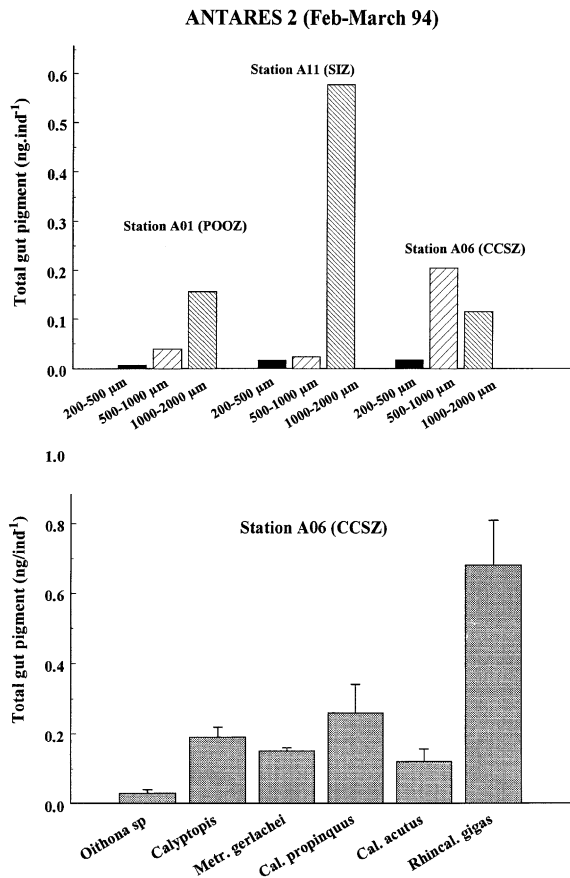


Fig. 3. Gut pigment content for three size class categories of the zooplankton community (top) and mean values ( $\pm$  standard deviation) for selected species (bottom) in the Antarctic coastal area (CCSZ) during ANTARES 2.

maximum gut contents were recorded for the large-size fraction, with the noticeable exception of the CCSZ where the medium size calyptopis larvae showed the highest values (Fig. 3). Overall, the summer period was characterised by relatively low chlorophyll gut content, ranging from 0.01 to 0.6 ng/ind. Station A06 (CCSZ) was further divided into major individual species, and the highest gut content ( $0.7 \pm 0.1$  ng/ind) was observed for the large copepod *R. gigas* (Fig. 3). Similar gut pigment levels were recorded for the copepods *C. acutus*, *C. propinquus*, *M. gerlachei* and the calyptopis of *E. superba*. Low levels occurred in the small cyclopoid *Oithona* spp. (Fig. 3).

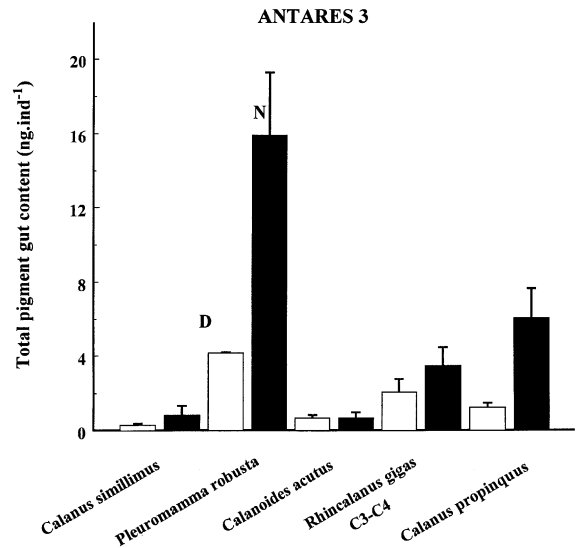


Fig. 4. Mean gut pigment content ( $\pm$  standard deviation) and day–night periodicity of the most abundant copepod species during the ANTARES 3 spring cruise. Symbols: D = day (white bars) and N = night (black bars).

A species-specific analysis was used during the next cruise. In spring (ANTARES 3), most of the biomass consisted of a small number of copepod species. Pigment gut content was measured from day- and night-time captures. The levels recorded were higher than in summer, with values ranging from 0.2 to 16 ng/ind (Fig. 4). A clear day–night feeding rhythm was noticeable, and the highest gut content was recorded for the copepod *P. robusta* at night ( $15.9 \pm 3.3$  ng/ind) followed by stage C3–C4 of *R. gigas* and *C. propinquus* (3.5–6.1 ng/ind, respectively). The lowest values were observed for *C. simillimus* (Fig. 4). In summer the zooplankton population sampled in the PFZ (ANTARES 4) showed a wide range of pigment gut content depending on the taxa considered (Fig. 5). Copepod showed typical summer low values ranging from 0.4 to 0.8 ng/ind as did some euphausiid species such as *Thysanoessa* sp. Higher gut content was recorded for pteropods (*Limacina* spp., *Cavolinia* sp.) or euphausiids (*Euphausia longirostris*, *Euphausia spinifera*), with values ranging from 3 to 98 ng/ind. Maximum gut content was observed for the salp *S. thomsoni* ( $272 \pm 60$  ng/ind).



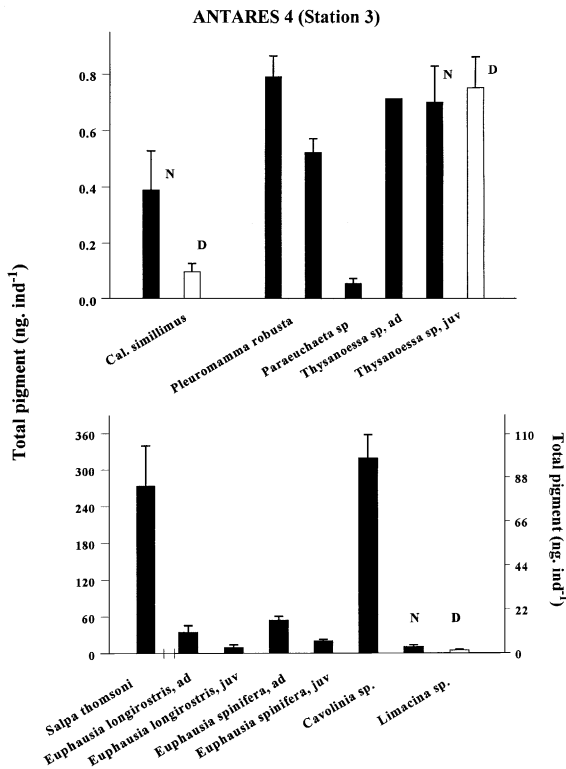


Fig. 5. Mean gut pigment content ( $\pm$  standard deviation) and day–night periodicity of the most abundant zooplankton species collected in the PFZ during ANTARES 4 summer cruise. Symbols: D=day (white bars) and N=night (black bars).

### 3.3. Ingestion rates from pigment gut content and energy requirements

Ingestion rates were computed using measured gut transit time (Tirelli and Mayzaud (1999), Perissinotto et al. (2001), literature data or unpublished data (see table legends)). Correction for pigment degradation was assumed to be 50% (mean degradation values for Antarctic and subantarctic species; Perissinotto, 1992), and results were compared with chlorophyll standing stock (Fiala and Oriol, 1995; Panouse et al., 1997; Fiala, unpubl.) and primary production (Caubert, 1997).

#### 3.3.1. Summer Antarctic population (ANTARES 2)

The grazing activity observed in summer for the copepod communities suggested an increasing

trend with increasing latitude (Table 4) without a direct relationship with either the phytoplankton standing stock or the level of primary production. The corresponding percentage of primary production removed appears very small in the POOZ (station A01), intermediate in the SIZ (station A11), and maximal, though limited, in the CCSZ (station A06). The feeding activity associated with *E. superba* adults or larvae in the CCSZ is far more important, as it represented an intake of 100% of the primary production (Table 3). Similarly, the non-crustacean taxa showed a significant contribution to grazing, with salps dominating in the POOZ. Pteropods showed a small but significant contribution in the POOZ and SIZ areas (Table 3). The influence of the entire zooplankton community showed a strong spatial variability related to taxonomic composition, with levels of total consumption representing 21% of the primary production in the SIZ, 66% in the POOZ and 143% in the CCSZ.

Comparison between carbon respiratory requirements and gut-pigment-derived ingestion for copepods showed that phytoplankton feeding did not correspond to the energetic requirements (Table 4). Interestingly, the percentage of respiration expenditure covered by pigment ingestion decreased from south to north, with 45% in the CCSZ, 26% in the SIZ, and 7% in the POOZ. Assuming that the difference corresponds to non-phytoplankton feeding, the ingestion rate on heterotrophic cells dominated in all areas, with values ranging from 63 to 68 mg C/m<sup>2</sup> d in the SIZ and CCSZ, respectively, and 155 mg C/m<sup>2</sup> d in the POOZ (Table 4). This represented 14–172% of the microzooplankton biomass measured by Becquevort et al. (2000).

#### 3.3.2. Spring Antarctic population (ANTARES 3)

Phytoplankton ingestion was measured for the adult stages of the five dominant species in the population. *C. propinquus* showed the highest ingestion, while *R. gigas* and *P. robusta* displayed intermediate values, and *C. similimus* and *C. acutus* showed the lowest rate (Table 5). These rates were on average higher than those recorded in summer during ANTARES 2, in agreement with the higher chlorophyll concentration.

Table 3

Ingestion rate computed from pigment gut content of the different components of the summer Antarctic zooplankton community sampled during ANTARES 2

	Station	Chl. <i>a</i> (mg/m <sup>2</sup> )	POC (g/m <sup>2</sup> )	POC/Chl	Ingestion rate (mg C/m <sup>2</sup> d)	Corrected ing. rate (1)	% Primary production
<b>Mesozooplankton</b>							
Copepod							
	A06	32.1	7.97	248	17.2±3.7	34.4	32.4
	A11	8.5	3.32	389	7.7±1.5	15.4	14.4
	A01	25.5	8.16	320	4.3±0.9	8.6	8.2
<b>Micronekton</b>							
<i>E. superba</i>							
	A06				106±18		100.0
Euphausiid larvae							
	A06				10±2		9.4
	A11				0.31±0.06		0.3
	A01				0.92±0.18		0.9
<b>Non-crustacean taxa</b>							
Salps ( <i>S. thomsoni</i> )							
	0.5–2 cm	A01			55±24		53.5
Pteropods (1 mm)							
<i>(Limacina spp.)</i>							
	A06				0.86		0.8
	A11				6.2±1.5		5.8
	A01				3.5±0.9		3.3

Chlorophyll *a* and particulate organic carbon (POC) were integrated over 100 m. Primary production (mg C/m<sup>2</sup> d): CCSZ (St06) 106.1; SIZ (St11) 106.7 and POOZ (St01) 104.2. (1): Copepod pigment gut content was corrected assuming 50% loss. Gut transit time averaged for each size category of the copepod population (small size *Oithona* spp. (1h), Atkinson, 1996; medium and large size transit time (1h30) derived from Tirelli and Mayzaud (1999) except for *Euphausia calyptopis* larvae (1h05), *S. thomsoni* (4h) and *Limacina* (1h), which were derived from Perissinotto (1992) and Pakhomov et al. (1997).

Table 4

Comparison of direct measurement of ingestion rate of copepods from pigment gut content with respiratory requirements

	POOZ A01	SIZ A11	CCSZ A06
Ing <sub>cor</sub> (corrected Ing) mg C/m <sup>2</sup> d	8.6	15.4	34.4
Mean dry weight (µg/copepod)	134.5	212.3	68.6
Respiration rates µg C/ind d	1.92	1.53	1.14
Respiration rates mg C/m <sup>2</sup> d	123	58	77
Ing <sub>resp</sub> equivalent to respiration (mg C/m <sup>2</sup> d)	164	78	102
Ing <sub>proto</sub> = Ing <sub>resp</sub> – Ing <sub>cor</sub> (mg C/m <sup>2</sup> d)	155	63	68
Ing <sub>proto</sub> % biomass microzoo	172	24	14

Respiration computed from size/respiration regression from ANTARES 3:  $\log \text{Resp} (\mu\text{l O}_2/\text{ind d}) = 0.78 \log \text{Dw} + 1.28$  ( $R^2 = 0.988$ ). Respiration converted to carbon assuming RQ = 0.9. Micro-protozoan biomass from Becquevort et al. (2000).

Spring is the period of maximum reproductive activity, and estimation of energy requirement must include both respiration and egg production losses (see below for terms of the calculation). The

comparison between phytoplankton carbon intake and energy requirements (Table 6) suggests a more balanced situation than that observed during the summer period. Indeed, feeding exceeds

Table 5

Ingestion rates of adult females computed from total gut pigment for spring populations (ANTARES 3) and corrected for a mean loss of 50%

Species	Station/area	Chl <i>a</i> (mg/m <sup>2</sup> )	POC (g/m <sup>2</sup> )	POC/Chl <i>a</i>	Ingestion (µg C/ind d)	Ingestion corr.
<i>C. propinquus</i>	SIZ	82.7	25.8	312	20.2±5.3	30.3
<i>C. acutus</i>	SIZ			312	2.5±0.8	3.8
<i>R. gigas</i>	SIZ			312	10.2±2.1	15.3
<i>P. robusta</i>	POOZ	47.1	5.1	107	11.1±5.7	16.7
<i>C. simillimus</i>	Mostly PFZ, POOZ	46.9	9.8	208	2.8±1.7	4.2

Gut transit time from Tirelli and Mayzaud (1999), Atkinson et al. (1992a, b) for *C. simillimus* and Atkinson (1996) for *P. robusta*.

Table 6

Carbon budgets (respiration + egg production) and equivalent ingestion rates of the dominant species of adult female copepods from the spring populations (ANTARES 3)

Species	Ing <sub>corr</sub> (µg C/ind d)	Respiration (µg C/ind d)	Egg production (egg/Fem d)	Egg production (µg C/ind d)	C requirements (µg C/ind d)
<i>C. propinquus</i>	30.3	9.4±3.7	51±28	25.5	34.9
<i>C. acutus</i>	3.8	6.4±2.1	20±9	10.0	16.4
<i>R. gigas</i>	15.3	8.6±2.7	15±7	13.5	22.1
<i>P. robusta</i>	16.7	5.4±0.9	0	0	5.4
<i>C. simillimus</i>	4.2	3.2±1.2	11±7	5.5	8.7

Carbon content of egg = 0.5 µg for *C. propinquus*, *C. simillimus*, *C. acutus* and 0.9 µg C for *R. gigas* (see text). Carbon requirements computed assuming 75% assimilation and an RQ = 0.9.

respiration expenditure in all cases except *C. acutus*. Respiration and egg production energy demands were almost met by ingestion for *C. propinquus* but not for the other species. However, egg production does not solely rely on immediate carbon intake but also on the energy stored as lipids, introducing a time lag between carbon intake and catabolism into egg.

To build a metabolic budget at the population level, total respiration was calculated for each dominant species using weighed means to take into account the differences in frequency of the different copepodite growth stages (Errhif, 1998). Values were then converted to carbon assuming an RQ of 0.9 (Omori and Ikeda, 1984) and converted to the population using the relative numeric abundance of each species. A carbon content of 0.37 µg C/egg was reported for *C. propinquus* (Kosobokova, 1994) and of 0.3 µg/egg for *C. acutus* (Lopez et al., 1993). An indirect estimate also could be obtained using the dry weight reported by Ward and Shreeve (1995) for

*C. simillimus* (1.1 µg/egg), *C. acutus* (1.2 µg/egg), and *R. gigas* (2.31 µg/egg), assuming 50% carbon. Most large arctic calanoids (*C. hyperboreus*, *C. glacialis*) display, for about the same size, carbon contents ranging from 0.4 to 0.56 µg C/egg (Huntley and Lopez, 1992). We choose to use a mean value of 0.5 µg/egg for *C. acutus*, *C. simillimus* and *C. propinquus*, and a value of 0.9 µg/egg for the larger species *R. gigas*, assuming that the ratio in dry weight applies to the carbon content. The sum of respiratory requirements and egg production gives the rate of minimum ingestion, which covered the energy expenditure. In the POOZ (Table 7), the contribution of *C. simillimus* and *R. gigas* dominated, followed by *C. acutus*, *C. citer* and to a minor extent *M. lucens*. Assuming that phytoplankton provided the bulk of the food, this minimum grazing rate represented a consumption of 66% of the local daily primary production. In the SIZ (Table 8), the same computation showed a dominant contribution of *C. acutus* and *R. gigas*, followed by *C. citer*, *C. propinquus* and *Oithona*

Table 7

Carbon budget and equivalent ingestion rates for the copepod population of the POOZ area during spring (ANTARES 3)

Species	POOZ				
	Respiration [R] ( $\mu\text{l O}_2\text{ mg/Dw d}$ )	Ing <sub>resp</sub> (mg C/ $\text{m}^2\text{ d}$ )	Egg prod. [E] (mg C/ $\text{m}^2\text{ d}$ )	Ing <sub>equivR+E</sub> (mg C/ $\text{m}^2\text{ d}$ )	% Prim. production
<i>C. acutus</i>	24.9±4.5	6.3	3.0	9.3	7.5
<i>C. propinquus</i>	17.9±2.6	0.3	0.3	0.6	0.5
<i>C. simillimus</i>	24.5±1.3	24.3	12.5	36.8	30.1
<i>C. laticeps</i>	38.2±6.0	0.2		0.2	0.1
<i>C. citer</i>	42.8±5.2	8.1		8.1	6.6
<i>M. lucens</i>	31.4±2.8	2.7		2.7	2.2
<i>O. frigida</i>	79.5 <sup>a</sup>	0.8		0.8	0.6
<i>O. similis</i>	79.5 <sup>a</sup>	1.3		1.3	1.1
<i>Oncaea antarctica</i>	51.5±6.2	0.2		0.2	0.2
<i>Paraeuchaeta</i> spp.	21.7	1.9		1.9	1.5
<i>R. gigas</i>	25.7±2.4	17.5	0.9	18.4	15.0
<i>Scolecithricella minor</i>	43.8 <sup>a</sup>	0.7		0.7	0.6
Total				81.0	66.0

Ingestion equivalent to respiration requirements (Ing<sub>resp</sub>) assumed an assimilation efficiency of 75%. Egg production of the large copepod species was converted at population level considering the % females of each species.

<sup>a</sup>Respiration rates derived from the regression between respiration and weight (see Table 2).

Table 8

Carbon budget and equivalent ingestion rates for the copepod population of the SIZ area during spring (ANTARES 3)

Species	SIZ				
	Respiration [R] ( $\mu\text{l O}_2\text{ mg Dw d}$ )	Ing <sub>resp</sub> (mg C/ $\text{m}^2\text{ d}$ )	Egg prod. [E] (mg C/ $\text{m}^2\text{ d}$ )	Ing <sub>equivR+E</sub> (mg C/ $\text{m}^2\text{ d}$ )	% Prim. production
<i>C. acutus</i>	25.9±4.8	21.9	10.1	32.0	13.3
<i>C. propinquus</i>	21.1±3.2	2.1	2.6	4.7	1.9
<i>C. simillimus</i>	24.9±1.5	0.4	0.6	1.0	0.4
<i>C. laticeps</i>	38.2±6.0	0.04		0.04	0.02
<i>C. citer</i>	42.8±5.2	7.4		7.4	3.1
<i>M. lucens</i>	31.2±2.8	1.9		1.9	0.8
<i>Microcalanus pygmaeus</i>	52.3 <sup>a</sup>	0.3		0.3	0.1
<i>O. frigida</i>	79.5 <sup>a</sup>	1.2		1.2	0.5
<i>O. similis</i>	79.5 <sup>a</sup>	3.6		3.6	1.5
<i>O. antarctica</i>	51.5±6.2	1.7		1.7	0.7
<i>O. curvata</i>	71.4 <sup>a</sup>	0.1		0.1	0.04
<i>Paraeuchaeta</i> spp.	21.7	1.6		1.6	0.7
<i>R. gigas</i>	22.8±2.1	17.6	9.7	27.3	11.3
<i>Scolecithricella minor</i>	43.8 <sup>a</sup>	1.4		1.4	0.6
Total				84.2	34.9

Ingestion equivalent to respiration requirements (Ing<sub>resp</sub>) assumed an assimilation efficiency of 75%. Egg production of the large copepod species was converted at population level considering the % females of each species.

<sup>a</sup>Respiration rates derived from the regression between respiration and weight (see Table 2).

Table 9

Grazing activity of the spring copepod communities (ANTARES 3) in relation with available daily primary production

	POOZ					SIZ				
	Chl <i>a</i> (mg/m <sup>2</sup> )	POC (g/m <sup>2</sup> )	POC/ Chl <i>a</i>	Ingestion (mg C/m <sup>2</sup> d)	% Primary production	Chl <i>a</i> mg/m <sup>2</sup>	POC g/m <sup>2</sup>	POC/ Chl <i>a</i>	Ingestion mg C/m <sup>2</sup> d	% Primary production
<b>Copepod species</b>										
<i>C. acutus</i>	47.1	5.0	107	0.6	0.5	40.5	12.6	250 <sup>a</sup>	3.4	1.4
<i>C. propinquus</i>	(±5.9)	(±1.1)		0.1	0.1	(±4.3)	(±1.8)		3.1	1.3
<i>C. simillimus</i>				4.7	3.8				0.6	0.3
<i>R. gigas</i>				0.4	0.3				7.7	3.2
<i>M. lucens</i>				11.4	9.3				40.4	16.7
Copepodite stages				59.3	48.4				65.6	27.2
Small calanoids				106.2	86.7				176.3	73.1
<i>Oithona</i> spp.				9.9	8.1				75.5	31.3
<b>Non-copepod taxa</b>										
Euphausiid larvae				0.1	0.1				1.3	0.5
Pteropods				9.2	7.5				7.5	3.1
<i>S. thomsoni</i>				—					5.7	2.4
Total				202	165				387	160

Values of Chl *a* and POC integrated over 200 m (depth of mixed layer). Primary production POOZ: 122.4, SIZ: 241.2 mg C/m<sup>2</sup> d.

<sup>a</sup>C:Chl ratio computed from Hewes et al. (1990).

*similis*. The percentage of primary production consumed daily is lower than in the POOZ, with a value close to 35%.

The use of copepod energetic requirements as a proxy of ingestion activity presents two potential biases: (1) it ignores the influence of the non-copepod taxa and (2) it is valid mainly for those populations or communities with reduced growth rates (adult populations). When young stages with very active growth dominate the population, the underestimation could be important. An alternate computation was attempted using the present data on adults and non-copepod groups as well as literature data on chlorophyll-derived ingestion rates for those species or group for which direct measurements were not made, i.e. *M. lucens* (Atkinson, 1996) and *Oithona* spp. (Atkinson, 1996), small calanoid copepods (*C. laticeps*, *C. citer*, etc.), and young copepodite stages of large species (Schnack et al., 1985). As anticipated, the ingestion rate computed at the population level showed a major impact of the small calanoid copepods and copepodite stages in both the POOZ and SIZ areas (Table 9). The

contribution of *Oithona* spp. in the SIZ was also major followed by the contribution of *M. lucens*. In the POOZ, the other groups or species that showed significant contribution were *Oithona* spp. and the pteropod *Limacina* spp. (Table 9). In terms of primary production consumed daily, the budget exceeds the estimates from energetic needs, with similar percentages in both POOZ and SIZ (165% and 160%, respectively).

#### 4. Discussion

During the course of this study mesozooplankton biomass ranged from values <2–16 g/m<sup>2</sup> in both spring and summer. This range brackets fairly well the values reported in earlier studies, from the relatively low estimates of Boysen-Ennen et al. (1991) for various parts of the Southern Ocean (0.8–3.6 g/m<sup>2</sup>) to the high values recorded by Ward et al. (1995) in South Georgia (13 g/m<sup>2</sup>). Regional studies (Hopkins, 1971) have shown that mesozooplankton biomass tends to increase

towards the polar front and localised coastal areas such as the Antarctic Peninsula (Hopkins, 1985; Huntley and Escritor, 1992), South Georgia (Ward et al., 1995), and Kerguelen archipelago (Razouls et al., 1995). Generally, two peaks of biomass have been observed over the seasons with the spring upward migration of overwintering species (Atkinson, 1991) and in summer the recruitment of the new generation (Hopkins, 1971). The seasonality and the spatial heterogeneity were well illustrated in the Indian sector of the Southern Ocean, with summer maxima of dry mass in the polar front and the POOZ (ANTARES 2 and 4). Spring biomass suggested a strong influence of the marginal ice zone with maximum values associated with a phytoplankton bloom in progress and, in contrast, minimum values in both the PFZ and the POOZ areas (ANTARES 3).

Antarctic zooplankton is usually dominated by crustacea (Yamada and Kawamura, 1986; Voronina et al., 1994; Hosie and Cochran, 1994), but other groups also can display significant contribution to the community, e.g., chaetognaths, salps, pteropods (Boysen-Ennen et al., 1991; Voronina et al., 1994; Hosie and Cochran, 1994; Ward et al., 1995). However, their contribution to the biomass remains small or irregular. In the present study, salps and pteropods were recorded mostly in summer in the polar front and POOZ areas, while euphausiid larvae displayed a North–South gradient at both seasons, with summer maximum density and biomass close to the Antarctic continent. The copepod biomass was dominated by the same species recorded in other sectors of the Antarctic Ocean, e.g., *C. acutus*, *C. propinquus*, *C. simillimus*, *R. gigas* and *M. gerlachei* (Vervoort, 1965; Hopkins, 1971; Hopkins et al., 1993; Boysen-Ennen et al., 1991; Voronina et al., 1994; Atkinson, 1996), but medium and small size species were also present, e.g., *M. lucens*, *C. citer*, *C. laticeps*, *Oithona* spp., (Yamada and Kawamura, 1986; Hopkins, 1987; Schnack et al., 1985; Errhif et al., 1997; Pakhomov et al., 1997).

Pigment gut content is to some extent related to chlorophyll availability, diel changes, and growth stage (Landry et al., 1994). The values recorded in the present study showed day–night periodicity in agreement with the diurnal variations reported for

most Antarctic and subantarctic copepod species (Perissinotto, 1992; Atkinson et al., 1992a, b, 1996; Pakhomov et al., 1997). The pigment gut content was usually low compared with the values observed off South Georgia (Pakhomov et al., 1997), but close to those reported by Perissinotto (1992) around Prince Edward archipelago for *C. simillimus*. The high chlorophyll content (30–300 mg/m<sup>2</sup>) off South Georgia, which contrasts with the low values observed in Prince Edward archipelago and the present study (respectively 70 and 8–80 mg/m<sup>2</sup>), probably explains such discrepancy. The somewhat higher values observed in spring compared to the summer period proceeds from the same difference in phytoplankton abundance (8–30 mg/m<sup>2</sup> in summer; 47–83 mg/m<sup>2</sup> in spring). Non-copepod taxa showed high pigment gut content, with *S. thomsoni* and the pteropod *Cavolinia* spp. exceeding 200 ng/ind. Pigment gut contents of other taxa, i.e. euphausiids, and the pteropod *Limacina* spp., agree relatively well with the values reported by Perissinotto (1992) for similar species.

The evaluation of the grazing impact of the entire community is always difficult since the full set of relevant measurements is rarely available and approximation must be made. Gut content of the different species and groups was not measured at all times, and summer estimates (pteropods, salps, and euphausiid larvae) have been used for the spring budget. Thus, because of the lower particulate chlorophyll and primary production in summer, the spring impact of these groups may have been underestimated. Similarly, the lack of measurements of gut clearance rate constants for all groups at all times may be a potential drawback. The response of gut evacuation ( $k$  in min<sup>-1</sup>) to changes in food availability is complex and has yielded contradictory results. Wang and Conover (1986), Dagg and Walser (1987), Pasternak (1994), Martaugh (1984), Mayzaud et al. (1998) reported that gut evacuation rates tended to increase (lower residence time) with increasing food level. Ellis and Small (1989) found no significant differences with changing food supply. Comparing different food sources Mayzaud et al. (1998) showed that the response varied with the nature of the food with a pattern, which agreed with the concept of

minimum transit time ( $1/k$ , min) at high food concentration for diatoms but not for dinoflagellates or detrital particles, which showed no differences. In this study, we used measured spring and summer values for  $k$  and literature data when  $k$  values for a given species were not determined. In this latter case, we only considered summer studies from regions of low primary productivity and similar chlorophyll standing stock (Prince Edwards Archipelago, north of South Georgia). The use of Schnack et al. (1985) data for spring feeding rates of key groups such as the small calanoids (*C. citer*, *C. laticeps*) and copepodite stages of large calanoids may not fully apply to our environment and may result in an over-estimation. They should be indicative of the expected order of magnitude. These data were acquired at the same season and for similar phytoplankton standing stock (their station 148), but the Weddell Sea system may not be directly comparable in terms of trophic environment. However, even if the actual rates were halved, the dominant impact of these two categories would remain unchanged.

Another source of uncertainty is the value of the chlorophyll to carbon ratio used to convert pigment intake to carbon equivalent. Classically ratios ranging from 35 to 60 (mean value = 50), characteristic of cultured phytoplankton, coastal bloom conditions or surface water (Antia et al., 1963; Strathman, 1967; Peterson and Festa, 1984; Hewes et al., 1990; Dehairs et al., 1992) are used. Such ratios correspond to the carbon and chlorophyll content of live, actively growing cells either from in vitro measurement or from indirect estimates using microscope counts and different

sets of relations between cell volume and carbon content (Strathman, 1967; Hewes et al., 1990). In their extensive study, Hewes et al. (1990) specifically addressed the problem of the carbon to chlorophyll ratio and demonstrated that the value of the conversion factor is linked in a non-linear mode to the chlorophyll concentration (microbial  $C:Chl a = 80Chl^{-0.4}$ ) and increases with depth in relation with the decrease in chlorophyll content and changes in physiological state. The C:Chl ratio of autotrophic eucaryotes from Antarctic blue waters exceeds 100 and approaches a threshold of 30 in Antarctic waters with high chlorophyll concentration ( $> 3 \text{ mg/m}^3$ ). In the ocean sector surveyed during the present study, plotting the regression between particulate carbon and chlorophyll (spring data in SIZ excepted) resulted in the following relationship:  $POC = 19.5 + 216 Chl a$  ( $R^2 = 0.833$ ,  $df = 29$ ;  $F = 134.8$ ;  $p = 0.0001$ ), which illustrates the tight link between carbon and chlorophyll.

From the study of Becquevort et al. (2000, Tables 9 and 10), it is possible to derive the standing stock of the different microbial groups in the upper mix layer during the ANTARES cruises and compare them with the mean total carbon concentration. The pool of live carbon (phytoplankton, bacteria, and protozoa) accounted for less than half of the total particulate carbon with the noticeable exception of the POOZ area in spring where it represented 73%. The authors used a C:Chl conversion factor of 35 for chlorophyll concentrations ranging from 0.1 to 0.4  $\mu\text{g/l}$ , which likely underestimated the autotrophic carbon. The actual value of detrital carbon is certainly lower than computed in Table 10, but the

Table 10

Mean biomass of total particulate carbon and the sum of the three main microbial groups (phytoplankton, bacteria, protozoa) in the surface mixed layer as reported by Bequevort et al. (2000)

Region station	ANTARES 2 (summer)			ANTARES 3 (spring)	
	POOZ A16–A14	SIZ A12–A07	CCSZ A06	POOZ A17–A13	SIZ A11–A12
Total protozoa groups ( $\text{mg C/m}^3$ )	17.2	20.0	31.2	25.4	26.8
Total POC ( $\text{mg/m}^3$ )	40.1	47.2	94.4	34.8	123.9
Total protozoa C (% total carbon)	43	42	33	73	22

underestimation is in part compensated by the bacterial contribution (collected on 0.2- $\mu\text{m}$  filters), which was only partially retained by the GF/F filters used for total POC determination. Whatever the basis considered, it appears that the contribution of detrital carbon is not negligible. It is interesting to note that the only region and season (POOZ in spring) where the C:Chl ratio is minimum (107, a value within the theoretical ones) is also the area that displays the largest contribution of live cells to the carbon pool (Table 10). The high significance of the regression between carbon and chlorophyll suggests that we are dealing with chlorophyll-containing particles, which probably contribute to the pigment gut content. Thus, the values of C:Chl ratio used in the present study not only considered the detrital carbon to be part of the zooplankton diet but also integrate the upper 200 m of the water column where the different groups of organisms feed at night. From a pragmatic viewpoint, our integrated value of the conversion factor yielded a level of predation on microzooplankton that matches the anticipated levels of protozoan production (see discussion below). The use of smaller ratios would increase the difference between respiration and pigment ingestion to a degree, which would result in a non-sustainable system. The same argument cannot apply to the SIZ in spring (ANTARES 3) where the changes in particulate carbon are independent of chlorophyll. The calculation of the conversion ratio was attempted two different ways: (1) using Hewes et al. (1990) and integrate the result for the 200-m water column and (2) using the protozoa carbon estimate of Becquevort et al. (2000), and subtract it from the total POC. The respective values of C:Chl obtained are 249 and 251. A value of 250 therefore seems appropriate.

The minor impact of mesozooplankton community grazing (Atkinson et al., 1996; Dam et al., 1993; Morales et al., 1991, 1993; Tsuda and Sugisaki, 1994; Ward et al., 1995; Irigoien et al., 2000) does not seem to apply to the grazing budget computed over two seasons for the Indian sector of the Southern Ocean. Indeed, the grazing pressure often exceeded the level of primary productivity but with different taxa responsible for the intake of phytoplankton. In summer, as

noticed by Perissinotto (1992) and Pakhomov et al. (1997), the copepod communities showed a very limited impact contrary to the non-crustacean taxa, which showed a strong but differential influence depending on the area considered: salps are the main phytoplankton consumers in the polar front and the POOZ, while adult krill (*E. superba*) and copepods were the key grazers in the CCSZ. In the SIZ, the grazing pressure is minimal, with a mixed influence of both copepods and pteropods. In spring, the copepod population showed a major influence at all locations, with the dominant impact of the small calanoid species and the copepodite stages of the large species. As noticed by Schnack et al. (1985), the strong influence of species contributing <10% the total copepod biomass (e.g., *Oithona* spp. or small calanoids) is a key feature of the spring period. As indicated earlier, the impact of the small calanoid species should be considered with caution and the high values of grazing impact should be viewed as indicative of a strong grazing pressure, which probably explains the low chlorophyll levels in an area of higher primary production (SIZ in spring). Computed in relation to the total particulate organic carbon, the impact of zooplankton feeding appears relatively constant with values ranging from 2.6% to 2.8% of POC in summer (ANTARES 2) and 3% to 4% in spring. Interestingly, the feeding pattern of protozoan is contrasted over the two seasons, with summer consumption on bacteria and spring feeding on phototrophic flagellates (Becquevort et al., 2000). As a result, the spring standing stock of phytoplankton was heavily controlled by the grazing activity of both micro- and mesozooplankton communities.

The relative contribution of phytoplankton and other food sources to copepod nutrition have been the object of several recent studies (Atkinson, 1994, 1995, 1996) and has suggested that the various sources of heterotrophic carbon could to a large extent explain the negative energy budget based on gut-pigment-derived ingestion rates (Dam et al., 1993, Irigoien et al., 2000; this study). Using such a difference as a minimum estimate of protozoan ingestion, the summer copepod population showed a significant rate of ingestion, which



decreased from the polar front to the Antarctic coastal waters. As a result, the impact of copepods on the protozoan biomass decreased from 172% in the POOZ to 14% in the CCSZ, in agreement with the observed gradient of protozoan biomass (Becquevort et al., 2000), which was minimum in the north ( $0.9 \text{ mg C/m}^3$ ) and increased with increasing latitude ( $2.6 \text{ mg C/m}^3$  in the SIZ and  $4.9 \text{ mg C/m}^3$  in the CCSZ). Though micro-protzoa growth rate was not measured directly, it is classically considered to be equivalent to the primary production (J. Dolan, personal communication). Thus, the percentages of protozoa production ingested varied from a maximum of 148% in summer in the POOZ to about 65% in the SIZ and CCSZ. If a conversion ratio of chlorophyll to carbon of 50 or 100 had been considered rather than the natural carbon to chlorophyll ratios, feeding pressure would increase (3–5 times) to exceedingly high levels. The relatively balanced budget observed for the spring copepod population (ANTARES 3) may indicate that protozoan was only marginally used as food. The parallel increase in grazing activity and protozoan biomass with increasing latitude ( $8.2 \text{ mg C/m}^3$  in the POOZ and  $11.3 \text{ mg C/m}^3$  in the SIZ) strongly suggests that heterotrophic carbon biomass and copepod feeding activity were not directly linked.

In conclusion, the concept of a microbial food chain with protozoa feeding on the large pool of bacteria and small phytoplankton and fuelling a mesozooplankton food web (Atkinson, 1995; Smetacek et al., 1990) does not apply to this sector of Antarctic Ocean and the period studied. Mesozooplankton communities remained an important player as consumers of phytoplankton, and the diversity of taxa involved confirmed that the definition of the zooplankton could not be limited to the dominant group of copepods if realistic figures are to be expected.

### Acknowledgements

We thank CNRS (through ANTARES programme and ESA 7076) and IFRTP for their financial support during the course of this study. Our thanks also go to the captain and the crew of

the R.V. *Marion-Dufresne* for the invaluable help and assistance during the different cruises. The French CNRS and the South African NRF (Science Liaison Centre) provided the funds for bilateral collaboration. We are very grateful to our cruise colleagues I. Bentaleb, T. Caubert, M. Fiala, and M. Panouse for supplying us and allowing us to use unpublished data. The technical assistance of S. Sabini was greatly appreciated.

### References

- Antia, N.J., McAllister, C.D., Parsons, T.R., Stephens, K., Strickland, J.D.H., 1963. Further measurements of primary production using large volume plastic sphere. *Limnology and Oceanography* 8, 166–183.
- Atkinson, A., 1991. Life cycle of *Calanoides acutus*, *Calanus simillimus* and *Rhincalanus gigas* (Copepoda: Calanoida) within the Scotia Sea. *Marine Biology* 109, 79–91.
- Atkinson, A., 1994. Diets and feeding selectivity among the epipelagic copepod community near South Georgia in summer. *Polar Biology* 14, 551–560.
- Atkinson, A., 1995. Omnivory and feeding selectivity in five copepod species during spring in the Bellingshausen Sea, Antarctica. *ICES Journal of Marine Science* 52, 385–396.
- Atkinson, A., 1996. Subantarctic copepods in an oceanic, low chlorophyll environment: ciliate predation, low food selectivity and impact on prey populations. *Marine Ecology Progress Series* 130, 85–96.
- Atkinson, A., Shreeve, R.S., 1995. Response of the copepod community to a spring bloom in the Bellingshausen Sea. *Deep-Sea Research II* 42, 1291–1311.
- Atkinson, A., Ward, P., Williams, R., Poulet, S.A., 1992a. Diel vertical migration and feeding of copepods at an oceanic site near South Georgia. *Marine Biology* 113, 583–593.
- Atkinson, A., Ward, P., Williams, R., Poulet, S.A., 1992b. Feeding rates and diel vertical migration of copepods near South Georgia: comparison of shelf and oceanic sites. *Marine Biology* 114, 49–56.
- Atkinson, A., Ward, P., Murphy, E.J., 1996. Diel periodicity of subantarctic copepods: relationships between vertical migration, gut fullness and gut evacuation rate. *Journal of Plankton Research* 18, 1387–1405.
- Becquevort, S., Menon, P., Lancelot, C., 2000. Differences of the protozoan biomass and grazing during spring and summer in the Indian sector of the Southern Ocean. *Polar Biology* 23, 309–320.
- Boysen-Ennen, E., Hagen, W., Hubold, G., Piatkowski, U., 1991. Zooplankton biomass and ice-covered Weddell Sea, Antarctica. *Marine Biology* 111, 227–235.
- Caubert, T., 1997. Production primaire, production de silice biogénique (BSi), dissolution de BSi, stock de BSi. In: Descolas-Gros, C., Mayzaud, P. (Eds.), ANTARES 3 (MD 102), Les Rapports de Campagnes à la Mer, Vol. 97-2.

- Institut Français pour le Recherche et la Technologie Polaires, pp. 158–162.
- Cohen, R.E., Lough, R.G., 1981. Length–weight relationships for several copepods dominant in the George Bank-Gulf of marine area. *Journal of Northwest Atlantic Fisheries Sciences* 2, 47–52.
- Conover, R.J., Huntley, M., 1991. Copepods in ice-covered seas—distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. *Journal of Marine Systems* 2, 1–41.
- Dagg, M.J., Walser Jr, W.E., 1987. Ingestion, gut passage and egestion by the copepod *Neocalanus plumchrus* in the laboratory and in the subarctic Pacific Ocean. *Limnology and Oceanography* 32, 178–188.
- Dam, H.G., Miller, C.A., Jonasdottir, S.H., 1993. The trophic role of mesozooplankton at 47°N, 20°W during the North Atlantic Bloom Experiment. *Deep-Sea Research II* 40, 197–212.
- Dehairs, F., Goeyens, L., Stroobants, N., Mathot, S., 1992. Elemental composition of suspended matter in the Scotia-Weddell confluence area during spring and summer 1988 (EPOS Leg 2). *Polar Biology* 12, 25–33.
- Ellis, S.G., Small, L.F., 1989. Comparison of gut evacuation rates of feeding and non-feeding *Calanus marshallae*. *Marine Biology* 103, 175–181.
- Errhif, A., 1998. Composition et structure du zooplancton du secteur Indien de l'Océan Austral. Rôle du métabolisme respiratoire. Thèse de Doctorat de l'Université Aix-Marseille III, France, unpublished.
- Errhif, A., Razouls, Cl., Mayzaud, P., 1997. Composition and community structures of pelagic copepods in the Indian sector of the Antarctic Ocean during the end of the austral summer. *Polar Biology* 17, 418–430.
- Fiala, M., Oriol, L., 1995. Biomasse des différentes classes de taille phytoplanctoniques dans le secteur Indien de l'Océan Austral durant l'été. In: Fiala, M. (Ed.), *ANTARES 2* (MD 78), Les Rapports de Campagnes à la Mer, Vol. 95-1. Institut Français pour le Recherche et la Technologie Polaires, pp. 158–162.
- Gifford, D.J., 1993. Consumption of protozoa by copepods feeding on natural microplankton assemblages. In: Kamp, P.F., Sherr, B.F., Cole, J.J. (Eds.), *Handbook of Aquatic Microbial Ecology*. Lewis Publishers, London, pp. 723–729.
- Hewes, C.D., Sakshaug, E., Reid, F.M.H., Holm-Hansen, O., 1990. Microbial autotrophic and heterotrophic eucaryotes in Antarctic waters: relationships between biomass and chlorophyll, adenosine triphosphate and particulate organic carbon. *Marine Ecology Progress Series* 63, 27–35.
- Hopkins, T.L., 1971. Zooplankton standing crop in the Pacific sector of the Antarctic. In: Llano, G.W., Wallen, I.E. (Eds.), *Biology of the Antarctic Seas*, Vol. 17. American Geophysical Union, Washington, DC, pp. 347–362.
- Hopkins, T.L., 1985. Food web of an Antarctic midwater ecosystem. *Marine Biology* 89, 197–212.
- Hopkins, T.L., 1987. Midwater food web in McMurdo Sound, Ross Sea, Antarctica. *Marine Biology* 96, 93–106.
- Hopkins, T.L., Lancraft, T.M., Torres, J.J., Donnelly, J., 1993. Community structure and trophic ecology of zooplankton in the Scotia Sea marginal ice zone in winter (1988). *Deep-Sea Research I* 40, 81–105.
- Hosie, G.W., Cochran, T.G., 1994. Mesoscale distribution patterns of macrozooplankton communities in Prydz Bay, Antarctica—January to February 1991. *Marine Ecology Progress Series* 106, 21–39.
- Huntley, M.E., Escritor, F., 1991. Dynamics of *Calanoides acutus* (Copepoda: Calanoida) in Antarctic coastal waters. *Deep-Sea Research* 38, 1145–1167.
- Huntley, M.E., Escritor, F., 1992. Ecology of *Metridia gerlachei*, Giesbrecht, in the western Bransfield Strait, Antarctica. *Deep-Sea Research* 39, 1027–1055.
- Huntley, M.E., Lopez, M.D.G., 1992. Temperature-dependent production of marine copepods: a global synthesis. *American Naturalist* 140, 201–242.
- Irigoién, X., Harris, R.P., Head, R.N., Lindley, J.A., Harbour, D., 2000. Physiology and population structure of *Calanus finmarchicus* (Copepoda: Calanoida) during a Lagrangian tracer release experiment in the North Atlantic. *Journal of Plankton Research* 22, 205–221.
- Kosobokova, K.N., 1994. Reproduction of the calanoid copepod *Calanus propinquus* in the southern Weddell Sea, Antarctica: observations in laboratory. *Hydrobiologia* 292/293, 219–227.
- Kubjeweit, F., 1993. Reproduction and life cycle of dominant copepod species from the Weddell Sea, Antarctica. *Berichte Polarforschung* 129, 1–237.
- Landry, M.R., 1981. Switching between herbivory and carnivory by the planktonic marine copepod *Calanus pacificus*. *Marine Biology* 65, 77–82.
- Landry, M.R., Peterson, W.K., Fagerness, V.L., 1994. Mesozooplankton grazing in the Southern California Bight. I. Population abundances and gut pigment contents. *Marine Ecology Progress Series* 115, 55–71.
- Lopez, M.D., Huntley, M.E., Lovette, J.T., 1993. *Calanoides acutus* in the Gerlache Strait, Antarctica. I. Distribution of late copepodite stages and reproduction during spring. *Marine Ecology Progress Series* 100, 153–165.
- Marin, V., 1987. The oceanographic structure of eastern Scotia Sea. Part IV. Distribution of copepod species in relation to hydrography in 1981. *Deep-Sea Research* 33, 177–194.
- Martaugh, P.A., 1984. Variable gut residence time: problem in inferring feeding rate from stomach fullness of a mysid crustacean. *Canadian Journal of Fisheries and Aquatic Sciences* 41, 1287–1293.
- Mayzaud, P., Tirelli, V., Bernard, J.M., Roche-Mayzaud, O., 1998. The influence of food quality on the nutritional acclimation of the copepod *Acartia clausi*. *Journal of Marine Systems* 15, 483–493.
- Metz, C., Schnack-Schiel, S.B., 1995. Observations on carnivorous feeding in Antarctic copepods. *Marine Ecology Progress Series* 129, 71–75.
- Morales, C.E., Bedo, A., Harris, R.P., Tranter, P.R.G., 1991. Grazing of copepod assemblages in the North-East Atlantic:

- the importance of small size fraction. *Journal of Plankton Research* 13, 455–472.
- Morales, C.E., Harris, R.P., Head, R.N., Tranter, P.R.G., 1993. Copepod grazing in the North East Atlantic during a six week drifting station: the contribution of size classes and vertical migrants. *Journal of Plankton Research* 15, 185–211.
- Omori, M., Ikeda, T., 1984. *Methods in Marine Zooplankton Ecology*. Wiley, New York.
- Pakhomov, E.A., Verheye, H.M., Atkinson, A., Laubscher, R.K., Taunton-Clark, J., 1997. Structure and grazing impact of the mesozooplankton community during late summer 1994 near South Georgia, Antarctica. *Polar Biology* 18, 180–192.
- Panouse, M., Fiala, M., Machado, C., Oriol, L., 1997. Distribution de la biomasse phytoplanctonique dans l'Océan Austral durant le printemps. Importance des différentes classes de taille. In: Descolas-Gros, C., Mayzaud, P. (Eds.), *ANTARES 3 (MD 102), Les Rapports de Campagnes à la Mer, Vol. 97-2*. Institut Français pour le Recherche et la Technologie Polaires, pp. 140–149.
- Pasternak, A.F., 1994. Gut fluorescence in herbivorous copepods: an attempt to justify the method. *Hydrologia* 292/293, 241–248.
- Perissinotto, R., 1992. Mesozooplankton size-selectivity and grazing impact on the phytoplankton community of Prince Edward Archipelago (Southern Ocean). *Marine Ecology Progress Series* 79, 243–258.
- Perissinotto, R., Mayzaud, P., Labat, J.P., Razouls, S., 2001. Grazing dynamics of *Euphausia spinifera* in the region of the subtropical convergence and the Agulhas front. *Canadian Journal of Fisheries and Aquatic Sciences* 58, 1–9.
- Peterson, W.T., Festa, J.F., 1984. Numerical simulation of phytoplankton productivity in partially mixed estuaries. *Estuarine and Coastal Shelf Sciences* 19, 563–589.
- Poulet, S.A., 1976. Feeding of *Pseudocalanus minutus* on living and non living particles. *Marine Biology* 34, 117–125.
- Razouls, S., de Bovée, F., Dellile, D., Fiala, M., Mayzaud, P., 1995. Temporal variability of bacteria phyto- and zooplankton assemblages of the subantarctic Morbihan Bay (Kerguelen Archipelago). In: Battaglia, B., Valencia, J., Walton, D.W.H. (Eds.), *Antarctic Communities, Species, Structure and Survival*. Cambridge University Press, Cambridge, pp. 86–92.
- Schnack, S.B., Smetacek, V., Bodungen, B., Stegmann, P., 1985. Utilisation of phytoplankton by copepods in Antarctic water during spring. In: Gray, J., Christiansen, M.E. (Eds.), *Marine Biology of Polar Region and Effects of Stress on Marine Organisms*. Wiley, New York, pp. 65–81.
- Smetacek, V., Scharek, R., Nöthig, E.M., 1990. Seasonal and regional variation in the pelagial and its relationship to the life history cycle of krill. In: Kerry, K.R., Hampel, G. (Eds.), *Antarctic Ecosystems: Ecological Changes and Conservation*. Springer, Berlin, pp. 103–114.
- Stoecker, D.K., Egloff, D.A., 1987. Predation by *Acartia tonsa* Dana on planktonic ciliates and rotifers. *Journal of Experimental Marine Biology and Ecology* 110, 53–68.
- Strathman, R.R., 1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. *Limnology and Oceanography* 12, 411–418.
- Swadling, K.M., Gibson, J.A.E., Ritz, D.A., Nichols, P.D., Hughes, D.E., 1997. Grazing of phytoplankton by copepods in the eastern Antarctic coastal waters. *Marine Biology* 128, 39–48.
- Tirelli, V., Mayzaud, P., 1999. Gut evacuation rates of Antarctic copepods during austral spring. *Polar Biology* 21, 197–200.
- Tsuda, A., Sugisaki, H., 1994. In situ grazing rate of the copepod population in the western subarctic North Pacific during spring. *Marine Biology* 120, 203–210.
- Turner, J.T., Graneli, E., 1992. Zooplankton feeding ecology: grazing during enclosure studies of phytoplankton blooms from the west coast of Sweden. *Journal of Experimental Marine Biology and Ecology* 157, 19–31.
- Uye, S., 1982. Length-weight relationship of important zooplankton from the inland sea of Japan. *Journal of the Oceanographic Society of Japan* 38, 149–158.
- Vervoort, W., 1965. Notes on the biogeography and ecology of free living marine copepods. In: Van Oye, P., Van Mieghan, J. (Eds.), *Biogeography and Ecology of Antarctica*. Junk, The Hague, pp. 381–400.
- Voronina, N.M., Kosobokova, K.N., Pakhomov, E.A., 1994. Composition and biomass of summer metazoan plankton in the 0–200 m layer of the Atlantic sector of the Antarctic. *Polar Biology* 14, 91–95.
- Waidyana, N.N., Rassoulzadegan, F., 1989. Selective feeding of *Acartia clausi* and *Centropages typicus* on microzooplankton. *Marine Ecology Progress Series* 53, 37–45.
- Wang, R., Conover, R.J., 1986. Dynamics of gut pigment in the copepod *Temora longicornis* and the determination of in-situ grazing rates. *Limnology and Oceanography* 31, 967–977.
- Ward, P., Shreeve, R.S., 1995. Egg production in three species of Antarctic Calanoid copepods during austral summer. *Deep-Sea Research I* 42, 721–735.
- Ward, P., Atkinson, A., Murray, A.W.A., Wood, A.G., Williams, R., Poulet, S.A., 1995. The summer zooplankton community at South Georgia: biomass, vertical migration and grazing. *Polar Biology* 15, 195–208.
- Webber, M.K., Roff, J.C., 1995. Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica. *Marine Biology* 123, 481–495.
- Yamada, S., Kawamura, A., 1986. Some characteristics of the zooplankton distribution in the Prydz Bay region of the Indian sector of the Antarctic Ocean in the summer of 1983/1984. *Memoirs of the National Institute for Polar Research* 44, 86–95.