Feeding, respiration and egg production rates of copepods during austral spring in the Indian sector of the Antarctic Ocean: role of the zooplankton community in carbon transformation

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Abstract

During the austral spring period of 1996, the composition, age structure and physiological activity of zooplankton were studied in the Indian sector of the Southern Ocean. Zooplankton biomass ranged from less than $1\,\mathrm{g\,m^{-2}}$ in the Northern Polar Front Zone (PFZ) to $16\,\mathrm{g\,m^{-2}}$ near the ice edge in the Seasonal Ice Zone (SIZ). Zooplankton communities were dominated by copepods associated with euphausiid larvae. At all stations, species composition of copepods was dominated in number by small species (*Oithona* spp, *Ctenocalanus citer*). Northern stations were characterized by *Calanus simillimus* and *Metridia lucens*. Southern stations showed high abundance of *Calanoides acutus*, *Calanus propinquus* and *Rhincalanus gigas*. Stage distribution was analyzed for the four main contributors to the copepod biomass (*Calanus simillimus*, *Calanoides acutus*, *Calanus propinquus* and *Rhincalanus gigas*).

Gut pigment content and gut transit time showed a strong day–night periodicity. Gut transit times were usually high with values ranging from 1 h (*Calanus propinquus*) to 1 h 30 min (*Rhincalanus gigas*). Maximum ingestion rates were recorded for *Calanus propinquus* and *Pleuromamma robusta*. Respiration rates were measured for 13 species of copepods and varied from $0.5–0.6\,\mu\mathrm{l\,O_2\,ind^{-1}\,day^{-1}}$ for smaller species to $20–62\,\mu\mathrm{l\,O_2\,ind^{-1}\,day^{-1}}$ for the larger ones. The impact of the copepod population was estimated from the CO_2 produced per $\mathrm{m^{-2}}$ and per day, which showed a release of 4.2–4.5 mmol. It corresponded to a minimum ingestion of 41.4% in the Permanent Open Ocean Zone (POOZ) and 22.6% in the SIZ of the daily primary production. The budget between carbon ingestion and respiratory requirements appears to be nearly balanced, but with the exception of *Calanus propinquus*, cannot accommodate the addition of the cost of egg production, which only partially relies on food intake. During austral spring, the population studied appeared to rely mostly on phytoplankton as food, though additional use of internal energy reserves and intake of protozoan cells was likely needed to fully balance the energy budget. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Zooplankton; Population; Copepods; Physiological activity; Antarctic; Indian sector

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1. Introduction

Our knowledge of the composition, structure and role of the mesozooplankton communities in the energy and carbon flows of the Southern Ocean has vastly improved over the past decade (Boysen-Ennen et al., 1991; Hopkins, 1985; Park and Wormuth, 1993; Schnack-Schiel and Mizdalski, 1994; Voronina et al., 1994; Ward et al., 1995), but remains to a large part limited to the summer situation and to a small number of locations in the Weddell Sea, the Antarctic Peninsula and the South Georgia system. Because of the logistic constraints, fewer studies have focused on the winter and spring situation (Hopkins et al., 1993; Siegel et al., 1992; Ward and Shreeve, 1999; Hernandez-Leon et al., 1999) despite the significant influence of the receding spring ice zone on the zooplankton community (Burghart et al., 1999). The winter–spring transition represents the onset of the period of high food supply with the development of the major spring bloom in the marginal ice zone (Sullivan et al., 1988), and this marked seasonality has shaped a variety of life-cycle/overwintering strategies of the key components of the zooplankton community (Schnack-Schiel and Hagen, 1994; Atkinson et al., 1997; Ward et al., 1997).

The influence of oceanic mesozooplankton grazing on phytoplankton biomass appears very variable, but usually is considered as relatively minor (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, although the percent of primary production consumed daily varies with season, location, population structure and population abundance, it is often found to be 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 impact is based largely on data limited to the copepod population, which ignore the other constituents of the zooplankton community despite their potential impact (Perissinotto, 1992). In addition, grazing rates are commonly derived from gut pigment estimates, but usually uncorrected for pigment degradation, and converted into carbon equivalent assuming live exponentially growing phytoplankton (C/Chl = 40–50), an assumption rarely verified. These considerations raise some doubts about our ability to generalize across different seasons and oceanic locations. Further quantification of the role of the zooplankton community is needed to complete the global picture of the Southern Ocean.

Increasing evidence suggests that copepod pigment-derived grazing rates often cannot match the respiratory and egg production requirements of individuals or populations (Dam et al., 1993; Drits et al., 1993, 1994; Pakhomov et al., 1997). The difference is ordinarily attributed to carnivorous feeding on protozoan cells (Atkinson, 1994, 1996) or on small zooplankters (Metz and Schnack-Schiel, 1995), which provide additional food sources. However, as shown by Atkinson et al. (1996), copepods may display a positive energy budget with high grazing rate but low overall impact during a period of high productivity and phytoplankton standing stock.

The aim of the present study was to clarify, for the Indian sector of the Southern Ocean during the austral spring of 1996, the composition, age structure and physiological activity of the copepod community. We attempted to evaluate, for both community and individual species, the impact of the copepods on phytoplankton production and the magnitude of the zooplankton population recycling rates via respiratory CO_2 for several oceanic areas: Polar Front Zone (PFZ), Permanent Open Ocean Zone (POOZ) and Seasonal Ice Zone (SIZ).

2. Materials and methods

2.1. Zooplankton abundance and biomass

Cruise track and sampling sites are presented in Fig. 1. *ANTARES* 3 cruises took place along 62°E during the austral spring, i.e., October–November 1995, between 49° and 58°S at the ice edge. Two "long" stations were surveyed over several days following a Lagrangian drifter (free drifting sediment trap) to assess small-scale population changes and processes. Station A16/M2 was
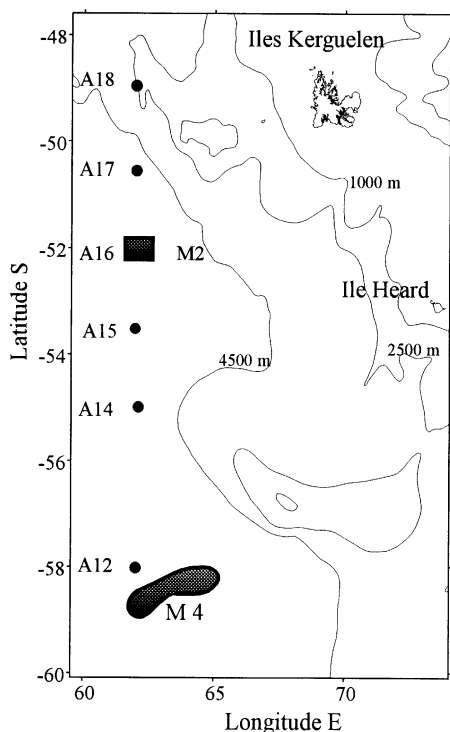
Fig. 1. Investigated zone and locations of sampling during the *ANTARES* 3 cruise (October–November 1995).

occupied from October 12 to October 16, and Station M4 at the ice edge was sampled between October 20 and October 26.

The abundance and biomass of mesozooplankton were estimated from vertical tows with a triple WP II net (200 μm mesh size). Hauls were made from 200 m to the surface. The content of the first net was preserved with formaldehyde and used for population structure analysis. Material from the second net was used for total biomass measurement; it was filtered on pre-weighed 200 μm net pieces, rinsed with ammonium formate and dried at 60°C to constant weight. The content of the third net was immediately diluted with surface seawater in a 40 l cooler and used for experiments on live animals.

2.2. Copepod feeding rates measured by gut fluorescence method

On retrieval of the net, the animals were transferred to a cold room at seawater temperature

and diluted. Groups of 15–20 individuals of the dominant stages of the same species were immediately picked out and filtered on Millipore 5 μm filters and deep frozen (−80°C) for pigment gut contents. Counts were checked under dim cold light and gut fluorescence analyzed on board.

Gut transit time experiments were carried out with animals from the same net, and detailed methodology can be found in Tirelli and Mayzaud (1999). Briefly, groups of 15–20 individuals of each species (mostly adults with few C5) were isolated in 250 ml beakers filled with 0.45 μm filtered seawater and placed in darkness. The sorting took 10–15 min, and only animals with visible full gut were chosen. At given time intervals (usually 6), all copepods from duplicate beakers were removed, rinsed and filtered on Millipore 5 μm membrane filters. The animals were then deep frozen at –80°C and later analyzed on board, as described below.

Copepods were homogenized in 6 ml of 90% acetone and extracted for at least 1 h at 2°C. Samples were then centrifuged and fluorescence measured before and after acidification with a Turner-design 10 fluorimeter. No correction for background fluorescence was applied. Gut pigment content was calculated as the sum of chlorophyll *a* and phaeopigments. The decline in gut fluorescence over time was fitted with a negative exponential model using Systat statistical package (Wilkinson, 1996).

Ingestion rates (*I*) were computed as the product of gut pigment content and the inverse of gut transit time (gut evacuation rate; K^{-1}). Assuming a nocturnal feeding period of 14 h, ingestion rate was then expressed by

$$I = \text{nocturnal gut content} \times \text{nocturnal } K^{-1} \times 14.$$

For two species an insufficient number of animals were collected, and literature data were used. Specifically, we adopted a gut evacuation rate of $1.13\,h^{-1}$ for *Calanus simillimus* (Atkinson et al., 1992b) and $0.179\,h^{-1}$ for *Pleuromamma robusta* (recalculated with a Q_{10} of 3,5 obtained from the data of Atkinson (1996) and Morales et al. (1993).

2.3. Respiration rates

Individuals from the diluted tow were placed in a cold room adjusted at seawater temperature (2°C). Animals from night collection were sorted to species, copepodite stage and sex under a binocular microscope (for the larger forms directly by eye) and placed in 1 l beakers filled with filtered seawater (0.45 μm) for 1–2 h. The animals were then incubated 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 used. Animal density was about 400 ind l^{-1} for the smallest species (*Oithona* or *Ctenocalanus*) and 20–40 ind l^{-1} (3–6 per 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 in darkness at seawater temperature for periods varying around 15–24 h.

Oxygen concentration was monitored with 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 and weight measurements. All data were normalized per unit dry weight. Values of individual biomass of each species were obtained from both direct measurements and 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 (Cohen and Lough, 1981; Uye, 1982; Kurbjeweit, 1993; Webber and Roff, 1995).

2.4. Egg production rate

Experiments on egg laying were performed on the five most abundant species at different stations along the transect: *Calanus simillimus* at A16/M2, *Rhincalanus gigas* at A12 and M4, *Calanus propinquus* at A15, A12 and M4, *Calanoides acutus* at M4 and A15, *Pleuromamma robusta* at A16, A15, A12 and M4. Females were immediately diluted and stored in a cold room at the temperature near that of in situ water, about 2.5°C in the north and near 1°C in the south. Females were then picked out by eye and isolated individually in vials filled with 30 ml of natural seawater from the field. They were then allowed to spawn under controlled conditions (cold room temperature, dim light). Females were kept in the laboratory for 5–6 days. Vials were inspected every day, eggs counted and females transferred into new natural seawater. The egg number reported is then the mean egg production rate per individual female and per day for the duration of the experiment.

2.5. Species contribution to total biomass

To compute the relative contribution of the different species to the total biomass, values of individual biomass of each species were taken from literature data. The values used are summarized in Table 1. Although, individual dry weights of the major species were measured from cruise samples, our values were limited to the dominant, mostly late copepodite stages. Since our values were reasonably close to the published one (*Calanus propinquus* C5 = 0.827 mg ind^{-1}; *Calanoides acutus* C4 = 0.158 mg ind^{-1}; *Rhincalanus gigas* C5 = 0.497 mg ind^{-1}; *Paraeuchaeta antarctica* fem = 2.21 mg ind^{-1}), we choose to use published data sets to minimize variability between stages. When specific dry weights were not available (mostly for the youngest copepodite stages), values were computed from the relationships between size and weight for that species as described earlier. For each large species (*Calanoides acutus*, *Calanus propinquus*, *Calanus simillimus*, *Rhincalanus gigas*, *Metridia lucens*) the actual copepodite stage composition was used to calculate its contribution to the total biomass of each zone. This contribution is then 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 μm mesh net and were composed mainly of adult and C5 stages. Thus, their contribution to total

Table 1
Summary of dry weight data used for the different copepodite stages of the main species of Antarctic copepod

Species	Growth stage	Dry weight ($\mu g\ ind^{-1}$)	References
Calanoides acutus	C1	25	Cohen and Lough (1981) (formula)
	C2	35	Cohen and Lough (1981) (formula)
	C3	48	Mizdalski (1988)
	C4	110	Conover and Huntley, 1991
	C5	445	Conover and Huntley, 1991
	C6 fem	608	Conover and Huntley, 1991
Calanus propinquus	C1	50	Cohen and Lough (1981) (formula)
	C2	79	Cohen and Lough (1981) (formula
	C3	118	Conover and Huntley (1991)
	C4	163	Conover and Huntley (1991)
	C5	807	Conover and Huntley (1991)
	C6 fem	1343	Conover and Huntley (1991)
Calanus simillimus	C1	8	Cohen and Lough (1981) (formula)
	C2	12	Cohen and Lough (1981) (formula)
	C3	17	Atkinson (1996)
	C4	45	Atkinson (1996)
	C5	179	Atkinson (1996)
	C6 fem	284	Atkinson (1996)
Rhincalanus gigas	C1	36	Atkinson et al. (1996)
	C2	62	Atkinson et al. (1996)
	C3	118	Conover and Huntley (1991)
	C4	309	Conover and Huntley (1991)
	C5	560	Conover and Huntley (1991)
	C6 fem	1287	Conover and Huntley (1991)
Ctenocalanus citer	C6	16	Cohen and Lough (1981) (formula)
	C5	12	Cohen and Lough (1981) (formula)
Oithona spp.	C4+C5+C6	1.54	Atkinson (1996)
Oncaea antarctica	Female	10	Webber and Roff (1995) (formula)
	Male	4	Webber and Roff (1995) (formula)
Oncaea curvata	Female	2,5	Webber and Roff (1995) (formula)
	Male	1,5	Webber and Roff (1995) (formula)
Candacia maxima	C6	627	Webber and Roff (1995) (formula)
Euchirella rostromagna	C6	3360	Hagen (1988)

biomass was computed from weight data only for these two stages.

Statistical significance of the difference in chlorophyll gut content between stations or oceanic areas was tested by an ANOVA test using the SYSTAT 10 statistical package.

3. Results

3.1. Hydrography and trophic conditions

The surface layer down to 200 m was nearly homogeneous in temperature and salinity as

confirmed by the hydrographic data collected during the cruise (Park et al., 1997). In spring, the polar front was located at 49°40′S and the limit of ice was observed at 58°45′S. Station M4 north of the ice zone displayed a surface lens of minimum temperature and salinity (−1.5°C, <33.8) and thus minimum density. North of this area a gradual increase in temperature (up to 2.5°C) was recorded in the upper 100 m.

Chlorophyll biomass, integrated between the surface and 200 m was usually low, though slightly higher than in summer. Values ranged from 40 to 60 mg m^{-2} with most of the biomass located in the first 100 m. Maximum chlorophyll concentrations were recorded in the marginal ice zone with values around 0.5 μg l^{-1}, while minimum values (0.3 μg l^{-1}) were observed in the POOZ (Panouse

et al., 1997). The levels of integrated primary production varied with the area considered, with mean values of 122.4±28.7 mg C m^{-2} day^{-1} in the POOZ and 241.2±61.5 mg C m^{-2} day^{-1} in the SIZ (Caubert, 1997). Protozoan biomass varied between 4.4 and 11.3 mg C m^{-3} with maximum concentrations north of the receding ice edge (Becquevort et al., 2000).

3.2. The zooplankton community

The zooplankton biomass integrated over 200 m increased from north to south (Fig. 2). The northern stations (PFZ) presented extremely low biomass with values lower than 1 g m^{-2} dry weight. The three stations sampled between 52° and 55°S (POOZ) showed higher values with
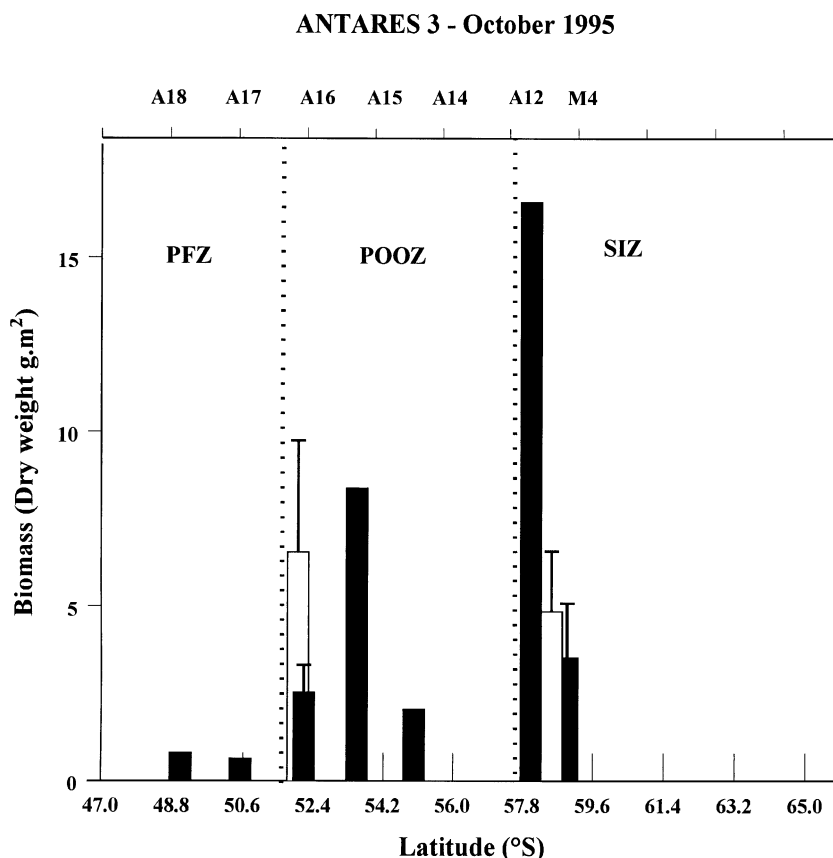

Fig. 2. Distribution of mesozooplankton dry mass along the transect surveyed during *ANTARES* 3. White bars—day time and black bars—night times. Vertical bars indicate standard deviation of multiple sampling at the same location ($n = 4$ at A16 and $n = 6$ at M4).

biomass ranging from 2 to $8 \, \mathrm{g \, m^{-2}}$. The most southern ice edge stations at 59°S (SIZ) displayed a small-scale spatial variability with values ranging from 4 to $16 \, \mathrm{g \, m^{-2}}$. No clear pattern could be seen between day and night tows suggesting a minor influence of vertical migration from populations located below 200 m (Fig. 2).

The composition of the mesozooplankton community is presented in Table 2, where the main taxa are grouped by hydrodynamic province. In terms of abundance, the communities were dominated by copepods associated with euphausiid larvae, pteropods, ostracods, chaetognaths and low abundances of salps and polychaetes. Because of the spatial scale of sampling, a large heterogeneity was recorded along the transect and within hydrodynamic provinces. A trend toward higher abundance in the SIZ was evident for copepods, euphausiid larvae and chaetognaths.

Species composition of the copepod populations is presented in Table 3. The list is limited to the 15 species that dominated the communities, and a detailed list can be found in Errhif (1998). They usually accounted for 97–99% of the copepod densities. In terms of numerical abundance small species largely dominated at all stations (*Oithona similis*, *Ctenocalanus citer*, *Oithona frigida*). The importance of some small species (*Oncea antarctica*, *Scolocethricella minor*) was limited to certain areas. Larger species (*Rhincalanus gigas*, *Calanoides acutus*, *Calanus propinquus*, *Paraeucheata* spp, *Calanus simillimus*) made a smaller contribu-

tion, which varied with the sampling location. Usually, the northern stations (PFZ and POOZ) were characterized by *Calanus simillimus*, *Metridia lucens* and to a minor extent *Clausocalanus laticeps*. The southern stations (south of POOZ and SIZ) showed large abundance of the larger species (*Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas*) as well as of smaller species (*Oithona similis*, *Oithona frigida*, *Oncaea antarctica*, *Oncaea curvata* and *Scolocithricella minor*).

Stage distribution was analyzed for the four main contributors to copepod biomass (Fig. 3). As indicated earlier, *Calanus simillimus* dominated in the PFZ where 77% of the population was composed of adult females and copepodite stage C5. Adult male and younger stages accounted, respectively, for 4% and 18% of all stages with C2 and C3 as the main contributors. A similar distribution was observed in the POOZ with a slightly larger contribution of adult males. In the SIZ, *Calanus simillimus* was less abundant and was mostly C5 and adult stages. The complete absence of C2 and C3 stages was noted. *Rhincalanus gigas* was mostly present in the POOZ and the SIZ with a major contribution of copepodite C3 and C4. Stages C5 and C3 made the next largest contribution, respectively, in the POOZ and the SIZ area. In the PFZ, only C3 and to a minor extent C4 stages were recorded at very low densities. *Calanoides acutus* and *Calanus propinquus* showed relatively similar distributions with a complete absence in the PFZ and increasing numbers from

Table 2
Abundance estimates (number $\mathrm{m^{-3}}$) of the main taxa constituting the mesozooplankton community during austral spring in the Indian sector of the Antarctic Ocean

| | ANTARES 3 (spring) | | | | | |
	PFZ (2)	SD	POOZ (6)	SD	SIZ (7)	SD
Copepods	299	203	198	117	591	201
Euphausiid larvae	1.6	0.4	3.2	1.5	14.4	7.8
Ostracods	5.7	1.8	10.1	5.7	3.6	2.6
Chaetognaths	5.2	1.3	7.3	4.6	11.8	6.5
Pteropods	0.6	0.8	0.9	0.7	0.3	0.3
Polychaetes	0.7	0.5	0.5	0.5	0.7	0.5
Salps	0	0	0	0	0.1	0.1

PFZ includes stations A18 and A17, POOZ includes stations A16 (replicated), A15 and A14, SIZ includes stations A12 and M4 (replicated). SD = standard deviation, (n) = number of stations in means.

Table 3
Species composition and abundance (number m^{-3}) of copepod populations at the different stations sampled above 200 m during *ANTARES* 3 in the different zones of the Indian sector of the Antarctic Ocean

Species	Stations														
	POOZ		POOZ						SIZ						
Station #	A18	A17	A16[a]	A16	A16	A16	A15	A14	A12	M4	M4	M4	M4	M4	M4
Date			12/10	12/10	14/10	16/10				20/10	21/10	22/10	23/10	24/10	25/10
Calanoides acutus	—	—	0.34	0.59	—	0.43	3.6	9.4	19.7	6.8	27.9	30.6	13.3	22.5	19.7
Calanus propinquus	—	—	—	—	—	—	0.17	0.17	1.7	1.7	3.7	5.1	2.7	6.5	5.8
Calanus simillimus	51.1	16.7	21.1	32.7	13.2	16.4	34.7	39.5	8.2	1.1	0.34	5.8	2.7	3.1	6.8
Clausocalanus laticeps	0.9	0.2	—	0.5	0.17	0.51	0.34	3.1	0.68	—	—	0.85	0.51	1.1	—
Ctenocalanus citer	226	43.5	117	183	22.5	35.6	34.1	53.1	59.9	92.6	187	166	103	204	174
Metridia lucens	52.1	0.9	6.5	—	—	5.6	11.2	3.2	18.4	5.1	0.34	6.2	2.0	3.2	7.8
Microcalanus pygmaeus	—	—	—	—	—	—	—	—	1.4	5.4	1.4	10.2	7.8	10.9	5.1
Oithona frigida	49.1	44.9	57.2	39.5	0.85	8.85	19.1	23.1	40.8	59.9	81.7	84.4	122	89.9	100
Oithona similis	57.2	43.6	80.3	99.4	6.9	22.5	11.6	28.6	142	125	363	174	258	250	362
Oncaea antarctica	—	—	1.5	—	0.85	—	10.2	0.09	2.6	24.9	9.5	40.8	40.9	76.3	76.3
Oncaea curvata	—	—	—	—	—	—	—	—	0.34	1.4	4.8	5.4	5.1	17.1	8.5
Paraeuchaeta spp.	0.68	0.51	1.2	0.5	0.09	1.2	2.9	—	—	2.7	—	2.4	3.2	1.7	2.4
Rhincalanus gigas	0.17	0.42	10.9	0.77	5.3	9.5	30.6	29.3	16.9	2.9	12.3	10.3	4.3	11.2	92.6
Scolecithricella minor	2.9	1.9	3.4	3.9	0.85	3.7	8.9	1.9	12.9	10.9	1.4	25.8	14.3	32.7	12.9

PFZ = Polar Front Zone, POOZ = Permanent Open Ocean Zone, SIZ = Seasonal Ice Zone.
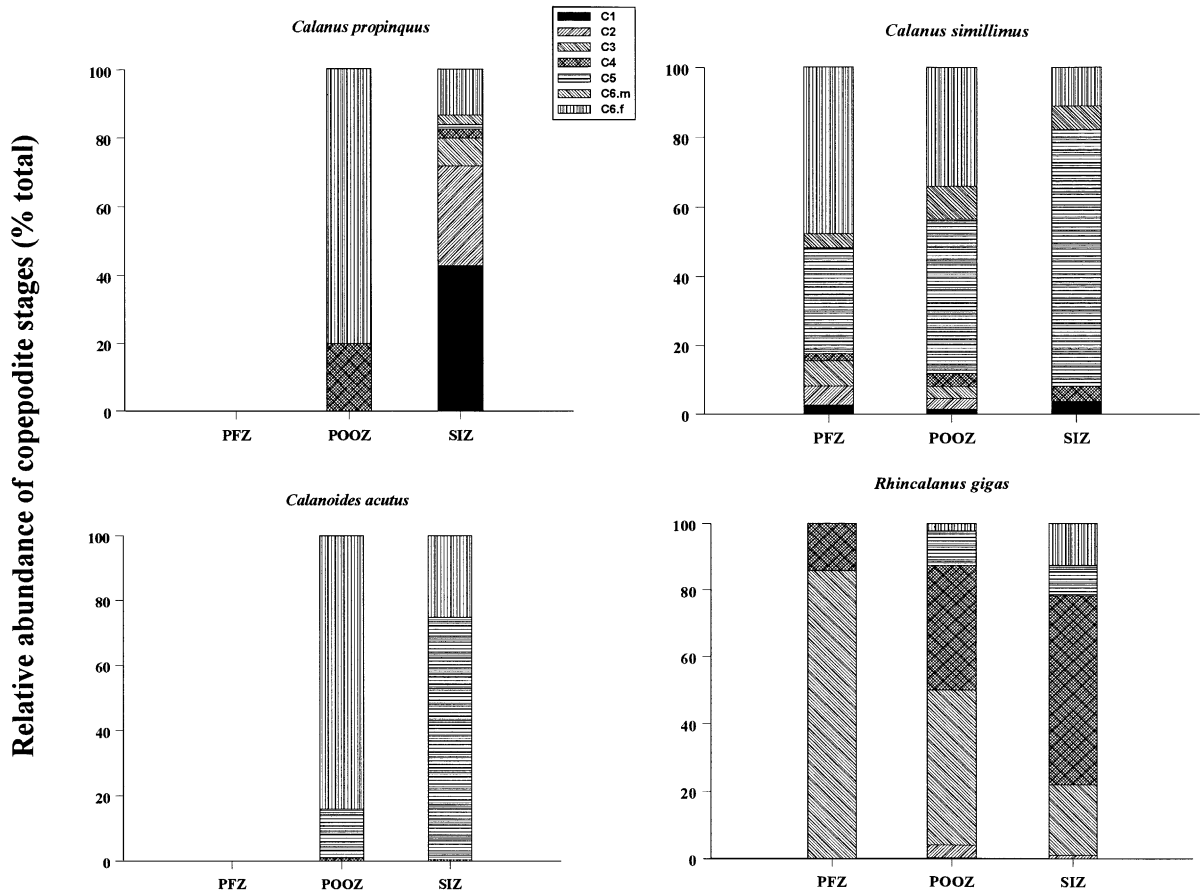[a] Day time tow.

Fig. 3. Copepodite stage distribution of the four main copepod species collected in the Polar Front Zone (PFZ), Permanent Open Ocean Zone (POOZ) and Seasonal Ice Zone (SIZ). C6m = copepodite 6 male, C6f = copepodite 6 female.

north to south. Late stages usually prevailed, with adult females dominating in the POOZ. A more complex picture was observed in the SIZ, with stage C5 and to a minor extent adult female contributing most of the *Calanoides acutus* population, whereas young C1 and C2 stages and to a minor extent adult females made up the bulk of the *Calanus propinquus* population.

The contribution of the different copepod species to the total biomass varied with the area considered (Table 4). In the PFZ more than 75% was *Calanus simillimus* (57%) and *Metridia lucens* (22%). The other species contributed less than 1–2% each. In the POOZ *Calanus simillimus* and *Rhincalanus gigas* made up the bulk of the biomass

(respectively, 42% and 29%). *Calanoides acutus* and *Ctenocalanus citer* were the second group in importance. *Metridia lucens* and *Paraeuchaeta* spp made a minor contribution with values larger than 3% of the total biomass. In the SIZ *Calanoides acutus* and *Rhincalanus gigas* accounted for 75% of the biomass, with *Ctenocalanus citer*, *Calanus propinquus*, *Paraeuchaeta* spp, *Metridia lucens* and *Oithona similis* as the second group in importance (21%). Though dominant in numbers, the group of smallest species (*Oithona* and *Oncaea*) never represented a large contribution to the total biomass, a result which could be related to the relatively large mesh size used to collect these species.

Table 4
Contribution of the different copepod species to total biomass sampled in the top 200 m during austral spring in the different hydrographic areas of the Indian sector of the Antarctic Ocean

Species	% total copepod biomass		
	PFZ	POOZ	SIZ
Calanoides acutus	—	10.74	38.98
Calanus propinquus	—	0.61	4.56
Calanus simillimus	56.95	42.17	0.79
Clausocalanus laticeps	0.12	0.17	0.05
Ctenocalanus citer	15.50	8.06	7.92
Metridia lucens	22.47	3.62	2.75
Microcalanus pygmaeus		—	0.25
Oithona frigida	0.83	0.41	0.71
Oithona similis	0.89	0.70	2.06
Oncaea antarctica	0.10	0.16	1.55
Oncaea curvata	—	—	0.06
Paraeuchaeta spp.	2.34	3.70	3.40
Rhincalanus gigas	0.36	28.99	35.50
Scolecithricella minor	0.44	0.66	1.43

3.3. Chlorophyll gut content and gut transit time

Gut pigment content and gut transit time were measured for the main species present at the different stations of the transect, and data were pooled because no significant differences could be related to either the area or the station for any of the species studied. Results for *Calanus simillimus* were collected in the northern part from stations A18 to A14 ($F_{1,12} = 0.156$; $p = 0.594$), and those of *Calanoides acutus* (stations A12 and M4; $F_{1,8} = 0.094$; $p = 0.777$), *Pleuromamma robusta* (stations A12 and M4; $F_{1,8} = 0.020$; $p = 0.893$) and *Rhincalanus gigas* (stations A2, M4, A14, A15; $F_{5,3} = 4.72$; $p = 0.116$) were collected in the central and southern part of the transect. Data for *Calanus propinquus* derived from the ice edge populations at station M4. With the exception of *Calanoides acutus*, gut fluorescence showed a strong day–night opposition with active feeding at night resulting in an increase of chloropigments by factors of 1.5–5 (Table 5). Gut transit times were generally high, with values ranging from 1 h (*Calanus propinquus*) to 1 h 30 min (*Rhincalanus gigas*). Pigment ingestion rates showed maximum and minimum values for *Calanus propinquus*/*Pleuromamma robusta* and *Calanus simillimus*/*Calanoides acutus*, respectively.

Table 5
Gut pigment content and ingestion rates of some copepod species during austral spring in the Indian sector of the Antarctic Ocean

Species	Station	Gut pigment (ng ind⁻¹)	Gut pigment (ng ind⁻¹)	K (h⁻¹)	K (h⁻¹)	Ingestion (ng pigm ind⁻¹ day⁻¹)	Ingestion (µg C ind⁻¹ day⁻¹)
	Night/day	Night	Day	Night	Day		
Calanus propinquus	M4/M4 (SIZ)	6.1±1.6 (7)	1.2±0.2 (6)	0.66	1.01	64.8±16.5	20.2±5.3
Calanoides acutus	M4/A12 (SIZ)	0.7±0.3 (12)	—	0.84	—	8.8±3.6	2.5±0.8
Rhincalanus gigas	A15-16/M4 (POOZ/SIZ)	3.5±0.9 (9)	2.1±0.7 (5)	0.68	—	38.1±10.8	10.2±2.1
Calanus simillimus	A15-16/A16 (POOZ)	0.8±0.5 (11)	0.3±0.1 (5)	1.13[a]	—	12.8±7.9	2.8±1.7
Pleuromamma robusta	A15-16/M4 (POOZ/SIZ)	15.9±3.3 (3)	4.2±0.1 (2)	0.18[a]	—	62.2±13.1	11.1±5.8

[a] Literature data (see text); (*n*) = number of replicates.

Intermediate values were recorded for *Rhincalanus gigas* (Table 5). Ingestion was also computed in carbon equivalents using measured particulate C/Chl ratio in the PFZ and the northern POOZ, with values between 100 and 150 (Panouse et al., 1997; Bentaleb et al., 1997) and a value of 250 at the southern stations in the POOZ and the SIZ (Mayzaud et al., in press).

3.4. Respiration of major copepod species

Respiration rate was measured for 13 species of copepods (Table 6). Mainly copepodite stages (adults, C5 and C4 stages) were considered for the larger species (*Calanoides acutus*, *Calanus propinquus*, *Calanus simillimus* and *Rhincalanus gigas*), and mixed C5-adult were used for the smaller species (*Clausocalanus laticeps*, *Ctenocalanus citer* and *Oncea antarctica*). Respiratory rates varied from 0.5–$0.8 \, \mu l \, O_2 \, ind^{-1} \, day^{-1}$ for the small copepods and $61.6 \, \mu l \, O_2 \, ind^{-1} \, day^{-1}$ for female *Paraeuchaeta antarctica*. Other large calanoids (*Calanoides acutus*, *Calanus simillimus*, *Calanus propinquus*, *Rhincalanus gigas*) showed values ranging from 2 to $23 \, \mu l \, O_2 \, ind^{-1} \, day^{-1}$. As anticipated, weight corrected rates indicated maximum values for the smaller species or copepodite stages (40–$42 \, \mu l \, O_2 \, ind^{-1} \, day^{-1}$) and lower rates for the larger one (10–$13 \, \mu l \, O_2 \, ind^{-1} \, day^{-1}$ for *Paraeuchaeta antarctica* and *Euchirella rostamagna*). The relationship between log respiration and log size was highly significant

$$\log R = 0.78 \log Dw + 1.28 \, (R^2 = 0.998)$$

and fitted the anticipated allometric values (0.75) despite the limited number of species considered and irrespective of the sampling locations (Fig. 4).

To evaluate the global impact of the copepod biomass, we computed the oxygen and CO_2 budget

Table 6
Respiration rates per individual and per mg dry weight of 13 copepod species present during austral spring in the Indian sector of the Antarctic Ocean during *ANTARES* 3

Species	Stage	n	Respiration rates	
			$\mu l \, O_2 \, ind^{-1} \, day^{-1}$	$\mu l \, O_2 \, mg \, dry \, wt^{-1} \, day^{-1}$
Calanoides acutus	CIV	1	4.41	40.11
	CV	1	11.81	26.53
	CVI fem	3	15.01 ± 2.74	24.69 ± 4.5
Calanus propinquus	CIV	1	5.11	31.36
	CV	2	18.35 ± 1.40	22.74 ± 1.73
	CVI	4	23.52 ± 3.60	17.51 ± 2.68
Calanus simillimus	CIV	1	2.11	46.98
	CV	2	4.45 ± 0.22	24.89 ± 1.25
	CVI fem	5	6.74 ± 1.69	23.74 ± 5.94
Clausocalanus laticeps	CVI	2	0.81 ± 0.12	39.46 ± 6.00
Candacia maxima	CVI	2	15.74 ± 2.06	25.10 ± 3.28
Ctenocalanus citer	CVI	3	0.60 ± 0.07	42.82 ± 5.22
Euchirella rostromagna	CVI	3	38.16 ± 4.28	10.43 ± 1.17
Metridia lucens	CVI	3	3.71 ± 0.34	30.94 ± 2.83
Oncaea antarctica	CV-CVI	3	0.49 ± 0.07	40.71 ± 6.23
Paraeuchaeta antarctica	CVI fem	5	61.56 ± 6.17	10.86 ± 1.09
	CVI male	2	43.65 ± 2.30	13.60 ± 0.72
Paraeuchaeta sp.	CIV	1	10.38	21.72
Pleuromamma robusta	CV	3	8.55 ± 1.03	24.79 ± 2.98
	CVI	4	13.87 ± 2.15	24.25 ± 3.76
Rhincalanus gigas	CIV	2	8.21 ± 0.73	26.57 ± 2.36
	CV	4	12.85 ± 1.87	20.67 ± 3.01
	CVI fem	3	22.66 ± 1.38	18.70 ± 1.14

N = number of replicates, fem = females.
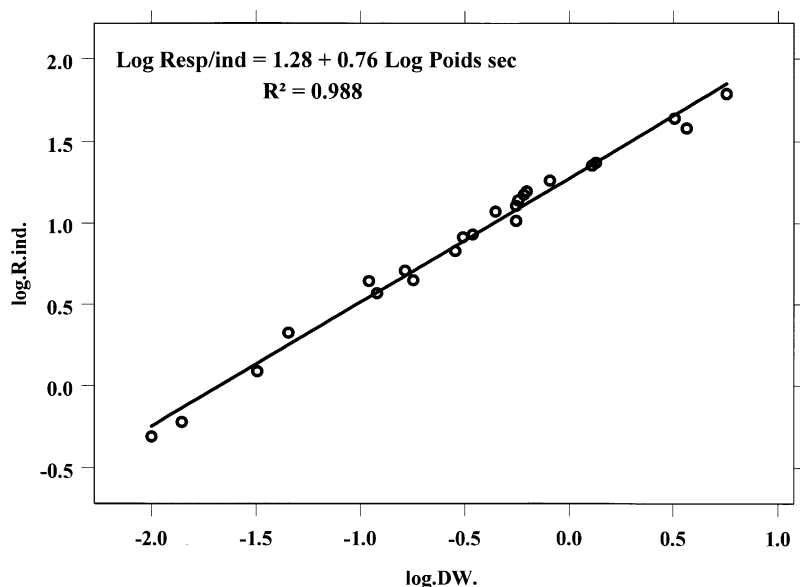
Fig. 4. Log transformed regression between respiration rate and individual dry weight.

per m^2, for two of the three zones studied (POOZ and SIZ) using weighted mean respiration rates, i.e., the mean taking into account the frequency distribution in growth stages. Actual frequencies were used for the larger species while small ones were assumed to be represented solely by C5 and adults. Individual contributions to total biomass were computed from the actual biomass per m^2 measured and the percent contribution of each species corrected for the presence of non-copepod group estimated at 27% (Voronina, 1966; present data). The results (Table 7) showed that the copepod community consumed 99.6 ml $O_2 m^{-2}$ day^{-1} in the POOZ and 107.1 ml $O_2 m^{-2} day^{-1}$ in the SIZ. In the permanent open ocean zone the highest rates were recorded for *Calanus simillimus* (37.7 ml $O_2 m^{-2} day^{-1}$) and *Rhincalanus gigas* (27.2 ml $O_2 m^{-2} day^{-1}$) and intermediate values for *Ctenocalanus citer* (12.6 ml $O_2 m^{-2} day^{-1}$) and *Calanoides acutus* (9.8 ml $O_2 m^{-2} day^{-1}$). In the marginal ice zone the total oxygen consumption was associated mostly with *Calanoides acutus* (38.5 ml $O_2 m^{-2} day^{-1}$) and *Rhincalanus gigas* (30.8 ml $O_2 m^{-2} day^{-1}$) but with a significant contribution of two small species: *Ctenocalanus citer* and *Oithona* spp (respectively, 12.9 and 8.4 ml

$O_2 m^{-2} day^{-1}$). Assuming a respiratory quotient (RQ) of 0.95 corresponding to ammonotelic species (Omori and Ikeda, 1984), it is possible to compute the quantity of CO_2 respired into the environment by the copepod community within the top 200 m. In both zones, the contribution of copepods was quite similar with rates of 4.2 and 4.5 mmol $CO_2 m^{-2}$ day^{-1} in the POOZ and the SIZ, respectively (Table 7). Since a single value of RQ was used, those species which showed the highest oxygen consumption rates were also the largest CO_2 producers.

3.5. Egg production rate

Mean egg production was recorded for four species mostly located in a single oceanic area: POOZ for *Calanus simillimus* and SIZ for *Calanoides acutus* and *Rhincalanus gigas*. *Calanus propinquus* was the only species sampled in both areas. However, no significant differences in *Calanus propinquus* egg production rate could be attributed to the sampling location ($F_{2,13} = 0.26, p = 0.77$) and all data were pooled. Rates per female and per day of spawning ranged from 11 for *Calanus simillimus* to 51 for *Calanus propinquus*

Table 7

Integrated respiration and CO_2 production rates of the copepod communities sampled in the upper 200 m in spring in the Indian sector of the Antarctic Ocean. Mean total dry weights of copepods were: 3.65 g m^{-2} in the POOZ and 3.80 g m^{-2} in the SIZ

Species	POOZ			SIZ		
	ml O_2 m^{-2} day^{-1}	Mg C m^{-2} day^{-1}	mmol CO_2 m^{-2} day^{-1}	ml O_2 m^{-2} day^{-1}	mg C m^{-2} day^{-1}	mmol CO_2 m^{-2} day^{-1}
Calanoides acutus	9.77	4.97	0.41	38.46	19.57	1.83
Calanus propinquus	0.40	0.20	0.02	3.64	1.85	0.15
Calanus simillimus	37.72	19.20	1.60	0.74	0.38	0.03
Clausocalanus laticeps	0.24	0.12	0.01	0.07	0.04	0.003
Ctenocalanus citer	12.60	6.41	0.53	12.89	6.56	0.55
Metridia lucens	4.15	2.11	0.18	3.26	1.66	0.14
Microcalanus pygmaeus	—	—	—	0.49	0.25	0.02
Oithona spp.	3.22	1.64	0.14	8.38	4.27	0.35
Oncaea antarctica	0.31	0.16	0.01	3.04	1.55	0.13
Oncaea curvata	—	—	—	0.17	0.09	0.01
Paraeuchaeta spp.	2.93	1.49	0.12	2.80	1.43	0.12
Rhincalanus gigas	27.15	13.82	1.15	30.81	15.68	1.31
Scolecithricella minor	1.06	0.54	0.04	2.38	1.21	0.10
Total	99.55	50.66	4.22	107.14	54.52	4.54

Table 8
Egg production rate of four copepod species collected during the _ANTARES_ 3 cruise

Species	Sampling	Egg produced per female		Egg produced
	Station	Range	Mean per day	μgC per day
Calanus propinquus	A15, A12, M4 (POOZ & SIZ)	2–114	51 ± 28 (15)	25.5 ± 14
Calanoides acutus	M4 (SIZ)	11–28	20 ± 9 (4)	10.0 ± 4.5
Rhincalanus gigas	A12, M4 (SIZ)	1–45	15 ± 14 (7)	13.5 ± 6.3
Calanus simillimus	A16 (POOZ)	1–25	11 ± 7 (13)	5.5 ± 3.5

(n) = number of individual female in experience. Carbon content of egg = 0.5 μg for _Calanus propinquus_, _Calanus simillimus_, _Calanoides acutus_, and 0.9 μg C for _Rhioncalanus gigas_.

Table 9
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 $_{corr}$ μgC.ind^{-1}.day^{-1}	$I_r \cong$ Respiration μgC.ind^{-1}.day^{-1}	$I_{egg} \cong$ egg prod μgC.ind^{-1}.day^{-1}	C. requirements μgC.ind^{-1}.day^{-1}
Calanus propinquus	30.3	15.1 ± 2.3	34.0 ± 18.7	49.1
Calanoides acutus	3.8	9.7 ± 1.7	13.3 ± 6.0	22.9
Rhincalanus gigas	15.3[a]	6.8 ± 0.8[a]	18.0 ± 8.4	—
Pleuromamma robusta	16.7	8.9 ± 1.4	0	8.9
Calanus simillimus	4.2	4.3 ± 1.1	7.3 ± 4.7	11.6

Carbon content of egg = 0.5 μg for _Calanus propinquus_, _Calanus simillimus_, _Calanoides acutus_, and 0.9 μg C for _Rhincalanus gigas_ (see text). Carbon requirements computed assuming 75% assimilation and an RQ = 0.9. Corrected ingestion (Ing$_{corr}$) assumed 50% pigment degradation during gut transit.

[a] Copepodite C4 ingestion and respiration rates; I_r—ingestion rate equivalent to respiration requirements; I_{egg}—ingestion rate equivalent to egg production cost.

(Table 8). A large individual variability was observed related to unequal intervals between spawning cycle and the gonad conditions. As might be expected, all the females were not at the same maturation state: 30–43% of the females of _Calanus simillimus_ and _Calanus propinquus_, respectively, spawned, within the first day after capture, but only 20% for _Calanoides acutus_ and only 6% for _Rhincalanus gigas_. As a result, interspecies differences in fecundity were observed despite similarity in size. Thus _Calanus propinquus_ and _Calanoides acutus_, though similar in size and collected in similar trophic environment, showed a difference in egg production by a factor of 2.5, while _Calanus simillimus_ and _Rhincalanus gigas_ though double in size showed similar fecundity. Daily egg production rates were expressed as carbon equivalent using 0.5 μg C for _Calanus propinquus_, _Calanus simillimus_, _Calanoides acutus_, and 0.9 μg C for _Rhincalanus gigas_.

3.6. Comparison between chlorophyll derived ingestion rate, respiration and egg production requirements

To compare ingestion rates to respiratory and egg production requirements, respiration data for female stage were converted to carbon equivalents assuming an RQ of 0.95. Ingestion data were corrected for pigment degradation assuming a mean value of 50%. Correspondence between respiration, egg production and ingestion were computed assuming an assimilation efficiency of 75%. If we except _Calanoides acutus_, for which ingestion rate failed to fulfill the minimum energy requirements, all other species appears to ingest in excess of (_Calanus propinquus_, _Rhincalanus gigas_, _Pleuromamma robusta_) or equal to (_Calanus simillimus_) their energy expenditure (Table 9). In the case of _Calanus propinquus_, _Calanoides acutus_ and _Calanus simillimus_, the addition in the energy

budget of the cost of egg production yielded a different picture, with *Calanus propinquus* being the only species whose ingestion rate almost balanced the carbon required by both processes.

4. Discussion

As indicated by Ward and Schreeve (1999), there have been relatively few investigations in the Southern Ocean during austral spring, and we have little comparable data for open ocean and receding ice zone areas. In the present study, mesozooplankton biomass integrated over 200 m ranged from less than 0.8 g m^{-2} to 16 g m^{-2}. The large degree of variability observed between stations was not unexpected because of the known patchiness along a north–south transect (Schalk, 1990). This range brackets fairly well the values reported at different seasons in earlier studies, from the relatively low estimates of Boysen-Ennen et al. (1991) (0.8–3.6 g m^{-2}) to the high values recorded by Ward et al. (1995) and Ward and Schreeve (1999) at South Georgia in summer (13 g m^{-2}) and spring (6.5–12.5 g m^{-2}). Regional studies (Hopkins, 1971) have illustrated that mesozooplankton biomass tended to increase towards the polar front and localized coastal areas such as the Antarctic Peninsula (Hopkins, 1985), 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). Spring biomass suggested a strong influence of the marginal ice zone, with maximum values associated with enhanced primary production and, in contrast, minimum values in both the PFZ and the POOZ areas. A trend of an increase in biomass from the PFZ to the SIZ certainly fits with this global picture. The reduced biomass observed at the ice edge (station M4) agreed with the observations of Burghart et al. (1999) probably in relation to changes in population structure and recruitment.

One of the main features of Antarctic zooplankton communities is the dominance by crustaceans (Voronina et al., 1994; Hosie and Cochran, 1994). However, other groups may also display a significant contribution, e.g. chaetognaths, salps, pteropods (Boysen-Ennen et al., 1991; Voronina et al., 1994; Hosie and Cochran, 1994; Ward et al., 1995). In the present survey, their contribution to the total biomass is quite variable and usually remains limited or irregular. Euphausiid larvae (maximum in the SIZ), chaetognaths, ostracods, polychaetes and pteropods were present at all stations sampled. This appears to be a characteristic of oceanic waters for spring time or a receding ice zone as observed by Ward and Schreeve (1999). In contrast to the previous studies, salps were present only in the SIZ in small numbers, and we found no appendicularians or siphonophores. The copepod biomass was dominated by the same species recorded in other sectors of the Antarctic Ocean, e.g. *Calanoides acutus*, *Calanus propinquus*, *Calanus simillimus*, *Rhincalanus gigas* and *Metridia gerlachei* (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 and often dominated in numbers, e.g. *Metridia lucens*, *Ctenocalanus citer*, *Clausacalanus laticeps*, *Oithona* spp. (Hopkins, 1987; Schnack et al., 1985; Errhif et al., 1997; Pakhomov et al., 1997). Predominance of small species, in particular *Oncaea* and *Oithona*, in Antarctic waters has been reported in recent years (Schnack et al, 1985; Fransz, 1988), but, as indicated by Fransz (1988), densities above 100 individual per m^3 are rare in these observations. In the present study, densities of *Oithona similis* higher than 250 ind m^{-3} seemed characteristic of the receding ice zone (Table 3) and may even be underestimated because of the 200 μm mesh size net used (Fransz, 1988).

Growth stage distribution of the main species of large calanoids is tightly coupled to the life cycle and recruitment strategies of the different species (see Schnack-Schiel and Hagen, 1994; Atkinson et al., 1997). A prevailing view has long been that most herbivorous species followed a cycle similar to that of the Arctic copepods: migration into the surface layers of deep overwintering individuals in spring and reproduction; developing copepodids feed within the surface phytoplankton rich layer

and late copepodids descended to depth to over-winter in diapause. Timing of such migration was found to vary with latitude in relation to the north–south advance of the spring bloom (Voronina, 1978). However, Marin (1988) suggested that the large calanoid species may have different life cycles both in timing and duration. The results presented here illustrate clearly that the four species considered (*Calanoides acutus*, *Calanus simillimus*, *Calanus propinquus* and *Rhincalanus gigas*) have different patterns of distribution. However, within the context of the present study, the influence of latitudinal gradient on development in spring can only be considered for *Calanus simillimus* and *Rhincalanus gigas*. Indeed, recruitment of a new generation had not started for *Calanoides acutus* (only C5 and C6 present in both POOZ and SIZ), and *Calanus propinquus* was sampled only at its northern limit of distribution. *Rhincalanus gigas* showed a pattern of distribution in growth stages that agrees with the life cycle proposed by Atkinson (1991) and Schnack-Schiel and Hagen (1994), i.e., overwintering stages dominated by C3 and C4 copepodids, which moult into adult on the onset of spring and active recruitment of younger copepodids (C1–C4) during spring. A clear latitudinal gradient was also observed with only C3 and C4 present in the PFZ, C3 and C4 and an increasing proportion of C5 and adults from the POOZ to the SIZ suggesting that recruitment of reproducing stages was initiated in the marginal ice zone at the time of sampling. The growth stage distribution of *Calanus simillimus* showed a large proportion of C5 and adults with a decreasing contribution of younger copepodids (C1–C4) from the PFZ to the SIZ. This agrees with the general pattern described by Voronina et al. (1978) and Atkinson (1991), who showed that this species overwinters as C5 and an increasing proportion of adults occurs towards the end of winter–early summer to produce a new generation (Atkinson, 1991). However, in contrast to *Rhincalanus gigas*, *Calanus simillimus* seemed to initiate its reproduction in the warmer water of the PFZ. A clear latitudinal trend was also recorded for *Calanus propinquus* despite the limited survey of the SIZ: only C4 and female stages were observed in the southern part of the POOZ, but a large

contribution of C1–C4 stages characterized the marginal ice zone, confirming that the recruitment of the new generation was well under way in this area.

Spawning of the four species of large calanoids studied was under way at the time of sampling (October), and the mean clutch sizes recorded are in fair agreement with those observed for the same species in other Antarctic regions, though somewhat lower for *Calanus simillimus* and *Rhincalanus gigas*. The daily egg-laying rate of *C. propinquus* in the Eastern Weddell Sea ranged from 15 to 31 eggs fem^{-1} (Fransz et al., 1989; Kurbjeweit, 1993) with a maximum of 100 eggs fem^{-1} late December–early January. Clutch size of *Calanoides acutus* in South Georgia, showed a mean value of 26 ± 23 eggs fem^{-1} day^{-1} in summer (Ward and Shreeve, 1995), and a range of 4–37 eggs fem^{-1} day^{-1} are reported for the Antarctic Peninsula (Lopez et al., 1993). For *Rhincalanus gigas*, the mean clutch size ranges from 22 eggs fem^{-1} day^{-1} in Eastern Weddell Sea (Fransz et al., 1989) to 33 ± 27 in South Georgia (Ward and Shreeve, 1995). For *Calanus simillimus*, the egg production rates recorded in January near South Georgia showed a mean value around 25 ± 14 eggs fem^{-1} day^{-1} (Ward and Shreeve, 1995). Interspecies differences in the time of spawning are suggested by the localization of egg laying females:

- For *Calanoides acutus* all reproducing females were sampled at the marginal ice zone station (M4), while females collected up north in the POOZ failed to spawn. This, coupled with the absence of young copepodite stages, suggests that the spawning season had only started in the surface layer for the new adult generation after the overwintering season (Schnack-Schiel and Hagen, 1994; Atkinson et al., 1997). *Calanoides acutus* is known to be an ontogenic seasonal migrant with a spawning period extending from October to January according to spatial or interannual variations. Such an early beginning in egg production supports the hypothesis of a maximum egg production in spring (Huntley and Escritor, 1991; Lopez et al., 1993; Schnack-Schiel and Hagen, 1995; Atkinson and Shreeve, 1995) rather than summer (Andrews, 1966).

- The rearing and egg-laying experiments carried out with *Calanus propinquus* females were successful at all sites in the POOZ as well in the SIZ. This species seems to inhabit the upper 500 m depth layer, and both males and females were found from October to late January in the eastern Weddell Sea (Schnack-Schiel and Hagen, 1995). Maximum egg-laying rate (>100 eggs fem^{-1}) was recorded during late December–early January (Fransz et al., 1989; Kurbjeweit, 1993), but egg laying may last until late February (Kosobokova, 1994). Our observations showed that almost all females reared in the laboratory were spawning every 2 days. The significant contribution of the younger stages of C1–C4 in the SIZ support the conclusion that the reproductive periods of the two species appear to be slightly shifted, *Calanus propinquus* preceding *Calanoides acutus*. Another difference appears in the reproduction strategy: in contrast to *Calanoides acutus*, *Calanus propinquus* females showed important accumulations of ovocytes at different maturation stages, the anterior diverticula of the ovary extending into the latero-dorsal part of the head, and the posterior diverticula swelling at each intercept between thoracical segments (unpublished observations, S. Razouls).

- In contrast to the previous two species, relatively few data seemed to exist concerning the spawning strategy of *Rhincalanus gigas*. We observed a clear north–south trend in age structure, which suggested an earlier reproduction in the SIZ, with only C3 and C4 in the PFZ and increasing percentages of C5 and females towards the marginal ice zone. Indeed, C1 individuals are found as early as late autumn (May) in the eastern part of Bransfield strait (Marin and Schnack-Schiel, 1993), in agreement with a reproduction period initiated early in autumn. The occurrence of nauplii and C1 from November to February and again in late April and May in the Scotia Sea may be indicative of a more extended reproductive period (Atkinson, 1991). Shifts in the age composition of *Rhincalanus gigas* populations with depth, locality and season likely add confusion in the interpretation of the life cycle of this species (Voronina, 1970).

- The spawning rates recorded with *Calanus simillimus* were obtained with females collected in the POOZ (St A16) with the most advanced development from C1 to adults. Earlier studies in the Scotia Sea have shown that *Calanus simillimus* inhabits preferentially the area between the sub-Antarctic and the Polar Front (Atkinson, 1991). Stage C1 has been found to be most abundant early summer (November–January), suggesting egg release earlier in the season, probably as early as August (Voronina et al., 1978).

Pigment gut content is to some extent related to chlorophyll availability, diel changes and growth stage (Landry et al., 1994). The values reported in the present study for the adults and C5 of *Calanoides acutus*, *Calanus simillimus*, *Calanus propinquus*, *Pleuromamma robusta* and C3 and C4 copepodites of *Rhincalanus gigas* showed day–night periodicity in agreement with the diurnal variations reported for most Antarctic and sub-Antarctic copepod species (Perissinotto, 1992; Atkinson et al., 1992a, b, 1996; Pakhomov et al., 1997). The pigment gut contents recorded were overall low compared to the values observed off South Georgia (Atkinson et al., 1992a, b, 1996; Pakhomov et al., 1997) or late summer in the Weddell Sea (Drits et al., 1994) or in the Bransfield Strait (Hernandez-Leon et al., 2000), but close to those reported by Perissinotto (1992) around Prince Edward Archipelago for *Calanus simillimus* and late summer in the Weddell Sea for *Calanus propinquus* at low phytoplankton concentrations (Drits et al., 1993). The differences in chlorophyll content (30–300 mg m^{-2} off South Georgia versus 70 mg m^{-2} and 8–80 mg m^{-2}, respectively, off Prince Edward Archipelago and the present study) only partially explain the discrepancy. Indeed, the level of gut pigment in *Calanoides acutus* reported by Drits et al. (1994) was also higher than those observed in the present study despite a similar range of in situ chlorophyll concentrations (0.1–0.5 µg l^{-1}).

Because estimates of gut transit time were quite in line with most published data (see Tirelli and

Mayzaud, 1999), ingestion rates computed as pigment consumed per day followed the same trend. The proportionally higher contribution of grazing in terms of carbon is linked, on the one hand, to the necessary correction for gut pigment degradation (Conover et al., 1986) and, on the other hand, to the non-linear relationship between chlorophyll standing stock and C_a:Chl a ratio shown by Hewes et al. (1990). Correction for pigment degradation was often omitted, despite the increasing number of reports on many different copepod species (see Tirelli and Mayzaud, 1998) and growing evidence that such destruction is linked to the nutritional activity (Penry and Frost, 1991; Cary et al., 1992; Head and Harris, 1996). Defining specific values of degradation for all species and several location is not feasible at sea, but an alternate possibility is to consider a mean value of degradation efficiency of 50% (Atkinson, 1996; Pakhomov et al., 1997), derived from the pigment degradation data on Antarctic and sub-Antarctic species by Perissinotto (1992) and Mayzaud and Razouls (1992). The non-linear relationship (C_a:Chl $= 80 \times$ Chl$^{-0.4}$) between chlorophyll standing stock and C_a:Chl a ratio described by Hewes et al. (1990) resulted in C_a:Chl ratio exceeding values of 100 for autotrophic eucaryotes from Antarctic blue waters and only approaches a threshold of 30 when Antarctic waters displayed high chlorophyll concentration (> 3 mg m^{-3}). In the present study this gave integrated values (over 200 m) of the ratio ranging from 107 to 250 in the POOZ and SIZ, respectively. Applying these corrections, it appears that except for *Calanoides acutus*, the spring rates of ingestion were high enough to cover the respiratory requirements of the different species studied, suggesting that phytoplankton could meet non-reproducing carbon demands. However, the addition of the reproductive costs for *Calanus propinquus* and *Calanus simillimus* suggested that alternate carbon sources were necessary for egg production (internal lipid reserves or alternate food sources; Huntley and Escritor, 1991). Like many Antarctic copepod species *Calanus acutus* can balance its energy budget via ingestion of an alternate food source such as protozoan (Atkinson, 1996), which represented a potential food supply of 8–11 mg C m^{-3} (Becquevort et al., 2000).

There are relatively few estimates of respiration costs of Antarctic copepods, and most studies are limited to the large calanoid species: *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas*, *Metridia gerlachei* and *Paraeuchaeta antarctica* (Rakusa-Susczewski et al., 1976; Ikeda and Mitchell, 1982; Hirche, 1984; Schnack-Schiel et al., 1991; Drits et al., 1993, 1994) or global population fractionated by size class (Hernandez-Leon et al., 1999, 2000). Weight specific respiratory rates are known to show a relatively large variability in relation to experimental protocols (acclimation to laboratory conditions or not; temperature of incubation, etc.), method of collection at sea, season, level of ambient food (see Hirche, 1984). Weight specific respiration rates of *Calanus propinquus*, measured at $-0.5°C$ to $0°C$, ranged between 7.2 and 23.7 for females and between 16.3 and 28.8 µl O$_2$ mg dry wt^{-1} day^{-1} for copepodite C5 (Ikeda and Hing-Fay, 1981; Ikeda and Mitchell, 1982; Schnack et al., 1985; Schnack-Schiel et al., 1991; Drits et al., 1993). Specific respiration rates of *Calanoides acutus*, measured at $-1°C$ to $0°C$, varied between 9.6 and 31.4 µl O$_2$ mg dry wt^{-1} day^{-1} for females and between 2.1 and 43.4 for copepodite C5 (Ikeda and Hing-Fay, 1981; Hirche, 1984; Schnack et al., 1985; Schnack-Schiel et al., 1991; Drits et al., 1994). Fewer measurements on *Rhincalanus gigas* (Rakusa-Susczewski et al., 1976; Hirche, 1984) and *Paraeuchaeta antarctica* (Biggs, 1982; Hirche, 1984) showed weight-specific respiration rates for females ranging between 3.8 and 14.8 µl O$_2$ mg dry wt^{-1} day^{-1} and between 3.8 and 17.8 µl O$_2$ mg dry wt^{-1} day^{-1}, respectively. The rates reported in the present study fit within the range of published data, though generally in the upper range as expected from incubation at a mean seawater temperature of 1.5–2°C rather than below 0°C. The respiration rates measured in the present study covered 13 different species and usually 2–3 developmental stages (C4 to adults) from the smaller poecilostomatoid species to the larger calanoids. A simulation of the total carbon uptake of the copepod population can be computed to estimate the minimal impact of grazing in spring

along 62°E. For levels of primary production of 122.4 and 241.2 mg C m^{-2} day^{-1} in the POOZ and SIZ, respectively, the minimum respiratory requirements of the copepod population amount for 41.4% in the POOZ and 22.6% in the SIZ of the daily primary production. Such minimum estimates greatly exceeded the low impact (< 5%) reported by Hopkins (1987), Atkinson (1996), Atkinson and Shreeve (1995), Swadling et al. (1997), Bradford-Grieve et al. (1998) for other locations and seasons in the Southern Ocean but are closer to the estimates of Ward et al. (1995) for South Georgia in summer and Perissinotto (1992) for the Prince Edward Archipelago in autumn.

The magnitude of CO_2 recycling by zooplankton has never been computed at the population level, despite the potential importance such a process on the global CO_2 budget of the photic zone. Studies on organic carbon recycling have been, almost exclusively, limited to the contribution of microbial respiration (bacteria and phytoplankton) (see Aristegui et al., 1996). In Antarctic waters Lancelot et al. (1991) summarized the mean carbon fluxes in the marginal ice zone, with an average loss via phytoplankton respiration of 48% of gross primary production and mean respiration via microheterotrophs (bacteria and protozoa) of 25–30% of gross production. Recycling by zooplankton was not considered, but the results of the present study indicate that the magnitude of such recycling was similar to that of the microheterotrophs. Computation from the population respiratory budget yielded mean values of 4.2–4.5 mmol CO_2 m^{-2} day^{-1} for the period considered, equivalent to a mean value of 32% of the daily integrated primary production. Quantification of the recycling processes should consider the entire community of heterotrophic organisms. Mesozooplankton communities deserve more attention than given thus far in studies of the biological processes related to the dynamics of CO_2 in oceanic waters.

Acknowledgements

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