Grazing impact of copepods and salps on phytoplankton in the Atlantic sector of the Southern Ocean

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Abstract—During the SO-JGOFS-*Polarstern* cruise in October/November 1992, grazing of the dominant calanoid copepods (*Calanoides acutus, Calanus propinquus* and *Rhincalanus gigas*) and of *Salpa thompsoni* was determined. *Calanoides* acutus and *R. gigas* were very abundant in the Polar Frontal region (PFr). *Calanus propinquus* was abundant at the ACC–Weddell Gyre Boundary (AWB). Grazing by copepods was very low and accounted for less than 1% of the primary production (PP) for all three species. *Salpa thompsoni* occurred in swarms in the southern part of the Antarctic Circumpolar Current (ACC) where its ingestion rates accounted for more than 100% of the PP. We conclude that grazing by copepods had a negligible effect on build-up of the phytoplankton biomass recorded in the PFr and—to a much lesser extent—at the AWB, whereas high grazing pressure of *S. thompsoni* was likely to have constrained phytoplankton biomass levels in the ACC. © 1997 Elsevier Science Ltd. All rights reserved

INTRODUCTION

Several hypotheses have been proposed to explain low phytoplankton biomass in the Southern Ocean despite generally high concentrations of macro-nutrients (i.e. phosphate, nitrate and silicate) (Priddle *et al.*, 1992). High wind speeds occurring in this area produce very deep mixed layers, resulting in low phytoplankton production rates (Hayes *et al.*, 1984; Sakshaug, 1989). The micro-nutrient iron may limit phytoplankton growth in land-remote areas (de Baar *et al.*, 1990; Martin *et al.*, 1990, 1991). A third hypothesis assumes that high zooplankton grazing pressure prevents the build-up of phytoplankton blooms in these areas (Smetacek *et al.*, 1990).

To test the third of these hypotheses, we examined whether the grazing pressure of dominant mesozooplankton species was high enough to prevent the development of phytoplankton blooms. During the SO-JGOFS cruise with R.V. *Polarstern* in October/ November 1992, the grazing of dominant mesozooplankton species was studied between 47°S and 60°S along the 6°W Meridian (Smetacek *et al.*, 1997; Fig. 1). According to satellite images, phytoplankton blooms occur relatively rarely in that region (Comiso, 1991). Three major transects were carried out, leading from the Polar Frontal region (PFr) in the north to the ACC–Weddell Gyre Boundary (AWB) in the south crossing the southern part of the Antarctic Circumpolar Current (ACC). During the investigation, zooplankton communities in the PFr and at the AWB were dominated by copepods (Fransz and

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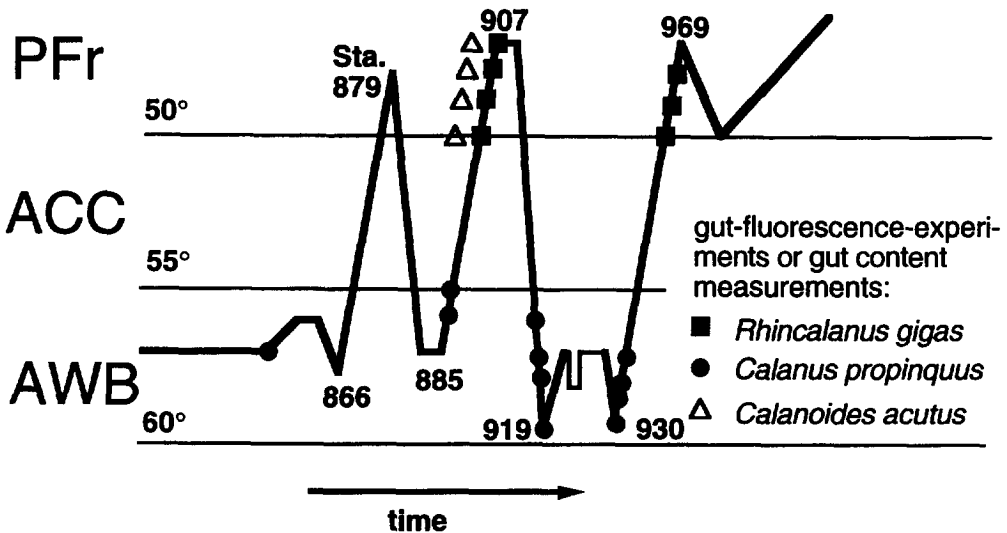
Fig. 1. Cruise track of the SO-JGOFS-*Polarstern* cruise in austral spring 1992. All transects were carried out along the 6°W meridian and are plotted against time. The symbols indicate stations where gut evacuation series or gut content measurements with the different copepods were carried out. PFr: Polar Frontal region; ACC: Antarctic Circumpolar Current; AWB: Antarctic Circumpolar Current–Weddell Gyre Boundary.

González, 1997), whereas, in the ACC, the salp *S. thompsoni* occurred in large swarms and was very abundant (Dubischar *et al.*, 1994). To investigate the grazing pressure of the dominant zooplankton in the upper 200 m of the water column in the respective areas, the ingestion rates of dominant calanoid copepods in the PFr (*C.acutus* and *R.gigas*), of a dominant calanoid copepod at the AWB (*C. propinquus*) as well as of *S. thompsoni* in the ACC were determined.

Calanoides acutus, *Calanus propinquus* and *Rhincalanus gigas* are abundant calanoid copepod species in the Southern Ocean (Ommaney, 1936; Andrews, 1966; Voronina, 1972; Marin, 1988; Huntley and Escritor, 1991; Bathmann *et al.*, 1993; Voronina *et al.*, 1994). *Calanoides acutus* and *Rhincalanus gigas* hibernate at great depths and migrate into surface layers during spring (Andrews, 1966; Marin, 1988), whereas *Calanus propinquus* also is found in ice covered surface layers during winter (Marin, 1988; Nöthig *et al.*, 1991; Bathmann *et al.*, 1993). Hopkins (1985), Hopkins and Torres (1989) and Hopkins *et al.* (1993) examined the gut contents of most of the Antarctic mesozooplankton species. They demonstrated that "only two species were found to be exclusively herbivorous: *C. acutus* and *R. gigas*" (Hopkins *et al.*, 1993). Furthermore, non-chlorophyll-containing particles such as smaller cyclopoid copepods, calanoid copepodite stages, and even debris of *Euphausia superba* have been found in the guts of *C. propinquus* in addition to phytoplankton remains (Hopkins, 1985; Hopkins and Torres, 1989). This suggests an omnivorous feeding behaviour. *Salpa thompsoni* has a circumpolar distribution mainly between the subtropical convergence and 70°S (Foxton, 1966). The ability of salps to proliferate asexually by budding (Chamisso, 1819) as well as their ability to grow very fast (Tsuda and Nemoto, 1992) enables them to increase in numbers very quickly under favourable conditions.

MATERIAL AND METHODS

Following the suggestions of the JGOFS-protocol (JGOFS, 1989), the ingestion rates (IR) of dominant mesozooplankton species were determined using the gut-fluorescence-method (Mackas and Bohrer, 1976). Gut content (GC) and gut clearance rate (GCR) of animals were used to calculate IR in ng chlorophyll a-equivalents (chl a-eq, the sum of chlorophyll a and phaeopigments) per individual and time. A phytoplankton carbon (PPC) to chl a ratio of 50:1 was assumed to convert this IR into units of PPC. At some stations, the GCR could not be determined. To obtain the IR at these stations, the measured GC values were multiplied by the average GCR measured at the other stations.

The grazing activity of the copepod community (stages CV/CVI) was calculated by using the abundance data determined at the same stations by Fransz and González (1997). The biomass of the salps was determined by using a RMT-net and the echo-sounder (P. David, unpublished data). The percentage of the daily primary production (PP) grazed by the mesozooplankton was determined by using the PP data determined at the same stations (Jochem et al., 1995).

Gut pigment measurements of copepods

Copepods were captured in the upper 200 m with a 200-μm mesh-size Bongo-net with sealed cod ends. Immediately after capture, copepods were sorted under dim light in a cool-container at 4°C. For each station, five to seven individuals of each species were placed into the test tubes and immediately deep-frozen (-80°C) for analysis of gut pigments within the next 3 days. Three to six replicates were taken. Wang and Conover (1986) demonstrated that no pigment destruction occurs within 6 days while freezing the samples at -20°C. For the analysis of the gut pigments, 6 ml acetone (90% v/v) and about 2.5 g of glass beads were added to the test tubes, and gut pigments were extracted by homogenizing the animal tissue twice for 5 min in a cell homogenizer. Between treatments, the samples were stored for *ca* 10 min at -20°C. The samples were then centrifuged at 4000 r.p.m. for 10 min at 0°C. Fluorescence of the supernatant was determined with a Turner-Design fluorometer before and after acidification (two drops of 10% HCl). Concentrations of chlorophyll a and phaeopigments were calculated using the equations of Evans et al. (1987).

Gut pigment measurements and carbon/nitrogen content of salps

The salps were caught either with a Bongo-net (mesh-size 200 μm) from the upper 200 m or with a RMT-net (two nets with mesh-sizes 200 and 2000 μm, respectively) which was towed for 30 min obliquely to a depth of 150 m. After retrieval, the catch was transferred immediately to a 20-l seawater container. Intact animals were sorted and analysed for gut pigment contents as described for the copepods, except that pigments were extracted in 100% acetone to compensate for the high water content of the salps (95%; Clarke et al., 1992). Particulate organic carbon (POC) and nitrogen (PON) were determined by sorting single organisms in filtered sea water, placing them on Whatman GF/F glassfibre filters, and deep freezing them (-30°C) prior to analysis in the laboratory. Within 6 months following the end of the cruise, filters were thawed and dried (24 h, 60°C), and carbon and nitrogen content was determined by means of a CHN-Analyzer (Carlo-Erba 1500).

Determination of the gut clearance rates of copepods

Immediately after capture with a Bongo net (capturing time 10 min), 15–20 individuals of a species were sorted under dim light in the cool container (4°C), and individuals for initial gut content determinations were deep-frozen (−80°C) within 10 min after capture. Other individuals were placed into each of several containers (1 l) containing 0.2 μm-filtered seawater at *in situ* temperature (1°C). Screens with a mesh-size of 200 μm at the bottom of these containers allowed sinking faecal pellets to pass but precluded the passage of copepods. At 20, 40, 60, 90, 120, 150 and sometimes also 180 min, the copepods were taken from the respective vessels, put into small plastic tubes, and deep frozen at −80°C. The determination of the gut pigments was carried out as explained above without correction for background fluorescence. The GCR was calculated by using a negative exponential equation (Mackas and Bohrer, 1976).

Salp feeding rates

Determination of salp feeding rates was carried out using two different approaches. First, the gut content was measured as described above. To calculate the IR of these individuals, the measured gut contents were multiplied by the GCR for *S. thompsoni* determined as gut evacuation rates in 16-h experiments by Drits and Semenova (1989) during feeding experiments near the South Shetland Islands in early spring 1985. Secondly, feeding experiments were carried out with intact, actively swimming, single individuals in 3-l containers. The net towing time was 30 min as mentioned above, and therefore pigment egestion by salps during capture might have occurred. The buckets were filled with filtered sea-water enriched with natural phytoplankton to *in situ* concentrations. Grazing was calculated as differences of chlorophyll *a* concentrations with time following Frost (1972). Chlorophyll *a* was determined in time intervals up to 72 h as described above.

<div align="center">RESULTS</div>

Grazing rates of the copepods

Calanoides acutus. Two gut evacuation series were carried out for *C. acutus* [Table 1, Fig. 2(a)]. The GCR was 0.96 and 0.84 h^{-1} (Table 1). The ingestion rates (IR) accounted for 0.82–3.07 μg phytoplankton carbon (PPC) ind^{-1} day^{-1} [Fig. 3(a)]. The IR of all CV and CVI stages corresponded to 0.46–6.86 mg PPC m^{-2} day^{-1}, i.e. to 0.03–0.42% of the PP at the respective stations [Fig. 3(b and c)].

Table 1. *Gut content (GC) given with standard deviation (SD), gut clearance rate (GCR) and ingestion rate (IR) of* Calanoides acutus *at stations 901 and 903, both in the PFr*

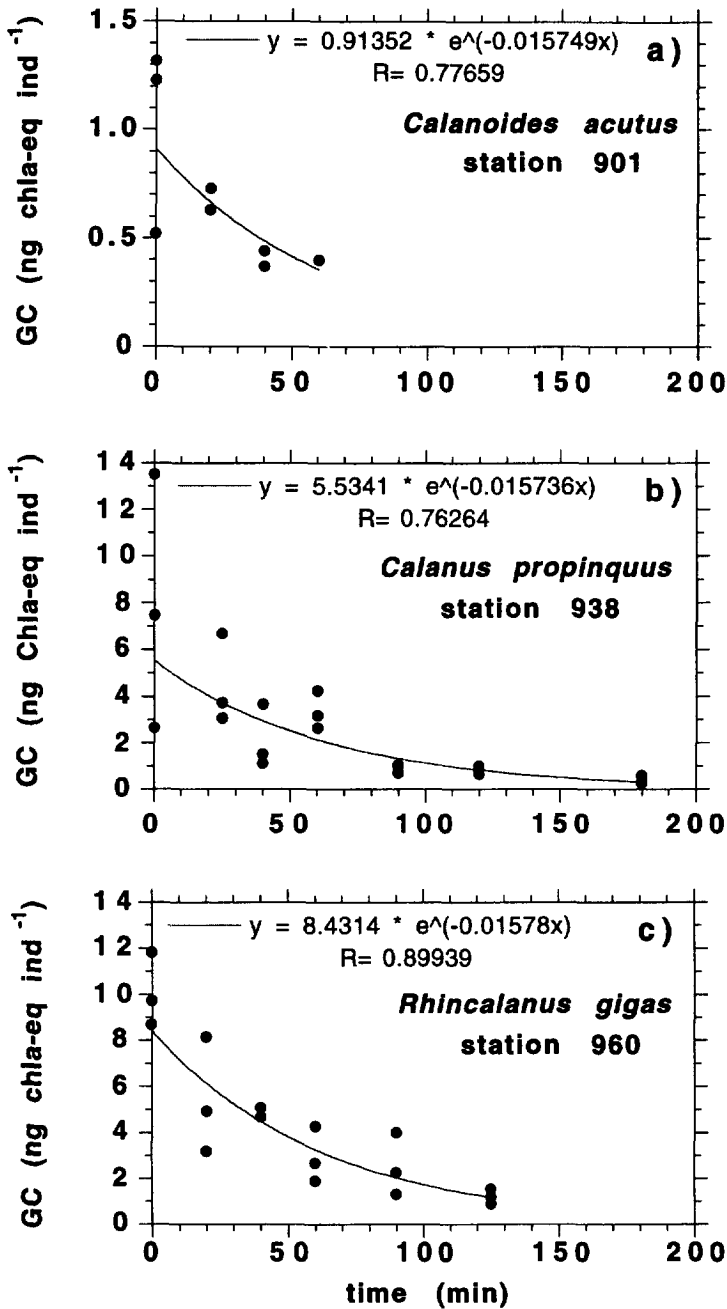| Station	Mean GC ± SD (ng chl *a*-eq. $ind.^{-1}$)	GCR (h^{-1})	IR (μg PPC $ind.^{-1}$ day^{-1})	n	r^2
901	1.21 ± 0.52	0.96	1.39	8	0.78
907	2.96 ± 0.74	0.84	2.98	9	0.68

PPC = phytoplankton carbon.

Fig. 2. Three examples of a total of 14 gut evacuation series indicated by the decrease of gut content of freshly caught *Calanoides acutus* (a), *Calanus propinquus* (b) and *Rhincalanus gigas* (c) placed in filtered sea water. GC: gut content.
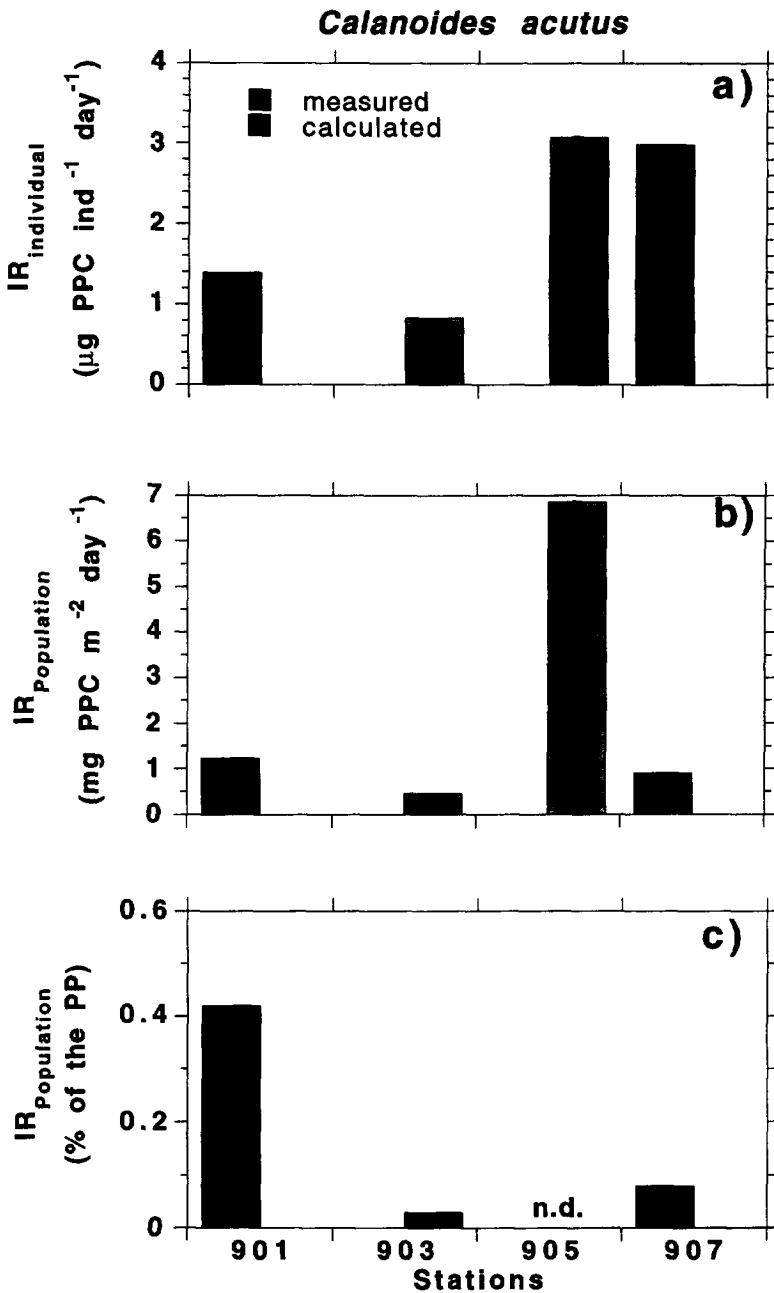
Fig. 3.   Ingestion rates of *Calanoides acutus* at different stations along the PFr (a) per individual and day, (b) per population and day and (c) as a percentage of the daily primary production (PP) (biomass data from S. González (NIOZ, NL), PP-data from Jochem *et al.*, 1995). Measured values were obtained by means of gut evacuation series, calculated values by multiplying the measured gut content with the average gut clearance rate determined at other stations. Bars indicate standard deviation. n.d.: no data.

Calanus propinquus. Seven gut evacuation series were carried out [one example is given in Fig. 2(b)]. The GCR was very variable and ranged from 0.20 to 3.20 h^{-1} (Table 2). The IR accounted for 0.15–23.04 μg PPC ind^{-1} day^{-1} [Fig. 4(a)]. The IR of all CV and CVI stages accounted for 0.01–2.07 mg PPC m^{-2} day^{-1}, corresponding to 0.01–0.69% of the PP at the respective stations [Fig. 4(b and c)].

Rhincalanus gigas. Five gut evacuation series were carried out for this species [Fig. 2(c); Table 3]. The GCR accounted for 0.25–0.95 h^{-1} (Table 3). The IR per individual accounted for 1.06–11.49 μg PPC ind^{-1} day^{-1} [Fig. 5(a)]. The IR of all CV and CVI stages accounted for 1.16–5.5 mg PPC m^{-2} day^{-1}, corresponding to 0.08–0.46% of the PP at the respective stations [Fig. 5(b and c)].

Grazing rates of the salps

For *S. thompsoni*, a direct linear relationship between the length of the animal and gut content was found (Fig. 6); data for the carbon and nitrogen content of four salps are given in Table 4. The gut content of 3-cm-long salps accounted for 2392 ± 250 ng chl *a*-eq, corresponding to 250 ± 67 ng Chl *a* plus 2143 ± 212 ng phaeopigments (Table 5). The chl *a*/phaeopigment ratio was very low (0.12 ± 0.03, Table 5). The ingestion rates calculated from these GC data and the GCR for *S. thompsoni* determined by Drits and Semenova (1989) were high: 660 ± 69 μg PPC ind^{-1} day^{-1} for a 3-cm-long individual, and 786 μg PPC ind^{-1} day^{-1} for a 4-cm-long individual, corresponding to 44.6 ± 5.6% of the carbon content of the animal for a 3-cm-long individual and 34.9% for a 4-cm-long individual (Table 5). The filtration rates calculated from these ingestion rates accounted for 44 ± 4.6 l ind^{-1} day^{-1} for a 3-cm-long individual, and 52 l ind^{-1} day^{-1} for a 4-cm-long specimen (Table 5).

Ship-board experiments with *S. thompsoni* yielded grazing rates of 102 ± 21 μg PPC ind^{-1} day^{-1} for 3-cm-long specimens and 163 ± 43 μg PPC ind^{-1} day^{-1} for 7-cm-long specimens (Fig. 7).

Table 2. *Gut content (GC) given with standard deviation (SD), gut clearance cate (GCR) and ingestion rate (IR) of* Calanus propinquus *at different stations along the AWB*

Station	Mean GC ± SD (ng chl *a*-eq. ind.$^{-1}$)	GCR (h^{-1})	IR (μg PPC ind.$^{-1}$ day^{-1})	n	r^2
863	1.66 ± 0.41	0.31	0.62	9	0.42
887	4.72 ± 2.60	3.20	18.12	8	0.84
915	4.43 ± 0.94	0.59	3.14	18	0.71
916	8.91 ± 5.43	0.87	9.30	12	0.81
930	0.64 ± 0.12	0.20	0.15	12	0.35
934	11.85 ± 5.16	1.62	23.04	19	0.83
938	7.89 ± 5.44	0.94	8.90	21	0.76

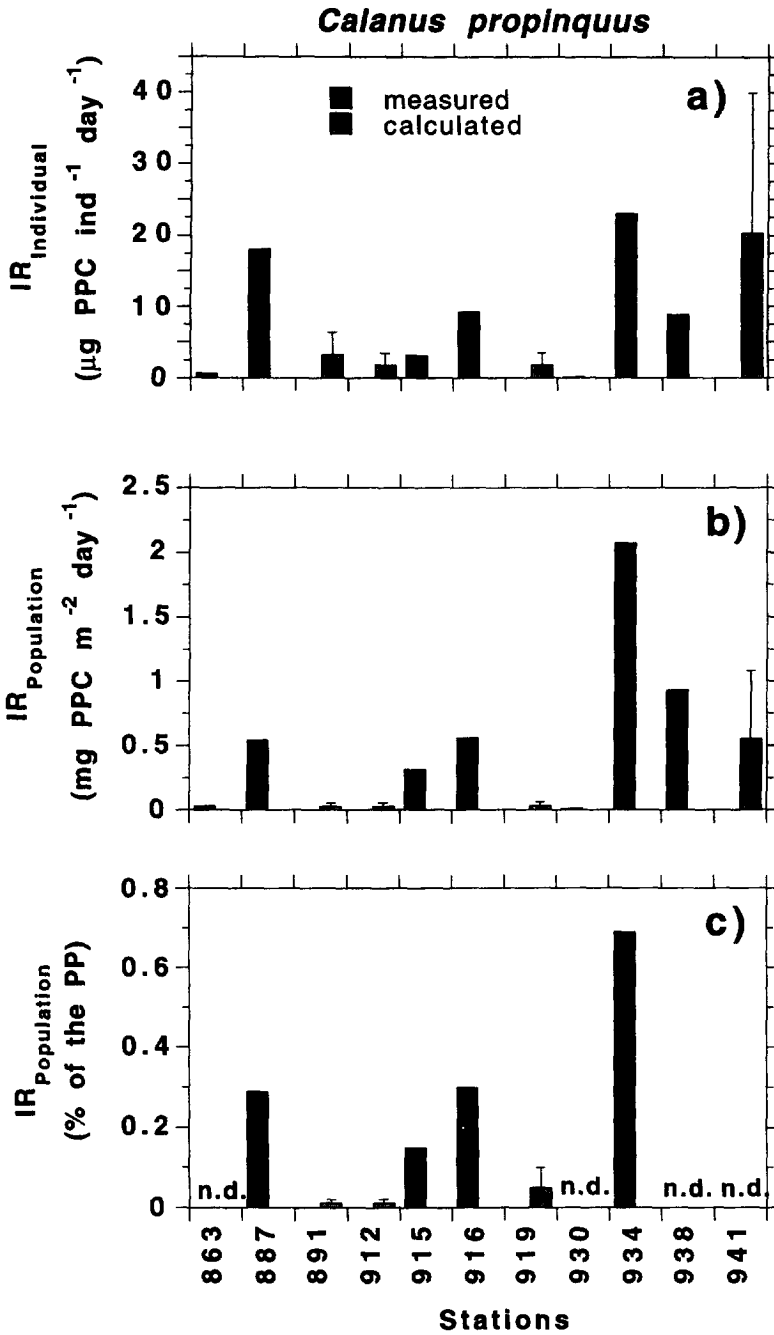PPC = phytoplankton carbon.

Fig. 4.   Ingestion rates of *Calanus propinquus* at different stations along the AWB (a) per individual and day, (b) per population and day and (c) as a percentage of the daily PP. See also legend of Fig. 3.

Table 3. *Gut content (GC) given with standard deviation (SD), gut clearance rate (GCR) and ingestion rate (IR) of* Rhincalanus gigas *at different stations in the PFr*

Station	Mean GC ± SD (ng chl *a*-eq. ind.$^{-1}$)	GCR (h^{-1})	IR (μg PPC ind.$^{-1}$ day^{-1})	*n*	r^2
901	3.52 ± 1.06	0.25	1.06	28	0.47
903	2.90 ± 1.34	0.69	2.40	11	0.65
956	4.85 ± 2.07	0.51	2.97	18	0.68
960	10.08 ± 1.61	0.95	11.49	18	0.90
964	5.63 ± 1.77	0.62	4.19	18	0.73

PPC = phytoplankton carbon.

DISCUSSION

Characterisation of the dominant mesozooplankton species, Calanoides acutus

Calanoides acutus is one of the most abundant mesozooplankton species in the Southern Ocean (Huntley and Escritor, 1991). It shows a circumpolar distribution that ranges from near the continent northwards to the Antarctic Convergence (Andrews, 1966). During the summer months, this species is found in the surface waters, but during winter, it hibernates between about 500 and 1000 m (Andrews, 1966). The upward migration during spring starts in October. This takes place sooner in the northern than in the southern areas (Andrews, 1966). Voronina (1966, 1978) postulated that this migration is mainly conducted by late copepodite stages. Vervoort (1965), Andrews (1966) and Zmijewska (1985) found very few or no male adults of this species during their investigations in surface waters. Marin (1988) discussed whether this was due to the occurrence of mating in deeper layers in a way that upward migration is conducted by fertilized females.

In the northern part of our investigation area (in the PFr, 47–50°S), most of the *C. acutus* CV and CVI were already present between 50 and 200 m at the beginning of October, whereas most of the *C. acutus* south of 50°S were still below 200 m. By the end of October, *C. acutus* was close to the sea surface north of 50°, but still below 200 m south of 50°S (Fransz and González, 1997).

Hopkins *et al.* (1993) examined the gut contents of *C. acutus* and classified this species as exclusively herbivorous. Typical phytoplankton fatty acids, such as 16:1 and 18:4, are incorporated without any modifications by copepods and therefore can be used as a marker for ingested phytoplankton (Lee *et al.*, 1971; Sargent and Henderson, 1986). The fatty acid composition of *C. acutus* also indicates a strictly herbivorous feeding behaviour (Graeve *et al.*, 1994).

Using the gut-fluorescence-method, we measured ingestion rates for *C. acutus* of about 0.82–3.97 μg phytoplankton carbon (PPC) ind^{-1} day^{-1} (Fig. 3), corresponding to 0.0005–0.03% of body carbon. Drits and Pasternak (1993), using the same method, determined slightly higher values (1.5–5.3 μg PPC ind^{-1} day^{-1}), but their experiments were carried out during the summer. The values of Schnack (1985) were also higher than our values and accounted for 0.03–0.3% of body carbon per day (see below).

Conover and Huntley (1991) calculated that only the highest ingestion rates determined by Schnack (1985) would enable *C. acutus* to develop from an egg to the overwintering stage CV from mid-October until mid-March. Because our values are rather low, it has to be
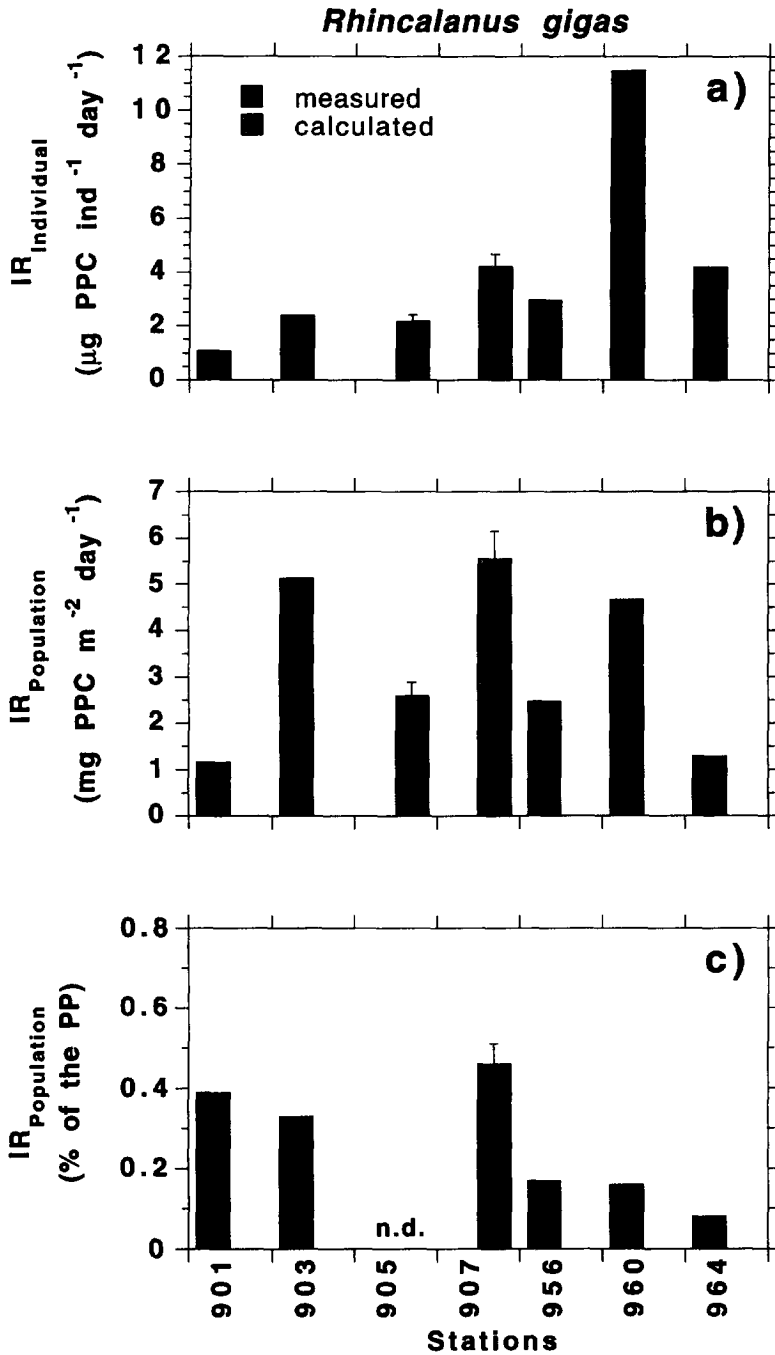
Rhincalanus gigas

Fig. 5.   Ingestion rates of *Rhincalanus gigas* at different stations in the PFr (a) per individual and day, (b) per population and day and (c) as a percentage of the daily PP. See also legend of Fig. 3.
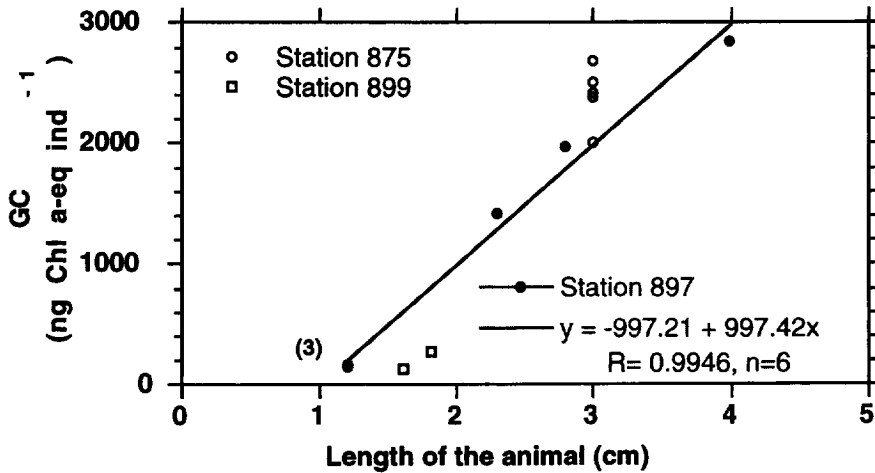
Fig. 6. Gut content (GC) of *Salpa thompsoni* as a function of body length. Closed symbols and regression from data determined at Station 897; (3): triplicate samples. Open symbols: data from other stations.

assumed that grazing by *C. acutus* will increase later in the year or that copepod grazing was underestimated by the method used (see below). The higher values measured by Drits and Pasternak (1993) during summer support these suggestions.

Calanus propinquus

Calanus propinquus also is a dominant copepod in the Southern Ocean (Hubold and Hempel, 1987). It shows a more southerly distribution than *R. gigas* and *C. acutus*. Part of the population hibernates in deeper layers (below the permanent thermocline), and part stays in the surface waters under the ice (Marin, 1988; Nöthig *et al.*, 1991; Bathmann *et al.*,

Table 4. *Carbon and nitrogen content ± SD (standard deviation) of* Salpa thompsoni

Length (cm)	Carbon content (mg) ± SD	Nitrogen content (mg) ± SD	C/N (by atoms) ± SD	n
3	1.48 ± 0.03	0.37 ± 0.02	4.6 ± 0.2	3
4	2.25	0.59	4.5	1

Table 5. *Gut content, ingestion rate (IR) and filtration rate (FR) ± SD (standard deviation) of* Salpa thompsoni

Length (cm)	Gut content ind^{-1} ± SD					IR ± SD		FR ± SD (litres ind^{-1} day^{-1})
	ng chl a-eq.	ng chl a	ng phaeopigment	chl a/phaeoration	n	μg PPC ind.$^{-1}$ day^{-1}	Body carbon (%)	
3	2392 ± 250	250 ± 67	2143 ± 212	0.12 ± 0.03	6	660 ± 69	44.6 ± 5.6	44 ± 4.6
4	2848	533	2315	0.23	1	786	34.9	52

A

3 cm sized salps
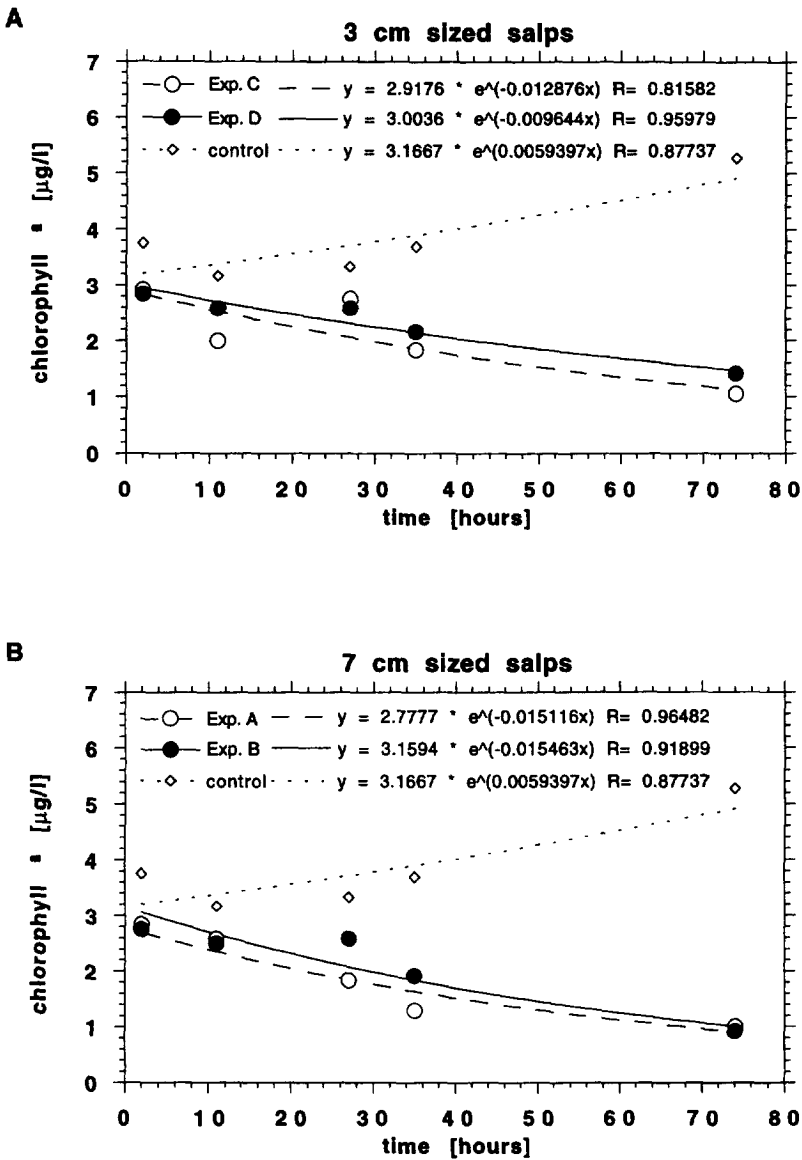

B

7 cm sized salps

Fig. 7. Development of chlorophyll *a* concentrations during grazing experiments of *Salpa thompsoni.* (A) Experiments C and D with 3 cm sized individuals and (B) experiments A and B with 7 cm sized individuals (open and closed circles). Open diamonds, controls without salps. The experiments were performed with single organisms; equations of exponential regression for each experiment are given.

1993). *Calanus propinquus* continues feeding in autumn (Hopkins, 1985)—in contrast to *C. acutus* and *R.gigas*—and it feeds actively under the ice during winter (Bathmann *et al.*, 1993). During spring, the animals from deep winter layers start to migrate into the surface layers. Their upward migration begins before *R. gigas* but after *C. acutus* (Voronina, 1970; Atkinson, 1991). During our expedition, *C. propinquus* was present in the upper 200 m near

the AWB during the entire investigation period. However, their distribution was very patchy.

Calanus propinquus has an omnivorous feeding mode (Hopkins and Torres, 1989). Not only phytoplankton but also protozooplankton as well as smaller metazoa have been found in its gut (Hopkins, 1985; Hopkins and Torres, 1989). The fatty acid composition of *C. propinquus* also indicates an omnivorous feeding behaviour (Hagen *et al.*, 1993).

We measured ingestion rates of *C. propinquus* ranging from 0.15 to 23.04 μg PPC ind^{-1} day^{-1} (Fig. 4). The gut-fluorescence-method determines only the ingestion of phytoplankton. Since *C. propinquus* feeds omnivorously and, therefore, also ingests non-chlorophyll containing particles, these ingestion rates may be underestimates of total ingestion. However, our rates correspond to those measured by Bathmann *et al.* (1993) during winter in the Weddell Gyre using a different method—that of Frost (1972). Our feeding rates for *C. propinquus* are higher than those measured for *C. acutus* and *R. gigas* (Figs 3 and 5). Our values for *C. propinquus* are, however, in the same order of magnitude as the values measured by Drits *et al.* (1993) later in the year, during February (2.8–23.4 μg PPC ind^{-1} day^{-1}). We assume, therefore, that the grazing activity of *C. propinquus* was already fully developed.

Rhincalanus gigas

Rhincalanus gigas is also a dominant mesozooplankton species in the Southern Ocean (Ommaney, 1936), showing a circumpolar range in its distribution northwards into sub-Antarctic waters (Voronina, 1972; Bathmann *et al.*, 1993; Voronina *et al.*, 1994). It overwinters in deeper water layers (1000 m) and returns during spring to the surface (Marin, 1988).

Arashkevich (1978) demonstrated the omnivorous feeding mode of *R. gigas* in experiments. Investigations of gut contents of *R. gigas* showed that it is a herbivorous species (Hopkins, 1985). This is also indicated by the fatty acid composition of the animals, where the dominance of short-chain alcohols resembles the lipid pattern found in the omnivorous *Metridia gerlachei* (Graeve *et al.*, 1994). Graeve *et al.* (1994) assume, therefore, that *R. gigas* shows an opportunistic feeding mode in between herbivorous and omnivorous feeding behaviour.

During our expedition, the abundance of *R. gigas* in the upper 500 m was highest in the northern part of our investigation area (Fransz and González, 1997). At the beginning of our investigation period, most of the individuals were found in deeper water layers. Only north of 51°S in the PFr, were numerous *R. gigas* already present at depths of 50–200 m. At the end of October, *R. gigas* still remained in deeper layers south of 51°, whereas CV and CVI of this species had reached surface layers in the PFr (Fransz and González, 1997).

Ingestion rates of *R. gigas* accounted for 1.06–11.49 μg PPC ind^{-1} day^{-1} (Fig. 5). Drits and Pasternak (1993) reported rates in the same order of magnitude for *R. gigas* (2.6–8.3 μg PPC ind^{-1} day^{-1}) later in the year. Therefore, we conclude that *R. gigas* was grazing at maximal rates at the end of our investigation period.

It is also remarkable that no faecal pellets were found in the containers with *R. gigas* in the grazing experiments (following Frost, 1972) carried out on board, although the chlorophyll and ammonia data and the cell numbers indicated active grazing (Dubischar, 1994). Using the same experimental design with *C. propinquus*, faecal pellets were numerous. Therefore, either the faecal pellets produced by *R. gigas* were much more fragile and disintegrated more

easily than the faecal pellets of *C. propinquus*, or the feeding rate of *R. gigas* on its own faecal pellets was high enough to clear the faecal pellets very quickly from the whole container so that they did not appear in the samples.

Salpa thompsoni

The gut content of *Salpa thompsoni* was high (e.g. 2.0–2.7 μg chl *a*-eq. ind^{-1} for 3-cm-long individuals). A positive linear relationship between the gut content and the length of the animal was found (Fig. 6). The chl *a*/phaeopigment ratios of the gut content of the animal accounted for 0.12 ± 0.03 for 3-cm-long animals (Table 5) and were below the ratios of the other particles in the water column (chl *a*/phaeopigment ratio of 5.68).

The experiments conducted on board resulted in ingestion rates for 3-cm-long salps of about 100 μg PPC ind^{-1} day^{-1}, which corresponds to 6.8% of body carbon ind^{-1} day^{-1}. Huntley *et al.* (1989), by calculating respiration rates and measuring egestion rates of *S. thompsoni*, calculated ingestion rates of about 25% of the body carbon ind^{-1} day^{-1}. Thus, our rates measured directly in ship-board experiments range at the lower end of the ingestion spectrum reported for salps.

Drits and Semenova (1989) determined the gut clearance rate of *S. thompsoni* using the gut-fluorescence-method (Mackas and Bohrer, 1976). Multiplication of this rate with the gut contents that we determined, leads to ingestion rates of 551–739 μg PPC ind^{-1} day^{-1} (3-cm-long animals), corresponding to 37–50% of body carbon. This ingestion rate corresponds to a filtration rate of 37–49 l ind^{-1} day^{-1} (3-cm-long animals). Huntley *et al.* (1989) determined values of 24 l ind^{-1} day^{-1} for an 11-cm-long individual. They determined these rates by using experimental containers of 10 l where the animals were left for several hours. Ingestion rates of salps are strictly correlated to swimming activities (Reinke, 1987) so that the effect of enclosure in a 10-l container may lead to a decreased ingestion rate.

This ingestion rate of 37–50% of body carbon represents only the contribution of the phytoplankton to the ingested food. In the guts of *S. thompsoni*, also cyclopoid copepods (Hopkins and Torres, 1989), calanoid copepods (Hopkins and Torres, 1989; Hopkins *et al.*, 1993) and even debris of *E. superba* (Hopkins, 1985; Hopkins and Torres, 1989) have been found. The total ingestion rate is, therefore, expected to be higher than the 37–50% of body carbon because of the non-chlorophyll part of the ingested food that we did not determine.

Thus, by using two different approaches for the determination of salp ingestion rates, we found a discrepancy by a factor of 5–8. Two possible reasons may have contributed to this uncertainty. The above-mentioned "container effect" may have reduced salp feeding in our experiments, and therefore probably results in an underestimation of natural ingestion rates. On the other hand, due to the stress during capture and being maintained in a small container, salp egestion rates in gut clearance rate experiments may be increased. This might result in a very rapid decrease of animal pigment concentrations and, thus, to overestimation of gut clearance rates that are used to calculate the ingestion rates after Mackas and Bohrer (1976). We conclude that both methods should give the extremes of the "true" feeding *in situ*, which definitely needs further investigation.

The gut-fluorescence-method

Based on the assumption that chl *a* is only degraded into phaeopigments but not into non-

fluorescent substances in the guts of copepods (Shumann and Lorenzen, 1975), Mackas and Bohrer (1976) developed the gut-fluorescence-method. Many experiments carried out to test this assumption (e.g. Conover *et al.*, 1986; Head, 1986,1988, 1992; Mayzaud and Razouls, 1992), indicate that part of the chl *a* ingested by the copepods is indeed degraded to non-fluorescent substances. Head (1988, 1992) demonstrated that the amount of pigment degraded to non-fluorescent substances is dependent on food concentration and feeding history of the animals. More recent studies using HPLC-techniques (high performance liquid chromatography) demonstrated that 10–80% of the ingested chl *a* is converted into phaeopigments, whereas the remainder is degraded to non-fluorescent substances (Head and Harris, 1992, 1994). Thus, the gut-fluorescence-method of Mackas and Bohrer (1976) may lead to an underestimation of total ingestion rates by a factor of up to 10. Other pigments, such as chl *b*, interfere with the fluorometric measurements of chl *a* leading to higher values; this may have caused an overestimation of chl *a* in our study by about 10% as this was equivalent to the ambient chl *b* concentration (Peeken, 1997). As the gut-fluorescence-method per definition only considers fluorescent particles, the heterotrophic proportion of the animal's food is ignored. In total, the ingestion rates presented in our paper range most likely at the lower end of the "true" species ingestion rates. Because of the uncertainty about the retrieval rate of pigments after gut passage (Mayzaud and Razouls, 1992) and because the general conclusions in our paper would not be altered, we do not apply any correction factors for pigment loss during gut passage.

The ingestion rates for *R. gigas* and *C. propinquus* determined during our cruise in shipboard experiments differed very little from the rates determined by using the gut-fluorescence-method (Dubischar, 1994). In the former experiments, phytoplankton associations derived from melting sea-ice and from the surface water layers were fed to different copepod species; the ingestion rates in these experiments were calculated by using the formula of Frost (1972). Thus, in the present study the gut-fluorescence-method gives a good estimation of ingestion rates of phytoplankton by mesozooplankton. Whether the egestion rates of copepods are best represented by negative power or negative exponential functions (Huntley *et al.*, 1987) is contentious, but it should not concern us here as it would not significantly alter our results and conclusions.

Several factors may have contributed to the relatively low copepod ingestion rates observed in this study compared to the values of Schnack (1985). Firstly, *R. gigas* may not have been actively feeding at the beginning of the study. The research was done in the beginning of spring, and most of the *R. gigas* population had just started to migrate to the surface layers. Microscopical observation revealed that most animals at the beginning of our study still had high lipid contents, indicating that they still had reserves from their overwintering stage. Secondly, the gut-fluorescence-method only measures the ingestion of phytoplankton and does not take into account the ingestion of detritus or smaller zooplankton. As mentioned above, for example, *C. propinquus* feeds also on non-chlorophyll particles. Consequently, the ingestion rates determined with this method are expected to lie below the total energy requirements of the copepod. Our aim was not to find the exact values of the total carbon ingested, but rather to determine the impact of grazing on phytoplankton biomass.

Ecological impact of calanoid copepods and salps in the investigation area

Based on our results, the ecological impact of grazing of the zooplankton communities in

the three regions of the investigation area may be as follows. In the southern parts of the investigation area, at the AWB and in the ACC, the chlorophyll concentrations and the primary production remained very low during the entire investigation period (Bathmann *et al.*, 1996; Jochem *et al.*, 1995). In the PFr, on the other hand, a phytoplankton bloom with chl *a* concentrations of $>4 \mu g \, l^{-1}$ and primary production rates $\geq 3 \, g \, C \, m^{-2} \, day^{-1}$ had developed (Bathmann *et al.*, 1997; Jochem *et al.*, in press). We next examine whether the zooplankton could have caused this situation.

Ingestion rates of populations of *R. gigas*, a dominant calanoid copepod in the upper 200 m in the PFr (Fransz and González, 1997), accounted for less than 1% of the daily primary production (PP). To estimate the grazing impact of the whole mesozooplankton community in the PFr, we assumed that the IR measured for *R. gigas* was the same as for the other mesozooplankton species. Calculations based on such an assumption resulted in 0.3–3.7% grazing of the daily PP in the PFr. Thus, the IR of the whole mesozooplankton community was probably very low in this area. The development of a phytoplankton bloom in the PFr, then, would not be suppressed to any great extent by this small grazing impact of the mesozooplankton. Other factors such as favourable physical conditions (Veth *et al.*, 1997), relatively high iron concentrations (de Baar *et al.*, 1995) and grazing by protozooplankton (Klaas, 1997) also may have stimulated the development of phytoplankton blooms.

At the AWB, the grazing of *C. propinquus* also had only a minor effect on phytoplankton biomass, as it consumed $<1\%$ of the PP. By using the same approach as for *R. gigas*, total mesozooplankton ingestion resulted in 0.1–1.6% of daily PP. The low phytoplankton biomass in the AWB therefore may be the result of other factors such as the observed deep mixing of the upper water column (Veth *et al.*, 1997) and the low iron values (de Baar *et al.*, 1995). Further, microzooplankton was very abundant in this area (Klaas, 1997).

In the ACC, the grazing pressure of *S. thompsoni*, expressed as a percentage of the daily PP, accounted for more than 100% of the amount of carbon fixed by the phytoplankton— even by applying the lowest ingestion rates that we determined (see above). We conclude that the salps could have prevented the build-up of a phytoplankton bloom in this area. Similarly, Makarov and Solyankin (1990) found a huge abundance of salps in the modified ACC waters at the eastern boundary of the Weddell Gyre in early summer. In this "super patch" of salps, a strong impact on phytoplankton was evident. Moreover, salp grazing had a negative effect, either directly or indirectly, on the seasonal development of dominating copepod species (Makarov and Solyankin, 1990). In our study, such grazing impact of salps on phytoplankton and other zooplankton in the southern ACC therefore seems likely.

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