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Zooplankton response to a phytoplankton bloom near South Georgia, Antarctica

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ABSTRACT: A shelf site near the island of South Georgia was sampled during a spring bloom in January 1994. Chlorophyll *a* (chl *a*) values declined from 19 to 6 mg m^{-3} during the 8 d of sampling. The bloom comprised mainly long pennate diatoms and large colonies of centric diatoms; a 200 µm sieve retained over two-thirds of the chl *a*. Mesozooplankton biomass was high, 12.3 g dry mass m^{-2} within the top 200 m, and comprised mainly copepods. A series of Longhurst Hardy Plankton Recorder profiles showed that the numerical dominants (*Oithona similis*, *Drepanopus forcipatus* and pteropods) resided mainly within the top 20 m, whereas the large, biomass-dominant copepods had secondary maxima rather deeper within the thermocline. Diel vertical migration was not a feature of this community, being limited to metridiid and euchaetiid copepods. Gut fluorescence measurements on 7 large copepod species showed that all fed during both day and night, although guts tended to be fullest during afternoon and night. About 20% of chl *a* grazed by these copepods occurred below the mixed layer, thus representing a potentially direct export of carbon from the system via sinking faecal pellets. Algal carbon rations (% body carbon ingested per day) of mixed layer copepods ranged from 3% (*Rhincalanus gigas*) to 20% (small copepods). With the exception of *R. gigas*, these values from gut fluorescence agreed with independent estimates from the site following the decline of chl *a* during incubations in ambient seawater. Despite low clearance rates, ingestion rates (per copepodid) were at the upper end of recorded Antarctic values, suggesting food saturation. *Calanoides acutus* and *R. gigas* cleared diatoms (including the highly elongated 0.5 to 1 mm forms) at maximal rates. *Metridia* spp., *Calanus propinquus* and small copepods, by contrast, cleared dinoflagellates and ciliates faster than diatoms of similar size. The total mixed layer zooplankton probably removed <5% of daily primary production and <5% of protozoan standing stocks per day.

KEY WORDS: Southern Ocean · Zooplankton · Copepods · Feeding rates · Diets · Diatom bloom

INTRODUCTION

Low productivity characterises large areas of the Southern Ocean, but inshore shelf waters are an exception. In these locations, stabilization of the mixed layer due to freshwater input or shelter from winds, coupled with nutrient enrichment is thought to contribute to intense phytoplankton blooms (Boden 1988, Mitchell & Holm-Hansen 1991). One such area is the large shelf surrounding the island of South Georgia (Priddle et al. 1986, 1995, Whitehouse et al. 1996). Productive inshore waters can support large stocks of mesozooplankton (Boden 1988, Ward et al. 1995) and krill (Marr 1962, Brinton 1991, Huntley & Brinton 1991). Although these hotspots comprise a small fraction of the Southern Ocean, they may be responsible for high carbon fixation and fluxes within the food web, making them key areas for study (Huntley et al. 1991).

For an herbivorous or omnivorous zooplankter, a spring bloom could be important in providing a brief but plentiful supply of food, against a background of generally low chl *a* levels and small food cells (Smetacek et al. 1990). Copepods can respond to

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increased quality or quantity of food with rapid egg production, moulting or lipid build up, depending on the species and maturity stage (Lopez et al. 1993, Hagen & Schnack-Schiel 1996). However, Antarctic blooms are often ephemeral events and characterised by extremely large diatoms which may be unpalatable (Perissinotto 1992). It is still not known how fast Antarctic zooplankton can feed, and whether they can ingest or digest the large or spiny bloom forming diatoms (Perissinotto 1992, Atkinson 1994, 1995, Pond et al. 1995).

During January 1994, we investigated an intense bloom of large diatoms at a site near South Georgia. A large biomass of zooplankton was feeding on the bloom, which declined from ~19 to 6 mg chl *a* m^{-3} during the 8 d study. Because vertical carbon fluxes were probably significant, we monitored the vertical distributions of both zooplankton and of copepod gut fullness. Feeding rates derived from gut fluorescence were compared with those from incubations monitoring clearance of diatoms, protozoans and total chl *a*. The 3 aims were (1) to estimate copepod ingestion and clearance rates attainable during a bloom, (2) to compare their clearance rates on protozoans, on diatoms of similar size and on longer (~1 mm) taxa, and (3) to estimate zooplankton grazing impact on primary production and on protozoans.

METHODS

Zooplankton abundance, biomass and diel vertical migration. From 11 to 19 January 1994, RRS 'James Clark Ross' occupied an inshore site (53° 43' S, 38° 4' W) located over the shelf at the western end of South Georgia. The abundance, biomass and vertical distribution of the zooplankton were estimated from 7 tows with a Longhurst Hardy Plankton Recorder (LHPR; Longhurst & Williams 1976) within the top 200 m. These hauls were conducted at generally 3 to 4 h intervals within a 24 h period on 17 to 18 January, and were aimed at monitoring the fine-scale vertical distribution and diel migrations of the major zooplankton species. The LHPR was interfaced with a PRO-PLUS® control system (Spartel Ltd., Plymouth, UK), enabling control of net trajectory on a double oblique profile from the surface to 200 m. Hauls lasted about 0.5 h with each sample being of 1 min duration (i.e. ~160 m distance towed). Volume filtered during each haul was provided by a flowmeter mounted within the nose-cone. Loss of our 38 cm nose-cone on the mid afternoon haul necessitated replacement with a 20 cm nose-cone. A single sample from the larger nose-cone, at our sampling interval of 1 min, represented 10 to 15 m^3, while that from the smaller one was 5 to 8 m^3.

On retrieval of the sampler, the individual samples were cut from the roll of 200 µm gauze and preserved in 4% formaldehyde in seawater. The descent portions of the profiles were not analysed because their flow rates were low and variable, with the possibility that plankton were recirculated in front of the recorder box and not washed back onto the retaining gauzes. Analysis of the LHPR samples was either on whole samples or on Folsom splitter aliquots of $\frac{1}{2}$ to $\frac{1}{64}$, depending on species abundance. Biomasses of non-copepod taxa (euphausiids, pteropods, amphipods, ostracods and chaetognaths) were determined by drying batches at 60°C and weighing on a Sartorius® microbalance. With the exception of the pteropods, these values were then multiplied by 1.25 as an adjustment for tissue loss in formaldehyde (Hopkins 1971). Dry masses of the major copepod taxa, which were used for feeding experiments, were determined from frozen material. The determination of community grazing required dry mass estimates of rarer species and life stages. These were obtained by length-mass regressions derived from those copepodites which were weighed.

Copepod feeding rates measured by the gut fluorescence method. Feeding rate measurements were restricted to copepods, which dominated both in numbers and biomass. Diel feeding periodicity was assessed for material from a 75 cm diameter, 200 µm mesh closable ring net, which provided 16 hauls from the top 70 m layer and 13 hauls from the 70 to 200 m layer. 70% of these hauls came from the same 24 h period as the LHPR sampling. These samples were frozen immediately (–60°C) for analysis of gut fluorescence, 18 mo later in the United Kingdom.

Laboratory procedures were described by Atkinson (1996), with the exception that prior to transferring the copepods to 10 ml aliquots of 90% aqueous acetone, they were rinsed in distilled water. Between 10 and 50 (mean of 22) individuals per haul were sorted for gut fluorescence, of *Calanoides acutus*, *Calanus simillimus*, *Calanus propinquus*, *Rhincalanus gigas*, *Metridia lucens*, *M. gerlachei* and *Pleuromamma robusta*. Replicates were processed where numbers were sufficient for rapid processing.

Chlorophyll and phaeopigment content of the copepods were calculated from the fluorescence readings before and after acidification (Parsons et al. 1984) using a Turner® 112 fluorometer. Chlorophyll was usually <10% of phaeopigment values and because it might have come from diatoms adhering to the feeding appendages of the copepods, gut contents were calculated from phaeopigment only. These values were multiplied by 1.5 as an adjustment for an unmeasured degree of pigment destruction (Kiørboe & Tiselius 1987, Dam & Peterson 1988). Unfortunately, gut clear-

ance rates could not be measured because it was not possible to separate copepods rapidly from the large colonial diatoms which were also retained in the nets. Daily chl *a* consumption was therefore estimated from the diel mean gut content multiplied by the turnover rate, calculated from temperature (Dam & Peterson 1988) and assuming food saturation.

Feeding experiments. Four experiments (A to D) provided independent estimates of copepod daily carbon rations based on chl *a* consumption, and allowed comparison of their clearance rates on various food taxa in the seawater. Copepods for these incubations were obtained from slow tows with the ring net from 70 m to the surface. Undamaged individuals were sorted from the solid cod-end and placed in 1.2 l bottles of unscreened surface seawater for an acclimation period of 18 to 24 h. Species incubated were *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas*, *Metridia* spp. and a mixed assemblage of small copepods [mainly *Drepanopus forcipatus*, *Ctenocalanus* sp. and *Metridia* spp. (CI–CIII)].

Natural seawater was used as a food assemblage. In order to reduce death or disruption of delicate items (e.g. athecate protozoans and some colonial diatoms), the water was collected with a plastic bucket from the sea surface and was not pre-screened (Gifford 1993). Bad weather, however, forced us into using water from the pumped non-toxic supply for Expt C. The experimental water was stored in a 50 l carboy at 2 to 3°C in the dark for 2 to 4 h prior to setting up each experiment. The seawater was then mixed, siphoned into the glass experimental bottles (1.2 or 2.4 l depending on grazer size) and the copepods added. Density of grazers (2 to 41 l^{-1}) was adjusted for their size and approximate feeding capabilities. These bottles (normally 2 replicates per experiment) plus 2 control replicates without copepods were then placed on a grazing wheel and rotated end over end (0.5 rpm) at 2°C in the dark.

In Expts A, B and D, feeding was monitored by microscope cell counts of taxa in the incubation water, and two 200 ml subsamples of water from each bottle were preserved in 2% acid Lugol's solution before and after incubation. In Expts A, B and C, feeding was also monitored from the drop in chl *a* concentration during the incubation. For these experiments, two 250 ml aliquots were filtered onto GF/F filters before and after incubation. The samples were extracted immediately in 8 ml of 90% aqueous acetone for measurement of chl *a* as described previously. Experimental duration was 21 to 26 h, after which the copepods were checked for mortality (which was negligible) and frozen for dry mass determination.

Cell counts and feeding rate calculations. Microscope counts of food items in the incubation water were completed on two 50 ml aliquots from each grazed or control bottle, using the Utermöhl settling technique. Only selected larger taxa were enumerated (Table 1) which, while hastening analysis time, precluded estimates of total carbon intake. Clearance rates on both the individual cell taxa and total chl *a* were calculated from Frost's (1972) equation modified to:

$$F = \ln(C_c/C_g)\cdot V/(m_g t)$$

where F is the clearance rate (ml mg^{-1} dry mass d^{-1}); C_c is the final concentration in control; C_g is the final concentration in grazer bottle; V is the experimental volume (ml); m_g is the copepod dry mass (mg); and t is the experimental duration (d). One justification for not using Frost's (1972) equation incorporating an algal growth term was that total chl *a* in the controls changed by less than 6% during the experiments. The other reason was that the initial and final control counts of the various food taxa were usually within the expected range of counting variation (Venrick 1978) making selection of realistic growth or loss terms problematic. Therefore to maintain consistency between

Table 1 Characteristics of the counted food items, listed for Expts A, B, and D respectively. Dashes represent food items not enumerated. The 'motile taxa' category comprises dinoflagellates and ciliates longer than 50 µm

Food taxon counted	Largest dimension (µm)			Smallest dimension (µm)			Carbon conc. in control (ng ml^{-1})			Mean no. cells per bottle		
Thalassionema sp.	–	34	–	–	5.4	–	–	0.42	–	–	165	–
Centric diatoms	73	74	–	36	35	–	6	27	–	86	433	–
Motile taxa	56	113	68	35	54	47	13	26	18	60	89	46
Eucampia sp.	–	–	160	–	–	15	–	–	25	–	–	173
Odontella sp.	110	168	230	22	26	22	29	29	26	735	810	653
Corethron spp.	74	116	408	22	22	27	5	21	48	113	542	478
Large pennate diatoms	967	–	890	13	–	30	8	–	7	98	–	49
Thalassiothrix sp.	–	1100	–	–	8	–	–	2	–	–	114	–
Chaetoceros spp.	–	1106	–	–	55	–	–	6	–	–	49	–

taxa and experiments and allow for possible changes in controls, the final control number (C_c) was used as a 'baseline' concentration for each food type (see 'Discussion'). For colonial cells the clearance rates were based on the numbers of cells counted rather than the number of colonies, in case of colony fragmentation during grazing (Deason 1980).

The lengths and widths of the food items were calculated from measurements of 20 to 50 cells, and their volumes were calculated from approximations to simple geometric shapes. Carbon contents of diatoms and dinoflagellates were calculated using the equations of Eppley et al. (1970). Ciliate carbon was estimated using Putt & Stoecker's (1989) value of 0.19 pg μm^{-3}.

Microbial production experiments. Production was estimated from oxygen flux measurements on water samples from 10 m depth, collected with Niskin bottles mounted on a CTD. Seven experiments were conducted at approximately daily intervals during our occupation of the site. Incubations were performed in 50 cm^3 or 100 cm^3 glass stoppered bottles for 24 h in either light or dark deck incubators. Near *in situ* temperatures were maintained by seawater circulating through the incubators. Initial and final dissolved oxygen concentrations were determined by Winkler titrations using a microcomputer-based system with a photometric endpoint detector (Williams & Jenkinson 1982). Microbial production was determined from oxygen values using a photosynthetic quotient of 1.2.

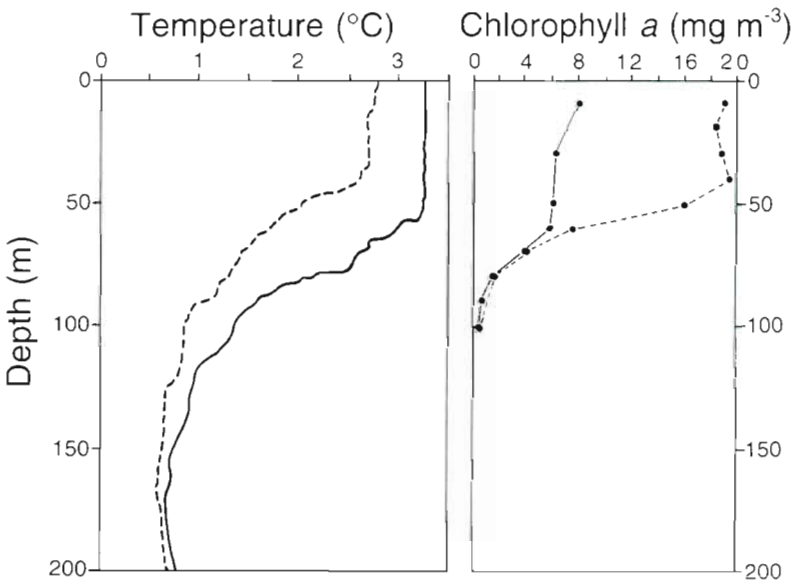

Fig. 1. Temperature and chl *a* profiles obtained on 11–12 January (----) and after the rough weather, on 16–17 January (——)

RESULTS

Environment

The environment changed during our 8 d occupation of the site (Fig. 1). Evidence for advective change was a 0.5°C increase in temperature of the mixed layer, an increase too large to be explained by seasonal warming. Chl *a* decreased from a maximum of 19 mg m^{-3} at the beginning of the study period to 6.5 mg m^{-3} at the end. There was a period of rough weather half way through our visit (prior to the LHPR and diel series of ring-net hauls) which was associated with a deepening of the mixed layer from ~40 to ~60 m.

The size composition of the phytoplankton reflected the large colonial diatoms (e.g. *Eucampia* sp., *Odontella* sp., *Thalassiosira* spp.) which characterised the bloom and accounted for most of the primary production. Over $^2/_3$ of the chl *a* was retained by a 200 µm mesh; nanoplankton comprised <10%. Massive clumped colonies of a small celled centric diatom were another feature of this site. These colonies were comparatively rare (usually <10 l^{-1}), so we could not evaluate whether the copepods were eating them. Their presence in the incubation water of Expt D also precluded the total chl *a* budget method of measuring grazing, as they caused a large measurement imprecision in this experiment.

A high net production of the whole community was determined from oxygen flux measurements. Results of 7 experiments spanning a week varied from 0.067 to 0.261 g C m^{-3} d^{-1} (mean 0.178 g C m^{-3} d^{-1}) but primary production decreased in line with the overall decline in chl *a*. Both chl *a* (Fig. 1) and primary production decreased sharply below the surface mixed layer.

The zooplankton community

Zooplankton biomass was high: 12.3 g dry mass m^{-2} within the top 200 m layer. This was dominated by large copepods (55%) although small pteropods (*Limacina* spp.) also characterised the site, contributing significantly to both total numbers and biomass (Fig. 2). Numerical dominants were *Oithona similis* and the neritic species *Drepanopus forcipatus*. Together with unidentified copepod nauplii these small copepods comprised 57% of metazoans caught in the top 200 m (Fig 2).

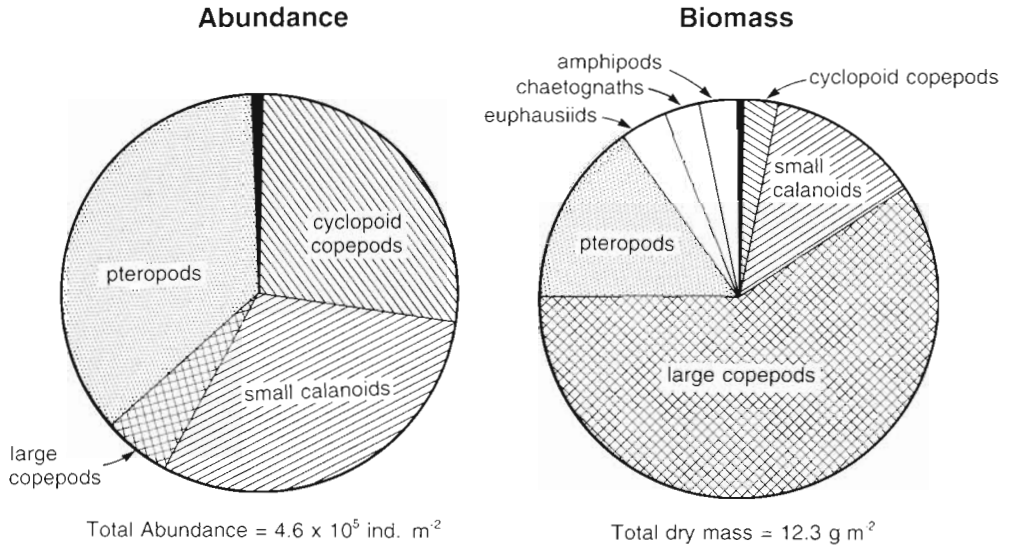

Fig. 2. Composition of the zooplankton community within the top 200 m, compiled from mean values across 7 LHPR hauls. Large copepods are defined as all copepodite stages of *Calanoides acutus, Calanus propinquus, Rhincalanus gigas, Calanus simillimus, Metridia lucens, M. gerlachei* and *Pleuromamma robusta*. Unidentified nauplii are included in the small calanoid group. Solid segment represents remaining taxa

Vertical distribution and diel vertical migration

On average, 69% of the 0 to 200 m biomass resided in the surface mixed layer. To summarise vertical distribution and diel migration, the median depths of major zooplankters were calculated from each haul, and the mean daytime (4 hauls) and nighttime (dusk, midnight and pre-dawn hauls) values of these medians were plotted (Fig. 3). Both this summary and the individual hauls (2 of which are presented in Fig. 4) suggest little diel vertical migration on the night of sampling. Most of the zooplankters occupied the top 50 m layer during both day and night and coordinated population movements (sensu Pearre 1979) were generally less than 20 m. Exceptions were several deeper living taxa: adult females of *Metridia lucens, M. gerlachei, Pleuromamma robusta* plus euchaetiids (all species and copepodites pooled) which tended to rise into the thermocline at night.

Although Fig. 3 shows differing median depths among the inhabitants of the mixed layer, the individual profiles (Fig. 4) show that their abundance maxima during both day and night were generally in the top 10 m. Within this topmost stratum metazoans were extremely abundant, with a mean total of 15524 ind. m^{-3} (range of 2471 to 32592 ind. m^{-3}). The slightly deeper median depths of the larger inhabitants of the mixed layer (*Calanoides acutus, Calanus propinquus, Rhincalanus gigas*) reflect the presence of secondary abundance maxima within the thermocline (Fig. 4).

Diel feeding periodicity

All 7 copepod species analysed for gut fluorescence had fullest guts at night (Fig. 5) but they differed in the detail of their feeding cycles. In the top 70 m layer, CV *Calanoides acutus* fed throughout the 24 h period but most actively from early afternoon through to dawn. From dawn to midday gut contents were only about 30 to 50% of values during the rest of the diel cycle. This morning lull in feeding is unlikely to have been a sampling artefact, being suggested by 5 samples over 3 separate days. The 0 to 70 m diel feeding signals for the other species are more irregular than those of *C. acutus* (Fig. 5), which probably reflects the fewer individuals analysed and poorer replication. The overall pattern for CV and CVI♀ *Rhincalanus gigas*, however, resembles that for *C. acutus*, with lower gut contents for the short period from late morning to midday.

Relative to the 0 to 70 m layer the overall gut fullness of the copepods below 70 m (Fig. 5) was higher than would have been predicted from the sharp decline in chl *a* below 70 m (Fig. 1). It is unknown whether the relatively full individuals below 70 m were feeding there or were performing episodic and asynchronous migrations from the richer waters above (Pearre 1979). In any case, 20% of their total digestion would have occurred below the mixed layer, based on the abundance and gut fullness of the 8 species/copepodite stages in the 0 to 70 m versus the 70 to 200 m layer. Significant defecation below the mixed layer would imply a rapid export of faecal carbon from the system.

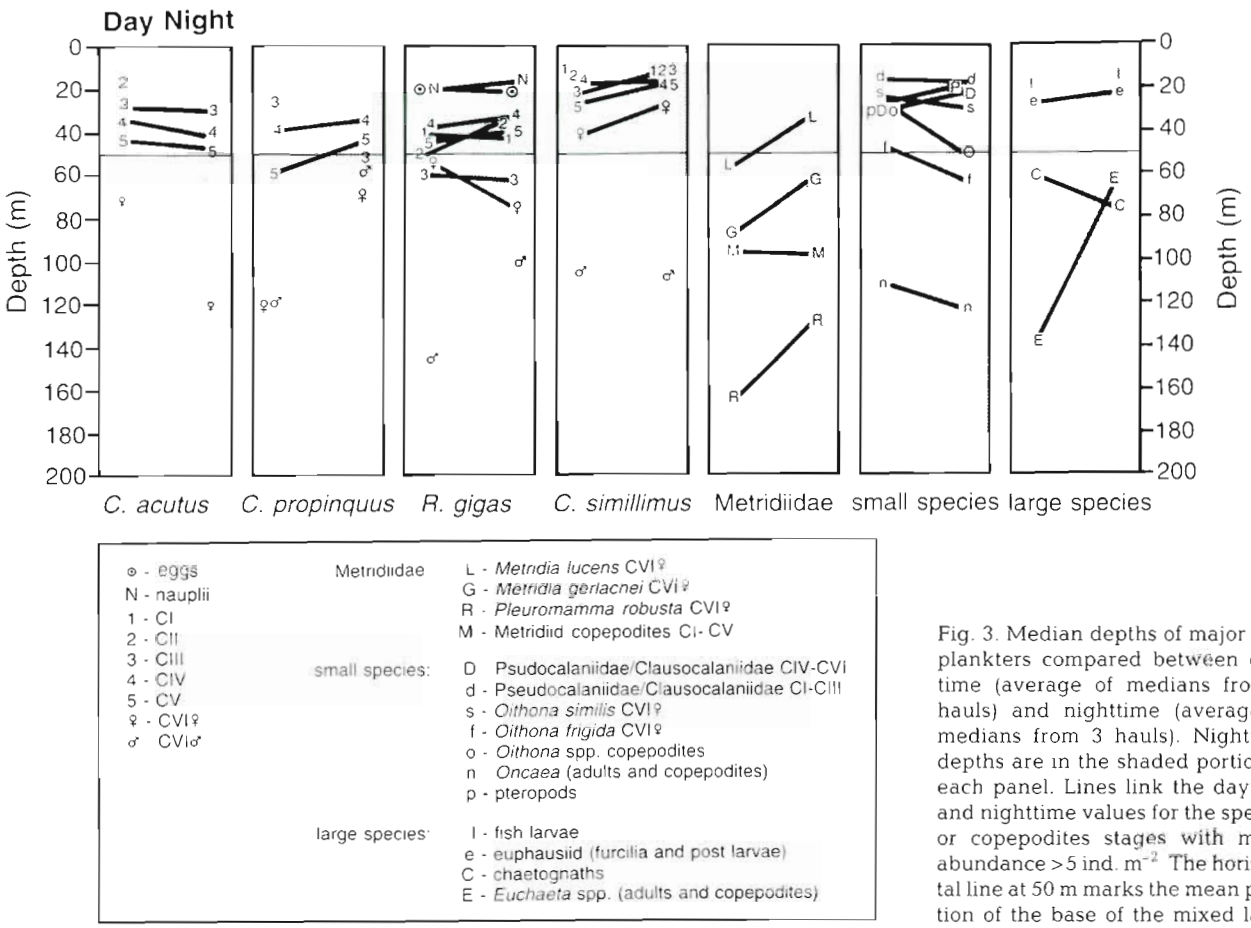

Fig. 3. Median depths of major zooplankters compared between daytime (average of medians from 4 hauls) and nighttime (average of medians from 3 hauls). Nighttime depths are in the shaded portion of each panel. Lines link the daytime and nighttime values for the species or copepodites stages with mean abundance >5 ind. m^{-2}. The horizontal line at 50 m marks the mean position of the base of the mixed layer

Feeding selectivity

Mass-specific clearance rates on individual food taxa are plotted in relation to their length in Fig. 6. It appears as if the copepods differed in their clearance rates of motile taxa and diatoms, with species in the right hand panel of Fig. 6 more efficient at clearing motile taxa (solid symbols) than those in the left hand panel. To counteract measurement imprecision and highlight this trend, mean clearance rates were calculated for 3 broad categories of food (Fig. 7). These categories are motile, non-diatom taxa (i.e. ciliates and dinoflagellates), diatoms in the same size range (i.e. <120 µm), and diatoms >120 µm. Even using this crude grouping the grazers form 2 categories. *Calanoides acutus* and *Rhincalanus gigas* appeared to clear motile taxa less rapidly than diatoms of the same broad size-range, whereas the opposite held for the remaining species. Clearance rates on large and small diatoms differed less, although the smaller copepods (*Metridia* spp. CV, CVI and copepodites of small species) cleared long diatoms less rapidly than <120 µm cells. Even small copepods, however, were capable of removing the long (~0.5 to 1 mm) cells of *Rhizosolenia* spp. and *Thalassiothrix* sp. (Fig. 6).

Daily carbon rations

The chl *a* contents of the incubation water in Expts A, B, C, and D were respectively 10, 13, 11 and 6.2 mg m^{-3}, which reflects the chl *a* decline at the station. Table 2 compares algal carbon rations from our 2 methods of measuring chl *a* consumption: gut fluorescence and bottle incubation. The ingestion rates based on gut fluorescence were converted to carbon rations by assuming a conservative carbon:chl *a* ratio of 50 for ingested microplankton (see 'Discussion') and that copepod body carbon was 45% of dry mass (Schnack 1985). Ingestion rates were obtained from the incubations by multiplying the clearance rate of total chl *a* by the initial chl *a* value in the incubation water (Marin et al. 1986). The same ratios of carbon:chl *a* and copepod carbon:dry mass were then used to derive rations which were directly comparable with those from gut fluorescence. Daily rations

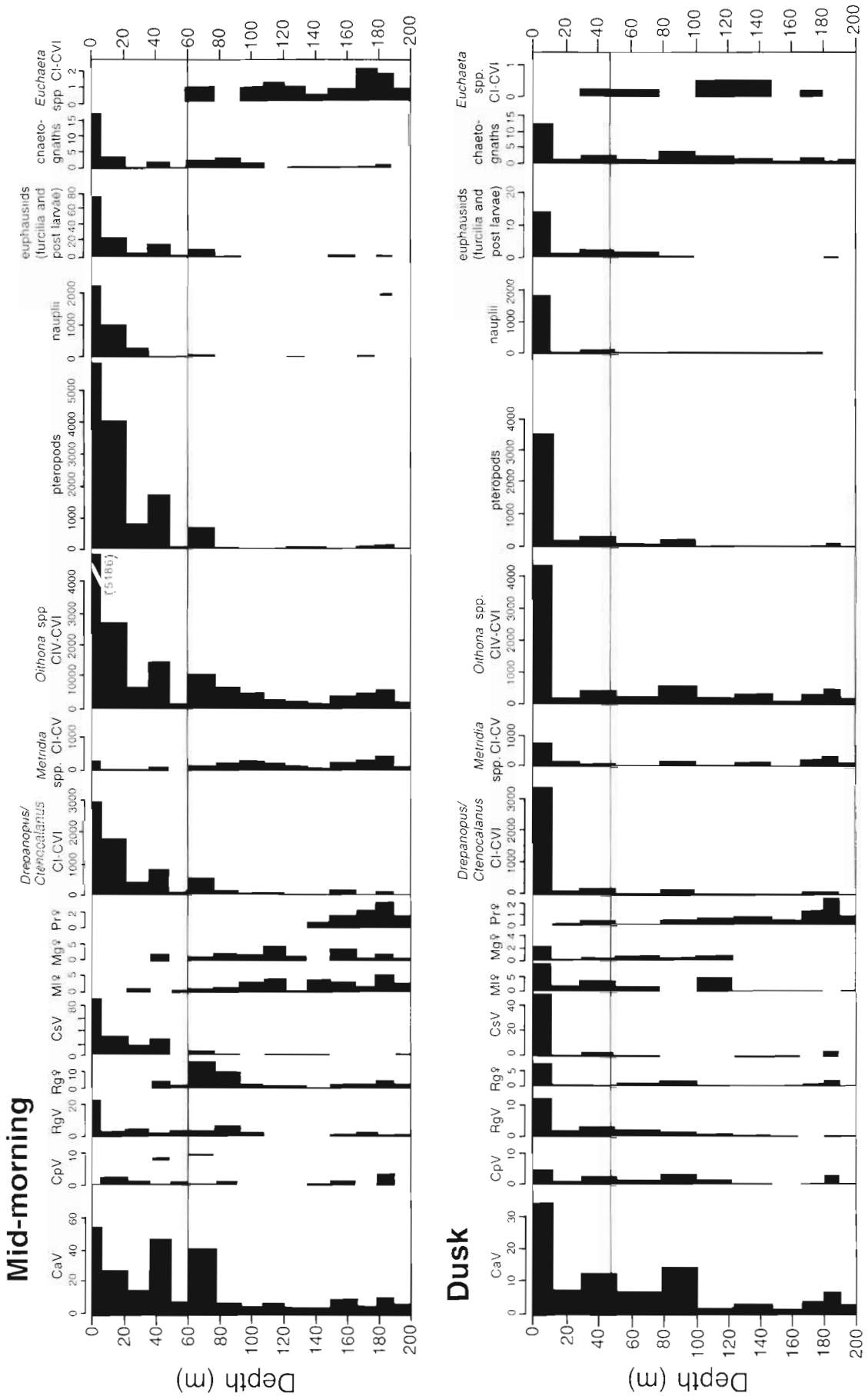

Fig. 4. Two LHPR profiles which typify the respective daytime and nighttime vertical distributions of the major species. Note that abundance scale (ind. m^{-3}) differs between species. The horizontal line marks the base of the mixed layer recorded by the LHPR's temperature sensor during the profile. CaV, *Calanoides acutus* CV; CpV, *Calanus propinquus* CV; Rg♀, *Rhincalanus gigas* CVI♀; Ml♀, *Metridia lucens* CVI♀; Mg♀, *Metridia gerlachei* CVI♀; Pr♀, *Pleuromamma robusta* CVI♀

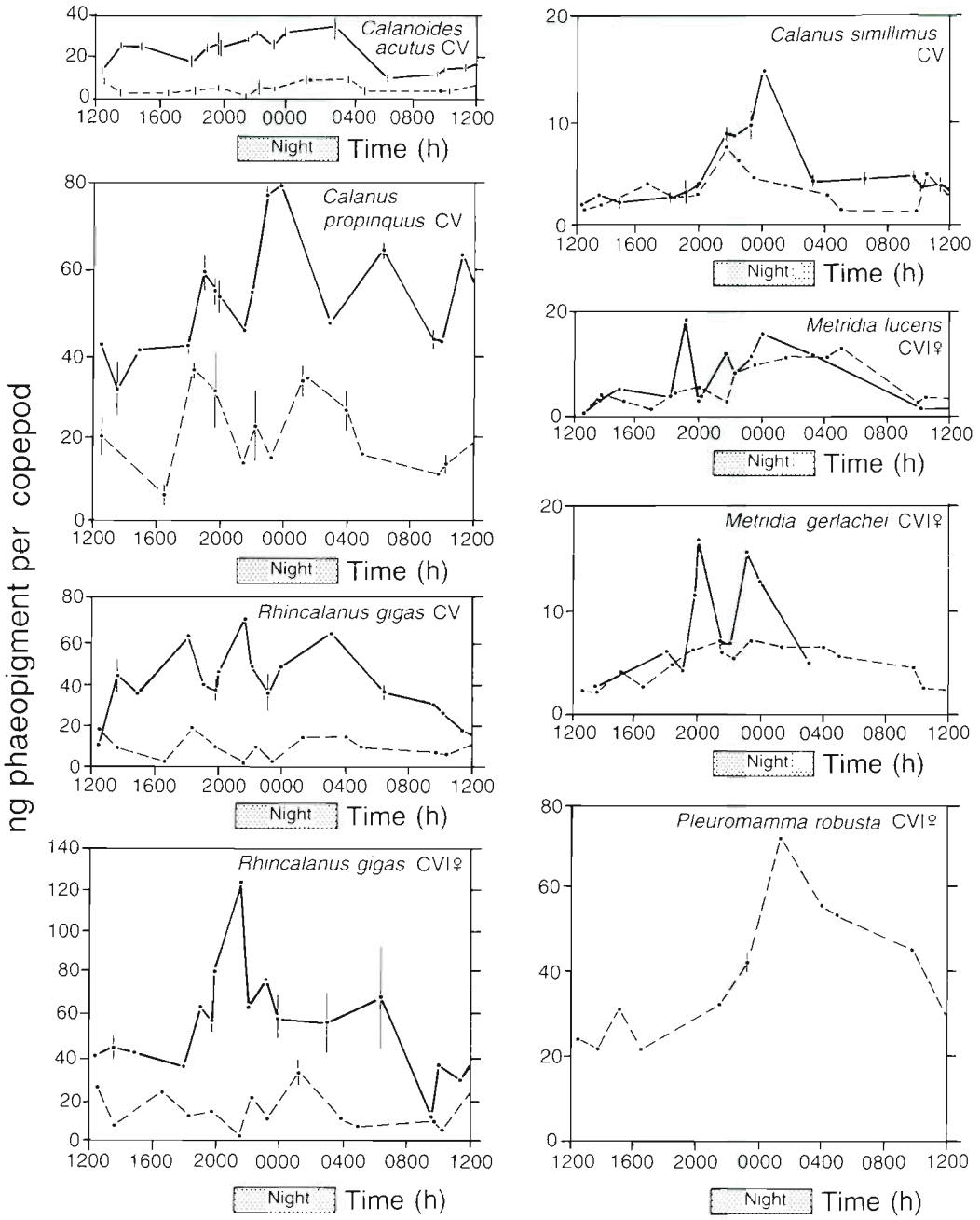

Fig. 5. Diel periodicity in copepod gut fullness, from hauls in the 0 to 70 m layer (——) and 70 to 200 m layer (– – –). Bars represent ranges between replicate batches, where these were processed

were also calculated from the incubations based on the mean clearance rate across all counted diatom taxa, rather than clearance of total chl *a* (Table 2 last column).

The calculated rations varied among the 4 experiments, with B and D providing lower values than the other two. Nevertheless, for the comparable species *Metridia* spp. CV, CVI♀, *Calanoides acutus* CV and *Calanus propinquus* CV the 2 methods gave similar mean values. For both CV and CVI♀ *Rhincalanus gigas*, however, the rations derived by the incubations were much lower than those from gut fluorescence. The rations of this species were also much lower than those of the other large copepods. This result echoes all previous studies, using either gut fluorescence or incubation methods.

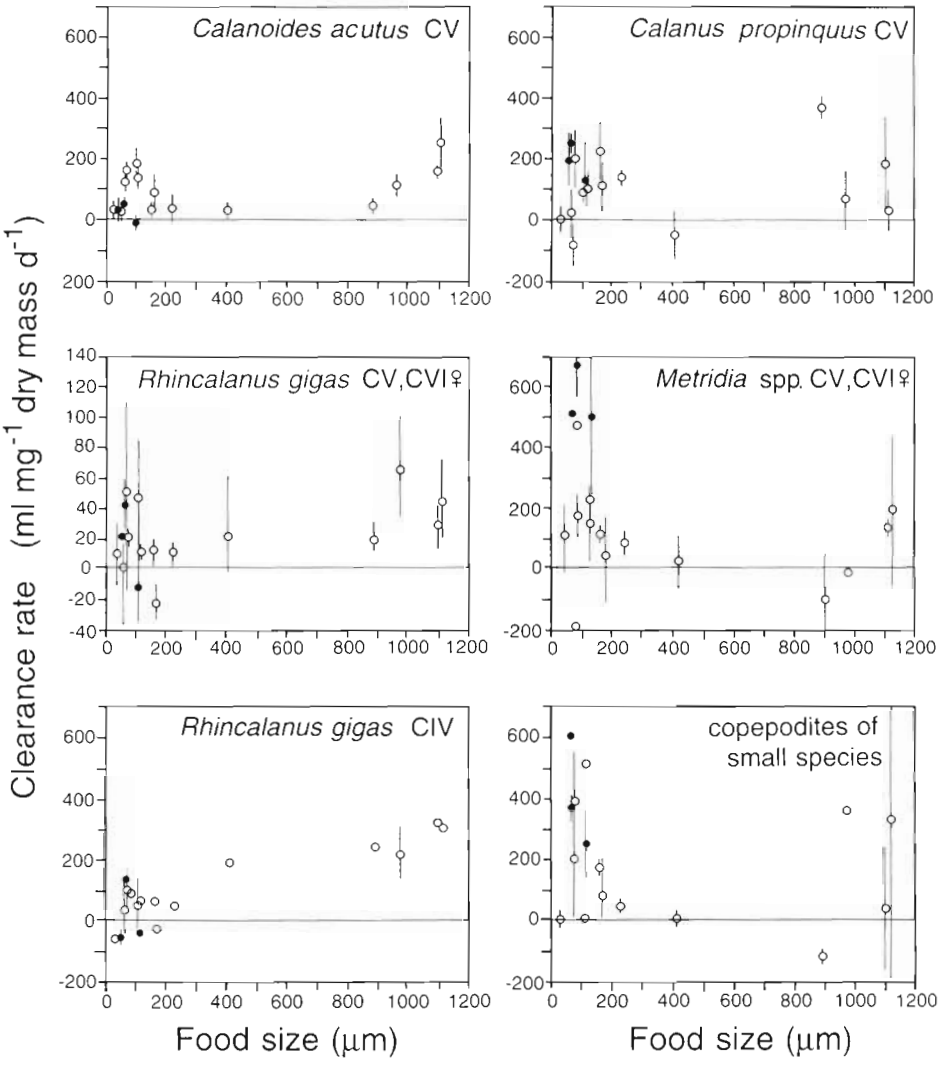

Fig. 6. Mass specific clearance rates on various food taxa, whose sizes are expressed as mean length of colony (or individual cell for non-colonial forms). Each data point represents a single food taxon in Expt A, B or D. (●): Motile taxa (dinoflagellates plus ciliates); (○) diatoms. Bars represent ranges between experimental replicates, where available. Results for *Rhincalanus gigas* CV and CVI♀ have been averaged to ease presentation

Community grazing impact

Grazing rates of zooplankters are considered to be predictable, to some extent, from their body masses (Peters & Downing 1984, Moloney & Field 1989, Morales et al. 1990). Both experimental data (e.g. Paffenhöfer 1971, Kiørboe & Sabatini 1995) and scaling considerations (Peters 1983) reveal that small organisms can have high mass specific rates of feeding and metabolism. Therefore an allometric approach was used to provide estimates of total copepod grazing which are as realistic as possible. This involved the construction of feeding rate/body mass regressions based on the copepodites whose feeding was measured, in order to estimate feeding rates of the remaining copepodites from their body mass. Allometric relationships (Table 3) were derived from the incubations only, because of the small size range of grazers monitored by gut fluorescence. Regressions were based on clearance rates on dinoflagellates and ciliates, on mean clearance across all the counted diatom taxa and on total chl *a*. The result from each grazer bottle in each experiment was used, although where calculated clearance rates were negative (Fig. 6), these values were excluded.

The total grazing impact of those copepodites incubated were obtained simply from the product of their clearance per individual and their abundance in the mixed layer, based on the mean of 7 LHPR hauls. For the remaining copepodites, individual clearance rates were estimated from body mass by the allometric equations, and these values were multiplied by their abundance. Total copepod clearance was then obtained by summation. Table 4 summarises the contributions of the various copepod groups to total grazing.

The copepodite stages which were incubated comprised 79% of total mixed layer copepod biomass but only 50 to 66% of their estimated predation/grazing impact. The large calaniid and eucalaniid species accounted for only 30% of the estimated copepod impact on motile cells, but contributed more to grazing on large diatoms (Table 4). Despite the high biomass and abundance of copepods, their impact on both the diatoms and motile taxa was <3% of the mixed layer cleared per day. The fact that the impact on the motile fraction was higher than on diatoms reflects selective feeding by some of the species (Figs. 6 & 7)

The slopes of the regressions in Table 3 (i.e. the body mass scaling coefficients) reflect the relative grazing rates of large and small copepods. Frequently quoted coefficients range from 0.65 to 0.75 (e.g. Peters 1983, Moloney & Field 1989, Kiørboe & Sabatini 1995). Both this study and previous Antarctic studies (Atkinson 1994, 1996, Atkinson & Shreeve 1995) found scaling coefficients lower than this. If the regressions were based on structural mass rather than total dry mass, however, the slope coefficients would be higher, because the lipid stores of CV and CVI stages of large Antarctic copepods greatly increase their dry masses. Paffenhöfer (1984) also pointed out that the food resource (or the portion of the diet actually assessed) will partly determine the scaling coefficient.

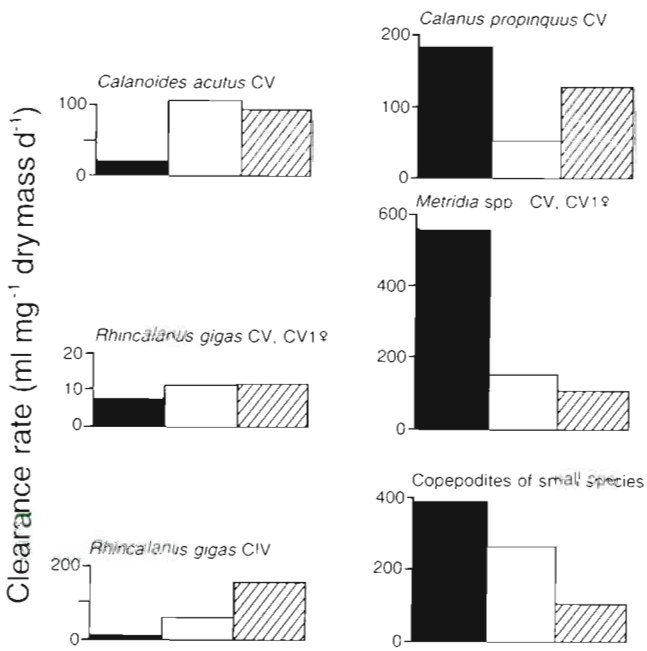

Fig. 7 Mean clearance rates of motile taxa (solid bars), diatoms of similar size range, i.e. <120 µm (open bars), and diatoms >120 µm (hatched bars)

DISCUSSION

Zooplankton response to a bloom

This study describes an atypical situation for the Southern Ocean, where a large zooplankton biomass was feeding on an intense phytoplankton bloom. A similar zooplankton biomass, 13 g dry mass m^{-2}, was found at this site in January 1990 by Ward et al. (1995). They suggested that this dry mass, 4 to 5 times higher than any other records for the Southern Ocean, reflected the productivity of the South Georgia shelf, the exact time of year of sampling and the catching efficiency of the LHPR. That *Calanoides acutus* and *Rhincalanus gigas* were benefitting from the bloom is suggested by their extensive lipid stores (Ward et al. 1996) resulting in high body masses (Table 2; cf. Conover & Huntley 1991, Hagen & Schnack-Schiel 1996). Zooplankton biomass remained high, 9.3 g dry mass m^{-2} later during the same season, based on net survey around the island in February/March (Pakhomov & Perissinotto 1996). We speculate that a degree of dependability of blooms near South Georgia, the ability of zooplankton to use them and possibly a retentive circulation pattern (Atkinson & Peck 1990) enable a high grazer biomass to build up and be maintained, in a similar way to the Gerlache Strait (Huntley & Brinton 1991).

To assess how the bloom was being utilized, we compared the rates, periodicity and selectivity of copepod feeding. Because vertical carbon fluxes could have been large, emphasis was placed on vertical distribution in relation to feeding. These topics were also studied on the previous visit to the site when the bloom was more modest, 1 to 4 mg chl *a* m^{-3} (Atkinson et al. 1992a, Ward et al. 1995). Several features are common to both visits, which gives some confidence to speculate on this system.

First, the biomass dominant copepods, *Calanoides acutus* and *Rhincalanus gigas*, had median depths near the base of the mixed layer during both studies (Fig. 3; cf. Fig. 2 in Atkinson et al. 1992a). This reflected individuals feeding (or digesting) below the chl *a* rich mixed layer. Also common to both studies is their unusual feeding cycle, from afternoon to dawn. Likewise the shallower distribution of *Calanus simillimus* and its feeding cycle are mirrored in the 2 studies. Vertical migrations were not extensive in either study, in contrast to generally greater migrations in oceanic water to the north, at lower chl *a* values (Atkinson et al. 1992b, 1996). Landry et al. (1994b) commented on this seemingly counterintuitive situation in a lower latitude study, where both feeding periodicity and diel vertical migration were less pronounced when more food was available. Predators might be impli-

Table 2. Copepods used for feeding experiments, listed in order of increasing dry mass (number of individuals weighed after the dry masses). Algal carbon rations are mean values (ranges between experiments)

Species	Stage	Dry mass (mg ind.$^{-1}$)	Algal carbon ration (% body carbon ingested d^{-1})		
			Gut fluorescence	Incubation method: total chl *a* budget, Expts A, B, C	Incubation method: mean clearance of counted diatom taxa, Expts A, B, D
Copepodites of small species		0.041 (142)	–	23 (2.7–40)	19 (4.5–32)
Rhincalanus gigas	CI	0.036 (12)	–	3.3 (0–5.4) for mixed stages CI–CIII	7.4 (6.8–8.0) for mixed stages CI–CIII
Rhincalanus gigas	CII	0.062 (54)			
Rhincalanus gigas	CIII	0.152 (71)			
Metridia lucens	CVI♀	0.120 (26)	8.4	–	–
Calanus simillimus	CV	0.137 (30)	10	–	–
Metridia gerlachei	CVI♀	0.268 (54)	6.1	7.8 (0.97–13)	9.8 (2.5–19)
Pleuromamma robusta	CVI♀	0.572 (12)	9.6	–	–
Rhincalanus gigas	CIV	0.602 (71)	–	7.5 (4.9–9.8)	11 (8.7–16)
Calanoides acutus	CV	0.650 (130)	9.5	9.6 (4.5–14)	11 (2.4–19)
Calanus propinquus	CV	1.19 (36)	12	12 (10–13)	9.6 (3.7–14)
Rhincalanus gigas	CV	1.47 (57)	7.8	2.8 (0.84–5.8)	3.2 (0.9–6.9)
Rhincalanus gigas	CVI♀	2.96 (42)	4.9	0.47 (0–0.77)	1.4 (0.54–2.8

Table 3. Regression analysis of relationships between $\log_{10}$ body mass (mg, *x*-value) and $\log_{10}$ clearance rate (ml ind.$^{-1}$ d^{-1}, *y*-value)

Food source	Slope	SE of slope	Intercept	*F* ratio	No. of data points	p
Dinoflagellates plus ciliates	0.485	0.116	1.90	17	31	<0.001
Mean of counted diatom taxa	0.647	0.107	1.64	36	40	<0.001
Total chl *a*	0.591	0.128	1.59	22	35	<0.001

Table 4. Estimated clearance of the copepod community in relation to abundance and biomass within the surface mixed layer. Clearance values are percentages, determined for the different food sources and measurement methods. The large copepods are defined as all copepodite stages of *Calanoides acutus*, *Rhincalanus gigas*, *Calanus simillimus* and *C. propinquus*

Species group	Mean no. (m^{-3})	Mean dry mass (mg m^{-3})	Percentage of surface mixed layer cleared daily		
			Dinoflagellates plus ciliates	Mean for counted diatom taxa	Total chl *a*
Species/copepodite stages incubated	1517	88	1.4	0.93	0.79
Large species only	444	95	0.89	0.87	0.65
Total copepod estimate	3785	112	2.8	1.3	1.2

cated in this, as they can force periodicity in feeding and/or migration of prey assemblages (Haney 1988, Bollens & Stearns 1992). The 1% light level in our study would have been at 15 to 30 m, using Fenton's (1991) equations for the minimum and maximum chl *a* values. Perhaps the low light levels or the abundance of large diatoms would have allowed copepods to feed in the afternoon, especially at the base of the mixed layer, with little risk of being detected by predators.

The overall gut pigment values are also in general agreement between the 2 studies. If gut evacuation rate constants are assumed to have been similar in both, the fact that gut fullness per copepodite in the present study (with >6 mg chl *a* m^{-3}) was overall no greater than in January 1990 (1 to 4 mg chl *a* m^{-3}) would imply that chl *a* was at saturating levels. The contrast between high ingestion rates and low clearance rates in this study also implies this. At lower food concentrations, comparable copepodids are capable of clearance rates (per individual) which are 2 to 3 times as high as those recorded here (e.g. Schnack 1985, Schnack-Schiel et al. 1991, Atkinson 1995). Individual ingestion rates, however, are among the highest recorded for these species (cf. Schnack 1985, Atkinson et al. 1992a, Drits et al. 1993, Pasternak et al. 1994, Atkinson & Shreeve 1995, Lopez & Huntley 1995,

Atkinson 1996). This implies that food was sufficient for rather low levels of feeding activity to provide maximal ingestion.

Considering that excess food was probably available the ~10% daily rations of calaniids seem quite low compared to those of their boreal counterparts (e.g. Ohman & Runge 1994). How realistic are they? One factor is that the lipid stores of *Calanoides acutus* and *Rhincalanus gigas* at this site were unusually high, so rates expressed on a mass specific basis tend to be depressed. Our ingestion rate estimates, as well as being at the upper end of recorded Antarctic values, are also in line with estimates for Arctic copepods during summer (Smith & Schnack-Schiel 1990). Of course the fact that our feeding rate methods agree broadly with each other and with other high latitude studies is not confirmation that they are correct; both incubations and gut fluorescence are being increasingly criticised for underestimating feeding rates. However, Barthel (1990) and Pasternak et al. (1994) have shown that cold water copepods can have low respiratory costs, allowing fairly modest food intake to suffice for growth. The few estimates of summertime respiration or egg production against which to balance our estimates are listed in Table 5. These suggest that ingestion rates during a bloom comfortably exceed normal carbon expenditure for respiration and female egg production.

Although these estimated rations may be in the right ballpark, several aspects of methodology may have conspired to make the actual carbon ingested differ from the values in Table 2. A problem with the incubations is that 'sloppy feeding' could fragment large cells, with incomplete ingestion of their contents (Roy et al. 1989). Although we did not assess this, the clearance rates on colonies were similar to those on the component cells, suggesting that fragmentation of colonies into cells was not occurring. Alternatively our gut fluorescence estimates can be criticised because neither pigment destruction nor gut evacuation rate constants were measured. Both methods could have used the wrong carbon:chl *a* ratio to convert ingested chl *a* into ingested carbon. In the absence of any direct data, a conservative value of 50 was selected, but during the bloom at this site in January 1990 the carbon:chl *a* ratio averaged 74 (Priddle et al. 1995). Choosing this value would raise all carbon rations by 50%. We stress that these carbon ingestion rates have been converted from consumption of chl *a* only; copepods preferentially selecting non-phytoplankton prey would obtain supplementary carbon. The preservation and counting procedures preclude assessments of the dietary contributions of protozoans and phytoplankton but nevertheless, heterotrophic taxa such as *Gyrodinium* spp. featured strongly in the motile cell category. Therefore, *Calanus propinquus*, *Metridia* spp. and the small

Table 5. Comparison of mean ingestion rates derived in this study with carbon expenditure for female egg production and for respiration from other studies by CV and adult females. All values are expressed on a percentage carbon basis

Reference	Notes	*Calanoides acutus*	*Calanus simillimus*	*Calanus propinquus*	*Rhincalanus gigas*	*Metridia gerlachei*
This study	Mean ingestion rate of CV and CVI♀ Chl *a* range: 6–12 mg m^{-3}	10	10	11	3.4	7.9
Ward & Shreeve (1995)	Egg production around South Georgia in January Egg carbon calculated from volume (Eq. 12 in Huntley & Lopez 1992) Chl *a* range: 0.5–6 mg m^{-3}	1.2	1.6		0.62	
Lopez et al. (1993)	Egg production in Gerlache Strait in November Chl *a* mean: 4.5 mg m^{-3}	4.5				
Kosobokova (1994)	Egg production in Weddell Sea in February > 300 mg carbon m^{-3}			2.4		
Schnack et al. (1985)	Respiration rate of CV and CVI♀ in Bransfield Strait/Drake Passage in December Chl *a* mean: 2.3 mg m^{-3}	3.8		3.0	1.8	
Pasternak et al. (1994)	Respiration rate of CV and CVI♀ in Atlantic sector Chl *a* mean: ~0.2 mg m^{-3}	3.4		2.2	1.6	

copepods, which selected these protozoans, would have rations exceeding our estimates from chl *a* consumption.

Metridia gerlachei and *Calanus propinquus* are known to be more omnivorous than *Calanoides acutus* and *Rhincalanus gigas* (e.g. Hopkins et al. 1993a, Atkinson 1995, Metz & Schnack-Schiel 1995) The former 2 species are also characterised by their different lipid storage patterns, and carnivorous feeding has been suggested as a winter survival strategy (Bathmann et al. 1993, Hagen et al. 1993, Hopkins et al. 1993b, Schnack-Schiel & Hagen 1994). Whether the diets of the 4 species differ in summer is arguable. Based on lipid compositions, Graeve et al. (1994) suggested that *M. gerlachei* was more omnivorous than *C. acutus*, with *R. gigas* between the two. However, no other evidence from any season has yet appeared to suggest that the diets of *C. acutus* and *R. gigas* are different, despite the fact that the latter has a conspicuously low ration of algal carbon. Studies during spring, summer and autumn have shown either similar diets among all 4 species (Voronina & Sukhanova 1976, Schnack 1985, Hopkins 1987) or more omnivorous feeding in *M. gerlachei* and *C. propinquus* (Hopkins et al. 1993b, Metz & Schnack-Schiel 1995). This study, and a similar one in the Bellingshausen Sea (Atkinson 1995) suggest that even during bloom conditions *C. propinquus* and *M. gerlachei* can feed more omnivorously than *C. acutus* and *R. gigas*.

Methodology could partly explain these conflicting reports. Gut content analysis, while being an *in situ* approach, suffers from inability to enumerate soft-bodied dietary items, and these far outnumbered loricate motile taxa in this study. The incubation method can be criticised for 'bottle effects' (Roman & Rublee 1980) such as differential growth or 'food chain effects' in grazed assemblages relative to controls. This is not easily controlled for, so our emphasis was to compare the responses of a variety of copepods exposed to the same food assemblage. The range of patterns seen therefore suggests differences in selective feeding behaviour between species, rather than incubation artefacts. The fact that 3 copepod taxa cleared motile taxa more rapidly than similar size diatoms, whereas 2 species did not, is plausibly explained by the ability of the former to detect prey movement remotely (Paffenhöfer 1988, Price 1988, De Mott 1990, De Mott & Watson 1991). However, Price (1988) suggested that such foods also differ in chemical signals, ease of handling, digestibility etc., any of which could elicit species-specific pre- or post-capture responses.

Although incubations in natural seawater cannot provide a mechanistic understanding of feeding, they do tell us whether copepods eat certain food items. Fig 6 shows that copepods could ingest highly elongated cells about 1 mm long, and do so when confronted with a natural mixture of food. Vanderploeg et al. (1988) came to this conclusion for a freshwater copepod, but found that it had more trouble ingesting cells which were elongated in 2 dimensions. Several studies have shown that certain large and/or spiny cells are not preferred by copepods (e.g Haq 1967, Corkett & Mc Laren 1978, Perissinotto 1992). Because large, long cells often dominate South Georgia blooms, the ability of copepods to ingest them could be important, even if they are not so nutritious, per unit volume, as motile cells.

Impact of the zooplankton community on the bloom

Was the decline in chl *a* during the study caused by zooplankton grazing? Two independent chl *a* budget methods concur that copepods cleared only 1.2 to 1.3% of mixed layer chl *a* d^{-1}, equating to <2.5% of mixed layer primary production. Not included in this estimate are small copepods which would have passed through the 200 µm mesh of the LHPR, plus pteropods and euphausiids. The small fraction was assessed by 2 consecutive pairs of hauls with 100 µm and 200 µm nets. Their additional grazing impact, estimated from length/mass regressions and the allometric equations (Table 3), would have increased the community grazing estimate by <25%. Pteropods were a conspicuous but unassessed part of the community. Perissinotto (1992) found that *Limacina* spp. near the Prince Edward Islands (Antarctic) accounted for 2 to 7% of zooplankton numbers and biomass, but an average 23% of their total grazing impact. Although inclusion of pteropods, euphausiids and <200 µm copepods would increase the estimate, even doubling it would leave the zooplankton cropping <5% of primary production.

Indeed, a simple carbon budget could rule out mesozooplankton as primary candidates for removing the bloom. Mean zooplankton biomass in the mixed layer was 0.060 g C m^{-3}, assuming carbon as 45% of dry mass. This biomass would need a daily carbon ration of nearly 300% to match the average microbial production of 0.178 g C m^{-3} d^{-1} which, at 3°C, seems an unrealistically high average for the whole community. The copepod impact on the motile taxa was higher, nearly 3% of the mixed layer population removed per day. Although turnover rates of these prey items were not measured, their slow removal by copepods suggests that other factors might have been more important in controlling their populations.

Mesozooplankton grazing impact is often low, <10% of daily primary production (Dam et al. 1993, Morales et al. 1993, Tsuda & Sugisaki 1994). Several studies,

however, have shown that high latitude zooplankton can consume a large portion of phytoplankton production (e.g. Hansen et al. 1990, Nielsen & Hansen 1995). This variability might reflect seasonal and regional shifts in the ratio between grazers and primary production (Landry et al. 1994a). Indeed the grazing impact of zooplankton near South Georgia during February/March of the same season varied from 6% to over 100% of daily primary production. (E. Pakhomov unpubl. data). This resulted from the high resident grazer biomass being exposed to a much lower biomass and turnover rate of food.

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