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Role of microplankton in the diet and daily ration of Antarctic zooplankton species during austral summer

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ABSTRACT: Predation rates of the 9 most abundant Antarctic meso- (4 copepods) and macrozooplankton (3 euphausiids, 1 hyperiid and 1 salp) species on microplankton (20 to 200 µm) were estimated using *in vitro* incubations during the fourth cruise of the South African Antarctic Marine Ecosystem Study (SAAMES IV) to the ice-edge region of the Lazarev Sea during austral summer (Dec/Jan) 1994/1995. Chlorophyll *a* concentrations during the incubations ranged between 0.187 and 1.410 µg l^{-1} and were dominated by ice-associated chain-forming microphytoplankton (>20 µm) of the genera *Nitzschia* and *Chaetoceros*. The microplankton assemblages were entirely dominated by protozoans comprised of ciliates and dinoflagellates. Densities of protozoans ranged from 1375 to 2690 cells l^{-1} Based on previously published results, meso- and macrozooplankton species generally consumed >120% of their minimum daily ration, i.e. minimum carbon uptake (MCU), when offered microplankton. Exceptions were *Euphausia crystallorophias* and *Vibilia antarctica* for which microplankton carbon contributed 68 and 30% of MCU, respectively. Microplankton carbon contributed between 17 and 24% of the total carbon requirements for the 4 copepod species examined and between 21 and 73% for the macrozooplankton. The daily rations of juveniles were, however, twice those of the adults, suggesting that the relative importance of microzooplankton to the daily ration of macrozooplankton shifts with life stage. Carnivory by metazoan grazers may, therefore, potentially reduce the high grazing impact of microzooplankton on the local phytoplankton stock.

KEY WORDS: Antarctica · Carnivory · Zooplankton · Microzooplankton

INTRODUCTION

Recent observations have shown that the role of microzooplankton (20 to 200 µm) in aquatic food webs is more important than previously thought. Microzooplankton consume a significant proportion of daily primary production (Paranjape 1990, Froneman & Perissinotto 1996, in press, for review see Pierce & Turner 1992) and are important agents in nutrient regeneration (Probyn 1987, Goeyens et al. 1991). In addition to these roles, microzooplankton are considered to be an important source of carbon for larger zooplankton (Stoecker & Capuzzo 1990). Since microzooplankton consume bactivorous flagellates, they may be regarded as important trophic intermediaries between bacterioplankton and larger meso- and macrozooplankton (Gifford & Dagg 1988, 1990). On the basis of these observations, the classical paradigm of pelagic food webs simply composed of diatoms, copepods and fish has been revised (Sherr & Sherr 1984).

Microzooplankton are an ubiquitous component of the plankton assemblages in the Southern Ocean (Garrison 1991, Garrison et al. 1993) and are now recognised as major consumers of phytoplankton production (Bjornsen & Kuparinen 1991, Garrison et al. 1993, Burkill et al. 1995, Froneman & Perissinotto 1996, in press). Phytoplankton consumed by microzooplankton contribute less to particulate organic flux due to the

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close association between microzooplankton, nanoflagellates and bacteria (microbial loop) which results in the recycling of carbon in the surface waters. Thus, in regions where microzooplankton represent the most important grazers of phytoplankton production, the biologically mediated carbon flux, the so called biological pump, is inefficient (Longhurst 1991). Grazing by larger zooplankton on microzooplankton may, however, represent an important source of carbon that can potentially be transferred from the microbial loop to the long-living pool in the deep ocean.

Feeding studies of larger zooplankton in the Southern Ocean have largely used the gut fluorescence technique to estimate daily rations and grazing impact (Conover & Huntley 1991, Perissinotto 1992). Because the gut florescence technique uses chlorophyll and its degradation products as indices of feeding, the contribution of heterotrophic food items, e.g micro- and mesozooplankton, to total daily carbon intake is not measured. Consequently, the daily rations of these grazers may be substantially underestimated using this method alone. Indeed, energy budgets for the dominant Antarctic grazer *Euphausia superba* and some copepod species show that carbon derived from the grazing of phytoplankton alone can hardly meet the daily metabolic requirements (Bathmann et al. 1993, Drits & Pasternak 1993, E. Pakhomov, R. Perissinotto, P. Froneman & D. Miller unpubl., R. Perissinotto, E. Pakhomov, C. McQuaid & P. Froneman unpubl.). These data suggest that other sources of carbon are important in meeting the energy demands of Antarctic zooplankton.

Gut content analysis of the dominant grazers in the vicinity of the marginal ice zone has repeatedly shown that protozoans comprise a significant proportion of the total number of items identified (Hopkins & Torres 1989, Hopkins et al. 1993). A recent study has shown that protozoans constitute ~25% of the total identifiable items in the gut of the 2 dominant Antarctic euphausiids, *Euphausia crystallorophias* (Pakhomov et al. in press) and *E. superba* (Perissinotto et al. unpubl.), in the Atlantic sector of the Southern Ocean. These estimates are, however, likely to be gross underestimations due to the fragility of microzooplankton components (Tanoue & Hara 1986). Also, these studies do not provide any quantitative data on the grazing impact of the 2 euphausiids on microzooplankton or the contribution of these organisms to their daily energy intake.

Although several quantitative studies of zooplankton feeding on microzooplankton have been carried out in the northern hemisphere (Stoecker et al. 1987, Tiseleus 1989, Jeong 1994, Wickham 1995), few data are available for the southern hemisphere. A recent *in vitro* grazing study, conducted by Atkinson (1994), has shown that the consumption of dinoflagellates, ciliates and cryptomonads by the dominant copepods in the shelf region of South Georgia contributes a median of 43% of their total carbon uptake. Furthermore, this study has suggested that larger copepods consume microzooplankton at rates equivalent to those observed using diatoms of similar size (Atkinson 1994, Atkinson & Shreeve 1995). Small copepods, however, appear to feed selectively on motile taxa such as protozoans (Atkinson 1994, 1995). At present, no data on the grazing impact of larger zooplankton on microzooplankton are available.

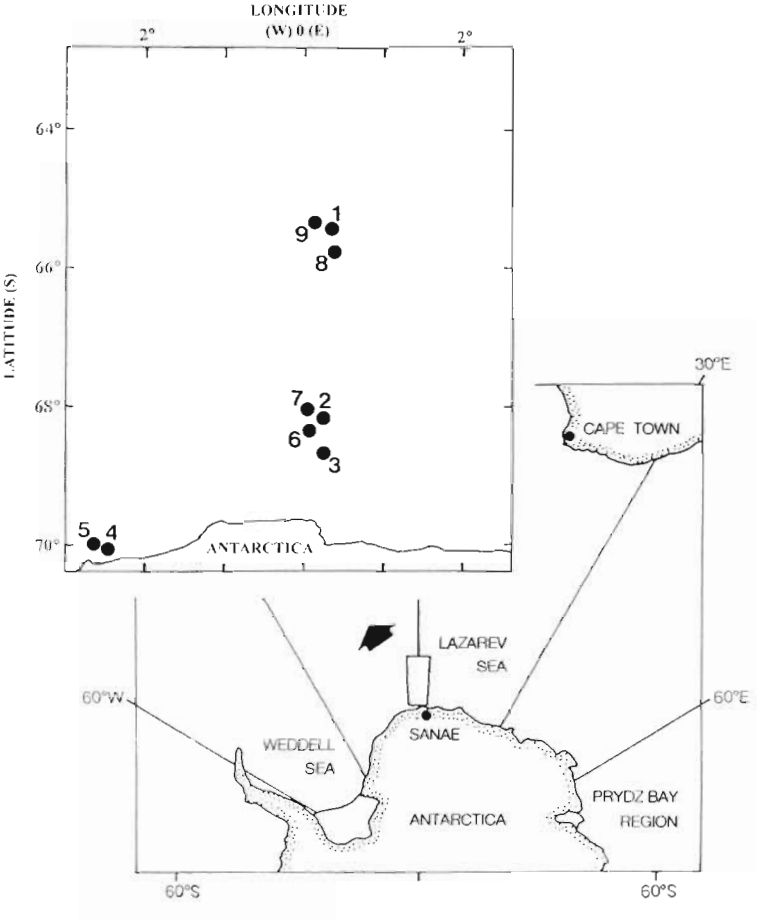

Fig. 1. Study area and inset illustrating positions of the stations where carnivory experiments were carried out during the SAAMES IV cruise to the region of the ice-edge zone of the Lazarev Sea in austral summer (Dec/Jan) 1994/1995. (1) *Euphausia superba*; (2) *Salpa thompsoni*; (3) *Thysanoessa macrura*; (4) *Euphausia crystallorophias*; (5) *Calanus propinquus*; (6) *Metridia gerlachei*; (7) *Rhincalanus gigas*; (8) *Calanoides acutus*; (9) *Vibilia antarctica*

The aim of our study is to present quantitative grazing data on the most abundant meso- and macroplankton species feeding on microzooplankton in the vicinity of the Marginal Ice Zone (MIZ) of the Lazarev Sea during austral summer 1995.

MATERIALS AND METHODS

Carnivory experiments with selected meso- and macrozooplankton on microplankton (20 to 200 µm) were conducted during the fourth South African Antarctic Marine Ecosystem Study (SAAMES IV) cruise in the MIZ of the Lazarev Sea during summer (Dec/Jan) 1994/1995 (Fig. 1). The consumption of microzooplankton was estimated employing the techniques of Gifford & Dagg (1988, 1990). The predation impact of the 5 most abundant macrozooplankton species, adult *Euphausia crystallorophias*, juvenile *E. superba*, *Thysanoessa macrura* (adults and juveniles), the hyperiid *Vibilia antarctica* (adults) and the aggregate form of the tunicate *Salpa thompsoni*, were investigated. In addition, rates of carnivory by the 4 dominant Antarctic copepod species, *Rhincalanus gigas*, *Metridia gerlachei*, *Calanus propinquus* and *Calanoides acutus*, were also measured.

Zooplankton were collected with net tows (500 µm Bongo nets) and acclimated in natural seawater for 24 h in 20 l polyethylene carboys under ambient conditions. Prior to the onset of the carnivory experiments, 6 replicate samples were prepared in 20 l polyethylene containers filled with natural seawater and allowed to stand for 2 h. According to Gifford (1993), this time period is sufficient to allow the stabilization of the plankton assemblage in the containers.

For each macrozooplankton carnivory experiment, 2 replicate samples in 20 l polyethylene carboys containing only natural seawater were used as controls. In the experimental treatments, 4 replicate samples, each containing 1 macrozooplankton individual, were used. The controls and treatments were then incubated on deck under ambient conditions for 24 h. Each container was gently stirred with a plastic spatula at 6 h intervals to prevent the settlement of plankton. The same procedure was followed in the mesozooplankton carnivory experiments, except that 3 to 8 animals (see Table 1) were incubated in 2 l polyethylene containers.

At the beginning of the experiment, two 250 ml water samples were taken from each container for the determination of initial chlorophyll *a* (chl *a*) concentration and microzooplankton species composition and abundance. This procedure was repeated at the end of the experiments to estimate the final chl *a* concentration and microplankton densities. Chl *a* concentrations were determined fluorometrically (Turner 111 fluorometer) after extraction in 100% methanol for 6 h (Holm-Hansen & Riemann 1978).

Water samples for the determination of microplankton species composition and abundance were fixed with 10% Lugol's solution (Leakey et al. 1994). Microplankton species composition and densities were estimated within 6 mo of collection using the Utermöhl settling technique after sedimentation in a 10 ml settling chamber (Reid 1983). From each sample, 3 subsamples of 10 ml, representing 30% of the total, were counted. A Nikon TMS inverted microscope operated at 400× magnification was used for this analysis. A minimum of 100 fields or 500 cells was counted for each sample. No distinction between the autotrophic and heterotrophic components of the microplankton assemblages were made. The total carbon of the microplankton fraction was estimated by calculating the mean biovolume of 50 ciliates and 50 dinoflagellates (Boltovskoy et al. 1989). The carbon biomass of the microzooplankton was then estimated assuming that 1 μm^3 = 0.19 pg C (Putt & Stoecker 1989, Sime-Ngando et al. 1992).

In all experimental treatments, meso- and macrozooplankton organisms were preserved in buffered formalin at the end of the incubation period. The dry weight of all specimens from each grazing study was determined by oven drying at 60°C for 36 h. The % carbon dry weight for each species was then estimated using the values reported in Ikeda & Mitchell (1982), Schnack (1985) and Torres et al. (1994).

The grazing impact of meso- and macrozooplankton on microplankton was estimated by employing a modification of Frost's (1972) equation:

$$F = \ln(C_c/C_g)\,V/(Nt)$$

where F is clearance rate, C_c is the final microplankton concentration in the control, C_g is the final microplankton concentration in the grazing bottle, V is the volume of the experimental container, N is the number of grazers, and t is the duration of the experiment.

The minimum carbon uptake (MCU; µg C $ind.^{-1}$ h^{-1}), representing the energy required to meet respiratory losses (Price et al. 1988), was then calculated for all the zooplankton species considered in the investigation. For *Euphausia superba*, MCU was calculated from the equation:

$$MCU = 0.452\,W^{0.97.5}$$

where W is the dry weight of an individual krill (Holm-Hansen & Huntley 1984). MCU values for the Antarctic neritic krill *E. crystallorophias* and the amphipod *Vibilia antarctica* were estimated at ~1.72 (mean value) and 1.28% of their carbon body weight per day, respectively (Ikeda & Bruce 1986). For the salp *Salpa thompsoni*, MCU was calculated assuming that indi-

viduals require ~2.57% (mean value) of body carbon (dry weight) per day (Ikeda & Bruce 1986). Finally, MCU values for the copepods and *Thysanoessa macrura* were estimated from the daily respiration rates available in the literature (Schnack 1985, Torres et al. 1994), assuming that 1 ml O_2 = 4.86 cal and 1 mg C = 10 cal (Vinogradov & Shushkina 1987).

RESULTS

Microplankton community

A summary of the initial conditions for the zooplankton grazing experiments is presented in Table 1. During the incubations, mean chl *a* concentrations ranged between 0.187 and 1.410 µg l^{-1}. Size-fractionation studies indicated that microphytoplankton (>20 µm) dominated total chlorophyll, contributing between 54 and 70% of the total. Amongst the microphytoplankton, chain-forming species of the genera *Chaetoceros* and *Nitzschia* numerically dominated the cell counts. Also well represented were large diatoms such as *Corethron criophilum*, *Rhizosolenia indica* and the silico-flagellate *Distephanus speculum*. The single most abundant diatom species during the investigation was *Chaetoceros dichaeta*, which comprised >40% of total cell counts in all the incubations. The concentration of the <20 µm chlorophyll fraction was always <0.08 µg l^{-1} and was dominated by unidentified nanoflagellates.

The microplankton (20 to 200 µm) fraction was entirely dominated by protozoans, with densities ranging from 1375 to 2690 cells l^{-1} (Table 1). Among these, aloricate (*Strombidium* sp.) forms numerically dominated with densities ranging from 750 to 1375 cells l^{-1} (size range 7.1×10^2 to 5.3×10^3 µm^3; $\bar{x} = 4.1 \times 10^3$ µm^3). Tintinnid abundances were always <100 cells l^{-1}. Dinoflagellates constituted the second most abundant group, with densities ranging between 625 and 750 cells l^{-1}. *Protoperidinium*, *Amphisolenia* and *Goniaulax* species were the main components of this group. Dinoflagellates volumes ranged from 2.5×10^2 to 5.6×10^3 µm^3 ($\bar{x} = 3.7 \times 10^3$ µm^3). Abundances of the larger protozoans, such as acantharians and foraminiferans, were <25 cells l^{-1} throughout the study. No metazoan larvae were recorded in the microplankton assemblages.

Grazing experiments

Among the copepods, feeding rates were highest for *Metridia gerlachei* and lowest for *Rhincalanus gigas* (Table 2). Indeed, analysis of variance indicates that the daily ration of *M. gerlachei* was significantly higher than those of the 3 other copepod species (F = 12.4, $p < 0.05$). The specific carbon ingestion rates for *M. gerlachei* ranged between 9.0 and 14.8 µg C ind.$^{-1}$ d^{-1} ($\bar{x}$ = 13.6 ± 5.2 µg C ind.$^{-1}$ d^{-1}), whilst for *R. gigas* the specific carbon ingestion rate ranged between 3.8 and 11.9 µg C ind.$^{-1}$ d^{-1} ($\bar{x}$ = 8.5 ± 3.1 µg C ind.$^{-1}$ d^{-1}). These rates correspond to a daily ration of between 5.7 and 13.6% body carbon ($\bar{x}$ = 9.1 ± 3.4%) for *M. gerlachei* and between 0.8 and 2.8% body carbon ($\bar{x}$ = 2.0 ± 0.7%) for *R. gigas* (Table 2).

The feeding rates of *Calanoides acutus* and *Calanus propinquus* corresponded to specific carbon ingestion rates of between 4.5 and 7.0 µg C ind.$^{-1}$ d^{-1} ($\bar{x}$ = 6.2 ± 1.4 µg C ind.$^{-1}$ d^{-1}) and between 9.8 and 11.7 µg C ind.$^{-1}$ d^{-1} ($\bar{x}$ = 10.1 ± 1.3 µg C ind.$^{-1}$ d^{-1}), respectively. These rates correspond to daily rations between 3.9 and 5.7% body carbon ($\bar{x}$ = 4.9 ± 0.9%) for *C. acutus* and between 4.2 to 6.4% body carbon (5.5 ± 0.9%) for *C. propinquus* (Table 2).

Table 1. Initial conditions of the carnivory experiments conducted using selected meso- and macrozooplankton species during the SAAMES IV cruise in the Marginal Ice Zone of the Lazarev Sea during austral summer (Dec/Jan) 1994/1995

Stn	Temperature (°C)	Zooplankton species	Total chl *a* conc. (µg l^{-1})	Microplankton densities (cells l^{-1})	No. grazers per incubation bottle
1	-1.15	*Euphausia superba*	0.709	1975	1
2	-1.27	*E. crystallorophias*	0.305	2280	1
3	-0.30	*Salpa thompsoni*	1.410	2690	1
4	-0.30	*Rhincalanus gigas*	0.907	1375	4-8
5	-1.27	*Metridia gerlachei*	0.931	1750	4-8
6	-0.86	*Calanoides acutus*	0.187	1875	4-8
7	-0.54	*Calanus propinquus*	0.215	2125	4-8
8	-1.15	*Vibilia antarctica*	0.247	1850	3-5
9	-0.59	*Thysanoessa macrura*	0.654	1675	3-5
10	-0.59	*T. macrura* (juveniles)	0.489	1800	3-5

Among the macrozooplankton species, feeding rates were highest for the tunicate *Salpa thompsoni* and lowest for the hyperiid *Vibilia antarctica* (Table 2). The specific carbon ingestion rate of *S. thompsoni* ranged between 152 and 356 µg C ind.$^{-1}$ d^{-1} ($\bar{x}$ = 232 ± 83 µg C ind.$^{-1}$ d^{-1}), corresponding to an average daily ration of 72.7% body carbon (Table 2). For *V. antarctica* the specific carbon ingestion rate during the incubations ranged from 7.8 to 11.1 µg C ind.$^{-1}$ d^{-1} ($\bar{x}$ = 9.5 ± 0.1 µg C ind.$^{-1}$ d^{-1}), corresponding to an average daily ration of ≤0.4% body carbon (Table 2).

The specific carbon ingestion rates for adult *Euphausia crystallorophias* and *Thysanoessa macrura* varied between 124 and 247 µg C ind.$^{-1}$ d^{-1} ($\bar{x}$ = 158 ± 61 µg C ind.$^{-1}$ d^{-1}) and between 83 and 149 µg C ind.$^{-1}$ d^{-1} ($\bar{x}$ = 125 ± 19 µg C ind.$^{-1}$ d^{-1}), respectively (Table 2). Based on these rates, the daily ration was equivalent to 1.2% body carbon for *E. crystallorophias*, and 1.1% for *T. macrura* (Table 2).

During the carnivory experiments conducted with juvenile *Euphausia superba* and juvenile *Thysanoessa macrura*, the specific carbon ingestion rates ranged between 50 and 301 µg C ind.$^{-1}$ d^{-1} ($\bar{x}$ = 187 ± 88 µg C ind.$^{-1}$ d^{-1}) and between 34 and 68 µg C ind.$^{-1}$ d^{-1} ($\bar{x}$ = 54.7 ± 3 µg C ind.$^{-1}$ d^{-1}), respectively (Table 2). These rates correspond to an average daily ration of 3.1% body carbon for juvenile *E. superba* and 2.3% for juvenile *T. macrura* (Table 2).

DISCUSSION

The dominance of typical ice-associated microphytoplankton species such as *Nitzschia* and *Chaetoceros* suggests that the microphytoplankton community encountered during this study may have originated from ice melt (Heywood & Whitaker 1984, Horner 1985). Dinoflagellates and ciliates numerically dominated the microplankton community, which is consistent with the results of previous studies in the MIZ (Garrison & Buck 1989, Garrison et al. 1993). Our estimates of microzooplankton biomass ranged between 24 and 34 µg C l^{-1} and are among the highest values recorded for the Southern Ocean (for review see Garrison 1991). These elevated microzooplankton abundances are likely the result of increased phytoplankton biomass typically associated with the MIZ during summer.

During this study, all species of the meso- and macrozooplankton heavily consumed microplankton despite the presence of substantial chlorophyll concentrations (Tables 1 & 2). The MCU values representing energy required to meet respiratory losses, for the species used in this investigation are shown in Table 3. From these data, it is evident that carbon derived from the consumption of microplankton contributed >120% of the MCU in most species. Exceptions were *Euphausia crystallorophias* and *Vibilia antarctica*, in which

Table 2. Summary of carnivory experiments carried out with selected meso- and microzooplankton species feeding on microzooplankton at the ice-edge zone of the Lazarev Sea during austral summer (Dec/Jan) 1994/1995. Values shown are means (±SD) for the 4 to 5 individuals in each experiment. DW: dry weight; CDW: carbon content of total dry weight; *F*: clearance rate; *I*: ingestion rate; *C*: carbon specific ingestion rate

	DW (mg)	CDW (mg)	*F* (ml ind.$^{-1}$ h^{-1})	*I* (cells ind.$^{-1}$ d^{-1})	*C* (µg ind.$^{-1}$ d^{-1})	Ration (% body C)
Rhincalanus gigas (n = 5)	0.9 (±0.1)	0.4 (±0.001)	12 (±7.7)	5 (±0.4)	8.5 (±3.1)	2.0 (±0.7)
Metridia gerlachei (n = 4)	0.3 (±0.1)	0.2 (±0.002)	7 (±2.3)	8 (±3)	13.6 (±5.2)	9.1 (±3.4)
Calanoides acutus (n = 5)	0.3 (±0.1)	0.1 (±0.001)	7 (±1.7)	6 (±1)	6.2 (±1.4)	4.9 (±0.9)
Calanus propinquus (n = 5)	0.4 (±0.2)	0.2 (±0.003)	8 (±1.7)	6 (±0)	10.1 (±1.3)	5.5 (±0.9)
Euphausia superba (juveniles; n = 8)	13.6 (±0.4)	6.1 (±0.3)	318 (±77)	624 (±301)	187.5 (±88)	3.1 (±0.2)
E. crystallorophias (n = 8)	29.9 (±1.3)	13.5 (±0.5)	133 (±53)	449 (±9)	157.9 (±61)	1.2 (±0.3)
Salpa thompsoni (n = 8)	2.4 (±0.6)	0.3 (±0.1)	253 (±26)	781 (±280)	232.6 (±83)	72.7 (±4.3)
Vibilia antarctica (n = 4)	5.1 (±1.5)	2.5 (±0.2)	6 (±2)	132 (±24)	9.5 (±0.1)	0.4 (±0.1)
Thysanoessa macrura (adults; n = 4)	23.0 (±4.6)	11.4 (±1.9)	733 (±35)	741 (±65)	125 (±33)	1.1 (±0.2)
T. macrura (juveniles; n = 2)	4.8 (±2.5)	2.4 (±1.1)	21 (±6)	206 (±63)	54.7 (±3)	2.3 (±0.4)

Table 3. Daily carbon ingestion rates expressed as % of minimum carbon uptake (MCU) for respiratory requirements of selected meso- and macrozooplankton species obtained from feeding experiments conducted within the ice-edge zone of the Lazarev Sea during austral summer (Dec/Jan) 1994/1995

	MCU (% body C d^{-1})	% MCU d^{-1}
Rhincalanus gigas	1.65	122
Metridia gerlachei	1.14	721
Calanoides acutus	3.95	155
Calanus propinquus	2.96	185
Euphausia superba	1.02	135
E. crystallorophias	1.72	68
Thysanoessa macrura (juveniles)	0.85	137
T. macrura (adults)	0.82	264
Salpa thompsoni	2.57	362
Vibilia antarctica	1.28	30

microplankton contributed only 68 and 30% of MCU, respectively (Table 3). This indicates that, with the exception of the Antarctic neritic krill and the hyperiid, all species of zooplankton examined in this study can meet their minimum metabolic requirements by feeding on microplankton. It should be noted that MCU values for the macrozooplankton were determined from the dry weight of samples preserved in formalin. No correction factors were applied to the dry weights to account for losses due to formalin preservation. This may have resulted in the over-estimation of the contribution of microplankton to the MCU of the larger zooplankton.

Among the copepods, daily rations of *Rhincalanus gigas* feeding on microplankton were the lowest recorded during this investigation (Table 2). Analysis of variance indicated that daily rations for this species were significantly lower than for the other 3 copepods ($F = 12.83$, $p < 0.001$). There is some evidence in the literature that *R. gigas* exhibits low feeding and respiration rates and has low growth efficiencies when incubated *in vitro* (Conover & Huntley 1991, Atkinson et al. 1992, Drits & Pasternak 1993). The low daily rations obtained during this study probably reflect those previously reported. The daily rations of the 3 other copepods also did not differ substantially from those reported in the literature (Conover & Huntley 1991, Atkinson et al. 1992, Atkinson 1994).

The contribution of microplankton to the total carbon ration of the 4 copepod species used in this investigation was estimated from the average daily carbon rations reported in Conover & Huntley (1991). Microplankton accounted for ~17% of the daily carbon ration in *Calanoides acutus* and *Rhincalanus gigas* while in *Calanus propinquus* and *Metridia gerlachei* the microplankton contribution was 19 and 24%, respectively. From these results, it is clear that the low daily rations of *R. gigas* reflect the normally low metabolic characteristics of this species (see above). Our estimates of daily ration, calculated by employing the average daily rations of Conover & Huntley (1991), compare well with results obtained in a recent study conducted by Atkinson (1994)

The daily ration of *Vibilia antarctica* was the lowest found during the entire investigation, corresponding to <0.5% body carbon (Table 2). Gut content analyses have shown that *V. antarctica* preferentially feeds on large crustaceans such as euphausiids (Hopkins 1985). During this study, however, the carnivory experiments were conducted in the absence of prey >200 µm. The data indicate that *V. antarctica* feeds on microzooplankton only to supplement its dietary requirements while larger prey items, such as euphausiids and copepods, are the main source of carbon for this hyperiid.

The daily ration of the juvenile *Thysanoessa macrura* was more than twice that of adults (Table 2). According to Nordhausen (1994), *T. macrura* can be considered a truly omnivorous species. Our data suggest, however, that the relative importance of microplankton in the diet of *T macrura* changes with life stage. It is of particular interest that, the daily ration of juvenile *Euphausia superba* (on average 61% of the total carbon requirement) was amongst the highest recorded during the entire investigation (Table 2). These data suggest that juvenile macrozooplankton are more efficient grazers of microplankton than adults.

In this study, the tunicate *Salpa thompsoni* had the highest specific carbon ingestion rates (Table 2). Although these rates are in the same range as those observed by Reinke (1987) and Huntley et al. (1989) within the same species, they are generally lower than those of tunicates of similar size cited in the literature (see Huntley et al. 1989). Reductions in salp clearance rates may result from bottling effects or the inability of salps to regulate their feeding rates. A recent parallel study has shown that the feeding efficiency of *S. thompsoni* decreases dramatically at chlorophyll concentrations >1 µg l^{-1} (R. Perissinotto & E. Pakhomov unpubl.). It is also worth noting that another study conducted in the Southern Ocean reported filtration rates for *S. thompsoni* ranging between 410 and 600 ml $ind.^{-1}$ h^{-1} in regions where chlorophyll concentrations were <0.6 µg l^{-1} (Drits & Semenova 1989). Using an *in situ* technique, Perissinotto & Pakhomov (unpubl.) obtained rates averaging 430 ml $ind.^{-1}$ h^{-1} for salps in the size range 1 to 5 cm length. These data suggest that the carbon specific ingestion rates obtained for the salp during this investigation can probably be regarded as conservative.

The daily rations of the macrozooplankton species used in the incubations are shown in Table 2. Assuming that all the euphausiids used in this investigation require ~5% of body carbon per day to meet their entire metabolic costs (Clarke & Morris 1983), carbon derived from the consumption of microplankton contributed 23% of total carbon requirements for *Euphausia crystallorophias* and 61% for *E. superba* juveniles. For adult *Thysanoessa macrura*, carbon derived from microplankton contributed 21% of the total while for juveniles it accounted for 45% of the total. These data clearly indicate that the consumption of phytoplankton still represented an important carbon source for both the copepods and the euphausiids during this investigation. The contribution of microplankton to total carbon requirements for the salps was, however, higher. Assuming that salps require daily ~21% of their body carbon to meet their metabolic demands, carbon derived from the consumption of microplankton would have contributed >300% of their total requirements.

The tunicate *Salpa thompsoni* had the highest daily ration of all zooplankton species investigated (Table 2). Salps have been shown to retain all particles >2 µm with almost 100% efficiency and produce compact, quick sinking faecal pellets with high carbon content. Salps are, therefore, efficient agents in transferring carbon from surface waters to depth (Fortier et al. 1994). Salps grazing on micro- and bactivorous nanoplankton may thus represent an important source of carbon that can be transferred from the microbial loop to the long-living pool. Recently, it has been shown that salp abundances in some regions of the high Antarctic have increased in response to localised warming in seawater temperature, at times dominating total zooplankton biomass (Pakhomov 1991). A recent *in situ* grazing study has demonstrated that *S. thompsoni* is able to consume up to 100% of the daily phytoplankton production (Perissinotto & Pakhomov unpubl.). Salps may, therefore, play a key role in the Southern Ocean carbon pump. In the case of the copepods, on the other hand, although they exhibited relatively high daily rations (Table 2), their contribution to carbon flux is reduced because they often re-ingest their own faecal material (Fortier et al. 1994).

It is clear that during the summer 1994/1995 microplankton represented an important source of carbon for all the meso- and macrozooplankton species studied (Table 2). These results are consistent with those obtained during similar studies conducted in different regions of the Southern Ocean (Conover & Huntley 1991, Atkinson 1994, 1995). It should be noted, however, that our estimates do not provide precise data on the contribution of heterotrophic carbon to total daily intake since some of the dinoflagellate taxa represented in the protozoan assemblages were autotrophic. Also, daily rations derived from the consumption of protozoans may have been severely underestimated since the contribution of the <20 µm (nanoplankton) component was not considered during this investigation. Studies conducted in the Southern Ocean have shown that nano-heterotrophs may comprise up to 20% of total plankton biomass (Garrison et al. 1991, Sorokin 1993). Further inaccuracies in estimates of microplankton contribution to daily ration of larger zooplankton during this study may have resulted from the experimental procedure. For example, the estimates of carbon ingestion were derived from the biovolume of microzooplankton cells fixed with Lugol's solution. Recent studies have shown that cell shrinkage in samples fixed with Lugol's solution may be as high as 25% (Leakey et al. 1994). Finally, the removal of water samples for the determination of microplankton cell counts at the onset of the incubation may have resulted in inaccuracies associated with lysis of protists or changes in feeding behaviour due to increased turbulence in the incubation chambers (Saiz et al. 1992).

Seasonal grazing rates of larger zooplankton feeding on microzooplankton are poorly documented (for review see Conover & Huntley 1991). Recent studies conducted during winter in the Weddell Sea and in early summer in the vicinity of Elephant Island (Antarctica) have shown that energy derived from the consumption of phytoplankton alone cannot meet the daily metabolic requirements of copepods (Bathmann et al. 1993, Drits et al. 1994). Alternative sources of food have been suggested to meet copepod energetic demands, including detritus and protozoans (Bathmann et al. 1993). A carnivorous feeding mode in copepods has been suggested as a possible mechanism allowing them to remain active during winter when chlorophyll concentrations are low (Atkinson 1994). Indeed, another recent study conducted in the vicinity of the Antarctic Peninsula has shown that carnivory by zooplankton probably represents the dominant trophic mode during winter (Huntley & Nordhausen 1995). Alternatively, zooplankton may utilise their lipid and protein supplies to overwinter (Hagen et al. 1993). Microzooplankton appear to represent an important carbon source for larger zooplankton in both summer and winter. The ability of metazoans to consume both autotrophic and heterotrophic prey may be a necessary adaptation to the seasonality and patchiness of food distribution in the Antarctic (Atkinson 1994). During winter, in the absence of microphytoplankton (Garrison et al. 1993), the predation impact of zooplankton on microzooplankton can be expected to increase. These shifts may have important consequences for the biological pump. Microzooplankton are recognised as major consumers of phytoplankton production in the

Southern Ocean (Garrison et al. 1993, Kivi & Kuosa 1994, Froneman & Perissinotto 1996, in press). Predation by metazoans as a consequence, may reduce the high grazing impact that microzooplankton generally exert on the phytoplankton.

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