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Feeding rates and diel vertical migration of copepods near South Georgia: comparison of shelf and oceanic sites

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Abstract. Seventeen Longhurst Hardy Plankton Recorder profiles were taken over a diel cycle in January 1990 to study the feeding of four major copepods over the South Georgia shelf. Ontogenetic changes in vertical migration were followed and feeding cycles determined by gut fluorometry for *Calanoides acutus* Stage CV, *Calanus simillimus* CV and CVI♀, *C. propinquus* CV and *Rhincalanus gigas* CV and CVI♀. In common with a neighbouring oceanic site visited two weeks later and reported elsewhere, all four species had a diel cycle of feeding and migration. The vertical distributions of *C. simillimus* (all stages), *R. gigas* (nauplii) and *Euphausia frigida* (postlarvae) were similar at both sites, the night being spent within the chlorophyll maximum at 15 to 30 m. However, the biomass dominants, *C. acutus* and *R. gigas*, dwelt below the chlorophyll maximum, about 30 m deeper than their oceanic counterparts. Unlike the oceanic site, feeding at the shelf site was not restricted to darkness, but increased 6 to 10 h before nightfall and finished at dawn; the intervening period coincided with sinking and digestion. Daylight feeding may have been induced by the shorter night, lower light levels or greater food requirements at the shelf site, despite planktonic predators being over three times more abundant. Daily ration estimates for *R. gigas* at both sites were only ~2% body carbon per day. These low values contrast with its smaller competitors, whose rations were in the range 5.6 to 27%.

Introduction

In the Southern Ocean, studies of zooplankton feeding and behaviour have been devoted almost exclusively to *Euphausia superba*. This is partly due to its high biomass and swarming behaviour, which allows exploitation by human and other higher predators. However, smaller organisms with higher turnover rates can make a proportionately greater contribution to carbon cycling (see Fenchel 1988, Boysen-Ennen et al. 1991). Large areas of the Southern Ocean are dominated by copepods (Hopkins 1971), and yet very little is known about their feeding. The work by Schnack (1983, 1985), Schnack et al. (1985, 1991), Hopkins (see Hopkins and Torres 1989), Huntley and Escritor (1991), Drits et al. (1990) and Atkinson et al. (1992) represent the few examples of feeding studies on Southern Ocean copepods. Of these, ingestion rates have only been measured by Schnack's bottle incubations.

The present study addresses feeding of copepods over the South Georgia shelf. With such a dearth of information for the Southern Ocean as a whole, it may seem premature to monitor a shelf site, as shelf seas comprise a tiny fraction of the ice-free zone and are surely atypical. However, shelves are often highly productive (El Sayed 1988); South Georgia waters are a good example, with high summer chlorophyll levels, vast flocks of seabirds (Croxall et al. 1985) and operating trawler fleets. The present paper focusses on four oceanic copepods which dominate biomass over the South Georgia shelf. Diel cycles of feeding and migration are compared (a) between species and life stages and (b) with a neighbouring oceanic site sampled two weeks later (see Atkinson et al. 1992). Daily ingestion rates are also presented for both sites.

Materials and methods

Field sampling

The shelf site (53°49'S; 38°16'W) was 20 km from the northern tip of South Georgia, in water 200 m deep, and was occupied from 6 to 10 January 1990. The sampling procedure was identical to that used at the oceanic site and involved a series of nine double oblique tows with a Longhurst Hardy Plankton Recorder (LHPR; Longhurst and Williams 1976, Williams et al. 1983). Hauls were made from the surface to 180 m every 2 to 3 h, with a 1 min gauze advance-time. This provided about 25 samples during a typical double oblique tow. Methodology is fully detailed in Atkinson et al. (1992). Simultaneous measurements of temperature, salinity, light and fluorescence were provided by an environmental logger bolted to the LHPR frame. Night-time coverage was hampered by technical problems and a fish jamming the codend, so a midnight and a midday double LHPR haul (20 and 200 μm gauzes) were included

from the following two days to improve resolution of vertical distribution. Times of net hauls are given in Table 1.

In addition to the LHPR hauls, vertical hauls were made with a 500 μm mesh, 70 cm diam, ring net from 80 m to the surface. These hauls obtained copepods for gut-evacuation experiments, in which their gut-passage times were estimated. The procedure is detailed in Atkinson et al. (1992), and involved transferring the catch to filtered seawater and obtaining subsamples at intervals over the following 3 h. These subsamples were then frozen at −60 °C for laboratory determination of gut fluorescence. High concentrations of the long diatom *Thalassiothrix antarctica* clogged several of the vertical net hauls. Our inability to separate copepods from their food caused all but one of these experiments to be aborted (see Table 1).

Table 1. Sampling times (Greenwich Mean Time) of Longhurst Hardy Plankton Recorder (LHPR) and vertical zooplankton net. Both the ascent and descent portions of each haul were analysed, except where noted otherwise ("Comments")

Date (1990) GMT (hrs)	Time of day	Net type	Comments
6 Jan.			
22.02–23.30	dusk	LHPR	
7 Jan.			
01.02–01.37	pre-midnight		
05.18–05.50	pre-dawn		ascent profile lost
07.06–07.30	early morning		
10.02–10.24	morning		
13.01–13.28	late morning		
16.02–16.26	early afternoon		
19.06–19.30	late afternoon		
22.06–22.29	evening		
8 Jan.			
16.00–16.29	early afternoon		descent profile not analysed
10 Jan.			
03.48–04.03	midnight		descent profile not analysed
8 Jan.			
17.25–17.47	afternoon	vertical net	

Treatment of samples

The gut-fluorescence method was applied, which measures fluorometrically the amount of pigments in copepods' guts. This is used as an index of recent feeding activity. To estimate ingestion rates (I), these gut-fullness values (C) were combined with laboratory estimations of passage time (t) using the equation:

$$I = C/t. \quad (1)$$

"t" was approximated as $1/k$, where "k", the gut evacuation-rate constant, comes from

$$C = C_0 e^{-kT} \quad (2)$$

fitted to the gut-evacuation data (C_0 is the initial gut pigment and C is the pigment after time T.

The frozen samples were analysed within 5 mo of collection. The procedure was to thaw each sample and sort the dominant species into 10 ml of 90% aqueous acetone at 0°C. Copepodites picked were *Calanoides acutus* CV, *Calanus simillimus* CV and CVI♀, *C. propinquus* CV and *Rhincalanus gigas* CV and CVI♀. Each copepodite stage was processed in two batches of 30 to 40 individuals where numbers on the gauze allowed. Mean numbers of individuals processed per profile for the above species and stages were 421, 32, 50, 62, 198 and 239, respectively.

The samples were homogenised and left to extract overnight at 0°C in the dark. The tubes were then shaken, centrifuged and the

Table 2. Comparison of some important characteristics of shelf and oceanic sites and differences in copepod behaviour

Characteristic	Shelf	Ocean
Time of sampling	early January	late January
Period of darkness	about 6.5 h	about 8 h
Temperature of mixed layer	2.2–2.4 °C	3.7 °C
Depth of mixed layer	50–65 m	40–50 m
Mean chlorophyll value	223 mg m^{-2}	96 mg m^{-2}
Depth of chlorophyll maximum	20–30 m	20–30 m
Microplankton composition	mainly large diatoms	dinoflagellates and smaller diatoms
Planktonic predators	abundant	about one-third as abundant as shelf
Krill swarms	present in vicinity	absent
Assumed age of CVs:		
Calanoides acutus	probably overwintered	mainly summer generation
Calanus simillimus	overwintered and summer generation	summer generation
Calanus propinquus	mainly overwintered	summer generation
Rhincalanus gigas	overwintered	mainly overwintered
Daily feeding periods	~16 h (afternoon and night)	8 h (only at night)
Depth of feeding	15–30 m and 50–70 m	15–30 m
Vertical mismatch between maxima of species abundance and their gut-fullness maxima	usually at coincident depths	fullest copepods usually below abundance maxima

fluorescence of the supernatant was read on a Shimadzu RF-540 scanning spectrofluorometer. Excitation and emission wavelengths were 428 and 668 nm, respectively, and readings were calibrated daily against acetone blanks and a refrigerated chlorophyll *a* standard. Acidification was with 2 drops of 10% hydrochloric acid. This methodology is fully described by Atkinson et al. (1992), the only difference being that sorting was done in a cold room (0 °C) rather than under ice in the laboratory. Tests on halves of the same sample showed that the two methods gave comparable results. Only the phaeopigments in the copepods were used as a tracer of feeding, following Mackas and Bohrer (1976) and Atkinson et al. (1992). These were calculated using the equations of Parsons et al. (1984). Agreement between replicates from the same sample was usually good (see Fig. 4 in Atkinson et al. 1992).

A simple zooplankton-community analysis was performed on both the ascent and descent profiles of each haul. This involved counting the copepodite stages (plus nauplii of *Rhincalanus gigas*) of the four copepod species in each sample. Other important taxa counted were postlarvae of *Euphausia superba*, *E. frigida* and *Thysanoessa* plus *Themisto gaudichaudii*, chaetognaths, fish and Stages CIV, CV and CVI of *Euchaeta* spp. (mainly *E. antarctica*).

Results

The following results refer to the shelf site, but a comparison with the oceanic site (reported in detail by Atkinson et al. 1992) is shown in Table 2.

Environment

A 50 to 65 m mixed layer (Fig. 1 a) was observed throughout the sampling, below which was a pronounced thermocline. Chlorophyll levels (Fig. 1 b) reached nearly 4 µg/litre, with three water-bottle profiles giving values of 157, 217 and 295 mg/m^2, integrated over the top 160 m. All of these had a slight subsurface maximum within the top 40 m. The chlorophyll retained on the 20 µm gauze of the fine-meshed double-LHPR achieved maximum levels at rather greater depths (Fig. 1 b). During the diel sampling period, chlorophyll levels did not vary greatly. Maximum integrated values (during the pre-midnight haul) were only 1.6 times the minimum value (during the dusk haul), and no temporal trends were apparent.

Population structure of the copepods

A detailed community analysis has been made by P. Ward (British Antarctic Survey unpublished data). *Calanoides acutus* and *Rhincalanus gigas* together comprised 68% of the copepod dry weight. All four copepod species were earlier in their developmental cycle than at the oceanic site, which was sampled two weeks later. *C. acutus* was dominated by Stage CV, presumed to be the overwintered stock; *Calanus simillimus* and *C. propinquus* had bimodal age structures, with modes of younger and older copepodites presumably comprising the summer and overwintered generations, respectively. *R. gigas* was dominated by Stages CV and CVI (overwintered) with nauplii and Stage CI of the summer generation also present.

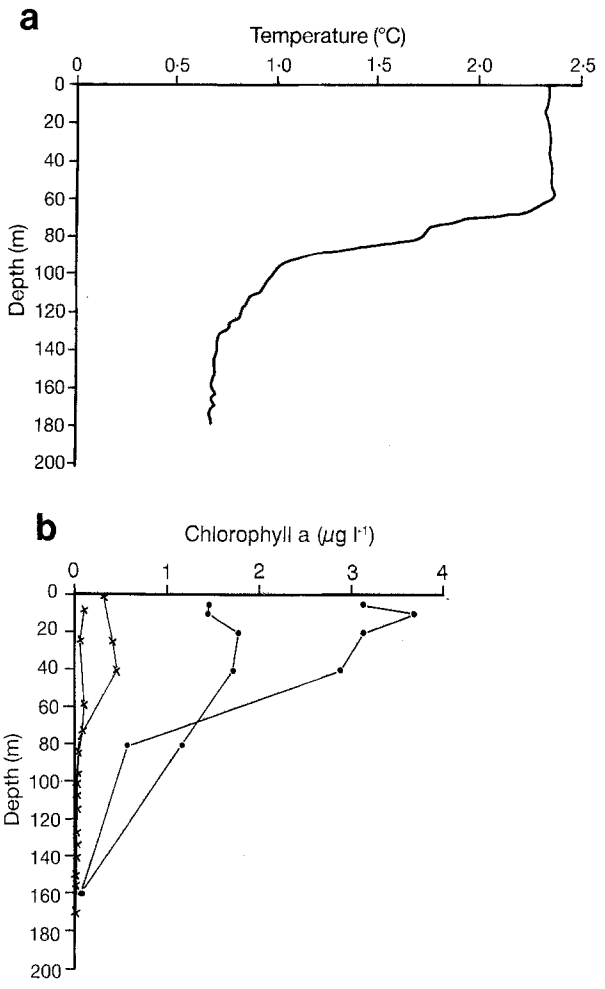

Fig. 1. (a) Temperature profile obtained during first haul of 24 h series; (b) profiles of chlorophyll *a* obtained by high-performance liquid-chromatography analysis of unfiltered water samples (•) and 20 µm-mesh double LHPR samples (×), assuming 100% filtration

Vertical distribution

With only five night-time profiles available, we were forced into a simple day/night comparison of median depths of the copepodite stages (Fig. 2). Calculations of median depths and pooling of data can obscure important aspects of vertical distribution. The following conclusions are therefore a cautious consensus, supported by the majority of individual profiles.

The four copepod species

During the day, the vertical pattern of all four species was similar to that at the oceanic site, with younger copepodites tending to live at shallower depths than the older stages (Fig. 2). The species also showed a similar daytime separation in depth, following the order (for CV, from shallowest to deepest): *Calanus simillimus*, *Rhincalanus gigas*, *Calanoides acutus*, *Calanus propinquus*. However *Calanoides acutus* and *R. gigas* resided mainly within the top of the thermocline, 20 to 30 m deeper than at the oceanic site.

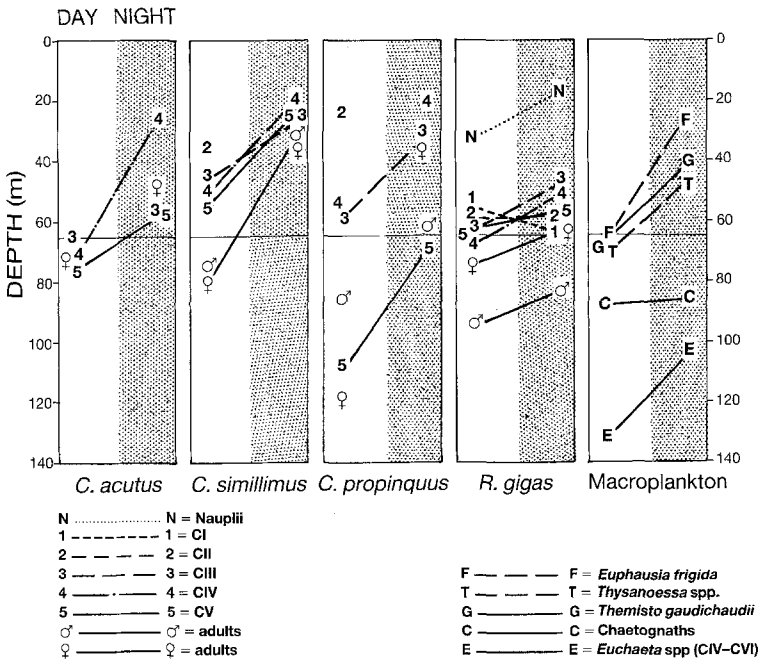

Fig. 2. Median depths of four copepods and their abundant predators and competitors. Their daytime and night-time depths are compared by averages of the medians of 13 daytime and 6 dusk or night-time profiles (see Table 1). Lines link daytime and night-time values only where numbers were $>100\ m^{-2}$ in each. Migration was significant (Mann-Whitney test, $p<0.05$) for *Calanoides acutus* CIV, CV, *Calanus simillimus* CV, CVI, *C. propinquus* CV, CVI♀, *Rhincalanus gigas* CVI♀, *Euphausia frigida*, *Thysanoessa* spp., *Themisto gaudichaudii* and *Euchaeta* spp. Horizontal line at 65 m indicates bottom of mixed layer

All four copepod species made a vertical migration into the mixed layer at night (Fig. 2). All stages older than CII appeared to migrate, and later stages (including CVI♀ and CVI♂) displayed the largest diel change. The greater movement of later stages tended to disrupt the vertical order of life stages observed in the daytime (Fig. 2); a result which parallels the situation at the oceanic site.

Fig. 3a presents the diel changes in depth of the six copepodite stages measured for pigment contents. Migration amplitude was greatest in *C. propinquus* and *Calanus simillimus*, and their ascent was gradual, taking about 8 h to complete. The descent of all four species was also gradual, starting before dawn and lasting until mid-morning. For *Calanoides acutus* and *Rhincalanus gigas*, afternoon depths appeared to be shallower than morning depths, implying an ascent during the daytime.

Macroplankton

As at the oceanic site, chaetognaths and *Euchaeta* spp. remained below the herbivorous copepods throughout the day (Fig. 2) *Euchaeta* spp. showed a cohesive night-time ascent, whereas chaetognaths did not. The diel migration of *Themisto gaudichaudii* was similar at both sites but, like the copepods, this species was consistently 20 m deeper over the shelf. Its vertical distribution did not correspond to that of any particular prey group. During the day it was generally dispersed throughout the water column but at night tended to concentrate within the top 10 to 20 m. Fish were rare in the samples; usually fewer than four larvae per profile.

Diel feeding activity

The diel change in gut pigments of the six species/stages is shown in Fig. 3b. A feeding rhythm is evident in all, except possibly *Rhincalanus gigas* Stage CV. Gut pigments were lowest around late morning and feeding began to increase around midday (15.00 hrs Greenwich Mean Time). Daytime feeding is supported by the pigment levels in the copepods from the afternoon vertical net haul (Fig. 4). Gut contents increased throughout the afternoon and evening, and for *Calanus simillimus* and *C. propinquus* this coincided with an afternoon ascent. The timing of maximum recorded gut content varied with species, and for 5 of the 6 stages there were two maxima. This, together with the long period between midday and dawn, would strongly suggest two distinct feeding periods. However, the spacing of our samples makes this rather speculative. The decrease in gut contents between dawn and midday coincides with sinking of the copepodites.

The fullest copepods tended to be sited within the stratum in which they were most abundant. An exception to this was *Calanoides acutus*; in half of the profiles, the fullest individuals of this species occurred *below* the abundance maximum. This type of mismatch was much commoner at the oceanic site, where it was postulated to be due to sinking after asynchronous feeding bouts (Atkinson et al. 1992).

Gut-passage times

Gut-evacuation rates for CVs of *Calanoides acutus* and *Rhincalanus gigas* are compared in Fig. 4. During this afternoon experiment the decrease was assumed to be exponential over the first hour (see Eq. 2 in "Materials and methods"). Gut-passage time estimates of *C. acutus* CV, *R. gigas* CV and *R. gigas* CVI♀ were 24 min, 4 h 17 min and 1 h 29 min, respectively. These values were obtained from the first hour of the experiment in order to reduce the effect of hunger on pigment kinetics.

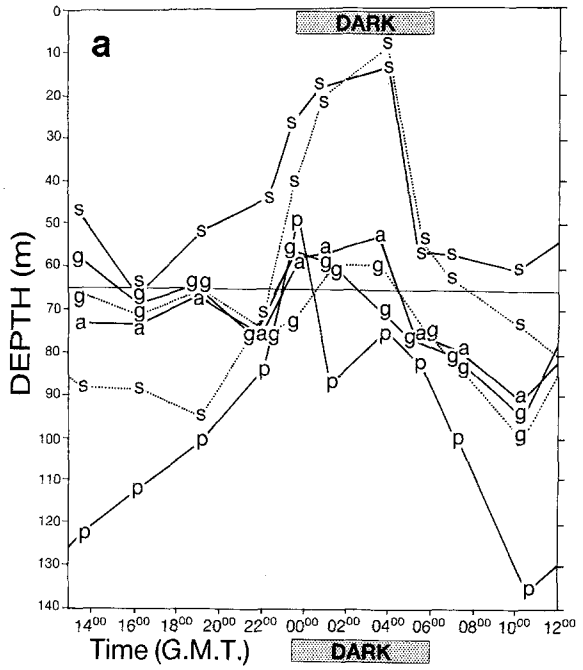

Fig. 3. (a) *Calanoides acutus*, *Calanus simillimus*, *C. propinquus* and *Rhincalanus gigas*. Median depths of six copepod species/stages measured for gut pigment content; depths are average of ascent and descent of each haul, where available (see "Comments" column in Table 1). (b) Diel changes in gut content of copepods within top 175 m. a——a = *Calanoides acutus* CV, s——s = *Calanus simillimus* CV, s·····s = *Calanus simillimus* CVI♀, p——p = *Calanus propinquus* CV, g——g = *Rhincalanus gigas* CV, g·····g = *Rhincalanus gigas* CVI♀

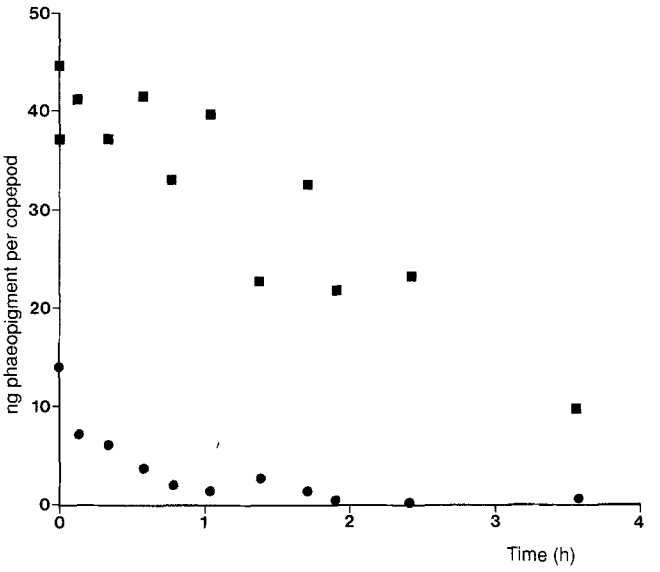

Fig. 4. *Calanoides acutus*. (●) and *Rhincalanus gigas* (■). Comparison of gut evacuation of CVs

Discussion

Feeding rates and grazing pressure

Grazing rates are presented for both the shelf and oceanic sites in Table 3. Ingestion rates are here calculated as the hourly mean gut content divided by the passage time (see Eq. 1 in "Materials and methods"). However, as Head (1986) and Penry and Frost (1990) have pointed out, this assumes a steady state situation (known not to apply to copepod feeding) and that passage time does not vary. For copepods with feeding rhythms, the variation in gut fullness, gut-passage time and extent of pigment destruction are difficult to simultaneously assess. Our 2 to 3 h spacing of hauls is at the limit of resolution of changes in gut pigments; a diel cycle of gut-throughput experiments is also needed to fully document feeding rates. The values in Table 3 are therefore best estimates, but nevertheless they outline some interesting points.

First, the guts of the copepods were on average fuller at the shelf site (Table 3, Column 2). This resulted partly from the longer feeding period (at least 16 h vs 8 h); however, their maximum pigment levels were also greater. Total daily consumption by *Calanoides acutus* CV plus *Rhincalanus gigas* CV was about twice that at the oceanic site (Table 3, Column 5). Chlorophyll *a* concentration at the shelf site was also about double that at the oceanic site (Table 2).

Second, the weight-specific ingestion rates varied between species. This is summarised for both sites in Table 4. Gut fullness, gut-passage times and ingestion rates of *Calanoides acutus* and *Calanus simillimus* are broadly in line with summer values from northern boreal and arctic waters (see Smith and Schnack-Schiel 1990, Morales et al. 1990); However, at both sites the values for *Rhincalanus gigas*, the largest epipelagic copepod in the Southern Ocean, are conspicuously low. Other indications that the overall metabolism of *R. gigas* may be slow are its low ingestion rates from the bottle incubations of Schnack et al. (1985), who reported 2 to 6% of body carbon per day. Its life cycle also differs markedly from the other large species, since it spawns late in the year and possibly has a 2 yr life cycle (see Marin 1988, Atkinson

Table 3. *Calanoides acutus*, *Calanus simillimus*, *C. propinquus* and *Rhincalanus gigas*. Estimation of phaeopigments ingested under 1 m^2. Values for the shelf are given, with those for oceanic site in parentheses. Ingestion rates (I) can only be calculated when gut passage times (t) are known. These have been taken from only one experiment (shelf) or averaged from three experiments (oceanic site; Atkinson et al. 1992). –: no data

Species/stage		Mean pigment content/copepod (C) throughout day (ng)		Mean gut passage time, t (h)		Meanly daily ingestion rate/copepod $I = C \cdot 24/t$ (ng/d)		Daily pigment consumed within top 190 m ($I \cdot 10^{-3} \times$ no m^{-2}) (µg)	
	[1]	[2]		[3]		[4]		[5]	
Calanoides acutus	(CV)	12.6	(6.29)	0.39	(0.94)	775	(160)	892	(215)
Calanus simillimus	(CV)	2.54	(3.04)	–	(0.89)	–	(82)	–	(180)
	(CVI♀)	6.96	(–)	–	(–)	–	(–)	–	(–)
Calanus propinquus	(CV)	31.4	(21.9)	–	(–)	–	(–)	–	(–)
Rhincalanus gigas	(CIII)	–	(2.33)	–	(1.1)	–	(51)	–	(55)
	(CV)	32.7	(12.1)	4.3	(1.2)	182	(243)	258	(353)
	(CVI♀)	34.3	(15.6)	1.5	(–)	549	(–)	673	(–)

Table 4. *Calanus simillimus*, *Calanoides acutus* and *Rhincalanus gigas*. Comparison of daily rations of three species, arranged in order of increasing body size. These estimates are percentages of body carbon ingested per day, and are calculated from Column 4 in Table 3 with dry body weight estimated from material obtained on a previous cruise (P. Ward unpublished data). The calculations are conservative, assuming (i) that body carbon comprises 50% of copepod dry weight; (ii) that daily phaeopigment weights are multiplied by 1.51 to provide equivalent chlorophyll ingested; (iii) that the carbon chlorophyll ratio is 30. nd: no data

Species/stage	Mean body dry wt (mg/individual)	Daily food ration (%)	
		shelf site	oceanic site
Calanus simillimus (CV)	0.062	nd	12.0
Calanoides acutus (CV)	0.257	27.0	5.6
Rhincalanus gigas (CV)	1.12	1.5	2.0

1991). *R. gigas* therefore seems atypical, and may be of less trophic impact during summer than its high biomass would suggest. The low ingestion rates of *R. gigas* fit the surmise of Morales et al. (1991) and others, that large species can dominate biomass but smaller ones may dominate carbon turnover. However, there is the possibility of detritivorous or carnivorous feeding; neither is detected by the gut-fluorescence method.

Vertical separation, migration and feeding

Figs. 2 and 3, as well as our unsummarized data, suggest two separate groups of species over the shelf. The lower group comprised the dominant biomass copepods *Calanoides acutus* and *Rhincalanus gigas*, which were both present at similar depths (around the top of the thermocline) during their feeding period. The other group was then 20 to 30 m shallower in the chlorophyll maximum, and was comprised of *Calanus simillimus* (all stages), *R. gigas* (nauplii) and *Euphausia frigida*. This vertical separation contrasts with the situation at the oceanic site, where all the feeding herbivores were concentrated at a similar depth.

Active feeding of species located within the chlorophyll maximum is expected, so why were *Calanoides acutus* and *Rhincalanus gigas* feeding at depth in chlorophyll levels which were only three-quarters that of the maximum? Indeed where vertical displacements from the chlorophyll maximum occur, the zooplankton are usually above it, feeding within the production maximum (e.g. Roman et al. 1986, Harris 1988). Two explanations are plausible:

First, they might have been exploiting different food from the upper group. In vitro feeding experiments at this site (our unpublished data) suggested that CVs of *C. acutus* and *R. gigas* fed mainly on large diatoms. The phytoplankton retained on the 20 µm mesh of the double LHPR was much sparser than that from unfiltered bottle profiles (Fig. 1 b), but its maximum was rather deeper. A feeding separation would parallel the situation recorded by Boyd et al. (1980) off Peru. These authors found that *Eucalanus* spp. tended to feed at depth (apparently on detritus) during the daytime, whereas *Calanus chilensis* and *Centropages brachiatus* had daytime and night-time feeding patterns, respectively, within the surface layer.

Second, predation could have forced the copepods deeper. Feeding occurs during the day as well as at night, and the predators *Themisto gaudichuaudii*, chaetognaths, and *Euchaeta* spp. were each about three times more abundant than at the oceanic site. Predation pressure may therefore have been greater, and deeper feeding could have been in order to reduce detection. The 1% irradiance depth was 48 m (calculated from mean chlorophyll values: N. Fenton, B.A.S, unpublished data). Therefore the daytime feeding of *Calanoides acutus* and *Rhincalanus gigas* at 50 to 80 m would have been at very low light levels, especially as it was foggy on the afternoon of sampling.

That feeding increased at least 8 h before darkness is an unusual aspect of this study. The majority of reported feeding rhythms are unimodal, with feeding starting around dusk (e.g. Dagg et al. 1989). Initiation of feeding

well before dark is rare (Head et al. 1985, Head and Harris 1987, Daro 1988). With the exception of the work of Head and Harris, short nights characterised these studies, so daytime feeding may be necessary for sufficient food intake. It may also allow time for a bimodal feeding rhythm to develop, enabling restoration of gut epithelial cells between feeding bouts (Nott et al. 1985). Another possible advantage in starting feeding before darkness may be enhanced quality of food (Enright 1977). Against these benefits must be weighed increased visibility to predators.

Conclusions

There were some notable similarities between the two sites. Both were characterised by a cycle of feeding and migration of the four copepods. Ontogenetic development of diel migration was similar. Ingestion rates of *Rhincalanus gigas* were low at both. Table 2 summarizes the main differences between the two sites. The physical/biological environment differed between the two, and the oceanic site was sampled slightly later, so it is hard to deduce which factors cause the differences in feeding behaviour. For example, the long feeding period over the shelf could have been forced, despite abundant predators, by high energy requirements of copepods prior to spawning. Equally it might be a simple response to greater availability of food.

A concensus is being reached that, in both marine and freshwater environments, predation has had a large influence on the evolution of diel behaviour (see Frost 1988, Gliwicz and Pijanowska 1988). Predation pressure is particularly difficult to study in the sea, and few studies to date even mention predators. A way forward in understanding diel cycles might be to progressively cover a larger number of sites, giving the herbivores, their food and predators equal attention.

The above approach, using the gut-fluorescence method has the advantage of leading to an understanding of behaviour. However, to measure rates of feeding in the Southern Ocean this has two serious drawbacks. First, there is growing doubt over quantitative aspects of the gut-fluorescence method (Lopez et al. 1988, Dam et al. 1991) and validity of gut-evacuation experiments (cf. Peterson et al. 1990 and Penry and Frost 1990 with Head 1988 and Ellis and Small 1989). Second, the Southern Ocean is unusual in that it is not overwhelmingly dominated by large copepods. Swarms of euphausiids, salps and small copepods are locally important, and studies elsewhere have stressed the potential importance of microplankton to carbon turnover (see Fenchel 1988). The spectrum from krill to ciliates requires different methodologies, each possessing unknown and potentially large errors. Simultaneous measurement and comparison of rates between groups is logistically difficult and subject to numerous errors.

An alternative approach towards community feeding rates might be to directly estimate total grazing using sediment traps, bottle casts and biomarkers (Welschmeyer et al. 1984, Welschmeyer and Lorenzen 1985) and simultaneously monitor species abundance and behaviour. This approach, if applied to patchy environments with contrasting grazers, could eventually reveal the contribution of individual taxa to total grazing.

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