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Omnivory and feeding selectivity in five copepod species during spring in the Bellingshausen Sea, Antarctica

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Copepod grazing experiments were undertaken along a transect of five stations in the Bellingshausen Sea during austral spring. The stations spanned unproductive, nanoflagellate-dominated waters under pack ice to an open water bloom of large diatoms in the north. The feeding habits of five dominant species were compared by incubating them in natural sea water. Feeding rates on individual food taxa were calculated from optical cell counts. The larger species (*Rhincalanus gigas*, *Calanus propinquus*, and *Calanoides acutus*) tended to eat larger cells than did *Oithona* spp. and *Metridia gerlachei*, and cleared cells up to 100–200 μm in length with increasing efficiency. Their clearance of longer cells remained high. *Oithona* spp. was the only species with high clearance rates on cells smaller than 10 μm. Clearance rates on elongated cells were compared with those of shorter and fatter cells of similar volume. The longer cells were eaten at higher rates in 65% of comparisons, suggesting that cell elongation did not protect against ingestion by large copepods. Clearance rates of motile cells were compared with those of non-motile diatoms of similar size and shape. The copepods ranged widely, with *Oithona* spp. at one extreme, ingesting motile cells almost exclusively. *M. gerlachei* and *C. propinquus* showed a preference for motile taxa compared with similar sized diatoms. The fact that the motile fraction comprised an array of taxa (nanoflagellates, dinoflagellates, and ciliates), all with a tendency to be cleared more rapidly than diatoms by the above three species, suggests that they were using mechanoreception to detect prey. *Oithona* spp., *M. gerlachei*, and *C. propinquus* were actively feeding under the ice before the bloom, in low productivity waters characterized by a nanoflagellate community and a high inorganic detritus content. The selection for motile taxa persisted, by *M. gerlachei* at least, into the bloom, even though motile cells comprised only a small fraction of available carbon at that time. *C. acutus* and *R. gigas* by contrast, migrated to the surface layers to start feeding on the bloom. These two species appeared to have fed indiscriminately on both motile and non-motile taxa. The contribution of motile taxa to copepod diets depended on their contribution to the overall food source, the extent of motile/sessile selection, and also on their size and shape relative to the diatoms. Consequently the proportion of motile taxa in copepod diets ranged from 100% (*Oithona* spp. before the bloom) to 3% (*R. gigas* during the bloom).

Key words: Bellingshausen Sea, copepods, omnivory, selective feeding, Southern Ocean.

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Introduction

Evidence is increasing that oceanic copepods often graze only a small fraction of daily primary production (e.g. Morales *et al.*, 1991, 1993; Dagg *et al.*, 1993). In several habitats, protozoans have been either directly or indirectly identified as the major grazers (Turner and Granéli, 1992; Tsuda *et al.*, 1989; Frost, 1993). Nevertheless, copepods have a potential role, through selective grazing, in shaping the species composition of microplankton (Granéli *et al.*, 1993; see Banse, 1992). For example, they may eat protozoan grazers as well as primary producers (e.g. Kleppel *et al.*, 1988; Turner and Granéli, 1989; Gifford, 1993a; Stoecker and Egloff, 1987; Fessenden and Cowles, 1994). Copepods may thus act on microplankton as "herbivorous grazers" and as "top predators", the relative balance depending on whether copepods are indiscriminate feeders (e.g. Huntley, 1981; Turner and Tester, 1989; Tiselius, 1989) or tend towards carnivory (Landry and Fagerness, 1988; Turner and Granéli, 1992). Carnivorous feeding provides a source of nutrition for the copepod that is not detected by the most commonly used study approaches based on chlorophyll assays. Studying

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Table 1. Station positions and environment along transect in Bellingshausen Sea.

Station, latitude	Date	Extent of ice cover	Temperature of mixed layer	Depth of mixed layer	Chlorophyll *a* in incubation water ng l^{-1}
G (70°17′S)	15/11/92 to 18/11/92	Solid pack	−1.8°C	(>100 m)	52
H (70°15′S)	29/11/92	Solid pack	−1.8°C	(>100 m)	107
I (69°39′S)	1/12/92 to 2/12/92	Ice edge	−1.8°C	70 m	174
J (68°18′S)	4/12/92 to 5/12/92	Ice-free	−1.3°C	50–70 m	894
K (67°41′S)	7/12/92 to 9/12/92	Ice-free	−1.0°C	50–70 m	3244

selective feeding in copepods is therefore a prerequisite to quantifying their food intake and to understanding population dynamics and species composition of the microplankton.

That copepods eat protozoans and micrometazoans as well as autotrophs is now well known, from gut contents analysis (e.g. Turner, 1991; Øresland and Ward, 1993; Hopkins *et al.*, 1993a, b) and from feeding experiments (e.g. Landry, 1981; Stoecker and Egloff, 1987; Gifford, 1993a). Indeed, protozoans are often numerous (Garrison, 1991), highly nutritious (Stoecker and Capuzzo, 1990), and within the size range on which copepods can graze (Berggreen *et al.*, 1988). However, whether copepods ingest protozoans selectively or indiscriminately is a more open question. Gut content analysis suffers from being only semi-quantitative and from not representing athecate taxa, which often dominate the protozoan community but are unrecognizable in copepod guts. Alternatively, both incubation methods and film observation can be criticized for not mimicking the natural environment.

The question of selective grazing was considered on a cruise of RRS "James Clark Ross" in the marginal ice zone in the Bellingshausen Sea, Antarctica. Feeding experiments were completed along a five-station transect out of the ice during early spring (November/December 1992). The copepods were incubated in natural sea water and uneaten food items were counted under a microscope before and after the experiments. This enabled feeding rates on individual taxa to be determined. The distinction between protozoans and autotrophs is not clear-cut, so the approach in this study was to classify cells as motile (i.e. free-swimming) or non-motile, rather than as animal or plant. This is a more natural distinction, easier to make, and addresses the question of whether copepods might have been using mechanoreception to detect prey movement remotely. Because food selectivity is also dependent on cell size, shape, and taste (see Price, 1988) a range of motile and non-motile taxa (nanoflagellates, dinoflagellates, ciliates, and diatoms) were enumerated and each classified broadly according to size and shape. This approach aimed to differentiate some of the attributes of a cell that might influence the rate at which it is grazed. Five copepod species were incubated, ranging in size from *Oithona* spp. (mainly *O. similis*) up to *Rhinocalanus gigas* (approximately ≈2 μg to ≈1750 μg range in adult female dry mass). With several copepod species simultaneously exposed to natural assemblages of diverse food types, some comparative questions could be addressed on their feeding behaviour: (1) Were the species capable of feeding on particles across the full size range of food (6 μm to 600 μm) which was measured? (2) Did the species differ appreciably in the sizes of food which they ate? (3) Were elongated cells eaten at different rates to more spherical cells of a similar volume? (i.e. does cell elongation provide a refuge from predation?) (4) In comparisons of cells of similar size and shape, did any of the copepods select motile taxa, rather than non-motile diatoms?

Materials and methods

Copepod feeding experiments were conducted at five stations on a transect along 85°W out of the ice in the Bellingshausen Sea in austral spring 1992 (Table 1). The copepod community and their overall feeding activity at these stations is described by Atkinson and Shreeve (1995). The environment, zooplankton/phytoplankton relationships, and microzooplankton composition and grazing are covered respectively by Turner and Owens (1995), Robins *et al.* (1995) and Burkill *et al.* (1995).

Copepods for feeding experiments were obtained from slow, vertical hauls with a 70 cm ring net (mesh size 200 μm) from either 50 m or 100 m to the surface. Undamaged and actively swimming individuals were sorted from the diluted contents of the 5 l solid codend and placed in 1.2 l bottles of unscreened surface sea water. The predominant species in the catches were selected for incubation (Table 2). The seasonal migrants, *R. gigas*, *Calanoides acutus* and *Metridia gerlachei* were rare in the surface layer prior to the bloom, which

Table 2. Species and stages used in grazing experiments, listed in descending order of mean body mass. Numbers of jars incubated per experiment are listed under each station.

Species	Stage	Mean drymass (μg individ.)$^{-1}$	Mean no. l^{-1}	Station G	H	I	J	K
Rhincalanus gigas	CVI♀	1507	5	—	—	—	2	2
Calanus propinquus	CVI♀	902	3	1	2	1	2	2
Calanoides acutus	CVI♀	532	7	—	1*	—	2	1
Metridia gerlachei	CVI♀	183	8	—	—	2	3	1
Oithona similis	>70% CVI	2.15	81	2	2	1	—	—

*CV and adults incubated together, but they did not feed.

tended to preclude their use in grazing experiments at stations G, H, and I. Difficulties in shipboard identification precluded separation of living *Oithona* spp. into species and stages. These were confirmed by subsequent analysis to comprise over 70% of adult females of *O. similis*, the remainder being their late stage copepodites and those of its larger congener *O. frigida*. Unfortunately, *Oithona* spp. could not be incubated at the two bloom stations because it was nearly impossible to separate them from numerous large diatoms and small metazoans in the catches.

Natural sea water was used as the food medium. This was collected from the surface with a clean plastic bucket, 1–3 h before the start of each experiment. Its chlorophyll content was obtained by filtering 1 l under gentle vacuum onto a GF/C filter. Filters were then frozen (−60°C) and chlorophyll *a* content measured by the fluorometric method (Parsons *et al.*, 1984) using a Shimadzu RF 540 Scanning Spectrofluorometer. These surface values (Table 1) are broadly in line with surface values from HPLC profiles (R. Barlow, unpublished cruise report). Barlow's chlorophyll profiles show that subsurface maxima were either slight or non-existent, so the incubation water was a reasonable representation of food available in the mixed layer.

All experiments were set up at midnight, after the copepods had acclimated in the 1.2 l bottles of ambient sea water for ≈18 h. The incubation water was mixed with a plastic plunger in an acid washed 50 l carboy and transferred to 2.4 l glass grazing jars. It was not prescreened, to reduce mortality of delicate aloricate ciliates (Gifford, 1993b) and to retain long filamentous and spiney diatoms, which were being tested as a food source.

After adding the copepods, one initial 100 ml subsample of water from each jar was preserved in acid Lugol's solution. The jars were then topped up with incubation water and placed on a grazing wheel (0.5 rpm) in a modified chest freezer. All incubations were for 24 h in dim light and at −1°C to 0°C. Rotation of the jars was end-over-end. Two or three control jars, containing no copepods, were treated identically.

On termination of the experiments two 200 ml subsamples of water from each jar were preserved in Lugol's solution. Experimental copepods were then checked for mortality. For *Oithona* spp. this was difficult because of their small size, their large numbers (Table 2) and because they move very irregularly. Mortality was checked by touching 30 individuals in each jar several times with a thermometer, to check for an escape response. Estimated mortality in *Oithona* spp. was less than 10%; that of the other species was negligible. The experimental copepods were concentrated onto a GF/C filter and frozen (−60°C) for subsequent counting and species/stage verification and dry mass measurement (see Atkinson and Shreeve, 1995).

Cell counts and calculation of feeding rates

A 50 ml aliquot of each subsample (i.e. two replicates for each grazing jar) was settled for >24 h and enumerated under an inverted microscope. The aliquots were selected randomly and "blind" in order to reduce potential bias due to subjective identifications, for example of small nanoflagellates or partially empty diatom frustules. The whole of the receptacle of the settling chamber was analysed for large taxa at × 100 magnification. Small and numerous cells (nanoflagellates and small pennate and centric diatoms) were counted on either two or three scans across the full diameter of the slide at × 200. Table 3 gives the food taxa sufficiently abundant (>30, on average, in initial and control aliquots) for inclusion in calculations of feeding rate. The emphasis in identification was not towards an exhaustive taxonomic breakdown but rather to group diatoms, nanoflagellates, dinoflagellates, and ciliates according to their size and shape. The majority of both dinoflagellates and ciliates were athecate forms (Burkill *et al.*, 1995). Counts of both thecate and athecate forms of each were pooled in order to increase sample sizes. Likewise, the group "large pennate diatoms" comprises several uncommon taxa of similar

Table 3. Food taxa sufficiently abundant for use in calculations of filtration and ingestion rates. Taxa are listed in ascending order of length.

Station	Food taxon	Mean length (μm)	Mean width (μm)	Mean volume (μm³)
G	Nanoflagellates	7.3	4.5	103
	Small dinoflagellates	20	10	1709
	Nitzschia kerguelensis[1]	22	8.5	2554
	Medium dinoflagellates	35	19	10351
	Large pennate diatoms	80	35	24122
	Nitzschia spp.	60	4.9	408
H	Nanoflagellates	6.2	4.1	95
	Thalassionema spp.	17	2.9	141
	Small dinoflagellates	19	11	1753
	Ciliates	20	15	2018
	Nitzschia kerguelensis[1]	35	13	3461
	Nitzschia closterium	43	2.5	50
	Medium dinoflagellates	43	24	18895
	Large pennate diatoms	87	22	18984
I	Nanoflagellates	6.4	4.9	108
	Small dinoflagellates	20	12	1994
	Nitzschia kerguelensis[1]	22	9.6	1190
	Ciliates	27	19	8932
	Medium dinoflagellates	36	24	14618
	Large pennate diatoms	72	19	12385
	Nitzschia closterium	114	7.1	700
J	Nanoflagellates	8.1	5.4	168
	Small dinoflagellates	22	13	2187
	Nitzschia kerguelensis[1]	38	15	2118
	Medium dinoflagellates	44	26	18239
	Distephanus spp.	48	15	2714
	Medium centric diatoms	62	25	33418
	Large centric diatom	83	43	122532
	Large pennate diatoms	98	19	31539
	Large dinoflagellates	102	39	73109
	Nitzschia kerguelensis[2]	137	33	3442
	Nitzschia spp.	144	7.6	2250
	Thalassia tumida?	242	50	171947
	Corethron sp.	356	47	277443
	Rhizosolenia spp.	465	19	135977
	Thalassiothrix antarctica	586	8.0	30321
K	Nanoflagellates	8.1	5.2	152
	Small centric diatom sp.	10	3.8	116
	Small dinoflagellates	20	13	1853
	Small centric diatoms	23	18	5895
	Medium dinoflagellates	40	26	12930
	Small/medium ciliates	43	19	12534
	Distephanus sp.	43	14	2350
	Large dinoflagellates	73	44	95765
	Nitzschia kerguelensis[2]	85	34	70026
	Large centric diatoms	90	36	207543
	Large ciliates	90	57	244333
	Eucampia antarctica	95	20	106477
	Large pennate diatoms	100	23	66790
	Nitzschia spp.	120	6.3	2010
	Chaetoceros spp.	132	9.4	≈5000
	Rhizosolenia spp.	250	10	62496
	Thalassiothrix antarctica	327	8.1	15761

[1]Colonies of up to four individuals.
[2]Colonies of more than four individuals.

dimensions which have been pooled to provide statistically meaningful feeding rate estimates. In these incubations the mean number of cells remaining at the end of the experiment was 71% of the final control values.

For each experiment the dimensions of each food category were obtained by measuring between 10 and 50 individuals, depending on variability in size. Cell volumes were then calculated from approximations to simple geometric shapes. Carbon content per cell was then estimated using the equations of Eppley *et al.* (1970). Ingestion rates and clearance rates of each food taxon were calculated using the equations of Frost (1972). Each strand of the long diatom *Thalassiothrix antarctica* encountered was measured, with feeding rates then being based on differences in the total measured length of strands, rather than simply on differences in the number of strands. The dimensions and volumes of cell categories listed for each experiment in Table 3 refer to the mean values that a grazer would encounter. Variable mean dimensions of colonial species between experiments therefore reflect different colony sizes. Likewise, effective volumes do not correspond to plasma volumes for colonial cells such as *Eucampia antarctica*, where there is a gap between adjacent cells.

A potentially serious error in such experiments is that preservation and handling procedures may cause some food items to change in length between the start of the experiment and the final Lugol's sample. Colonial diatoms could fragment, from either grazer activity (Deason, 1980) or sample handling procedure (see Turner and Tester, 1989). Ciliates can shrink on preservation in Lugol's (e.g. Leakey *et al.*, 1994). Feeding rates of colonial diatoms were based on numbers of cells rather than numbers of colonies, to make an allowance for colony break-up. Colony size data were compiled from both initial and control samples to gauge the effective sizes that the copepods would encounter. No allowance has been made for shrinkage of aloricate cells because this seems rather variable for ciliates (see Leakey *et al.*, 1994). Decreases in their linear dimensions will not be so severe as volume shrinkage; a 30% loss in volume corresponds to a 12% decrease in length or width. The emphasis in these experiments was on comparing between species presented with identical food sources. This aimed to allow for any systematic errors in methodology.

Results

Comparisons of feeding rates are based on clearance rather than ingestion, because the latter depends on both the feeding effort of the copepod (i.e. clearance rate) and the numbers and/or biomass of the food taxon. Clearance-rate measurements do not need to take account of the sizes of the food items, being based only

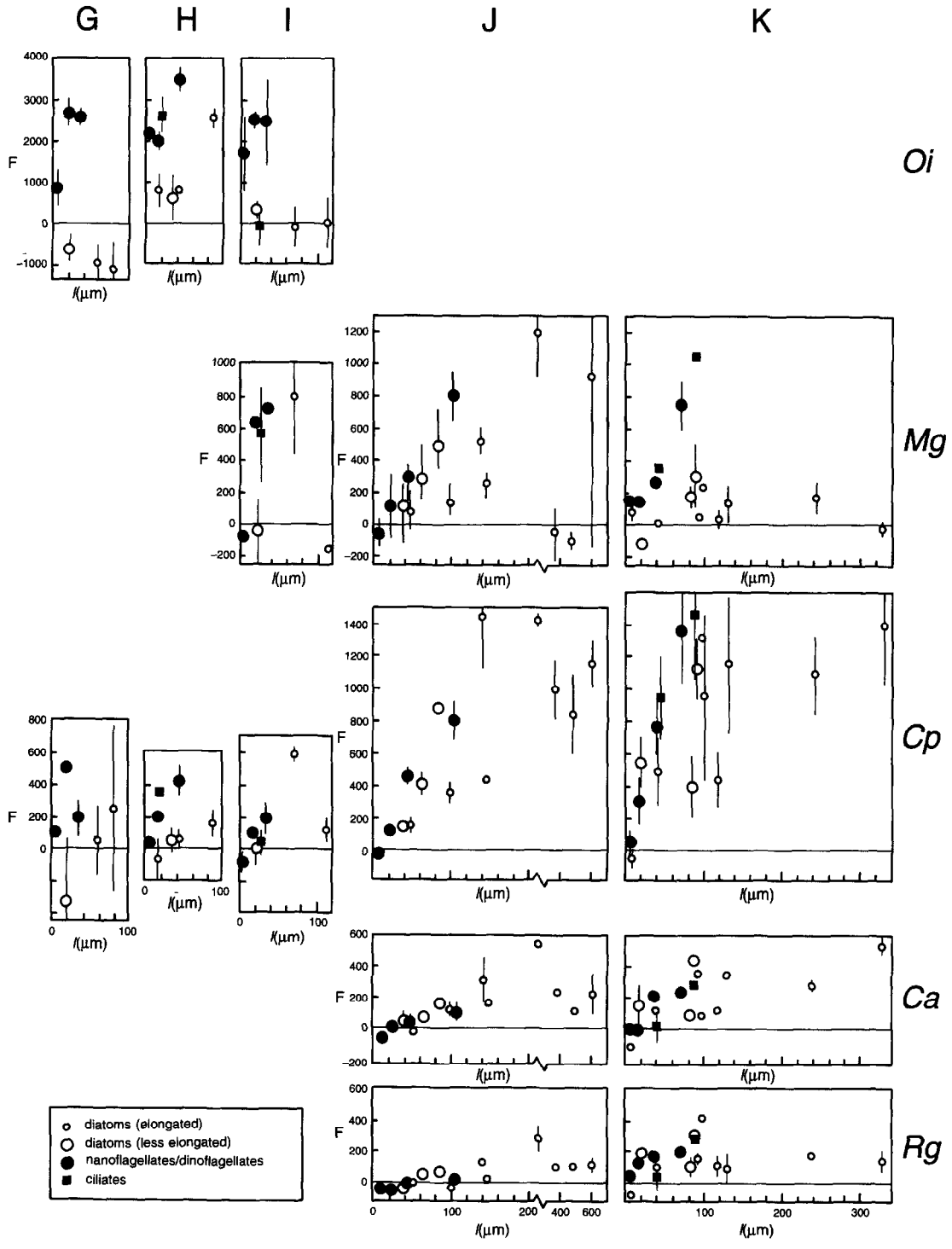

Figure 1. Oi = *Oithona* spp.; Mg = *Metridia gerlachei*; Cp = *Calanus propinquus*; Ca = *Calanoides acutus*; Rg = *Rhincalanus gigas*. Clearance rate (F) versus mean length of food taxa (l) for the five species at pre-bloom stations G, H, I and bloom stations J and K. Ratios of mean length to mean width for motile food taxa ranged up to 2.6 in these experiments, so diatoms with comparable ratios up to 2.6 are portrayed by large open circles. More elongated diatoms are given smaller open circles. Filled symbols represent motile taxa (see Table 3). Each bar on clearance scale represents 200 ml mg drymass^{-1} d^{-1} for all species except *Oithona* spp., where it represents 5 times this value. Error bars represent either the range of clearance rates obtained from two counted samples from a single grazing jar, or, where two or three jars were available (Table 2), the range in mean rates between jars.

Table 4. Mean food index (k) for the grazers incubated at each station. Ranges between replicate jars are in parentheses.

Species	Station				
	G	H	I	J	K
Rhincalanus gigas				22.6 (10–34)	2.0 (1.9–2.0)
Calanus propinquus	0.85	0.96 (0.42–1.5)	5.8	7.1 (4.8–9.4)	2.5 (2.3–2.7)
Calanoides acutus		(not feeding)		5.1 (4.9–5.2)	3.9
Metridia gerlachei			0.93 (0.61–1.3)	4.0 (2.1–5.4)	2.0
Oithona spp.	0 (0.0)	0.86 (0.85–0.87)	0.011		

on the proportion of them remaining. This makes it easier to use as a measure of selective grazing. Figure 1 shows clearance rates for the five species, at the stations where they were measured, plotted against mean lengths of the food taxa. *Oithona* spp. had the highest mass specific clearance rates, followed by *M. gerlachei* and *C. propinquus*. The large species, *C. acutus* and *R. gigas* had the lowest mass specific feeding rates. Overall feeding rates are compared between species and stations, and related to their life cycles and the changing environment in Atkinson and Shreeve (1995).

Clearance rate and food size

The counted food items ranged in size from nanoflagellates 6–8 μm long up to pennate diatoms 600 μm long. For the four larger copepod species, clearance rates on nanoplankton were low and increased up to food sizes of 100–200 μm. Clearance of cells larger than this remained high. Interpretations of cell size selection are hindered by the fact that copepods may also select food on the basis of shape, motility, taste, particle volume distribution, and previous feeding history. Some of these characteristics are denoted by the symbols in Figure 1 and are described in the following two sections. For each station, the preferred food sizes of the copepods can be compared using a simple size index, k:

$$k = \frac{\text{mean clearance rate on taxa longer than 50 μm}}{\text{mean clearance rate on taxa shorter than 50 μm}}$$

The 50 μm cut-off, although arbitrary, was chosen because in each experiment there were sufficient cells both larger and smaller than this to enable k to be calculated. These indices (see Table 4) tend to be greater than unity for the large species, *R. gigas*, *C. propinquus*, and *C. acutus*, particularly at the bloom stations J and K. This reflects their effective clearance of large diatoms during the bloom (Fig. 1). The smaller two species, *M. gerlachei* and particularly *Oithona* spp., had smaller k values, reflecting a higher proportion of small cells in their diet. *Oithona* spp. was the only species with high clearance rates on nanoflagellates, 6–8 μm long (Fig. 1).

Clearance rate and food shape

The food assemblage comprised a wide diversity of cell shapes. At the two bloom stations, J and K, the large cells tended to be highly elongated or filamentous. Although it is clear from Figure 1 that the copepods, particularly the largest ones, are capable of eating these cells, the question being asked here is whether long thin cells are eaten at lower rates than shorter and fatter cells of similar volume.

For this analysis the clearance rates on pairs of diatom taxa were compared. Ciliates, dinoflagellates, and nanoflagellates could not be compared validly with diatoms because several species appeared to have selected these motile taxa in preference to diatoms of similar size (see following section). Two diatom taxa were defined as having similar volumes if they differed by no more than 20%. Across all the experiments, seven such pairs of diatoms could be compared, giving 54 comparisons of clearance rate across all species and replicates. Of this 54, only 20 (35%) yielded filtration rates that were higher for the shorter and fatter taxon. This infers that for the range of food and grazer size analysed (admittedly the larger ends of both spectra), cell elongation in one dimension is no defence against predation. To the contrary, the long thin cells, which frequently clogged our zooplankton nets at the bloom stations, were often cleared at near maximum rates by the larger species (Fig. 1).

Clearance rates on motile versus sessile cells

Figure 1 suggests that *Oithona* spp. and *M. gerlachei* cleared motile taxa (solid symbols) more rapidly than diatoms (open symbols). Interpretations are obscured by factors such as size and shape, so for a more rigorous approach, the question was posed as to whether, when motile and sessile taxa of similar size and shape are compared, the motile taxa are cleared at higher rates. Again a series of pairwise comparisons was possible. The motile taxa had length/width ratios ranging up to 2.6 between the experiments, so diatoms within this range of length/width ratios were defined as having a broadly similar shape. These diatoms are portrayed by

the large open circles in Figure 1. Similar size was defined as: lengths varied by no more than 20%, or widths varied by no more than 20%, or both. Across the 14 comparable pairs of taxa, cell dimensions were similar; the median ratio of their length (motile taxon/diatom) was 0.89 and the median ratio of their width was 1.17. The flattened silicoflagellate *Distephanus* spp. (43–48 μm diameter) was cleared at low rates and was not included in these comparisons.

For each pairwise comparison a selectivity index, s was calculated as *the clearance rate of the motile taxon minus the clearance rate of the sessile taxon*. Because the species differed in their overall clearance rates, these were first normalized to percentages of the maximum rate observed for the species in each experiment. Negative clearance rates were assigned as zero. Figure 2 illustrates the value of s among the replicate grazing jars for each of the available comparisons. The species differ appreciably in both the proportion of positive values of s and the average value of s. This is summarized in Table 5. The species appear to follow a trend of increasing selection for motile food, in the order *C. acutus*, *R. gigas*, *C. propinquus*, *M. gerlachei*, *Oithona* spp.

Whether *M. gerlachei* and *C. propinquus* changed in their degree of selectivity between pre-bloom and bloom stations is uncertain. *C. propinquus* was the only species incubated at all stations, and the strongest selection for motile cells was at the pre-bloom stations G and H. At the bloom stations J and K, however, the largest values of s were positive values (Fig. 2). This implies that their selection of motile cells persisted into the bloom.

Among the three species showing evidence for selection of motile prey, there are no indications that clearance rates of ciliates were different from those of dinoflagellates (Fig. 1). An exception to this was at station I, where *Oithona* spp. and *C. propinquus* had low clearance rates on ciliates compared with dinoflagellates of similar size.

Contribution of motile taxa to copepod diets

Table 6 compares the percentages of total carbon in diatoms between the incubation water and the diets of the five species. The remainder of the carbon estimates comprise motile taxa: nanoflagellates, dinoflagellates, and ciliates. The percentages in the incubation water reflect the changing environment, between the ice-dominated pre-bloom stations and the bloom in the open sea to the north (Robins *et al.*, 1995). Small flagellates were dominant under the ice, with small pennate diatoms comprising less than ≈25% of the carbon. At the open water bloom stations (J and K) large diatoms heavily dominated the total carbon. The diets of the larger species broadly reflected this change, with an increase in the contribution of diatoms. *Oithona* spp. preyed almost exclusively on motile taxa at the pre-bloom stations. *M. gerlachei* and to a lesser extent *C. propinquus* tended to select motile taxa, so it would be expected that these would comprise a greater percentage of their diet than seen in available food. Although this is sometimes the case (e.g. *M. gerlachei* at station K), size-based selection appears to have obscured this in other instances. For example, at station K the carbon in the motile component was mainly in medium-sized dinoflagellates (mean length 40 μm), whereas that in diatoms was mainly in cells over twice as long. Although *C. propinquus* appeared to prefer motile taxa to diatoms of similar size, the fact that larger cells were eaten more readily tended to counteract this.

Discussion

Three features of these experiments were (1) that natural assemblages of food were offered to the copepods, (2)

Table 5. Comparison of selectivity indices (s).

Species	No. of comparisons	Percentage of comparisons yielding positive value of s	Mean value of s, median value of s
Oithona spp.	10	90%	63, 70
Metridia gerlachei	20	75%	18, 18
Calanus propinquus	25	72%	18, 10
Rhincalanus gigas	16	25%	−3.1, −3.0
Calanoides acutus	12	25%	−3.9, −6.9

Table 6. Percentages of total carbon contributed by diatoms in the incubation water and in the diets of the five species. Values are means, with ranges between replicates in parentheses.

Station	Incubation water	Species				
		Oithona spp.	*Metridia gerlachei*	*Calanus propinquus*	*Rhincalanus gigas*	*Calanoides acutus*
G	22	0 (0,0)		15		
H	16	7.5 (7.3–7.7)		10.4 (6.8–14)		(not feeding)
I	9.4	0.4	8.4 (6.2–11)	19		
J	89		88 (85–91)	92 (90–93)	97 (96–98)	95 (93–97)
K	82		45	83 (82–83)	86 (83–89)	89

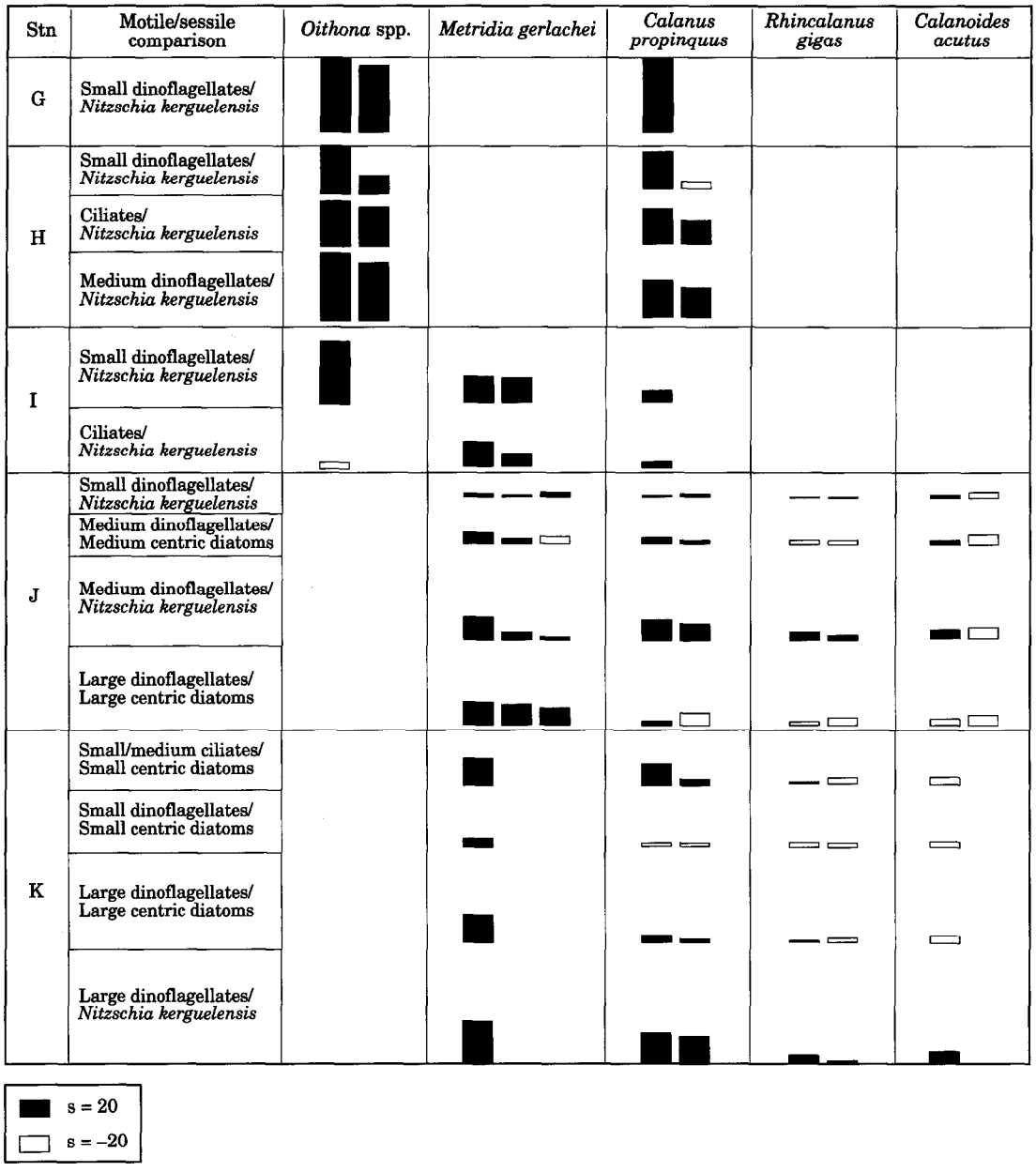

Figure 2. Selectivity indices, s, calculated from 14 motile/sessile clearance rate calculations. Each bar represents a replicate grazing jar. Positive values of s are represented by filled bars, negative values by open bars.

responses of a variety of copepods to identical food were compared, and (3) feeding rates were based on optical cell counts of individual food taxa. This combination was chosen to reduce some of the problems of feeding selectivity experiments. A particular problem is that the size, shape, and identity of the prey items need to be assessed simultaneously in order to gauge whether "carnivorous" behaviour is occurring, in addition to selection based on size and shape (Wiadnyana and Rassoulzadegan, 1989). Studies using optical cell counts and natural sea water have clearly demonstrated the importance of protozoans in the diets of the genera *Acartia* and *Neocalanus* (Stoecker and Egloff, 1987; Gifford and Dagg, 1991; Gifford, 1993a; but see Tiselius, 1989). In some of these studies, however, the animal and plant food items were of different size, making it difficult to decide whether the protozoans had been selected actively or eaten indiscriminately (Tiselius, 1989).

Another serious problem in experiments employing natural sea water is that, being a living assemblage with turnover times of the order of a few days, individual

taxa can increase or decrease during the experiment. This might be independent of copepod grazing and attributable to microzooplankton grazing during the experiment (Turner and Granéli, 1992) or to reproduction of autotrophs (Granéli *et al.*, 1993), especially of small species (Roman and Rublee, 1980). Aloricate ciliates are also delicate and susceptible to high mortality (Tiselius, 1989; Gifford, 1993b). Probably as a result of these factors, diatoms increased in numbers in the incubations of *Oithona* spp. at station G, as indicated by the "negative" clearance rates (Fig. 1). In an attempt to allow for this, several species were exposed to the same prey assemblage, with the emphasis being on comparison. The range of patterns seen (Tables 4–6) lends credance to their being due to behavioural traits of the species, rather than to artifacts of incubation.

Copepods tend to be inefficient at filtering particles smaller than 5–10 μm (Nival and Nival, 1976; Berggreen *et al.*, 1988) but the upper and lower size limits of food have been established for only a small number of species. Berggreen *et al.* (1988) described the optimum food sizes (equivalent spherical diameter) for *Acartia tonsa* as 2 to 5% of prosome length. Applying this rule would give optimum food sizes of approximately 10–25 μm for *Oithona* spp., 55–138 μm for *M. gerlachei*, 85–213 μm for *C. propinquus* and *C. acutus*, and 140–350 μm for *Rhincalanus gigas*. Based on these results it would be predicted that the larger species could eat the large diatoms which characterized the bloom. This result was also found near South Georgia (Atkinson, 1994). Likewise, Vanderploeg *et al.* (1988) concluded from microcinematography and grazing experiments that elongation of cells in one dimension was no defence against ingestion by a freshwater copepod. However, the females incubated at the bloom stations represent the largest extremes of copepod size; it would be of interest to determine whether the early copepodite stages and smaller species could also tackle these long cells. Differences in preferred food size, related to copepod size, are suggested by Table 4. As suggested by Berggreen *et al.* (1988) and Atkinson (1994), this may tend to reduce competition for food between extremes of body size.

Against this background of food size selection, the species range widely in the extent of their selection for motile food. *Oithona* spp. appeared to have selected almost entirely for motile cells, whereas *C. acutus* and *R. gigas* appeared to have fed indiscriminately. It must be reiterated that not all of these motile taxa are heterotrophic; the presence of chlorophyll cannot be determined from Lugol's preserved samples. Nevertheless, many of the large dinoflagellates, which comprised a significant proportion of biomass of the motile fraction, were heterotrophic forms such as *Gyrodinium* spp. (Burkill *et al.*, 1995). With the proviso that predation rates on nauplii were not measured (they were too rare), the trends in selection for motile taxa are likely to reflect the differing degrees of carnivory between the species.

The experiments could not test whether it was the motility, or other factors such as taste or ease of handling, which influenced selection. Nevertheless, the fact that a diverse grouping of taxa (nanoflagellates, dinoflagellates, and ciliates) all shared the characteristic of motility and tended (with two exceptions) to follow a common trend suggests that it was their motility which was somehow causing their selection. Mechanoreception of moving prey has been described in several copepod genera (Price, 1988; Landry and Fagerness, 1988). In contrast, Huntley *et al.* (1986) showed that the taste of certain noxious dinoflagellates caused rejection by copepods.

The diets of these copepod species are known mainly from gut contents analysis (e.g. Hopkins and Torres, 1989; Hopkins *et al.*, 1993a, b) as well as from feeding experiments (Schnack, 1985; Atkinson, 1994). Taken together, the results suggest seasonal differences in the degree of carnivory of *M. gerlachei* and *C. propinquus*, relative to *C. acutus* and *R. gigas*. Hopkins *et al.* (1993b) described *C. acutus* and *R. gigas* as the only herbivorous species found during spring, all others having a higher incidence of loricate protozoans/metazoans in their guts. In contrast, during summer and autumn, when food is presumably more abundant, both gut content analyses (Voronina and Sukhanova, 1976; Hopkins and Torres, 1989) and incubation studies (Schnack, 1985) suggest that the diets of all four species might be broadly similar, comprising mainly diatoms. Likewise, Huntley (1981) found that copepods fed indiscriminately during a bloom in the Labrador Sea. His reasoning was that if food was super-abundant and contains little detritus, then feeding does not need to be selective. Food availability increased dramatically along the present transect, which makes it a possible test for the above hypothesis. Although there is not enough data to be conclusive, Figure 2 suggests that *M. gerlachei* (and possibly *C. propinquus* as well) tended to select motile taxa, even when they contributed a small percentage of biomass during the bloom.

The dietary picture for *Oithona* spp. is not clear. In winter this genus was found with empty guts (Hopkins *et al.*, 1993a), whereas in autumn it contained almost exclusively diatoms (Hopkins and Torres, 1989). Turner (1986) and Paffenhöfer (1993) could find no clear consensus on the natural diet of this genus, despite several studies (e.g. Lampitt and Gamble, 1978; Uchima and Hirano, 1986; Turner and Granéli, 1989) finding, like this one, a preference for motile cells.

The trend in selection of motile food among the copepods might be linked to other aspects of their life cycles, discussed for these stations by Atkinson and Shreeve (1995). This is summarized in Table 7. Suggested strategies towards surviving the winter are, first, to cease feeding, to descend to the meso- or bathy-

Table 7. Trophic aspects of the life cycles of five major copepod species, with the species ordered to summarize trends between them.

Species	Aspect of life cycle: Extent of feeding on motile food	Extent of winter feeding	Reliance on lipid store	Extent of seasonal vertical migration
Oithona spp.	Tends to select motile food	Feeds prior to spring bloom	Lower lipid content	Relatively small
Metridia gerlachei *Calanus propinquus* *Rhincalanus gigas* *Calanoides acutus*				
	More indiscriminant in diet	Diapause in winter	High lipid content	Extensive migration
Comments/exceptions	*Oithona* spp. food selectivity not tested during a bloom, although their diets comprised diatoms during autumn (Hopkins and Torres, 1989). Diets change seasonally (see Hopkins *et al.*, 1993a)	Hopkins *et al.* (1993a) found *Oithona* spp. with empty guts in winter	*Oithona* spp. not tested. *Calanus propinquus* has extensive store of triacylglycerol (Schnack-Schiel *et al.*, 1991)	*M. gerlachei* resides deeper than the other species (Schnack-Schiel and Hagen, 1995) Extent of migration may vary regionally and inter-annually (Bathmann *et al.*, 1993)

pelagic, and to enter diapause (Voronina, 1978; Marin, 1988; Schnack-Schiel *et al.*, 1991). Second, a species could remain active in the surface layers, feeding, possibly carnivorously, underneath the ice during the winter (Bathmann *et al.*, 1993; Schnack-Schiel and Hagen, 1995; Atkinson and Shreeve, 1995). The latter strategy appears to be adopted, in varying degrees, by *Oithona* spp., *M. gerlachei*, and *C. propinquus*. Although there appear to be some exceptions and *Oithona* spp. has been little studied (Metz, 1995), the species seem to follow a systematic gradient between these alternative winter survival strategies.

Carnivorous feeding may be a prerequisite if a species is to remain active in a low chlorophyll environment during winter. As well as the fact that a higher proportion of organic carbon resides in motile forms, the selection of motile prey may help a copepod to cut its feeding costs. *Oithona* spp., for example, appeared to spend most of their time motionless at the pre-bloom stations, darting only occasionally (to capture food?). A large portion of the particulates, especially at stations in the vicinity of the ice, were inorganic detritus (Robins *et al.*, 1995). By selecting only nutritious motile cells a copepod could increase its feeding efficiency.

This explanation of selective feeding before the bloom is analogous to "peak tracking", where copepods feed efficiently on the particle type which dominates the numbers, volume or carbon in their food source. Both observations of selective grazing and their explanations are debated (Huntley, 1981; Turner and Tester, 1989), but it seems that large particles can be selected from mixtures (e.g. Runge, 1980), possibly by raptorial feeding (Price *et al.*, 1983). This is one possible explanation for the high feeding rates on large diatoms, exhibited by the larger copepods during the bloom. Decreased efficiency in handling small cells may have contributed to this effect. However, it is clear that during the bloom the copepods had not switched to feeding solely on the single cell type (large centric diatoms) that dominated the volume and carbon of the food at stations J and K. These cells (83–90 μm long) were cleared at similar rates to other rarer diatoms of equivalent size (Fig. 1).

The grazing impact of the copepod community was estimated to reach at most (which was at station K) only 8% of daily production by cells >2 μm (Atkinson and Shreeve, 1995). Heterotrophic dinoflagellates and ciliates appeared to be the major grazers (maximum estimate, again at station K, was 271% of daily primary production; Burkill *et al.*, 1995). If copepods selectively ingest large protozoans, or at least ingest them at near maximum rates (Fig. 1), then by acting as a "top

predator" on the microbial food web they would relieve some of the high protozoan grazing impact. The extreme discrepancy between the algal grazing impact of copepods and protozoans suggests that the role of copepods as "top predators" rather than "algal grazers" would be a more appropriate one to consider in this food web.

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