

# Feeding of *Calanus helgolandicus* on Phytoplankton Mixtures

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**ABSTRACT:** In order to examine feeding selectivity by copepods, females of *Calanus helgolandicus* were allowed to graze on a mixture of three different chain-forming diatoms: *Thalassiosira rotula* ( $40 \times 15 \mu\text{m}$ ), *Chaetoceros pseudocurvisetus* ( $\varnothing 15 \mu\text{m}$ ) and *Stephanopyxis palmeriana* ( $85 \times 45 \mu\text{m}$ ). *T. rotula* was deliberately offered at higher abundancies. *C. helgolandicus* filter a higher rate of *C. pseudocurvisetus* than of *S. palmeriana* and *T. rotula*, and graze preferentially on this spiny form. During experiments, *T. rotula* rarely decrease, and electivity regarding this species was always negative; in contrast, on *S. palmeriana* and *C. pseudocurvisetus* it was always positive. Net particle production occurred only in the smaller chains (2, 3 and 4 cells per chain) of *S. palmeriana*; net particle removal was recorded on all phytoplankton species, but in *S. palmeriana* only on single cells and longer chains. Within a given species, removal pressure was high on large chains of *S. palmeriana* and *T. rotula*, whereas in *C. pseudocurvisetus* a greater variability prevailed. Maximum removal occurred at or near modal peaks.

## INTRODUCTION

Since Harvey's (1937) report on size-selective feeding by copepods, a great number of papers have been published on this theme. For reviews consult 'Marine Ecology', Volume III: Kinne, 1977, and Volume IV: Conover, 1978. Although there is general agreement that copepods do indeed feed selectively, experimental results are frequently contradictory with regard to actual feeding behaviour. Selective feeding is evidently regulated by a large number of factors such as quality and quantity of available food and previous feeding history of the copepods.

In the present study grazing experiments were conducted using three chain-forming diatoms as food. While *Thalassiosira rotula* is known as a good food source for *Calanus* species (Paffenhöfer, 1976, Schnack, 1978), *Stephanopyxis palmeriana* is a relative

poor one (Schnack, 1978). Contrasting results were obtained with spiny *Chaetoceros* species as food for copepods (e. g. Harvey, 1937, Marshall and Orr, 1955). The question addressed here is: How do *Calanus helgolandicus* females behave in a mixture of these three different diatoms, when the most suitable food organism (*T. rotula*) is much more abundant than the two other species?

## MATERIAL AND METHODS

Selective feeding experiments were carried out with adult female *Calanus helgolandicus* in December 1977. The copepods used in the experiments were collected in the North Sea. 25 healthy females were placed in each of four 4-l beakers containing 3 l of a suspension of algal mixture. One control beaker was used containing identical algal cultures but no copepods. The contents of the beakers were kept homogeneous by using Plexiglas stirrers rotating at 2 rpm (Frost, 1972). The copepods were conditioned for one day before experimentation began. The experiments were conducted in dim light at a temperature of  $15^\circ\text{C}$  for 15 h. Food concentrations were measured by counting 5–10 subsamples of 50 ml each under an inverted microscope. Three chain-forming diatom species were used in the experiments. The phytoplankton was cultured at  $15^\circ\text{C}$  before experimentation. Average cell volumes were estimated after Smetacek (1975).

Table 1. Mean size and estimated cell volume of diatom species used in feeding experiments. The species were isolated and cultured from the NW-African upwelling area by H. K. Schöne

Phytoplankton species	Mean cell size ( $\mu\text{m}$ )	Mean cell vol. ( $\mu\text{m}^3$ )
<i>Chaetoceros pseudocurvisetus</i>	$\varnothing 15$	2 200
<i>Thalassiosira rotula</i>	$40 \times 15$	13 000
<i>Stephanopyxis palmeriana</i>	$85 \times 45$	136 000

Table 2. Filtration rates of female *Calanus helgolandicus* Mono-algal diet

Phytoplankton species	Mean particle conc. ( $\mu\text{m}^3 \text{ml}^{-1}$ )	Filtration rates ( $\text{ml copep}^{-1}\text{h}^{-1}$ )
<i>Chaetoceros pseudocurvisetus</i>	$59 \times 10^4$	6.39
	$72 \times 10^4$	6.17
	$60 \times 10^4$	5.03
<i>Thalassiosira rotula</i>	$62 \times 10^4$	5.96
	$88 \times 10^4$	4.62
	$90 \times 10^4$	5.89
	$97 \times 10^4$	6.31
<i>Stephanopyxis palmeriana</i>	$88 \times 10^4$	5.46
	$62 \times 10^4$	5.60
	$87 \times 10^4$	5.26
	$77 \times 10^4$	5.44
	$71 \times 10^4$	4.87

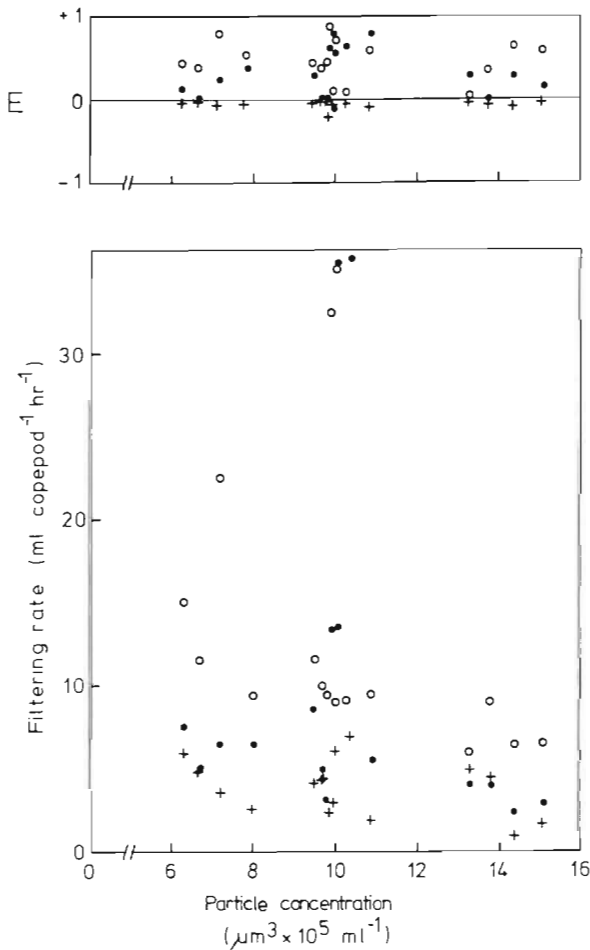


Fig. 1 Filtration rates and food electivity plotted against mean total particle concentration available (all three species combined).  $\circ$  *Chaetoceros pseudocurvisetus*;  $+$  *Thalassiosira rotula*;  $\bullet$  *Stephanopyxis palmeriana*

The size of the chains varied over a broad range depending on the number of cells per chain. The mean size and volume of the cells are presented in Table 1. Filtration rates on each species were calculated after the formula given by Gauld (1951). Selection was

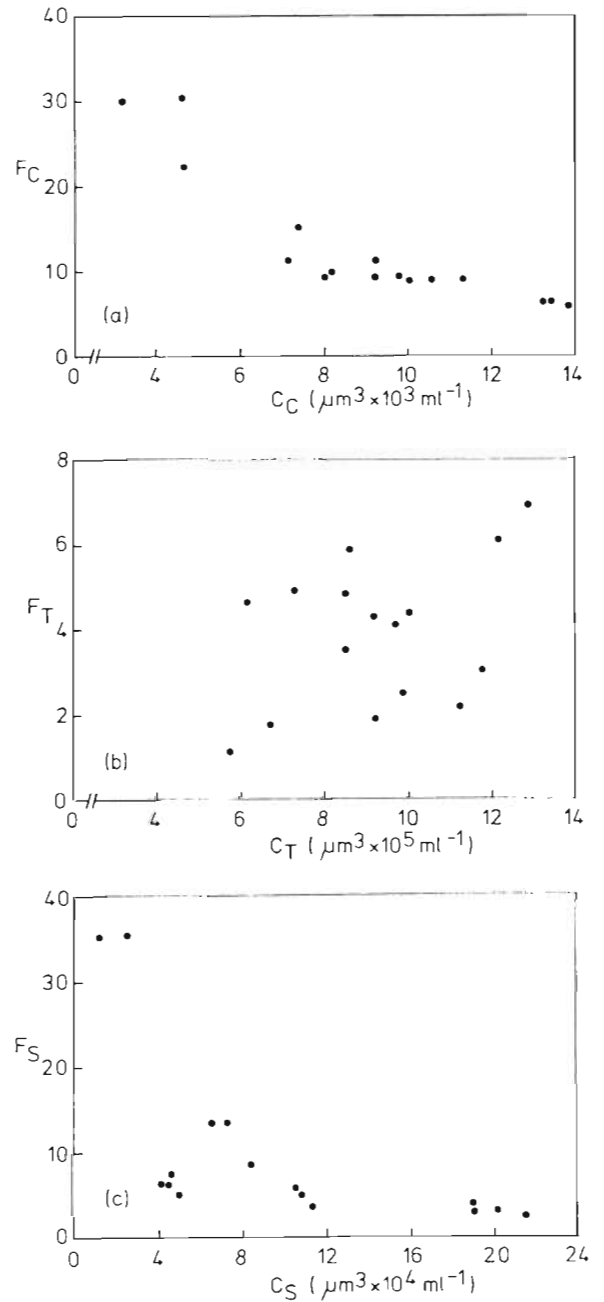


Fig. 2. Filtration rates of *Chaetoceros pseudocurvisetus* (a), *Thalassiosira rotula* (b) and *Stephanopyxis palmeriana* (c) versus concentration of the respective species.  $C_C$ : Concentration of *C. pseudocurvisetus*;  $C_S$ : Concentration of *S. palmeriana*;  $C_T$ : Concentration of *T. rotula*;  $F_C$ : Filtration rate ( $\text{ml copepod}^{-1}\text{h}^{-1}$ ) of *C. pseudocurvisetus*;  $F_S$ : Filtration rate ( $\text{ml copepod}^{-1}\text{h}^{-1}$ ) of *S. palmeriana*;  $F_T$ : Filtration rate ( $\text{ml copepod}^{-1}\text{h}^{-1}$ ) of *T. rotula*

quantified by means of Ivlev's (1961) electivity index:

$E = (r_i - p_i) / (r_i + p_i)$ , where  $r_i$  is the relative proportion of one phytoplankton species in the ration and  $p_i$  the relative proportion of the same phytoplankton species in the total available food particles.

## RESULTS

No great difference was found between filtration rates of *Calanus helgolandicus* when feeding on mono-specific cultures of the three phytoplankton species

Table 3. Summary of *Calanus helgolandicus* grazing experiments. C : *Chaetoceros pseudocurvisetus*, T : *Thalassiosira rotula*, S : *Stephanopyxis palmeriana*

Food organism	Mean food conc. ( $\mu\text{m}^3 \text{ ml}^{-1}$ )	Percent avail.	F ( $\text{ml cop}^{-1}\text{h}^{-1}$ )	I ( $\mu\text{m}^3 \times 10^3 / \text{eaten cop}^{-1}\text{h}^{-1}$ )	Percent eaten	Electivity (E)		
						C	T	S
C	2 664	0.3	30.5	141	4.6			
T	920 010	93.2	2.2	1989	64.5	+ 0.89	- 0.18	+ 0.65
S	65 008	6.6	13.2	952	30.9			
C	9 963	1.0	9.0	95	1.3			
T	972 790	97.8	6.1	6084	87.0	+ 0.09	- 0.12	+ 0.78
S	12 376	1.2	35.3	816	11.7			
C	4 600	0.5	30.5	141	3.7			
T	922 701	92.3	3.0	2769	71.7	+ 0.78	- 0.13	+ 0.55
S	72 488	7.2	13.6	952	24.6			
C	10 494	1.0	9.0	94	1.2			
T	996 281	96.6	6.9	6877	86.8	+ 0.08	- 0.05	+ 0.66
S	25 024	2.4	35.6	953	12.0			
C	9 207	0.8	9.4	79	3.2			
T	985 621	90.3	1.9	1885	75.2	+ 0.58	- 0.09	+ 0.79
S	96 288	8.8	5.3	544	21.6			
C	7 099	0.8	11.4	88	2.0			
T	857 285	90.3	4.1	3536	82.2	+ 0.46	- 0.05	+ 0.28
S	84 864	8.9	8.4	680	15.8			
C	8 010	0.8	9.3	79	2.3			
T	854 880	87.6	4.3	3005	86.0	+ 0.47	- 0.00	+ 0.00
S	113 288	11.6	3.4	408	11.7			
C	8 096	0.8	9.9	86	2.0			
T	849 537	88.0	4.4	3757	85.6	+ 0.40	- 0.01	+ 0.05
S	108 120	11.2	4.8	544	12.4			
C	9 786	1.3	9.5	99	4.5			
T	733 577	93.3	2.5	1820	83.1	+ 0.57	- 0.06	+ 0.39
S	42 568	5.4	6.5	272	12.4			
C	7 430	1.5	15.1	130	3.2			
T	581 711	91.3	5.9	3523	86.8	+ 0.46	- 0.03	+ 0.17
S	45 424	7.2	7.4	406	10.0			
C	9 214	1.4	11.3	112	3.3			
T	614 458	91.2	4.8	3029	88.7	+ 0.41	- 0.01	+ 0.03
S	50 320	7.4	5.0	272	8.0			
C	4 567	0.6	22.5	141	5.2			
T	668 356	93.4	3.5	2327	84.9	+ 0.78	- 0.05	+ 0.25
S	42 432	5.9	6.5	271	9.9			
C	13 812	1.0	6.0	84	1.1			
T	1 123 551	84.7	4.8	5525	73.5	+ 0.04	- 0.07	+ 0.28
S	189 448	14.3	4.1	1904	25.4			
C	13 350	0.9	6.5	88	4.4			
T	1 215 006	84.2	1.1	1391	68.8	+ 0.65	- 0.10	+ 0.29
S	215 560	14.9	2.3	544	26.8			
C	11 198	0.8	9.0	106	1.7			
T	1 175 369	85.4	4.6	5400	84.6	+ 0.34	- 0.01	+ 0.00
S	189 448	13.8	3.9	880	13.7			
C	13 171	0.9	6.6	88	3.2			
T	1 288 456	85.3	1.7	2158	77.3	+ 0.57	- 0.05	+ 0.17
S	208 896	13.8	2.8	544	19.5			

(Table 2). In feeding experiments using a mixture of all three species, *Thalassiosira rotula* was most abundant. More than 90% of the total available cells and more than 80% of the available cell volume were represented by this species. The relative frequency of the species was the same in all experiments (Table 3). With two exceptions *C. helgolandicus* filtered at the highest rate on *Chaetoceros pseudocurvisetus*. Usually higher filtration rates were found on *Stephanopyxis palmeriana* than on *T. rotula* (Table 3). There are significant differences in filtration rates: between *C. pseudocurvisetus* and *T. rotula* at the 1% level and between *C. pseudocurvisetus* and *S. palmeriana* at the 5% level (Wilcoxon and Wilcox test for multiple comparison). The filtration rates on *T. rotula* and *S. palmeriana* were not related either to the total available particle concentration (Fig. 1) or to the density of the respective species (Fig. 2). The filtration rate on *C. pseudocurvisetus* was also independent of the total concentration (Fig. 1), but not of the density of *Chaetoceros* cells (Fig. 2). The electivity on the most abundant species, *T. rotula* was always negative but close to zero, but on *C. pseudocurvisetus* and *S. palmeriana* it was always positive (Table 3). For all species the electivity was independent of total abundance of food (Fig. 1).

The chain-length frequency for the three species at

the beginning and end of one experiment is shown in Fig. 3; the variance between beakers and experiments was below 3%.

Only in *Stephanopyxis palmeriana* were the chains much shorter at the end than at the beginning. When plotting the differences between chain-length frequencies in 'grazing beakers' (with copepods) and control beakers (without copepods) against the number of cells per chain, the resulting curves are below zero in *Thalassiosira rotula* and *Chaetoceros pseudocurvisetus* (Fig. 4). In *S. palmeriana* however, there is an increase in short chains (2, 3 and 4 cells per chain) and the values are below the zero line only for single cells and longer chains. According to O'Connors et al. (1976) and Donaghay and Small (in prep.) values below zero indicate net removal by breaking of large chains into smaller ones and/or by ingestion, while those above zero represent net production of particles resulting from breakage of long chains.

In *Chaetoceros pseudocurvisetus* and *Thalassiosira rotula* it is apparent that only net removal occurred, whereas in *Stephanopyxis palmeriana* there was also net production. The greatest removal occurred at or near the modal peaks (Fig. 4, a, b, c). Donaghay and Small (in prep.) described an index of removal pressure on different size classes relative to the volume of algae present in this size class [(grazed-control)/con-

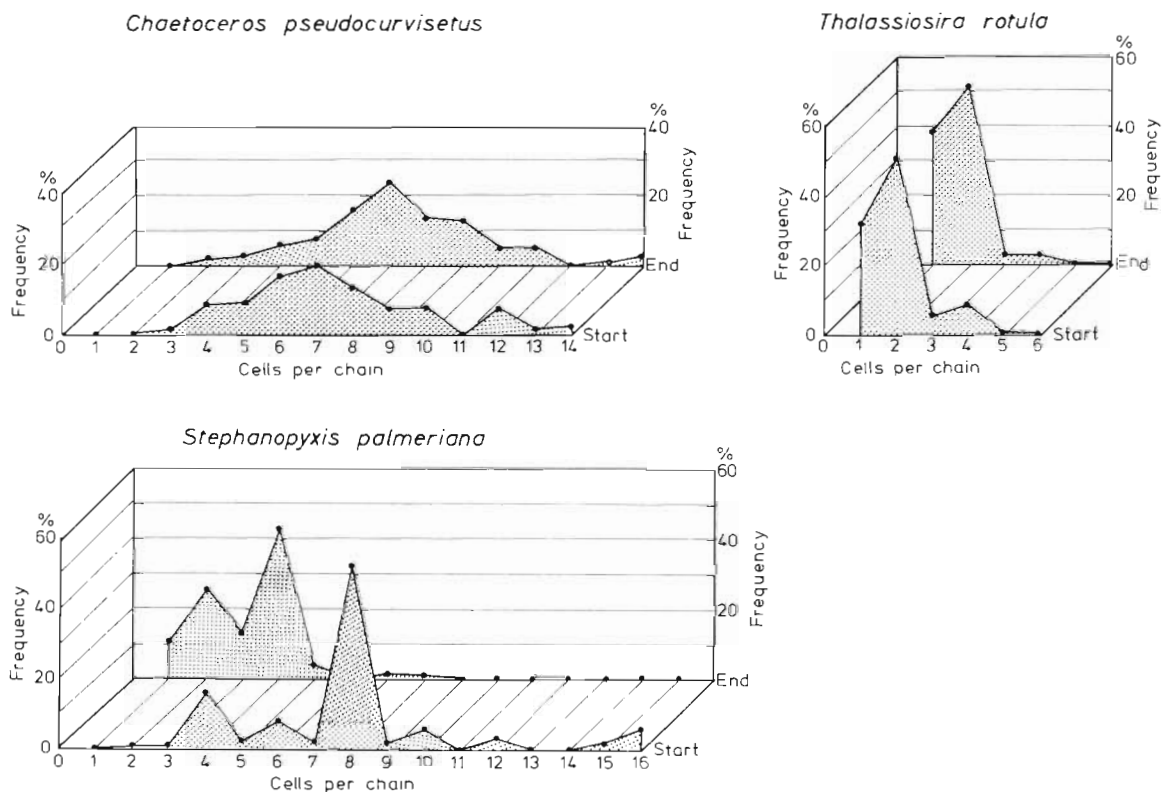


Fig. 3. Chain-length frequency of three diatom species at beginning and end of experiments

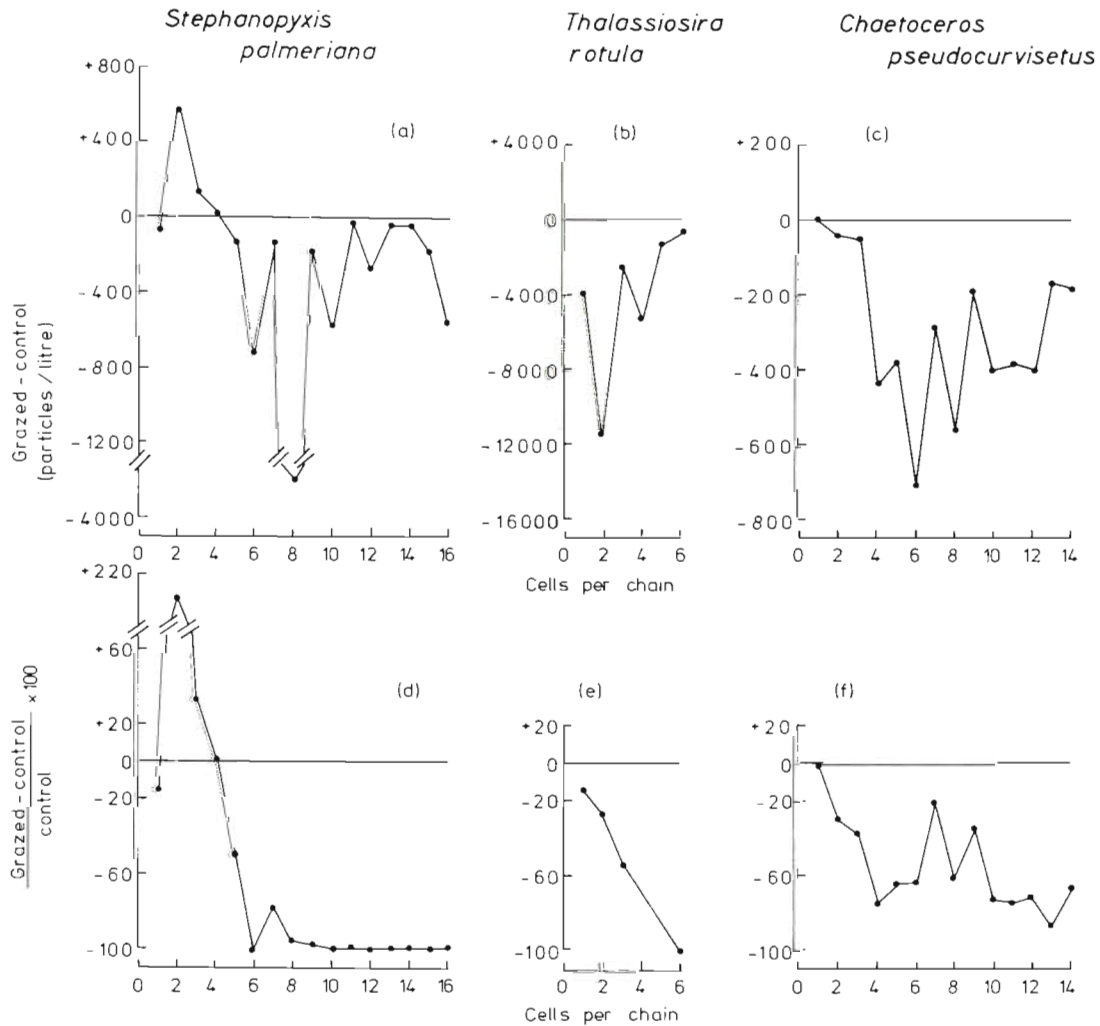


Fig. 4. Grazing effects on chain-length. Data presented as difference plots of grazed and control beakers (4a, b, c) and as indices of relative removal (4d, e, f)

tol × 100]: the more negative the index, the greater the removal pressure. Removal pressure was high on large chains of *S. palmeriana* with a steep decrease of the index between particle production and particle removal (Fig. 4d). For *T. rotula* a continuously increasing removal pressure was present as chains became longer (Fig. 4e). For *C. pseudocurvisetus* there was great variability in the removal pressure index (Fig. 4f). The index was low at the model peak (7 cells per chain), which is in contrast with the results obtained for *T. rotula* and *S. palmeriana*.

## DISCUSSION

Several factors, such as shape, size, chemical composition and concentration of food particles can cause selective feeding by copepods. It is obvious from the results of the experiments presented in this paper that

*Calanus helgolandicus* did not feed preferentially on the most abundant species offered. Furthermore, *C. helgolandicus* grazed heavily in most experiments on the spiny *Chaetoceros pseudocurvisetus*. Different opinions concerning feeding on *Chaetoceros* occur in the literature. Harvey (1937), Parsons et al. (1967) and Hargrave and Geen (1970), for instance did not find feeding by copepods on *Chaetoceros* species. Their results contrast with those given in this study and by Raymond and Gross (1942), Marshall and Orr (1955), Paffenhöfer and Strickland (1970) and Heinle et al. (1976). In contrast to *Thalassiosira rotula* and *Stephanopyxis palmeriana*, the chains of *C. pseudocurvisetus* have a semicircular shape with a diameter of about 150 µm, which may contribute to the difference in how they are handled.

The mean-spherical diameter or cell volume of *Chaetoceros pseudocurvisetus* is less than that of *Stephanopyxis palmeriana* and *Thalassiosira rotula*

Table 4. Mean length and chain volume of diatom species. For *Chaetoceros* the volume has been calculated (a) with spines and (b) without spines

Phytoplankton species	Cells/ chain	Length/ chain ( $\mu\text{m}$ )	Chain a	Volume ( $\mu\text{m}^3$ ) b
<i>Chaetoceros pseudocurvisetus</i>	7	105	15 400	1 071 739
<i>Thalassiosira rotula</i>	2	46	45 239	-
<i>Stephanopyxis palmeriana</i>	8	680	1 081 493	-

(Table 1), but the *C. pseudocurvisetus* cells occupy a greater volume due to their long projecting spines. Table 4 gives the mean lengths and volumes of the chains for all the species; for *C. pseudocurvisetus* the value including spines is also given. From these data it is clear that the volume of *C. pseudocurvisetus* with spines is very close to that of *S. palmeriana*. The spines of *C. pseudocurvisetus* possibly increase the effective diameter of the chains and thus copepods would encounter *C. pseudocurvisetus* more often than expected if spines were not included in volume measurements. The evident preference for this species shown by *Calanus helgolandicus* could thus be explained by the larger volume occupied by it. Heinle et al. (1976) also found preferential feeding on *Chaetoceros* and proposed a similar explanation.

The importance of the size of the food organisms, independent of the species, was demonstrated by Mullin (1963). He found *Calanus helgolandicus* to feed preferentially on the larger chains of *Asterionella japonica* and larger cells of *Rhizosolenia setigera*. Martin (1970) reported that although *Acartia clausi* preferred *Skeletonema costatum* to the larger *Rhizosolenia delicatula* the larger chains of *Skeletonema costatum* were selected. When phytoplankton chains become long, the probability that a whole chain can be swallowed by a copepod decreases, and therefore the possibility of chain breakage increases. Breaking of long chains into smaller ones during grazing activity has been described by Parsons and Seki (1970), Paffenhöfer (1971, 1976), O'Connors et al. (1976), Donaghay and Small (in prep.). It is difficult to determine whether copepods filtered the larger chains in a suspension more efficiently and broke the chain during feeding or whether the larger chains were broken into smaller ones by the swimming activities of the copepods. The chains of *Chaetoceros pseudocurvisetus* and *Thalassiosira rotula* are much more fragile than those of *Stephanopyxis palmeriana*. Hence, *C. helgolandicus* is probably more likely to accidentally break longer chains in *T. rotula* and *C. pseudocurvisetus* than in *S. palmeriana*. Hence, true selective feeding on the longer chains of *Stephanopyxis* seems to be likely.

These experiments clearly show that female *Calanus*

*helgolandicus* do not feed preferentially on the most abundant and suitable food organism, but select *Chaetoceros pseudocurvisetus*, whose spiny shape occupies a greater space. The results are particularly important because spiny forms such as *Chaetoceros* frequently dominate in the phytoplankton. More research on 'actual' and 'encounter' volumes is called for before we can deepen our understanding of trophic relationships in the pelagic ecosystem.

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