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SIZE AND PHYTOPLANKTON SELECTION BY OOSTERSCHELDE ZOOPLANKTON*

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ABSTRACT

Grazing of adults of the copepods *Acartia* spp., *Temora longicornis*, *Centropages hamatus* and nauplii of *Balanus* spp. on natural particulate matter from the Oosterschelde was studied using a Coulter counter. Two types of particulate matter distributions were found to occur in the Oosterschelde: 1. distributions with distinct peaks in the >20 μm size range (A) and 2. more flattened distributions which were bell-shaped or contained multiple small peaks spread over the entire 4-100 μm size range (B). In A-type distributions, peak tracking was performed in all species studied, especially in *Acartia* spp. and *T. longicornis*. In B-type distributions, the animals tended to spread their grazing activity towards the smaller particles.

Quantitative microscopical analysis of the phytoplankton distributions shows that A- and B-type distributions were caused by the presence (A) or absence (B) of blooms of phytoplankton species with an SED of >20 μm, reaching concentrations of $>1.40 \cdot 10^6$ $\mu m^3 \cdot cm^{-3}$.

The demonstrated clearance rate distributions are shown to result in a concentration of phytoplankton in the ingested material as compared to the medium for all copepod species studied. *Balanus* spp. nauplii did not demonstrate this systematic selection of phytoplankton. When B-distributions occurred, only *Acartia* spp. switched its feeding activity towards smaller particles to such a degree that a substantial contribution of the <20 μm size range to the ingested material resulted. Whether this behaviour represents a higher selection capacity for small phytoplankton species or a detritivorous behaviour remains an open question.

1. INTRODUCTION

Studies of zooplankton feeding on naturally occurring particulate matter with electronical particle counters have repeatedly demonstrated the capability of adult pelagic copepods to feed on a broad range of particle sizes. Usually, within this range, selection of larger particles and peaks of particulate matter is reported (POULET, 1973, 1974, 1978; RICHMAN *et al.*, 1977; COWLES, 1979; GAMBLE, 1978). Because microscopical observation has shown the presence of phytoplankton species of appropriate size, this peak selection is interpreted as a selection of phytoplankton (POULET, 1973; GAMBLE, 1978). In recent years, the capacity of copepods to actively select phytoplankton cells has been demonstrated by high speed cinematography (PRICE *et al.*, 1983; PAFFENHÖFER *et al.*, 1982).

On the other hand, ATP and chlorophyll-based determinations of the relative importance of living and non-living carbon in the diet of copepods have shown the latter to be an important component (POULET, 1976; CHERVIN, 1978; CHERVIN *et al.*, 1981 and earlier references in these papers). This is especially so in coastal and estuarine ecosystems, where detritus forms a major part of the particulate suspended matter. So at present, there is relatively little quantitative knowledge on the role of the different components of particulate matter as food source to coastal or estuarine zooplankton.

This paper reports the results of a series of experiments designed to obtain quantitative information on the relative role of phytoplankton and detritus, and of particle size in the diet of the dominant zooplankton species in an estuarine system (S.W. Netherlands).

There are several copepod species of the genus *Acartia* (*A. bifilosa, A. clausi* and *A. tonsa*) and nauplii of the cirripeds *Balanus balanoides* and *B. crenatus* in the inner part of the estuary, whereas the copepods *Temora longicornis* and *Centropages hamatus* occur in the outer part of the estuary. In the grazing measurements no distinction of species was made for *Acartia* spp. and *Balanus* spp.

This study was carried out as part of an ecological survey programme accompanying the construction

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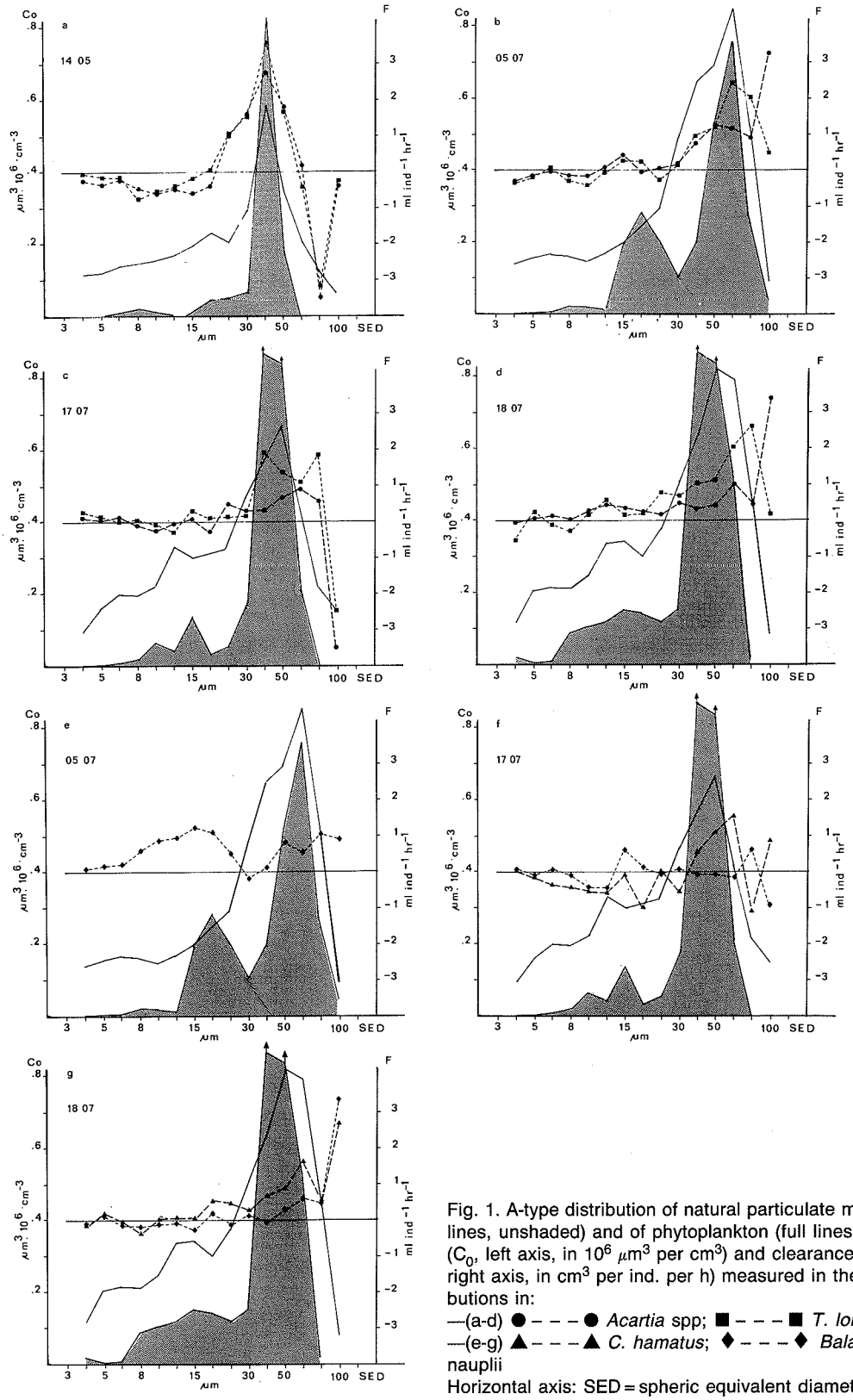

Fig. 1. A-type distribution of natural particulate matter (full lines, unshaded) and of phytoplankton (full lines, shaded) (C_0, left axis, in 10^6 μm^3 per cm^3) and clearance rates (F, right axis, in cm^3 per ind. per h) measured in these distributions in:
—(a-d) ● – – – ● *Acartia* spp; ■ – – – ■ *T. longicornis*
—(e-g) ▲ – – – ▲ *C. hamatus*; ♦ – – – ♦ *Balanus* spp. nauplii
Horizontal axis: SED = spheric equivalent diameter in μm.

of a storm-surge barrier in the seaward part of the Oosterschelde. Results presented in this paper are restricted to the aspect of selectivity of grazing.

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2. MATERIAL AND METHODS

Experiments were carried out during the growing season of 1985. Oosterschelde water was collected in the inland part of the estuary with a 5-dm^3 water sampler at 0.5 m beneath the surface. Zooplankton was caught with a 300 μm net at the same depth.

In the laboratory, the water was filtered through a 150 μm screen and animals were sorted into groups of 50 individuals (adult copepods of one species or *Balanus* spp. nauplii) and put in beakers containing 100 cm^3 of 150 μm screened Oosterschelde water. Each group of animals was then brought into a plastic container filled with 1325 cm^3 of 150 μm screened Oosterschelde water. A number of control containers were filled with the same volume of water. From these containers 4 samples of 50 cm^3 were taken with a pipette for determination of particle concentration at time 0 of the experiment. The remaining volume was poured into 1125 cm^3 glass flasks, which were mounted on a wheel and rotated at 2 rpm for 6 h in the dark. Temperature was kept constant at the value measured *in situ* at the time of sampling.

At the end of the experiment, 4 samples of 50 cm^3 were taken from each bottle for Coulter counter analysis.

In each experiment 2 control bottles were used. Grazing bottles were usually taken in triplicate. In a few experiments, the low abundance of some zooplankton species necessitated a reduction in the number of replica grazing bottles.

Particle concentrations were measured with a Coulter counter model TAII, equipped with 100, 280 and 560 μm aperture tubes. This combination of tubes allowed reliable analysis within the 4 to 100 μm size range of the particulate matter.

Clearance and ingestion rates were calculated according to FROST (1972). Because the time-0 samples sometimes showed substantial differences in particle concentrations between control and grazing bottles, values of particle concentration at the end of the experiment were calculated as:

$$C^* = C_{z0} \cdot e^{kt} \qquad (\mathrm{p \cdot cm^{-3}})$$

with C_{z0} = particle concentration in a given grazing bottle at time 0 and

$$k = 1/t \; ln \; C_t / C_0 \qquad (\mathrm{h^{-1}})$$

where

C_0 = average particle concentration in the control bottles at time 0

C_t = average particle concentration in the control bottles at time t

t = grazing time (h)

When no differences occur between C_0 and C_{z0}, this formula is equivalent to the original formula of FROST (1972) (TACKX & VAN DE VRIE, 1985). Mean clearance and ingestion rates of replicates were calculated including negative values when such occurred.

At the beginning of each experiment, a sample of 150 μm-screened water was taken and preserved with lugol's solution for microscopical analysis. The method used for counting phytoplankton is given in BAKKER *et al.* (1985).

Size distributions of algae were determined by a similar approach as applied by VAN VALKENBURG *et al.* (1978) and HARBISON & MCALLISTER (1980). Between 20 and 100 cells of each phytoplankton species present in the sample were measured. Cell volumes were calculated according the most appropriate geometric form (BAKKER *et al.*, 1985). From these cell volumes, the frequency distribution (expressed in %) of each phytoplankton species within the Coulter size classes was recorded. By applying this distribution to the cell concentration in the sample, the number of cells of each species falling in a given size class was calculated. Total phytoplankton concentration (in μm^3·cm^{-3}) per class was obtained by adding up volumes of all species present in each size class.

3. RESULTS

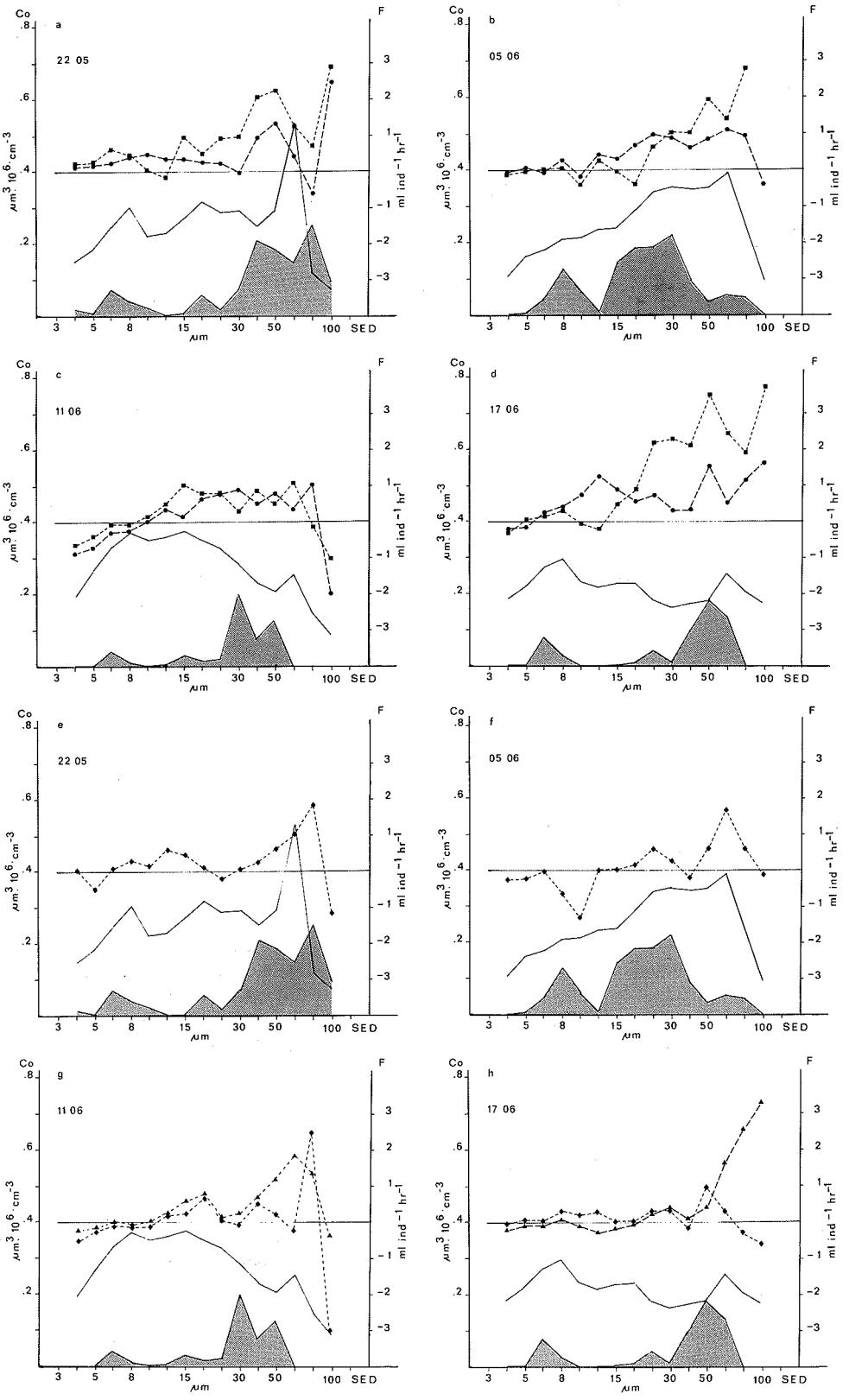
Figs 1 and 2 show the particulate matter distributions measured by Coulter counter and the distributions of phytoplankton within each sample studied, as determined by microscopical analysis. The Coulter counter data enabled us to distinguish two types of particulate matter distributions .

—A) those showing a distinct peak in the size range >20 μm SED (Fig. 1: a-g) and

—B) more flattened distributions, with no, or multiple small peaks, occurring over the entire 4 to 100 μm size range (Fig. 2: a-h).

The microscopical data showed that the A-type distributions contained high concentrations of phytoplankton, of which the bulk is situated in the >20 μm size range. Peaks in this size range mainly consisted of phytoplankton.

The B-type distributions contained less phytoplankton, which was more evenly spread over the entire 4 to 100 μm size range.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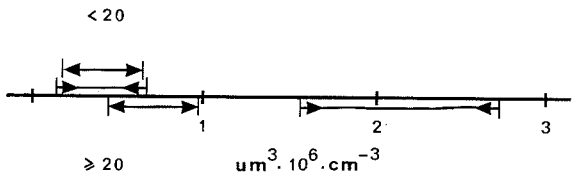

Fig. 3. Ranges of phytoplankton concentrations (in 10^6 μm^3 per cm^3) occurring in the <20 μm and >20 μm size range in ▶——◀ A- and ◀——▶ B-type distributions.

Fig. 3 shows that, while phytoplankton concentrations in the $\leqslant 20$ μm size range overlapped strongly in A- and B-distributions, the concentration of phytoplankton in the $\geqslant 20$ μm size range was significantly higher in the A- than in the B-type distributions (Mann-Whitney test, $p<0.05$). Thus, A-type distributions were caused by blooms of phytoplankton species with a SED of >20 μm, obtaining concentrations of more than $1.4 \cdot 10^6$ $\mu m^3 \cdot cm^{-3}$ in the 20 to 100 μm size range.

In both A- and B-type distributions, the <20 μm size range was dominated by flagellates and small pennate chain-forming diatoms, while centric diatoms, including large chain-forming species, prevailed in the >20 μm size range.

Clearance rate curves for all species studied are also presented in Figs 1 and 2. For clarity, only mean values of the replicates in each experiment were drawn. When feeding on A-type distributions, both *Acartia* spp. and *T. longicornis* exerted high clearance rates on the peaks in the >20 μm size range (Fig. 1: a-d).

C. hamatus and *Balanus* spp. nauplii showed a similar, but less consistent, feeding pattern in this type of distributions (Fig. 1: e-g).

In the B-type distributions, all species studied extended their feeding activity over a broader size range. While the highest clearance rates were generally still measured in the >20 μm size range, a distinct feeding activity was also measured on particles <20 μm (Fig. 2: a-h).

The percentage of phytoplankton (% PI) in the ingestion of the animals was calculated from the data presented in Figs 1 and 2 as:

$$\%PI = \sum_{i=1}^{n} pi \cdot xi$$

With

n = number of size classes in which grazing occurs

pi = fraction of particulate matter concentration made up by phytoplankton in size class i

xi = percentage of total ingestion obtained from size class i

This calculation provides a minimal estimation of the percentage of phytoplankton in the ingestion, as it is based only on the occurring distributions of ingestion rate among the size classes, and possible active selection of phytoplankton in disproportion to its concentration within a given size class is not taken into consideration.

The percentages obtained were plotted against the percentage of phytoplankton present in the medium

$$(PC_0 = \sum_{n=1}^{15} pi^*100)$$

in Fig. 4.

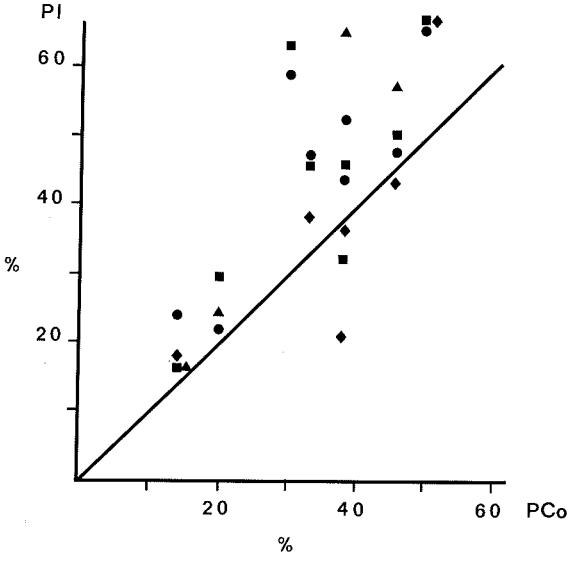

Fig. 4. Percentage of phytoplankton in the ingestion (PI) as a function of percentage of phytoplankton in the medium (PC_0) for the following taxa: *Acartia* spp.: ●, *T. longicornis*: ■, *C. hamatus*: ▲ and *Balanus* spp. nauplii: ◆.

Fig. 2. B-type distribution of natural particulate matter (full lines, unshaded) and of phytoplankton (full lines, shaded) (C_0, left axis, in 10^6 μm^3 per cm^3) and clearance rates (F, right axis, in cm^3 per ind. per h) measured in these distributions in:
—(a-d) ●– – –● *Acartia* spp; ■– – –■ *T. longicornis*
—(e-g) ▲– – –▲ *C. hamatus*; ◆– – –◆ *Balanus* spp. nauplii
Horizontal axis: SED = spheric equivalent diameter in μm.

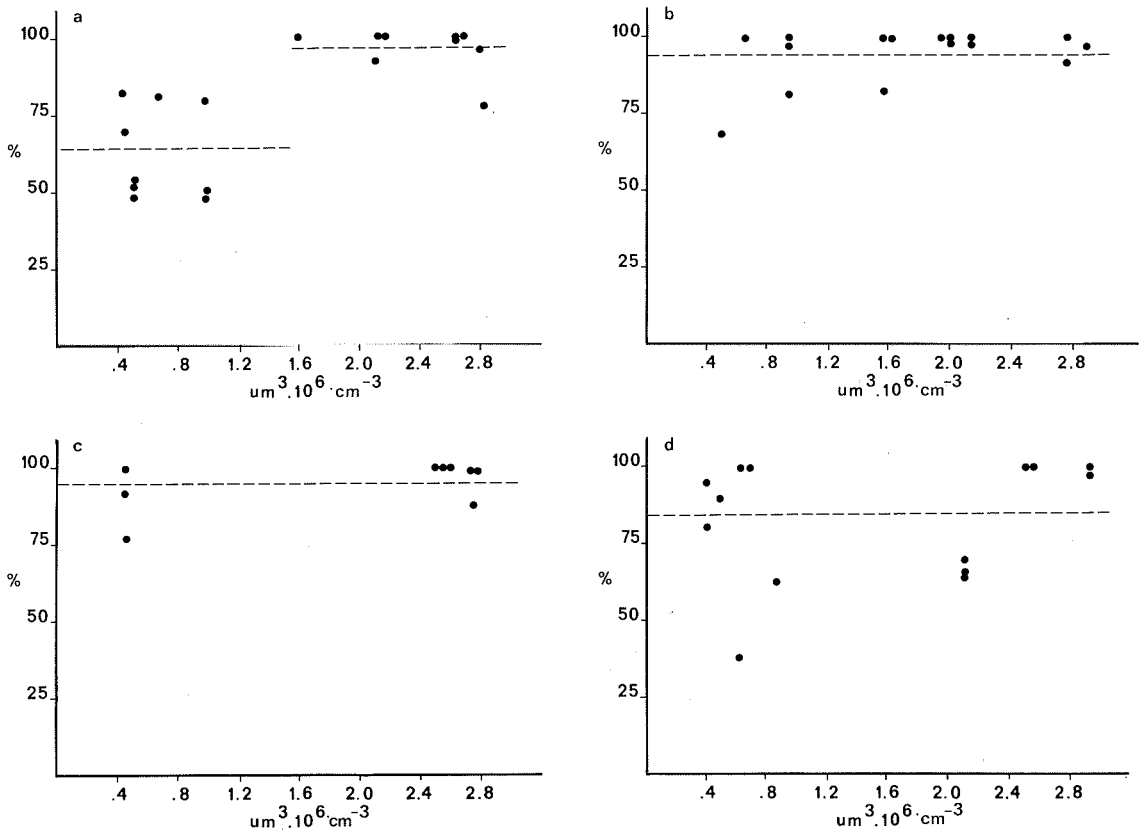

Fig. 5. Percentage of the ingestion (in volume) obtained from the ≥ 20 μm size range as a function of phytoplankton concentration (in 10^6 μm^3 per cm^3) in the ≥ 20 μ size range, as observed in a) *Acartia* spp.; b) *T. longicornis*; c) *C. hamatus* and d) *Balanus* spp. nauplii.

The position of the data relative to the bisector shows that all copepod species studied concentrated phytoplankton in their ingestion (compared to the proportion in the medium). Within each experiment, no obvious differences in apparent concentration of phytoplankton between the different zooplankton species studied were detectable, except a slight tendency of *Balanus* spp. nauplii to obtain smaller amounts of phytoplankton than copepods.

To evaluate the result of the difference in clearance rate distribution on A- and B-type distributions in terms of amounts of particulate matter removed from the ⩽20 and >20 μm size range, the ingestion rate obtained from the >20 μm size range was calculated as percentage of total ingestion rate (in volume). These percentages were plotted against phytoplankton concentration in the >20 μm size range in Fig. 5: a-d. In this figure, x values above and below $1.4 \cdot 10^6$ $\mu m^3 \cdot cm^{-3}$correspond with A- and B-type distribution, respectively. Only *Acartia* spp. (Fig. 5a) had a significantly lower percentage of ingestion obtained from the >20 μm size range when feeding on B-type than on A-type distribution (Mann-Whitney, $p < 0.05$). *T. longicornis* (Fig. 5b) obtained 20 to 30% of its ingestion from the <20 μm size range in some B-type distributions, and fed exclusively on the >20 μm size range in others. In the A-type distributions, *T. longicornis* always fed 90 to 100% on the >20 μm size range. *C. hamatus* (Fig. 5c) fed 90 to 100% on the >20 μm size range when feeding on A-type distributions. In B-type distributions it sometimes obtained a considerable amount (up to 25%) of its ingestion from the <20 μm size range. In *T. longicornis* the average percentages of the ingestion obtained from the >20 μm size range in both A- and B-type distributions did not differ significantly. *Balanus* spp. nauplii (Fig. 5d) obtained varying percentages of their ingestion from the >20 μm size range in both types of distribution. In A- and B-type distributions, the food of *Acartia* spp. consisted on average 96 and 64%, respectively, of >20 μm-sized particles. In both types of distribution, the ingestion of *T. longicornis*, *C. hamatus* and *Balanus* spp. nauplii consisted 93, 94 and 84%, respectively, of the >20 μm size range. *Balanus* spp. nauplii obtained on average only 84% of their ingestion from the >20μm size range.

4. DISCUSSION

The applied combination of Coulter counter data and microscopical phytoplankton analysis allows phytoplankton and seston distributions to be related quantitatively.

The shape of the Oosterschelde seston distributions is essentially determined by the concentration of phytoplankton species with a SED >20 μm. Presence or absence of blooms of these species causes the occurrence of A- or B-type distributions, respectively. Throughout the growing season (April-September), the two types of distributions alternated about 4 to 5 times (unpubl. observations). Below 20 μm SED, high phytoplankton concentrations are rare; in this size range, detritus is the dominant seston component.

In the >20 μm range, we sometimes measured a peak of phytoplankton which was higher than the peak in particulate matter measured by the Coultercounter. Similar methodological problems are mentioned by VAN VALKENBURG *et al.* (1978), who was working on natural seston. The most probable cause of this discrepancy is that the size distribution of the phytoplankton species in question is broader than measured in the subsample.

The general concordance between Coulter counted and microscopically determined SED has been reported by HARBISON & MCALISTER (1980) for several pure algae cultures. However, for some species encountered in natural samples, it is indeed difficult to determine the size distributions, either because they have a shape which is difficult to approach as a known geometric form, or because they are present in low concentrations in the sample. A critical analysis of this methodology is given by BAKKER *et al.* (1985). Based on their findings, great care was taken to optimize the accuracy of both Coulter and microscopical analysis. For the Coulter counter analysis, this was made by using an appropriate combination of aperture tubes, with a ratio less than 4 (VANDERPLOEG, 1981). For the microscopical analysis, care was taken to measure as many cells as feasible for each species, also for species present in low concentrations. With the restrictions mentioned above, this technique provides satisfactory results concerning the matching of phytoplankton and Coulter counter distributions. Its major drawback is its high labour intensity.

In the seston distributions occurring in the Oosterschelde, *Acartia* spp. and *T. longicornis* tend to focus their feeding activity on particles >20 μm. In B-type distributions *Acartia* and, to a much smaller extent, *T. longicornis* and *C. hamatus* extend their grazing activity towards smaller particles. *Balanus* spp. nauplii show a similar, but less consistent, grazing behaviour. On average, they obtain a considerable percentage (16%) of their ingestion from the <20 μm size range. The variability in results obtained with *Balanus* spp. nauplii could be partly caused by the experimental procedure: for each experiment, nauplii of similar size were isolated. This selection criterion is less strict than the selection of adult organisms which was done for the copepod species. Moreover, the selected size of nauplii is influenced by the dominance of (a) certain size class(es) of nauplii in the catch. Consequently, the variability in grazing behaviour measured may, at least to a certain extent, be ascribed to variation at the population level rather than at the individual level.

In our experiments, grazing activity in the <20 μm size range may be masked by particle production in the grazing bottles resulting from either enhanced phytoplankton growth or sloppy feeding on larger particles (DEASON, 1980, and references therein). This effect could bias our findings on the relative contribution of <20 and >20 μm particles to the diet of adult copepods and *Balanus* spp. nauplii. We have attempted to minimize this effect by using a short (6 hours) grazing time and relatively low (50 individuals per 1125 cm^3) animal concentrations in our experiments (ROMAN & RUBLEE, 1980; TACKX & POLK, 1986). Nevertheless, negative average clearance values were sometimes found in the <20 μm size range (Figs 1 and 2), so that some degree of overestimation of the relative importance of the >20 μm size range cannot be excluded completely. However, the results obtained with *Acartia* spp. and *Balanus* nauplii show that considerable feeding activities are detectable in the <20 μm size range with the experimental setup used.

The data presented in Fig. 4 show that the grazing behaviour demonstrated by all copepod species studied results in an "automatic" concentration of phytoplankton in the ingestion: *i.e.* the apparent preference for certain size classes would lead to a selection of phytoplankton cells *versus* detritus, even if particles were selected only on the basis of their size, and not on their nature. The evidence of active phytoplankton selection given in the literature (PRICE *et al.*, 1983; PAFFENHÖFER *et al.*, 1982) makes it quite clear that the observed clearance rate curves are the result of selection based on quality of particles, rather than on size. Nevertheless, it is possible to quantify the minimum degree of such a selectivity by using data such as shown in Fig. 4, which can be obtained by grazing experiments using the particle-count method directly on suspensions of natural particles.

Acartia spp. are the only organisms studied which, when feeding on B-type distributions, obtain a substantial percentage of their diet from the <20 μm size range (Fig. 5a). That phytoplankton concentrations are usually low in the <20 μm range suggests

that *Acartia* spp. are detritivorous under these circumstances. In grazing experiments using ^{14}C-prelabelled natural Oosterschelde seston, clearance rate values obtained for *Acartia* spp. were always lower than for the other species (Daro, unpublished results). CHERVIN (1978) reports that *A. clausi* and *A.tonsa* obtain respectively 31 and 81% of their diet (in terms of carbon) from detritus in the Hudson River estuary (U.S.A.). ROMAN (1984) has shown that addition of detritus obtained from the macrophyte *Thalassia testudinum* to a phytoplankton diet can increase the growth rate of *A. tonsa* and decrease its mortality.

On the other hand the size at which algal cells can be individually detected and captured increases with copepod size (PRICE & PAFFENHÖFER, 1986). The maximal dry weights found for *Acartia* spp. in the Oosterschelde amounted to 20.2 μg ind^{-1}, while the dry weight of *Temora longicornis* ranged from 10 to 54 μg ind^{-1} (BAKKER & VAN RIJSWIJK, 1987). Hence it seems possible that *Acartia* spp. more readily switch their feeding activity to the <20 μm size range, because they are more efficient in detecting and capturing the algal cells present in this range.

So, from the data presented here, it is not possible to determine whether the switching of feeding activity to smaller-sized particles in situations where abundant phytoplankton peaks of >20 μm SED are absent is the result of selection of smaller phytoplankton species, or of a more detrivorous behaviour.

The tendency of *Acartia* spp. to feed more readily on small particles than the other dominant copepods in the Oosterschelde could represent a competitive advantage in situations where B-type distributions prevail.

Although literature data suggest a herbivorous diet for cirriped nauplii (MACKAS & BOHRER, 1976; YULE, 1986), the clearance rate distributions of *Balanus* spp. seem less linked with phytoplankton than those of the copepod species studied. Like the other dominant genus in the inland part of the Oosterschelde, *Acartia* spp., *Balanus* spp. tend to feed more on smaller particles (16% on average) than the species typical of the outer part of the estuary (*T. longicornis* and *C. hamatus*).

Integration of these results into the carbon cycling and ecological functioning of the Oosterschelde system will be presented elsewhere.

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