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Uptake of sub-micrometre- and micrometre-sized detrital particles by bacterivorous and omnivorous ciliates

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ABSTRACT: We used a new model type of detritus to observe and quantify the uptake of detrital particles by bacterivorous and omnivorous ciliates. It consisted of freshly prepared, fluorescently labeled dead organic particles. To represent autochthonous dead organic matter we chose the diatom *Cyclotella meneghiniana*, the green algae *Monoraphidium minutum* and *Scenedesmus acutus*, the copepod *Cyclops abyssorum praealpinus* and leaves of the macrophyte *Elodea canadensis*. Leaves of the copper beech *Fagus sylvatica* and grass stalks of *Poa annua* were considered as allochthonous detritus. The different types of organic matter were stained with the fluorescent dye DTAF and artificially disrupted to produce 7 different kinds of fluorescently labeled detritus (FLD) with a size spectrum of 0.2 to 20 µm (depending on the organic material we used). The uptake of 6 different kinds of FLD by the ciliates *Dexiostoma campylum* and *Paramecium caudatum* was demonstrated. Furthermore, a size dependent uptake of FLD was observed for the ciliate *D. campylum* and ciliates of the *Stylonychia mytilus* complex. Our study suggests that fine particulate detritus can be an additional food source besides bacteria or other picoplankton in the pelagic zone of lakes. This may increase the complexity of microbial food webs as well as the decomposition rate of particulate detritus.

KEY WORDS: Ciliates · Feeding · Detritivory · Detritus · Protozoa · Sub-micrometre particles

INTRODUCTION

Detritus has generally been considered only as a part of the decomposer food chain parallel to the grazing food chain. The idea of the present study was to investigate whether or not detritus can be incorporated directly into the microbial food web by suspension-feeding ciliates. In particular, sub-micrometre- and micrometre-sized detrital particles seem to be an important part of dead particulate organic matter (POM) in aquatic ecosystems (Lenz 1972, Wotton 1984, Georgi 1985). According to Koike et al. (1990), the abundance of sub-micrometre particles (0.36 to 1.0 µm) in the ocean is often higher than the abundance of bacteria. In lakes sub-micrometre particles in the size range 0.2 to 0.7 µm can represent 3 to 30% of what has been considered as dissolved organic matter (DOM) (Middelboe & Søndergaard 1995). These particles have often been neglected due to the use of GF/F filters for measuring DOM. Sub-micrometre particles can partly pass this type of filter, although they do not really belong to the dissolved fraction of organic material (Søndergaard & Middelboe 1993). Besides the sub-micrometre particles there is a large pool of dead organic matter in the size range of a few µm (Lenz 1972, Georgi 1985, Melack 1985 and references therein).

As laboratory studies have shown, the autochthonous and allochthonous origin of these particles as well

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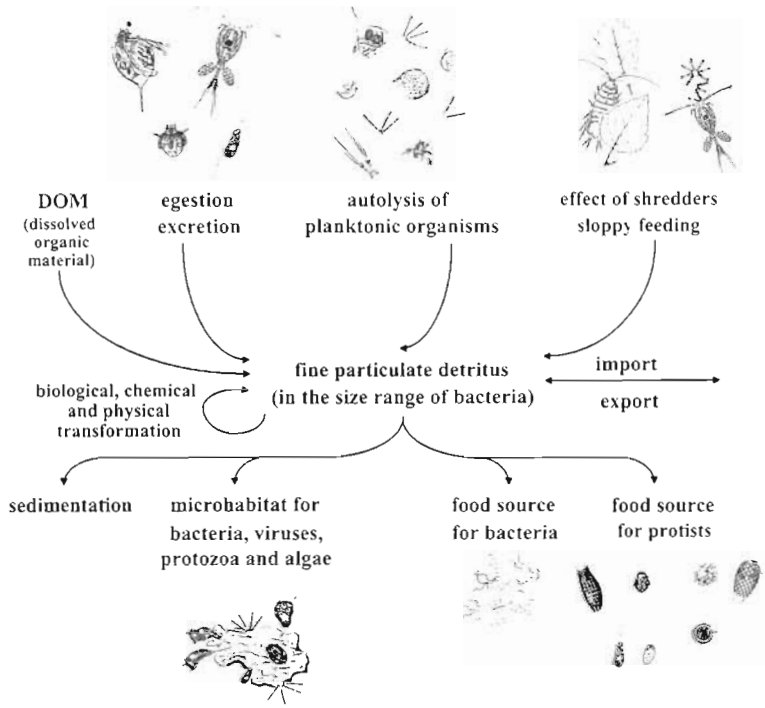

Fig. 1 Possible mechanisms for the formation and transformation of sub-micrometre- and micrometre-sized detrital particles and their importance as a habitat and a food source in the microbial food web

as the biological, chemical and physical mechanisms responsible for the formation of this kind of detritus are very complex (Fig. 1): (1) Particle formation out of dissolved organic matter by air bubbles (Johnson & Cooke 1980) or by aggregation of dissolved compounds to and onto detrital particles of every size range (Kepkay 1994). (2) Formation of fragile, fine particulate detritus in the size range of picoplankton by egestion and excretion. This was shown for phytoplankton (Passow & Alldredge 1994), for flagellates (Elbrächter 1991), for ciliates (Stoecker 1984) and also for cladocerans (Kersting & Holterman 1973, Lampert 1978, Olsen et al. 1986). (3) Particle formation by autolysis of small planktonic organisms caused by senescence or parasitism (e.g. by viruses; Suttle et al. 1990). (4) Formation of particles by feeding processes (shredding, sloppy feeding; Lampert 1978). The particle spectrum itself is continuously transformed by physical, chemical and biological processes (Wotton 1984). Furthermore, detrital particles with a diameter of several µm and larger provide a potential microhabitat for colonizing bacteria and protozoa (Fenchel 1970, Silver et al. 1984, Grossart & Simon 1993). Even very small detrital particles in the size range of only a few µm are important substrates for attached bacteria (Pedrós-Alió & Brock 1983) and may in this way become a more attractive food source for flagellates and ciliates. However, it is not clear yet if the smallest size class of detrital particles (sub-micrometre) is also colonized by microbes.

Although detritivory is often reported to occur among protozoa (Kahl 1930–1935, Sandon 1932, Gast 1985, Fenchel 1987, Sherr & Sherr 1992) there are nearly no data available on the quality and quantity of the dead organic material protozoa can ingest. This is astonishing because there is a large pool of fine particulate detritus in the pelagic zone, which ciliates and flagellates should be able to graze upon. It is well known that many ciliates (Fenchel 1980, 1986) and flagellates (Marchant & Scott 1993) ingest pico-sized and even smaller particles such as colloids (Sherr 1988, Tranvik et al. 1993) and viruses (González & Suttle 1993). In this study we investigated the direct uptake of non-colonized particles by ciliates. Different kinds of fluorescently labeled detritus (FLD) originating from algae, plants, macrophytes and zooplankton were tested as a potential food source for suspension-feeding ciliate species.

MATERIALS AND METHODS

Cultivation of ciliates. All batch cultures were kept at a temperature of 20°C and in continuous dim light. The hymenostome ciliate species *Dexiostoma campylum* (syn. *Colpidium campylum*; see Ganner & Foissner 1989) and *Paramecium caudatum* were cultivated in 10 ml glass tubes and fed with bacteria growing on wheat grains. As cultivation medium we used 0.2 µm prefiltered autoclaved tap water. Cultures of *D. campylum* were kindly provided by M. Macek (Institute of Hydrobiology, Czech Academy of Sciences, České Budějovice). *P. caudatum* and hypotrich ciliates of the *Stylonychia mytilus* complex were isolated from a culture of the isopod *Asellus aquaticus* cultivated at the Institute of Limnology in Mondsee (Austria). For the *S. mytilus* culture, we used 0.2 µm prefiltered lake water from Lake Mondsee and fed with *Chlamydomonas reinhardti* cells growing in a modified Woods Hole MBL medium (K. O. Rothhaupt pers. comm.). Cell dimensions of each species were measured from cells fixed with Lugol's solution (0.5% final conc.) and formaldehyde (3% final conc.; Sherr et al. 1989) using bright-field microscopy. *D. campylum* mean cell size (mean ± SD) was 53 ± 6 × 24 ±

3 µm and a cell volume of 16000 µm^3 was calculated (n = 300). *P. caudatum* had a mean cell size of 202 ± 3 × 60 ± 6 µm, corresponding to a cell volume of 380800 µm^3 (n = 120). The mean cell size of *S. mytilus* was 141 ± 21 × 50 ± 7 µm with a mean volume of 185000 µm^3 (n = 160).

Origin of the detrital material. The green algae *Monoraphidium minutum* and *Scenedesmus acutus* and the diatom *Cyclotella meneghiniana* were grown in a modified Woods Hole MBL medium in a chemostat system under constant conditions (temperature 20°C, continuous light). Cultures of the algae were kindly provided by K. O. Rothhaupt (Max Planck Institute of Limnology, Plön, Germany). Copepods (*Cyclops abyssorum praealpinus*) were collected by net from Lake Mondsee in February 1994. Living animals were isolated in a light trap according to Behrendt & Krocker (1990). Leaves of the macrophyte *Elodea canadensis*, dry leaves of the copper beech *Fagus sylvatica* and fresh grass stalks of *Poa annua* were collected in the Lake Mondsee area in February 1994. Plants were cut into small pieces before staining. *C. a. praealpinus*, *C. meneghiniana*, *E. canadensis*, *M. minutum* and *S. acutus* were considered to represent autochthonous material and *F. sylvatica* and *P. annua* allochthonous material.

Staining procedure. The organic material was fluorescently labeled by a slightly modified method for the staining of bacteria described by Sherr et al. (1987) with 5-(4,6-dichlorotriazin-2-yl)aminofluorescein (DTAF, Sigma). Before staining, each type of organic material was washed and centrifuged. Staining time was 6 h at a temperature of 45°C and 0.25 mg of DTAF was added to 1 ml suspension of each type of organic matter. For storage the labeled material was frozen in small plastic vials. For each experiment the thawed fluorescently labeled material was homogenized for 2 to 3 min (Ultraturrax homogeniser) and sonicated (3 short pulses with maximal intensity) to produce fluorescently labeled detritus (FLD) with an equivalent spherical diameter (ESD) of 0.2 to 20 µm. Particle counting was done by filtering 0.5 to 1 ml of the feeding suspension on a black polycarbonate filter (Nucleopore-Costar) with a pore size of 0.2 µm. At least 200 particles were counted by epifluorescence microscopy with a Zeiss Axioplan under blue excitation [excitation filter (BP) 450 to 490 nm, beamsplitter (FT) 510 nm, barrier filter (LP) 520 nm]. The size of the particles was measured with an ocular micrometer. In one experiment an automatic image analysis system (LUCIA M, Nikon) was used to determine size distributions of 6 different types of FLD. In addition, 0.5 to 1 ml of each feeding suspension was counted by bright-field microscopy using small settling chambers to control the ratio of stained to unstained particles.

Determination of FLD uptake. Ciliates of the species *Dexiostoma campylum* and *Paramecium caudatum* show a strong negative gravitaxis. Thus they could be separated from bacteria by upward migration into sterile medium through cotton wool (over 4 to 6 h). During this time ciliates had to live in a nearly food-free medium. Therefore animals were most probably starved at the beginning of the experiments. Living ciliates of the *Stylonychia mytilus* complex were collected under the microscope using a micropipette and transferred into 0.2 µm prefiltered lake water to separate ciliates from their food organisms. Ciliates were kept in this food-free medium for 2 h before we started the experiments. A 0.5 ml volume of the cleaned *D. campylum* (~3500 cells) or *P. caudatum* (~500 cells) ciliate culture was added in 4 parallels to 2 ml plastic vials mounted on a rotation wheel (1 rpm) to avoid settling of food particles. After 15 min the experiment was started by adding 1 ml of the prepared feeding suspension. In the experiments with *S. mytilus*, 3 ml of feeding suspension was added to 2 ml (~40 cells) of the ciliate culture. For both single point and time course experiments, we prepared 4 parallel vials for each uptake measurement. To stop feeding, ciliates were fixed with Lugol's solution (0.5% final conc.) followed by immediate addition of formaldehyde (3% final conc.; Sherr et al. 1989). A part of the sample (300 to 500 µl) was filtered on a 0.8 µm pore size black polycarbonate filter (Nucleopore-Costar). Fixed *S. mytilus* cells were collected under the microscope using a micropipette and placed on the filter. Filters were washed 3 times with 5 to 10 ml 0.2 µm prefiltered tap water. The ciliates were stained with 4',6-diamidino-2-phenylindole (DAPI, Merck) and the filter was mounted with silicon oil (for gas chromatography, Merck) between a slide and a coverslip. A total of 50 (*D. campylum*, *P. caudatum*) or 25 (*S. mytilus*) ciliates per sample were counted under UV excitation (BP 365, FT 395, LP 397) and sizes of ingested particles were measured with an ocular micrometer under blue excitation at a magnification of 500 to 1250×. Uptake selectivity for different size classes of FLD was calculated according to Jacobs (1974):

$$D = \frac{r - p}{r + p - 2rp} \quad (1)$$

where D is a selectivity index (relative difference in uptake), r is the proportion of a particular food component ingested by the animal, and p is the proportion of this component in the food suspension. When $D = 0$ there is no preference for this food type. Selective uptake of a food component is reflected in a D-value between 0 and +1. D-values between 0 and −1 indicate negative selection of a food type with respect to total available food.

RESULTS

Characteristics of the fluorescently labeled detritus (FLD)

In our preliminary experiments we noticed differences between the various FLD suspensions with respect to the shape of the particles, the intensity of the fluorescence and the ratio of stained (50 to 80%) to unstained (20 to 50%) particles within the food suspensions. Therefore we observed in our first experiment only the visible uptake of 6 different types of detritus but were not able to give a quantification of the total ingestion. For another experiment we chose the *Cyclops abyssorum praealpinus* FLD because of its larger size range (0.2 to 15.4 µm ESD) and its relatively constant ratio of about 80% stained to 20% unstained particles. In the last experiment the *Scenedesmus acutus* FLD was chosen as model detritus whereby nearly 95% of the particles were stained. By using this type of FLD a first quantification of the uptake of detritus was possible.

Ingestion of six different types of detritus by *Dexiostoma campylum* and *Paramecium caudatum*

The size distribution of the offered suspensions was similar for all types of FLD with maximum abundances of particles in the smallest size class (0.2 to 3 µm ESD). An exception was the food suspension of *Monoraphidium minutum* detritus (Fig. 2) in which the applied method for disrupting the cells was not effective. Total food concentrations (consisting of stained and unstained material) ranged from 0.4 to 2.3 × 10^6 particles ml^{-1} and the ratio of stained to unstained particles was not constant (see above). FLD uptake was described as the percentage of examined ciliates with ingested FLD particles after a feeding period of 15 min (Fig. 3a). In addition the numbers of vacuoles with at least 1 ingested FLD particle were counted (Fig. 3b). Both species consumed all types of detritus irrespective of the origin of the material. Generally *Paramecium caudatum* showed higher percentages of cells with ingested FLD and higher numbers of vacuoles containing FLD. This may be due to the larger cell size of *P. caudatum* in comparison to *Dexiostoma campylum*. Lower percentages of *D. campylum* cells with incorporated *M. minutum* FLD may be caused by high abundances of particles >3 µm ESD in this food suspension which were not consumed by *D. campylum* (see below).

Comparison of the feeding behaviour of *Dexiostoma campylum* and ciliates of the *Stylonychia mytilus* complex

Dexiostoma campylum is known as a typical bacterivorous ciliate (Laybourn & Stewart 1975, Taylor & Berger 1976). *Stylonychia mytilus* is considered as a typical omnivorous species (Pfister & Arndt 1995). *Cyclops abyssorum praealpinus* FLD was used for these experiments because this detritus consisted of a broad size spectrum of particles ranging from <0.4 to 15.4 µm ESD. Nine size classes were created and the frequency of each size class to the total FLD number was determined (Fig. 4a). After 15 min ingestion time, ciliates were fixed and the ingested FLD particles were sized using an ocular micrometer. For each size class we calculated the ratio of ingested to totally available particles. Using Jacobs' (1974) Selectivity Index,

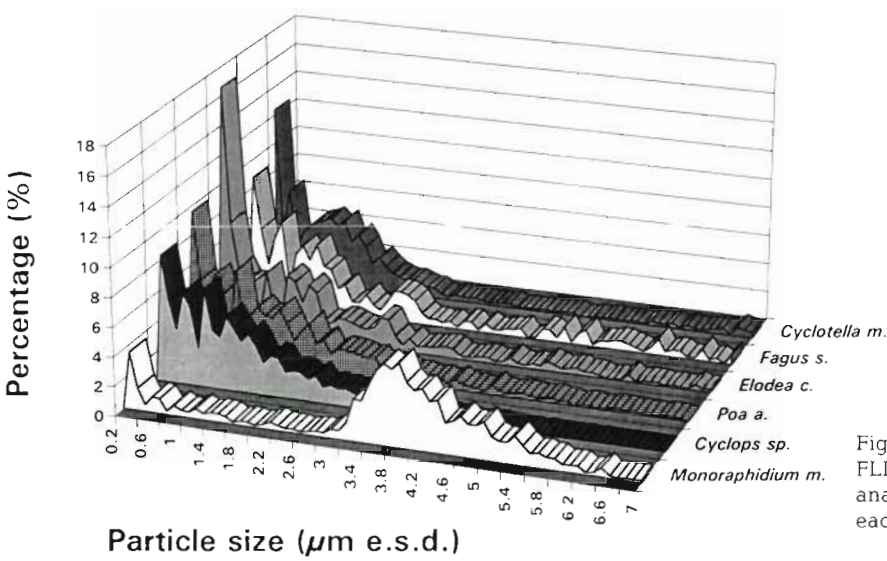

Fig. 2. Size spectrum of 6 different kinds of FLD particles measured by automatic image analysis. The relative contribution (%) of each size class to the total number of every kind of detritus is shown

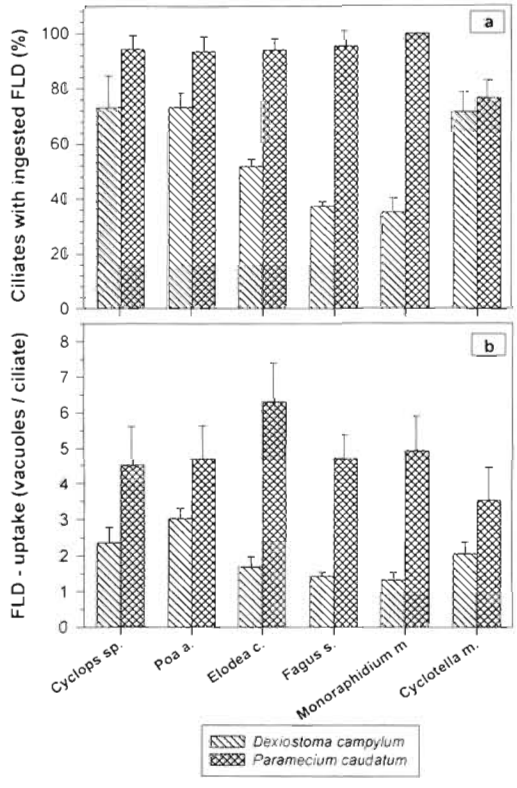

Fig. 3. *Dexiostoma campylum* and *Paramecium caudatum*. (a) Percentage of individuals with ingested FLD particles (mean of the 4 parallel vials + SD). (b) Numbers of vacuoles with at least 1 ingested FLD particle per ciliate (mean of the 4 parallel vials + SD)

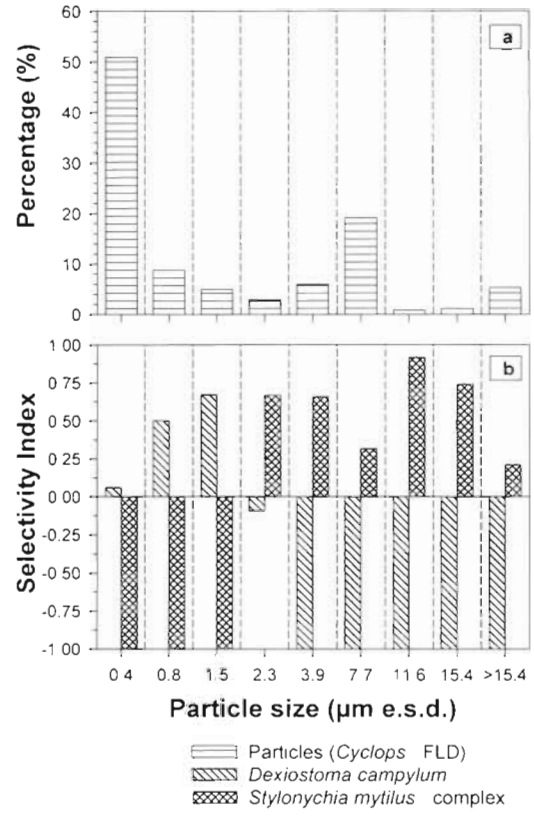

Fig. 4. (a) Size spectrum of FLD particles obtained from homogenized, DTAF-stained copepods *Cyclops abyssorum praealpinus*. The relative contribution (%) of each size class to the total abundance is shown. (b) Comparison of the size-selective feeding of *Dexiostoma campylum* and a ciliate clone of the *Stylonychia mytilus* complex offered *C. a. praealpinus* FLD

D. campylum was found to prefer particles in the size range 0.8 to 1.5 µm whereas *S. mytilus* did not ingest particles smaller than 1.5 µm (Fig. 4b). There was a clear separation of the food size niches of both species.

Time series of FLD uptake by *Dexiostoma campylum* using *Scenedesmus acutus* FLD

The feeding suspension consisted of FLD particles with an ESD of 0.2 to 1.3 µm. A particle concentration of 9.7×10^5 particles ml^{-1} corresponded to a total detrital volume of about 8.0×10^4 μm^3 ml^{-1}. Size-selective feeding was examined in the course of 20 min. There was already a reduction of FLD uptake after 5 min. The ingestion rate was approximately constant from 0 to 5 min and from 5 to 20 min (Fig. 5). Therefore 2 linear regressions were calculated. By the first regression (0 to 5 min) an uptake rate of 39.5 particles $ciliate^{-1}$ h^{-1} and a clearance rate of 40.7 nl $ciliate^{-1}$ h^{-1} were determined. A cell volume-specific clearance rate (VSCR) of 2.5×10^3 h^{-1} was calculated. From the second regres-

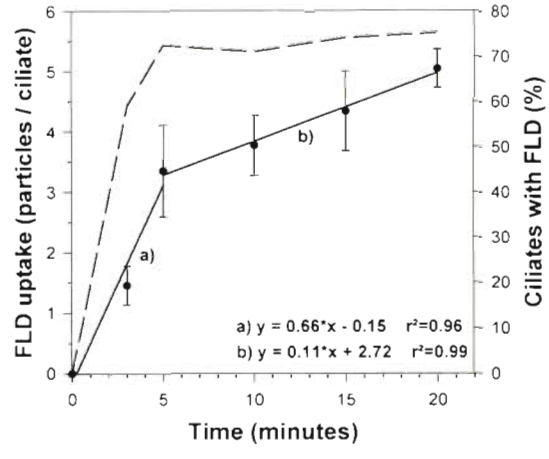

Fig. 5. Time-dependent uptake of *Scenedesmus acutus* FLD particles by *Dexiostoma campylum* (●, mean of the 4 parallel vials ± SD). Two regression lines were calculated: (a) 0 to 5 min, (b) 5 to 20 min. Particle uptake (y) was assumed to be a function of time (x). (— —) Percentage of examined ciliates with ingested particles

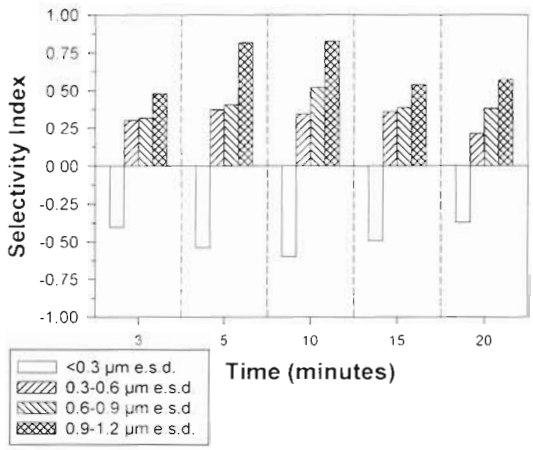

Fig. 6. Size-selective feeding behaviour of *Dexiostoma campylum* on *Scenedesmus acutus* FLD particles during the time course experiment (0 to 20 min)

sion (5 to 20 min), we calculated an uptake rate of 9.3 particles ciliate^{-1} h^{-1} and a clearance rate of 9.6 nl ciliate^{-1} h^{-1} (VSCR = 6×10^2 h^{-1}). The percentage of ciliates containing FLD particles remained fairly constant after 5 min of the experiment (Fig. 5). We noted a strong uptake preference for the largest particle size class (0.9 to 1.3 µm ESD). Selectivity did not significantly change with time (Fig. 6).

DISCUSSION

Detritivory or detritivory as a part of omnivory has often been reported to occur among planktonic protozoa, especially ciliates (Kahl 1930–1935, Sandon 1932, Gast 1985, Fenchel 1987, Sherr & Sherr 1992). Its significance as a food source, however, is not well understood, for many reasons. Firstly, there is a problem with the definition of the term detritus, and there is no reliable method to quantify dead organic matter in aquatic energy fluxes (Lenz 1972, Melack 1985). Generally, the measurement of uptake rates of detrital particles by ciliates is even more difficult. Nevertheless, there are several studies that demonstrate the uptake and assimilation of detritus by cladocerans (Naumann 1918, Rodina 1963, DeMott 1988a), copepods (Paffenhöfer & Knowles 1979, Roman 1984, DeMott 1988b) and rotifers (Starkweather & Bogdan 1980). Ciliates, however, have seldom been examined with regard to the type and quantity of detritus they are able to consume, although not only size-selective feeding of filter-feeding ciliates has been shown (Fenchel 1980, 1986), but also selectivity for surface, shape or taste (e.g. Sanders 1988, Verity 1991). To consider these potentially important qualities of detritus, we offered several model types of FLD rather than using inert particles (FP), microspheres or carbon particles. Of course, the artificial destruction of the organic material is a simplification of the complex decomposition *in vivo* (see Fig. 1). However, simple destruction of pelagic organisms into fine particulate detritus can play an important role in the pelagic environment during sloppy feeding and excretion of crustaceans, which provide significant amounts of easily digestible fractions of phytoplankton (Lampert 1978, Olsen et al. 1986).

All 3 ciliate species were found to consume the offered detrital particles. We can assume that the chosen ciliate species were representative organisms for detritivory, because they are ubiquitous in lakes and rivers and prefer nutrient-rich conditions (Foissner et al. 1994). Therefore, especially at seasonally higher concentrations of natural detrital particles (Middelboe & Søndergaard 1995) or during eutrophication, certain ciliate species are likely to profit from this additional food source. The percentage of *Dexiostoma campylum* individuals which consumed detritus of *Fagus sylvatica* and *Monoraphidium minutum* was lower than the fraction of individuals feeding upon detritus of *Cyclops abyssorum praealpinus*, *Cyclotella meneghiniana*, *Elodea canadensis* and *Poa annua* (Fig. 3a). The lower percentage of *D. campylum* cells incorporating *M. minutum* FLD particles may be caused by size-selective feeding. This kind of detritus had a size distribution different from that of all other kinds of offered detritus, with a predominance of large particles (4 to 5 µm; see Fig. 2). *D. campylum* is known from the literature to feed effectively on very small particles (Fenchel 1980). Our results also showed that *D. campylum* did not consume particles larger than 2.3 µm (Fig. 4b). But we do not know the reasons for the low uptake rates of *F. sylvatica* FLD. On the other hand, we did not find an explanation for the nearly constant feeding behaviour of *Paramecium caudatum* irrespective of food type and the size distributions of the different kinds of detritus (Fig. 3a). Ciliates of the *Stylonychia mytilus* complex, in contrast, only consumed particles larger than 1.5 µm (Fig. 4b). This species is known as a typical omnivore (Pfister & Arndt 1995) Thus not only the lower consumable size but also an upper size limit may contribute to the food niche separation of coexisting suspension-feeding ciliates.

The time course experiment with *Dexiostoma campylum* revealed 2 uptake rates of detrital particles (Fig. 5). Though ciliates had been acclimated to the experimental vials, they were perhaps still stressed at the beginning of the experiment. This may have caused an arbitrary ingestion behaviour (Choi 1994). Massana et al. (1994) noticed an acclimation time of at least 2 h before ciliates showed regular feeding behaviour again. However this does not explain the observed shift, which had already occurred after 10 min. Fur-

thermore, a stress effect should result in lower rather than higher ingestion rates at the beginning of an experiment (Massana et al. 1994). Another explanation may be the establishment of an equilibrium between uptake and egestion after 10 min. On the other hand, there was no atypical size-selective feeding noticed over the 20 min (Fig 6). Therefore the higher uptake rates within the first 5 min were most likely due to a starvation effect as *D. campylum* had to live in a nearly food-free medium for 4 to 6 h prior to the experiment (see above). A comparison of the observed uptake rates with published feeding rates of *D. campylum* (Table 1) showed that in most studies significantly higher food concentrations (bacteria or latex beads) were offered at lower ciliate abundances (Laybourn & Stewart 1975, Fenchel 1980). Similar low food concentrations were used by Sanders (1988) for the scuticociliate *Cyclidium* sp., for which an uptake rate of 23 or 25 microspheres ciliate^{-1} h^{-1} at a food concentration of 4.8 or 5.6 × 10^5 microspheres ml^{-1} was observed. This value is comparable to uptake rates observed during our experiments. In general the concentrations of detrital particles used in our experiments seem to be low in comparison with expected concentrations in nature. Further investigations should pay attention to this fact and perhaps use even higher abundances of detrital particles, which exceed bacterial numbers commonly determined in nature.

Since the discovery of high abundances of submicrometre particulate detritus (Koike et al. 1990, Middelboe & Søndergaard 1995) there has been an open question about the fate of this organic source in pelagic ecosystems. Our results suggest that this size class of detritus should also be considered as an additional food source for ciliates (and probably other protists) besides bacteria and other picoplankton. Living and dead organic matter are probably ingested simultaneously in the form of colonized particles. Even if consumed detrital particles are only partly digested, suspension-feeding ciliates could transform them via excretion with respect to size, shape, coating or aggregation behaviour (cf. Stoecker 1984, Elbrächter 1991). This may contribute significantly to particle transformation and metabolism in pelagic and benthic environments.

Another question concerns the effects of different concentrations of detrital particles on the feeding behaviour of ciliates. Roman (1984) reported a higher feeding activity of copepods fed with diatoms and detritus than those fed only with diatoms; however, a diet consisting only of detritus caused a reduction of the growth rate and/or the reproduction rate (Rodina 1963). Further studies are required to investigate if similar effects can also be observed for suspension-feeding ciliates. Moreover there is a need to determine the nutritive value of these detrital particles (e.g. car-

Table 1. A comparison of the observed uptake rates with published feeding rates of *Dexiostoma campylum*. nd: not determined

Food type	Particle size (µm ESD)	Abundance (ciliates ml^{-1})	Food concentration (particles or bacteria ml^{-1})	Ingestion rate (particles or bacteria ciliate^{-1} h^{-1})	Clearance rate (nl ciliate^{-1} h^{-1})	Source
FLD particles	0.2–1.3	~2300	9.68 × 10^5	9[a]	10[a]	This study
				40[b]	41[b]	
Moraxella (bacterium)	nd	~500	1.25 × 10^8	5208	42	Laybourn & Stewart (1975)
Moraxella (bacterium)	nd	~500	2.00 × 10^9	52083	26	Laybourn & Stewart (1975)
Latex beads	0.36	~50	2.05 × 10^9	53215	26	Fenchel (1980)
Latex beads	0.36	~50	3.68 × 10^{10}	274264	7	Fenchel (1980)

[a]0 to 5 min ingestion time. [b]5 to 20 min ingestion time

bon:volume, carbon:nitrogen ratios) and the assimilation efficiency of protozoa feeding on detritus. Our experiments give new evidence that detrital particles of various origins can be directly incorporated into microbial food webs by suspension-feeding ciliates. This indicates that the division into detritus and grazing food chain is partially artificial and the fate of detritus is more complex than generally considered (Fig. 1).

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