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Role of TEP in the microbial food web structure. II. Influence on the ciliate community structure

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ABSTRACT: The structure of the bacterial population (free vs. attached bacteria), variations in bacterial abundance and ciliate group composition were monitored as a function of transparent exopolymeric particle (TEP) concentration during *Phaeocystis globosa* blooms that developed in mesocosms. Two ciliate groups dominated at different stages of the blooms. The oligotrichous ciliate *Strombidium* spp. were dominant during the growth phase of the blooms, when TEP volume concentration was lower than 20 ppm. The hypotrichous ciliate *Euplotes* spp. emerged and became dominant after blooms peaked, when TEP concentration reached values between 20 and 50 ppm. The succession from *Strombidium* spp. to *Euplotes* spp. was closely related to TEP variation. *Strombidium* spp. depletion was apparently not caused by a reduction of prey availability due to TEP aggregation, as the bacterial concentration increased over time and the fraction of available bacteria for *Strombidium* spp. remained close to 90%, irrespective of variations in TEP concentration. Instead, the results of incubations conducted by adding *S. sulcatum* to seawater collected in the mesocoms suggest that *Strombidium* spp. disappearance may have been caused by direct TEP-mediated aggregation of the ciliates. The emergence of *Euplotes* spp. coincided with the formation of macroaggregates (favored by high TEP concentration), which provide them with the physical support required for feeding on attached bacteria. Our results suggest that variations of the size in the TEP pool may induce a ciliate population succession, modify the size distribution of the bacterial population and ultimately control the microbial food web structure and function.

KEY WORDS: Transparent exopolymeric particles · *Phaeocystis globosa* · Ciliates · *Strombidium* · *Euplotes* · Succession · Microbial food web · Bacteria

INTRODUCTION

Since the discovery of transparent exopolymeric particles (TEP) a decade ago (Alldredge et al. 1993), many studies have focused on the effect of environmental changes on the TEP pool characteristics and distribution. The aims of these previous studies on TEP were to define their source, describe their mode of formation and discuss their fate in relation to ecosystem function. One of the main outcomes was to show that the size of the TEP pool is highly variable and depends on various factors, such as phytoplankton bloom events and seasonal variations (Passow & Alldredge 1994, Riebesell et al. 1995, Mari & Kiørboe 1996, Grossart & Simon 1997, Hong et al. 1997, Mari & Burd 1998, Mari et al. 2001, Passow et al. 2001), growth stage and phytoplankton species (Schuster & Herndl 1995, Grossart & Simon 1997, Hong et al. 1997, Grossart et al. 1998, Mari & Burd 1998, Mari 1999, Passow 2002), turbulent regime (Stoderegger & Herndl 1999, Passow 2000), light regime (Hong et al. 1997) and carbon dioxide concentration (Engel 2002).

Field studies conducted in various regions of the ocean indicate that TEP volume concentration can vary by more than 2 orders of magnitude, depending on the

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trophic status of the area (Passow & Alldredge 1994, Passow et al. 1994, Kiørboe et al. 1998, Mari & Burd 1998) and on phytoplankton bloom dynamics (Mari & Kiørboe 1996, Mari & Burd 1998, Mari et al. 2001). Due to their physico-chemical properties TEP play a key role in coagulation processes (Kiørboe & Hansen 1993, Dam & Drapeau 1995, Mopper et al. 1995, Passow & Alldredge 1995, Hansen & Kiørboe 1997). Consequently, variations in the size of the TEP pool affect the overall particle size spectra by increasing aggregation rates and efficiency (Alldredge & Jackson 1995, Jackson 1995, Jackson & Burd 1998).

As most protozooplankton select their food according to size (Bernard & Rassoulzadegan 1990, Epstein & Shiaris 1992, Sherr et al. 1992, Simek & Chrzanowski 1992, Simek et al. 1994, 1995, 1997, Pernthaler et al. 1996), selective removal of picoplankton-size particles (e.g. bacteria for bacterivorous protozoans) should depend both on the intrinsic particle size and on its stage of aggregation (i.e. inclusion into aggregates and size of the aggregates). As particle size spectra are modified via TEP-mediated coagulation processes, food abundance for a given ciliate group may be affected by changes in TEP volume concentration. Mari & Rassoulzadegan (2004, this volume) showed that the availability of picoplankton-size particles for the ciliate *Strombidium sulcatum* was reduced when TEP volume concentration increased. Whether changes in TEP concentration in the field modify the structure of the microbial food web is still unknown. Enhanced TEP concentration may disadvantage heterotrophic bacterivorous ciliates, such as *Strombidium* spp., by aggregating their food source (Mari & Rassoulzadegan 2004) and the subsequent formation of large aggregates may favor the emergence of ciliate groups adapted to macroaggregate-rich environments, such as Hypotrichida ciliates (Caron et al. 1982, Davoll & Silver 1986, Artolozaga et al. 2000, Woerner et al. 2000).

The aim of this work was: (1) to study changes in the ciliate community structure as a function of TEP concentration during *Phaeocystis globosa* blooms, (2) to examine the repartition of the bacterial population over the size spectra in order to assess the availability of bacteria for micro-grazers, and (3) to discuss the role of TEP produced during *P. globosa* blooms in the community structure of microbial food webs.

MATERIALS AND METHODS

Mesocosms. Three 850 l indoor mesocosms were filled with natural coastal North Sea water enriched with nitrate and phosphate in order to reach the following initial N:P ratios: 16 (40:2.5 µM, Mesocosm 1), 4 (40:10 µM, Mesocosm 2) and 44 (66:1.5 µM, Mesocosm 3). No silicate was added. Total concentrations of the limiting nutrient were determined in order to reach similar a *Phaeocystis globosa* biomass in all 3 mesocosms. *P. globosa* were grown at 15°C, with a 12 h light:12 h dark cycle and under a light intensity of 150 µE m^{-2} s^{-1}. Each mesocosm was inoculated with 1% v/v of an exponentially growing *P. globosa* culture at the beginning of the experiment. The water in mesocosms was kept in motion to prevent sedimentation and wall growth (C. P. D. Brussaard et al. unpubl. data). Chlorophyll *a* data were provided by C. P. D. Brussaard et al. (unpubl. data). This study was part of a large joint effort aimed at investigating the effect of nitrogen to phosphorus ratios on *P. globosa* bloom dynamics during a mesocosm study. Since our objectives within this framework were to describe the effect of TEP pool accumulation on the ciliate community structure, the eutrophication issue was not examined. In our study, we consider the mescosms as experimental triplicates of the role of TEP as a factor controlling the ciliate community structure.

Samples for determination of TEP, bacteria and ciliates were collected from inside each mesocosm during 5 sampling occasions covering the main phases of *Phaeocystis globosa* blooms, i.e. initial phase, early exponential phase, late exponential phase, senescent phase and post senescent phase (i.e. when chlorophyll *a* concentration reached pre-bloom levels). All samples were immediately filtered for TEP and bacteria slides preparation (see following sections).

Incubations. Incubations, aimed at determining the role of TEP as a loss factor for the ciliate *Strombidium sulcatum*, were conducted in triplicate with seawater collected from each mesocosm during the 5 sampling occasions described above (a total of 45 incubations were conducted). Prior to incubation with *S. sulcatum*, seawater was pre-filtered through a 200 µm mesh in order to remove large aggregates and mesozooplankton. The ciliate *S. sulcatum* was added to 250 ml subsamples to yield a final concentration of ca. 10 ciliates ml^{-1} (initial concentration ~1000 ml^{-1}). Prior to inoculation, *S. sulcatum* were maintained in stationary-phase on a wheat-grain media at 15°C. Incubations were conducted at 15°C under continuous light intensity (150 µmol photon m^{-1} s^{-1}) and the bottles were gently shaken twice a day. Time-course samples were taken at 24 h intervals for 2 d. *S. sulcatum* was counted in 100 ml sub-samples fixed with alkaline Lugol's solution (final conc. 2%) and refrigerated until analysis. Blanks were prepared as above without addition of ciliates, but with ciliate growth media, filtered by gravity onto 0.4 µm polycarbonate filters.

TEP determination. TEP slides were prepared following Passow & Alldredge (1994). Aliquots (2, 5 and 10 ml) of each sample were filtered through 0.2 µm

polycarbonate filters (Osmonics, Poretics), in order to avoid potential artifacts linked to coagulation in the filter funnel (Mari & Kiørboe 1996). TEP retained on the filter were stained with 500 µl of a solution of Alcian Blue, and transferred to a microscope slide using the Filter-Transfer-Freeze technique (Hewes & Holm-Hansen 1983). For each slide, 10 images were taken under the microscope at 100×, 200× and 400× magnifications using a digital camera. For each image, all TEP were counted and sized using a semi-automatic image-analysis system. The cross-sectional area of each TEP was measured, and its equivalent spherical diameter (ESD) was calculated. For each sample, counts from the 3 magnifications were combined and TEP were classified according to their ESD into 20 logarithmic size classes (Mari & Burd 1998). TEP size distributions were described using a power relationship (Mari & Rassoulzadegan 2004).

Bacterial concentration. The abundance of non-attached bacteria (so called 'free') in each mesocosm was determined in 5 ml samples filtered onto 0.2 µm pore polycarbonate black filters after fixation with glutaraldehyde (final conc. 1%) and staining with DAPI for 10 min (final conc. 0.5 µg ml^{-1}) (Porter & Feig 1980, King & Parker 1988). Free bacteria were counted in 10 fields on each slide with an epifluorescence microscope at 1000× magnification. Total bacterial abundances were determined using flow cytometry (FacsCalibur, Becton Dickinson) according to Marie et al. (1999) (C. P. D. Brussaard et al. unpubl. data).

TEP-attached bacteria and bacteria fraction available for ciliate grazing. The number of TEP-attached bacteria was estimated for each sample by combining the TEP size spectra with a relationship between TEP size and number of attached bacteria. Since this relationship was not established during the present study, we used a relationship obtained from re-examination of data from Mari & Kiørboe (1996). During their study of a spring bloom, the number of TEP-attached bacteria (n) scaled with TEP size (diameter, d; µm) raised to an exponent of 1.48 ($n = 0.45\ d^{1.48}$; $r^2 = 0.82$; n = 340) during the growth phase of the bloom and of 1.05 ($n = 1.38\ d^{1.05}$; $r^2 = 0.67$; n = 140) during the senescent phase, i.e. after the bloom peaked. Since no other study has provided tools that allow prediction of the fraction of TEP-attached bacteria from TEP size spectra, the above relationships were used.

Ciliate concentration and community composition. For ciliate counts and group determination in each mesocosm and during the incubations with *Strombidium sulcatum*, 100 ml samples were fixed with alkaline Lugol's solution (final conc. 2%) and refrigerated until analysis. Aliquots were settled for >12 h in a 10 ml Hydrobios chamber. The total surface area of the chamber was examined at 200× magnification using an inverted microscope. For protistan concentration and community composition in the mesocoms, all the ciliates were enumerated and the different groups identified according to their morphological characteristics. During the incubations with *S. sulcatum*, the fraction of ciliates attached to mucous aggregates was estimated only for the added ciliate species, in order to distinguish between ciliates that may become attached to aggregates during preparation and handling of the fixed samples (considered as artifacts) and the ciliates that naturally become attached to mucous aggregates (due to TEP stickiness).

RESULTS

TEP concentration and TEP size spectra

TEP occurred in significant concentrations (i.e. >5 ppm) on all sampling occasions and in all mesocosms (Fig. 1). TEP volume concentration increased continuously from Day 0 to Day 20, from 5.4 to 118.5 ppm, 6.1 to 76.1 ppm and 5.9 to 115.9 ppm in Mesocosms 1, 2 and 3, respectively. TEP volume concentrations were low until Day 9 in all mesocosms (approximately 5 ppm) and increased after *Phaeocystis globosa* blooms peaked, i.e. during the senescent phase of the blooms (119, 76, and 116 ppm in Mesocosms 1, 2 and 3, respectively).

For all sampling occasions, the power relationship fitted the TEP size spectra well. In Mesocosms 1 and 2, the spectral slope, δ, increased significantly ($p < 5\%$) from Day 2 to Day 18 (from −3.96 to −2.38 and from −4.38 to −2.11 for Mesocosms 1 and 2, respectively), i.e. the fraction of large TEP increased. Although δ remained relatively constant in Mesocosm 3 during the course of the bloom, large TEP were produced between Day 2 and Day 14 (i.e. larger TEP appeared between successive sampling occasions).

Free, attached and total bacterial concentration

Bacterial concentration obtained using flow cytometry was compared with predicted total bacterial concentration estimated as the sum of microscope counts of free bacteria and expected number of TEP-attached bacteria. We excluded data for which the slope, δ, of the TEP size spectra was >−3 from the regressions, because when the fraction of large TEP increases (i.e. when δ increases) large TEP distribution is too sparse and counting statistics may become inaccurate and utilizing these data may, thus, introduce an error when estimating the number of attached bacteria. Free bacterial concentrations, determined using epifluorescence microscopy, represented 59 ± 13% of the total bacter-

ial population, and TEP-attached bacteria represented ~40% (slope of bacterial concentration estimated by microscopy versus bacterial concentration estimated by flow cytometry; Fig. 2). Comparison between predicted and observed total bacterial concentrations showed that attachment to TEP explains up to 95% of the observed total bacterial concentration (Fig. 2).

In all mesocosms, bacterial concentrations (total observed, total expected or free) were positively correlated to TEP concentration (Fig. 3). Estimates of the fraction of bacteria available for protozoans, as a function of the maximum particle size on which a given group can graze upon, were obtained by combining TEP size spectra from the 3 mesocosms and the TEP size versus number of attached bacteria relationships. Depending on food size-selectivity, over the size range investigated (particles < 12 µm), 73 to 97% of the total bacterial population is available for protozoan grazing (Fig. 4).

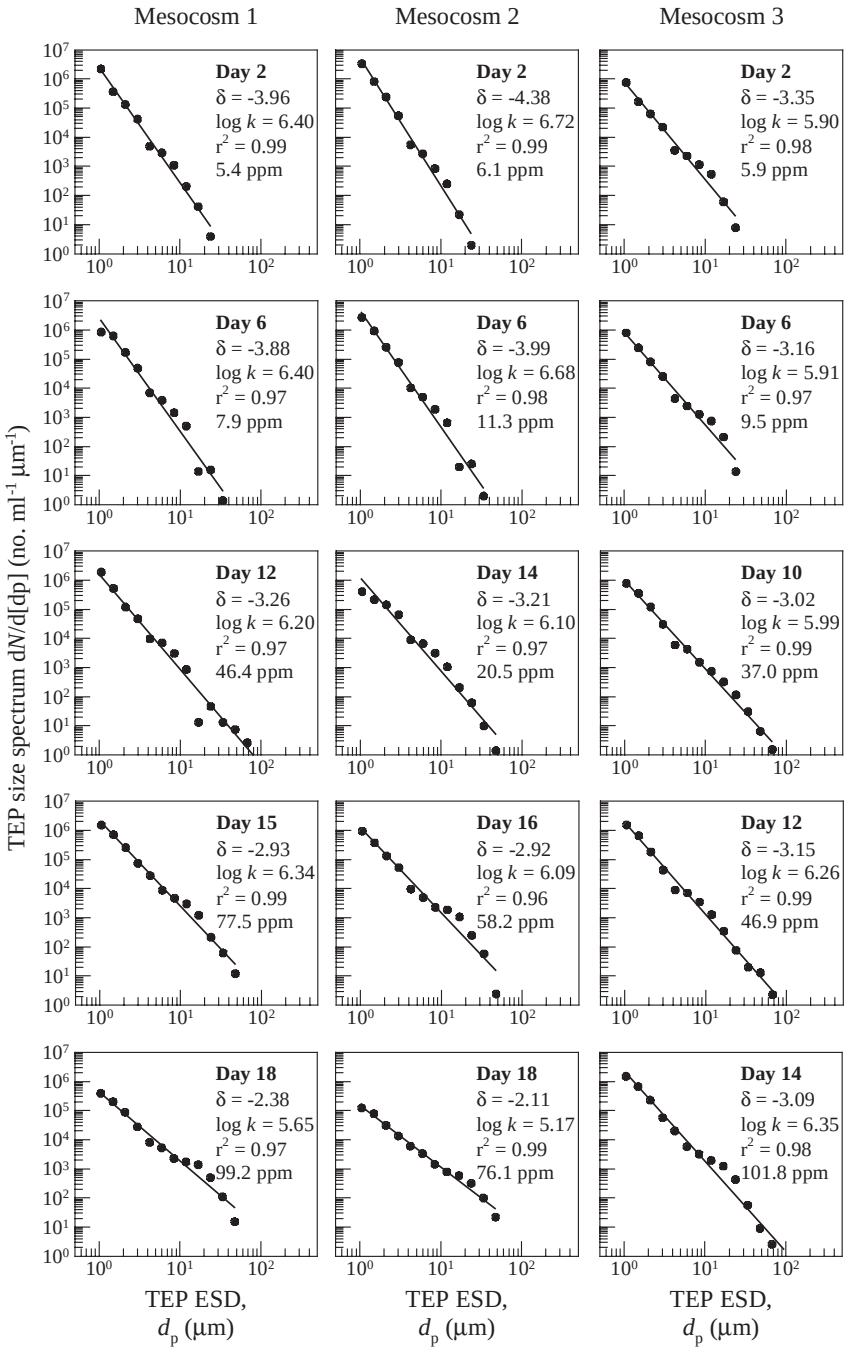

Fig. 1. Differential transparent exopolymeric particle (TEP) size distribution and TEP volume concentrations during bloom growth under contrasting N:P molar ratios. Regression lines were fitted to the data using $dN/d[d_p] = kd_p^{\delta}$, where d_p is the equivalent spherical diameter (ESD) and dN is the number of TEP particles per unit volume and per size class (no. ml^{-1} µm^{-1}) in the size range d_p to $[d_p + d(d_p)]$ (µm). δ = spectral slope

Protistan community composition and concentration

Strombidium spp. and *Euplotes* spp. (mainly *E. vannus*) dominated the mesocosms at different stages of *Phaeocystis globosa* blooms (Fig. 5). A few Tintinnids and *Mesodinium* spp. were also observed, but their abundance remained very low (<2 ml^{-1}) and their occurrence was not correlated to variations in TEP volume concentration.

In Mesocosms 1 and 3, the concentration of *Strombidium* spp. was high (from 5 to 20 ml^{-1}) and dominated the protistan community until TEP volume concentration rose from less than 10 ppm up to ~40 ppm (Days 10 to 12); thereafter *Euplotes* spp. emerged. For TEP volume concentration >40 ppm, *Strombidium* spp. simply disappeared, while *Euplotes* spp. became the dominant species with concentrations ranging from 5 to 12 ml^{-1}.

In Mesocosm 2, the protistan community behaved somewhat differently, as *Strombidium* spp. did not disappear when TEP volume concentration reached >40 ppm, but only slightly decreased. *Euplotes* spp. also emerged when TEP volume concentration reached ~40 ppm and thereafter dominated the ciliate community with concentrations as high as 44 ml^{-1}.

Variations in the relative percentages of *Strombidium* spp. and *Euplo-*

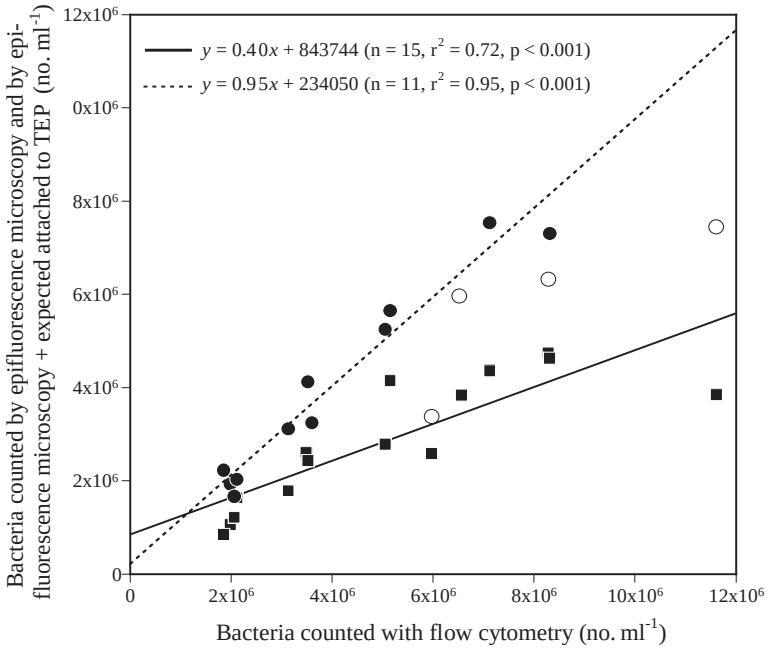

Fig. 2. *Phaeocystis globosa*. Comparison between total bacterial concentration ($Bact_{Total}$; estimated by flow cytometry) and free bacterial concentration ($Bact_{Free}$; estimated by epifluorescence microscopy, squares), and expected total bacterial concentration ($Bact_{Expected\ Total}$; calculated as $Bact_{Free}$ + $Bact_{Expected\ Attached\ to\ TEP}$, circles). Regression lines have been fitted to the data, but utilizing only data described by closed symbols

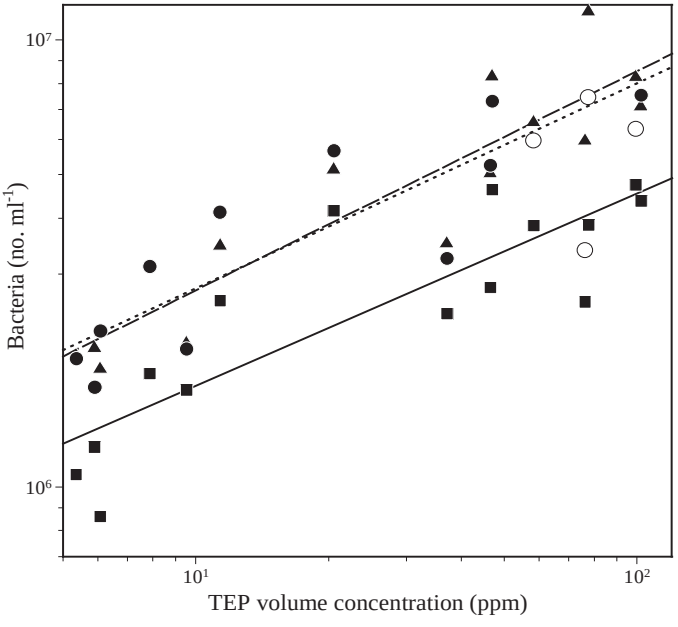

Fig. 3. Correlation between TEP volume concentration and the concentrations of: free bacteria (squares) ($r^2 = 0.73$; n = 15; $p < 0.001$), total bacteria measured by flow cytometry (triangles) ($r^2 = 0.84$; n = 15; $p < 0.001$), and expected total bacteria (circles) ($r^2 = 0.75$; n = 11; $p < 0.001$). Regression lines have been fitted to the data, but utilizing only data described by closed symbols

tes spp. were closely correlated with changes in TEP volume concentration (Fig. 6). The inversion point (i.e. from *Strombidium* spp. to *Euplotes* spp. dominance) coincided with the early senescent phase of the blooms and the concomitant increase in TEP volume concentration (ultimately leading to the formation of large marine snow aggregates).

Incubations with *Strombidium sulcatum*

After 24 h of incubation, the percentage of *Strombidium sulcatum* attached to mucous aggregates increased from 13 to 20% to a maximum of 37 ± 8% in seawater collected at Day 14 (Fig. 7). For the incubations conducted with seawater collected from Mesocosms 1 and 2 at Day 18 (during the senescent phase of the blooms), the percentage of *S. sulcatum* attached to mucous aggregates decreased drastically. In the mean time, the fraction of *S. sulcatum* still present in the medium (calculated as a function of initial concentration and for the 15 incubations) decreased to 51 ± 22% after 24 h and to 37 ± 18% after 48 h. *S. sulcatum* associated with large mucous aggregates were both present at their surface and embedded inside them (Fig. 8), suggesting that they were trapped rather than intentionally sitting on aggregates.

The percentage of *Strombidium sulcatum* attached to aggregates after 24 h of incubation correlated positively with TEP volume concentration,

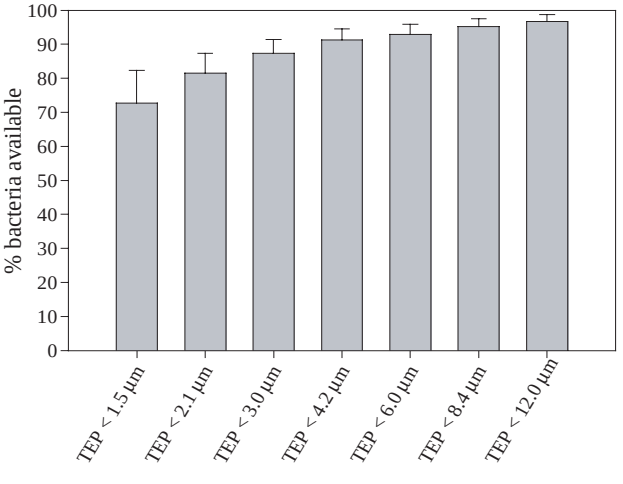

Fig. 4. Fraction of bacteria available for ciliate grazing according to the possible maximum aggregate size the ciliate *Strombidium sulcatum* can graze upon. The selected sizes (i.e. from 1.5 to 12.0 µm) correspond to the medium size of the TEP logarithmic size classes in the small size range

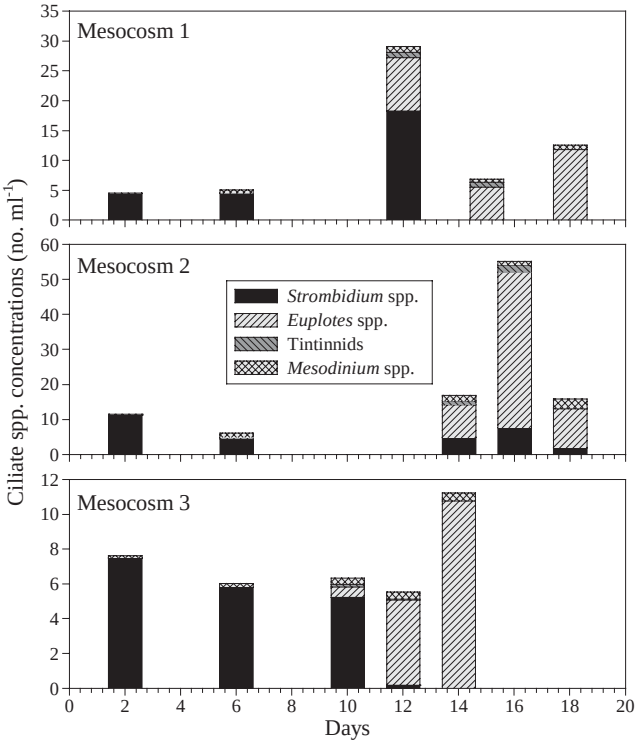

Fig. 5. Temporal variations of protozoan community composition in Mesocosms 1, 2 and 3 (note the different scales of the *y*-axes)

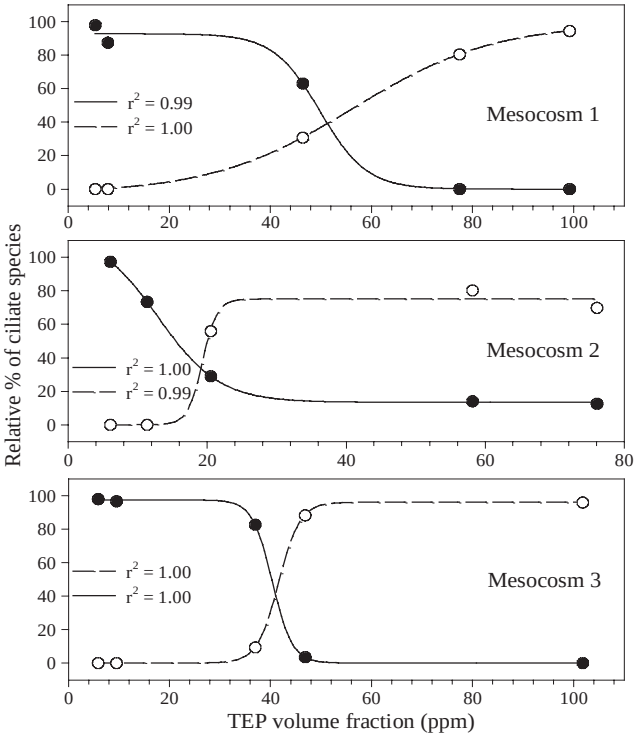

Fig. 6. Correlation between TEP volume concentration and relative percentage (d*P*) of *Strombidium* spp. (●) and *Euplotes* spp. (○). Sigmoidal regression lines ($dP/d[TEP_{vol}] = a\{1+e^{-[(TEPvol-TEPvol0)/b]}\}^{-1}$) have been fitted to the data for each mesocosm

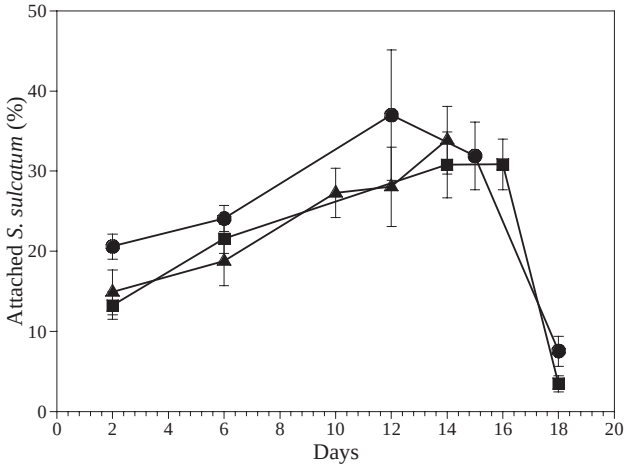

Fig. 7. *Strombidium sulcatum*. Temporal variations of the percentage attached to mucous aggregates after 24 h of incubation for Mesocosms 1 (●), 2 (■) and 3 (▲)

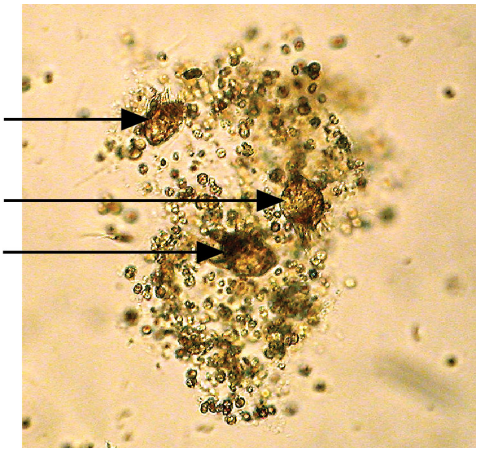

Fig. 8. *Strombidium sulcatum*. Examples (shown by arrows) attached to a macroaggregate

and the fraction of attached ciliates scaled with TEP volume raised to an exponent of 0.23 (Fig. 9), i.e. as the TEP pool accumulates, a larger fraction of the *S. sulcatum* population may become attached. We excluded the results obtained during the incubations with seawater collected from Mesocosms 1 and 2 on Day 18 from the regression analysis.

DISCUSSION

Partitioning of the bacterial population

The bacterial population in aquatic systems usually appears as both free and attached to particles, and estimations of the attached fraction vary from less

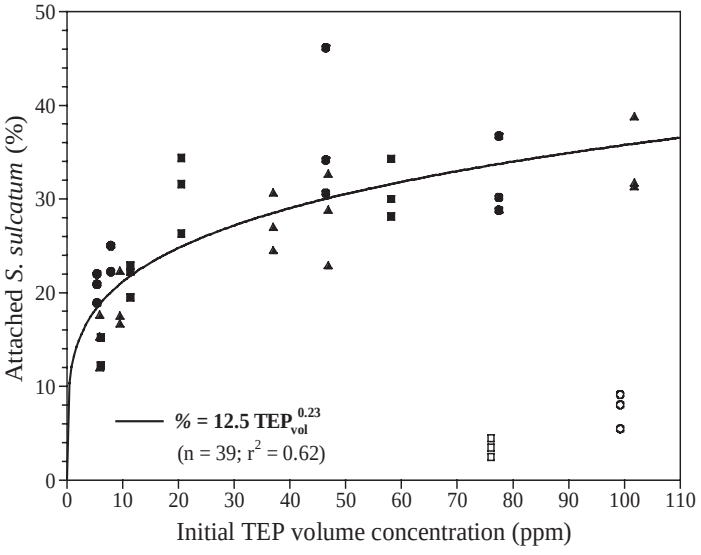

Fig. 9. *Strombidium sulcatum*. Percentage attached to mucous aggregates (%) as a function of TEP volume concentration (TEP_{vol}, ppm) for Mesocosms 1 (●,○), 2 (■,□) and 3 (▲). Regression line (% = $aTEP_{vol}^{b}$) has been fitted to the data, but utilizing only data described by closed symbols

than 10% up to 90% of the total population (Bell & Albright 1981, Robertson & Newell 1982, Alldredge & Youngbluth 1985, Albright et al. 1986, Alldredge et al. 1986, Herndl 1988). While the fraction of free bacteria is easily accessible microscopically, an estimate of the attached fraction is more difficult to obtain since it requires determination of the size distribution of the particles hosting bacteria and establishment of a relationship between the size of the particles and the number of attached bacteria. Therefore, for convenience and because large aggregates hosting bacteria are under-represented when studied in a limited number of fields at 1000× magnification, the number of bacteria attached to organic aggregates is generally not determined microscopically (especially when the concentration of large aggregates is high).

The number of TEP-attached bacteria was estimated from the TEP size spectra using the TEP size versus number of TEP-attached bacteria relationship obtained by compiling data recorded in the Kattegat (from Mari & Kiørboe 1996). Although this relationship can only provide a crude estimate of the fraction of TEP-attached bacteria, this approach allowed us to confirm the hypothesis that attachment to TEP could explain the difference between free (determined microscopically) and total (determined by flow cytometry) bacterial populations. Therefore, the combined use of both methods can help to describe the structure of the bacterial population.

In the present study, the fraction of attached bacteria was ~40% of the total bacterial population, which is high compared to previous estimates (i.e. average values from 0.5 to 25%; Passow & Alldredge 1994, Schuster & Herndl 1995, Mari & Kiørboe 1996). Our results support the hypothesis that the fraction of attached bacteria may increase along productivity gradients (Schuster & Herndl 1995), as the *Phaeocystis globosa* mesocosms were highly eutrophic systems (i.e. TEP concentration up to 100 ppm and chlorophyll *a* concentrations >20 µg l^{-1}; C. P. D. Brussaard et al. unpubl. data).

Succession of protists: influence of TEP concentration

The present study suggests that TEP concentration is a significant controlling factor of the ciliate community structure. The ciliate *Strombidium* spp. dominated the protozoan community in all mesocosms when TEP concentration was relatively low (i.e. <20 ppm), while the ciliate *Euplotes* spp. became dominant in all mesocosms when TEP concentration reached a critical value (from 20 to 50 ppm). However, the observed difference between the community composition varied among mesocosms, suggesting that additional mechanisms besides TEP volume concentration may be important in structuring the ciliate community.

Strombidium spp. are typical filter feeders feeding on small-suspended food particles, such as nanoflagellates, bacteria and, to a lesser extent, picoplanktonic organisms (Allali et al. 1994, Dolan & Šimek 1997, Christaki et al. 1998). They have an optimum food particle size of ~3 µm (Fenchel & Jonsson 1988, Bernard & Rassoulzadegan 1990, Mari & Rassoulzadegan 2004) and are able to graze on free bacteria and aggregates ≤6 µm (Bernard & Rassoulzadegan 1990, Mari & Rassoulzadegan 2004). Additionally, like most Oligotrichina, *Strombidium* spp. are truly free swimming protists and do not usually inhabit aggregates (Artolozaga et al. 2000). During their study of picoplankton-size prey analog grazing by *S. sulcatum* as a function of TEP concentration, Mari & Rassoulzadegan (2004) showed that the food size spectrum was modified subsequent to enhanced TEP production and demonstrated that this process had a negative effect on the studied ciliate, which could ultimately lead to its disappearance. If prey concentration for *Strombidium* spp. decreases due to transfer of its food source to unreachable size classes, this ciliate population may decline and may gradually be superseded by other populations of ciliates feeding on larger particles or needing to sit on a physical support to feed.

The bacterial population structure (free vs. attached bacteria) was modified due to TEP-mediated aggrega-

tion. However, the fraction of bacteria available for *Strombidium* spp. was high and relatively constant (ca. 90%), and even increased over the course of the blooms, as bacterial and TEP concentrations were positively correlated. Therefore, reduction of bacteria availability does not seem to be directly responsible for the observed *Strombidium* spp. disappearance. The results obtained during the incubations conducted with *S. sulcatum* suggest that attachment to mucous aggregates may act as a loss factor for this ciliate (i.e. *S. sulcatum* were embedded inside mucous aggregates and, thereby, disabled). Assuming that TEP control upon *Strombidium* spp. abundance is due to their high sticking properties and subsequent direct scavenging by TEP aggregation, the diminution of the fraction of attached *S. sulcatum* observed for Mesocosms 1 and 2 at Day 18 could be due to a diminution in TEP stickiness or to a bad estimation of the fraction of attached *S. sulcatum* when aggregates started to age and to become denser (i.e. content hardly identifiable).

Euplotes spp. are poor swimmers, commonly found in benthic habitats, and the presence of large mucous aggregates in the water column may help them 'colonize' the epibenthic zone (and to some extent the pelagic zone). Such colonization may be achieved by swimming from one aggregate to another, using an active reversal response to the food gradient to locate food patches (Jonsson & Johansson 1997). Unlike *Strombidium* spp., *Euplotes* spp. prefer to graze on attached bacteria while temporally attached to a solid surface (Albright et al. 1987, Patterson et al. 1993, Artolozaga et al. 1997). Therefore, large marine snow aggregates can be considered as environments in the pelagic zone that support populations with combined features allowing success in both pelagic and benthic systems. This mechanism of colonization may explain why benthic protists, known to be poorly adapted to pelagic lifestyle, are often observed inhabiting marine snow aggregates (Caron et al. 1982, Patterson & Fenchel 1990). Hypotrichous ciliates, such as *Euplotes* spp. are specifically adapted to inhabit the surface and are known to be abundant in aggregate-rich environments (Caron et al. 1982, Davoll & Silver 1986, Artolozaga et al. 2000, Woerner et al. 2000). An accumulation of TEP may, thus, favor the dominance of *Euplotes* spp. by promoting the formation of macroaggregates.

Consequences for the microbial food web structure and function

The consequences of high TEP production for the microbial food web structure and function could be divided into 2 processes. First, TEP production and the subsequent formation of mixed aggregates could act as a 'trophic elevator' by providing a direct lift for micrometer-size particles and dissolved organic carbon to higher trophic levels (Mari & Rassoulzadegan 2004). Second, due to high sticking properties, the TEP-mediated aggregation of active components of the microbial food web (i.e. bacteria, heterotrophic nanoflagellates, ciliates) could cause a 'trophic jam' activating the trophic elevator by forcing a detour to higher trophic levels, thus inhibiting the microbial food web. Both mechanisms would minimize the significance of the microbial trophic web for the transfer of energy from the dissolved phase back to higher trophic levels.

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