



Aggregation and sinking behaviour of resuspended fluffy layer material

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Abstract

The influence of pelagic diatom addition (*Skeletonema costatum*) on aggregation dynamics of resuspended fluffy layer material containing natural microorganism assemblages (bacteria and pennate diatoms) was studied during two roller table experiments. Sediment samples were taken at a fine sand site (16 m water depth) located in Mecklenburg Bight, south-western Baltic Sea. Fluff was experimentally resuspended from sediment cores and aggregation processes with and without *S. costatum* were studied in rotating tanks. Total particulate matter was incorporated into artificial aggregates in equal shares after both roller table experiments. However, biogenic parameters (particulate organic carbon, particulate organic nitrogen, and carbohydrate equivalents), as well as cell numbers of bacteria and pennate diatoms were found in higher percentages in *S. costatum* aggregates compared to aggregates without *S. costatum*. Transparent exopolymer particles were apparently irrelevant in the aggregation process during both experiments. Settling velocities of *S. costatum* aggregates exceeding 1000 µm in diameter showed a significantly higher mean settling velocity compared to aggregates without *S. costatum* of the same size. The pronounced effect of pelagic diatoms on aggregation processes of fluff in terms of particle attributes, size, and therewith sinking velocities could be demonstrated and may lead to further insight into near bed particle transport in coastal waters.

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1. Introduction

Particle aggregation in the water column is controlled by the collision rate and efficiency with which two colliding particles stick together (see [Simon et al., 2002](#) for a review). Especially pelagic diatoms were found to form aggregates in the water column (e.g. [Takahashi, 1986](#); [Kranck and](#)

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Milligan, 1988; see Thornton, 2002 for a review), a process that has been hypothesized to be due to an increase in particle stickiness at the decline of a diatom bloom (Smetacek, 1985). Dissolved polysaccharides exuded from pelagic microorganisms coagulate in the water column, forming gel-like, transparent exopolymer particles ('TEP') that provide the glue for the aggregation of diatom blooms (see Passow, 2002 for a review). Laboratory devices were constructed to study aggregate formation of diatoms (Kranck and Milligan, 1980; Shanks and Edmondson, 1989; Kioerboe et al., 1990; Crocker and Passow, 1995). Thus, *Skeletonema costatum* was found to form aggregates depending on cell–cell sticking (Kioerboe and Hansen, 1993; Thornton and Thake, 1998) as well as sticking to lithogenic material (Hamm, 2002). This species also contribute to the TEP pool in the water column during spring blooms (e.g. Alldredge et al., 1993; Passow and Alldredge, 1995a; Engel, 2000).

Aggregates that settle out of the water column form an unconsolidated, fluffy surface layer at the sediment–water interface (Stolzenbach et al., 1992; Beaulieu, 2002) which will be resuspended at lower critical shear velocities compared to the underlying sediment (Beaulieu, 2003; Ziervogel and Bohling, 2003). Benthic diatoms were found to be abundant in fluffy layers (Lund-Hansen et al., 2002). Due to the mobility of fluff, the potential for benthic microorganisms to be resuspended appears high. Most benthic phototrophic microorganisms secrete copious amounts of carbohydrate-rich substances (EPS; Smith and Underwood, 1998; Decho, 2000) that may act as glue for particle aggregation, too. To our knowledge, the influence of benthic microorganisms on particle aggregation remains uninvestigated. Nevertheless, numerous authors measured elevated concentrations of photopigments in bottom waters after sediment resuspension containing benthic diatoms (Grant and Bathmann, 1987; Grant and Gust, 1987; Wiltshire et al., 1998).

Previous field studies stressed that resuspended material interact with fine suspended particles in the BBL influencing aggregate formation and transport processes near the sea floor (Jähmlich et al., 1999, 2002). The transport of fluff aggregates

contributes appreciably to the advection of organic pollutants (Witt et al., 2001) and organic carbon in shallow waters (Christiansen et al., 2002; Leipe et al., 2000), and the deep sea (Thomsen and van Weering, 1998).

This study investigates the relative changes of aggregation and sinking behaviour of fluffy layer particles caused by pelagic diatoms. Fluffy layer material was experimentally resuspended from their natural deposition site and mixed with cells of the pelagic diatom *S. costatum* simulating sedimentation of an algal bloom.

2. Material and methods

2.1. Experimental set-up

In the first laboratory experiment, aggregation of fluffy layer particles was determined (Exp I). The influence of *S. costatum* on aggregation behaviour of the same material was measured in a second experiment (Exp II). For this purpose, sediment cores with a diameter of 20 cm were taken with a box-corer from a site with fine sand (54°12.00'N, 11°58.00'E, 16 m water depth), situated in Mecklenburg Bight, south-western Baltic Sea. Unconsolidated particles from the top layer of the sediment surface were experimentally resuspended with the erosion device microcosm (Gust and Müller, 1997) into which one sediment core with overlying in situ seawater (height of water over the core: 10 cm) was inserted. The device consists of a removable lid with a stirring disc and a water input and output. Water is pumped into an external water cycle through a central axis and back into the overlying water of the core. By controlling the rotational speed of the disc and the pumping rate, the device generates a spatially homogeneous shear stress velocity (u_*) at the bottom. Calibration of this bottom shear stress in the erosion chamber was done by several approaches, e.g. skin friction probes (Gust and Müller, 1997).

The threshold of measurable erosion of fluffy layer material for this sediment type has been determined as 1.15 cm s^{-1} (Ziervogel and Bohling, 2003). After reaching the erosion threshold, the lid

of the device was removed and the water overlying the sediment core containing resuspended fluff particles was immediately collected. To describe the composition of resuspended particles in suspension, subsamples were taken and analysed for different parameters (see below for particle analysis). For the second experiment (Exp II), 5 ml of a non-axenic *S. costatum* culture (F/2-media) were mixed with particles resuspended from a second sediment core. This species is abundant in the southern Baltic Sea during spring bloom (Wasmund et al., 1998). The addition resulted in a median diatom cell number of $25.4 \times 10^4 \text{ l}^{-1}$ found in the tanks after roller table incubation. This number is approximately three orders of magnitude lower than cell abundances found in coastal surface waters of Mecklenburg Bight during spring bloom (Wasmund, pers. comm.).

One litre of water overlying the sediment core was transferred into three replicate cylindrical, transparent tanks (radius: 7.5 cm; height: 7.9 cm) and filled with filtered seawater (0.7 μm pore size) to a final volume of 1.4 l each. The tanks, thus filled with a water-fluff suspension were placed in a plastic tube equipped with a video camera system (Sony Handycam with close-up lens +4). The tanks together with the camera were rotated for 18 h on a roller table (Shanks and Edmondson, 1989) at a rotation speed of 6.4 rpm and a temperature of 15 °C. Solid body rotation, i.e. the point when the water inside the tank rotated at the same speed as the wall of the tank, is achieved after a spin up time of 1000 s. Under these conditions particle aggregation is mainly controlled by differential settlement (Jackson, 1994). With the camera 10 cm in front of the first tank, particles > 100 μm diameter could be identified. In an earlier study Jählich (1996), using a camera system with a close-up lense +3, determined the accuracy of size measurement with fluorescent microspheres (163 μm) and fishing lines with 200, 400 and 600 μm in diameter. Calibration measurements resulted in an overestimation of the diameter of particles $\leq 200 \mu\text{m}$ of 10%, and an underestimation of 3% for particle diameters > 200 μm .

During roller table incubation, particle aggregation was recorded every hour for 1 min in an area

of 3 × 2 cm in size at a radial distance of 3 cm from the centre of the tank. Video pictures were digitized on a Macintosh computer and analysed with the software “Image 1.4”. At each time interval the following parameters of between 17 and 58 sharp edged aggregates were measured: the largest diameter of an aggregate (major axis), length of the minor axis, as well as the largest expansion in the horizontal (*x*-ferret length) and the vertical (*y*-ferret length) direction.

At the end of both roller table experiments, the tanks were carefully turned to one side and aggregates were allowed to settle to the bottom for approximately 15 min. The overlying water (*W*) above the settled macroscopic aggregates, i.e. ~1 l of tank water was then sampled. Small aggregates invisible for the naked eye were certainly present in *W*. Individual large aggregates and original water (*W+A*, ~0.4 l in volume), left over in the tanks after sampling of *W*, were analysed for the same parameters. Prior to filtration of *W+A*, large aggregates were removed using a syringe and transferred to a glass cylinder with a volume of 2 l to determine settling velocities (*V_s*) under low turbulent conditions. Aggregates were carefully placed into the centre of the cylinder and sinking particles were recorded in the lower part of the water column with the same video camera as described above. After sedimentation, aggregates were collected in a Petri dish at the bottom of the cylinder and recombined with *W+A*.

To get an indication of the attributes of artificial aggregates formed during roller table experiments, the excess density ($\Delta\rho$) was calculated according to Engel and Schartau (1999):

$$\Delta\rho = \frac{V_s^2 C_D \rho_f A_p}{2gV V_A}$$

where C_D is the dimensionless drag coefficient, ρ_f stands for the fluid density (1.01 g cm⁻³), and g is the acceleration due to gravity (981 cm s⁻²). Because Reynolds numbers of artificial aggregates exceeded 0.5, the drag coefficient had to be determined empirically according to White (1974). The area of the particle perpendicular to the direction of the fall (A_p) was calculated as the maximum cross-sectional area either of a prolate (*y*-ferret length > *x*-ferret length) or of an oblate

ellipsoid (see Engel and Schartau, 1999 for details). The visible volume of each aggregate (VV_A) was calculated as the volume of an ellipsoid.

2.2. Analysis

In order to complement the results from image analysis, tank water samples of 50 and 100 ml originating from W and $W+A$ were filtered onto glass fibre filters (0.7 μm pore size) and analysed for different parameters after roller table experiments. Values for A were calculated by subtracting mean concentrations of parameters, i.e. $(A+W)-W$ (Table 1). Data in Table 1 are given as the concentration of each parameter and cell number in 1 l tank water, respectively.

Total particulate matter (TPM) was measured according to von Bodungen et al. (1991) using pre-weighed glass fibre filters (0.7 μm pore size). Particulate organic carbon (POC) and particulate organic nitrogen (PON) were measured using an elemental analyzer. Chlorophyll equivalents (Chl) were measured using the acidification method of Holm-Hansen et al. (1965) and chlorophyll a and phaeopigments were analysed in a Turner fluorometer and calculated using the JGOFS protocol (UNESCO, 1994). Besides the former parameters

(POC, PON, pigments) carbohydrate equivalents (CHE) as a further indicator for biogenic particles were determined using the phenol–sulphuric acid assay (Underwood et al., 1995). Particles were filtered onto glass fibre filters and CHE were extracted by adding 2 ml of distilled water, followed by 1 ml of 5% aqueous phenol (wt./vol.) and 5 ml of concentrated sulphuric acid. The assay measures total carbohydrate concentration, including intra- and extracellular detrital material, in the sample. Values are expressed as Glucose equivalents, a standard used to measure a calibration curve. TEP were determined according to Passow and Alldredge (1995b). Twenty millilitres of tank water preserved in formaldehyde at a final concentration of 4% were filtered onto a 0.4 μm Nucleopore filter and stained with Alcian blue. Results are expressed as Xanthan equivalents, a standard used to measure a calibration curve. Alcian blue absorbs onto TEP and TEP precursor as well as onto mineral particles that are covered by organic matter possibly being of TEP-like origin. Because mineral particles are abundant in resuspended material, results of Xanthan equivalents will be given as ‘TEP’. Both CHE and ‘TEP’ include biogenic sticky particles in the tanks.

Table 1

Proportion of parameters, algae and bacterial cell abundance distributed between water and aggregates ($n = 3$, except TEP with $n = 9$, mean \pm SD)

	Exp I				Exp II			
	W	$A+W$	A	$A/A+W$ (%)	W	$A+W$	A	$A/A+W$ (%)
TPM (mg l^{-1})	41.3 \pm 1.5	92.7 \pm 8.1	51.4	55	41.3 \pm 1.5	92.7 \pm 4.2	51.4	55
POC ($\mu\text{g l}^{-1}$)	228.5 \pm 38.1	852.5 \pm 73.3	624	73	208.8 \pm 14.9	1288.9 \pm 149.5	1080.1	84
PON ($\mu\text{g l}^{-1}$)	39.5 \pm 2.8	111.3 \pm 6.4	71.8	65	52.7 \pm 2.5	188.5 \pm 36.4	135.8	72
Chl ($\mu\text{g l}^{-1}$)	0.03 \pm 0.01	0.23 \pm 0.09	0.20	87	0.06 \pm 0.01	0.46 \pm 0.11	0.40	87
Phaeopigments ($\mu\text{g l}^{-1}$)	0.17 \pm 0.02	1.15 \pm 0.2	0.98	85	0.27 \pm 0	1.81 \pm 0.19	1.54	85
CHE (mg Glucose Equiv. l^{-1})	1.35 \pm 0.1	1.76 \pm 0.43	0.41	23	0.50 \pm 0.13	1.58 \pm 0.49	1.08	68
TEP (mg Xanthan Equiv. l^{-1})	2.45 \pm 0.11	2.69 \pm 0.19	0.24	9	3.13 \pm 0.6	2.81 \pm 0.17	—	0
Pennate diatoms (10^4l^{-1})	0.57	1.3	0.73	56	0.5	1.6	1.1	69
<i>S. costatum</i> (10^4l^{-1})	0	0	0	0	7.6	25.4	17.8	70
Bacteria (10^8l^{-1})	7.8 \pm 1.4	6.6 \pm 3.0	—	0	5.4 \pm 0.8	9.1 \pm 1.9	3.7	41

Number of pennate diatoms and *S. costatum* cells per litre are median values of three replicate tanks. Concentrations are given per litre of water. TPM—total particulate matter; POC—particulate organic carbon; PON—particulate organic nitrogen; Chl—chlorophyll equivalents; CHE—carbohydrate equivalents; TEP—transparent exopolymeric particles; W —water overlying the settled aggregates in the tank after incubation, and $A+W$ —aggregates and water after incubation. For each parameter A is calculated as $(A+W)-W$. “—” means calculated values are negative.

2.3. Diatom and bacteria enumeration

For the determination of bacterial abundance, 10 ml of tank water were preserved with formaldehyde at a final concentration of 4%. Bacteria were enumerated by epifluorescence microscopy according to Porter and Feig (1980). Diatom cells were counted using an inverted microscope according to Utermöhl (1958) from 20 ml of water fixed with formaldehyde at a final concentration of 4%. We distinguished between cultured cells of the genus *Skeletonema* and pennate diatoms that were resuspended from the sediment surface during microcosm experiments.

3. Results

3.1. Aggregate formation

3.1.1. Experiment I

Visible aggregates of fluffy layer particles (major axis $>100\ \mu\text{m}$) appeared in both roller table experiments after 1 h incubation time (Figs. 1 and 2, upper graphs). In Exp I the formation of aggregates can be separated into a growth phase and a stationary phase. Within the first 6 h, mean aggregate diameter and incubation time showed a significant positive correlation ($r = 0.93$, $P < 0.01$). During this period, aggregates had a mean diameter growth rate of $260\ \mu\text{m h}^{-1}$. After 6 h rotation time, mean aggregate diameters remained constant. During Exp I, the size class distribution of artificial fluff aggregates was dominated by the smallest one (Fig. 1, lower graph). Aggregates reached up to $5320\ \mu\text{m}$ in diameter.

Excess densities ($\Delta\rho$) of aggregates formed during Exp I ($n = 30$ for calculation) ranged between 1.2×10^{-4} and $1.8 \times 10^{-1}\ \text{g cm}^{-3}$ with a median value of $4.1 \times 10^{-3}\ \text{g cm}^{-3}$.

3.1.2. Experiment II

S. costatum aggregates showed a continuous mean diameter growth rate of $100\ \mu\text{m h}^{-1}$ over 18 h rotation time with a stronger significant correlation between mean aggregate diameter and incubation time compared to Exp I ($r = 0.94$, $P < 0.001$, Fig. 2, upper graph). Towards the end of the experiment, the size class distribu-

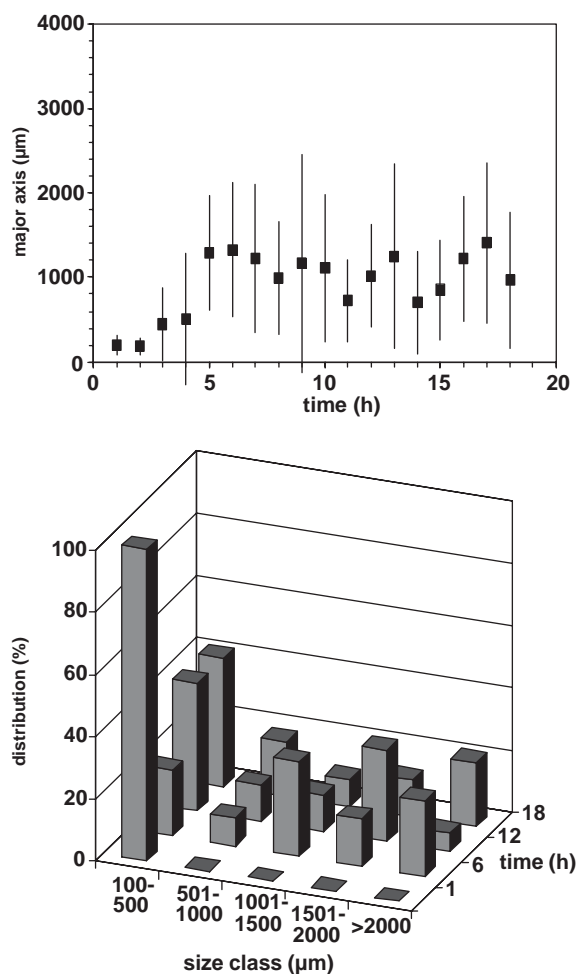


Fig. 1. Mean particle diameter \pm standard deviation during roller table incubation of Exp I (upper graph, $n = 17-41$). Distribution of particles in size classes at four representative times are illustrated in the lower graph.

tion reveals that $>60\%$ of aggregates had diameters exceeding $2000\ \mu\text{m}$ with maximum diameters of $6910\ \mu\text{m}$ (Fig. 2, lower graph).

Values for $\Delta\rho$ of *S. costatum* aggregates were in the same range with a slightly higher median value of $7.7 \times 10^{-3}\ \text{g cm}^{-3}$ ($n = 38$ for calculation) compared to Exp I.

3.2. Sinking velocities

Sinking velocities (V_s) ranged from 0.06 to $1.0\ \text{cm s}^{-1}$ for particles with diameters of $140-4420\ \mu\text{m}$

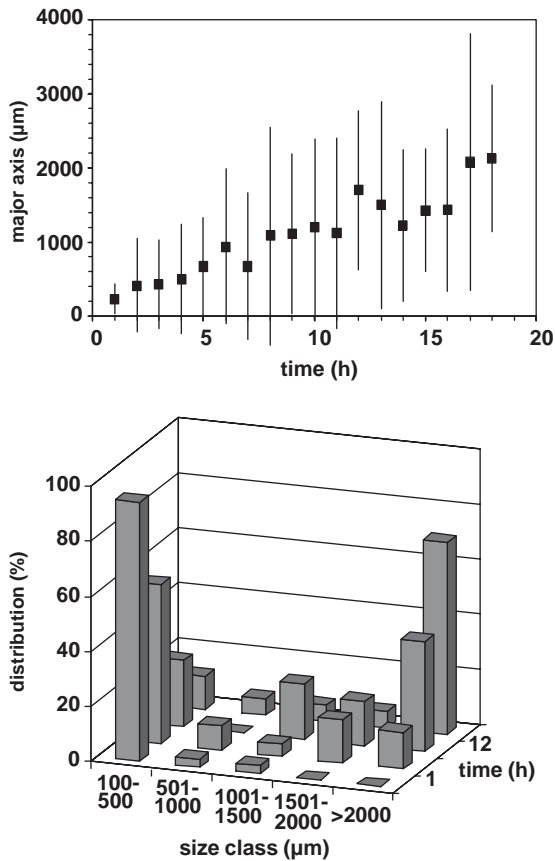


Fig. 2. Mean particle diameter \pm standard deviation during roller table incubation of Exp II (upper graph, $n = 25-58$). Distribution of particles in size classes at four representative times are illustrated in the lower graph.

(Fig. 3). Sinking velocities of aggregates without *S. costatum* increased with particle diameter following a power-law function:

$$V_s = 0.02 (\text{major axis})^{0.35}$$

Also in Exp II, particle diameter and sinking velocities increased exponentially following the power-law function:

$$V_s = 0.0002 (\text{major axis})^{1.02}$$

Using linear correlation coefficients, the relationship between V_s and major axis was less pronounced in Exp I ($r = 0.35$, $P < 0.05$) compared to Exp II ($r = 0.82$, $P < 0.001$). Aggregates used for sinking velocity measurements were distinguished into two size classes varying from $< 1000 \mu\text{m}$ to $> 1000-2350 \mu\text{m}$ in diameter. This classification is

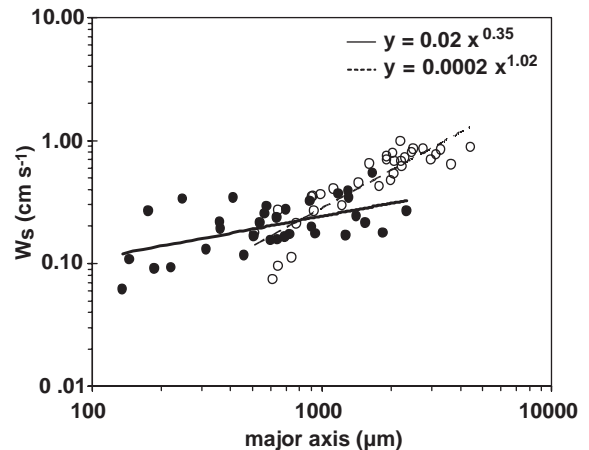


Fig. 3. Relation between settling velocities (V_s) and particle diameter (major axis) of artificial fluff aggregates without *S. costatum* (circles, Exp I, $n = 33$) and *S. costatum* aggregates (open circles, Exp II, $n = 33$). Artificial aggregates were formed during roller table experiments (Exps I and II) and placed into a settling chamber afterwards.

based on in situ observations revealing that the dominant aggregate size in the BBL of Mecklenburg Bight and an adjacent area are presumably less than $1000 \mu\text{m}$ (Christiansen et al., 2002; Jählich et al., 1999, 2002). Mean aggregate sinking velocities in Exp I ranged between $0.2 \pm 0.08 \text{ cm s}^{-1}$ for aggregates $< 1000 \mu\text{m}$ and $0.3 \pm 0.12 \text{ cm s}^{-1}$ for those $> 1000-2350 \mu\text{m}$. *S. costatum* aggregates $< 1000 \mu\text{m}$ showed mean sinking velocities comparable to aggregates of the same size class formed in Exp I, while the mean V_s value of *S. costatum* aggregates $> 1000-2350 \mu\text{m}$ ($0.6 \pm 0.18 \text{ cm s}^{-1}$) was significantly higher compared to Exp I aggregates of the same size (ANOVA, $F_{4,17} = 33.96$, $P < 0.001$).

3.3. Chemical analysis, algae and bacteria cell abundance

Data in Table 1 compare the proportional distribution of attributes between water and aggregates, and the differences in distribution onto aggregates with and without *S. costatum*, since starting conditions were very similar. Prior to rotation, the amount of TPM in the tanks ranged between 58.8 mg l^{-1} in Exp I and 55.2 mg l^{-1} in Exp II (results not shown). This indicates no

measurable influence of *S. costatum* addition on TPM concentrations. In Exp I, the value of CHE was 60% higher compared to Exp II. In contrast values of POC, PON, photopigments, and TEP were 20–30% higher in Exp II compared to Exp I, possibly due to the addition of *S. costatum*. Concentrations of phaeopigments exceeded those of chlorophyll *a* in both experiments indicating a high amount of detrital material in the tanks.

The same amount of TPM, i.e. 55% from *A+W*, was incorporated into *A* in both experiments (Table 1). After roller table incubation of Exp II, all biogenic parameters, as well as cell numbers were incorporated in equal (photopigments) or higher (POC, PON, CHE and cell numbers) percentages into *A* compared to Exp I. *S. costatum* aggregates further revealed no incorporated TEP.

Resuspended cells of pennate diatoms and bacteria were abundant in tanks of both experiments while cells of *S. costatum* were only found in samples of Exp II. In Exp I, 56% of pennate diatoms from *A+W* were found in *A*, whereas no bacterial cell number could be calculated for *A*. Contrarily, 69% of pennate diatoms together with 70% of *S. costatum* were incorporated into *A* while 41% of bacterial cells from *A+W* were incorporated into *A* in Exp II.

4. Discussion

4.1. Aggregate formation

Results from roller table experiments with resuspended fluff material (Exp I) and added pelagic diatoms (Exp II) showed a significant increase of mean aggregate diameter during the first 6 h of incubation. After this initial phase mean aggregate sizes remained nearly unchanged in Exp I but increased further in Exp II. Aggregation dynamics observed in Exp I correspond to the results of Jähmlich and Graf (1998) who measured initial increase of average aggregate diameters in the first 10 h of roller table incubation and subsequently mean aggregate diameters remained constant. The authors argued that differences in particle composition within the tanks lead to different aggregate sizes. We changed particle

composition in Exp II deliberately by adding a small amount of *S. costatum* and demonstrated a pronounced effect of pelagic diatoms on sizes and attributes of artificial aggregates.

‘TEP’ were present in our samples with slightly higher values in Exp II compared to Exp I. Concentrations reported here exceeded those of seawater concentration in the Baltic Proper by one order of magnitude (Engel et al., 2002) and were in the same range as measured in a diatom assemblage dominated by *S. costatum* (Engel, 2000). Engel and Passow (2001) presented TEP concentrations in aggregates sampled in the euphotic zone of the Baltic Proper that were 30-fold higher compared to our results. Here, ‘TEP’ was not involved in particle coagulation during Exp II. In both experiments, TPM was nearly in equal shares in *W* and *A*, whereas over 65% of POC, PON and pigments were found in *A* (Table 1). Therefore, less than 35% of mineral particles possibly associated with ‘TEP’ were incorporated into artificial aggregates. Nevertheless, a possible close association between ‘TEP’ and mixed layer minerals being abundant in the original fluff material (results of mineralogical composition are not shown) may explain the predominant absence of ‘TEP’ in *A*.

Our microscopic examinations of aggregates showed that bacteria and pennate diatoms were incorporated into aggregates in a higher proportion in Exp II compared to Exp I (Table 1) possibly due to an increase of particle coagulation rate and efficiency in the former compared to the latter experiment. This was either caused by increasing particle stickiness, number or sizes in the tanks due to *S. costatum*. Fluff particles that were filled into the tanks were at least two orders of magnitude larger than cells or chains of *S. costatum* (5–8 µm in diameter; Wasmund, pers. comm.) as indicated by the initial mean particle diameter of ~100 µm in both experiments (see Figs. 1 and 2, upper graph). Unfortunately, particle abundance could not be calculated from video analysis because particles within the cylinders are not uniformly distributed (Tooby et al., 1977). We therefore assume no measurable influence of *S. costatum* addition on particle number or sizes and rather propose differences in particle stickiness at the beginning of both experiments.

In our experiments both benthic diatoms and bacteria were likely coated with EPS which is frequently sticky. The cells possibly acted as coagulation kernels in the tanks gluing other particles. In the absence of *S. costatum* the majority of benthic cells might be enclosed by inorganic, less sticky particles after 6 h incubation time resulting in constant mean aggregate diameters as determined in Exp I. The addition of *S. costatum* likely increased the ratio of sticky to non-sticky particles in the tanks leading to bigger aggregates in Exp II. As the same amount of TPM were incorporated into *A* in both experiments (Table 1), aggregate number rather than aggregate excess density were likely lower in Exp II compared to Exp I (see below).

4.2. Aggregate settling velocities

Maximum aggregate settling velocities of 1 cm s^{-1} determined in the settling chamber exceeded those from literature data by approximately one order of magnitude. A rather uniform value of in situ floc sinking speed of 0.1 cm s^{-1} was proposed by Hill and Mc Cave (2001). This discrepancy may be caused by methodological artefacts. Handling of aggregates during transfer from the tank into the settling chamber using a syringe may break up or compact aggregates. The porosity of aggregates formed in rotating tanks may be much lower than of natural flocs (Lick et al., 1993). Furthermore, Alldredge and Gotschalk (1988) compared sinking velocities of marine snow aggregates measured in situ and in the laboratory. Sinking velocities derived from laboratory measurements were 2–4 times higher than in situ measured values. This is also true for the comparison of excess densities of artificial and natural aggregates. Engel and Schartau (1999) reported values for excess densities of *Nitzschia closterium* aggregates, which were up to two orders of magnitude higher than values obtained for natural flocs. Thus, our values of sinking velocities and excess densities are likely an overestimate. However, the relative effects of the addition of *S. costatum* on aggregate sinking velocities could be demonstrated and are discussed.

Image analysis revealed that aggregates without *S. costatum* tended to be more porous than those formed in Exp II. The large percentage of bacteria and diatom cells may have elevated excess density of *S. costatum* aggregates compared to aggregates formed in Exp I, resulting in a slightly higher median value of $\Delta\rho$ and a higher mean settling velocity of aggregates $>1000 \mu\text{m}$ in diameter. These findings correspond to in situ (Thomsen and Mc Cave, 2000) and laboratory observations (Beaulieu, 2003), proposing higher settling velocities of phytodetritus aggregates compared to inorganic flocs. Furthermore, the addition of *S. costatum* in Exp II resulted in a stronger significant relationship between settling velocity and aggregate size. Numerous authors reported a relationship between aggregate size and settling velocity (Gibbs, 1985; Alldredge and Silver, 1988), especially for marine snow containing high numbers of pelagic diatoms (Alldredge and Gotschalk, 1988). A lack of this relationship was reported by Diercks and Asper (1997) who studied predominately flocs of minerals together with diatom frustules. Aggregate settling behaviour depends on composition and structure of the flocs as permeability of aggregates determines flow conditions around them and thus their settling velocities.

4.3. Considerations for the field

Artificial aggregates with *S. costatum* reach sizes similar to those found in natural waters. Large, organic-rich aggregates reaching $2000 \mu\text{m}$ in diameter were observed in deep sea waters (Thomsen and Gust, 2000; Thomsen and Mc Cave, 2000) whereas in situ aggregate size measurements in the BBL of coastal areas reveal mean aggregate diameter less than $1000 \mu\text{m}$ (Jähmlich and Graf, 1998; Christiansen et al., 2002; Jähmlich et al., 2002). Deep sea aggregates had higher scavenging residence times ($^{234}\text{Th}/^{238}\text{U}$) compared to those from coastal waters (Turnewitsch and Springer, 2001). Kersten et al. (1998) measured residence times of approximately one week for suspended matter including aggregates in bottom waters of Mecklenburg Bight based on $^{234}\text{Th}/^{238}\text{U}$ disequilibrium method. The corresponding settling velocities for these particles would be two orders of

magnitude lower than mean values presented here. This dissimilarity is likely to result from particle attributes in both systems. Median values of excess densities of artificial fluff aggregates were one order of magnitude higher than values obtained for natural diatom aggregates (Alldredge and Gotschalk, 1988) and aggregates including minerals together with diatom frustules (Diercks and Asper, 1997). These observations correspond to the observed higher excess densities and sinking velocities of artificial aggregates.

Finally, turbulence in the BBL which carries particles upwards in a statistical sense (Hill and Mc Cave, 2001) has to be considered in this regard. In the field, particle residence time is modified not only by settling velocities but also by turbulent transport. Including turbulence would provide a better mechanistic understanding of aggregate transport in coastal waters.

5. Conclusions

This study emphasises that experimentally formed fluff aggregates with added cells of pelagic diatoms (*S. costatum*) showed increased rate and efficiency of particle coagulation compared to original fluff material with natural microorganism assemblages. *S. costatum* aggregates incorporated higher percentages of biogenic parameters (POC, PON, and CHE), and higher cell numbers of bacteria and pennate diatoms compared to aggregates without pelagic diatoms. Artificial aggregates of the former type were less porous and had higher experimentally measured sinking velocities compared to aggregates of the same size without *S. costatum*. ‘TEP’ were virtually absent in aggregates of both types. Mineral particles contribute little to TPM in aggregates, too, supporting a close association to ‘TEP’. Our results further show that measurements of sinking velocities are necessary because the use of literature derived equations to calculate aggregate settling velocities may lead to wrong conclusions of particle transport behaviour. A pronounced effect of pelagic diatoms resulting in a relatively higher sinking velocity of fluff aggregates was clearly shown and has to be considered in regard to particle transport within the water column.

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