Vol. 154: 241–252, 1997 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published July 31

Particle capture and deposition by deep-sea sponges from the Norwegian-Greenland Sea

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ABSTRACT: Particle uptake and deposition by the 2 most abundant deep-sea demosponge species from the Norwegian and Greenland Sea (*Thenea abyssorum*) and the deep fjords of western Norway (*Thenea muricata*) were studied in flume experiments. Fluorescent particles of 1, 2, 3, 6, 10 and 16 µm diameter (microspheres, Duke Scientific Corporation®) with a density of 1.05 g cm^{-3} were used at 2 current velocities, 1.5 and 5 cm s^{-1}. Both species ingested small particles exclusively (<6 µm and <10 µm, respectively), with a preference for the smallest fraction at both current speeds. The results suggest that the size spectrum actually ingested depends on the supplied particle sizes rather than on current velocity. Current velocity fields around dead specimens were recorded and turbulence intensity calculated in order to determine the influence of the sponge acting as a biogenic structure on the near-bottom current regime. Disruption of flow conditions was detected as far as 14 cm downstream and several cm laterally from the biogenic obstacles. Bulk biodeposition rates calculated from sponge biomass and volume of ingested particles range between 7 and 10 mg d^{-1} g^{-1} ash-free dry weight.

KEY WORDS: Deep sea · Sponge · Suspension feeding · Biodeposition · Biogenic structure · Flow regime

INTRODUCTION

Most benthic communities in deeper waters rely on particles in the bottom nepheloid layer (BNL) for food. The composition and abundance of these particles depend on a variety of processes, and field studies have revealed a high particle exchange between sediments and BNL. Particles may have rather short residence times in the BNL (Bacon & van der Loeff 1989) but re-enter the benthic resuspension loop several times (for review see Graf & Rosenberg in press). As even slow near-bottom current velocities exceed high sedimentation rates, these particles form a laterally moving flux situated high above many benthic organisms. Among the processes driving the suspension/deposition loop are bioresuspension and biodeposition: deposit feeders build pits that mediate enhanced deposition (Yager et al. 1993) and epibenthic suspension feeders like sponges extract drifting particles from the water and — by expelling faeces or pseudofaeces — make them available for other benthic organisms.

In the deep sea, however, suspension feeders markedly decrease in overall importance with depth due to the scarcity of water-borne particles, and suspension feeding consequently is of much less importance in abyssal benthic communities than in energetic coastal habitats (Gage & Tyler 1991). Deep-sea members of taxa hitherto believed to be suspension feeders have even been found to be carnivorous: the Sorberacea among the tunicates (Monniot & Monniot 1978), now categorized as a separate class, the septibranch mollusc *Cuspidaria* (Reid & Reid 1974) and members of the family Cladorhizidae in sponges, discovered only recently (Vacelet & Boury-Esnault 1995).

In polar deep seas, on the other hand, sponges seem to dominate the epibenthic megafauna. The composition and distribution of sponge associations of the abyssal Norwegian and Greenland Sea have been studied by Barthel & Tendal (1993), who were able to

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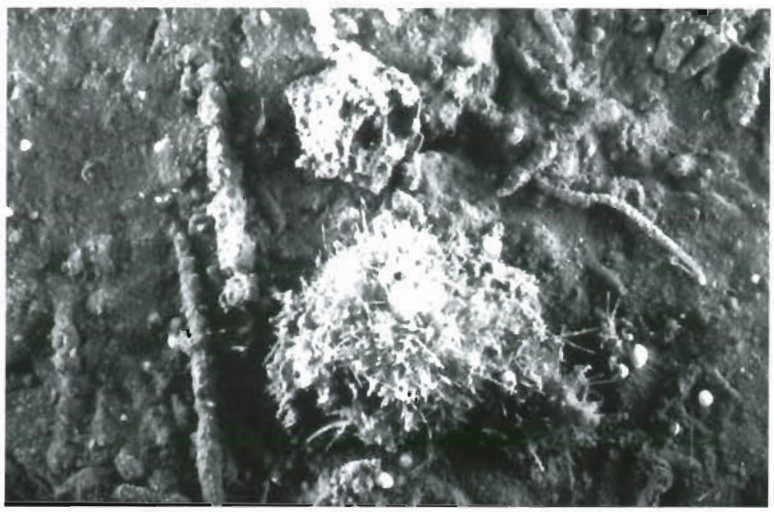

Fig. 1 *Thenea abyssorum* in its natural position half buried in the sediment. Diameter of specimen 1.8 cm

delineate a core association of 8 regularly occurring sponge species that is distributed throughout the deep Norwegian and Greenland Sea. Its most abundant species, the demosponge *Thenea abyssorum*, is used as a character species in some high Arctic areas (Paul & Menzies 1974) and at many stations comprised more than 50% of the individuals of all taxa caught in trawls (Witte unpubl.). It can thus be expected to play a major role in exchange processes at the sediment/water interface.

For the first time, flume experiments with living deep-sea sponges have been performed to investigate the nutrition of 2 dominant species, *Thenea abyssorum* and *Thenea muricata*. In this paper, data on particle size preferences, clearance rates and the fate of ingested particles are presented. The small scale flow regime around sponge specimens is depicted to illuminate mechanisms of particle capture, and bulk deposition rates are calculated to gain insight into the role of this sponge community in exchange processes at the sediment/water interface.

MATERIALS AND METHODS

Species descriptions

Thenea abyssorum Koltun, 1959

Thenea abyssorum is part of the core association dominating the poriferan communities of the Greenland-Iceland-Norwegian (GIN) Seas (Barthel & Tendal 1993), where it contributes more than 80% to sponge community respiration (Witte & Graf 1996). It can be so abundant that it is used as a character species in Arctic areas (Paul & Menzies 1974), and it was the most abundant species at all stations sampled for this study in the deep Norwegian and Greenland Seas. The individuals are small, with a diameter of up to 2.5 cm, and colonize soft bottoms exclusively. The sponges live half buried in the sediment (see Fig. 1), and are anchored in the sediment with a spicule root tuft that can be longer than the animal's height. In- and exhalant openings lie on opposite sides of the sponge above the sediment and can be surrounded by a screen of several-millimeter-long spicules. The angle of the spicules in this corona is variable. In the lab, the animals were observed to contract at irregular intervals, reducing their volume to ca 50%. Together with contraction and closure of the spicule corona, this might aid in controlling the water volume pumped through the sponge.

Thenea abyssorum, like many sponge species, carries heterotrophic bacteria in its tissue, and it has been suggested that these species might—at least in part—live by uptake of DOC. As a sponge that feeds via DOC uptake is not a suitable object for particle uptake experiments, the uptake of radioactively labelled amino acids was tested prior to other experiments. The sponges, perhaps not too surprisingly, were able to take up DOC. However, with 700 pg ind.$^{-1}$ d^{-1} the uptake rates were too low to play a major role in the energy budget of the species.

Thenea muricata (Bowerbank, 1858)

Thenea muricata is the most abundant sponge species in deep fjords of western Norway. Similar to *T. abyssorum*, the species colonizes soft bottom, anchoring itself in the sediment with 1 or several spicule root tufts. Individuals reach a diameter of 6 to 8 cm. Small individuals are mushroom-shaped with 1 central osculum; larger specimens appear more flattened with several oscula. For detailed descriptions see Sollas (1882), Babic (1916) and Steenstrup & Tendal (1982). For the experiments, sponges of varying size up to 5 cm in diameter were used.

Sampling

Specimens of *Thenea abyssorum* were sampled during 2 cruises with the RV 'Meteor' to the Norwegian

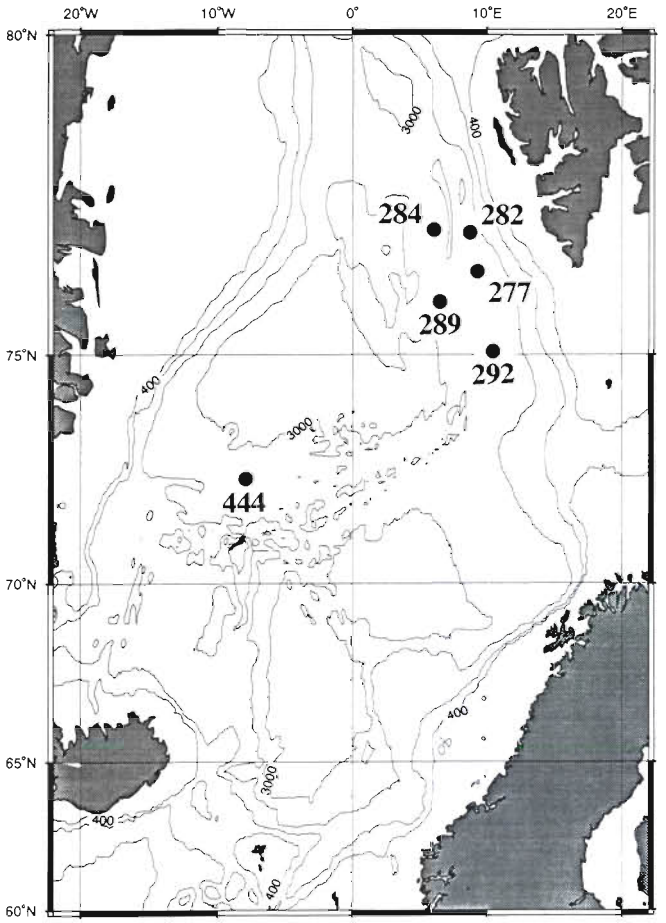

Fig. 2. Location of stations in the Norwegian-Greenland Sea. For additional station information see Table 1. Depth represented along contours at 400, 1000, 2000 and 3000 m

and Greenland Sea at depths of 2000 m or more (Fig. 2, Table 1). The sponges were sampled with a modified box corer (50 × 50 cm) that carries 4 plexiglass tubes of 19 cm inner diameter. The low surface water temperatures in the study area allowed sampling with only minor heating and thus made it possible to obtain living specimens that had not been subjected to rapid temperature changes: on deck, the overlying water in the box cores had a temperature of 1 to 2°C, compared to −0.9°C at the sea floor. Generally, sediment cores of 20 to 25 cm length with fairly undisturbed surfaces were obtained, with an overlying water column of ca 20 cm. Immediately after recovery of the gear these microcosms were removed and transferred to a specially designed cooling container, where they were maintained at *in situ* temperatures. Twice a week about one third of the overlying water column was removed and replaced by precooled bottom water. Following each cruise the cooling container was shipped to Kiel, where experiments could thus be carried out about 4 to 6 wk after sampling. For maintenance and experiments, water from >2000 m was sampled and stored during the cruises. Heat production measurements, which had also been carried out on board (Witte & Graf 1996), were conducted before flume experiments were started in order to insure that the specimens used were healthy.

Specimens of the closely related species *Thenea muricata* were sampled during 2 cruises with the RV 'Hans Brattström' on 19 and 29 February 1993 at 630 m depth in the Korsfjord, western Norway (60° 08.8' N, 05° 07.0' E). The sponges were maintained at *in situ* temperatures of 5 to 6°C in a constant temperature room at the Dept of Fisheries and Marine Biology, University of Bergen, where flume experiments were carried out during the following days. For maintenance and experiments, filtered fjord water from 100 m depth was used.

Flume experiments

All flume experiments were carried out at *in situ* temperatures in recirculating flumes. According to Nowell & Jumars (1987) no flume design is applicable to all problems in benthic biology. Our flumes are basically designed as outlined in Vogel (1981), with some modifications considering design criteria given in Nowell & Jumars (1987). The channels of the 2 flumes are 3 (2) m long and 0.4 (0.3) m wide and high, i.e. length/width ratios are 7.5 and 6.7, respectively. Water level was 15 (10) cm giving width/water depth ratios of 2.7 (3). Nowell & Jumars suggest a minimum value of 5 for the width/depth ratio in order to reduce side wall effects. However, for the current velocities used in this study side wall effects end 7 cm from the side walls. As the test section was situated with 10 cm distance to each side wall, boundary effects as described by Nowell & Jumars (1987) were assumed to be negligible. In addition, they themselves have used a width/depth

Table 1. Cruises, locations and depth of stations. BC: box corer. For details see Suess & Altenbach (1992) and Pfannkuche et al. (1993)

Cruise-Leg	Stn	Latitude	Longitude	Depth (m)	Gear
Meteor 17-1	444	72° 21.1' N	07° 48.4' W	2630	BC
Meteor 21-4/5	277	76° 28.6' N	08° 44.5' E	2020	BC
Meteor 21-4/5	282	76° 51.0' N	08° 24.3' E	2360	BC
Meteor 21-4/5	284	77° 04.0' N	06° 21.8' E	2150	BC
Meteor 21-4/5	289	75° 59.5' N	06° 21.4' E	2160	BC
Meteor 21-4/5	292	75° 18.5' N	09° 46.2' E	2570	BC

ratio of 3 in experiments on flow dynamics within seagrass beds (Gambi et al. 1990).

For the particle uptake experiments, the smaller flume was used (2 m long and 30 cm wide; for details see Ziebis 1991), which allowed the 20 cm tubes (microcosms) to be introduced and set level with the sediment surface inside the flume. The sponges thus stayed in their natural position half buried in the sediment and did not have to be touched or removed from the sediment. Fluorescent particles (microspheres, Duke Scientific Corporation®) with a density of 1.05 g cm^{-3} were used to study particle uptake by the sponges. As sponges are unable to distinguish between digestible and non-digestible particles (Pourbaix 1933, Kilian 1952, Willenz & van de Vyver 1982), a protein coating was not applied. Particles of 1, 2, 3, 6, 10 and 16 µm diameter were used. All flume experiments lasted 5 to 6 h. At each flow speed, 2 replicate experiments were carried out with *Thenea abyssorum* and 3 with *T. muricata*. In the case of *T. abyssorum*, the biomass of the sponges in the flume was too low to cause considerable reduction of particle concentration in the flume water. Number and size of particles taken up by this species therefore had to be determined directly. For this purpose, 2 methods were used. (1) Histological sections of tissue samples from some of the sponges were prepared for TEM analysis in order to ensure that particles had been taken up into the sponge tissue (Witte unpubl.). (2) The remaining sponges were dissolved in nitric acid. From the mixture of sponge spicules and microspheres, the latter were separated out by means of density separation with calcium bromide (modified according to Thomsen 1991) and counted using an epifluorescence microscope. Prior to this procedure sponges were placed in glass beakers with filtered seawater to allow for cleaning of the canal system in order to exclude particles trapped in the canal system but not taken up into the tissue.

During the experiments with *Thenea muricata*, particle concentration in the flume water was determined every 30 min by means of a coulter counter. To account for the unavoidable 'natural loss' of particles, e.g in the recirculation tube and resulting from passive deposition of particles on the sediment surface not due to the presence and activity of sponges, an identical experiment without sponges was run for each experiment. The reference values achieved this way were then subtracted from the raw data. After the termination of each experiment, size and ash-free dry weight (AFDW) of all sponges were determined. Prior to each experiment the flume bottom was covered with a sediment layer and the flume was then filled with filtered (10 µm) deep-sea water. The system was run for 2 d at medium flow speed (ca 3 cm s^{-1}), with the water being permanently aerated. After 2 d, sediment cores and sponges were implanted and given another 3 d to adjust to the system. Water samples were analysed to determine the natural particle freight (2 to 16 µm) of the water and a microsphere suspension was prepared that would result in an equal amount of natural and artificial particles of each size class in the flume water Following these 3 d the aeration was stopped and the particle suspension was slowly added. Five minutes after injection the first water sample was taken. From the decreasing particle concentration the clearance rate was calculated for 30 min intervals.

For determination of flow fields around the sponges, the large flume, equipped with a system for measuring current velocity with high spatial resolution (Springer 1996) that was not available in 1993, was used. An acoustic Doppler current meter (Sontek, San Diego, CA, USA) was mounted onto a movable unit that allowed positioning of the sensor with an accuracy of 0.2 mm. Measurements of all 3 orthogonal components of the velocity vector (v_x, v_y, v_z) were taken and, as measurements were taken 5 cm below the sensor, the influence of the probe itself was assumed to be negligible. The measurements of flow fields were taken around 2 dead *Thenea abyssorum* individuals that were placed onto a sediment layer in the flume in their natural position (see Fig. 1). The sponges had diameters of 18 and 13 mm, and their height above the sediment was 13 and 8 mm, respectively; they were positioned ca 100 cm downstream from the leading edge (rectifier grid). For the current velocities used here, the flume allows development of a boundary layer thickness of 5 cm over smooth surfaces. The boundary layer is fully developed about 0.9 m from the leading edge. The animal height/boundary layer height ratios are 0.2 and 0.37 for the 2 species respectively and thus are close to the ratio of 0.33 recommended by Nowell & Jumars (1987). Current velocity profiles were measured at 2 free stream velocities, 1 and 5 cm s^{-1} Vertical profiles were taken 5 cm in front, directly above and 4 cm behind the larger of the 2 specimens. Horizontal profiles were measured 1 cm above the bottom (which is approximately the height of the in- and exhalent openings) with a grid resolution of 4.83 mm. From the 3 velocity components, turbulence intensity *TI* was calculated as

$$TI = 100 \times \frac{\sqrt{\Delta v_x^2 + \Delta v_y^2 + \Delta v_z^2}}{\sqrt{v_x^2 + v_y^2 + v_z^2}}$$

(Gambi et al. 1990). Shear velocity u^* and the roughness length z_0 were calculated from the Karman-Prandtl log profile (e.g. Middleton & Southard 1984, Mann & Lazier 1991). From these parameters near-bed particle dynamics can be inferred (Jumars 1993).

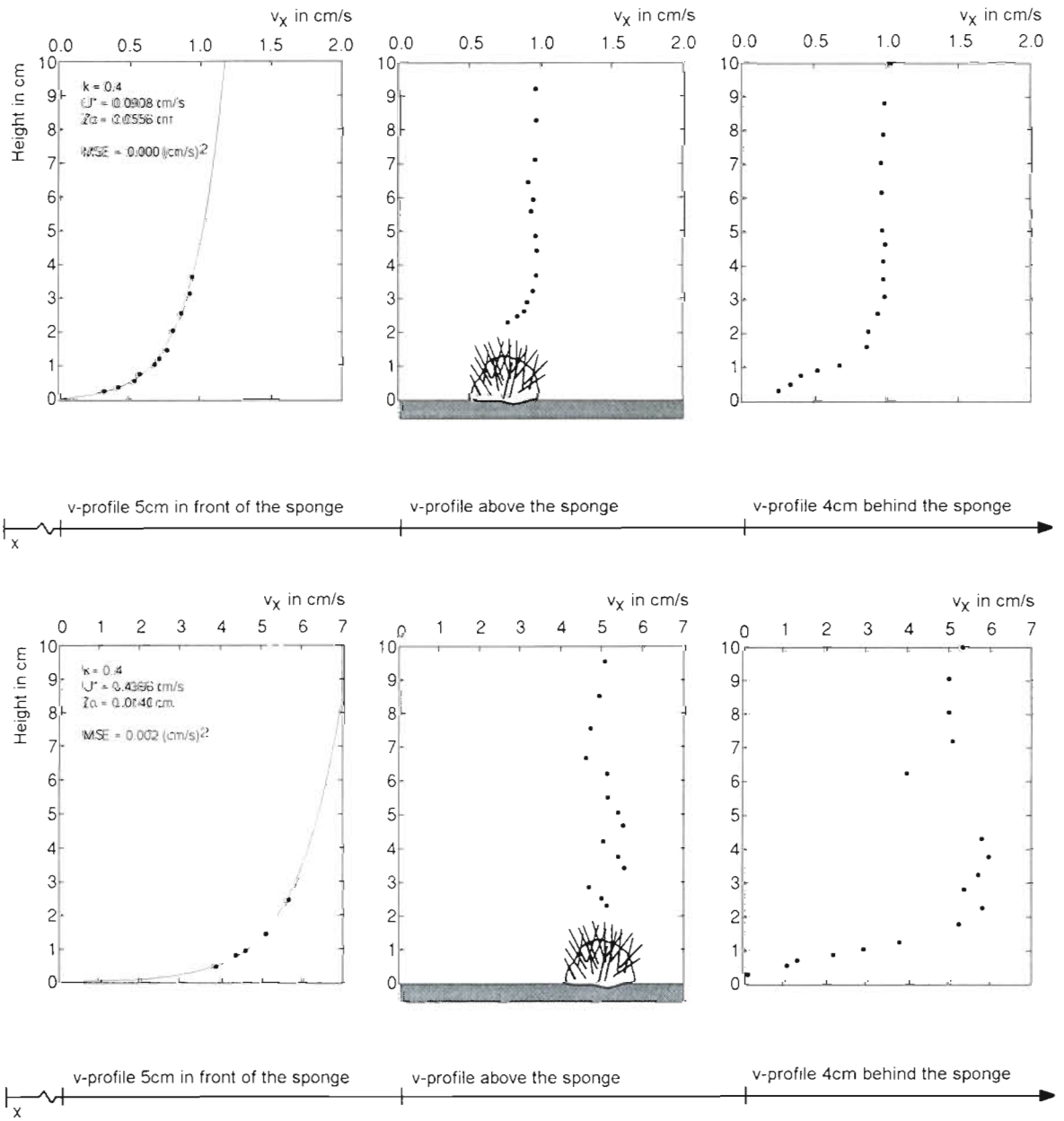

Fig. 3. Profiles of current velocity in front of, above and behind a specimen of *Thenea abyssorum* at free-flow velocities of 1 cm s^{-1} (top) and 5 cm s^{-1} (bottom). Grey dots: data not used for calculation of log profiles

RESULTS

The vertical current profiles show that a well developed boundary layer (see above) existed in front of the sponges (Fig. 3). For the free-flow velocity v = 1 cm s^{-1} (5 cm s^{-1}), u^* and z_o were calculated as u^* = 0.09 cm s^{-1} (0.44 cm s^{-1}) and z_o = 0.05 cm (0.01 cm). Above and behind the sponges the boundary layer formation was disturbed and the current profiles had a different shape. Here, calculation of u^* and z_o from the log profile is not sensible. At v = 1 cm s^{-1} the log profile seems to be shifted upwards by ca 1 cm. Horizontal profiles (Fig. 4) show that the influence of the large sponge on hydrodynamic conditions was visible 14 cm downstream of and several cm lateral to the sponge. *TI* rose from 20% in front of to 160% behind the sponge, where a leeward deceleration of the flow occurs.

The data obtained on size and relative abundance of particles found in the specimens of *Thenea abyssorum* are summarized in Fig. 5. At both the low and higher current velocities, only microspheres 1 to 3 µm in diameter were found inside the sponges. None of the

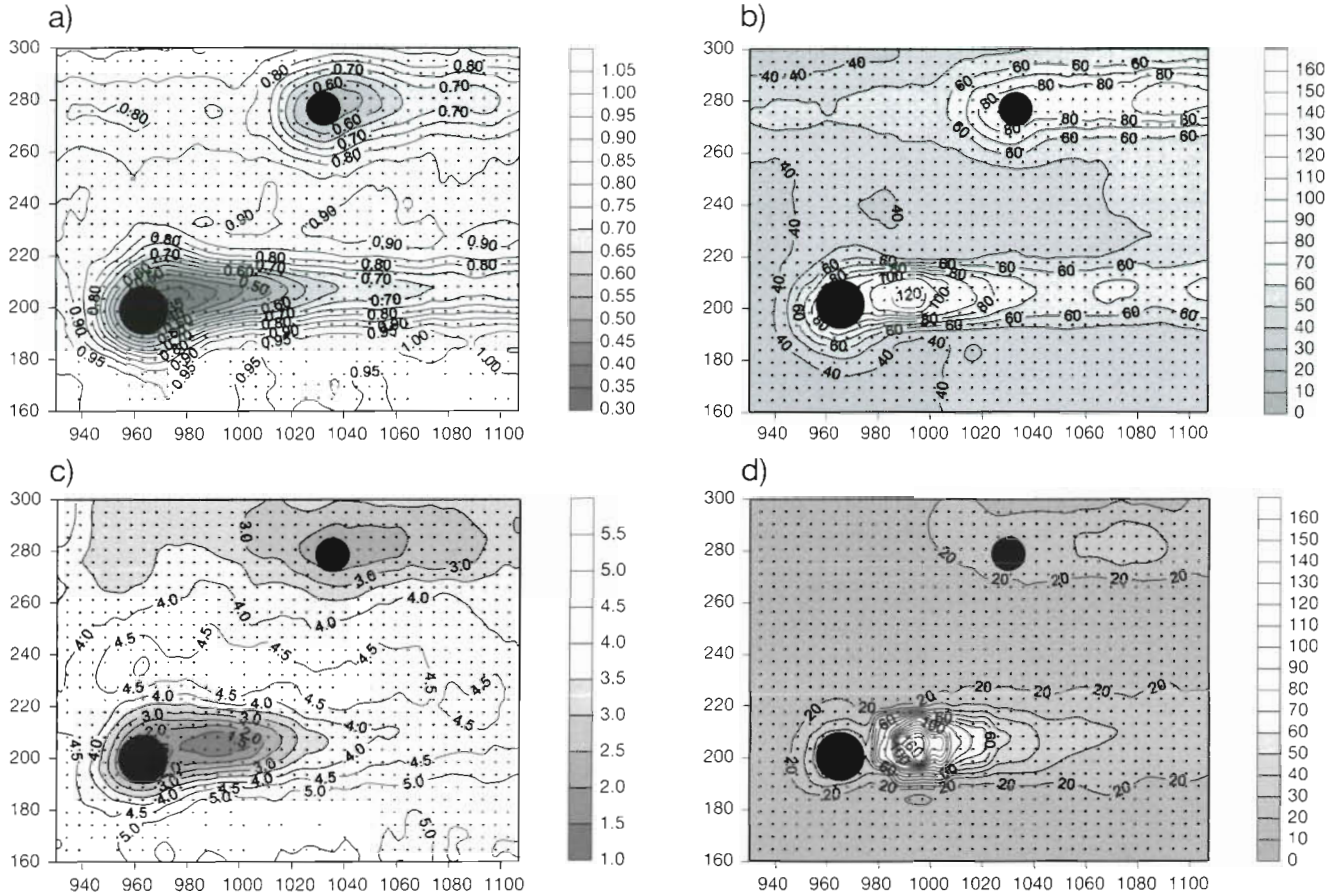

Fig. 4. Current velocity (a, c) and turbulence intensity (b, d) field around specimens of *Thenea abyssorum* at 1 cm height above bottom. (a, b) Free-flow velocity v = 1 cm s^{-1}; (c, d) free-flow velocity v = 5 cm s^{-1} x-axis: distance downstream from collimator (mm); y-axis: position between the sides of the canal (mm). Small dots mark points of current measurements. Black circles symbolize sponge specimens

specimens contained larger particles. The concentration of particles in the flume water at the beginning of the experiment was fairly even, with approximately 2000 particles ml^{-1} for all 3 sizes (1, 2 and 3 µm). Particle uptake, however, was selective: 40% of the particles found inside the sponges were small (1 µm), ca 30% were 2 µm and only 15 to 20% were 3 µm. Varying current speeds, on the other hand, did not influence the size spectrum taken up. As *T. abyssorum* is a very small species and only a limited number of living specimens was available, the sponge biomass in the flume was not sufficient to cause a significant decrease in particle concentration in the flume water Additional experiments were carried out with *T. muricata* from Korsfjord, western Norway. Again, experiments were carried out at 2 different current speeds. The particle concentrations during the experiments (calculated as the difference between the main experiment with sponges and an identical experiment without sponges) are shown in Figs. 6 & 7 As shown in Fig. 6, at a low current speed the concentration of small particles continually decreased, whereas the coarser fraction (10 and 16 µm) was not affected. During the second set of experiments with higher current speed (Fig. 7) this decrease was much faster. The concentration of the 2 and 3 µm fractions sank within 4 h to ca 300 particles ml^{-1} and then stayed more or less constant. Whether this constant particle concentration resulted from an equilibrium between removal and addition cannot be decided. The 6 µm particles decreased constantly throughout the experiment and the 10 µm particles, unaffected at low flow speed, decreased rapidly after 3.5 h.

From the decrease in particle concentration between t = 60 min and t = 240 min, mean clearance rates were calculated for the 2 to 6 µm size fractions and both flow speeds. The clearance rate (a theoretical value describing the volume of water per unit time that an organism filters free of particles, given in l h^{-1} g^{-1} AFDW) ranged between 5 and 9 l h^{-1} g^{-1} AFDW or 17 and 30 ml min^{-1} g^{-1} DW (AFDW is ca 20% of DW for *Therea muricata*, Witte unpubl.). It was higher for smaller particles and

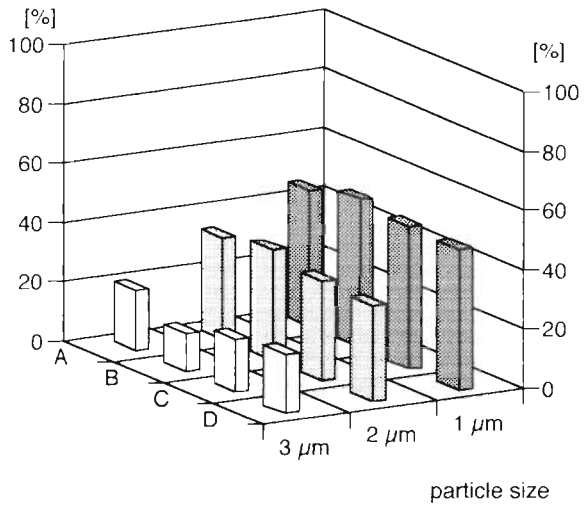

Fig. 5. *Thenea abyssorum*. Percentage of particles of different sizes ingested by sponges during 4 experiments at 2 current speeds. (A, B) 1.5 cm s^{-1}, (C, D) 5 cm s^{-1}. (Larger particles were not ingested and are thus not shown in the diagram)

increased with increasing current velocity. In addition to the mean clearance rate, clearance rates were calculated for 30 min intervals throughout the experiment to monitor possible variations (Fig. 8). As can be seen, the clearance rate was not constant throughout the experiment: at low current speed it increased for 3 and 6 µm particles until the end of the experiment whereas it increased then decreased again for the 2 µm size fraction. At a higher current speed it decreased after 3 to 4 h for both 2 and 3 µm particles; only for 6 µm particles did it remain high until the end of the experiment.

DISCUSSION

As benthic organisms, sponges live in the current gradient of the benthic boundary layer However, with the exception of *in situ* studies conducted by Reiswig (1971a, 1975) with 3 marine demosponge species and by Frost (1978, 1980) with the freshwater sponge *Spongilla lacustris*, particle uptake of sponges has mainly been studied in laboratory experiments either under still-water conditions or in uncontrolled turbulent conditions created to keep the particles in suspension This flume study was an attempt to address the phenomenon of sponge particle uptake under nature-like boundary layer conditions. Flow conditions in boundary layers can be divided into laminar and turbulent flow, characterized by Reynolds numbers ($Re = v \times l/\nu$, where v is current velocity, l is the characteristic length, and ν is the kinematic viscosity of a fluid). In our flume experiments we attempted to create smooth turbulent flow conditions (Re = 40 to 200000; Vogel 1981) that frequently occur in the field. For v = 1 cm s^{-1} (v = 5 cm s^{-1}) Re was calculated at 5000 (25000) (using l = distance from sponge to leading edge) and thus falls into the range defined above. Turbulence intensity in front of the sponges was ca 20% and thus somewhat higher than field data of TI = 5 to 10% reported by Middleton & Southard (1984). However, it is not indicated in that study whether all 3 velocity components were chosen to calculate TI as in the method described by Gambi et al. (1990). Both Re and TI thus confirm the existence of nature-like conditions. Note that turbulence intensity is used as a means to compare flow

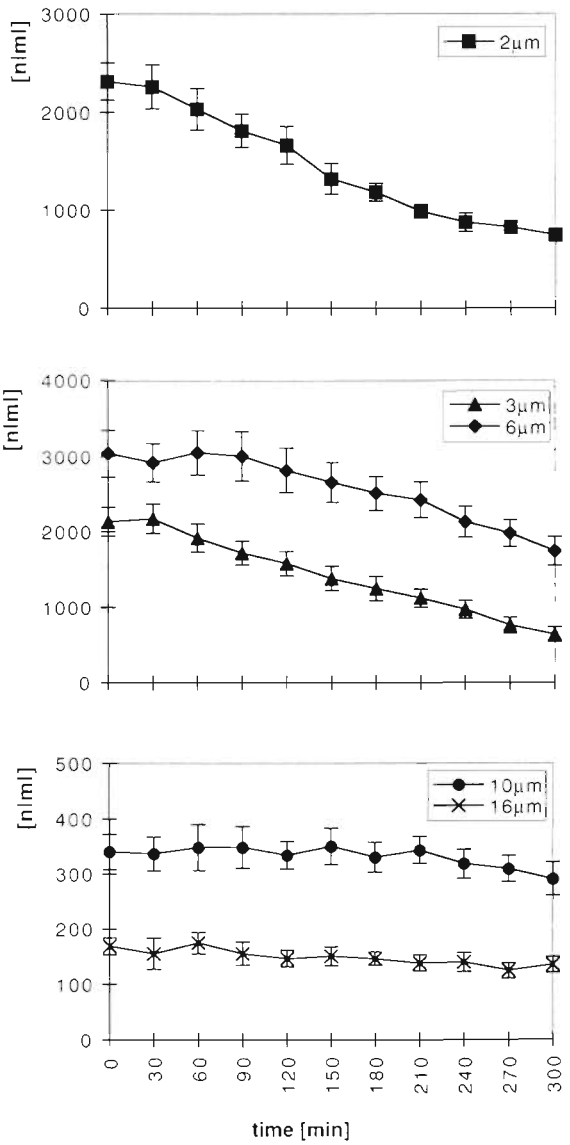

Fig. 6. Particle concentration (mean ± SD) during 5 h flume experiments (calculated as the difference between the main experiment with sponges and an identical reference experiment without sponges) with *Thenea muricata* at v = 1.5 cm s^{-1}. Sponge biomass 4.2 g AFDW

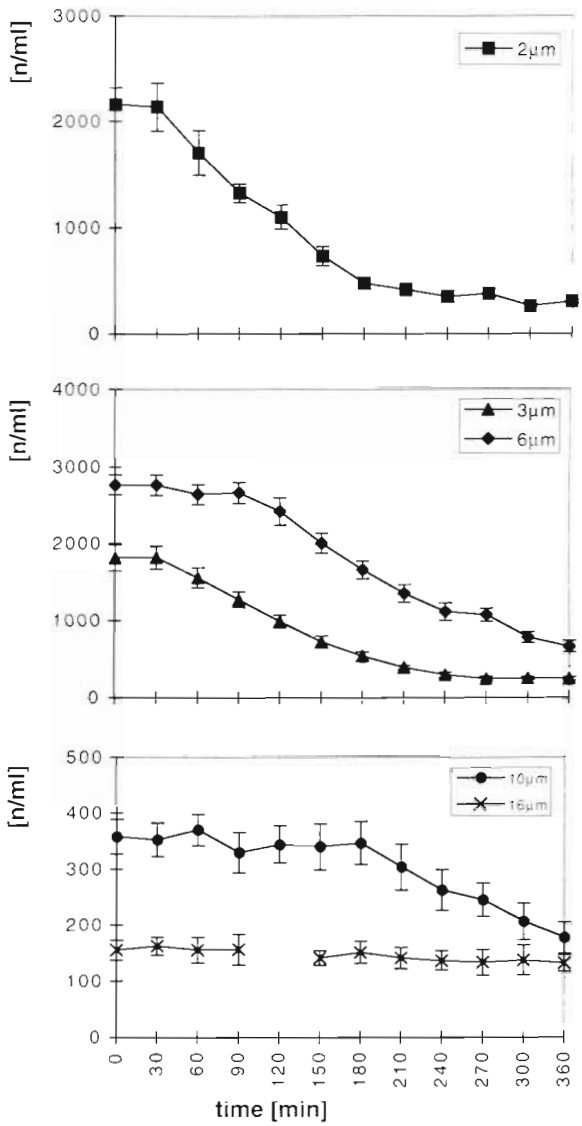

Fig. 7 Particle concentration (mean ± SD) during 6 h flume experiments (calculated as the difference between the main experiment with sponges and an identical reference experiment without sponges) with *Thenea muricata* at v = 5 cm s^{-1} Sponge biomass = 4.6 g AFDW

regime at varying free-flow velocities. High values of *TI* thus do not necessarily mirror strong forces, as the standard deviation from flow velocity can be relatively high, especially at low flows. Thus the high turbulence intensity at the leeward side of the sponges, although indicating the presence of wake perturbations, represents an area of low energy.

Particle capture

Thenea abyssorum took up particles of up to 3 µm, whereas *T. muricata* took up particles of up to 6 µm and in the second set of experiments up to 10 µm. This is in accordance with qualitative results of Göbel (1993), who studied particle uptake in 8 shallow-water sponges of different taxa that all accepted particles 0.15 to 6 µm in diameter. Only 2 species, the calcareous sponge *Leucosolenia* sp. and the freshwater sponge *Spongilla lacustris*, were able to cope with larger particles of 9.6 and 21 µm, respectively. For particles <63 µm, however, mean transport velocity does not differ significantly from mean current speed (Eisma 1993). Particles are assumed to behave like water and follow the streamlines around obstacles. This raises the question of how they become available to the sponges. Several processes seem likely (Fig. 9): For irregular structures like specimens of *T. abyssorum* it is difficult to determine the surrounding 3D flow field without flow visualization. This has, however, been done for an animal tube mimic (Eckman & Nowell 1984): a down-

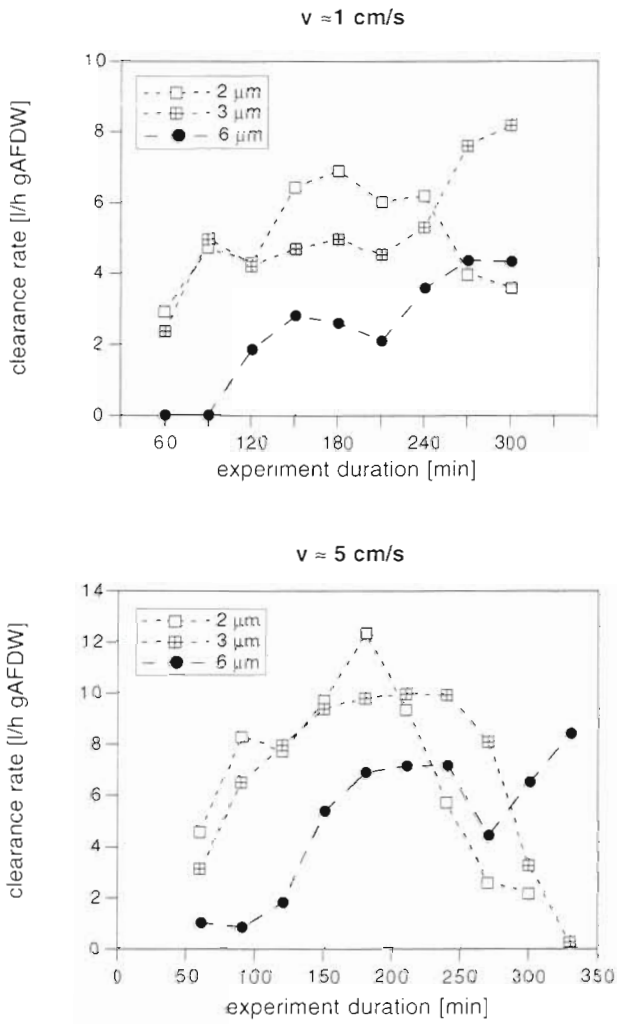

Fig. 8. Variation in clearance rates of *Thenea muricata* for different particle sizes during experiments with v = 1.5 cm s^{-1} (above) and v = 5 cm s^{-1} (below)

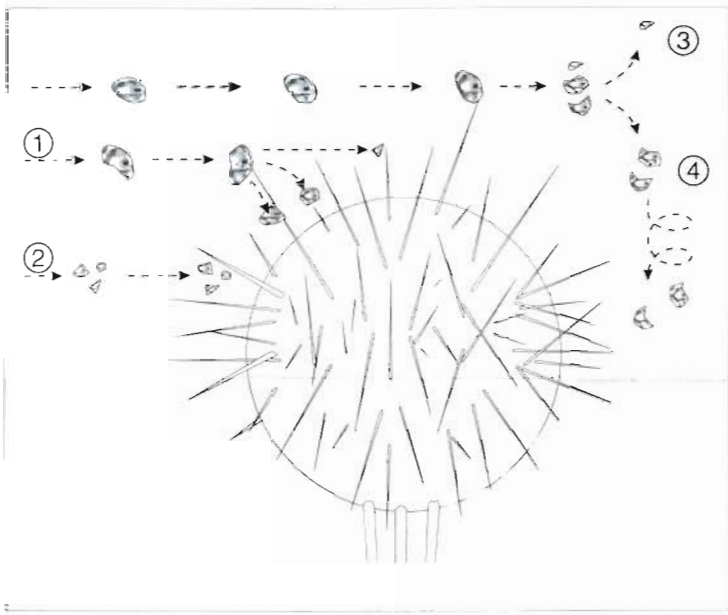

Fig. 9. Schematic drawing of possible particle capture modes in *Thenea abyssorum*. (1) Breakage of aggregates into smaller particles that decelerate and thus become available to the sponge; (2) intrusion of small particles into the sponge's spicule 'fur'; (3) uplift of small particles due to increased turbulence; (4) downward transport of particles due to vortex at the leeward side of the sponge

ward vortex developed downstream from the tube and the flow velocity strongly decreased, facilitating the deposition of particles. As the turbulence intensity field around *T abyssorum* (Fig. 4) also indicated strong current deceleration behind the sponge, it is assumed that a similar vortex developed. If this holds true, the flow deceleration and downward vortex on the leeward side might facilitate the ingestion of particles. As can be seen in Fig. 4, the deceleration of flow behind the sponges for both current speeds is much stronger behind the larger specimen, which would thus profit more from this phenomenon than smaller ones. In these specimens, the leeward side might be the main area of particle uptake. In areas with a rather stable flow regime or with a predominant flow direction it could then be advantageous to orient correspondingly. Unfortunately, no observations on the orientation of sponge ostia with repect to flow exist. Carey (1983), on the other hand, investigated the polychaete *Lanice conchilega* and demonstrated resuspension in upward spiral vortex filaments downstream from the tube. Both scenarios, although contrasting, provide the sponge with otherwise non-available particles and might thus increase food supply for the animal at the leeward side. The high turbulence intensity behind the larger individuals can also cause an opposite phenomenon: at high *TI* and low flow, low excess density particles can experience uplift (Jumars 1993). Small organic particles, created e.g. by the disruption of aggregates, might thus be transported out of immediate reach of suspension-feeding benthic organisms.

The sponges might also profit from the permeability of their spicule 'fur': the intrusion of 10 µm particles into permeable sediments, driven by pressure gradients generated when boundary layer flows interact with topography, has recently been demonstrated (Hüttel et al. 1996). Small particles could also be decelerated and thus become available in the needle mesh around the sponge where flow is reduced. The needles probably also cause the breakage of larger aggregates. This breakage of aggregates possibly is of great importance: up to 65% of the bacterial population in near-bottom deep waters lives in association with particles. Free-living bacteria that match the preferred sponge food size are correspondingly scarce (Thomsen & Graf 1994) and aggregate breakage could thus provide the sponges with food of high nutritional value. It must, however, be kept in mind that sponges are active suspension feeders able to create water circulation that by itself might supply a sufficient amount of food particles. To separate the importance of the varying processes and weigh the role of active pumping in deep-sea sponge feeding, a detailed survey of flow patterns around actively pumping specimens would be necessary.

Selection of particles

If particles <63 µm become available for deep-sea sponges, a filter mechanism obviously prevents the ingestion of particles >6–10 µm. Göbel (1993) gives a compilation of ostial diameters determined by various authors, and states that—although they function as a filter—the ostia, which have a diameter of 20 to 70 µm, are far too large to filter out the smaller particles. Göbel suggests that the limit is set by the size of choanocytes, endopinacocytes and archaeocytes as all particles have to be ingested by the one or the other cell type. This is, however, not fully convincing as freshwater sponges are able to take up much larger particles than marine sponges without having correspondingly larger archaeocytes. In addition, it is difficult to envisage a passive filtering mechanism in which ostial diameter or mean cell size mediates the preferential uptake of certain size classes within the acceptable size range. Hydrodynamical sorting of particles in the benthic boundary layer is a well known phenome-

non (e.g. Muschenheim 1987a, b), but as mean transport velocity differs significantly from mean current speed only for particles >63 µm (Eisma 1993), the selection effects observed here cannot be explained as an effect of hydrodynamical sorting either. Is the preferential uptake of smaller particles in *Thenea* then created by an active selection process? A striking capability of selective particle retention was described by Wilkinson et al. (1984), who found that sponges were able to descriminate between bacteria from ambient waters—which were retained—and symbiotic bacteria which were not retained. Our experiments with *Thenea muricata* support this hypothesis: in both experiments the concentration of smallest (2 and 3 µm) particles declined rapidly, as did the 6 µm fraction 2 h later. This could indicate that it is the decline of small (i.e. preferred?) particles that leads to the uptake of the larger size fraction. We have, however, stated above that particles can be taken up via 2 pathways. The delayed uptake of 6 µm particles might thus reflect the fact that pathway 2 needs a 'reaction time' until a sufficient number of archaeocytes has gathered. Also, cells might reach a saturation point as reported by Willenz & Rasmont (1979) for choanocytes of *Ephydatia fluviatilis*. However, during the second set of experiments the 10 µm particles started to decrease 3 h after the beginning of the experiment. As 6 and 10 µm particles are ingested via the same pathway, selection here must have taken place independently from the ingestion mechanism. In addition, the 10 µm particles were not affected at low flow speed when smaller particles decreased far more slowly. This supports the hypothesis that the uptake of larger particles is connected to the disappearance of smaller food items. The uptake of particles of a certain size class would thus depend on the availability of certain particles rather than on current velocity, as described for other suspension feeding taxa (e.g. Okamura 1990).

Clearance rates

Clearance rates were determined from $t = 60$ min instead of $t = 0$ min as the experiments showed a time lag between the start of the experiment and the beginning of a decrease in particle loads. Pumping activity is not necessarily constant in sponges: long-term studies of pumping activities in 3 tropical demosponges (Reiswig 1971b) revealed that one species maintained a constant level of activity, one species displayed high pumping activity for long periods interrupted by short periods of complete cessation, and one species maintained an alternating active-inactive cycle over a long time span. On the other hand, active pumping without filtering has also been described by Wilkinson et al. (1984). A possible explanation could be the existence of bypasses connecting the inhalant and exhalant canal system directly, as described by Bavestrello et al. (1995). From our experiments it cannot be determined whether the sponges were inactive or instead pumping but not filtering during the initial period. As these periods have been excluded from calculations, the mean clearance rates of 17 to 30 ml min^{-1} g^{-1} DW obtained have to be regarded as maximum values. They are in the range of filtration rates estimated for *Haliclona urceolus* and *Halichondria panicea* (Riisgård et al. 1993, Thomassen & Riisgård 1995). As can be seen in Fig. 8, clearance rates varied considerably both between different-sized particles and over the course of the experiment, indicating that the size classes are retained with varying efficiency. This is in agreement with findings of Reiswig (1971a), who found retention rates to vary considerably between different food items, which underlines the sponges' ability to actively select particles.

Deposition of particles

Most sponges are suspension feeders, but the fate of indigestable food items has long remained unknown. Both Kilian (1952) and Weissenfels (1976), during their studies of freshwater sponges, noted the ejection of pellets. However, they only recorded single observations. Wolfrath & Barthel (1989) studied pellet production in the shallow-water sponge *Halichondria panicea* Pallas. Laboratory feeding experiments with both latex beads and algal cultures demonstrated the production of oval to rounded pellets of 15 to 50 µm diameter. The pellets were always covered by a thin membrane. This cover proved to be very labile but the pellets did not fall apart when it was destroyed. Göbel (1993) continued this investigation with another 5 marine demosponge species and demonstrated that all species studied produced similar pellets of 30 to 100 µm length. Single, uncoated particles never were ejected. As Göbel studied representatives of various demosponge groups and found all of them to produce pellets, and as histological preparations of the species studied here (Witte 1996) contained cysts filled with food remains, it is assumed that these pellets can be regarded as typical for suspension-feeding sponges. This implies that the deep-sea species studied here ingest small particles up to 6 µm in diameter which after digestion are ejected as pellets up to 50–100 µm in size and thus become available to deposit feeding organisms. The filtration activity of these sponges thus mediates the deposition of very fine grained material. Such coupling has, for example, been observed by Amouroux et al. (1990) and Ziebis (1991) in microcosm experiments with shallow-water bivalves and polychaetes.

Table 2. Biodeposition mediated by the deep-sea sponge community of the GIN Seas

Stn	Depth (m)	Sponge biomass (mg AFDW m^{-2})	Biodeposition (mg C m^{-2} d^{-1})
277	2020	664	0.97
289	2160	1524	2.24
292	2570	240	0.59
444	2630	536	0.79

Biodeposition rate of the poriferan community from the deep GIN Seas

As outlined above, suspension feeders can mediate the deposition of laterally transported particles by their feeding activity. In addition, being passive obstacles for bottom currents, they increase sediment roughness and can thus—depending on form, size and frequency—create sediment deposition or erosion (e.g. Eckman et al. 1981, Luckenbach 1986, Vogel 1994), although a consistent functional grouping of organisms as stabilizers or destabilizers, or as decreasers or enhancers of erosion, respectively, is not possible (Jumars & Nowell 1984). In this study, active and passive deposition of particles could not be separated. Nevertheless, a bulk biodeposition rate could roughly be calculated from the volume of particles extracted from the water column. Biodeposition amounted to 6.7 mm^3 d^{-1} g^{-1} AFDW (low current speed) and 9.3 mm^3 d^{-1} g^{-1} AFDW (high current speed) or 7.3 and 10.2 mg d^{-1} g^{-1} AFDW, respectively, assuming a density of 1.05 g cm^{-3}. As particles smaller than 2 µm are not included, this has to be considered a conservative estimate. Filtering activity was assumed to be constant. This is in accordance with the work of Reiswig (1971b), who monitored excurrent velocity in the oscula of 3 demosponge species and found it to be constant for months in 2 of the species. The third species showed a clear diurnal pumping rhythm, which, however, is not to be expected in deep-sea species. The combination of biodeposition rates with biomass data for the Norwegian and Greenland Seas allows a rough estimate for sponge community biodeposition, which is given in Table 2. Biodeposition rate for the sponge community of the deep Greenland and Norwegian Seas ranges between 0.5 and 2.0 mg C m^{-2} d^{-1}. If biomass is taken into account, this is comparable to shallow-water benthos of other taxa, e.g. 0.02 mg C g^{-1} wet wt d^{-1} for the antarctic bivalve *Laternula elliptica* (Ahn 1993) compared to 0.03 mg C g^{-1} wet wt d^{-1} for *Thenea muricata*. Thomsen et al. (1995) give a biodeposition rate of 25 mg C m^{-2} d^{-1} for the entire benthic community (ca 1000 ind. m^{-2}) in an interface feeder field at 1400 m depth on the Barents Sea continental slope. A comparison with sedimentation rates from the GIN Seas (annual mean: 5 to 6 mg C m^{-2} d^{-1}; maximum flux: 20 to 30 mg C m^{-2} d^{-1}; von Bodungen et al. 1995) shows that the poriferan community possibly adds up to 10% to vertical particle flux by the deposition of fine, laterally transported material.

Acknowledgements. Thanks are due to the masters and crews of RV 'Meteor' and RV 'Hans Brattström' for their assistance during sampling, to W. Queisser and J. Nittikowski for technical assistance and to G. Unsöld for valuable discussions. The manuscript benefited from the thorough work of 3 anonymous reviewers. This is a GEOMAR publication and publication no. 309 of Sonderforschungsbereich 313, University of Kiel.

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This article was submitted to the editor

Manuscript received: August 8, 1996
Revised version accepted: May 16, 1997