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Passive suspension feeding in *Amphiura filiformis* (Echinodermata: Ophiuroidea): feeding behaviour in flume flow and potential feeding rate of field populations

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ABSTRACT: Experimental studies in a laboratory flume show that the sediment-living brittle-star *Amphiura filiformis* captures suspended particles. Feeding activity is a function of flow velocity with few animals extending feeding arms in still water. Flow velocity also affects the orientation of feeding arms, and we suggest that this orientation is partly controlled by *A. filiformis*. By combining field measurements of current velocity and seston concentration with morphometrics and filtration models, a theoretical encounter rate of suspended particles was calculated for *A. filiformis*. In terms of organic content, *A. filiformis* can potentially balance growth and respiration with ingested seston although balance will strongly depend on retention efficiency and particle quality. Detailed measurements of flow around feeding arms revealed complex flow patterns that will limit the applicability of available models of food encounter for passive suspension feeders, but our sensitivity analysis indicates that suspended aggregates may be especially important in the nutrition of this species.

KEY WORDS: *Amphiura filiformis* · Behaviour · Bio-energetics · Brittle-star · Encounter rate · Flume · Passive suspension feeder · Skagerrak

INTRODUCTION

Energy transfer through suspension feeding is an important route from the pelagic to the benthic ecosystem (e.g. Baird & Ulanowicz 1989, Loo 1991). A major source of energy to the benthic ecosystems is sinking particulate material ('marine snow') formed both above and below the photic zone. This particulate material originates from several sources, e.g. declining phytoplankton blooms (e.g. Alldredge & Gotschalk 1989), fecal pellets and larvacean houses (Simon et al. 1990).

Suspension feeders can be either passive or active. Passive suspension feeders utilise the natural flow to bring particles in contact with feeding structures. In contrast, active suspension feeders use ciliary or muscular activity to create feeding currents. Several studies describe feeding mechanisms and uptake dynamics of benthic, active suspension feeders, e.g bivalves (Møhlenberg & Riisgård 1978), ascidians (Fiala-Médioni 1978), sponges (Reiswig 1974), and some polychaetes (Riisgård 1989, 1991). Active suspension feeders often encounter particles in direct proportion to the pumping rate. Encounter rate for passive suspension feeders will depend both on the exogenous flow pattern and the exposure of the feeding apparatus, which makes quantification of feeding rates difficult. There may even be interactions between flow and feeding behaviour as reported by Warner & Woodley (1975) who found that the brittle-star *Ophiothrix fragilis* altered the orientation of its tube feet in response to varying flow regimes.

Few studies have treated particle encounter mechanisms of passive suspension feeding. LaBarbera (1978) showed that a suspension-feeding brittle-star, *Ophio-*

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pholis aculeata, was capable of removing artificial particles from sea water by mechanisms other than sieving LaBarbera explained his results in terms of predictions from aerosol filtration theory. Muschenheim (1987) showed that the polychaete *Spio setosa* could build sand tubes that allow it to feed several centimetres above the bed, where hydrodynamic sorting provides low-density, high-quality organic seston. Leonard et al. (1988) and Leonard (1989) studied the influence of flow speed and food availability on feeding activity of crinoids, and Best (1988) measured feeding rate and filtering efficiency for a sea pen.

To our knowledge no study has attempted to combine information about feeding mechanisms and natural fluxes of suspended particles to yield estimates of feeding rates of passive suspension feeders in the field. Such estimates are necessary to understand energy transfer from the pelagic to the benthic ecosystem. Benthic-pelagic coupling has a central role in large-scale processes in most coastal and shelf areas. Across the interface between water and sediment there are complex fluxes of energy, nutrients and contaminants. These fluxes are affected by e.g. water flow, oxygen concentration, sediment structure and biological activity. A potential 'key' species affecting sediment-water exchange processes in the Kattegat, the Skagerrak and the North Sea is the brittle-star *Amphiura filiformis*. According to Buchanan (1964) and Ockelmann & Muus (1978) *A. filiformis* feed on suspended material in flowing water, but will in stagnant water shift to deposit feeding. Interestingly, the related species *A. chiajei* is only known to feed on deposited material (Buchanan 1964).

This study is part of a larger investigation of the role of *Amphiura filiformis* in the removal of suspended particles and benthic biomass production (Sköld et al. 1994). The major objective of the present paper is to estimate the potential feeding rate of natural populations of *A. filiformis*. It is accomplished through an indirect calculation of encounter rate using filtration theory and behavioural studies of feeding *A. filiformis* together with field measurements of seston concentration, and flow speed.

MATERIALS AND METHODS

Filter model. A possible way to approach the problem of potential feeding rate would be to estimate encounter rate for individual tube feet, on the arms of *Amphiura filiformis* (O. F. Müller, 1776), from measured near-bed flow speeds and the size-specific concentration of suspended particles. Encounter rate of a collector in a flow of particles has received some attention, particularly in aerosol filtration theory (e.g. Fuchs 1964). Aerosol models have been applied more or less successfully to suspension feeding in aquatic environments (see the thorough review by Shimeta & Jumars 1991). Using available encounter theory for particles in fluids moving at low collector Reynolds number (Re_c), the tube feet of *A. filiformis* are here modelled as an infinite row of equally spaced, parallel circular cylinders (Tamada & Fujikawa 1957, Silvester 1983).

Owing to the hydrodynamic drag imposed on the fluid, there will be a pressure drop across the filter It will divert fluid and reduce flow speed compared to the ambient flow. Since encounter rate of particles depends on the flow speed through the filter, this reduction should be related to the ambient flow speed. The first step is thus to find a model that expresses flow speed through the filter as a function of ambient flow speed.

The pressure drop, Δp, across a filter consisting of an infinite plane of cylindrical fibres is given by Tamada & Fujikawa (1957) as:

$$\Delta p = \frac{\mu u_0}{h}\frac{8\pi}{\Lambda} \quad (1)$$

where μ is dynamic viscosity of the fluid, u_0 the ambient flow speed, $\Lambda = 1 - 2\ln\tau + \tau^2/6 - \tau^4/144 + \tau^6/1080$ and $\tau = 2\pi a/h$ where a is the radius of a cylindrical fibre and h is the centre-to-centre spacing. The expression for Λ was used when $Re_c < 1$, where $Re_c = 2a\bar{u}\rho/\mu$ and ρ is fluid density. For $1 \le Re < 5$ a correction for Λ was calculated from Tamada & Fujikawa (1957). Following the derivation in Silvester (1983) the average flow speed through the filter is found as:

$$\bar{u} = \sqrt{\frac{e^2}{\rho^2} + u_0^2} - \frac{e}{\rho} \quad (2)$$

where $\bar{u}$ is the mean flow speed through the filter and e is the pressure drop per unit flow speed calculated as:

$$e = \frac{8\pi\mu}{h\Lambda} \quad (3)$$

Several mechanisms may account for the encounter between suspended particles and a filter fibre. Here we consider direct interception, inertial impaction and gravitational deposition (Rubenstein & Koehl 1977, Shimeta & Jumars 1991). Sieving is not considered since the distance (300 µm) between adjacent tube feet of *Amphiura filiformis* (see Fig. 1) exceeds the largest measured size-class of suspended particles (but see 'Discussion'). Diffusive deposition was also excluded since most encountered particles were assumed to be non-motile. Any turbulent diffusion in the feeding flow is neglected (see 'Discussion'). Encounter rate due to direct interception, F_R, is modelled as:

$$F_R = 2C\bar{u}\ r_p l_c \quad (4)$$

where C is particle concentration, r_p is radius of particle and l_c is length of a cylindrical filter fibre. Inertial impaction, F_I, of particles on a cylindrical filter fibre is modelled as:

$$F_I = \begin{cases} 2C\bar{u}\ l_c l_s & l_s \le r_c \quad (5a) \\ 2C\bar{u}\ r_c l_c & l_s > r_c \quad (5b) \end{cases}$$

where r_c is the radius of a cylindrical filter fibre and l_s is the stopping distance for a particle with density ρ_p calculated as:

$$l_s = \frac{\bar{u}(\rho_p - \rho)(2r_p)^2}{18\mu} \quad (6)$$

A more or less arbitrary density of suspended particles of 1.04 g cm^{-3} was assumed (Jackson 1989), although sensitivity to particle density was examined over a range of densities. Suspended particles may also encounter a cylindrical filter fibre through gravitational deposition, F_G, and this rate is modelled as:

$$F_G = 2Cw_s(r_c + r_p)l_c \quad (7)$$

where w_s is the settling velocity of a particle calculated from Stokes' law as:

$$w_s = \frac{g(\rho_p - \rho)(2r_p)^2}{18\mu} \quad (8)$$

where g is gravitational acceleration. Since inertial impaction and gravitational deposition do not act independently, a combined encounter rate, F_{I+G}, is calculated according to Shimeta & Jumars (1991) as:

$$F_{I+G} = \frac{1}{2}F_I + \max\left(\frac{1}{2}F_I, F_G\right) \quad (9)$$

The applicability of the encounter-rate models above relies on several assumptions. They require Re_c to be much less than unity, upstream flow to be laminar and steady and filter fibres to be oriented perpendicular to the flow. Possible violations of these assumptions are treated in the 'Discussion'.

Particle analysis. Water for particle analyses was sampled with a flow-through water sampler that closes immediately upon hitting the bottom. The 1.7 l sampler is a 40 cm tall cylinder placed 10 cm above the closing mechanism. Samples were taken on 34 occasions between August 1990 and November 1991 at the mouth of the Gullmarsfjord, west Sweden (58° 14.72' N, 11° 25.80' E), at 40 m depth, where a 'typical' *Amphiura filiformis* community (*sensu* Petersen 1915) has been monitored annually since 1983 (Sköld et al. 1994). Tidal influence on particle load was assumed to be minor since tidal amplitude is small (ca 20 cm) on the Swedish west coast. The sampler was set gently on the sediment surface to reduce resuspension. Size-specific particle concentration was measured in an Elzone 80 XY electronic counter with 128 channels. Particle sizes ranging from 5 to 50 µm were counted using a 95 µm orifice tube and those from 20 to 250 µm using a 300 µm tube. Sizes from 20 to 50 µm were means from both tubes.

Flow measurements. Near-bed flow speed was measured *in situ* at a depth of 40 m on sediment bottoms with dense populations of *Amphiura filiformis* (Sköld et al. 1994), at stations similar to those where suspended particles were sampled. Measurements of current speed were carried out with an underwater video-recording system (S-VHS, 50 Hz). Velocities of small particles in the flow were measured by analysing video-recorded sequences frame by frame. From measurements of particle velocities at different heights above the sediment, ranging from 0.2 to 8 cm, a vertical velocity profile was calculated. The profile represents a time average over 30 min. Flow at these depths is steady on time scales of several minutes and wave-driven oscillatory components are weak. Assuming a logarithmic velocity profile, shear velocity was calculated by fitting data to the Karman-Prandtl equation (Schlichting 1979):

$$u_z = \frac{u_*}{\kappa}\ln\frac{z}{z_0} \quad (10)$$

where u_z is flow velocity at height z, u_* is shear velocity, κ is von Karman's constant (here 0.4) and z_0 is roughness length. Because these near-bed flow measurements covered only short time scales we used another data set to estimate the variability of flow velocity on longer time scales. This data set was collected in April 1973 at the same locality 5 m above the sediment and is reported in Rydberg (1975). Current speed and direction were simultaneously recorded every hour for 30 d. From this time series of flow speed measurements, the average and variance of free-stream velocity were calculated.

Observations in flume flow. The response of living individuals of *Amphiura filiformis* was observed in flow generated by an indoor flume tank (3.5 m long and 0.5 m wide with a water depth of 0.15 m). Benthic samples were collected with a Smith McIntyre grab (0.1 m^2) at a station east of the Kosterfjord at the border between Sweden and Norway (close to Tjärnö Marine Biological Laboratory) at a depth of 30 to 40 m. The brittle-stars were gently rinsed and picked out from the sediment using forceps. Animals with a mean oral width of 1.5 mm (range 1.1 to 2.0 mm) and a mean weight of 0.011 g DW (Josefson & Jensen 1992) were used in the flume experiments. Oral width shows less seasonal variance than disk size, which increases during gonadal development (O'Connor et al. 1983). Sediment for the flume experiments was collected from the benthic samples but was first sieved (1 mm mesh) to remove any macrobenthic fauna before placement in the flume tank. About 10 individuals were placed in the sediment box (0.08 m^2) which was flush with the flume floor. The animals were left to acclimate for 1 d before the start of an experiment. In the recirculating flume there was a slow exchange of fresh sea water collected at a depth of 40 m. Apart from particles occurring in the added natural sea water, animals were not fed before or during the experiments. In a typical experiment *A. filiformis* was exposed to each flow speed, including still water, for about 1 h before observations were performed on the number of extended arms, the position of arms and particle trajectories around arms. Only individuals more than 10 cm from the flume wall were used in the experiments. The flume used in the present study yields a logarithmic boundary layer of ca 4 cm at the working section. However, arms of *A. filiformis* never extended more than 2 cm into the water and were contained within the logarithmic part of the boundary layer. *A. filiformis* feeds in the benthic boundary layer where flow speed declines towards the sediment surface. To allow for this reduction in ambient flow speed over the length of feeding arms in our calculations of encounter rate, we measured the vertical velocity profile in experimental flows generated in the flume tank. In the flume it was possible to measure the velocity gradient closer to the sediment, and these measurements are complementary to the measurements *in situ*. A heated thermistor probe (Vogel 1981) measured speed at the working section from the water-sediment interface to a height of 30 mm in 1 mm steps. Measurements 7 cm above the sediment were used to characterise free-stream flow. Flume flow speed was adjusted to yield a shear velocity similar to the estimate from the *in situ* near-bed measurements described above. The velocity profile was fitted to the Karman-Prandtl Eq. (10). From this expression a mean flow speed ($\bar{u}$) through the tube-foot filter was calculated (Eq. 2) for every millimetre of an *A. filiformis* arm protruding into a velocity gradient, and averaged over the whole 20 mm arm.

Morphometrics. Measurements of linear dimensions and shapes of adult *Amphiura filiformis* arms were obtained from video recordings of live animals exposed to flume flow (Fig. 1). Each tube-foot of an active arm was considered as a filter fibre (diameter 100 µm) with a constant spacing (300 µm).

Conversion between particle volume and AFDW. To compare encounter rate with estimated growth and respiration rates, volume of particles was converted to energy content by first analysing the ash-free dry weight (AFDW) of seston from the samples described above. Seston was collected on GF/C glass-fiber filters, dried to constant weight at 60°C and combusted for 5 h at 550°C. A conversion factor between AFDW and energy of 20 kJ g AFDW^{-1} was assumed (Crisp 1984).

Assimilation efficiency. We could find no measurements of assimilation efficiency for *Amphiura filiformis* in the literature. Brittle-stars have a short oesophagus ending in a folded stomach occupying most of the disk volume. Undigested material is expelled through the mouth as feces. This cul-de-sac-like digestive tract makes measurements of assimilation efficiency difficult. To obtain at least a rough estimate we measured assimilation efficiency of newly caught animals by comparing the organic fraction (AFDW) of the stomach contents with the organic fraction of collected fecal pellets. AFDW was measured as above. Since the distribution of the organic fraction of stomach contents contained some very low values, possibly because of some period of non-feeding, we selected the median value to represent newly ingested food. Assimilation efficiency was calculated according to Conover (1966).

Error analysis. Conclusions about the significance of the estimated encounter and ingestion rates by *Amphiura filiformis* rely on some estimate of the error involved. The long-term encounter rate of suspended particles presented here is calculated from several other estimates of parameters associated with various sources of error. These errors are consequently compounded in the calculations of encounter and ingestion rates. Rarely is it possible to calculate accurately the error associated with higher-order estimates, mainly because of a lack of information about the sources of error involved. It is, however, possible to combine available estimates of errors together with subjective guesses in an error model which may be evaluated through a Monte-Carlo simulation. For 1000 simulations (MATLAB®, MathWorks Inc.) encounter and ingestion rates were calculated from current velocity, tube-foot morphometrics, concentration of particles, AFDW, growth rate, respiration rate and assimilation efficiency where an estimate of each parameter was sampled from normal distributions (Table 1). A 95% confidence interval was then constructed by setting 2-tailed boundaries at the 50 most extreme values. In this error analysis, the number of active tube-feet was fixed at 160 per individual.

Particle trajectories at $Re_c > 1$. During observations of flow around the tube feet of *Amphiura filiformis* it became evident that flow did not follow the creeping-flow motions assumed by aerosol filtration theory. Although we did not attempt to derive an empirical model applicable to the Re_c characterising flows in the present study, we performed observations and some experiments to document some of the flow structures discovered. Flow patterns around arms and tube feet of living individuals of *A. filiformis* were studied in frame-by-frame analysis of video-recorded (S-VHS, 50 Hz) sequences of particles in flume flow. The presence of attached vortices and flow separation was investigated at flow speeds between 2 and 15 cm s^{-1}.

In a series of experiments, model mimics of *Amphiura filiformis* arms were exposed to flume flow at different velocities. The arm mimic consisted of a 10 cm long nylon cord (diameter = 1.4 mm) with 3.7 mm long branches made of a thinner nylon cord (diameter = 0.5 mm) attached every 1.5 mm on both sides of the centre cord. In some experiments this arm mimic was contrasted with a mimic having only the centre cord but no branches. The arm mimic was 5 times larger than arms of living *A. filiformis* and flow velocity was reduced accordingly, yielding a logarithmic boundary layer of about 10 cm. The presence of attached vortices and other flow circulation was investigated at 4 flow speeds: 0.5, 1.0, 1.2 and 1.7 cm s^{-1} Observations were carried out at 3 vertical locations along the arm mimic: 0.5, 5 and 9 cm above the sediment. Each combination of flow speed and location was replicated 3 times and each replicate consisted of at least 4 particle trajectories. The presence of attached vortices and other flow circulation was detected by comparing particle trajectories (in focus) which passed through the tube-feet mimic with particles unobstructed by the arm mimic (slightly out of focus). The effect of flow speed on attached vortices, and the effect of flow speed, mimic type and vertical location on the presence of upward circulation, were tested with analysis of variance (ANOVA). Since presence-absence data generate means that may significantly deviate from central tendency we used a randomisation procedure to calculate the *F*-statistics (Manly 1991).

Table 1 *Amphiura filiformis*. Sources of error affecting estimated encounter rate and ingestion rate. Estimated or assumed errors are shown as SE in % of the mean

Source of error	Estimated error (%)	Assumed error (%)
Encounter rate		
Current measurement		7.5
Boundary-layer profile	25	
Non-linear relation between u_0 and u_s	2	
Variability in u_s due to variability in gaps between tube feet	4	
Length of tube feet	5	
Sampling of particle concentration		25
Measurements of particle concentration		3
Conversion between AFDW and energy		20
Ingestion rate		
Growth (Sköld et al. 1994)	20	
Respiration (Buchanan 1964, O'Connor et al. 1986)	15	
Assimilation efficiency	10	
Conversion between AFDW and energy		20

RESULTS

Morphometrics of *Amphiura filiformis* arms

Arms engaged in passive suspension feeding extended 10 to 20 mm up from the sediment surface. Each arm supported 2 rows of ca 40 tube feet. Tube feet measured ca 100 µm in diameter with a length of 750 µm, and the distance between adjacent tube feet was ca 300 ± 20 µm (mean ± 95% CI, n = 10). Orientations of tube feet were not quite perpendicular to the flow but made an angle of ca 80 to 85° (Fig. 1)

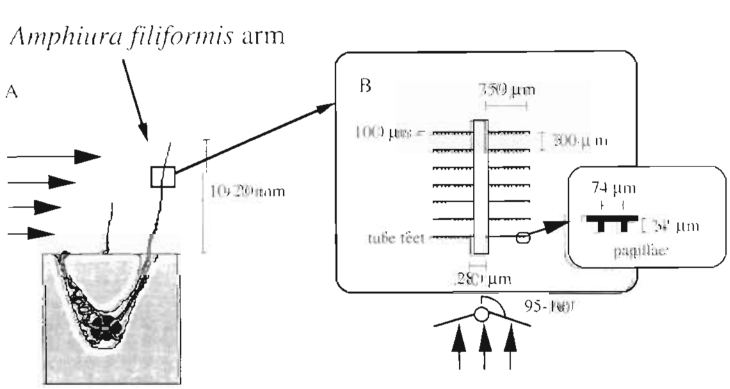

Fig. 1. *Amphiura filiformis*. (A) Height and shape of extended arms of *A. filiformis* during passive suspension feeding. Horizontal arrows indicate current direction and velocity gradient. (B) Schematic drawing of an *A. filiformis* arm showing morphometrics of the tube feet. The lower figure shows a cross section of the arm with the angle between the tube feet and the current

Assimilation efficiency

Organic fractions of the stomach contents of 15 individuals ranged from 14 to 85% with a median of 75%. Organic content of the fecal pellets was only 17 ± 1.5 (mean ± SD, n = 8). These estimates yield a calculated assimilation efficiency of 93% of ingested organics.

Feeding behaviour at various current speeds

In still water many *Amphiura filiformis* did not extend their arms into the water (Fig. 2A). At moderate flow velocities (up to 5 cm s^{-1} free-stream velocity) the proportion of individuals with at least 1 extended arm increased (Fig. 2A; Spearman rank correlation, $p < 0.05$) with increasing flow speed. On average, ca 2 arms were extended at a time (Fig. 2B). From video recordings in flume experiments, *A. filiformis* was observed to capture suspended food items. Particles

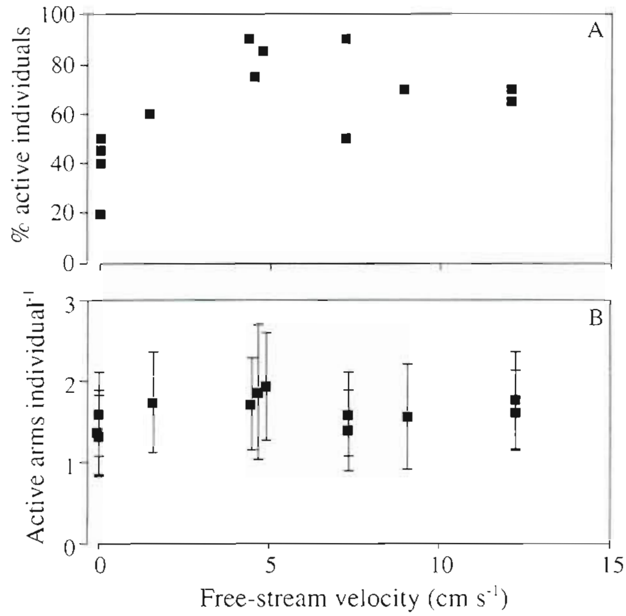

Fig. 2. *Amphiura filiformis.* (A) Proportion of active individuals (defined as individuals having at least 1 extended arm), and (B) mean number of active arms per individual (mean ± SD), as a function of flume free-stream velocity

encountered and retained on the tube feet were seen to be transferred between adjacent tube feet in the proximal direction along the arm. During transport, captured particles became entangled in mucus and were rolled into a bolus by the tube feet. Eventually the bolus was transported by tube feet below the sediment surface and possibly to the mouth. Occasionally, individuals picked deposited particles from the sediment surface, and this behaviour was most common in still water. *A. filiformis* seemed actively to change the orientation of its feeding arms in response to flow velocity. In flow velocities between 0.5 and 6 cm s^{-1} active arms were stretched nearly straight up into the water with a small bend downstream at the tip in the direction of flow. At increased free-stream velocities between 6 and 12 cm s^{-1} arms bent slightly further downstream and also across the flow. In fast flows between 12 and 25 cm s^{-1} arms bent even further, almost to the sediment surface (Fig. 3). Often, arms were bent in the form of a wave (Fig. 3). The rather complex change of arm orientation as a function of flow velocity indicates that *A. filiformis* can perceive the velocity of flow or some correlate, e.g. shear force. At the distal tip of each arm there is a small, flexible protrusion that orients itself in the flow, similar to a streamer. We suggest that this structure may give *A. filiformis* information about flow characteristics.

Encounter rate of suspended particles

From the size distribution of suspended particles (Fig. 4) we calculated encounter rates for *Amphiura filiformis* (Fig. 5) using filtration theory and long-term measurements of flow velocity in the field. The free-stream velocity of 8 ± 8 cm s^{-1} (mean ± SD) represents the average of a data set spanning 30 d at the sampling locality. Speed and direction often persisted for several hours. From the average free-stream velocity the near-bed velocity gradient was calculated from vertical velocity profiles measured *in situ* and in the flume (Fig. 6). Two arms with 80 tube feet per arm (5 tube feet mm^{-1}) were assumed to be active in suspension feeding (Fig. 2B). There was a nonlinear dependence of encounter rate on free-stream velocity caused by the relative increase in viscous resistance through the filter at low speeds (Fig. 7, Eq. 2). Encounter rate fluctuated over the studied period with both the total load of suspended particles and the size spectrum. Encounter rate increased substantially when large particle sizes dominated (e.g. Fig. 4, Day 48, October 8, 1990). On

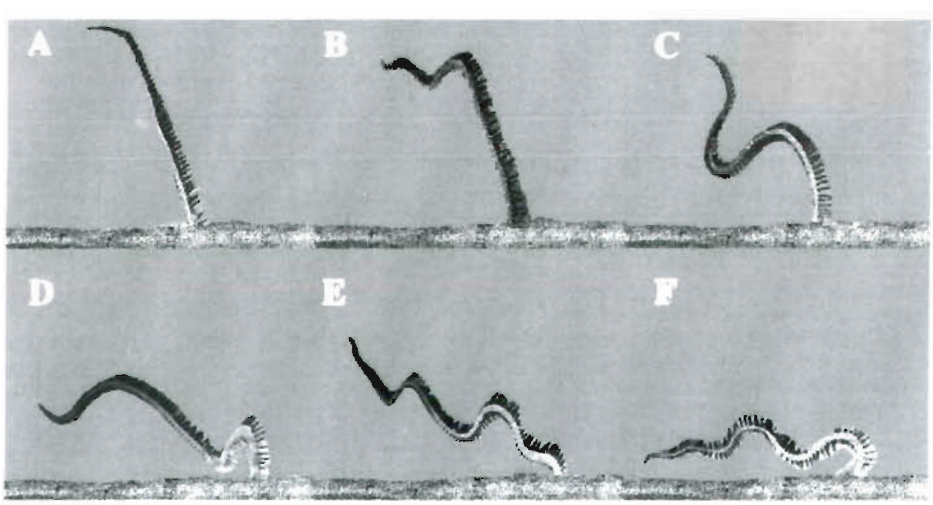

Fig. 3. *Amphiura filiformis.* Video frames of arm position as a function of flume free-stream velocity. Flow is from right to left. (A) In low flow velocities, 0.5 to 6 cm s^{-1}, arms stretched upwards 10 to 20 mm above the sediment surface. (B, C) In flow velocities between 6 and 12 cm s^{-1} the arms were closer to the sediment and positioned perpendicular to the current. (D, F) In high flow velocities, 12 to 25 cm s^{-1}, arms bent in the downstream direction close to the sediment

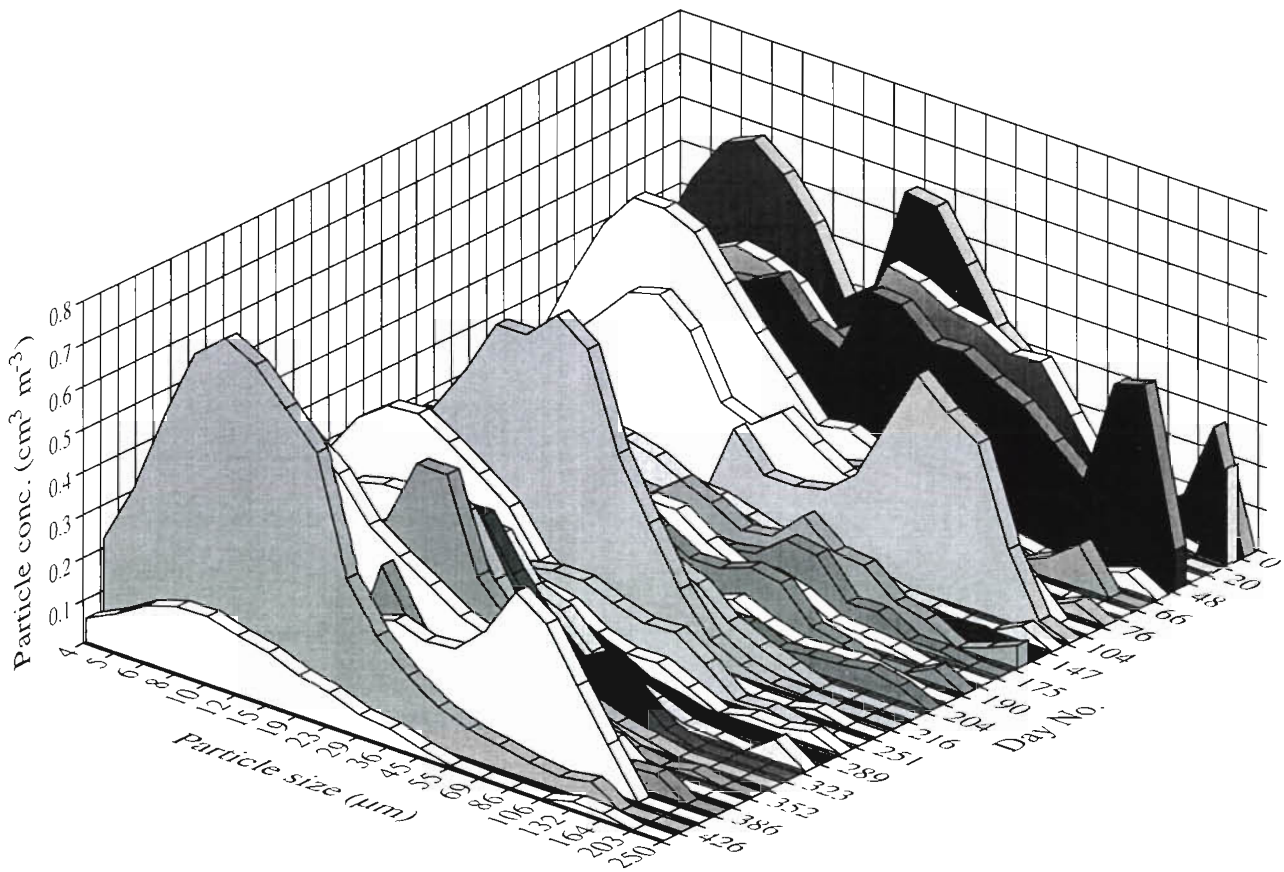

Fig. 4. Time series of the particle size distribution in bottom water (10 to 50 cm above the sediment) during the period August 21, 1990 to November 4, 1991. Concentration of particles is given for 20 size classes expressed as equivalent spherical diameter (µm)

average AFDW was 33% of total seston volume, and this fraction was negatively correlated with seston volume (Fig. 8). For the expected range of specific gravity of suspended particles (1.03 to 1.06 g cm^{-3}) and flow speeds (>5 cm s^{-1}) the combined effect of inertial impaction and gravitational deposition (F_{I+G}) accounted for less than 10% of the total encountered particulate volume (F_{I+G} + F_R) (Fig. 9).

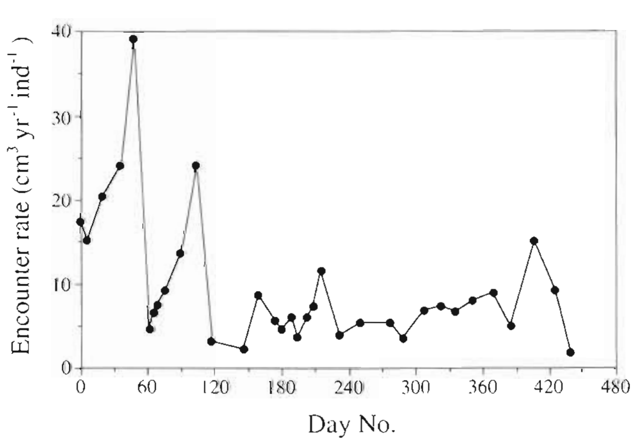

Fig. 5. *Amphiura filiformis*. Time series of calculated encounter rates with suspended particles of 5 to 250 µm (cm^3 particle volume yr^{-1} ind.$^{-1}$) at a near-bed flow velocity of 6.8 cm s^{-1}. Encounter rates are the sum of direct interception, inertial impaction and gravitational deposition

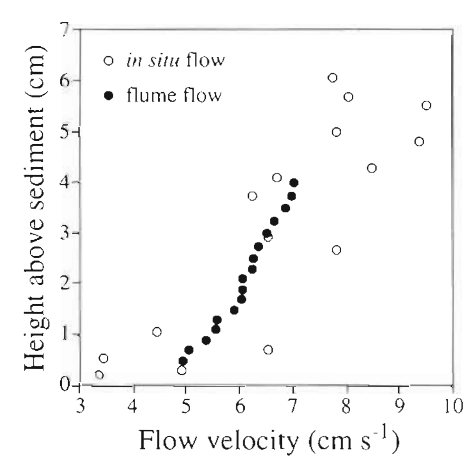

Fig. 6. Vertical velocity profiles in horizontal water flow above the sediment surface. (O) Measurements *in situ*, u_* = 0.57 cm s^{-1}; (●) measurements in flume flow, u_* = 0.41 cm s^{-1}. Velocities are averages over 30 and 2 min for *in situ* and flume measurements, respectively

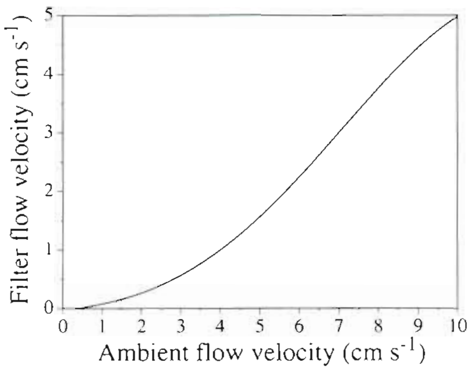

Fig. 7 *Amphiura filiformis*. Theoretical relationship (Eq. 2) between ambient flow velocity (u_0) and the mean flow velocity between tube feet ($\bar{u}$) of *A. filiformis*

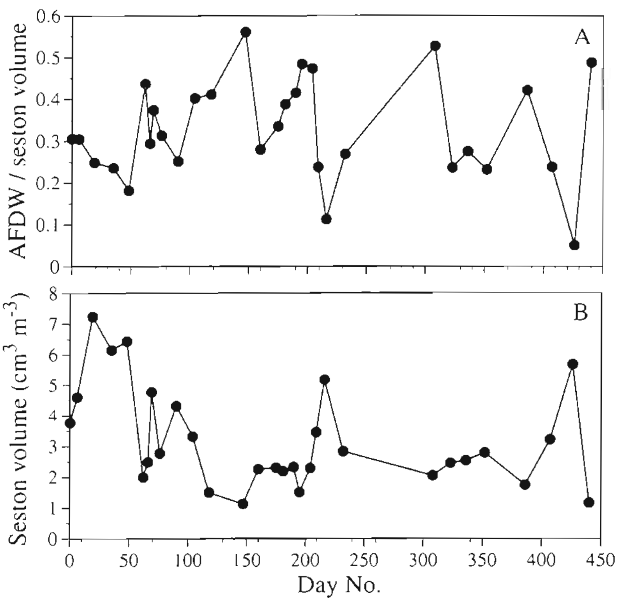

Fig. 8. Time series of (A) ratio between ash-free dry weight (AFDW) and seston volume (mg mm^{-3}); and (B) concentration of seston expressed as total particle volume per volume of sea water (mm^3 l^{-1})

Particle trajectories at $Re_c > 1$

Tracings of particles in the flow passing between tube feet of living *Amphiura filiformis* revealed 2 interesting patterns. At flow velocities around 6 cm s^{-1} (2 cm above the sediment, $Re_c = 6$) attached vortices formed on the downstream side of active arms (Fig. 10B–D). In addition, there was a slow flow from the sediment surface toward the distal end along the downstream side of active arms (Fig. 10A). These flow patterns recurred around a mimic of an *A. filiformis* arm. Attached vortices became frequent ($F_{1,48} = 16$, $p < 0.001$) in free-stream velocities between 1.2 and 1.7 cm s^{-1} ($Re_c = 7$) but sporadically occurred even at the lowest velocity of

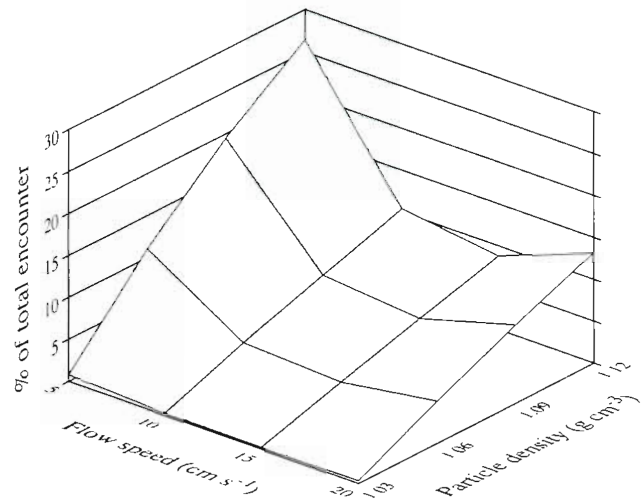

Fig. 9. *Amphiura filiformis*. Estimated contribution (%) of inertial impaction and gravitational deposition to total encountered volume of particles for *A. filiformis* as a function of particle density and free-stream flow speed. Encounter rates were calculated for the average size-frequency distribution of all samples (Fig. 4), and the vertical concentration profile was corrected according to Eq. (12). Shear velocity is assumed to be 5% of the free-stream flow speed

0.5 cm s^{-1}. Similar to the observations of living *A. filiformis* the arm mimic induced an upward current on the downstream side. The frequency of occurrence of upward flow increased with free-stream velocity ($F_{3,48} = 4.4$, $p < 0.01$) and was most pronounced at the proximal end of the mimic close to the sediment ($F_{2,48} = 15$, $p < 0.001$). The upward flow almost disappeared when the arm mimic was replaced by a centre cord without any tube-feet mimic ($F_{1,48} = 34$, $p < 0.001$).

DISCUSSION

Amphiura filiformis feeds on both deposited and suspended food items. Our study indicates that the flow regime, and the resulting particle flux, may influence the relative importance of these feeding modes. The main purpose of the present study is to investigate whether uptake of seston, i.e. suspension feeding alone, could account for estimated growth rates in natural populations.

Estimate of potential feeding rate

Potential feeding rate is here defined as the encounter rate between tube feet and suspended particles. The conversion between actual feeding rate and encounter rate is the retention efficiency which for potential feeding rate is assumed to be 100%. Assum-

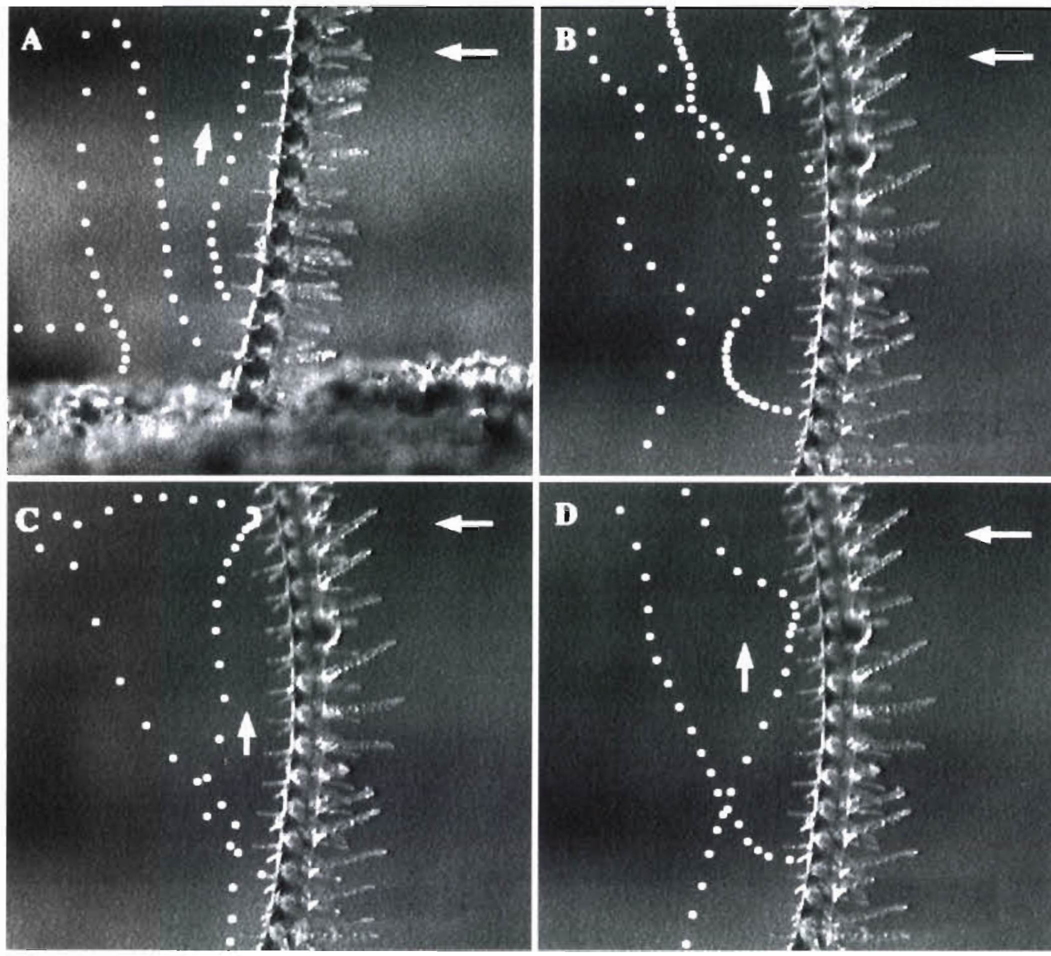

Fig. 10. *Amphiura filiformis.* Flow paths of particles passing between tube feet. (A) Water flows from the sediment surface toward the distal end along the downstream side of active arms. (B–D). At flow velocities ca 6 cm s^{-1} (Re_c = 6) attached vortices form on the downstream side of active arms

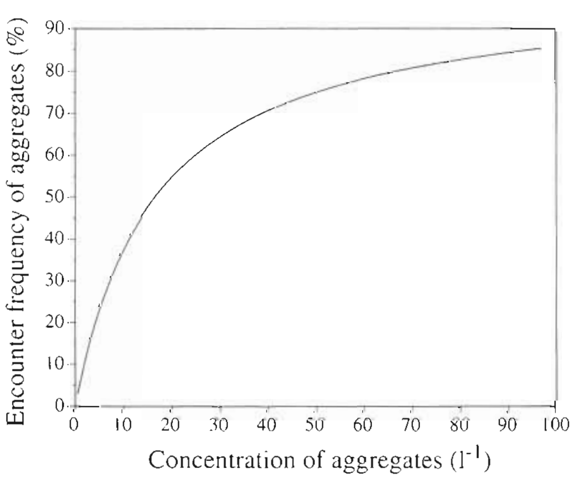

Fig. 11 *Amphiura filiformis.* Theoretical contribution (% of the particle volume encountered) of sieving to total encounter rate as a function of large aggregate concentration. The sieving model assumes a filter area of 3 mm^2, ambient flow of 6.8 cm s^{-1}, flow through filter of 2.8 cm s^{-1}, and 2 active arms

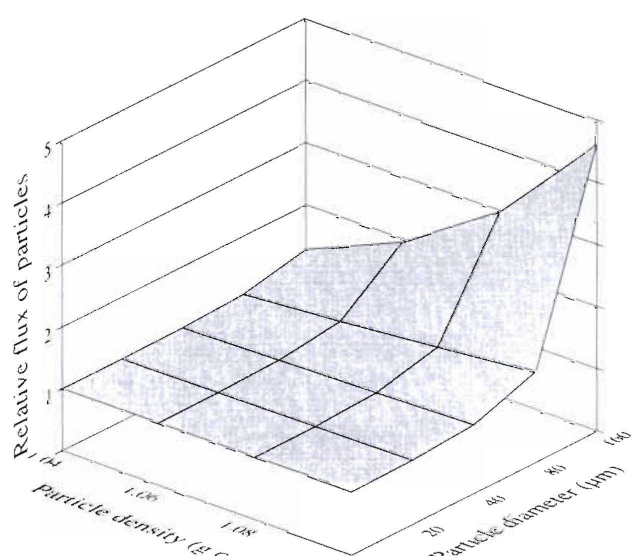

Fig. 12. *Amphiura filiformis.* Predicted effect of hydrodynamic sorting on the particle flux around an arm of *A. filiformis* calculated from Eq. (12) and the boundary-layer flow in Fig. 6. Flux as a function of particle size and density is expressed relative to the flux for a homogeneous particle suspension

ing no post-capture rejection the predicted encounter rates in Fig. 5 yield an average potential feeding rate per adult individual of 9.8 ± 4.1 g wet weight ind.$^{-1}$ yr^{-1} (mean ± 95% CI, from error model) or 56 ± 23 kJ ind.$^{-1}$ yr^{-1} (mean ± 95% CI). According to Sköld et al. (1994) the adult production (including gonads and regeneration) of an *Amphiura filiformis* population was 0.012 g AFDW ind.$^{-1}$ yr^{-1} or 0.23 kJ ind.$^{-1}$ yr^{-1}. If we assume a respiration rate of 2.4 ml O_2 g^{-1} wet weight d^{-1} (Ursin 1960, O'Connor et al. 1986; 1 ml O_2 = 20 J) and an average adult weight of 0.22 g wet weight (Sköld et al. 1994) the annual respiration is ca 4 kJ ind.$^{-1}$ yr^{-1}, suggesting a net growth efficiency of only 5%. An assimilation efficiency of 93% yields an ingestion demand of 4.5 ± 3 kJ ind.$^{-1}$ yr^{-1} (mean ± 95% CI, from error model). Thus, the average potential feeding rate per adult individual can account for more than 10 times the required ingestion rate, if retention efficiency is 100%. Although the large organic fraction of stomach contents may have been inflated by digestive fluids and scraped-off tissue, the high level implies very selective feeding. Since particles with similar organic contents may differ substantially in their nutritional values (Mayer et al. 1993) only a fraction of the encountered particles may be of sufficient quality to be selected. Such selectivity may seriously increase the required encounter rate.

Effect of large aggregates

One limitation in our calculations of encounter rates is the exclusion of large suspended particles (aggregates or marine snow), i.e. particles that may be captured by sieving. Firstly, our method of particle analysis considered only particles <300 µm, and secondly, not all suspended particles were quantified by the sampling procedure. The frequency distribution of particle sizes in marine environments is usually logarithmic, with few particles in large size classes (Sheldon et al. 1972). For the determination of particle size spectra we sampled 1.7 l of sea water, a sample size that will underestimate the abundance of large particles, e.g aggregates, occurring at densities <1 l^{-1}. It is also likely that large aggregates actually sampled are broken up into smaller parts during processing. This artefact will significantly reduce the encounter rate in terms of volume of suspended particles since the encounter models depend strongly on particle diameter. If we allow for the encounter of large aggregates, e.g. in the size range 0.6 to 9 mm (equivalent spherical diameter) (Lampitt et al. 1993), their encounter can be modelled as a sieving process as:

$$F_S = An\bar{u}C \qquad (11)$$

where F_S is rate of encounter, A is the area outlined by an active arm with its tube feet, n is the number of active arms and C is the aggregate concentration. As expected, addition of large aggregates will increase the predicted encounter rate (Fig. 11) Abundances and qualities of large aggregates vary greatly (Lampitt et al. 1993) but even conservative estimates (2 to 4 µg C, aggregate size >2 mm; Simon et al. 1990) of a few 1 mm aggregates l^{-1} will increase encountered particulate energy >30%. Floderus & Petersson (in press) found aggregates (size >0.5 mm) 20 cm above the bottom at concentrations of 0.5 ppm (volume) at the mouth of the Gullmarsfjord. These aggregates would increase the particle volume encountered almost 200%. Considering the large gap between adjacent tube feet, *Amphiura filiformis* may be well adapted to strain large volumes of water for large aggregates. This view is supported by calculations of the volume of water processed by *A. filiformis* compared to pumping rates of active suspension feeders specialised on small particles, e.g. *Mytilus edulis*. According to Eq. (11) about 6 l h^{-1} of flowing water will pass between the active tube feet in an adult *A. filiformis* (0.011 g DW). Individuals of *M. edulis* with similar pumping rates are considerably larger, 0.72 g shell-free DW (Møhlenberg & Riisgård 1979). The weight-specific processing rate of water is thus 65 times greater for the passive suspension feeder *A. filiformis*.

A further source of error is the possibility of near-bed gradients in seston concentration. In the present study we sampled seston by integrating particle concentration from 10 to 50 cm above the sediment surface, and we assumed a well-mixed boundary layer with a homogeneous particle concentration. The steady-state vertical distribution of suspended particles in horizontal shear flow above the sediment may be modelled as:

$$C_z = C_{z_1}\left(\frac{z_1}{z}\right)^{Ro}, \quad Ro = \frac{w_f}{\kappa u_*} \qquad (12)$$

where C_z is the particle concentration at a height z above the sediment, C_{z_1} is the particle concentration at some reference height z_1, and Ro is the Rouse number (Muschenheim 1987). The Rouse number is the ratio between particle fall velocity (w_f) and shear velocity (u_*) multiplied by von Karman's constant (κ). Particles with different fall velocities will have different vertical profiles and Muschenheim (1987) showed both theoretically and experimentally that hydrodynamic sorting of suspended particles will occur in the boundary layer. Inorganic particles tend to concentrate closer to the bottom compared to organic particles with small settling velocities. At low shear velocities when dense particles are not suspended at all hydrodynamic sorting may increase the encounter rate of organic particles for *Amphiura filiformis*. Only sampling with high resolution could reveal a vertical gradient in particle-specific concentration. To assess the error due to our assumption of homogeneous vertical profiles, Eq. (12) was evaluated for a u_* of 0.5 cm s^{-1} and a range of particle densities and diameters (Fig. 12). The error is probably small for the size range of particles involved in our calculations of encounter rate. However, for larger particles the error may be substantial, and future measurements of *in situ* near-bed concentrations will be essential. The effect of hydrodynamic sorting further emphasises the potential role of larger aggregates as an important food source for *A. filiformis*.

Filtration models

The filtration model used strictly applies only for $Re_c \ll 1$, i.e. at creeping flow with no streamline compression (that would carry flow closer to an object on the upstream side due to inertial forces). Calculated Re_c for *Amphiura filiformis* is in the range 0.1 to 10. Clearly the assumption of creeping flow is frequently violated. Shimeta & Jumars (1991) suggest an extension of classic aerosol models to include streamline compression. These modifications require that the degree of compression be specified, e.g. by detailed descriptions of flow lines around filter fibres. Flow with streamline compression may substantially increase encounter rate compared to creeping flow regimes. Further research about encounter by large passive suspension feeders is needed to investigate the dependence of streamline compression on Re_c and on fibre geometry. Streamline compression is not the only complication. Although previous authors have stated that flow separation does not occur in most suspension feeders (Jørgensen 1983, LaBarbera 1984), our flume studies show that complex flow geometries form downstream of feeding *A. filiformis*. Attached vortices were frequent at flow velocities exceeding 6 cm s^{-1} ($Re_c = 6$) and circulation with slow flow upwards on the downstream side of the arm was observed. These flow patterns were reproduced at similar Re_c using model mimics of an *A. filiformis* arm. Eckman & Nowell (1984) found similar flow patterns around simpler mimics of animal tubes, and they proposed that the slow, upward flow along the axis of a tube is caused by the velocity difference between the proximal and the distal end in the velocity gradient of the boundary layer. The velocity difference results in a pressure gradient moving fluid to the low-pressure region on the downstream side at the top of the tube. This interpretation is supported by our flume studies where the upward flow was more intense closer to the sediment in which the velocity gradient is steeper, and by the weaker flow induced by the 'low-drag' model stripped of tube-feet mimics. The slow flow along the downstream side of the arm may increase retention efficiency in fast ambient flows and will also allow encounters on the downstream face of the tube feet. These secondary flow patterns may greatly complicate the use of simple filtration models and strongly indicate that calculated encounter rates of large passive suspension feeders in the present and previous studies should be interpreted cautiously.

Flume studies also show that ambient flow around active arms of *Amphiura filiformis* is generally turbulent, further violating the assumptions of the aerosol models used. Ambient turbulence is expected to increase encounter rate, but at present it is not possible to parameterise this effect (Shimeta & Jumars 1991). Analyses of how ambient turbulence affects encounter rate will most certainly include empirical studies.

Retention efficiency

We have here avoided the highly difficult problem of retention efficiency by defining encounter rate as potential feeding, thus assuming a retention efficiency of 100%. This assumption is certainly false, and we observed on several occasions in the flume that encountered particles were lost. Retention efficiency should be a function of the balance of drag acting on encountered particles, particle inertia and the adhesive force between particles and filter fibres. Note that streamline compression and turbulence, which will increase encounter rate, will probably reduce retention efficiency. Retention efficiency will also critically depend on surface properties of the filter elements. The small, papillate protrusions observed on the tube feet of *Amphiura filiformis* (Fig 1) could act to improve retention efficiency by increasing adhesion to encountered particles. It may be that the reorientation of active arms shown by *A. filiformis* at increasing flow velocities (Fig. 3) is an attempt to adjust the height of arm extension to match some optimal flow velocity in the boundary layer with respect to encounter rate and retention efficiency. Such matching could be a means for a passive suspension feeder to control the rate at which particles are encountered and filtered. The observed wave-form posture of active arms at high flow speeds may further increase both total cross-stream area exposed by trailing arms and retention efficiency in induced secondary flows. Taghon et al. (1980) observed a similar behaviour for some spionid polychaetes that can capture suspended particles using 2 ciliated tentacles. At high flow speeds the trailing tentacles formed helices, and experiments showed that this posture was an active response to the increased flux of food particles rather than flow per se.

The shape of the retention efficiency function has been partly evaluated for a crinoid (Leonard et al. 1988) and a sea pen (Best 1988). These studies indicate retention efficiencies between 10 and 30% with declining efficiency as flow speed increases. The present lack of knowledge about retention efficiencies in ophiuroids makes it difficult to infer ingestion rates from encounter rates. Evaluation of retention efficiency as a function of flow velocity and particle size and shape will be a major challenge for future research. High-resolution video recordings (e.g. Leonard et al. 1988) of particles encountering tube feet, and the use of labelled food particles, may help. Passive suspension feeders may also actively reject captured particles. In flume studies of *A. filiformis* we occasionally observed active rejection of encountered and retained nematodes and marine mites (Halacaridae).

Conclusions

Calculated encounter rates indicate that seston potentially can account for estimated growth rates of *Amphiura filiformis*. We conclude that although calculated encounter rates by natural populations of large passive suspension feeders presented here represent a serious attempt to balance capture rates with metabolic requirements, a new approach to the problem is necessary. Our study illustrates the difficulty in predicting ingestion rates of passive suspension feeders, particularly in the field. As advocated by Shimeta & Jumars (1991), it will be imperative to develop methods and theory to include effects of flow in intermediate Re_c, of turbulent diffusion and of how retention efficiency depends on flow velocity, as well as on sizes, geometries and surface characteristics of fibres and particles.

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