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Suspension feeding in the brittle-star *Ophiothrix fragilis*: efficiency of particle retention and implications for the use of encounter-rate models

Abstract Dense beds of the suspension-feeding brittle-star *Ophiothrix fragilis* are common in European waters. Their potential importance in benthic–pelagic coupling has been highlighted, but little is known about the feeding dynamics of this species. Encounter-rate models provide a potential mechanism for the estimation of feeding rates on suspended material of varying sizes. This work investigates factors essential to the application of such models. Particle-retention efficiency (RE) converts encounter rate into capture, or clearance rate. Laboratory studies demonstrated that RE varied with the interactive effects of flow velocity and particle size. RE was lowest for large particles, particularly at high flow velocity where RE as low as 59% was observed. This indicates that if RE is not accounted for in encounter-rate models, significant overestimates of feeding rates on large particles may occur. Flow around feeding arms and tube feet was characterised by intermediate Reynolds numbers, precluding application of the most simple encounter-rate models. Complex secondary-flow patterns were observed, which carried particles along the downstream side of the feeding arms, but these did not appear to increase the area available for particle capture. Previously reported particle capture by arm spines was not observed. Evidence of active rejection of large particles by tube feet was recorded. Difficulties in the application of encounter-rate models for prediction of seston-removal rates are highlighted by these results. Predicted encounter rate may deviate from actual clearance rate due to the effects of retention dynamics, localised flow patterns and differential particle handling. Other methods of estimation of seston-removal rates are equally problematic however, so that encounter-rate models are likely to remain a useful tool for such estimates.

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Introduction

The common brittle-star *Ophiothrix fragilis* (Ophiuroidea: Echinodermata) is known to form very dense aggregations in European waters, over scales of several square metres to several square kilometres and in densities of up to 2000 individuals m^{-2} (Vevers 1952, 1956; Brun 1969; Warner 1971; Broom 1975; Davoult et al. 1990). Studies in the same areas over periods of more than a century have shown that the beds are stable over long time periods (Chadwick 1886; Brun 1969; Aronson 1987).

Suspension feeding in *Ophiothrix fragilis* has been reported by several authors in both the laboratory and the field (Vevers 1956; Roushdy and Hansen 1960; Warner and Woodley 1975). In the most detailed account of particle capture and handling, Warner and Woodley described particle capture by mucus-covered spines and tube feet, with periodic cleansing of spines by tube feet, and collection of food into a bolus which increased in size as it travelled down the feeding arm towards the mouth. A two-way (comb) and four-way (cruciform) arrangement of tube feet was described in unidirectional and turbulent flow, respectively. Feeding behaviour was observed in free-stream currents of up to 20 to 25 cm s^{-1} in the field; above this, distortion of the feeding-arm array occurred. Based on high levels of silt found in stomach contents, selection of particles was not thought to take place prior to ingestion. Selective ingestion, by rejection of some whole boluses has been reported for other ophiuroid species (Pentreath 1970).

The importance of *Ophiothrix fragilis* beds in removing and recycling suspended organic material, even potentially controlling phytoplankton standing crop, has been recognised (Davoult et al. 1991, 1992; Hily 1991). In areas of high abundance, suspension-feeding

brittle-stars are an important link between the benthic and pelagic ecosystems. In such areas, knowledge of seston-removal rates by *O. fragilis*, the type of seston removed, and the fate of such material, is essential to understanding coastal processes such as energy transfer, food web dynamics, nutrient recycling and fate of suspended-phase contaminants. Despite this, the dynamics of suspension feeding in ophiuroids has received relatively little attention in comparison to that of other taxa (e.g. bivalve molluscs).

A possible mechanism for predicting seston-removal rates by suspension feeders exists in the form of mathematical models of particle encounter based on the aerosol-filtration theory (Rubenstein and Koehl 1977; Shimeta and Jumars 1991). Particle capture by each of the possible encounter mechanisms is modelled separately (direct interception, inertial impaction, gravitational or diffusional deposition). Prediction of flux of seston to brittle-star beds over scales of square kilometres therefore relies on measurement and modelling of parameters on the scale of micrometres. Application of these models requires knowledge of the dimensions of the collector, diameter of particles, particle concentration and flow velocity at the filter, along with any behavioural modification of feeding in response to environmental conditions. The modelled particle-encounter rate can only equal removal rate, or indeed ingestion rate, if all encountered particles are retained. Retention efficiency (RE = proportion of encountered particles retained) is therefore a vital consideration in the application of encounter-rate models, but is a poorly studied parameter (Shimeta and Jumars 1991). In their modelling of potential feeding rates of field populations of the brittle-star *Amphiura filiformis*, Loo et al. (1996) assumed retention efficiencies of 100%, while acknowledging that this assumption was probably incorrect. While there have been studies that have resolved individual particle encounters or fates in a variety of suspension feeders (e.g. Strathmann 1982; McFadden 1986; Leonard et al. 1988), the only comprehensive investigation of RE has been carried out on suspension-feeding spionid polychaetes (Shimeta and Koehl 1997). Shimeta and Koehl modelled the balance of adhesive, lift and drag forces acting on particles to predict the response of RE over changing flow velocities and particle sizes. These models predicted that retention efficiency would be lower for larger particles and at higher velocities, with the effect of increasing velocity being more pronounced on larger particles. It was also predicted that animals with smaller tentacles would show stronger selection towards small particles. Such responses were confirmed in flow-tank experiments on spionid polychaetes, showing that retention dynamics can directly influence feeding ecology by placing constraints of flow speed and collector width on the diet available to tentaculate suspension-feeders (Shimeta and Koehl 1997).

Reynolds number of the collector (Re_c), indicates the effect of the collector on flow patterns around the filter. Such flow patterns influence encounter rate, and differ-

ent encounter rate models are required for low and intermediate Reynolds number flow (Shimeta and Jumars 1991) Low Re_c has often been taken as the rule for suspension feeding (Jørgensen 1983; LaBarbera 1984). Shimeta and Jumars (1991) challenged this view, and proposed that intermediate Re_c should be found in many taxonomic groups, including ophiuroids, based on published flows and filter dimensions. They also predicted that associated formation of attached vortices would enable particle encounter on the leeward side of collectors, greatly increasing potential capture rates. Intermediate Re_c has recently been reported in the brittle-star *Amphiura filiformis* (Loo et al. 1996), but the associated influence on site of particle capture has not yet been investigated.

Encounter-rate models are potentially a very useful tool in the prediction of the impact of *Ophiothrix fragilis* beds on suspended material. This aim of the research described here was to investigate aspects of feeding which have major implications for the application of such models. In particular, the retention efficiency of particles of different sizes and at different flow speeds was recorded. Filter dimensions, Reynolds numbers and associated small-scale flow patterns were also determined. The results are discussed with reference to their implications for use of encounter-rate models in the prediction of rates of transfer of pelagic material to brittle-star beds.

Materials and methods

Ophiothrix fragilis was collected by naturalist's dredge, from an extensive bed to the south of the Isle of Man, at 30 m depth. The brittle-stars were maintained in flowing seawater until use. Particle-retention efficiency was determined at two flow speeds and for two particle sizes. Experiments were carried out in a recirculating flow tank, 1.5 m × 0.25 m (after Vogel 1981) containing 70 litres of unfiltered seawater. Dimensions of the flow channel were 75 cm × 25 cm, and water depth was 15 cm. Flow was produced by a Citenco propeller-stirrer. A constant, slow replacement of fresh unfiltered seawater was added to stimulate feeding. Water temperature was maintained at 12.5 to 12.8 °C. Only fully intact *O. fragilis* individuals, with a disc diameter of >8 mm, were used. Sixty brittle-stars were placed in the working section (giving densities similar to those seen in the field) and allowed to acclimatise for ≃2 h or until normal aggregation and feeding behaviour was observed. Eight experimental runs were carried out between 14 June and 17 July 1997, four with high and four with low water-flow, in randomised order. For each run, retention efficiency of large and small particles was recorded separately, in random order, on six separate *O. fragilis* individuals for each particle-size range. All 60 individuals were replaced between experimental runs.

Nominal free-stream velocities of 10 or 5 cm s^{-1} were set at the start of each run by timed passage of suspended particles through the flow channel. At the end of each experimental run, a small gap (≃5 cm upstream) was cleared in the brittle-star aggregation. Within this, the vertical-flow profile was recorded, using a video system incorporating an Hitachi KPM3 black-and-white CCD camera with a UNIMAC MS50 macrozoom lens with supplementary long working distance lens (0.75×), linked to a Panasonic AG-7350 S-VHS video recorder and Sony b/w monitor. Recordings were taken at 1 cm intervals from the surface of the water (see Fig. 1). Flow velocity was determined from the number of video frames (each 0.02 s) taken for in-focus suspended particles to travel a known distance (minimum of ten particles per estimation). Flow

local to each feeding arm (from 0 to 3.5 mm upstream) at 5 cm height was also recorded from videotapes by tracking particles approaching the filter (mean of ten estimations taken per arm).

Particles used were Polystyrene DVB microspheres (Duke Scientific Corporation, polymer density 1.05 g ml⁻¹). Several microsphere size-ranges were combined, then wet-sieved to give nominal size ranges of 240 to 500 μm (large particle-size range) and 80 to 140 μm (small particle-size range). These size ranges were chosen as being or larger than, smaller than, the diameter of tube feet, so that differences in adhesive forces would be maximised. The actual size distribution of sieved particles was determined microscopically for 100 particles of each size range. Mean diameter was 358 μm (SD = 101.3) for large particles and 93.9 μm (SD = 14.0) for small particles. Microspheres were added slowly, by fine pipette, at least 30 cm upstream of the individual under study and just downstream of the flow-straightener. The passage of particles around and along brittle-star arms was recorded with the video system. Illumination was provided by a 60 W bulb covered with red acetate to prevent postural changes by brittle-stars in response to light. Only those individuals that lay in the downstream half of the flow channel, and >7 cm from the side wall of the tank were used. The field of view contained a length of brittle-star arm of ≃6.4 mm and was centred 5 cm from the floor of the flow channel. Length, diameter and spacing of the tube feet, width of central arm and length of spines were recorded from calibrated video images. The passage of microspheres over the feeding arms was examined on videotapes frame by frame, and the resting position and fate of the first ten encountered particles were recorded for each individual. An encounter was recorded if a particle remained stationary for at least two frames at the highest flow. At low flow this was extended in proportion with the ratio of flow velocity at 5 cm height in the two treatments (Shimeta and Koehl 1997). This ensured that bias due to particle encounter and subsequent removal by water flow in less than the designated number of frames remained constant between flow treatments. Thus, encounter in the low-flow treatment was recorded if particles remained stationary over $(6.0/2.8) \times 2 = 4$ frames (0.08 s). It was originally intended to record particle fate as loss or transferral to bolus (= retention). However, a third possibility was observed with large particles, in which the tube foot in contact with the particle was moved behind the plane of the feeding arm and, in many cases, scraped on spines or moved about rapidly with subsequent loss of the particle. It was considered possible that this was active particle rejection and was recorded separately. Retention efficiency (RE) is defined as the percentage of encountered particles that are retained. It was calculated in two ways, first including all recorded encounters, and then excluding encounters which resulted in presumed active rejection.

A three-factor ANOVA was carried out on RE data for velocity × particle size with experimental run as a nested factor within velocity. Cochran's test on untransformed data indicated that homogeneity of variance was within acceptable limits. Transformation of RE data was therefore not carried out prior to ANOVA.

Reynolds numbers of the tube feet or collector (Re_c) were calculated from the tube-foot diameter and local upstream-flow velocity. Flow patterns behind the feeding arms were studied in detail by tracking of individual particles. For each brittle-star examined ($n = 96$), a segment of recording was selected randomly from videotapes taken for RE calculations. The path of the first observed, in focus, particle entrained behind the arm was mapped frame-by-frame on acetate sheets. The trajectory, presence of vortical movement, speed and distance of closest approach to arm and spines were recorded for each particle.

Results

Flow velocities

Mean free-stream velocity, estimated from videotapes, was 9.2 and 5.1 cm s⁻¹ for high and low flow, respec-
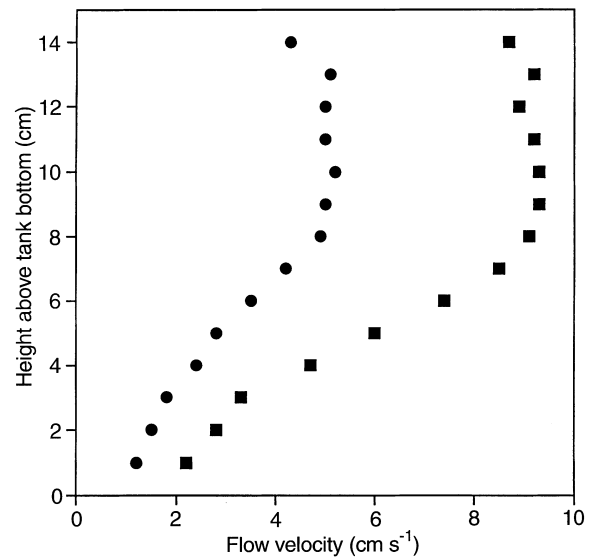

Fig. 1 Mean flow velocity as a function of depth in experimental flow tank during high- and low-flow treatments

tively (Fig. 1). Flow velocity was measured within the *Ophiothrix fragilis* patch, and profiles did not follow the classical log profile (e.g. Nowell et al. 1981). This was presumably due to flow disruption from the raised arms, which resulted in a two-layer flow, with flow increasing rapidly only above the height of raised arms (7 to 8 cm). Consequently, shear velocity, a useful parameter for comparing boundary shear stress, could not be calculated from these profiles. Average flow velocities at 5 cm from channel bottom (height of observation of particle capture) were 6.0 ± 0.66 and 2.8 ± 0.25 cm s⁻¹ (means ± SD). Flow local to the feeding arm at the same height was slightly lower at 5.3 ± 1.02 and 2.6 ± 0.46 cm s⁻¹ at high and low flow, respectively.

Dimensions of filter elements

Throughout the experiments, brittle-stars adopted a two-way orientation of feeding arms (Fig. 2), as most commonly observed in the field (Warner and Woodley 1975). Tube feet formed two rows, one each side of the feeding arm, held slightly into the current with an angle of ≃70° between tube feet and the direction of flow. Video footage for morphological measurements was taken from a side view, with the camera angled where possible to view the entire length of structures such as tube feet. However, some variability in angle of view remained, which is a source of error in such measurements. Dimensions of the feeding apparatus are summarised in Table 1. Mean distance between tube feet (323 μm) was smaller than the biggest particles of the large size range, and encounter by sieving was sometimes observed for such particles. However such large particles were normally retained until bolus formation by adhesion to a single tube-foot. Overall mean tube-

Fig. 2 *Ophiothrix fragilis.* Image from video tape, showing section of feeding arm
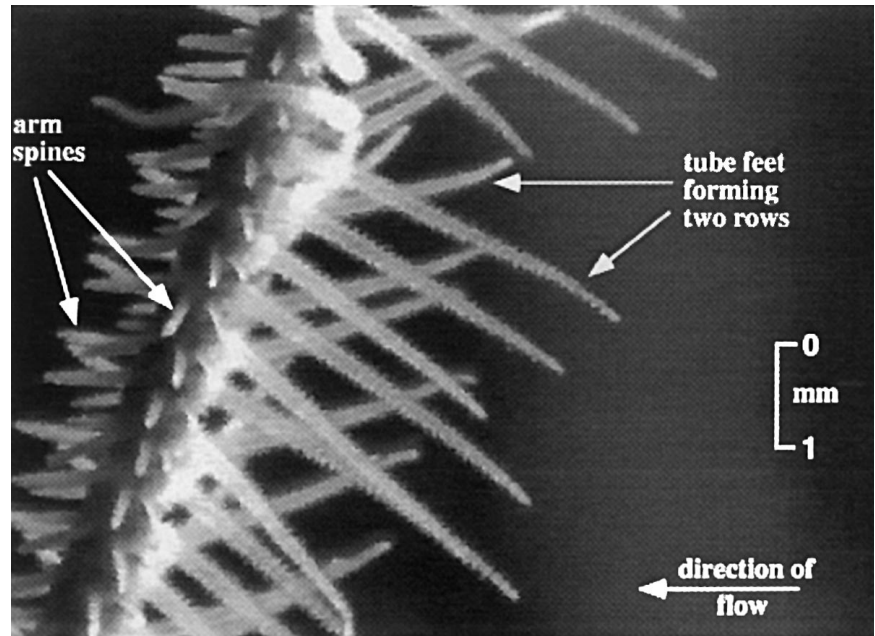

Table 1 *Ophiothrix fragilis.* Morphometrics (μm) of feeding apparatus. Values are means (±SD) of all individuals used in retention-efficiency estimations (*n* = 96)

Parameter	Mean (±SD)
Tube-foot length	3190 (±597)
Tube-foot width	192 (±31)
Tube-foot spacing	323 (±84)
Arm width	902 (±274)
Spine length	949 (±275)

foot diameter was 192 μm (Table 1), but comparison of measurements showed that tube feet observed at high flow were slightly narrower than those observed at low flow (183 μm compared to 200 μm). This difference was found to be significant (Student's *t*-test, *p* = 0.004). The difference was due to the postural changes made by *Ophiothrix fragilis* at different flow velocities. At high flow, arms were raised to a height of $\simeq$7 cm compared to >8 cm under low flow. Therefore smaller tube feet, closer to the tip of the feeding arm, were observed at 5 cm height under high flow. The retention efficiency of large particles would be expected to be reduced on narrow tube feet because of lower adhesive forces (Shimeta and Koehl 1997), thus possibly confounding the effects of flow velocity. The range of tube-foot width within the individuals examined at high flow was relatively large (140 to 240 μm), but for large particles at high flow there was no correlation between RE and tube foot width (*r* = 0.06, *n* = 24), despite the maximum effect of tube foot width on RE being expected under such conditions. It is therefore unlikely that any differences in RE between high and low flow was strongly influenced by the small differences in mean tube-foot width.

Retention efficiency

Mean retention efficiency as a percentage of all encounters was 59% for large particles and 93% for small particles at high velocity and 79% for large and 94% for small particles at low velocity (Table 2). Loss of particles involving active movements of tube feet, presumed to be rejection, was only observed for large particles. A higher rate of particle rejection was observed at high water flow.

Retention efficiency calculated from all encounters and from those excluding active particle loss were analysed separately. In both cases, the combined effects of velocity and particle size were found to have a significant effect on particle-retention efficiency, although higher significance levels were observed when all encounters were included (Tables 3 and 4). Interaction effects were such that the difference in RE between large and small particles was greater at higher velocities (Fig. 3). For small particles there was very little difference in RE be-

Table 2 *Ophiothrix fragilis.* Fate of encountered particles at high and low flow velocity, expressed as percentage of recorded encounters (mean values of observations on 24 individuals per treatment). Values in parentheses were calculated with encounters resulting in active particle rejection excluded. Particles were considered to be retained when gathered into a bolus

Flow, particle size	Percentage:		
	retained	lost	rejected
High			
large	59 (75)	18 (25)	23
small	93 (93)	7 (7)	0
Low			
large	79 (88)	9 (12)	12
small	94 (94)	6 (6)	0

tween the two flow velocities. While significant variation between runs was observed, both within velocity and in the level of response to particle size, the direction of this response remained constant.

Patterns of flow around arms and associated particle capture

Mean Re_c at the tube feet was 6.7 at high velocity and 3.6 at low velocity. Such Reynolds numbers are below those expected to cause separation of flow around a simple

Table 3 *Ophiothrix fragilis*. Analysis of variance of particle-retention efficiency (RE) as a function of flow velocity and particle size: all particle encounters are included in estimation of RE. Experimental run is nested within velocity (*SS* sum of squares; *MS* mean square)

Source	(*df*)	SS	MS	*F*	*P*
Velocity × particle size	(1)	2144.2	2144.2	10.617	.0016
Velocity	(1)	2455.3	2455.3	12.157	.0008
Particle size	(1)	14546.0	14546.0	72.023	.0001
Run (velocity)	(6)	5853.3	942.2	4.665	.0004
Particle size × run (velocity)	(6)	6354.3	1059.1	5.244	.0001
Residual	(80)	16157.0	202.0		

Table 4 *Ophiothrix fragilis*. Analysis of variance of particle-retention efficiency (RE) as a function of flow velocity and particle size: those encounters which resulted in active particle loss are excluded from estimation of RE. Experimental run is nested within velocity

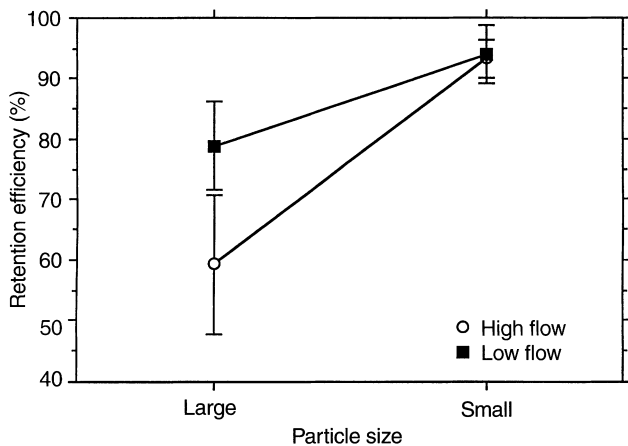| Source	(*df*)	SS	MS	*F*	*P*
Velocity × particle size	(1)	1038.2	1038.2	5.642	.0199
Velocity	(1)	1257.9	1257.9	6.835	.0107
Particle size	(1)	3590.5	3590.5	19.511	.0001
Run (velocity)	(6)	3127.5	521.3	2.833	.0149
Particle size × run (velocity)	(6)	3651.1	608.5	3.307	.0059
Residual	(80)	14721.7	184.0		

Fig. 3 *Ophiothrix fragilis*. Retention efficiency (% of all encountered particles). Interaction plot for velocity × particle size (±95% confidence intervals)
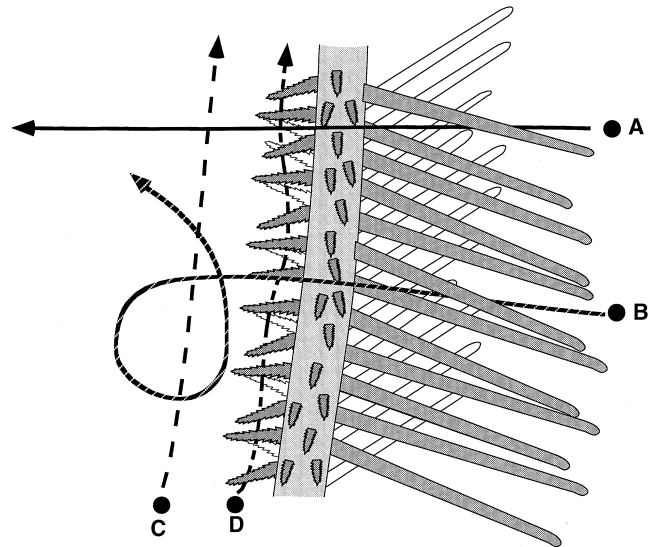
Fig. 4 *Ophiothrix fragilis*. Examples of particle paths around section of feeding arm, as traced from video sequences. Flow direction and orientation of feeding arm as in Fig. 2 (*A* normal trajectory of particles: passing between tube feet, but not deviating from main direction of flow; *B* vortical movement behind feeding arm; *C* particle following commonly observed upward trajectory behind arm; *D* particle entrained in upward flow behind arm, but providing example of particle moving between arm spines)

cylinder and, indeed, no evidence of flow separation or attached vortices was seen in flow directly behind tube feet. Particle encounter on the leeward side of tube feet was not observed, but encountered particles were often seen to roll around the tube foot to be retained on the downstream side. Particles passing between tube feet sometimes showed deflection in angle on approach, but usually continued in a straight trajectory on passing through. However, complex flow patterns were observed behind the central vertical portion of the brittle-star arm. Reynolds number of the arm was >10, with a mean of 29.8 at high flow and 17.8 at low flow. At these Reynolds numbers, attached vortices might be expected. Tracking of individual entrained particles demonstrated that the dominant flow pattern behind the arm was a steady upward flow (Fig. 4), with $\simeq$75% of observed particles showing simple upward movement within the field of view. Particles that had passed between the base of the tube feet occasionally became entrained within this flow. The velocity of the upward current was higher at high ambient flow (Table 5). Movements of entrained particles indicted the presence of attached vortices in 13% of cases at both high and low flows (Table 5). Particles within the leeward upward current often passed between the arm spines at both high and low flows (Fig. 4, Table 5), but adhesion of particles to spines was not observed during particle-tracking. Particle retention on spines was very rarely observed (only two observations) in studies of entire feeding tapes during which entrained particles were not tracked in detail. Such particles were not incorporated into passing boluses and remained adhered to spines for the duration of recordings.

Table 5 *Ophiothrix fragilis*. Movement of particles entrained behind feeding arms, indicative of downstream flow-structures. Percent occurrence of selected trajectory events was estimated from $n = 48$ observations of entrained particles for each flow treatment

Flow treatment	Particle velocity (cm s^{-1} ± SD)	Percentage:		
		vortical movement	particle adhesion	passage between spines
High	1.6 ± 0.74	13	0	20
Low	0.7 ± 0.40	13	0	27

Discussion and conclusions

Retention efficiency

The present study on particle fate in *Ophiothrix fragilis* has shown that particle retention varies due to a combination of both ambient flow velocity and particle size. Retention dynamics will bias particle-size distributions in the bolus towards smaller particles, particularly at higher ambient flows. These findings are in agreement with predicted trends and observations in tentaculate worms (Shimeta and Koehl 1997). Most small particles encountered were retained, with increasing water velocity resulting in only a very small reduction in retention (from 94 to 93%). Retention efficiencies for larger particles were much lower however, and the effect of flow velocity was more pronounced. Mean RE as low as 59% was recorded for large particles at the highest flow speed.

Encounter-rate dynamics alone will cause ingestion rate to increase with increasing velocity and will bias intake towards larger particles (Shimeta and Jumars 1991). Retention efficiency, however, acts in an opposing direction, particularly at higher velocities. Behaviour assumed to be active particle rejection will also select for smaller particles, and may also be more pronounced at higher flow rates. Ingestion rate of particles of different sizes will therefore reflect a combination of these passive and active selection pressures.

While particle loss or rejection was frequently the fate of encountered large Polystyrene DVB microspheres, this may not be the case for nutritive particles. A different behavioural response to encountered material was observed during experiments: occasional encounters with naturally occurring large prey items (small zooplankters) appeared to trigger envelopment by all surrounding tube feet, and initiation of a bolus immediately from that point on the arm. Such behaviour would greatly reduce the chances of loss of large particles, but was never observed with Polystyrene DVB microspheres. Further study of possible active selection and/or rejection at the level of the tube foot is required, using naturally occurring nutritive and non-nutritive particles.

Local flow patterns and particle capture

Enhancement of feeding by particle capture within downstream vortices has been previously described for octocoral colonies (Patterson 1984) and in simuliid larvae (Chance and Craig 1986). In *Ophiothrix fragilis* feeding in unidirectional current, complex secondary-flow patterns also develop downstream of the feeding arm. These flow structures carry particles close to the spines projecting from the rear of the arm. However, no particle capture onto either tube feet or spines was observed from within downstream flow-patterns. Particle capture onto spines with subsequent cleaning by tube feet and transferral to bolus, previously reported by Warner and Woodley (1975), was not observed on any occasion. This was surprising, as particles entrained into the upward flow behind the arms frequently moved on a trajectory passing between spines. Tube feet at the rear of a bolus were seen to wipe over spines, but this did not appear to be for the purpose of removing food particles, at least not those of a size that could be resolved by the video equipment (a minimum particle diameter of ~60 μm). Mucus-secreting glands are present within the spines of *O. fragilis* (Buchanan 1963), but the function of this mucus, if not for particle capture, is uncertain. The observations of Warner and Woodley were made by SCUBA diving using magnifying lenses, and it is not clear if handling of individual small food particles could be resolved by this method.

While localised, complex flow patterns around the brittle-star arms may not increase particle capture at the level of the individual; however, on the scale of the whole brittle-star bed, particle capture may be increased. Missed particles may be resuspended higher into the boundary layer, and captured by individuals downstream. Eckman and Nowell (1984) proposed that upward flows observed behind mimics of animal tubes, were due to pressure gradients over the length of the tubes resulting from their relative position in the boundary layer. It is likely that similar gradients are responsible for the upward flows behind brittle-star arms. An upward current to the rear of the arm has also been described in the brittle-star *Amphiura filiformis* (Loo et al. 1996), although its influence on capture site was not described.

While the experiments described here were carried out in free-stream flows of up to 10 cm s^{-1}, feeding by *Ophiothrix fragilis* at above-bed flows of up to 25 to 30 cm s^{-1} has been recorded (Warner and Woodley 1975; Davoult and Gounin 1995). It is therefore possible that secondary-flow patterns and capture sites might alter at higher speeds. However, observations in the field (Davoult and Gounin 1995) and in our flow tanks suggest that the feeding arm is held much lower at higher flow speeds. It is possible that *O. fragilis* utilises boundary-flow gradients to maintain an optimum maximum flow rate that is much lower than the recorded free-stream flows.

Implications for application of encounter-rate models

These findings highlight problems for the use of encounter-rate models to predict seston-removal rates by

Ophiothrix fragilis beds, as RE must be included as a factor within the models. This work indicates that an assumption of 100% retention in the application of encounter-rate models would result in significant errors for larger particles, as a high proportion of encountered particles would be returned to suspension. The application of the RE correction presents some difficulties, however, as it is likely to vary not only with both flow velocity and particle size, but also with particle characteristics such as density, surface properties and shape. Differential handling of particles of different types appears to be take place, a behavioural response which would further complicate the use of encounter-rate models.

In estimating the potential effect of recorded RE dynamics on feeding rates, detailed field studies of seston size-distribution and concurrent flow velocities is required. Such information has not been collected for *Ophiothrix fragilis* beds. These factors were measured by Loo et al. (1996) to facilitate modelling of encounter rate in the brittle-star *Amphiura filiformis*; however, particle-size frequency was only gathered for particles < 250 µm diam. Within this size range, seston was usually dominated (in terms of volume) by particles < 100 µm, while average recorded free-stream flow speeds were 8 cm s^{-1}. The studies presented here suggest that RE would be unlikely to have a significant effect on feeding rates under the average flow and particle conditions that were measured for the *A. filiformis* beds. RE recorded in the studies described herein was $> 90\%$ under such conditions, albeit for a different species. However, Loo et al. emphasised that the importance of larger particles may have been substantially underestimated in their field measurements, and suggested that estimates of encountered particle volume might increase by 200% if large aggregates were included. Also, on occasional sampling dates, particles at the upper end of the measured size range (to 250 µm) dominated. In *O. fragilis*, the retention efficiency of encountered particles > 240 µm was 79% at 5.1 cm s^{-1}, and as low as 59% at 9.2 cm s^{-1}-flow velocities within the range recorded by Loo et al.. Under conditions of large particle dominance, it is possible therefore that actual feeding rates in *A. filiformis* would be substantially lower than estimates from encounter-rate models, because of RE effects.

Variable retention efficiency and particle handling are not the only difficulty in the use of encounter-rate models: all calculated collector Reynolds numbers were intermediate values. The most simple encounter-rate models are designed for use at $Re_c \ll 1$, an assumption that is clearly violated. Although models are available for intermediate Reynolds number flow (Shimeta and Jumars 1991), these incorporate a factor for streamline compression that is very difficult to quantify.

While the use of encounter-rate models for estimation of seston removal has obvious limitations, it is likely that they will remain a useful tool. Accurate empirical models of seston removal would be difficult to achieve. In the laboratory, scaling factors involved in flume design (No-well and Jumars 1987) in respect to the height of feeding arms, would necessitate a flume of impractically large proportions, requiring very large numbers of brittle-stars to reproduce densities of individuals, and flow conditions, comparable to natural beds. Field measurements of clearance of different particle types by animals in situ, as carried out for some bivalves (e.g. Newell and Shumway 1992), would be difficult due to the inaccessibility of most brittle-star beds and the probable disturbance of local flow fields. It is likely, therefore, that encounter-rate models will continue to be useful to estimate potential feeding rates. Such models would be particularly useful for studies of removal rates of an individual seston type, where modelling could be more easily backed up by laboratory studies of retention efficiency and particle handling. The use of field-based, high-magnification video would provide further essential information on aspects of particle fate, local flow patterns and larger scale flow profiles under natural conditions.

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