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BRYOZOAN FILTER FEEDING IN LAMINAR WALL LAYERS : FLUME EXPERIMENTS AND COMPUTER SIMULATION

P.S. LARSEN, S.S. MATLOK*, H.U. RIISGÅRD***

** Department of Energy Engineering, Fluid Mechanics Section, Technical University of Denmark Building 404, 2800 Lyngby, Denmark*

*** Research Centre for Aquatic Biology (Institute of Biology, Odense University), Hindsholmvej 11, 5300 Kerteminde, Denmark*

AMBIENT FLOW VELOCITY
BOUNDARY LAYER
SUSPENSION-FEEDING
LOPHOPHORS

ABSTRACT. – Particle paths and velocities have been determined from video recordings above single-line colonies of bryozoans (*Celleporella hyalina*, *Electra pilosa*, *Alcyonidium hirsutum*, *Membranipora membranacea*, *Flustrellidra hispida*) placed at the bottom of a laminar flow flume in zones of constant velocity gradient (1 to 4 s^{-1}). The laminar wall layer simulated viscous sublayers found in the field for smooth surfaces. Incurrents to lines of 3 to 10 zooids typically distort paths of particles approaching the colony at heights 1 to 2 mm above the level of lophophore inlets and they capture particles from paths 0.7 to 1.2 mm above this level. The experiment was simulated numerically by computing the full three-dimensional laminar flume flow for the case of a line of 10 zooids that were modelled as sink-source pairs. Computed paths of discrete "fluid particles" show how the fraction of captured particles per zooid decreases downstream. Similar results were obtained by computing the continuous concentration distribution in the flow resulting from specifying uniform upstream concentration and sinks at zooids. Computed particle paths show the cross sectional area of approaching flow cleared of particles by the 10 zooid line colony to be about 16 times the frontal area of a simulated lophophore. Fluid particles were captured from paths about 1.3 mm above the sink. At twice the flowrate, the area cleared of particles reduced to about 7 times the frontal area while feeding rate increased by about 19 %.

HYDRODYNAMISME LOCAL
COUCHE LIMITE
SUSPENSIVORES
LOPHOPHORES

RÉSUMÉ. – Alimentation par filtration des Bryozoaires dans des couches laminaires : essais au laboratoire et simulation informatique. Les trajectoires et les vitesses des particules ont été déterminées à l'aide d'enregistrements video effectués au-dessus de colonies de Bryozoaires formant une colonne unique *(Celleporella hyalina, Electra pilosa, Alcyonidium hirsutum, Membranipora membranacea, Flustrellidra hispida)* placée à la base d'un écoulement laminaire dans des zones de gradient linéaire de vitesse (1-4 s^{-1}). L'écoulement laminaire simule les sous-couches visqueuses existant dans la nature le long de parois lisses. La trajectoire de particules approchant une colonne de 3 à 10 zooïdes est typiquement modifiée à une hauteur de 1 à 2 mm au-dessus de l'ouverture des lophophores et ceux-ci capturent les particules dans les couches situées entre 0,7 et 1,2 mm au-dessus de ce niveau. Les essais de laboratoire ont été simulés numériquement en calculant l'écoulement laminaire tri-dimensionel dans le cas d'une colonne de 10 zooïdes considérés comme des paires d'entonnoir capteur-source. Les trajectoires calculées des « particules de fluide » montrent comment la proportion de particules capturées par zooïde décroit vers l'aval de l'écoulement. Des résultats semblables ont été obtenus en calculant les taux de concentration en aval de la colonie provenant de concentrations uniformes en amont de la colonie, et d'un nombre donné d'entonnoirs par zooïde. Les trajectoires calculées des particules montrent que la proportion de section transversale d'écoulement qui est vidée de particules est équivalente à 16 fois la zone frontale d'un des lophophores simulés. Les particules de fluide sont capturées dans les trajectoires situées à environ 1,3 mm au-dessus des entonnoirs. Pour un courant deux fois plus fort, la surface vidée de particules est réduite à environ 7 fois la zone frontale, mais le taux de capture augmente d'environ 19 %.

INTRODUCTION

Bryozoans are active filter feeders working an energy-consuming lophophore filter-pump (Bullivant 1968, Gordon 1974, Ryland 1976, Winston 1978, Gordon *et al.* 1987, Grünbaum 1995, Riisgård & Goldson 1997, Riisgård & Manríquez 1997). Water from near the surface of a bryozoan colony is pumped downward by the lateral cilia on the crown-tentacles of the individuals. The flow velocity at the entrance of the lophophores is typically 2 to 3 mm s^{-1} (Riisgård & Manríquez 1997, Nielsen & Riisgård 1998). In encrusting colonial bryozoans, which form a continous and often fairly smooth layer, the filtered water moves laterally along the substratum between the individual lophophores, and finally in e.g. *Membranipora villosa*, the water emerges from 'chimneys' as a jet of substantial speed (about 20 mm s^{-1}) (Lidgard 1981).

Due to their small size bryozoans must be able to cope with thin boundary layers and steep velocity gradients above surfaces of marine macroalgae, rocky outcrops etc. on which they live. Therefore, it may be expected that the feeding success, choice of habitat, colony form and distribution are closely related to the way in which bryozoans deal with the flowing surrounding water (Okamura 1984, 1985, Eckman & Okamura 1998).

For a long time it has been recognized that a variety of processes of biological interest are strongly influenced by water motions at the boundary with the sea floor (Jumars & Nowell 1984, Jumars 1993). It has also been realized that the processes in the bottom boundary layer may be modelled in flumes (Nowell & Jumars 1987, Fréchette *et al.* 1989, Emlet 1990, Hart *et al.* 1991, Butman *et al.* 1994, O'Riordan *et al.* 1993, 1995, Anthony 1997). Nowadays, flumes with widely different size, shape and flow characteristics are used for manifold purposes (Wildish & Kristmanson 1997). But so far the use of flumes in benthic filter-feeding biology has mainly dealt with studies of boundary layer flows in supplying phytoplankton to mussels and other macro-benthic filter feeders. Thus, most studies deal with the 'logarithmic' layer where the velocity varies as the logarithm of the distance above the bottom. The logarithmic layer is turbulent but below this layer, due to viscous damping, there exists a thin layer of essentially laminar flow near hydrodynamically smooth surfaces. This layer is designated the viscous sublayer or the 'linear sublayer' because the velocity varies linearly with the distance above the substratum (Emlet 1990, Jumars 1993, Vogel 1994, Mann & Lazier 1996, Wildish & Kristmanson 1997).

The viscous sublayer is typically in the order of millimetres thick at low flowrates but decreases in thickness with increasing flowrate. Encrusting filter-feeding bryozoan colonies may often (or perhaps as a rule) reside within this viscosity-dominated layer (Lidgard 1981, Grünbaum 1995) although Eckman & Okamura (1998) have claimed that such conditions may occur only under restrictive circumstances or if the bryozoans foul flat blades of marine macroalgae. But in a recent study, Hurd *et al.* (1997) measured the velocity profiles of seawater flow along a blade of a giant kelp exposed to unidirectional laminar flow in a flume. At low free-stream velocities (< 2 cm s^{-1}) the boundary layer was laminar in the blade mid-region but turbulent at the blade end. However, no detailed information was given about the thickness of the viscous sublayer. At higher free-stream velocities (> 2 cm s^{-1}) the velocity boundary layer was turbulent and, depending on blade morphology, there were recirculating regions.

A detailed mathematical model of laminar feeding currents in encrusting bryozoans in the absence of external flow was recently presented by Grünbaum (1995). Closely spaced zooids forming a circular colony experience hydrodynamic interference that results in a significant reduction of feeding current per zooid as the number of zooids increases. This effect is especially strong in the absence of 'chimneys' because excurrents flowing in the substratum can only escape at the rim of the colony. For an in-line colony, however, the interference is minimal because excurrents escape to the sides of zooids. Eckman & Okamura (1998) solved the two-dimensional convection-diffusion equation for the concentration boundary layer developing in both turbulent and laminar flows over encrusted actively feeding bryozoans, and accounted for excurrents through a phenomenological model of mixing. This theoretical study shows how the per-lophophore rates of particle capture were predicted to decrease downstream of the first zooid in a colony, depending on flowrate and zooid spacing. It was also concluded that, in general, feeding was greater from turbulent flow than from laminar flow, except for closely spaced zooids where excurrent chimney effects could provide added mixing.

Due to the uppermost parts of the lophophores of encrusting bryozoans being typically raised only about 0.5 to 1.5 mm above the substratum, it seems obvious that filter-feeding in the viscous (linear) sublayer may frequently take place – or perhaps be the usual condition. Therefore, the physical environment experienced by encrusting bryozoan colonies living on brown algae, such as *Laminaria* sp., or less commonly on other algal substrates, is 'one of reduced flow within a boundary layer' (Lidgard 1981).

Our knowledge about viscous sublayers in the field is very limited and more empirical measurements are needed to understand the interactions between sessile organisms and the surrounding water (Shashar *et al.* 1996). Protected embayments may be subject only to tidal changes in water level and velocities that rarely exceed 10 cm s^{-1}. In areas that experience seawater velocities < 4 to 6 cm s^{-1}, seaweed productivity may be limited by the development of a boundary layer that reduces the transport of nutrients to the blade surface (Hurd *et al.* 1996). But this layer, inhabited by encrusting bryozoans, should perhaps also be regarded as a protected niche for these animals. Given the flexibility and closeness of tentacles these protrusions can hardly be compared to usual rigid roughness elements. Also, the boundary layer flow experiences 'suction' due to incurrents which are known to stabilize the flow or it may be obstructed by regions of spines that reduce the velocity gradient. It therefore seems relevant to consider situations of bryozoan filter feeding in a viscous layer.

The present work deals with flume studies and computer simulation of bryozoan particle capture in a viscous wall layer. The starting point – and assumption – is that filter feeding by bryozoans in nature takes place in the linear gradient region adjacent to the surface. Seen in that perspective it is of considerable interest to know how the filter feeders deal with velocity gradients in which they find themselves.

MATERIALS AND METHODS

Experimental animals and flume observations : Flume studies were performed with 5 species of bryozoans collected at low tide in the Menai Strait, UK, in May 1997 : *Celleporella hyalina, Electra pilosa, Alcyonidium hirsutum, Membranipora membranacea, Flustrellidra hispida.* Using a scalpel, the continuous encrusting layer of colonial zooids on fronds of seaweed was reduced to a single row of individuals. A rectangular piece of frond (30 × 15 mm), with the lengthwise located row, was placed in a small flume (Fig. 1). Measurements were commenced after a re-establishment period of about 24 h. In one case the bryozoans in the flume were replaced by a small glass tip (opening = 0.27 mm) connected to a thin tube thus enabling siphoning at different flowrates analogous to the pumping of a bryozoan lophophore.

Particle paths and velocities were recorded at 20 °C using a video camera (Kappa CF 11/1) attached to a horizontal placed microscope (Wild M3C), and a 50 half-frames per second video recorder (Panasonic NV-FS200 HQ). The depth of focus (about 4 mm) ensured that only particles in the mid plane of the flume were registred. The position of particles (6 µm flagellate cells of *Rhinomonas reticulata*) upstream as well as above the row of zooids were recorded and the position of the particles traced. This was done by mounting a

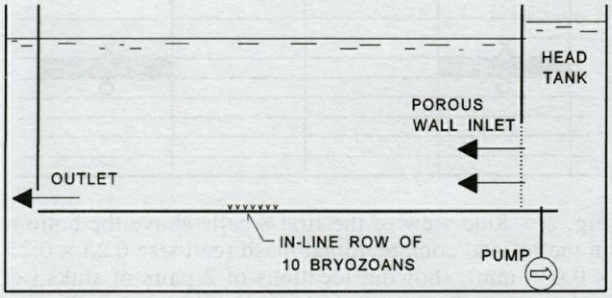

Fig. 1. – Flume (schematic) with row of 10 bryozoans positioned at bottom in mid-plane of flume chamber (200 × 70 mm by 15 mm deep), having uniform inflow through a 35 × 15 mm porous wall inlet (lower right wall) and an adjustable outlet (lower left wall).

transparent plastic sheet onto the video screen so that the tentacle contours as well as the position of suspended particles were marked with a time interval of 5 video frames = 0.1 s using a pen directly on the sheet. The length, width and height (distance from substratum with bryozoans to free water surface) of the flume were 200, 15 and 70 mm, respectively. The flow was set up by means of a pump recirculating the seawater, and the volume flow was regulated by means of an adjustable outlet placed 100 mm downstream of the bryozoans. All measurements were done at the School of Biological Sciences, University of Wales, Bangor, U.K.

Computational model : To ensure an accurate simulation the flow was computed in the whole flume chamber, from inlet to outlet (Fig. 1). Being interested in the trajectories of captured particles and hence the boundary layer depletion, only the net effect of cilia-driven feeding currents of each lophophore in the line of bryozoans was simulated by source-sink pairs of specified flow.

Thus, the computational domain of flume chamber (200 × 70 mm by 15 mm deep), had at the right face (lower half) a 35 × 15 mm uniform flow inlet (U = 10.9 mm s^{-1}, corresponding to a total flow of 5.7 ml s^{-1}, and at the left face (near bottom) a 5 × 15 mm outlet condition. The top was a free surface with imposed no-shear condition, and side walls were imposed the no-slip condition.

The numerical study used the finite volume method (Patankar 1980) available in a standard computer code (STAR-CD). The steady, three-dimensional Navier-Stokes equations were solved on an unstructured Cartesian mesh (about 190,000 nodes), employing a self-filtering central-difference scheme and the SIMPLE pressure-velocity coupling.

The computational mesh consisted of a coarse mesh (cell size 4 × 3.5 × 1.5 mm), refined in 6 steps to the finest mesh (cell size 0.25 × 0.25 × 0.036 mm) in which were placed a total of 10 sink-source pairs. These sink-source pairs simulated a line colony of lophophores of *Electra pilosa* (Riisgård & Maríquez 1997, Table 4 index no. #4 therein), each of strength 1.09 ml h^{-1}, located from 95.5 mm to 102.5 mm from the inlet and in cells in the midplane of the flume model. The sink of specified volume flow was located in one cell and a source of equal volume flow and of a corresponding

Fig. 2. – Side view of the first 8 cells above the bottom in the refined computational mesh (cell size 0.25 × 0.25 × 0.036 mm), showing locations of 2 pairs of sinks (×) and sources (○), separated by cell (cross-hatched) with impermeable horizontal faces.

downward directed momentum source was located two cells below (Fig. 2). To ensure a downward directed sink flow a horizontal cell-face between sink and source was separated by an impermeable wall.

Once a converged solution had been established, neutrally buoyant 'fluid particles' were started with the local velocity from a position 6.5 mm upstream of the first model zooid and tracked, in this way simulating the experiment. A total of 1050 particles were arranged in 21 columns of 50 particles, covering the central width of 2.5 mm and a height of 1.79 mm, which ensured that only a fraction of particles (typically about 10 %) would be captured. In this way the capture capacity in terms of upstream flow area cleared of particles could be determined. Capture was registred at a given lophophore when a particle entered its sink.

As an alternative approach to determine the theoretical feeding potential of zooids, given the steady velocity field and specifying a uniform upstream concentration of unity representing food particles, zero concentration at sources on the assumption of 100 % retention, and zero flux at all walls, the resulting concentration distribution was computed. Using a low value of diffusivity (3×10^{-9} m^2 s^{-1}) the solution of the convection-diffusion equation gave transport with negligible dispersion. Then, the value of concentration at each sink represented the feeding potential at that location since the product of volume flow and concentration at a sink equalled the feeding rate at that point.

RESULTS

Flume experiments

Figure 3 shows the upstream velocity profiles and particle trajectories above a line of 3 lophophores of *Celleporella hyalina* in two situations. In both cases (#1 and #2) it was verified that the upstream flow was laminar, and that the velocity varied linearly with height above the bottom (Fig. 3, lower fig., recorded about 50 mm upstream of the colony).

Figure 4 shows results obtained with a line of 10 *Electra pilosa*. The figure allows a comparison between individuals without long spines (Fig. 4A) and individuals with long spines (Fig. 4D). The upstream velocity profile (Fig. 4B & C) and the velocities above and within the long spines (Fig. 4E & F) clearly illustrate how the spines reduce the laminar flow velocity gradient.

The particle trajectories above a single row of zooids of 3 differently sized species of bryozoans *(Alcyonidium hirsutum, Membranipora membranacea* and *Flustrellidra hispida)* are shown in Fig. 5.

In Fig. 6 the bryozoans in the flume have been replaced by a small glass tip connected to a thin tube thus enabling siphoning at 3 different flowrates, analogous to the pumping of a bryozoan lophophore, except that flow corresponding to excurrent was not returned. It is seen that the strength of the sink highly influences the thickness of the 'feeding layer' from which particles are captured.

Computational results

Simulations were carried out with a specified volume flow of 1.09 ml h^{-1} for each sink-source pair, which corresponds to the data from the experiment shown in Fig. 4A, and for the nominal flume flow of 5.7 ml s^{-1}, as well as twice that flume flow. In both cases laminar boundary layers developed with a linear vertical velocity gradient near the bottom that decreased downstream. In the mid-plane of the flume, at positions 50 mm and 5 mm upstream of the first sink-source pair, the velocity gradient at nominal flume flow was $\partial u/\partial y$ = 3.1 s^{-1} and 1.6 s^{-1}, respectively. The former value should be compared to the experimental value $\partial u/\partial y$ = 3.26 s^{-1}, derived from data in Fig. 4B & C.

Figure 7 shows computed trajectories of fluid particles entering with the flow from right. For clarity only particles started in the vertical plane aligned with the sinks are shown. About 10 % of all particles released were captured. Figure 8 shows the fraction of these particles that were captured by each lophophore (+). These results obtained from trajectories are compared to those obtained from the concentration distribution (—). Also shown in the figure are corresponding results for twice the nominal flume flow, (○) and (---). In each case the sum of discrete values at the 10 zooids adds up to unity.

For the case of twice the nominal flume flow, because of the nature of the viscous boundary layer development along the bottom, velocity gradients at positions 50 mm and 5 mm upstream of the first sink-source pair increased to the values $\partial u/\partial y$ = 5.95 s^{-1} and 4.8 s^{-1}, respectively. While the distribution of relative feeding rate per zooid only changes little (Fig. 8), the magnitude of feeding rate increased by about 9 % at the first zooid

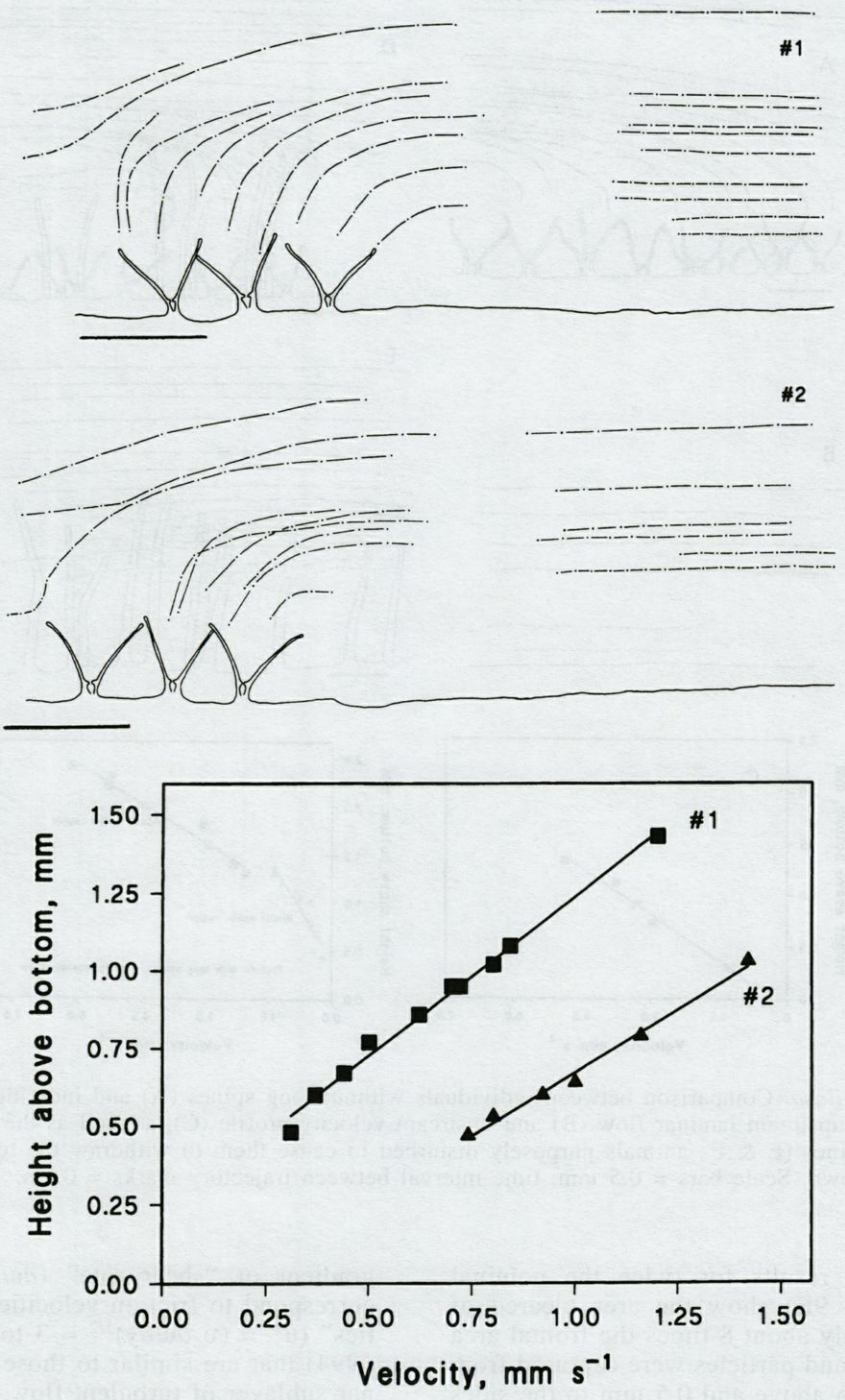

Fig. 3. – *Celleporella hyalina*. Upstream velocity profiles (#1 & #2 right side) and particle trajectories above 3 lophophores in flume. The lowest figure shows that the estimated flow velocity as a function of height above the bottom for 2 settings of the adjustable gate (Fig. 1) : 5 × 15 mm (#1) and 10 × 15 mm (#2) open outlet. Scale bar = 0.5 mm, time interval between trajectory marks = 0.1 s.

and 21 % at the 10th zooid, as compared to the case of nominal flow, hence becoming slightly more uniform at this higher flow.

Figure 9 shows a cross-section of the approaching flow, located 6.5 mm upstream of the colony where particles were started, each cross indicating that a particle started from this location was captured. Thus, the marked region gives an idea of the area of approaching flow cleared of particles. For nominal flow (Fig. 9A), the size of the area was about 16 times the frontal area of a simulated lophophore. Particles were captured from paths as high as about 1.3 mm above the sinks and as much as about 0.75 mm to the sides.

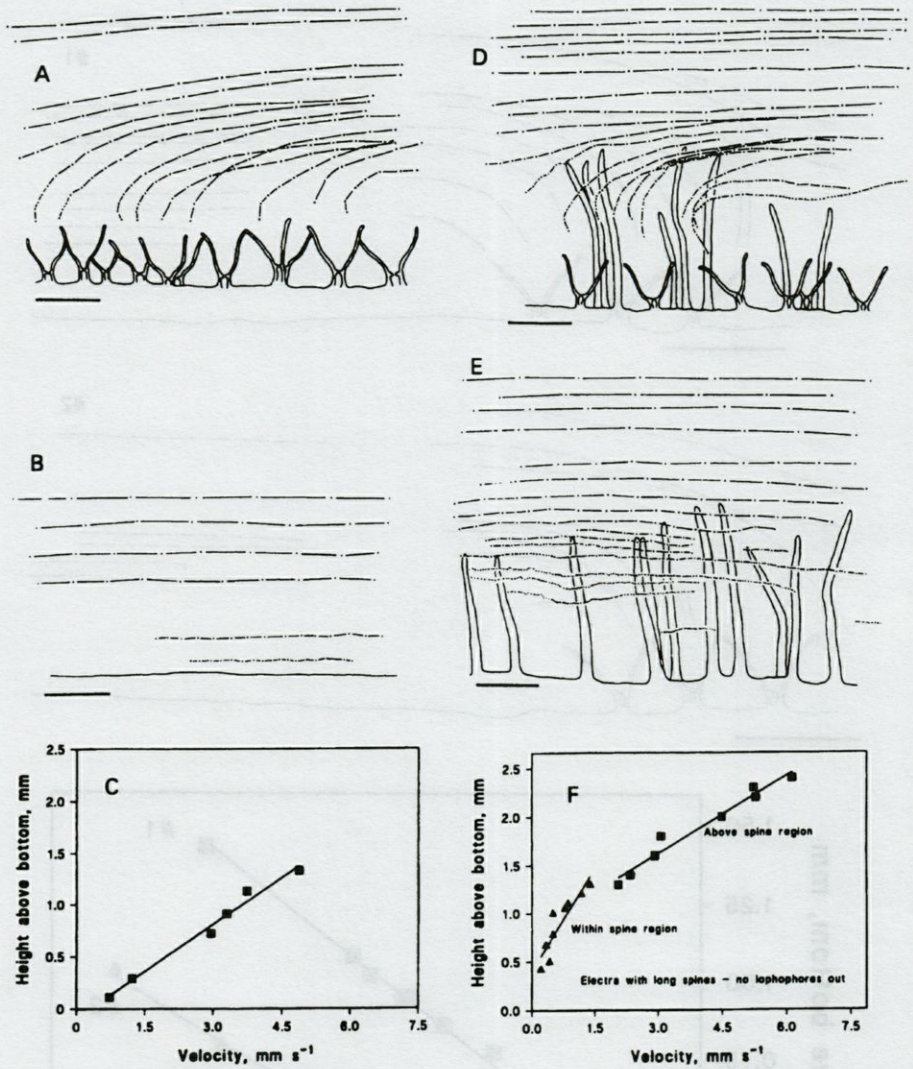

Fig. 4. – *Electra pilosa.* Comparison between individuals without long spines (A) and individuals with long spines (D) in flume. The upstream laminar flow (B) and upstream velocity profile (C), as well as the velocities above and within the long spines (E & F; animals purposely disturbed to cause them to withdraw the tentacular crowns into the casing) are shown. Scale bars = 0.5 mm, time interval between trajectory marks = 0.1 s.

Corresponding results for twice the nominal flume flow (Fig. 9B) show the area cleared of particles to be only about 8 times the frontal area of a lophophore, and particles were captured from paths about 1 mm above and 0.5 mm to the sides of the sinks. Due to the higher velocity the net flux in terms of number of particles captured per unit time increased by about 19 % on the average.

DISCUSSION

Using flume experiments and numerical simulation the present study has focussed on the feeding process in small line colonies of bryozoans in a laminar wall layer. Values of the velocity gradient or "shear rate" ($\partial u/\partial y$ = 1 to 4 s^{-1}) correspond to friction velocities or "shear velocities" ($u^* = (\upsilon\ \partial u/\partial y)^{1/2} \approx 3$ to 6 mm s^{-1}) (Vogel 1994) that are similar to those found in the laminar sublayer of turbulent flow over smooth surfaces (e.g. Muschenheim 1987, Fréchette *et al.* 1989, Shashar *et al.* 1996).

Flow pattern

The tracking of small food particles assumed to be neutrally buoyant provided information on both particle capture and fluid motion, because slip between fluid and particle motion was negligible. Experiments have shown how feeding currents distort a laminar wall layer above single-line colonies of a number of bryozoans (*Celleporella*

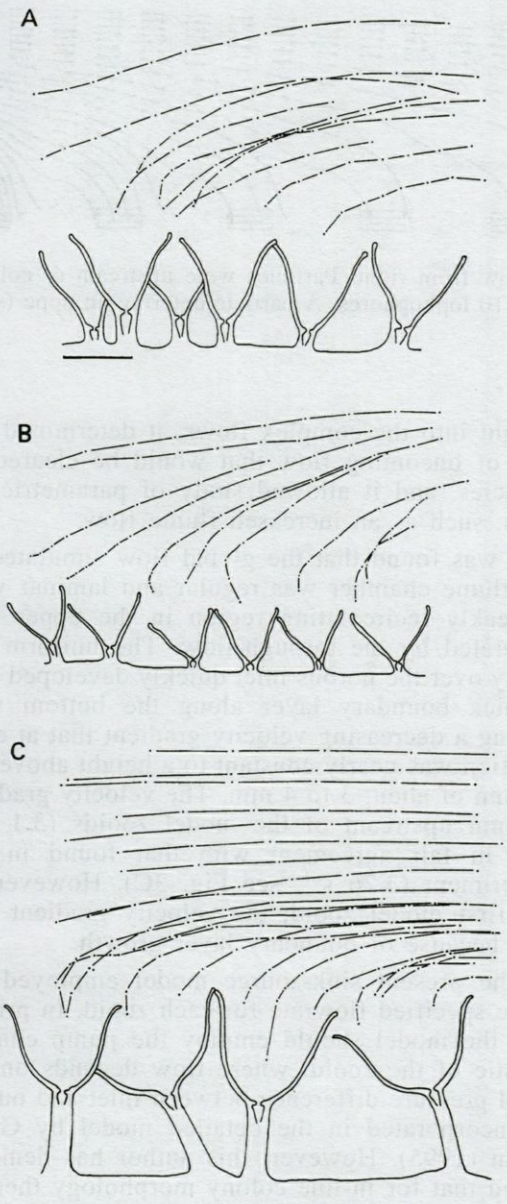

Fig. 5. – Examples of particle trajectories above the lophophores of 3 species of bryozoans in flume. (A) *Alcyonidium hirsutum*, (B) *Membranipora membranacea*, (C) *Flustrellidra hispida*. Scale bar = 0.5 mm, time interval between trajectory marks = 0.1 s.

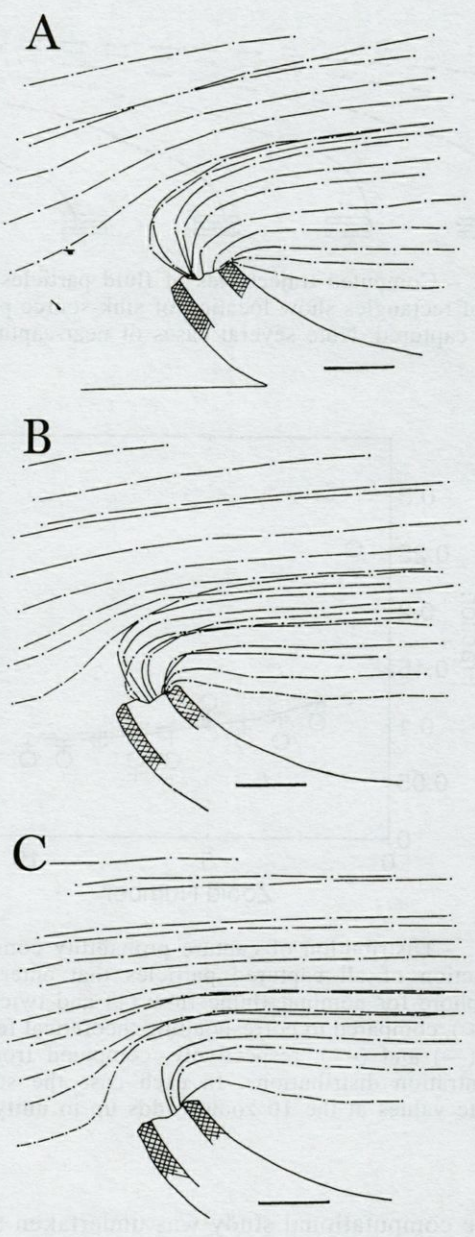

Fig. 6. – Bryozoans in flume replaced by a small glass tip (opening = 0.27 mm) and connected to a thin tube thus enabling siphoning at different flowrates (Q), analogous to the pumping of a bryozoan lophophore. (A) Q = 17 ml h^{-1}, (B) 11 ml h^{-1}, (C) 9 ml h^{-1}. Scale bar = 0.5 mm, time interval between trajectory marks = 0.1 s.

hyalina, Electra pilosa, Alcyonidium hirsutum, Membranipora membranacea, Flustrellidra hispida). Thus, incurrents to lines of 3 to 10 zooids typically distort paths of particles approaching the colony at heights 1 to 2 mm above the level of lophophore inlets and they capture all particles from paths 0.7 to 1.2 mm above the level of lophopore inlets, the higher values applying to the longer colonies of 10 zooids. Paths were observed to curve toward the zooids so that captured particles entered lophophores on nearly vertical paths. In reduced velocity gradients in the wall layer, when spines are present (Fig. 4D), particle paths even reversed direction turning upstream before entering the lophophore. This phenomenon, to be expected for flow to a strong sink, was also demonstrated by recording paths to a glass tip through which water was drawn at increasing volume flows for a fixed velocity gradient (Fig. 6). The number of particles tracked in the experiments was insufficient to deduce results on the per-zooid relative feeding rate.

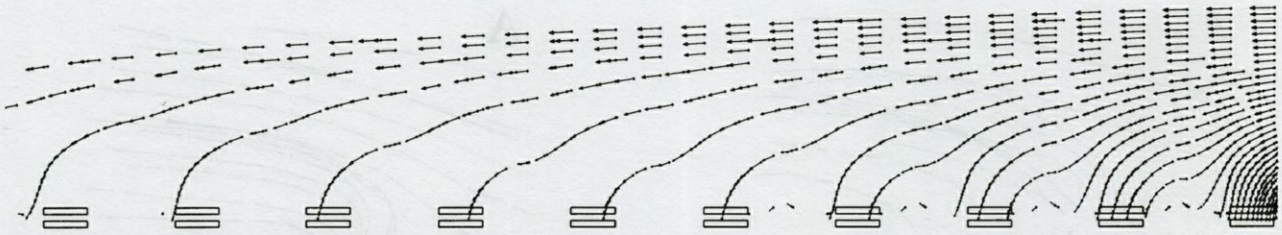

Fig. 7. – Computed trajectories of fluid particles entering with flow from right. Particles were upstream of colony. Pairs of rectangles show location of sink-source pairs representing 10 lophophores. A particle entering an uppe (sink) cell is captured. Note several cases of near-capture trajectories.

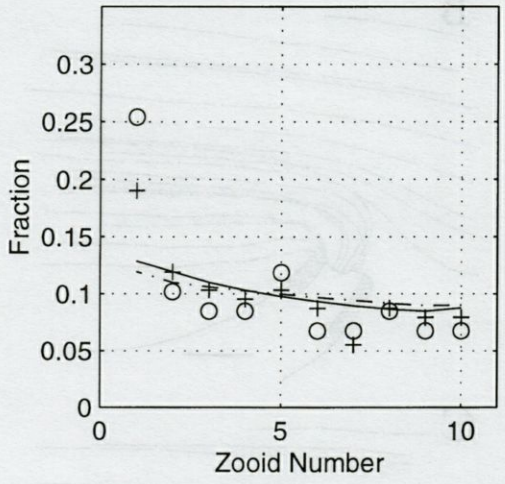

Fig. 8. – Distribution of capture probability computed as fraction of all captured particles that enter each lophophore for nominal flume flow (+) and twice that flow (○), compared to corresponding theoretical feeding rates (—) and (– –), respectively, computed from the concentration distributions. In each case the sum of discrete values at the 10 zooids adds up to unity.

The computational study was undertaken to determine the per-zooid capture rate along a 10-zooid line colony, a situation studied in one experiment (see Fig. 4A). In addition, it provided insight into the complex flows, it determined the part of oncoming flow that would be cleared of particles, and it allowed study of parametric effects, such as an increased flume flow.

It was found that the global flow simulated in the flume chamber was regular and laminar with a weakly recirculating region in the upper part generated by the through-flow. The uniform velocity over the porous inlet quickly developed into a thick boundary layer along the bottom wall having a decreasing velocity gradient that at each location was nearly constant to a height above the bottom of about 3 to 4 mm. The velocity gradient 50 mm upstream of the model zooids (3.1 s^{-1}) was in fair agreement with that found in the experiment (3.26 s^{-1}, see Fig. 3C). However, at the first model zooid, the velocity gradient was less because of boundary layer growth.

The present sink-source model employed the same specified flowrate for each zooid. In principle, the model should employ the pump characteristic of the zooid, where flow depends on the local pressure difference between inlet and outlet, as incorporated in the detailed model by Grünbaum (1995). However, this author has demonstrated that for in-line colony morphology there is a minimal interference (< 4 % for 10 zooids), i.e. each zooid will pump a volume flow essentially as an isolated zooid. This justified the use of the same volume flow for all model zooids.

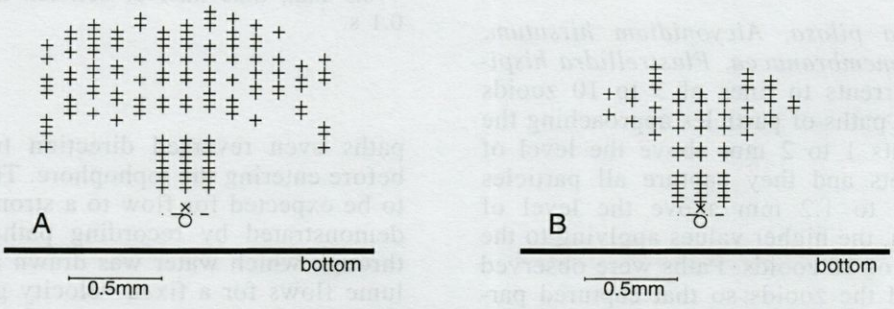

Fig. 9. – Cross section of flow 6.5 mm upstream of 10 zooid line colony, showing starting location (+) of particles captured. Nominal flow (A) and twice that flow (B). Also shown are positions of sinks (×), impermeable cell faces (- —) and sources (○) representing zooids located in sections further downstream.

Above the line colony the flow was systematically distorted due to the sinks, as seen from the particle tracks in the vertical plane through sinks (Fig. 7) being similar to those of the experiment (Fig. 4A). To the sides of each zooid, however, a complex three-dimensional flow prevailed. Downward directed source flows cleared of particles were deflected by the bottom, primarily to the sides of the line colony, creating two vortices of opposite sign aligned with the main flow and aiding the transfer of particles from the sides toward the center. Clearly, the line colony is very special and of simple geometry, but the last mentioned flow features may also be at play along edges aligned with the main flow for the normal geometry of fairly large encrusting bryozoans.

Particles that were started upstream in the vertical (symmetry) plane through sinks tended to stay in this plane (Fig. 7) dispite the induced secondary flows described above. Most of the particles from this and neighboring planes were captured (Fig. 9A), but not all because of the discrete nature of sinks leading to near-capture trajectories (Fig. 7). Particles which started further away from the center underwent complex motion and some were captured. The difference in shape of area of oncoming flow cleared of particles shown in Fig. 9A & B can be explained by the source flow induced vortices being less effective in bringing particles toward the center when flume flow was increased. Vortex centers were located about 0.7 mm above the bottom and about 0.5 mm to the sides of sink-source pairs, thus particles that started near the center of these vortices were not displaced sufficiently to be captured. Asymmetries in Fig. 9A & B are due to sink-source pairs being positioned in a plane offset 0.125 mm from the midplane of the flume chamber. Vacancies in the pattern of starting points of captured particles are due to near-capture trajectories.

Feeding rates

Feeding rates per zooid were computed in two ways; by tracking particles started upstream of the colony and recording those captured at each zooid, and by determining the concentration at each zooid given an upstream uniform distribution. The scatter in computed trajectory results for fraction of particle capture by each zooid (Fig. 8) is due to the small total number. The first zooid has about twice the capture rate of the followings zooids. For the latter, capture rate decreases moderately downstream. The computed results show that the last zooid has a slight advantage over the preceeding ones because it has no competition from downstream zooids. The present results for fraction of particle capture obtained from the concentration distribution do not show the abrupt decrease after the first zooid displayed by the trajectory results. In this regard the results are similar to those of Eckman & Okamura (1998) also obtained from concentration distributions, now for widely spaced lophophores.

The difference between the two computational schemes, although using velocity information from the same discrete mesh, lies with the *apriori* averaging of concentration over cell faces of sinks compared to the very accurate trajectories computed in small increments using interpolated velocities. The latter gives in effect a distribution of the flux of particles over the cell face of each sink. For this reason it is believed that particle tracking provides more realistic results. It dublicates the physical process and shows the sensitivity to upstream starting position of particles.

Both schemes showed that feeding rates increase with increasing flume flow, as also found by Eckman & Okamura (1998), which is to be expected with the associated thinning of the concentration boundary layer and increase in flux of particles. From particle tracking, feeding rate is proportional to the sum of products of captured particles and the velocity at their starting location (Fig. 9) which increases linearly with height above the bottom. At nominal flume flow and twice that value the number of captured particles decreased from 130 to 59, but the velocity gradient increased, leading to an increase in capture of about 19%. From the concentration distribution, feeding rate is proportional to the product of sink flow and concentration, showing a similar increase when flume flow was doubled.

Flow control and spinosity

It has been shown that e.g. *Membranipora membranacea*, within 1 to 2 days after the colony detects a molluscan predator, can produce spines as a mean of defense (Harvell 1990, Grünbaum 1997). But spinosity in *Flustrellidra hispida* has also been found to be highly correlated with the degree of water movement (Whitehead *et al.* 1996). Thus colonies from wave-swept turbulent conditions have more spines than colonies from sheltered habitats. This suggests that spinosity may also be partially controlled by the hydrodynamic environment (Bayer *et al.* 1997). The functional significance of spinosity in *Electra pilosa* (Fig. 4) is obscure; but the spines are too small to produce local turbulence near the lophophores. On the contrary, the spines clearly dampen the flow velocity of the viscous sublayer. The hydrodynamic interference of spines with water transport in the feeding process has recently been studied by Grünbaum (1997) who found that spi-

nation in *M. membranacea* reduced the exponential growth rate in 'fast flow' (1.1 cm s^{-1}).

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