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Summary
Patterns of water flow around steadily beating comb plates of Pleurobrachia pileus were tracked using suspended plastic beads. The positions of the beads and the comb plates in the plane of the central longitudinal axis of the comb row were digitised from high-speed ciné films covering several beat cycles. All of the data from each sequence were combined using a computer program which integrated them into a standard cycle, and the resulting data were plotted by a second computer program to produce charts for different stages in the beat cycle showing the flow velocity at a grid of points. On these charts, contour maps were drawn to indicate the speed and direction of the water flow.

Water is drawn towards each comb row from ahead and from the sides and accelerates strongly backwards in a fairly narrow stream which joins those from the other seven comb rows at the rear of the animal. At a beat frequency of 10Hz the comb plates move with a tip speed of up to 70mm s$^{-1}$ in their effective stroke; they have an estimated Reynolds number of 9 in this stroke. Changes in inter-plate volume between adjacent antiplectically coordinated plates are very important in propulsion, particularly near the end of the effective stroke when pairs of adjacent plates close together and cause the high-speed water from around the ciliary tips to be shed into the overlying stream as a series of jets at speeds of 50mm s$^{-1}$ or more. The antiplectic coordination of the comb plates makes a major contribution to the efficiency of propulsion.

Introduction
Typical ctenophores swim by means of eight rows of comb plates. Each comb plate is a simple rectangular paddle composed of a hundred thousand or more cilia (Afzelius, 1961). Water propulsion during swimming is produced by metachronal waves of beating passing along these rows of plates (Sleigh and Aiello, 1972); these waves are described as antiplectic because they are propagated in the direction opposite to the effective stroke of the beat (Knight-Jones, 1954). Antiplectic metachronism is also common in other swimming animals, e.g. in many crustaceans where pairs of complex lobed limbs move in

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sequence, but the simple comb plates of ctenophores provide a good model in which to study the principles of propulsion by antiplectically coordinated paddles.

Like the cilia of protozoa (Machemer, 1974), the comb plates of typical ctenophores are coordinated mechanically (Verworn, 1890; Sleigh, 1972, 1974), although in lobate forms the ciliated groove between plates is involved (Tamm, 1973). Child (1933) found that metachronal wave transmission could be blocked in *Pleurobrachia* or *Beroe* at a plate that was held stationary, and Sleigh (1972) described how the water drawn behind one plate as it commences its effective stroke lifts the next plate upstream and causes it to beat. This external hydro-mechanical coupling, independent of nervous conduction, allows the beat frequency of a whole comb row to be controlled for experimental purposes by the mechanical stimulation of a comb plate at the downstream end of the row (Sleigh and Jarman, 1973).

Water flows around propulsive structures have been observed and measured for ctenophores (Sleigh and Aiello, 1972), some anchored protozoa (Sleigh and Barlow, 1976) and copepods (Koehl and Strickler, 1981) by tracking the movements of particles suspended in the water. The previous study of *Pleurobrachia* by Sleigh and Aiello (1972) gave only a general picture of the flow because of the low filming rate and the limited ability to follow particles close to the comb plates. It did not therefore allow detailed study of the individual and cooperative contributions of comb plates to the generation of water flow. Improved information is necessary for comparisons to be made of comb plates operating under different conditions, or between propulsion by metachronally coordinated comb plates and metachronally coordinated paddle-limbs (D. I. Barlow and M. A. Sleigh, in preparation). Although better information can be obtained at higher filming rates and with improved illumination, there is still a disadvantage of following individual particles in that their spatial relationship to the propulsive structure changes during the course of the beat cycle as the particles flow through the system. To obtain the more reliable quantitative data that we seek from flow studies, it is important to measure the flow at all points around the propulsive structure at all stages of the beat cycle and to integrate these into a composite picture. This has been achieved by the development of a computer program to integrate data from the tracks of a large number of particles followed at different stages in several beat cycles.

**Materials and methods**

*Experimentation and data recording*

*Pleurobrachia pileus* Mueller were collected from Southampton Water by trawling. All experiments were carried out between April and July when these animals are abundant in this area. Trawled samples were carried to the laboratory in closed 5l jars. Here, healthy undamaged individuals were transferred to fresh filtered sea water (specific gravity 1.030) in a 5l beaker, and this was kept in a cold room at 4°C until animals were required for use.

The ctenophores were immobilised in a small Perspex tank mounted on the stage of a Reichert Zetopan microscope set up for bright field illumination. The animal was carefully gripped between two plastic clamps (Fig. 1), which avoided interference with
the comb rows or apical organ. Toothed clamps were used so that the teeth touched the body between the comb rows. The ctenophore was held so that a comb row could be seen in profile at one side of the animal, with a plane of focus that ran along the centre line of the comb row. The temperature of the tank was regulated by the gentle circulation of chilled sea water, the rate of flow being adjusted to exclude interference with the currents produced by the comb rows.

It was necessary to hold the animal still to follow the motion of water around individual comb plates. This tethering of the organism has an effect on the far-field flow around the

Fig. 1. The method of immobilising *Pleurobrachia*. A slow circulation of fresh sea water was maintained by a pump. The temperature of the sea water could be adjusted. The insert shows how the body of the ctenophore was held between the teeth of the Perspex gripper.
organism because a larger volume of water around the organism is circulated than the volume that would be disturbed as an animal swims through it (Blake and Sleigh, 1974; Higdon, 1979; Childress et al. 1987). This far-field effect is accentuated if the walls of the container are within a few cilium lengths of the organism, but rapidly decreases since in this region the velocity field falls off with the square of the distance (Blake and Sleigh, 1974). In this study the organism is at least 2 cm from the side walls and 5 cm from the end walls of the tank; although the depth of water above and below the ctenophore was limited to 1 cm for optical reasons, these surfaces are further than this from the plane in which the comb plates beat. The effect of tethering and the tank walls on the near-field flow around the comb plates, which is of prime interest here, is much less significant, but is probably worthy of further hydrodynamic study.

The beat frequency of the comb row under observation was regulated by the method of Sleigh and Jarman (1973). A fine glass needle attached at its base to the arm of an electromagnetic relay switch was placed with its tip against the shaft of the first comb plate at the aboral end of the comb row (Fig. 1). The microneedle depressed the comb plate towards the body surface and the comb plate responded with an effective stroke which triggered a wave of activity that was transmitted along the row. Observations were made on comb plates farther along the row, remote from the influence of movements of the microneedle itself.

Saran microspheres (Dow Corning) were introduced into the water around the animal so that particle tracks could be followed in the water flows. The beat patterns of a group of comb plates, their metachronal coordination and the movements of particles in the water around the plates were recorded on 16 mm film using a Mitchell high-speed ciné camera operating at 300 frames s⁻¹. An analysis projector was used to project the film onto the screen of a digitiser–plotter interfaced to a teletype terminal and paper tape punch to record the x and y coordinates of the positions of the plates and of the particles from successive frames of the film. This work was commenced some years ago, and if it were to be started now we would use a simpler and quicker computer-based digitising system, avoiding the need for paper tape.

Method of computation for analysis of flow patterns

The data obtained for use in mapping flows consisted of x,y coordinates of the positions of one or more comb plates and of numerous surrounding particles in relation to two fixed points on the antero-posterior axis of the animal, which provided both a reference line and a length scale for use in the computer program. These data were collected from consecutive frames of the film, the framing rate of which was indicated by timing marks along the edge of the film, and was also entered in the computer program. The number of data points in one series varied from 200 to 1000; 43 series of frames have been analysed.

The program calculated in three dimensions (x, y and time) the successive positions of all particles followed in a film covering 3–5 cycles of beat. The position on each frame within its cycle was integrated into one standard cycle. The framing rate of the film permitted calculation of the instantaneous velocities of the particles at any time within the cycle. The program was written in BASIC (by R.J.W.) and run on a DEC PDP 11/45 computer. Data processed by this program were transferred to a FORTRAN plotting
program which used a two-dimensional interpolation routine (Shepard, 1968) adapted (by R.J.W.) to interpolate a third dimension (time). This program was run on an ICL 2970 computer. (The programs used are available from R.J.W.)

Flow direction was plotted as arrows over a 40×40 point grid by interpolation between the velocities of the particle data points. Shepard’s method uses the average and derivatives of a set of 4–10 data points near to the required grid point, weighted by distance from the grid point. The formulae generalise easily to three (or more) dimensions. His algorithm uses a simple unweighted average if several data points are very close to the grid point and uses derivatives to adjust the weights to improve the estimation of the slope of the fitted surface. We fitted surfaces for the x and y component of water speed, then calculated velocity and direction from these components. There was a limit on the time axis to points within 0.1 cycle of the grid point in question. A series of contours showing water speed was superimposed on the direction grid. Maps drawn in this way provided the average flow over a period of 0.2 cycle. These limits were adjustable, but were considered to be accurate enough for the estimates required in this analysis.

The program permitted the integration of data from a very large number of particles, including measurements on distinctive particles visible in only two successive frames in rapidly changing flows, to produce accurate summary pictures of the flows from films in which patterns of particle movement appeared complex. The aim of this procedure was to give a statistically valid reconstruction of the flow and not a comprehensive hydrodynamic model. The accuracy of the result depended on the density of the data points, which could make this method laborious; however, in areas of uniform flow it was only necessary to measure coordinates for a few particle tracks, allowing data collection to be concentrated in areas where flows changed rapidly over short distances or short times.

The interpretation of the maps produced by the program requires a short explanation. Recording flows on film inevitably reduces all information to two-dimensional projections. Therefore, the maps produced from the analysis only provide the components of direction and speed that exist in the plane of observation. Since the organisms themselves are three-dimensional structures, the flows around them must also be three-dimensional. This results in maps that show closed contours as though there were small ‘packets of water’ flowing through the frame of view at different velocities, which could not occur in an incompressible fluid like water. Closed contours indicate that the flow has a three-dimensional character, i.e that there is a component moving into and out of the plane of view, and thus that water is being funnelled inwards upstream of the power source and spreading out downstream. The low Reynolds number and viscous forces ensure that the flow is laminar. It was an assumption of this analysis that contours represent a cross section through the fastest region of flow in a plane along the axis of an approximately circular jet. Observations of the type shown in Fig. 4B confirm that the jet is circular, rather than elliptical, in cross section; it is only from this view that the cross-sectional shape of the jet can be seen. By measuring the velocity profile close to the power source (the comb plate) in the region of peak flow, it was further assumed that the velocity component in a plane perpendicular to the axis of flow was negligible. The successful portrayal of even the local flows in these flow maps was regularly confirmed by comparing what is shown in the maps with repeated examination of the projected film.
Numerous individual measurements of particle velocities are entirely consistent with velocities portrayed at corresponding positions on flow maps.

Results

The beat cycle of *Pleurobrachia* comb plates beating at 27Hz is shown in Fig. 2. The basic cycle for each comb plate consists of an effective stroke when the whole plate swings stiffly about its base from right to left through an angle, quoted by Sleigh and Jarman (1973) as approximately 140°; in this study the average value of this excursion angle was $135 \pm 15.5^\circ$ ($N=46$). Once the comb plate reaches the end of this initial swing, a bend is propagated from the base to the tip of the plate. Sleigh and Jarman (1973) recorded rates of propagation between 6 and 18mm s$^{-1}$, depending on the frequency of beat; in this study a wider range of temperatures and frequencies has been used and rates between about 5 and 35mm s$^{-1}$ were found. This bend causes the plate to swing backwards on its base, and the structure unrolls itself back to the starting position close to the animal’s surface ready for the next beat. At high frequencies the plate may begin the next effective stroke immediately, or even before the recovery stroke has been completed, while at low frequencies the comb plates may come to rest in a pause or resting phase before the next cycle of activity begins. The starting and finishing points of the effective stroke have been defined by the start and finish of the forward swing of the base of the comb plate, irrespective of the state of the recovery bend.

Fig. 3A shows successive profiles of a single comb plate beating at 10Hz. Alongside the profiles is a plot of the change in the tip speed of the comb plate during the course of the cycle (Fig. 3B). The cycle is expressed on a scale of 0 to 1 of the cycle time; in this case the cycle time is 100ms. The dots are the measured speeds taken from digitised information from five cycles of the comb plate and plotted as one cycle. It can be seen from these superimposed data points that the beat is very regular when the beat frequency is controlled by a mechanical stimulator triggering a comb plate downstream of the photographed section. The first peak shows the change in speed during the effective stroke, whilst the second flatter peak shows the speed of the tip during the recovery stroke. The tip does not stop moving between the effective and recovery strokes, but only changes its direction; to emphasise this point, speed was plotted in preference to velocity. The traced profile nearest to the end of the effective stroke is marked with an arrow on the plot for reference. The broken line shows the relative position in the cycle of the phase-shifted speed profile for the next comb plate in the metachronal wave.

The speed of the comb plate changes continuously throughout the cycle and most markedly during the effective stroke. The comb plates reached their maximum speed when they were perpendicular to the surface of the animal (Fig. 2G). The change in inter-plate volume throughout the cycle is shown in the graph in Fig. 2.

Fig. 4 gives a diagrammatic summary of the flow observed around a single *Pleurobrachia* tethered as illustrated in Fig. 1. Viewed sagittally (Fig. 4A), particles in the water could be seen moving rapidly in the aboral direction close to the surface. More distant from the surface, particles could be seen being funnelled in towards the comb
Fig. 2. Comb plates of *Pleurobrachia* beating at 27Hz (20°C). The frames are printed from 16 mm film shot at 290 frames s⁻¹, and show the character and magnification of the film frames used for analysis. The time interval between successive frames is 3.5 ms. At this frequency, recovering comb plates start their effective stroke before the recovery bend has reached the tip of the comb plate (arrowed in A). The inset graph shows the relative expansion and compression of the space between any two adjacent comb plates (interplate space) during the cycle, expressed as a percentage of the maximum volume reached. The y-axis of the plot expresses the volume as a percentage of the maximum. The x-axis is the cycle time from 0 to 1. E is the effective stroke and R the recovery stroke of the leading plate. Frame E shows the suggested pressure distribution within the interplate spaces at an instant when two comb plates in the effective stroke are travelling at the same speed; the space between them has reached maximum volume, so there is no pressure difference (0P). Some spaces are getting larger and water is being drawn in (−P), whilst others are getting smaller and expelling water (+P). Frame G shows the pressure distribution within interplate spaces when the arrowed comb plate has reached maximum speed. The scale bar represents 1 mm.
When the animal was in ‘fast forward’ motion (Tamm and Moss, 1985), with all the comb rows propelling the animal forward, a stream of rapidly moving water could be seen at the aboral end, as shown also in free-swimming ctenophores by Matsumoto (1991).

Between the comb rows, water was drawn in relatively slowly towards the surface of the animal and posteriorly (towards the aboral end) until it reached the vicinity of the comb plate. At this point the water was accelerated strongly backwards and flowed too fast to see without recourse to high-speed ciné photography. Viewed from the aboral end (Fig. 4B), in optical section at about the level indicated in Fig. 4A, the particles could be seen being drawn in from all around each comb plate. In the shaded area extending beyond the tips of the comb plates, particles are seen travelling straight towards the observer in an approximately circular jet. The main disadvantage of the sagittal and aboral view points shown in Fig. 4, for detailed study of flow, was that it was very difficult to see the flow between the individual comb plates and to relate flow to the movement of the propulsive structures. The view shown in Fig. 5, from the side of the comb row, gave a good optical section through the fastest regions of the flow above the comb plates and in between them.

An example of a set of computer-generated maps of flows around a row of comb plates beating at 10Hz is shown in Fig. 5. We have plotted 23 sets of such data for six animals and partially analysed another 23 film sequences under a range of different conditions of temperature and frequency, and they all show the same general character (D. Barlow and M. A. Sleigh, in preparation). The maximum tip speed in the effective stroke in Fig. 5B,C is about 70mm s⁻¹. At a frequency of 10Hz, the minimum flow rate, reached at the end of the resting period, is still 20–30% of the maximum tip speed; this can be seen at the right-hand side of Fig. 5A and the left-hand side of Fig. 5D. In Fig. 5A, comb plates 1 and 2 are just starting their beat cycle, and water at the tips of both plates is accelerating and being drawn down between them; the influence of the accelerating comb plate extends upstream, so that the water is already starting to speed up at a point two plates upstream of comb plate 1.

Fig. 3. (A) Profiles of a comb plate at 6.3ms intervals taken from a film of comb plates driven at 10Hz (at 20˚C). (B) The tip speed of one individual comb plate at different times during several successive cycles (dots) is shown superimposed on the beat cycle of the next comb plate in the metachronal sequence (broken line). The arrow indicates the profile nearest to the end of the effective stroke.
Fig. 4. Summary diagram of the far-field flow around *Pleurobrachia*. In the lateral view (A) water is funnelled in towards the comb plates with regions of high-speed aboral flow forming at the comb plate tips. The aboral pole view (B), at the focal plane shown by the line X—X in A, shows slow water flow between and around the plates where particle movements could be followed by eye. The shaded areas are regions of maximum flow, directed towards the observer. *ao*, apical organ; *cr*, comb row; *cg*, ciliated groove.
By 50ms after this beat starts, the wave has travelled along the comb row to plates 4, 5 and 6 (Fig. 5C). A stream of water has developed tangential to the animal’s surface with maximum water velocities in the region of the ciliary tips. The space between plates 4 and 5 is decreasing and high-speed water is being shed into the main stream. Relatively small volumes of high-speed water are very obvious. Indeed, one reason for the observed variability of the ratio of water speed to plate tip speed may be that the small volumes of
high-speed water are ejected from the central point of the inter-plate space, with the result that slight variations in focus can cause the regions of highest flow to be missed. The computer program does not extrapolate above the maximum velocity observed and so to
achieve a contour line the program must detect one or more data points greater than the contour value.

Once the water has been propelled clear of the inter-plate space, the energy of the flow is dissipated downstream. Fig. 5D shows the flow after a further 25ms when the wave of activity has passed. A fast-moving exit stream can be seen at the right of the picture, bounded by the 15mm s\(^{-1}\) contour line. This stream of water decelerates towards the left of the picture as energy is dissipated into the far field. However, water can still be seen travelling at 10mm s\(^{-1}\) right to the edge of the frame. Flows at this speed are present continuously throughout the cycle at this frequency of beat, unlike at low frequencies where the flow stops between beats (D. Barlow and M. A. Sleigh, in preparation).

The passage of the recovery wave (Fig. 5D) causes the reversal of water flow between the comb plates, but the effect of the backward movement of plates does not extend beyond the comb plates to any extent. The water enclosed between two adjacent plates is carried bodily during the recovery stroke so that the speed of water flow between the plates is not dependent upon the tip speed of the individual comb plates, but on the average speed of movement of the comb plates bordering the space. The speed and volume of water transported in recovery are very low compared to the speeds and volumes transported in the effective strokes.

It is apparent that the regions of highest water flow are closely associated with the comb plate tips. Flow reaches its maximum speed at the same time as the associated plates reach their maximum velocity. That occurs when the plate is roughly perpendicular to the animal’s surface (Fig. 2).

**Discussion**

It has been suggested that antiplecetic metachronism may be responsible for the progressive acceleration of water to a much higher sustained speed than would be possible with a single paddle (Sleigh and Barlow, 1980). Whilst the data show that water is not accelerated beyond the tip speed of the comb plate, they do imply that antiplecetic coordination may increase the mechanical efficiency of the plate in two ways: first, by reducing drag losses due to backflow during the acceleration of each plate and, second, by reducing energy losses during the deceleration of the plate by increasing the shedding of water into the outflow at its maximum speed.

The flow that can be seen from the maps (Fig. 5) is in general as described by Sleigh and Aiello (1972). By combining this information with the patterns portrayed in Fig. 4 we can infer that water is drawn in behind each comb plate, from the sides and from above, in the filling phase at the start of the effective stroke, and jetted out posteriorly by the expulsion of water from between the plates towards the end of the effective stroke (Fig. 6). The predicted development of flow around the comb plates and especially around their tips is summarised in Fig. 6. The flow patterns shown suggest that it is important to consider how the interaction of adjacent plates contributes to the efficient functioning of the system.

Each comb plate acts as both a leading and a trailing comb plate at the same time. One comb plate starts its effective stroke when the plate ahead is at its maximum acceleration
(Fig. 3B); the increase in inter-plate volume as the plates separate draws particles and water into the inter-plate space. Suction, whose existence is inferred by the particle motions, is assumed to lift the lower plate and is probably the triggering stimulus (Sleigh, 1972; Tamm, 1973, 1984). Once this plate has been triggered, the inter-plate space behind it is similarly subjected to negative pressure and fills with water as it starts its effective stroke. As the trailing plate accelerates, the suction force in the space ahead of it diminishes until the plate reaches the same velocity as the leading plate (Fig. 2E). At this point the inter-plate volume reaches a maximum and the inter-plate pressure is zero. However, as shown in the speed profile (Fig. 3B), that point is transient and the leading comb plate is already decelerating. It is inferred from particle movements that, before any comb plate passes its maximum speed, the pressure in the inter-plate space ahead of it becomes positive whilst that in the inter-plate space behind it is negative (Fig. 2G). The inter-plate space ahead of a decelerating comb plate would then remain in compression until the end of the effective stroke and pressure in the inter-plate space behind it would increase as the trailing plate catches up.

Each inter-plate space therefore acts like a simple pump with a continuously expanding and shrinking volume. During the suction phase the comb plates are pointing upstream and as the inter-plate volume expands it fills with water from ahead. During the compression phase, the comb plates pivot to point downstream and so water is ejected to the rear. In this sense the row of comb plates acts rather like a paddle wheel. However, compression of water between the comb plates during the second half of the effective stroke leads to a jetting effect, confirming the suggestion by Sleigh and Aiello (1972).

The flow is affected by the Reynolds number ($Re$) of the system. The $Re$ can be deduced for cilia beating in water from the formula:

$$Re = \frac{\omega l^2 p}{\mu},$$

Fig. 6. Diagram summarising the water flow around comb plates of *Pleurobrachia*. Arrows show general directions of input and output flows; broken lines indicate the development of the flow at the comb plate tip and how it is shed into the water. Further details are given in the text.
where $l$ is the length, $\omega$ is the angular velocity of the structure and $\rho$ and $\mu$ are the density and dynamic viscosity, respectively, of the water (Blake and Sleigh, 1974). For comb plates with an average length of 0.8mm, beating at 10Hz, the average radian frequency in the effective stroke was $100 \, \text{s}^{-1}$ ($N=16$) and the $Re$ was 9. At this $Re$, inertial forces dominate, but viscous forces may not be totally neglected. At other stages of the beat, when the comb plate is moving more slowly, $Re$ will fall to less than 1.

If the comb plates act as paddles then one might expect the tip, as the fastest moving point, to generate the fastest flows. As the speed of a comb plate increases, the water most closely associated with the plate accelerates the most. As the plate tip accelerates, high-speed water developed at the tip trails behind it into the inter-plate space, which is under suction (see Fig. 5C). Maximum water speeds are therefore less than the plate tip speeds, especially where tips are frayed. The highest speed flows are seen around the ciliary tip at the start of the effective stroke (e.g. comb plate 6 in Fig. 5C) and in the trailing inter-plate space in the later stages of the cycle (e.g. behind plate 3 in Fig. 5B); this effect becomes most apparent at higher frequencies, where the Reynolds number is even higher and the water more easily separates from the plates. This result is achieved in the manner shown in Fig. 2, where pressure changes can be inferred from the constantly changing volumes enclosed between a pair of adjacent plates. When the leading comb plate starts to decelerate, pressure in the inter-plate space behind it increases as the trailing comb plate catches up. The inter-plate space ahead of the leading comb plate is already under pressure so the effect is for water to be ejected along the length of the comb plate from both inter-plate spaces (e.g. around plate 4 in Fig. 5C). The resultant ejection of water from the inter-plate spaces during the second half of the effective stroke apparently does not accelerate it to speeds higher than those already present at the tip of the plate, but the high-flow region separates from the decelerating comb plate tip and is shed into the main flow stream.

At the peak of the effective stroke the Reynolds number of a comb plate is about 9 at 10Hz; this means that the inertial forces are approximately ten times the viscous ones. The inertia confers a tendency for the boundary layer of high-speed water at the tip of the comb plate to separate during the acceleration phase and trail behind. However, as the Reynolds number falls during the deceleration of the comb plate, the effects of viscosity will become more significant. This will result in an increased tendency for water to stick to the plates. Both of these effects would result in drag on an isolated paddle.

In the case of single ciliary units, the wall effect is regarded as an important factor in preventing the fluid that is transported downstream by a cilium in the effective stroke from being dragged back upstream during recovery. Comb plates are much larger and the viscous drag exerted by the surface of the animal’s body is probably much less; Blake and Sleigh (1974) found that even at low $Re$ the effect of the cilium dominated over that of the body wall in a periciliary zone of radius equal to half the height above the body surface. However, boundary effects around the comb plates themselves may well still be important. It is possible that the antiplectic nature of the coordination creates an advantage here. By having the next plate in the sequence start to accelerate slightly behind the leading plate, the negative pressure in the trailing inter-plate space (Fig. 2) keeps the water shed from the comb plate tips within the radius of the comb plate at its
trailing edge. Thus, water lost from one comb plate can be captured and accelerated by the
next plate in the metachronal sequence. Then, as each comb plate decelerates during the
second half of its effective stroke, the increasing pressure in the inter-plate space creates a
squeezing effect that may facilitate the shedding of the higher velocity water created at
the tip into the main outflow at the maximum speed; this occurs at a time when the
decreasing Reynolds number of the decelerating comb plate might be expected to result in
deceleration of the water through viscous effects. This is what Sleigh and Aiello (1972)
detected as the ‘jetting’ of water. A more obvious separation of the water from the comb
plates occurs at higher frequencies, where inertial effects are even more dominant, as
discussed by D. Barlow and M. A. Sleigh (in preparation). However, the flow is still
laminar, and there is little evidence of turbulent flow around the comb plate tip even at the
maximum frequencies of beat.

These observations indicate that the arrangement of the plates in antiplectic
coordination not only smooths out the intermittent flows from the individual propulsive
units but also enables them to impart a greater momentum to the water than would be
achieved with an equivalent number of single plates because they cooperatively capture
‘partly accelerated’ backflow around each plate.

In *Pleurobrachia* the comb plates are separated by a distance of over half of the length
of a comb plate. Separation of the bases must reduce the jetting effect of acceleration
during compression. Several experiments have been performed on *Pleurobrachia*
(Sleigh, 1972, 1974) and other non-lobate and lobate ctenophores (Tamm, 1973) to
determine the effect, on wave transmission, of blocking the movement of comb plates,
cutting the surface of the animal between plates and even spacing out the comb plates.
However, as yet, no one has reported the results of reducing the inter-plate spacing. We
conclude that the coupling forces generated between comb plates that are too close
together may well result in synchronisation of the beating of adjacent comb plates and
loss of the main benefits of antiplectic coordination.

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