Fluid Flow through Filtering Appendages of Insects

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Many organisms use structures composed of arrays of cylinders to capture particulate food or molecules from the water or air around them. The performance of such filters depends on the velocity of fluid movement through them; hence, mathematical models of flow through fibrous structures can provide insights about the functional morphology of biological filters. In this paper, the authors address the case of feather-like biological filters of finite width and assess several possible models for fluid motion through them by comparing model predictions with observational data. Two examples of insect appendages are considered: the cephalic fans of black fly aquatic larvae that capture particulate food and the antennae of adult male moths that catch sex-attractant molecules released by female moths. The results suggest that flow through such structures can be much slower than ambient currents, that the finest hairs in the structure are the morphological features with the greatest effect on leakiness, and that the velocity of movement (or of ambient flow), as well as the morphology of such filters, can be critical in determining their performance.

1. Introduction

Many organisms use structures composed of arrays of cylinders to capture particulate food or molecules from the fluid (water or air) around them (for reviews, see, for example, Jørgenson, 1966, 1983; LaBarbera, 1984). The work of biologists studying the ecology, anatomy, physiology, or evolution of organisms utilizing such fibrous particle-catching structures would be much enhanced if we knew the mechanisms by which these filters operate, as well as how the differences in filter morphology observed for various species might affect their performance. The performance of filters depends on the flow of fluid around and through them as they are moved or held in ambient currents (Spielman, 1977). Therefore, the first step in understanding the functional morphology of biological filters is to determine which aspects of their structure affect the motion of air or water through them. Hence, mathematical models of fluid motion through arrays
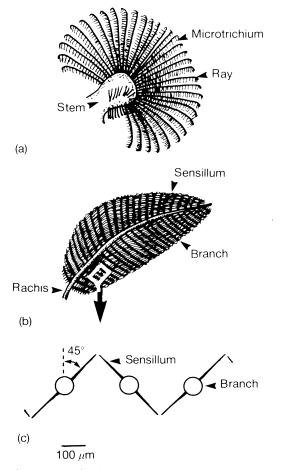
FIG. 1. Simplified diagrams (not to scale) of examples of feather-like filters of insects (dimensions are given in Table 1): (a) cephalic fan of an aquatic larva of the black fly *Similium vittatum*; (b) antenna of an adult male moth, *Acitas luna*; (c) magnified cross-sectional view of the portion of the antenna indicated by the rectangle in (b).

of cylinders or through porous plates should provide insights into the functional morphology of biological filters.

Many biological filters are feather-like in structure; that is, they are appendages of finite width composed of a stalk supporting a more-or-less planar array of cylinders, each of which bears an array of smaller cylinders (Fig. 1). The objective of the present study is to evaluate several models for the fluid flow through feather-like filters by comparing their predictions with observational data. We focus on two specific examples: the cephalic fans of aquatic black fly larvae and the antennae of adult male moths.

2. Some background about flow through filters

Reynolds number Re, which represents the ratio of inertial to viscous forces for a particular type of flow, is given by $Re = ulp/\mu$, where u is the velocity, l a linear dimension characterizing the size scale of the type of flow, and ρ and μ the density and viscosity, respectively, of the fluid. The fibres in both man-made and
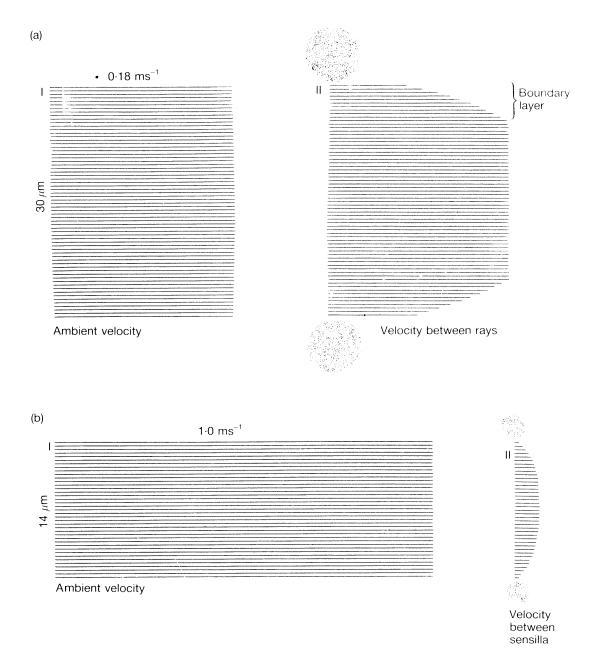
FIG. 2. Fluid velocity vectors of ambient flow compared with velocity vectors of flow between a pair of cylinders. Leakiness is calculated by dividing the area of the velocity profile between the two cylinders (area II) by the area of the ambient velocity profile in a region of equal width to the gap between the cylinders (area I). (a) Water flow calculated using the model of Cheer & Koehl (1987) between the rays of the cephalic fan of the black fly *Similium vittatum* if the microtrichia are ignored ($Re = 0.9$ for a ray; leakiness = 92%). (b) Air flow between the sensilla of the antenna of the moth *Acitas luna* calculated using technique 4 described in the text. Ambient wind velocity is $1.00 \, \mathrm{m \, s}^{-1}$, and u_s through antennal branches (i.e. the velocity encountered by the sensilla) is calculated to be $0.48 \, \mathrm{m \, s}^{-1}$ ($Re = 0.01$ for a sensillum; leakiness = 10.7%). The velocity vectors in (a) and (b) are not drawn to the same scale.

biological filters generally operate at low Re's, calculated using the fibre diameter for l (Davies, 1973; LaBarbera, 1984); hence, viscosity is more important than inertia in determining the flow around these cylinders.

When a viscous fluid flows over a solid surface, the layer of fluid in contact with the surface does not slip with respect to the surface. Therefore, a velocity gradient develops between the surface and the freestream flow (Fig. 2a). The same is true for an object moving through a stationary fluid; that is, some fluid sticks to and moves along with the object and a velocity gradient exists in the fluid around it. The lower the Re, the more gentle is this velocity gradient and the thicker is this sheared layer with respect to the dimensions of an object. Thus, for an appendage of finite width made up of an array of cylinders that operate at $Re \ll 1$, little fluid moves through the gaps between adjacent cylinders; the appendage functions more like a paddle than a rake (Cheer & Koehl, 1987). We define the 'leakiness' of an array of cylinders as the ratio of the volume of fluid per unit time moving through the gaps in the array to the volume of fluid per unit time that would move through those same gaps at freestream velocity if no boundary layers existed (Fig. 2).

The fluid flow through, and the particle capture by, fibrous filters have been modelled in various ways (for reviews, see, for example, Fuchs 1984; Davies, 1966; 1973; Rubenstein & Koehl, 1977; Spielman, 1977; Murray, 1977). Filters are able not only to sieve particles out of the fluid passing through them, but can also collect particles smaller than the width of the gaps between fibres by a variety of physical mechanisms. The efficiency of particle capture by a fibre in a filter is the ratio of the number of particles per unit time captured by a fibre to the number of particles per unit time that would be carried by the fluid through the space occupied by the fibre if the fibre were not there. The efficiency of capture of particles of different characteristics can be affected by flow velocity. For example, the inertial impaction of large, dense particles on to the fibres in a filter is enhanced as velocity is increased. In contrast, the efficiency of diffusive deposition of small particles and molecules on to the filter goes up as the flow slows down. Some interesting trade-offs must be considered in filter design. For example, a filter having many fibres per unit area presents more sites for collecting particles, but has a lower flux of particle-laden fluid through it than does a less dense, leakier filter of the same area. Furthermore, although faster flow carries more particles per unit time through a filter, the efficiency of capture of small particles is reduced and the chance that captured particles will be blown off the fibres is increased.

To understand the physical mechanisms by which biological filters collect particles or molecules, and to sort out how the morphology of these filters affects their efficiency and selectivity of particle capture under different conditions, we must explore how water or air moves through and around the filters.

3. Biological background

In this paper, we consider two specific examples of biological filters, both of which are feather-like structures on the bodies of insects: the cephalic fans of black fly aquatic larvae and the antennae of adult male moths.

3.1 *Cephalic Fans of Black Fly Larvae*

Certain groups of insects have aquatic larval forms that make their living by filtering particulate matter out of the water (for reviews, see Wallace & Merritt, 1980; Merritt & Wallace, 1981; Merritt *et al.*, 1984). One such insect, which has received considerable attention because the adult form is a pest which bites man, is the black fly. The feeding behaviour, diet, and distribution in rivers and streams of black fly larvae are reviewed in Kurtak (1978), Ross & Craig (1980), Craig & Chance (1982), and Chance & Craig (1986). These larvae attach the posterior ends of their abdomens to the substratum and, in flowing water, are pushed over by the current so that their heads are downstream. Black fly larvae have large feathery mouthparts called cephalic fans (i.e. head fans) that they spread in the current to capture suspended detritus particles and microorganisms (Fig. 1a). Several lines of evidence suggest that water velocity affects particle capture by black fly larvae. With a faster flow, more particles are suspended in the water and the flux of water past a larva is greater (for a review, see Craig & Chance, 1982). However, the efficiency of particle retention by the cephalic fans decreases as water speed increases, especially for large particles (Kurtak, 1978). The efficiency of capture of particles of different sizes as a function of water velocity has been found to vary from species to species. Larvae of various species show preferences for specific flow microhabitats, and it has been suggested that these relate to species-specific differences in the structure of the cephalic fans (Kurtak, 1978; Craig & Chance, 1982).

3.2 *Moth Antennae*

Many animals communicate via odours (Bossert & Wilson, 1963). A pheromone is a chemical released by an animal that elicits particular responses by other members of the same species. An example of such olfactory communication is the sex-attractant pheromone released by female moths to lure males. A large proportion of the sensory receptors on the feather-like antennae (Fig. 1b) of male moths are specialized for the female pheromone. If the antennae of a male collects sufficient sex-attractant molecules, he flies upwind in search of the female (Vogel, 1983; Schneiderman *et al.*, 1986). The male moves to the vicinity of the female by the process of anemotaxis: he flies upwind if activated by the pheromone, but flies laterally if the pheromone concentration falls too low (Bossert & Wilson, 1963; Schneiderman *et al.*, 1986).

Male moths can respond to low concentrations of female pheromone (Schneider, 1969; Murray, 1977). Adam & Delbruck (1968) and Murray (1977) have modelled the diffusion of molecules to receptor sites on the moth antenna, invoking three-dimensional diffusion to get the molecules in the vicinity of the sensory hairs, and then two-dimensional diffusion along the hairs to get the molecules to the receptor pores. They suggest that moth antennae are extremely efficient filters, collecting nearly all of the pheromone molecules in the air passing through them. However, the antenna of the silkmoth *Bombyx mori* has been measured to collect only 27% of the pheromone molecules in an airstream of the same cross-sectional area as the antenna (Schneider, 1969). Vogel (1983) has

suggested that this discrepancy arises because much of the airstream encountering a moth antenna flows around rather than through it.

Several studies have suggested that air speed should have important effects on the ability of male moths to sense the chemical signals of the females. The effects of wind speed and turbulent diffusion in the habitat on the distance from which a male can be attracted have been modelled by Bossert & Wilson (1963), who predicted that faster winds reduce the range. At the level of the feather-like antenna itself, the experiments of Vogel (1983) showed that the percentage of air moving through rather than around an antenna becomes greater as wind speed (or flight velocity) increases. However, Murray (1977) has pointed out that increased air velocity in the vicinity of the sensory hairs of antennae will decrease the efficiency of pheromone capture by reducing the time period during which molecules can diffuse to the receptors. The trade-off between an increase in volume of air processed per unit time and a reduction in efficiency of molecule capture as wind speed is increased may explain the finding of Kaissling (1971) that the percentage of pheromone molecules collected by antennae was independent of air velocity (Vogel, 1983).

4. Some methods of calculating flow through feather-like structures

A number of techniques can be used to calculate the flow through feathery filters composed of rows of cylinders, each of which bears arrays of smaller cylinders. Reviews of methods that have been used to calculate fluid motion through mesh-like structures can be found in Fuchs (1964), Davies (1973), Laws & Livesey (1978), and Silvester (1983), for example. We will summarize here a few approaches that are relevant to the insect filters described above.

4.1 *Murray's Model*

In his analysis of pheromone collection by moth antennae, Murray (1977) modelled air motion around a sensory hair (sensillum) (Fig. 1b) as low-Re flow around an isolated cylinder. He discussed how neighbouring sensilla would reduce the air velocity in the vicinity of a sensillum, thereby increasing the time allowed for molecules to diffuse to the hair's surface. He incorporated this phenomenon into his model by increasing the particle-capturing efficiency of the sensillum, using approximations described in the literature about aerosol filtration (Fuchs, 1964; Davies, 1966).

The other models summarized below specifically address the question: What fraction of the fluid encountered by a feather-like structure passes through the structure rather than flowing around it?

4.2 *Silvester's Model*

Another possible approach to calculating the flow through a feather-like filter is to use the approximation of Silvester (1983) for fluid flow through silk filtering nets spun by certain aquatic insect larvae. Such a net is a rectangular mesh

composed of two rows of parallel fibres at right angles to each other. A feathery structure might be considered a net: the large cylinders would be analogous to one row of fibres in the net, and the smaller hairs they bear would be analogous to the other row of fibres perpendicular to the first row. Silvester derived an expression for the pressure drop across a planar rectilinear array of fibres by modifying the equations of Tamada & Fujikawa (1957) for an infinite row of evenly spaced cylinders. He then used this pressure drop to estimate the average flow speed through the net for a given ambient current by treating the net as a porous disc of finite width in high-Re flow.

Silvester's (1983) analysis yields the following equations for calculating the mean speed u_s through a net exposed to an ambient current of speed u_0. A measure of the filter's porosity is the filter area h_e per unit length of fibre, which is given by

$$h_e = h_1 h_2 / h_1 + h_2, \tag{4.1}$$

where h_1 and h_2 are the centre-to-centre distances between the larger fibres and the smaller hairs, respectively. The pressure drop R across the filter per unit speed is given by

$$R = 8\pi\mu / h_e \Lambda_e, \tag{4.2}$$

where μ is the dynamic viscosity of the fluid, and Λ_e is given by

$$\Lambda_e = -\ln \beta - 1\cdot53 + 2\cdot09\beta - \beta^2 \cdots, \tag{4.3a}$$

where β is given by

$$\beta = \pi a^2 / h_e^2, \tag{4.3b}$$

where a is the radius of the slimmest hairs in the net. Then the mean velocity in the filter is given by

$$u_s = [(R/\rho)^2 + u_0^2]^{\frac{1}{2}} - R/\rho, \tag{4.4}$$

where ρ is the density of the fluid. The fraction of fluid encountering the net that flows through it is then given by u_s/u_0.

4.3   Porous Plate Model

If the feather-like filters of insects are considered as porous plates, the flow through them might be estimated using Darcy's law (for example, Spielman & Goron, 1968). Other approaches for porous plates are given in Taylor & Batchelor (1949) and Koo & James (1973).

Let us consider a feathery structure consisting of a finite number N of equally spaced cylinders of diameter d. The edge-to-edge distance between adjacent cylinders is h and the width L of the entire structure is given by $L = N(h + d)$. If the Reynolds number of the cylinders is small, then the flow field through them can be described by solution to Stokes equations. For a Stokes flow, the drag D on each cylinder is approximately $u_s\mu d$ (leaving numerical constants aside). The net resistance per unit area of the feathery structure is thus approximately

D/A^2d^2, where $A = h/d$. The mean pressure gradient ∇p across the structure is approximately D/A^3d^3. Hence, Darcy's law may be used in the form

$$u_s \mu d / A^3 d^3 \approx -\nabla p. \tag{4.5}$$

Solving for u_s, we get

$$u_s \approx A^3 d^2 \nabla p / \mu. \tag{4.6}$$

Substituting equation (4.6) into the equation of continuity, we see that the pressure field satisfies Laplace's equation. Solving the Laplacian in polar coordinates and taking the derivative with respect to L, we see that $\nabla p \approx p/L$. Substituting this expression into equation (4.6), we get

$$u_s \approx A^3 d^2 p / \mu L. \tag{4.7}$$

The Reynolds number for flow around the entire feathery structure is $Re_L = u_0 \rho L / \mu$. For the case where Re_L is small, the viscous forces are dominant and the pressure field p is approximated by $p \approx \mu u_0 / L$. For large Re_L, the inertial terms dominate in the flow and $p \approx \rho u_0^2$. This pressure field drives the flow through the porous plate. Substituting these terms for p into equation (4.7), we obtain the following crude approximations for the proportion of fluid flowing through the structure:

$$u_s/u_0 \approx \begin{cases} h^3/dL^2 & \text{if } Re_L < 1, \\ h^3 Re_L / dL^2 & \text{if } Re_L > 1. \end{cases} \tag{4.8}$$

4.4 Cheer and Koehl's Model

We have developed a model for fluid motion through an appendage composed of a finite number of bristles (Cheer & Koehl, 1987). Because fluid is free to move around the sides of such appendages as well as between the bristles, it is not appropriate to model them as an infinite array of cylinders between which all the fluid is forced to move. Rather, as a first approximation to the flow in the vicinity of the bristles on a structure of finite width, we consider flow around and between a two-dimensional cross-section of a pair of circular cylinders when the direction of ambient flow is perpendicular to the line intersecting the centres of both cylinders. The model is only appropriate for cylinders operating at $Re < 1$.

The details of how we calculate the velocity vector field around two equal circular cylinders moving with respect to a fluid of infinite extent are described by Cheer & Koehl (1987). In this analysis, the velocities close to the cylinders are calculated in a bipolar coordinate system using Stokes's (1851) low-Re approximation to the Navier–Stokes equations of motion, and velocities further from the cylinders are calculated in a polar coordinate system using Oseen's (1910) approximation. These two expansions are put together using the matched-asymptotic analysis of Umemura (1982). The volume of fluid moving per unit time between a pair of cylinders of unit length is then obtained by integrating the velocity profile between the two cylinders. The 'leakiness' of the structure is defined as the ratio of this volume to the volume of fluid that would have moved

without restriction through a space of equivalent width and length in the ambient current in the same time interval (Fig. 2).

To apply this model to the case of feather-like filters, we first calculate the velocity profile between a pair of the larger cylinders of the filter. The 'ambient' flow encountered by the smaller hairs attached to these large cylinders is assumed to be this velocity profile. We then calculate the flow between a pair of the smaller hairs at a position midway along their length using the same technique.

5. Methods used in this study

In the present study, we use several techniques to calculate the flow through feather-like structures of particular species of insects, and compare the results with published flow measurements for those species.

5.1 Cephalic Fans of Black Fly Larvae

We consider the flow of water through the cephalic fans of the larva of the black fly *Similium vittatum*. Each fan, which is illustrated in Fig. 1a, and described in Table 1, is made up of a stem from which radiates a fan-like array of cylindrical rays. Each ray bears a row of smaller cylinders, the microtrichia.

Craig & Chance (1982) have measured the velocity of marker particles in the water moving through *S. vittatum* cephalic fans. We have calculated u_s, using various approaches, for comparison with the data of Craig & Chance for $u_0 = 0.18 \text{ m s}^{-1}$.

Technique 1. The mean velocity u_s was calculated using Silvester's (1983) equations, treating the fan as a net and using the radius of a microtrichium for a.

Technique 2. The mean velocity u_s was calculated using Darcy's law by assuming the fan to be a porous plate composed only of microtrichia.

Technique 3. The velocity profile between a pair of rays was calculated using the model of Cheer & Koehl (1987). The microtrichia were assumed to encounter this velocity profile, and the velocity profile between them midway along their length was then calculated using the same technique. The maximum velocity attained between the microtrichia was chosen for comparison with the velocity data of Craig & Chance (1982).

Technique 4. The fan was considered to be a porous plate made up only of rays, and Darcy's law was used to calculate u_s between the rays. This value of u_s was then used as the ambient velocity to calculate the velocity profile between microtrichia using the approach of Cheer & Koehl (1987).

Technique 5. The microtrichia of *S. vittatum* are not long enough to extend across the entire width of the gap between adjacent rays in portions of the cephalic fan where the rays are most widely spaced. We assumed that the microtrichia serve to increase the functional diameter of the ray bearing them; hence, we used Darcy's law to calculate u_s for a porous plate composed only of rays whose diameters were the sum of the ray diameter and the microtrichium length.

TABLE 1

Insect filters examined in this study

Species:	*Similium vittatum*	*Acitas luna*
Individual:	Black fly, larva	Moth, adult male
Filter:	Cephalic fan	Antenna
Length (mm):	0·9[a]	13·5[b]
Width (mm):	1·2[a]	6·0[b]
Large cylinder:	Ray	Branch
Diameter (μm):	5[c]	70·8[d]
Gap width† (μm):	30 to 50[c]‡*	190[d]
Small cylinder:	Microtrichium	Sensillum
Diameter (μm):	0·2[c]*	3[d]
Gap width† (μm):	0·15[c]*	14[d]
Length (μm):	7[c]	149[d]
Fluid:	Freshwater	Air
Kinematic viscosity§ at 20 °C (m² s⁻¹):	$1 \cdot 004 \times 10^{-6}$[f]	$1 \cdot 5 \times 10^{-5}$[f]
Speed, u_0 (m s⁻¹):	0·18[g] to 0·8[c]	0·75 to 2·75[b]
Material caught:	Particulate food	Pheromone molecules

* Measured on published photograph.
† Distance from the edge of one cylinder to the closest edge of its neighbour.
‡ Measured on the area of the fan where the gaps were widest.
§ Kinematic viscosity = μ/ρ.
[a] Chance & Craig (1986).
[b] Vogel (1983).
[c] Ross & Craig (1980).
[d] Measured on *A. luna* antenna, as described in the text.
[e] Kurtak (1978).
[f] Vogel (1981).
[g] Craig & Chance (1982).

5.2 Moth Antennae

We consider the flow of air through the antenna of a male moth of the species *Acitas luna*. These antennae, which are illustrated in Fig. 1b, c, and described in Table 1, look like pennate feathers. The central rachis bears two rows of cylindrical branches, which in turn bear two rows of smaller hairs (sensilla) on which the sensory receptors are located. We used an ocular micrometer on a Zeiss compound microscope to measure the diameters of the gaps between the branches (magnified 100 times) and the sensilla (magnified 400 times) of an antenna of a male *A. luna*. In order to minimize investigator bias in the measurements, two portions of the antenna were located using coordinates taken from a random number table, and the first nine of each structure encountered in each of these areas were measured. There is variability within an antenna in the dimensions of cylinders and gaps; we found the standard deviations of each of our sets of measurements to be less than 20% of the mean ($n = 18$ in each case).

Vogel (1983) has reported measurements of the 'transmissivity' to air flow of *A*.

luna antennae; this transmissivity is analogous to the u_s/u_0 or to the leakiness described above. We have calculated, for comparison with Vogel's data, the percentage of the air encountering an antenna that passes through it using the following approaches.

Technique 1. The antenna was assumed to be a net and u_s/u_0 was calculated using Silvester's (1983) equations; the radius of a sensillum was used for a.

Technique 2. The antenna was assumed to be a porous plate made only of sensilla and Darcy's law was used to calculate u_s/u_0.

Technique 2'. Each branch bearing sensilla was considered to be a separate porous plate composed of sensilla and Darcy's law was to calculate u_s/u_0.

Technique 3'. Even at the lowest velocities used in Vogel's experiments (0·75 and 1·00 m s^{-1}), the Re's of the branches were slightly greater than 1 (3·5 and 4·7, respectively); hence, the model of Cheer & Koehl (1987) could not be used to calculate the velocity profile between branches. Instead, we calculated the velocity profile around a single branch using the technique of Tomotika & Aoi (1950); although the onset of a pair of standing eddies predicted by this model appears at a Re much smaller than is observed experimentally, the velocity profiles lateral to the cylinder at $Re = 3·9$ are in good agreement to the experimental results of Goldstein (1938: Plate 31). The sensilla were assumed to encounter this calculated velocity profile, and the velocity profile between them midway along their length was calculated using the model of Cheer & Koehl (1987). This velocity profile was then used to calculate leakiness, as described above.

Technique 4. The antenna was assumed to be a porous plate made up of only branches and Darcy's law was used to calculate u_s. We reasoned that this approximation, which assumes that the branches operate at low Re, might be appropriate to use since Vogel's (1983) data show that little fluid moves through the antenna. Nonetheless, we restricted our calculations to the lowest u_0's used in Vogel's (1983) experiments (0·75 and 1·00 m s^{-1}). The u_s estimated in this way was then used as the ambient velocity to calculate the velocity profile between and leakiness of a pair of sensilla using the approach of Cheer & Koehl (1987).

Because the sensilla of *A. luna* extend across the gap between adjacent branches (see Fig. 1c), technique 5 described above was not used for this species.

6. Discussion: comparison of different techniques

The results of our calculations of u_s and of the percentage of fluid moving through rather than around the cephalic fan of a *S. vittatum* are given in Table 2; results for the antenna of a *A. luna* are given in Table 3. Flow measured through real fans or antennae of these species are also presented in Tables 2 and 3 for comparison.

Silvester's (1983) model (technique 1) yields u_s's that are lower than those measured. In the case of the moth antenna, the predicted values are roughly half the magnitude of the measured values, but in the case of the black fly fan, the predictions are roughly three orders of magnitude too low. Thus, the assumption that feathery filters can be considered as nets does not appear to be valid in cases

Table 2

Flow through Similium vittatum *cephalic fans*

Technique	Gap between branches (μm)	u_0 (m s^{-1})	u_s (m s^{-1})	Leakiness (%)
Measured*		0·18	0·018–0·023	10–12·5[a]
1	30	0·18	$6·4 \times 10^{-5}$	$3·6 \times 10^{-2}$ [a]
2	—	0·18	$5·76 \times 10^{-6}$	0·03[a] .003
3	40	0·18	0·015[c]	8·0[b]
	30	0·18	0·014[c]	7·8[b]
4	40	0·18	0·014[c]	7·8[b]
	30	0·18	0·012[c]	6·6[b]
5	30	0·18	0·095	53[a]

* Craig & Chance (1982).
[a] Leakiness = u_s/u_0.
[b] Leakiness as defined in Fig. 2.
[c] Maximum velocity in calculated profile taken to be u_s.

where the fine hairs are not long enough to extend across the gap between adjacent cylinders.

The simplest way to estimate the flow through a feathery filter is to use Darcy's law for a porous plate composed only of the filter's slimmest hairs (technique 2). Another advantage of this approach is that effects of the size of the whole filter can be explored in addition to the fine-scale morphological features of the filter. Unfortunately, estimates made using this technique are orders of magnitude lower than measured values for the examples considered here. The same conclusions can be drawn about the use of technique 2'.

Table 3

Flow through Acitas luna *antenna*

Technique	u_0 (m s^{-1})	u_s (m s^{-1})	Leakiness (%)
Measured*	0·75	—	8·2
	1·00	—	8·6
1	0·75	0·025	3·3[a]
	1·00	0·045	4·5[a]
2	0·75	0·002	0·4[a]
	1·00	0·004	0·5[a]
2'	0·75	0·011	1·5[a]
	1·00	0·020	2·0[a]
3'	0·75	0·24[c]	16·1[b]
	1·00	0·66[c]	30·9[b]
4	0·75	0·06[c]	6·7[b]
	1·00	0·13[c]	10·7[b]

* Vogel (1983).
[a] Leakiness = u_s/u_0.
[b] Leakiness as defined in Fig. 2.
[c] Maximum velocity in calculated profile taken to be u_s.

Using the model of Cheer & Koehl (1987) to calculate the flow between both the larger and then the finer cylinders in a feathery filter (technique 3) is only valid when the Re of the larger cylinders is less than 1. In the example of the black fly fan, this technique yields results that are in the best agreement with measured values. Another advantage of this approach is that it provides a description of the velocity gradients next to the fibres in the filter; this information is important for analysis of mechanisms of particle capture by these fibres (Fuchs, 1964; Davies, 1973; Spielman, 1977).

When the Re of the larger cylinders in a feathery filter is slightly greater than 1, the use of the equations of Tomotika & Aoi (1950) to calculate flow around the large cylinders and then the equations of Cheer & Koehl (1987) to calculate flow between the small hairs (technique 3') predicts velocities and leakiness values that are too high. In contrast, the use of Darcy's law to estimate flow through the coarse cylinders and then the use of the model of Cheer & Koehl to calculate flow between the fine hairs (technique 4) yields results similar to measured values for both the moth antenna and the black fly fan.

Assuming that the fine hairs in a feathery filter merely function to increase the diameter of the coarser cylinders to which they are attached and then using Darcy's law to estimate flow through the filter (technique 5) predicts a much leakier filter than is observed in the case of the black fly fan.

7. Discussion: biological implications

We have developed a general model of fluid movement through fibrous biological filters of finite width to explore which aspects of the morphology and motion of these structures have important effects on the flow through them (Cheer & Koehl, 1987). As shown above, the predictions of this model are in good agreement with empirical data for certain insect filters.

We have used this model to investigate the effect of the Re (i.e. diameter or speed relative to the surrounding fluid) of the cylinders composing fibrous animal appendages on the flow through those appendages (Cheer & Koehl, 1987). We found that changes in diameter or speed have a large effect on leakiness if the cylinders operate at Re's of 10^{-2} to 1, as can be seen by comparing Figs 2a and b. In contrast, we found that changes in the Re of the cylinders in a filter have little effect on leakiness if the cylinders operate at Re's of 10^{-3} or, lower (Cheer & Koehl, 1987). Our model also predicts that changes in the width of the gap between adjacent cylinders has the biggest effect on the shear gradient next to a cylinder at Re's of the order of 10^{-2}, or at higher Re's only if the cylinders are very close together already. These general predictions of our model point to the importance of measuring the velocity of fibrous appendages relative to the surrounding fluid, in addition to the structural aspects of such filters that biologists more commonly measure, if the functional morphology of the appendages is to be understood.

Our theoretical analysis and the experimental results described above show that the leakiness of feather-like filters can be quite low. Our calculations suggest that this reduction in flow speed through such a filter is largely due to the presence of

small hairs on the larger cylinders composing the filter. For example, the leakiness of a black fly cephalic fan composed only of rays (Fig. 2a) would be 92% in an ambient water current of $0 \cdot 18 \, \text{m s}^{-1}$, whereas the leakiness when the microtrichia are added is reduced to only 7·8% (calculated using technique 3 described above). The velocity of fluid movement through a filter is important to its performance in a number of ways: it determines the flux of particle-carrying fluid processed; it affects the efficiency of capture of particles of various physical characteristics; and it affects the subsequent loss of captured particles.

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