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THEORETICAL MECHANICS OF PARTICLE CAPTURE: PREDICTIONS FOR HYDROPSYCHID CADDISFLY DISTRIBUTIONAL ECOLOGY

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Net-spinning caddisfly larvae (Insecta: Trichoptera) are filter feeders, capturing particles from the passing water with silken nets (Wiggins 1977). Nets spun by members of the family Hydropsychidae, attached to the substrate beside their retreats, project into the local current. Nets are flat or slightly curved in the direction of the current. They are constructed of rectangular meshes of such regularity that characteristic mesh sizes have been reported for several species and instars within species (Wallace 1975*b*; Malas and Wallace 1977; Georgian and Wallace 1981; Tachet et al. 1987).

The distributional ecology of hydropsychid larvae appears to relate to their species-specific net morphologies. Species that spin larger mesh are found in faster-current microhabitats (Wallace 1975*a*; Malas and Wallace 1977; Alstad 1981). Within a stream drainage, species are added to or lost from headwaters to downstream habitats, forming longitudinal distributional patterns that often relate to patterns in net morphology; species spinning smaller mesh are typically found farther downstream (Gordon and Wallace 1975; Wiggins and Mackay 1978; Alstad 1982, 1987*a*).

Although these field patterns suggest that net morphology may play an important role in caddisfly distributional ecology, many factors, including temperature, current, predation, and the size, concentration, and nutritional value of suspended particles, vary along the stream continuum. Correlational studies have generated a number of controversial hypotheses, which invoke different functional relationships of these environmental variables to caddisfly nets to explain the hydropsychid distributional patterns (Alstad 1986; Thorp et al. 1986).

Competing hypotheses that explicitly relate hydropsychid distributional patterns to aspects of net structure fall into two general categories.

1. *Particle-size hypothesis*.—This hypothesis states that hydropsychid distributional patterns result from selective particle capture by nets with large and small meshes. Nets with larger mesh are found in faster microhabitats, and they filter a greater volume of fast-moving water, which may carry larger particles. Therefore, nets with larger mesh should capture larger particles than nets with smaller mesh.

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Differences in mesh size may not translate into differences in total quantity of food captured, however. Because of their lower resistance, nets with larger meshes filter more water per unit of time and unit of area but capture particles with less efficiency. If species with large and small meshes ingest particles of different sizes or types, this may facilitate the coexistence of species in areas with broad distributions of particle size; environments with narrower ranges of particle size should support a correspondingly limited community composition (Wallace 1975*a*; Malas and Wallace 1977; Wallace et al. 1977). Dietary differences among species spinning meshes of different sizes are suggested by differences in gut morphology. Hydropsychid subfamilies characterized by finer mesh also have well-developed teeth in their gastric mills, which may play an important role in crushing diatoms (Boon 1985).

2. *Capture-rate hypothesis*.—According to the capture-rate hypothesis, caddisfly distributions are determined by species-specific marginal requirements for two partially substitutable resources: current velocity and resource concentration. For example, in localities where the particle concentration is low, insects situated in a fast current might still filter enough water to obtain a sufficient supply. Large, robust meshes might be required to withstand the force of such currents. At sites with higher food-particle concentrations, a slower current should suffice to produce the same capture rate; nets should require less strength, and nets with finer meshes might have an advantage, losing fewer items through narrower openings. It follows that the community composition should correspond more closely to the quantity of suspended food than to the size distribution of the particles (Alstad 1987*b*).

These two explanations relating hydropsychid distribution and community ecology to net functional morphology are not mutually exclusive, but they make different assumptions about how nets capture particles.

There is a theoretical basis, independent of field correlations, for predicting how a net functions in particle capture. Silvester (1983) developed equations based on fluid-mechanics theory to calculate particle capture by a net with rectangular meshes, such as those spun by hydropsychid caddisflies. Because the equations describe complex and nonintuitive relationships among many variables, the implications of these equations for hydropsychid distributional ecology have remained largely unexplored.

We performed a series of computer simulations based on Silvester's equations in order to identify the effects of mesh size, fiber diameter, temperature, and ambient water velocity on particle-capture rate. The objective of the simulations was not to determine whether caddisflies are building structures to optimal specifications but to test the theoretical plausibility of two assumptions that form the basis of established distributional hypotheses. (1) The particle-size hypothesis assumes that nets with larger mesh capture larger particles than nets with smaller mesh. (2) The capture-rate hypothesis assumes that, in a habitat with fast water and low food concentration, a net with larger mesh has a higher particle-capture rate than one with smaller mesh and that, in a habitat with slower water and higher food concentration, a net with smaller mesh has a higher particle-capture rate than one with larger mesh (Alstad 1987*b*).

TABLE 1

VARIABLES AFFECTING CAPTURE RATE BY DIRECT INTERCEPTION AND THE RANGES USED IN THE SIMULATIONS

Parameter	Symbol	Range
Water		
Viscosity	μ	0.8–1.8 mPa s (0°–30°C)
Density	ρ	996–1000 kg/m^3 (0°–30°C)
Velocity (ambient)	V_{amb}	1 mm/s–1 m/s
Net		
Mesh width	h_1	2 μm–1 mm
Mesh length	h_2	2 μm–1 mm
Fiber diameter	d_{f}	1–50 μm
Particle diameter	d_{p}	1 μm–1 mm

METHODS

A particle can be captured by a sticky filter through five mechanisms: sieving, direct interception, inertial impaction, gravitational deposition, and diffusive deposition (Rubenstein and Koehl 1977; LaBarbera 1984). Sieving refers to the capture of particles larger than the filter openings. The other four mechanisms describe capture of particles smaller than the filter openings, presuming that the elements of the filter are sticky to the particles.

Our computer simulations assumed that particles larger than the openings in the net were sieved (i.e., always caught). When particles were smaller than the openings in the net, we simulated their capture by direct interception, because this is the primary mechanism by which particles (of moderate density) of sizes from 0.3 to 50 μm in diameter are caught by hydropsychid nets (for analysis, see Silvester 1983). Particles in the water in which caddisflies are found and particles caught in their nets are commonly in this size range (Wallace et al. 1982; Fuller et al. 1983; Alstad 1987*a*). For larger particles that are still smaller than the filter openings, the assumption of direct interception remains a reasonable approximation (Silvester 1983). This analysis differs from the earlier work of Georgian and Wallace (1981), which presumed sieving exclusively.

We used a series of computer programs based on Silvester's equations to vary individual characteristics of the net, the water, and the particles, predicting their separate effects on particle-capture rate. The biologically relevant parameter ranges used in the programs are listed in table 1. Mesh size and fiber diameter are defined in figure 1.

Particle-capture rate of a caddisfly net is the product of four factors:

$$P = V_{\mathrm{net}}\, E_{\mathrm{net}}\, A\, C\,, \tag{1}$$

where (using SI units) P is the particle-capture rate (number of particles per second); V_{net}, the average velocity through the net (m/s); E_{net}, the efficiency of particle capture, that is, the proportion of particles passing through the net that get caught; A, the total area of the net (m^2); and C, the concentration of particles in the water (number of particles/m^3).

The first two factors in equation (1), V_{net} and E_{net}, were calculated from parame-

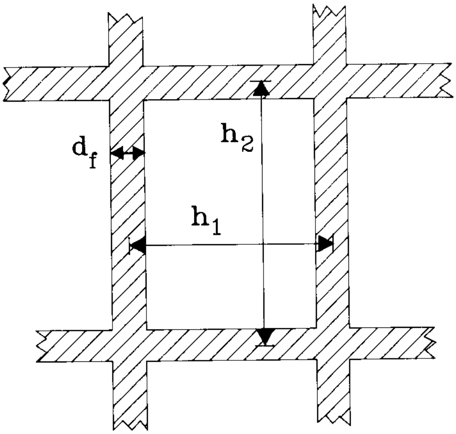

FIG. 1.—Morphology of nets. Fiber diameter (d_f) is the diameter of the silk strand. Mesh width (h_1) and mesh length (h_2) are the distances between the centers of adjacent parallel fibers and are measured perpendicular to each other. By convention, the smaller of the two perpendicular measurements is mesh width. Mesh size refers to the geometric mean of mesh width and mesh length (the square root of the product of mesh width and mesh length, $(h_1h_2)^{1/2}$).

ters listed in table 1 following Silvester's equations. Details of these calculations can be found in the Appendix. E_{net} is a maximal estimate because adhesivity between a particle and the silk strand was arbitrarily set at 100%.

The product of the two remaining factors from equation (1), A and C, was usually set equal to 1 (particles/m in SI units). This corresponds, for example, to a net area of 0.25 cm^2 (2.5×10^{-5} m^2) and a particle concentration of 40 particles/liter (4×10^4 particles/m^3). When the product of A and C is set equal to 1 in this manner, particle-capture rate is simply the product of V_{net} and E_{net}, the particle-capture rate per unit of net area per unit of particle concentration.

For simulations in which mesh size and fiber diameter were not of primary interest, mesh width and mesh length were set at 20 times the fiber diameter, in accord with empirically observed scaling (fig. 2). When temperature was not of primary interest, the viscosity and density of the water were set equal to 0.001 Pa s (pascals times seconds) and 1000 kg/m^3, respectively (corresponding within two significant figures to the viscosity and density of water at 20°C; Weast 1986).

RESULTS

The simulation results are organized in sections describing the individual effects of six variables (temperature, current velocity, mesh size, mesh eccentricity, fiber diameter, and total net area) on the simulated particle-capture performances of caddisfly nets.

Temperature

Both water viscosity and density decrease with increasing temperature (density above 3.98°C). Viscosity changes much more than density; if water temperature

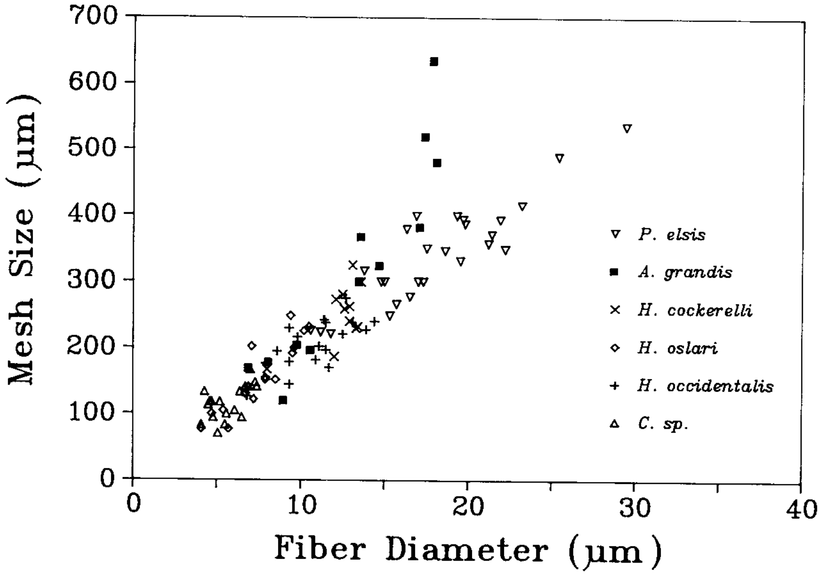

FIG. 2.—Mesh size (square root of the product of mesh width and mesh length) as a function of fiber diameter. Nets, spun by members of six hydropsychid species from Utah streams, were collected in the field. Each point is for a single net. Mesh size is based on the mean of 11–64 measurements per net; fiber diameter is based on the mean of 10 measurements per net. All measurements were made on whole mounts of nets using an ocular micrometer. *P*., *Parapsyche*; *A*., *Arctopsyche*; *H*., *Hydropsyche*; *C*., *Cheumatopsyche*. Regression equation: $y = 19.2x + 11.1$, where y is mesh size in µm and x is fiber diameter in µm ($r^2 = 0.82$). The intercept is not significantly different from 0 ($p = 0.33$).

increases from 5°C to 25°C, viscosity decreases by 41%, while density decreases by less than 1% (Weast 1986). Our simulations suggest that any net captures more particles in warmer water (fig. 3), primarily because of this decrease in viscosity. Because of the drag exerted by the silk fibers, only a portion of the water that approaches the net actually passes through. Reduced viscosity causes more water to go through the net rather than being diverted around it. E_{net} is independent of water temperature because efficiency is not a function of water viscosity or density (see eqs. A4, A5). Since particle-capture rate is proportional to the product of V_{net} and E_{net} (eq. 1), an increase in particle-capture rate follows from the increase in velocity through the net.

Does this mean that a larva filtering in warmer water has an advantage in terms of food supply? In the short term, increases in particle-capture rate seem unlikely to compensate for the greater nutritional demands associated with higher temperature. Typically, the rate of oxygen uptake increases about 50% with a 5°C increase in temperature (calculated from Hildrew and Edington 1979; Bales and Badcock 1987; see table 2), but our simulations suggest that the particle-capture rate increases approximately 11% with a 5°C increase in temperature (range, 9%–18% for simulations using a temperature of 5°–30°C, fiber diameter of 1–50 µm, ambient velocity of 5–50 cm/s, and mesh width and length each 20 times silk

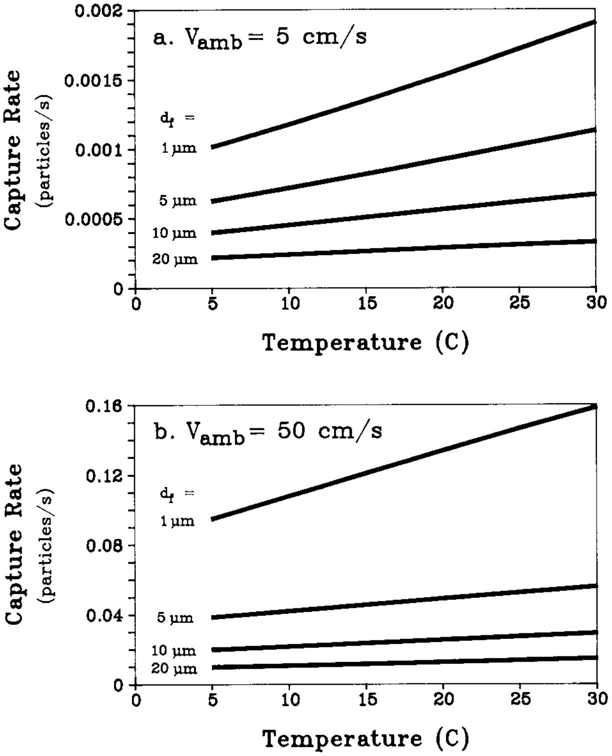

FIG. 3.—Particle-capture rate as a function of temperature for nets with fiber diameter of 1 µm, 5 µm, 10 µm, and 20 µm. Mesh length = mesh width = 20 times fiber diameter. Particle diameter, 10 µm. The product of particle concentration and net area is 1 particle/m. Ambient velocity: *a*, 5 cm/s; *b*, 50 cm/s. Note the difference in the scaling of the *y*-axes.

TABLE 2

PERCENTAGE INCREASE IN OXYGEN CONSUMPTION RATE BY HYDROPSYCHID LARVAE WITH 5°C INCREASES IN TEMPERATURE

	TEMPERATURE INCREASE (FROM–TO)				
SPECIES	5°–10°	10°–15°	15°–20°	20°–25°	Mean
Diplectrona felix[a]	15%	120%	71%	33%	60%
Hydropsyche instabilis[a]	55%	17%	131%	4%	52%
Hydropsyche pellucidula[a]	29%	25%	64%	64%	46%
Sericostoma personatum[b]					
Acclimated to 6°C	71%	34%	26%	—	44%
Acclimated to 18°C	151%	38%	22%	—	70%
Mean					54%

[a] Calculated from Hildrew and Edington 1979.

[b] Calculated from Bales and Badcock 1987, assuming a larval size of 7.4 mg.

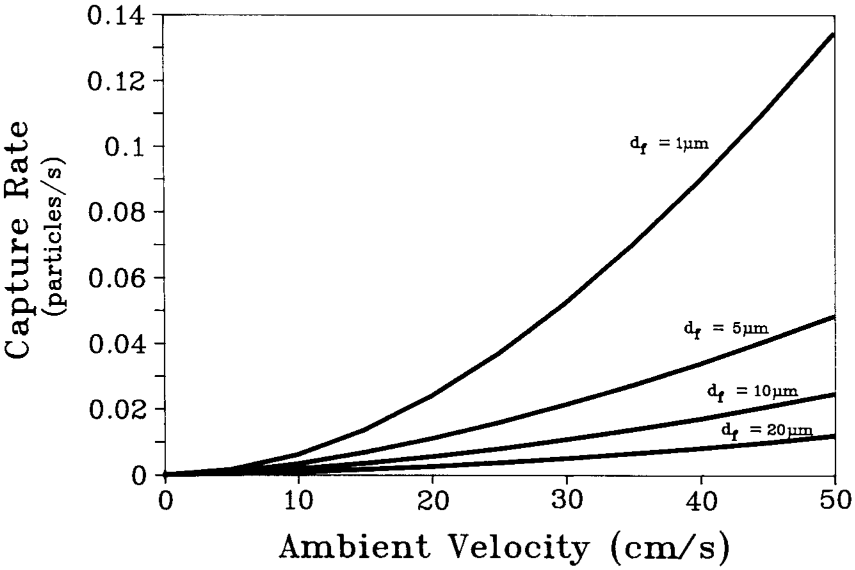

FIG. 4.—Particle-capture rate as a function of ambient velocity for nets with fiber diameter of 1 μm, 5 μm, 10 μm, and 20 μm. Mesh length = mesh width = 20 times fiber diameter. Particle diameter, 10 μm. The product of particle concentration and net area is 1 particle/m.

width). Therefore, a larva would not gain a net energetic advantage by moving into warmer water unless long-term acclimation to the higher temperature reduced its metabolic rate substantially.

Current Velocity

Any net theoretically captures more in faster water (fig. 4; also cf. fig. 3*a* with 3*b*). This is because velocity through the net increases with ambient velocity (fig. 5; eq. A1), although the efficiency of particle capture changes little. The proportion of approaching water that passes through the net, or "leakiness" (V_{net}/V_{amb}; Cheer and Koehl 1987*b*) also increases with ambient velocity and mesh size (fig. 6). The greater leakiness of larger-meshed nets is not a result of more open area in the net; because fiber diameter is scaled with mesh size for this set of simulations, the percentage of open net area is 90.25% in all cases represented in figure 6 (consistent with empirical scaling; fig. 2). Because any net theoretically captures more particles in faster water, there is no functional reason, on the basis of particle-capture rate, to think that some nets are more adapted to slower flows and some to faster flows. Therefore, the simulations of capture rate provide no mechanistic insight into the field correlations between mesh size and microhabitat velocity.

Mesh Size

As mesh size increases for a fixed fiber diameter, more of the water approaching the net passes through the net; that is, velocity through the net increases, although ambient velocity remains constant. In contrast, the efficiency of particle capture

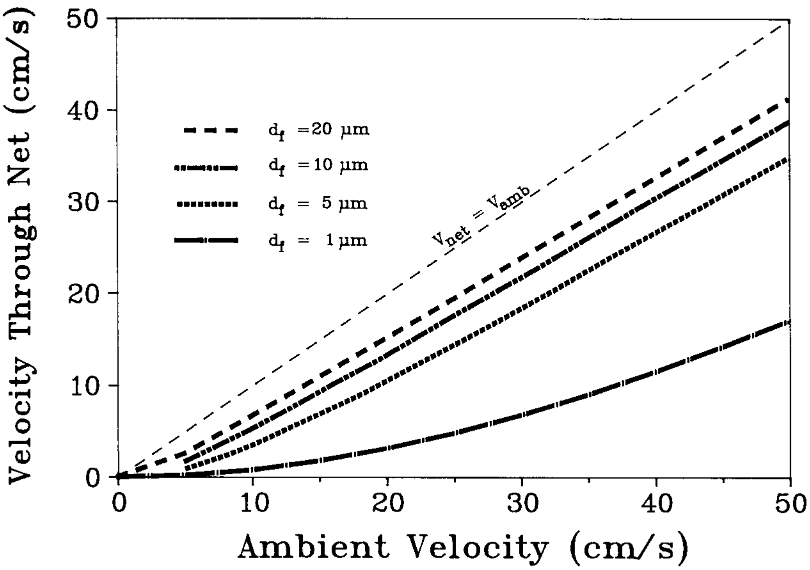

FIG. 5.—Velocity through the net as a function of ambient velocity for nets with fiber diameter of 1 μm, 5 μm, 10 μm, and 20 μm. Mesh length = mesh width = 20 times fiber diameter.

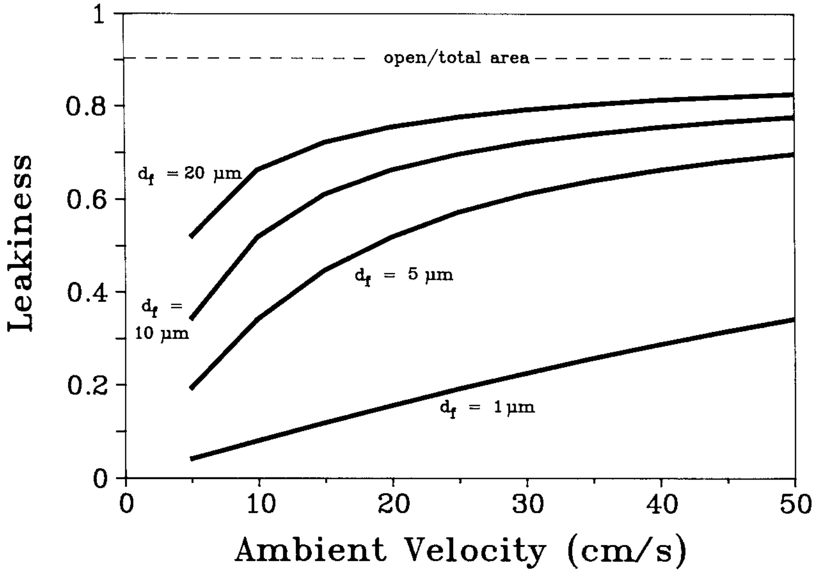

FIG. 6.—Leakiness, the proportion of water approaching the net that goes through (dimensionless), as a function of ambient velocity for nets with fiber diameter of 1 μm, 5 μm, 10 μm, and 20 μm. Mesh length = mesh width = 20 times fiber diameter. All nets have the same proportion of open area: 90.25% of total area.

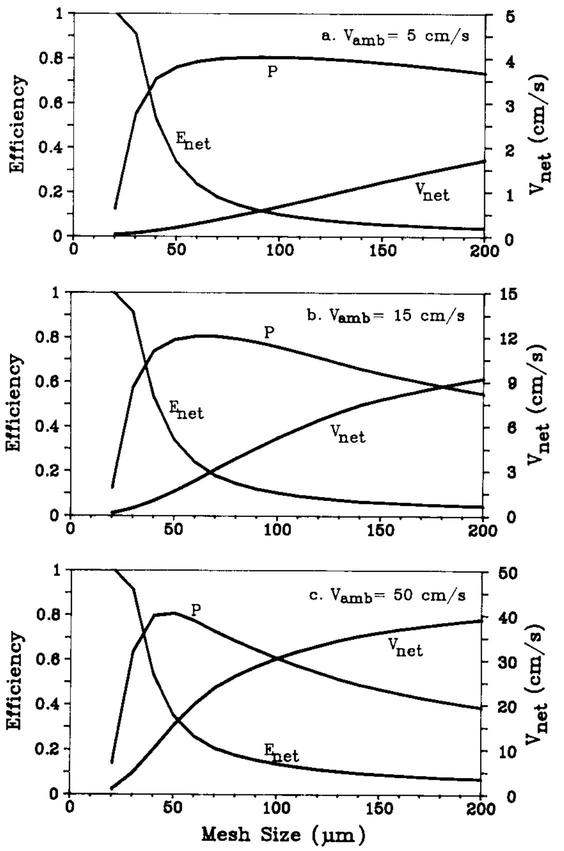

FIG. 7.—Efficiency of particle capture (E_{net}), velocity through the net (V_{net}), and particle-capture rate (P, particles/s) as a function of mesh size (the square root of the product of mesh width and mesh length). Particle diameter, 10 µm. Fiber diameter, 10 µm. The product of particle concentration and net area is 1 particle/m. *a*, Ambient velocity, 5 cm/s; maximal particle-capture rate, 0.00061 particles/s. *b*, Ambient velocity, 15 cm/s; maximal particle-capture rate, 0.0052 particles/s. *c*, Ambient velocity, 50 cm/s; maximal particle-capture rate, 0.052 particles/s.

decreases with increasing mesh size. This decrease can be understood intuitively as a lower probability that a particle will contact a silk fiber on its way through the net. Particle-capture rate, the product of these increasing (V_{net}) and decreasing (E_{net}) functions, is a curve with a maximum (fig. 7). Therefore, in our simulations, one mesh size theoretically maximizes particle-capture rate for a given fiber diameter, net area, ambient velocity, and particle size. For example, with a fiber diameter of 10 µm and an ambient velocity of 15 cm/s, the mesh size that theoretically maximizes the capture rate of 10-µm-diameter particles is approximately 60 µm (fig. 7*b*). Note that this larger mesh size (60 µm) captures more than sieving mesh sizes ($\leq$20 µm); the increase in water flow through the net due to the larger mesh more than compensates for the decrease in the efficiency of particle capture.

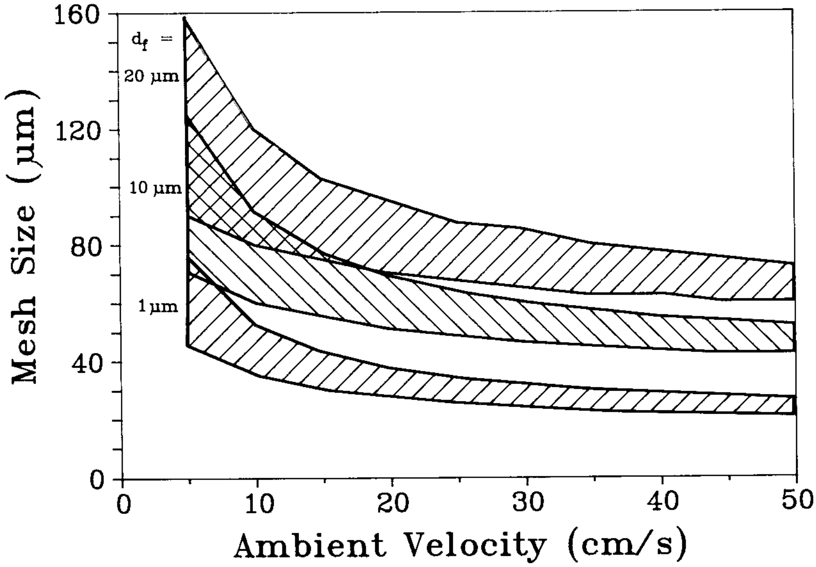

FIG. 8.—The range of mesh sizes (square root of product of mesh width and mesh length) that result in a capture rate of 10-µm particles within 1% of the maximum as a function of ambient velocity. Nets of three fiber diameters: 1 µm, 10 µm, and 20 µm.

These simulations also suggest that the effects of mesh size on capture performance vary with ambient current velocity. Since the particle-capture curve becomes more peaked with increasing velocity, a change in mesh size of the same magnitude has a larger effect on particle-capture rate in faster water (compare figs. 7*a*–*c*). This functional tolerance for a change in mesh size is graphed in figure 8, which gives the range of mesh sizes that result in a particle-capture rate within 1% of maximum. At higher velocities, the ranges are narrower, corresponding to more-peaked capture-rate curves. The mesh size that maximizes particle-capture rate is predicted to decrease with increasing velocity (for particles less than 70 µm in diameter).

The theoretical mesh size that maximizes capture rate increases with particle size. This means that if fiber diameter, mesh size, and ambient velocity are known for a net, the nominal particle size for which capture is maximized can be calculated (fig. 9). The exercise shows that even the largest hydropsychid meshes are maximizing the capture rate of particles less than 0.25 mm in diameter, although larger particles are still caught with higher probability. Larger particles are always more likely to be caught by any net. As a result, correlations between mesh size and particle size are predicted to be weak, and using a nominal particle size to characterize the selectivity of a net of a particular morphology indicates only a qualitative tendency toward the capture of a particular particle size.

The strength of the correlation between mesh size and particle size is also affected by the distribution of available particle sizes in the stream water. Where large items make up a major portion of available resources, there is relatively little specialization because large items preponderate in most nets (fig. 10*a*). Where the

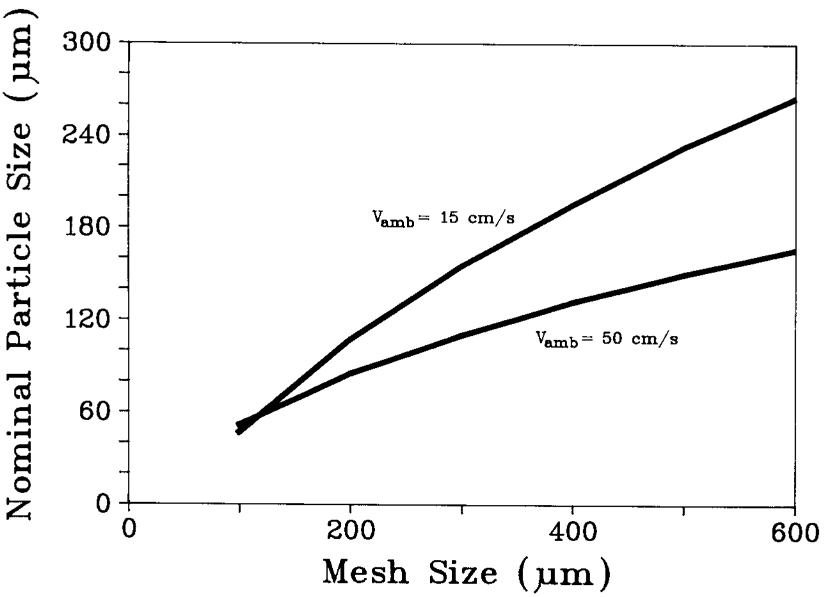

FIG. 9.—Nominal particle size (whose capture is maximized) as a function of mesh size for two ambient velocities: 15 cm/s and 50 cm/s. Mesh size (square root of product of mesh width and mesh length) is 20 times fiber diameter.

available particle volume is heavily dominated by small items, there will be little specialization because large items are rare in all nets (fig. 10*c*). Between these extremes, simulations suggest that the potential for particle-size partitioning is greater (fig. 10*b*). The distribution of suspended-particle sizes varies widely among stream sites (Naiman and Sedell 1979; Wallace et al. 1982; Alstad 1987*a*). Thus, feeding specialization resulting from differences in net function should depend on the distribution of locally available resources.

Temperature has only a slight effect on the mesh size that maximizes particle-capture rate. The predicted mesh size that maximizes particle-capture rate decreases by less than 5% for a 5°C increase in temperature.

Mesh Eccentricity

The meshes of hydropsychid caddisfly nets are usually not square but are 1.2 to 10 times longer than wide (Wallace and Malas 1976). Deviation from squareness is referred to as "eccentricity," analogous to the deviation of an eccentric ellipse from circularity, and it is defined as the ratio of mesh length to mesh width. This is the reciprocal of "lengthening of the mesh" (ratio of mesh width to mesh length) used by Tachet et al. (1987).

A net with more-eccentric mesh usually has a greater particle-capture rate than a net with less-eccentric mesh. This is because the proportion of open area of the net decreases with increasing eccentricity, and the resulting increase in the efficiency of particle capture is usually greater than the resulting decrease in velocity through the net. This pattern holds whether the total area of the net is

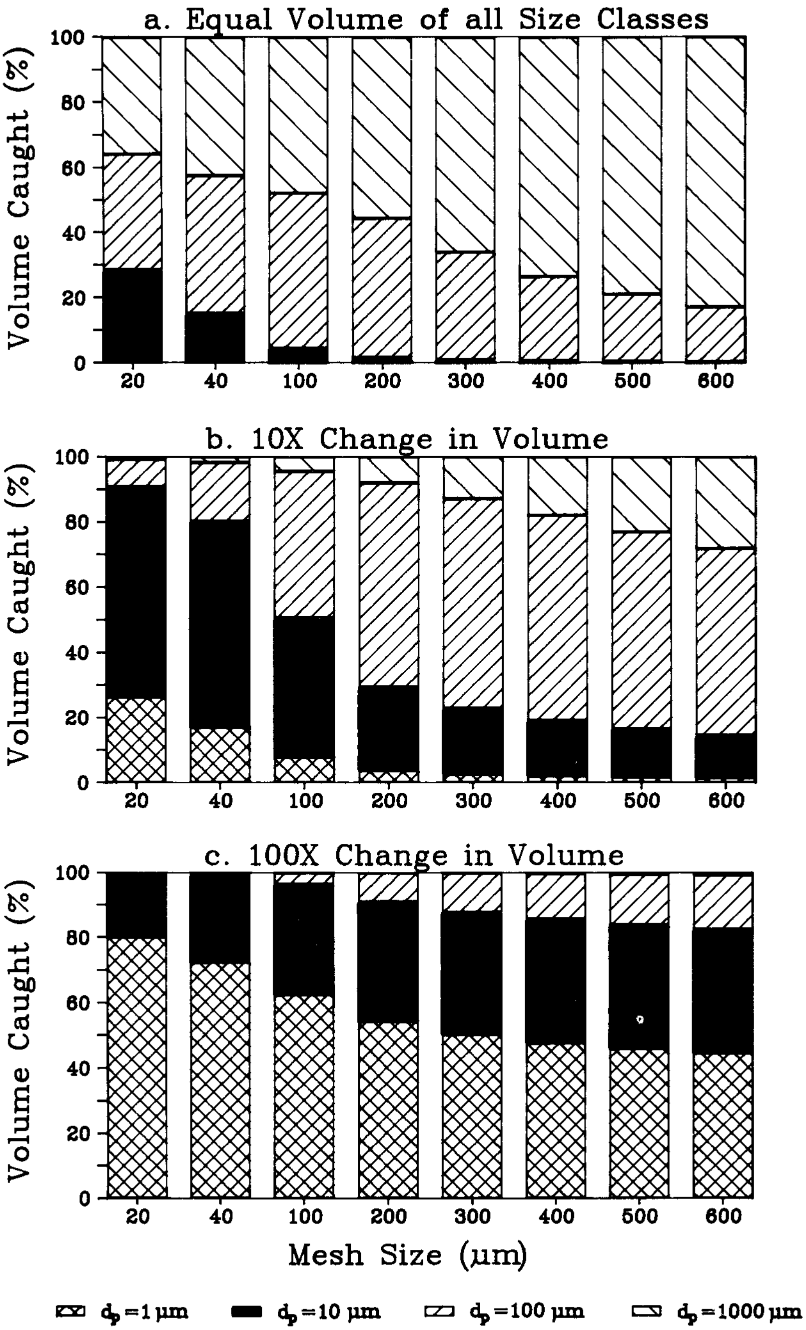

FIG. 10.—Volumetric proportions of different sizes of particles caught by nets of different mesh sizes. Four particle diameters: 1 µm, 10 µm, 100 µm, and 1000 µm. *a*, Equal volumes of all four particle-size classes. *b*, Larger particles are one-tenth as abundant as the next-smaller-size class; the ratios of total volumes of particle-size classes are 1000:100:10:1. *c*, Larger particles are 0.01 times as abundant as the next-smaller-size class. Ratios of total volumes of particle-size classes are 1,000,000:10,000:100:1. Mesh size (square root of product of mesh width and mesh length) is 20 times fiber diameter.

held constant or the total quantity of silk is held constant (they cannot be held constant simultaneously).

The effect of eccentricity on particle-capture rate is pronounced only for large degrees of eccentricity and for small fiber diameters. If mesh eccentricity is constrained to be less than 2, the increase in the particle-capture rate is less than 2% above that of square mesh (for fiber diameters in the range of 1–20 μm and ambient velocities in the range of 5–50 cm/s). If eccentricity is as high as 10, then the maximal particle-capture rate for eccentric mesh is 15% higher than the maximal particle-capture rate realized with square mesh, but only for small fiber diameters (1 μm). For larger fiber diameters (5–20 μm), eccentric mesh increases particle-capture rate by less than 5% (ambient velocities in the range of 5–50 cm/s). This result is consistent with empirical findings that pronounced eccentricity (≈10) has evolved independently in distantly related caddisfly genera that spin with a narrow silk strand (Wallace and Malas 1976). Wallace and Malas (1976), assuming that particles are caught only by sieving, suggested that this eccentric morphology leads to the capture of smaller particles than would be caught with a less-eccentric net with the same mesh area. Our simulations suggest that capture is enhanced even for particles too small to be caught by sieving and present a functional reason for the correlation between pronounced eccentricity and narrow silk strands.

The particle-capture rates predicted in previous sections for square mesh can be generalized to rectangular mesh of small eccentricity (the error is likely to be less than 5% for eccentricity under 2, which includes the mesh of nets spun by most members of the subfamilies Arctopsychinae, Diplectroninae, and Hydropsychinae). Moreover, the eccentric-mesh size that maximizes particle-capture rate is close (on the average, within 5%) to the square-mesh size that maximizes particle-capture rate. Thus, for nets of eccentricity less than 2, the mesh size can be adequately described for functional interpretation (particle-capture rate, specifically) as one number (geometric mean of length and width) rather than two numbers (width and length).

Fiber Diameter

Although there is a theoretical mesh size that maximizes particle-capture rate for a fixed fiber diameter, the converse is not true: there is no fiber diameter that theoretically maximizes particle-capture rate for fixed mesh size (fig. 11). A thinner silk strand always theoretically leads to greater particle capture for particles smaller than the sieving dimension because the increase in velocity through the net resulting from a thinner silk strand more than compensates for the decrease in the efficiency of particle capture. For example, fifth-instar *Arctopsyche grandis* larvae are predicted to catch more particles per area of net than are fifth-instar *Parapsyche elsis* larvae because they have a thinner fiber and approximately the same mesh size (fig. 2). This effect is stronger for small particles: fifth-instar *A. grandis* larvae are predicted to capture 10% more 10-μm particles per unit of net area than are fifth-instar *P. elsis* larvae, but less than 1% more 100-μm particles.

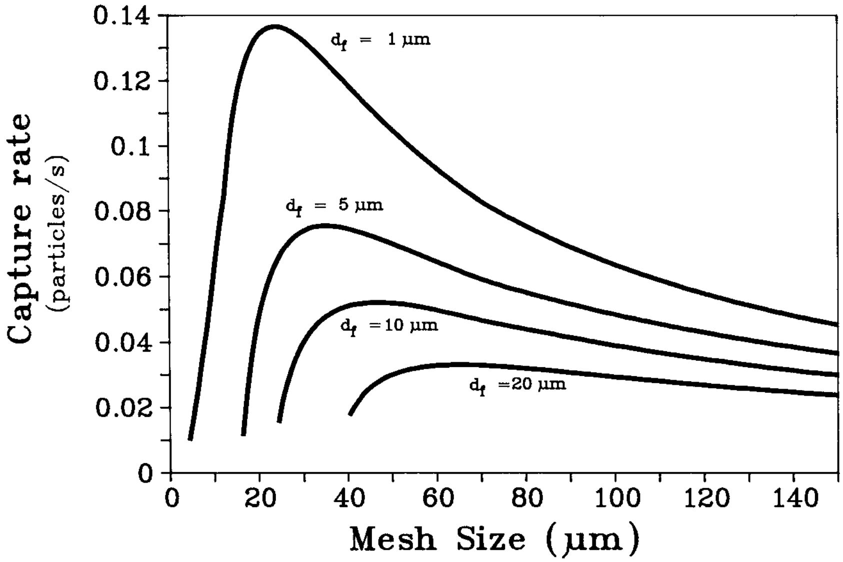

FIG. 11.—Particle-capture rate as a function of mesh size for four fiber diameters: 1 μm, 5 μm, 10 μm, and 20 μm. Ambient velocity, 50 cm/s; particle diameter, 10 μm. The product of particle concentration and net area is 1 particle/m.

The simulations predict that, to maximize the capture of any fixed particle size, mesh size should scale allometrically with fiber diameter, such that the ratio of mesh size to fiber diameter decreases with increasing fiber diameter. In contrast, the empirically observed relationship between mesh size and fiber diameter is isometric (fig. 2). This results in a tendency for nets of larger mesh to capture a greater proportion of larger particles and for nets of smaller mesh to capture a greater proportion of smaller particles.

Total Area of Net

In general, the total area of a net increases with mesh size and fiber diameter (Georgian and Wallace 1981; for an exception, see Fuller and Mackay 1980). Nets with smaller meshes and fiber diameters are predicted to capture more particles per unit of net area (fig. 4); therefore, it is possible to calculate whether a larger-area net with larger mesh would capture more or fewer particles than a smaller-area net with smaller mesh.

The larger area of larger-meshed nets is predicted to more than compensate for their lower particle-capture rates on a per-unit-of-area basis, assuming that total area scales with mesh size as reported by Georgian and Wallace (1981, p. 151). Larger nets with larger meshes are predicted to have 1.2 to 200 times the particle-capture rate of smaller nets with smaller meshes (fiber diameters, 1–20 μm; particle diameters, 1–20 μm; ambient velocity, 5–50 cm/s). Unless the basic food requirements of taxa with large and small meshes are quite different (i.e., much higher for those with big nets), this calculation implies that species with large nets

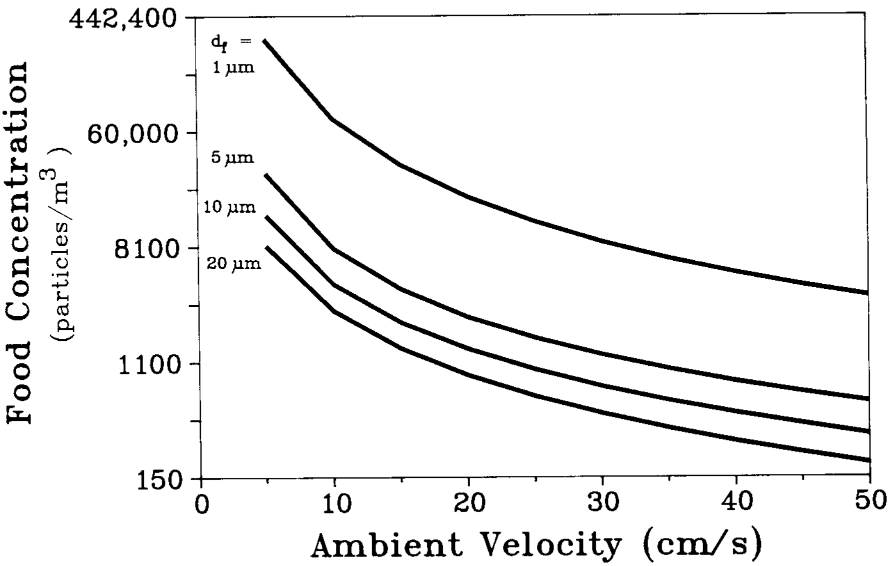

FIG. 12.—The predicted minimal levels of food concentration and ambient velocity required to sustain populations of four hypothetical species that differ in morphology of nets. All species have the same requirement for particle-capture rate: 50 particles/s. If the larger taxa, which spin larger meshes, require a higher rate of food intake, the vertical displacement between the curves is reduced. Fiber diameters: 1 µm, 5 µm, 10 µm, and 20 µm. Mesh size (square root of product of mesh width and mesh length) is 20 times fiber diameter. Total areas of nets are predicted from mesh size using an empirical relationship (Georgian and Wallace 1981, p. 151).

should be superior competitors, displacing species with smaller nets under all conditions of current and resource availability (fig. 12). This prediction is inconsistent with the capture-rate hypothesis because it implies that the patterns of caddisfly coexistence and community composition are not based simply on the rates of resource acquisition achieved by the different net morphologies.

DISCUSSION

Silvester (1983) adapted the theory of flow through rows of parallel cylinders to the case of a filter constructed of rectangular mesh, making it simpler to calculate the theoretical particle-capture rate of a hydropsychid caddisfly net. Our simulations using Silvester's equations suggest several points. (1) Nets with fine meshes capture suspended particles at a higher rate per unit of area than those with larger meshes. (2) However, species spinning large meshes have a greater particle-capture rate because of the correlation between mesh size and overall net area. (3) There is a mesh size that maximizes the capture rate of a given size of particle (for a given ambient current velocity and fiber diameter). (4) Particle-capture rates for all nets increase with current speed and temperature. Finally, (5) nets with larger mesh tend to capture larger particles, and nets with smaller mesh tend to capture smaller particles. (This last point was also discussed in Silvester 1983.) The simulations are based on fluid-mechanics principles and thus form an independent theoretical means for testing assumptions that underlie ecological models of caddisfly distribution.

Particle-Size Hypothesis

The particle-size hypothesis assumes that caddisfly nets are selective capture devices and that large meshes produce a diet of bigger particles. This assumption of differential particle-size capture by nets of different mesh size is supported by our simulations; they predict that particle sizes captured by large and small meshes should be broadly similar but that nets of larger mesh tend to capture larger particles and nets of smaller mesh tend to capture smaller particles. This prediction is supported by empirical research (Wallace 1975*b*; Alstad 1987*a*). As noted above, the amount of specialization expected depends on the size distribution of locally available particles. However, because the ecological significance of dietary differences depends on rates of both consumption and renewal of the different particle sizes, neither computer simulations of particle capture nor empirical observations of dietary specialization provide a logically sufficient test of the particle-size hypothesis (Alstad 1987*a*).

Capture-Rate Hypothesis

The capture-rate hypothesis is based on an empirical observation that suspended-diatom concentration is a better predictor of caddisfly community composition than is locally available particle size (Alstad 1987*a*,*b*). This theory assumes that caddisfly population densities are potentially limited by two resources: suspended-particle concentration and current velocity. Because suspended foods are delivered at a rate determined by ambient current, these resources are potentially substitutable; sufficient current might compensate for deficient particle concentration, and vice versa. The hypothesis assumes that net function affects the form of this trade-off, providing a mechanistic basis for the empirically observed distributional patterns. Coexistence requires each species to have a range of current speeds in which it is the superior competitor. Thus, in faster currents, species with large nets of coarse mesh should have a lower marginal food-concentration requirement than those spinning smaller nets of finer mesh; in slower currents, species with smaller, finer nets should have a lower food-concentration requirement than species with larger, coarser nets (Alstad 1987*b*).

To test this assumption of the capture-rate hypothesis, we assumed identical food-intake requirements for large and small species and used the simulations to estimate the particle concentration required by different net morphologies. The result, that large meshes should be competitively superior over all current speeds (fig. 12), means that the particle-capture performance of different net sizes is not a sufficient basis for predicting caddisfly distribution. To remain viable, the capture-rate hypothesis must make additional assumptions. For example, (1) taxa that spin large meshes might have higher food requirements than smaller taxa, which spin smaller-meshed nets, and (2) the limited strength of delicate meshes might exclude them from fast currents, where large nets achieve their highest capture rates (see below). Specific quantitative combinations of these two factors could cause each net morphology to be competitively superior at some current speed. Whether these assumptions are met in the wild, we cannot say.

Adequacy of Filtering Theory

Since these results are based entirely on Silvester's equations (1983), it is relevant to consider how accurately these equations are likely to predict capture by real caddisfly nets. Two separate quantities are calculated: velocity through the net (V_{net}) and the efficiency of particle capture (E_{net}).

Silvester suggested that the error in predicting velocity through a net using his equations is unlikely to be greater than 20%. This has been experimentally verified by measuring flow through stainless-steel mesh "nets" and through caddisfly nets under controlled conditions (Loudon 1990). Cheer and Koehl (1987*a*) found that Silvester's equations did not adequately describe flow through feather-like structures or short arrays of parallel cylinders, but the geometric arrangements that they were considering were quite different from the rectangular mesh assumed in Silvester's derivation.

Some estimate of adhesion must be used in calculating the efficiency of particle capture. We followed Silvester (1983) in arbitrarily assuming perfect adhesion between the particles and the sticky silk; hence, the estimates for particle capture are maximal. The adhesion may be closer to 0.2% than 100% (Loudon 1990), on the basis of calculations using data from Fuller et al. (1983). If the 0.2% figure is representative, then the reported theoretical capture rates are overestimates. This will not change the predicted relative performances of nets if adhesion does not change markedly with mesh size, fiber diameter, particle size, or water velocity. If the probability of remaining adhered correlates with these factors, then the results of our simulations will be affected. For example, if adhesion is not absolute, then particles may be less likely to remain adhered to a net in faster water. This could mean that some finite water velocity maximizes particle-capture rate, reducing the capture-rate advantage predicted for taxa that spin large meshes in fast current. In contrast, if adhesion is not absolute, an increase in the efficiency of particle capture could be abrupt, rather than asymptotic, as the particles reach the sieving dimension of the net. This could lead to greater differentiation between particle sizes captured by nets differing in mesh size than reported here. We have also ignored differences between particles other than size. Particles of different types may have different adhesive properties.

In order to quantify how the predictions in this paper would change if the drag forces tending to dislodge the particles from the silk were significant, one would have to know how the velocity gradients between fibers scale with fiber size and mesh size, how the drag forces on the particles scale with particle size and velocity gradient, and how the adherence of the particles scale with particle size and fiber diameter. Parts of these unknowns have been addressed theoretically (Silvester and Sleigh 1985; Cheer and Koehl 1987*b*), but there is not currently enough information to assess this complex issue adequately.

Phenomena with Low Reynolds Number

Reynolds number (*Re*) is a dimensionless quantity indicating the ease with which fluids shear rapidly. Viscous effects have greater impact with lower *Re*; in the context of filtering caddisfly nets, lower *Re* means a greater diversion of water (and suspended particles) around the net. Even if fluid density and viscosity are constant, a change in fiber size or water velocity will change *Re* (eq. A3). For hydropsychid nets in streams, *Re* (calculated using the fiber diameter and average velocity through the net) is usually less than 10, and changes in viscous effects are important in predicting fluid behavior. For example, a net with larger mesh (and larger *Re*) is leakier to approaching water than is a net with smaller mesh (lower *Re*), even though the proportion of open area is the same in both cases (fig. 6). In warmer water, viscosity decreases more than density decreases; thus, *Re* increases with increasing temperature, making a net leakier in warmer water.

A single length measurement is incorporated in the calculation of *Re*. Equation (A3) calculates the *Re* for a fiber diameter. In a filter, the distance between fibers is as important as the fiber size in influencing fluid behavior, and a separate *Re* for mesh size can also be calculated (Tamada and Fujikawa 1957). Therefore, the calculations for flow through a filter, or for flow through arrays of cylinders, always depend on two length measurements and cannot be summarized by a single *Re* (see also Cheer and Koehl 1987*b*).

Relationships between Morphology and Function

In functional studies, it is just as important to quantify when function is insensitive to morphological change as it is to indicate when sensitivity is pronounced. Functional change does not always intuitively follow morphological change. For example, the simulations predict that functional tolerance for a change in mesh size is greater at lower velocity. In an analysis of fluid flow through bristled appendages (low *Re*), Cheer and Koehl (1987*b*) have also reported size ranges in which morphological change barely influences leakiness, and other ranges in which morphological change has a substantial effect. Another nonintuitive result from the simulations is that isometric scaling of mesh size with fiber diameter (fig. 2) theoretically leads to functional differentiation, with larger meshes having a greater tendency toward capture of larger particles and smaller meshes tending toward capture of smaller particles.

This paper has focused entirely on a single mechanical aspect of nets: particle capture. Undoubtedly, another mechanical feature, structural integrity, may be of importance as a causal factor in caddisfly distribution. For example, the correlation between mesh size and local velocity might be partly explained by structural failure if finer meshes cannot tolerate faster microhabitats. Only by explicitly separating and quantifying the individual effects of changes in morphology and environmental parameters on different functions can mechanistic hypotheses relating physical processes with distributional ecology be supported or rejected.

SUMMARY

Computer simulations based on equations developed earlier were used to analyze theoretically the effects of six parameters on particle capture by hydropsychid caddisfly nets. If assumptions that form the basis of these simulations are valid, the following statements can be made. (1) Nets with fine meshes capture suspended particles at a higher rate per unit of area than those with larger meshes.

(2) Species spinning large meshes have a greater total capture rate because of a correlation between mesh size and overall net area. (3) Capture rates of all nets increase with current speed and temperature. (4) A specific mesh size maximizes the capture rate of a given particle size (for a fixed ambient current velocity and fiber diameter). Finally, (5) nets with larger meshes have a greater tendency to capture larger particles, and nets with smaller meshes have a greater tendency to capture smaller particles. These results are compatible with a particle-size hypothesis, but they compel a modification of a capture-rate hypothesis, suggesting that the particle-capture performance of different net morphologies is not a sufficient basis for explaining empirical correlations between resource concentration and caddisfly community structure.

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APPENDIX

Calculation of 'V_{net}'

Velocity through the net (V_{net}) can be calculated from the following parameters: h_1, mesh width (m); h_2, mesh length (m); d_f, fiber diameter (m); V_{amb}, ambient velocity of water (m/s); μ, water viscosity (Pa s); and ρ, water density (kg/m^3).

V_{net} was calculated following Silvester (1983):

$$V_{net} = [(\gamma/\alpha\rho)^2 + V_{amb}^2]^{1/2} - \gamma/\alpha\rho\,, \tag{A1}$$

where α is the ratio between the area of the net and the entrance area (deviation from 1 can be viewed as the deviation from flatness),

$$\gamma = 8\pi\mu/h_e\Lambda_e\,,$$

$$h_e = h_1h_2/(h_1 + h_2)\,,$$

and

$$\Lambda_e = 1 - 2(\ln\tau) + \frac{\tau^2}{6} - \frac{\tau^4}{144} + \frac{\tau^6}{1080}\,; \tag{A2}$$

here,

$$\tau = d_f\,\pi\,(h_1^2 + h_2^2)^{1/2}/h_1h_2\,.$$

(Cheer and Koehl used an alternative equation to calculate Λ_e [1987*a*, p. 191, eq. 4.3a]; their choice leads to slightly lower values for calculated velocity through nets than eq. A2, used in Silvester 1983 and in this paper.)

For all of the simulations, α was assumed to equal 1. Calculations suggest that the theoretical bias in the estimate of particle-capture rate is small for the common situation, when the net is curved, but it is flattened for the measurement of net area and assumed to be flat ($\alpha = 1$) for calculations of particle capture. If the true shape of the net is a hemisphere ($\alpha = 2$), the average bias in the calculation of particle capture assuming flatness is less than 0.1% above the theoretical "true" capture rate for the curved net (maximal deviation is ±10% of the theoretical rate for the following simulation parameter ranges: ambient velocities, 5–50 cm/s; fiber diameters, 1–20 μm; mesh sizes, 2–30 times silk width;

Erratum

Loudon, C. and D. N. Alstad. 1990. Theoretical mechanics of particle capture: predictions for hydropsychid caddisfly distributional ecology. Am Nat 135(3): 360-381.

p. 378, last paragraph:

"If the true shape of the net is a hemisphere ($\alpha=2$), the average bias in the calculation of particle capture assuming flatness is less than 0.1% above the theoretical "true" capture rate for the curved net..."

In fact, for the parameters listed, a flat net is predicted to average a 60% greater particle capture rate than a hemispherical net with the same filtering area.

particle size, 10 μm). This suggests that an estimation of particle-capture rate from a flattened net is unlikely to be substantially different from that calculated taking the true curvature of the net into account.

Once V_{net} is calculated, the Reynolds number for the fibers of the filter (Re_{f}) can be calculated:

$$Re_{\text{f}} = \rho d_{\text{f}} V_{\text{net}}/\mu\,. \tag{A3}$$

At higher Reynolds numbers, Λ_{e} deviates from the value calculated by equation (A2). Following Silvester, a new Λ_{e} was calculated from the graphs of Tamada and Fujikawa (1957) for the appropriate Re_{f}. This was incorporated smoothly into the computer simulations by digitizing the information in the graph and interpolating appropriate values. A log(log$x$) transformation was used to interpolate for values of h_1, h_2, and d_{f} that were not explicitly graphed. The new Λ_{e} was then used to recalculate γ and V_{net}, and this process was performed a total of three times. This resulted in a convergence between the new Reynolds number and the preceding Reynolds number to a difference of less than 5% (following Silvester 1983, p. 278). Unlike Silvester (1983), we invoked this iterative process for any Reynolds number, since we found that discontinuities could develop in graphs of simulations if a threshold Reynolds number (such as 0.1) was chosen.

Calculation of 'E_{net}'

The efficiency of particle capture (E_{net}) was calculated from the following parameters: d_{p}, particle diameter (m); d_{f}, fiber diameter (m); Re_{f}, Reynolds number of the fiber; h_1, mesh width (m); and h_2, mesh length (m).

The efficiency of a single fiber (E_{f}) was calculated:

$$E_{\text{f}} = \left[2\,\frac{d_{\text{f}} + d_{\text{p}}}{d_{\text{f}}}\ln\!\left(\frac{d_{\text{f}} + d_{\text{p}}}{d_{\text{f}}}\right) - \frac{d_{\text{f}} + d_{\text{p}}}{d_{\text{f}}} + \frac{d_{\text{f}}}{d_{\text{f}} + d_{\text{p}}}\right] \Big/ \Lambda_{\text{e}}\,. \tag{A4}$$

Equation (A4) is appropriate for low-Reynolds-number flows (Silvester 1983). Silvester also reported an alternative equation to calculate the efficiency of a single fiber, which is more appropriate for high-Reynolds-number flows. Equation (A4) was used for all simulations because the Reynolds number of the fiber was always below 10 for the reported results. In addition, there was no threshold Reynolds number obviously appropriate for determining which equation to use that would not lead to large discontinuities in some calculations.

The efficiency of the whole filter or net was calculated using the efficiency of the fiber calculated above:

$$E_{\text{net}} = E_{\text{f}} d_{\text{f}}/h_1 + E_{\text{f}} d_{\text{f}}/h_2 - (E_{\text{f}} d_{\text{f}})^2/h_1 h_2\,. \tag{A5}$$

The efficiency of the net is the proportion of particles going through the net that are retained by the net. If the particle size is greater than or equal to the width of the mesh opening, then the efficiency of the net is set equal to 1 to avoid the nonsense result of an efficiency greater than one. These calculations for efficiency assume complete adhesion; that is, if a particle touches the fiber, it sticks. The last term in equation (A5) compensates for particles caught by two silk strands near an intersection of strands (i.e., they are counted once instead of twice; Silvester 1983). If we assume that the adhesion may not in fact be absolute and that a particle simultaneously caught by two threads at a corner may have twice the probability of being retained as a particle caught by only one thread, then the efficiency of the net would be more appropriately expressed as

$$E_{\text{net}} = E_{\text{f}} d_{\text{f}}/h_1 + E_{\text{f}} d_{\text{f}}/h_2\,. \tag{A6}$$

All of the above simulations were rerun substituting equation (A6) for equation (A5). The substitution had only a trivial effect; clearly, low adhesion is not driving the patterns seen above.

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