Title
Empirical test of filtering theory: Particle capture by rectangular-mesh nets

Journal
Limnology and Oceanography, 35(1)

ISSN
0024-3590

Author
Loudon, Catherine

Publication Date
1990

DOI
10.4319/lo.1990.35.1.0143

Limnol. Oceanogr., 35(1), 1990, 143–148

Empirical test of filtering theory: Particle capture by rectangular-mesh nets

Abstract—Theoretical equations predicting particle capture by rectangular-mesh nets were evaluated empirically. Flow was measured through and around silk caddisfly nets and model nets (made of steel mesh) with a thermistor flowmeter. Measured speeds through nets were compared to theoretically predicted speeds based on net morphology and ambient water velocity. The median absolute percent difference between measured and predicted speeds was 20%, while the median absolute difference was 0.013 m s^{-1} (ambient speed range 0–0.60 m s^{-1}). Analysis of published distributions of particle sizes caught in caddisfly nets verified that larger particles in the water were more likely to be caught by the nets than smaller particles, but not by as great a factor as predicted. An adhesion probability of about 0.2% is necessary to make the theory agree with particle capture data.

Many aquatic organisms obtain their food by capturing suspended particles from the water with sticky filters (LaBarbera 1984). Silvester (1983) developed equations to calculate the rate of particle capture by rectangular-mesh nets, such as those spun by hydropsychid caddisflies (Trichoptera; Hydropsychidae). Particle capture rate is calculated as the product of four terms:

$$P = V_{net} \times E_{net} \times A \times C \qquad (1)$$

where P is the particle capture rate (particles s^{-1}), V_{net} the average velocity through the net (m s^{-1}), E_{net} the proportion of particles travelling through the net that get caught (dimensionless), A the total area of the net (m^2), and C the particle concentration in the water (particles m^{-3}) (Silvester 1983; Loudon and Alstad 1990). In empirical work, usually only two of the four terms (A and C) are measured or are set, and the other two (V_{net} and E_{net}) can be calculated from the properties of the net, the fluid, and the particles.

The theoretical derivation is made possible only by a number of simplifying assumptions that do not apply to real caddisfly nets. For example, caddisfly nets lie in velocity gradients, not a uniform velocity field; nets are not constructed of completely uniform meshes and are attached to rocks that have complex surfaces. The nets are slightly concave upstream and have irregular frames (formed of the particles and fibers that the caddisflies fasten together with silk). Given these complications, it is not clear whether these theoretical equations are accurate. Therefore, I assessed the validity of Silvester's derivation empirically.

Because estimates of the two calculated parameters (V_{net} and E_{net}) are based on different assumptions, it is particularly useful to analyze them separately. Velocity was measured through both stainless steel mesh and caddisfly nets with a thermistor flowmeter and compared with theoretical pre-

---

Acknowledgments

D. N. Alstad provided facilities where this work was done. The manuscript was improved by comments from D. N. Alstad, N. R. Silvester, and two anonymous reviewers. Partial financial support was provided by the University of Minnesota.

dictions. Distributions of particles caught in caddisfly nets (Fuller et al. 1983) were compared with theoretical predictions to test assumptions in calculating the efficiency term. Thus it is possible to evaluate how closely Silvester's equations predict filtering by caddisfly nets.

Local hydropsychid caddisfly larvae (genera *Hydropsyche* and *Cheumatopsyche*) collected in the field were placed singly on small rocks in a flow tank and allowed to spin nets (flow tank design of Vogel and LaBarbera 1978; two laminators, working cross-section 0.12 × 0.15 m, 0.90 m long between last laminator and propeller shaft). The temperature of the water in the flow tank was controlled at 20°C (total range 19°–21°C).

Twenty to twenty-eight hours after larvae were placed in the flow tank, flow was measured both around and through the center of the nets with a thermistor flowmeter having a probe tip of 1 mm (LaBarbera and Vogel 1976). These flow measurements were made before altering the set current speed of the flow tank or the position of the rock. Each net was used only once for estimates of flow for the conditions in which the net was spun. Upstream access to the net was less obstructed by larval construction, so flow through the net was measured directly upstream of the center of the net (~1 mm away from the mesh as the nets are slightly concave upstream). Ambient flow was estimated at four different locations at each net: 1 mm above the center of the top of the net; 2 mm above; 1 mm to one side of the net halfway up the edge; 2 mm to the same side. Because the four measurements did not differ significantly from each other, their average was used to estimate ambient flow (multivariate ANOVA with the four measurements as the four response variables, $P = 0.38$, $n = 20$ nets). Larvae were in their retreats but were not attending nets during flow measurements.

Thermistor flowmeters are sensitive to temperature and orientation in flow. All calibrations and measurements were made between 19° and 21°C, keeping orientation of the flowmeter probe constant with respect to local current. Each flow datum is the average of 10 measurements at a single point; voltage output was recorded every 2 s for 20 s (average SE for mean of 10 measurements = 0.016 m s^{-1}). The flowmeter probe was moved in the water and distances were measured to 0.1 mm with a micromanipulator (Brinkman model RP-III). To calibrate the flowmeter probe, I combined five different independent trials because the unexplained variance between trials was greater than the unexplained variance within trials. For calibration at slow speeds, velocity of the water relative to the probe was estimated by timing movement of dye in water or by timing the movement of a motor-driven platform. For calibration at higher speeds, the probe tip was held centrally near the end of a cylinder through which water was running. The volume flow rate through the cylinder was estimated by collecting water leaving the cylinder, and the velocity of water at the center of the cylinder could be estimated as twice the average flow rate because the length of the cylinder and the speed of the water were in the appropriate range to ensure a fully developed laminar flow. The median absolute difference between the measured velocity and the calculated velocity (resulting from regression) during calibration trials was 0.007 m s^{-1}, and the median absolute percentage difference was 8.0% ($n = 35$ data points for the combined calibration curve in the velocity range $0.02–0.65 \text{ m s}^{-1}$).

Twenty nets were spun by 10 larvae. After measuring the flow through and around the nets, each net was dissected from the supporting framework underwater with a dissecting microscope and mounted on a glass slide. Ten measurements of silk thickness at midpoints between silk intersections were made for each net with an ocular micrometer on a compound microscope (average SE for mean of 10 measurements = 0.16 μm). Average silk widths for the nine *Cheumatopsyche* nets ranged from 4.8 to 5.8 μm and for the 11 *Hydropsyche* nets from 5.8 to 11.6 μm.

Mesh size was measured by projecting the image of the net onto a digitizing tablet (Ken-A-Vision microprojector and Numonics 2210 tablet). Mesh length and width (distances between centers of adjacent silk fibers) were digitized and stored automatically in computer files for all meshes in each net (range, 50–1,120 meshes net^{-1}). The range in median mesh sizes was from 39 × 65 μm to 72 × 113 μm for *Cheumatopsyche* nets and from 144 × 177 μm to 239 × 311 μm for *Hydropsyche* nets (median mesh widths and median mesh lengths). The C.V. in mesh size for single nets averaged 16%, and the mesh sizes were not normally distributed.

Circles of stainless steel mesh (Small Parts, Inc.) were glued on annular Plexiglas frames. Four sizes of square mesh were used (corresponding wire diameters and mesh lengths: 380 and 1,270 μm, 280 and 845 μm, 255 and 635 μm, 190 and 425 μm). Mesh lengths are distances between centers of adjacent fibers as used above. Three sizes of frame were used (corresponding inner and outer diameters were 31.5 and 37.5 mm, 28.5 and 34.5 mm, and 19.3 and 25.3 mm; length, perpendicular to mesh, was 1.5 mm). Thus, there were 12 steel net "morphologies": three frame sizes × four mesh sizes. A steel "net" (frame + mesh) was held in the flow tank by a wire (1.1-mm diam) attached to the Plexiglas frame. As mesh was attached to one side of a frame, the net was asymmetrical and was always oriented with the mesh side downstream.

Flows were measured through the steel nets with the flow tank and the flowmeter described above. The steel nets were held centered in the flow tank, either halfway up the column of water (total water depth, 0.12 m) or touching the bottom of the flow tank. For each net the flow was set at fast, medium, or slow speed. Thus, there were six flow environments for each of the 12 net morphologies: two positions × three ambient water velocities. Flow through the net was measured between 1 and 2 mm downstream of the center of the mesh. Ambient velocity was measured by leaving the probe of the flowmeter clamped in place and removing the net from the water. Flow marker (aqueous solution of fluorescein disodium) was used to ensure that the water measured by the flowmeter had in fact gone through the mesh. This procedure was particularly crucial for fine meshes at higher speeds; vortices can form behind the mesh, rendering the flowmeter reading misleading.

Data appropriate for calculations of particle capture efficiency already existed in the form of particle capture by unattended hydropsychid caddisfly nets in a stream (Fuller et al. 1983, *Hydropsyche betteni*). Particles measured ranged in size from 12 to 45 μm. The mesh size of these caddisfly nets averaged 150 × 250 μm (Fuller and Mackay 1980), so these particles were not caught by sieving.

Theoretical velocity through the net (V_{net}) and efficiency of particle capture by the net (E_{net}) were calculated from measured ambient velocity and net morphology following Silvester (1983) with the following clarifications or modifications (explained in more detail by Loudon and Alstad 1990). The nets were assumed to be flat, direct interception was assumed to be the major mechanism for particle capture, and Tamada and Fujikawa's (1957) correction factor was always used in calculating the pressure drop through the mesh. To characterize morphology of a single net, I used the mean fiber diameter, median mesh width, and median mesh length. A single estimate of ambient velocity was used for each net (measurements explained above). Once V_{net} and E_{net} were calculated, particle capture rate could be calculated from Eq. 1.

To predict theoretically the particles caught in a net, it was necessary to know the number of particles in each size class in the water, as well as the ambient velocity and net morphology (morphological data from Fuller and Mackay 1980; particle data from Fuller et al. 1983). Parameters used in the calculations were: fiber diameter, 9.2 μm; ambient velocity, 0.50 m s^{-1} (which leads to a theoretical V_{net} of 0.38 m s^{-1}), particle concentration, 5.385×10^9 particles m^{-3} with size distribution as by Fuller et al. (1983) (*see Fig. 2*); total area of net, 77 mm^2; fluid viscosity, 0.001 Pa s; fluid density, 1,000 kg m^{-3}. An assumption must be made about the adhesive properties of the particles and the net; the adhesivity between them was arbitrarily set at 100% (following Silvester 1983).

Theoretical V_{net} was compared to measured V_{net} for both the steel nets and the caddisfly nets (Fig. 1). When steel and silk meshes were combined, the median abso-

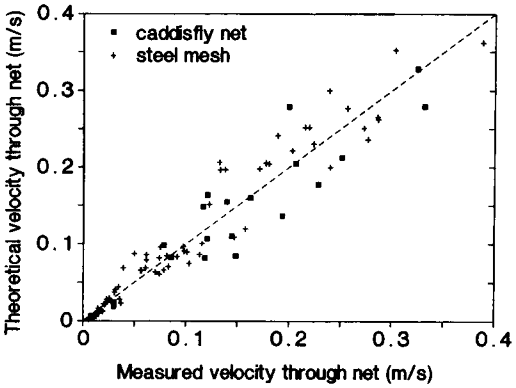

Fig. 1. Theoretical vs. measured velocity through caddisfly nets and steel mesh nets. Each point is for a single net and is the mean of 10 measurements (average SE for mean of 10 measurements = 0.016 m s^{-1}). Line describes the points for which theoretical velocity equals measured velocity and is indistinguishable at this scale from the regression line, slope = 0.98 (SE = 0.03), intercept = 0.003 (SE = 0.005), $r^2 = 0.92$, $n = 20$ for caddisfly nets, $n = 71$ for steel nets.

lute difference between measured and theoretical speeds was 0.013 m s^{-1}, and the median percent difference was 20%. At higher speeds absolute differences were greater but percent differences were lower.

Separate regression lines for steel and silk nets do not differ significantly in slope ($P = 0.14$) and neither has an intercept significantly different from 0 ($P = 0.54$, $P = 0.76$). Linear regression on the combined data results in the equation $y = 0.981x + 0.003$ [y = theoretical velocity through net (m s^{-1}), x = measured velocity through net (m s^{-1}), $r^2 = 0.92$, $n = 91$], the slope of which is not significantly different from 1 (t-test, $SE_{slope} = 0.032$, $P > 0.50$). Note that measured V_{net} was estimated immediately upstream or downstream of a net; exactly how it relates to the velocity between the filter elements is unknown.

This congruity between the results for steel and for silk nets is especially remarkable because of the differences in Reynolds number (Re). Re (for a fiber of the net and average flow speed through the net) ranged from 1 to 100 for the measurements through steel nets and from 0.03 to 3 for the measurements through silk nets. The proportion of water approaching a net that actually passed through ranged between 15 and 75% for steel mesh and from 20 to 90% for silk nets (a larger proportion of water passed through the net at higher Re).

The flow measurements through steel and through silk had different strengths and shortcomings for evaluating Silvester's (1983) equations predicting V_{net}. As the theoretical solutions were inspired by the silk nets of caddisflies (Silvester 1983), the silk nets had the advantage of obvious relevance in testing the applicability of the theory. One shortcoming of the silk nets was that the ambient velocity estimates were approximate by necessity; theoretically it would have been best to measure flow with and without the nets in place. This procedure was possible with the steel nets but not with the silk nets.

One advantage of the steel nets was that it was possible to construct any desired size of net and size of mesh and impose any position in the flow tank. The total size of a net did not affect the relationship between theoretical and measured V_{net} (within the ninefold difference in total area used); the three size classes significantly affected neither the slope ($P = 0.68$) nor the intercept ($P = 0.91$) in an ANCOVA with measured V_{net} as the covariate. Size of net does not enter into the equations (Silvester 1983), because it is assumed that the Reynolds number of the whole net in ambient flow was large enough to make the drag coefficient close to unity (Silvester pers. comm.). These results, therefore, validate this assumption.

The position of the net, whether in the center of the water column or touching the bottom of the flow tank, did not affect the relationship between theoretical and empirical V_{net}; the two position classes did not significantly affect the slope ($P = 0.74$) or the intercept ($P = 0.46$) in an ANCOVA. This result is important because the derivation assumes that a net is suspended in an infinite medium of constant velocity, while a real net is attached to the bottom and hence lies in a velocity gradient. As measurements were made only at the center of nets, this result should not be interpreted to mean that the velocity gradient across a net is independent of location in a water column.

Mesh size did influence the relationship between theoretical and empirical V_{net} for

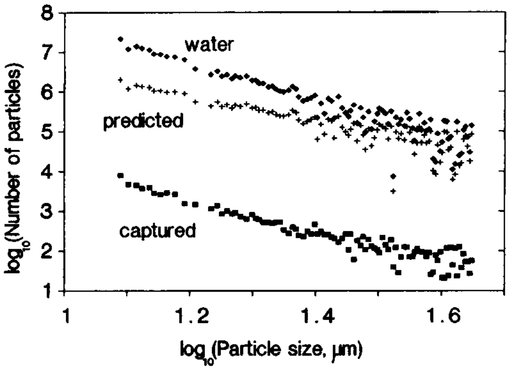

Fig. 2. Number of particles captured by a net in 1,200 s (■), predicted to be caught in that time (+), and in the water passing through the net in that time (◆), all as functions of particle size (particle data from Fuller et al. 1983). Regression lines are: particles captured, $y = -3.73x + 7.69$, $r^2 = 0.91$; predicted to be caught, $y = -3.22x + 9.73$, $r^2 = 0.77$; in the water, $y = -4.63x + 12.2$, $r^2 = 0.88$ [$y = \log_{10}$ (No. particles) and $x = \log_{10}$ (particle size, μm)].

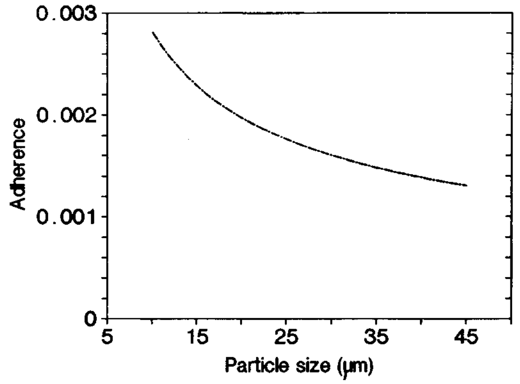

Fig. 3. Relative adherence (particles caught/predicted) as a function of particle size, calculated from difference in regression lines in Fig. 2.

the steel nets; slopes are significantly different between the four mesh classes ($P = 0.0002$). The slopes neither increase nor decrease monotonically with mesh size, and so the functional significance of this small but statistically significant result is not clear. The slopes were (in increasing order of mesh size) 1.103 (SE = 0.057), 0.928 (SE = 0.025), 1.132 (SE = 0.061), and 1.297 (SE = 0.079). The mesh size interaction was not statistically significant for the silk nets ($P = 0.60$), possibly because the silk nets varied less in percentage of open area than did the steel mesh. Hydropsychid caddisfly nets are typically about 90% open because of the isometric scaling between silk width and mesh size (Loudon and Alstad 1990), while the steel mesh ranged from 30 to 50% open (total proportion of projected area not occluded by fiber).

Larger particles are theoretically more likely to be captured by the silk fibers than smaller particles (Silvester 1983). This prediction was verified from the data of Fuller et al. (1983) by comparing sizes of particles caught in the net with those in the water (Fig. 2); the size distribution of particles was significantly different between net and water (slopes of numbers of particles regressed on particle size are significantly different, $P = 0.05$) (also noted by Fuller et al. 1983). The tendency toward the capture of larger particles is not as large, however, as predicted with Silvester's equations. The numbers predicted and captured differ by a factor of about 500 and have a significantly different distribution with particle size (slopes are significantly different, $P = 0.02$). This result is robust to a significance level of 0.05, even assuming an uncertainty of 20% in the parameters used in the calculations (morphological characteristics of the nets and ambient velocity). This difference in slopes means that the adherence of particles to silk might decrease with increasing particle size on average (Fig. 3). For example, if the theory is strictly correct, 15-μm particles remained adhered on average 2.3 times out of 1,000 theoretical contacts with a silk strand, and 40-μm particles remain adhered on average 1.4 times. Silvester (1983) pointed out that particles of different sizes may not have the same probability of adhering to a fiber. Note that it is not possible to rule out the alternative explanation that adhesion is in fact very strong and the theory does not adequately describe particle capture by caddisfly nets. More empirical work is needed to distinguish among these alternatives.

Catherine Loudon[1]

Department of Ecology, Evolution, and
Behavior
University of Minnesota
Minneapolis 55455

---

[1] Present address: Department of Biology, Ithaca College, Ithaca, New York 14850.

References

FULLER, R. L., AND R. J. MACKAY. 1980. Feeding ecology of three species of *Hydropsyche* (Trichoptera: Hydropsychidae) in southern Ontario. Can. J. Zool. **58**: 2239–2251.

———, ———, AND H. B. N. HYNES. 1983. Seston capture by *Hydropsyche betteni* nets (Trichoptera; Hydropsychidae). Arch. Hydrobiol. **97**: 251–261.

LABARBERA, M. 1984. Feeding currents and particle capture mechanisms in suspension feeding animals. Am. Zool. **24**: 71–84.

———, AND S. VOGEL. 1976. An inexpensive thermistor flowmeter for aquatic biology. Limnol. Oceanogr. **21**: 750–756.

LOUDON, C., AND D. N. ALSTAD. 1990. Theoretical mechanics of particle capture: Predictions for hydropsychid caddisfly distributional ecology. Am. Nat. In press.

SILVESTER, N. R. 1983. Some hydrodynamic aspects of filter feeding with rectangular-mesh nets. J. Theor. Biol. **103**: 265–286.

TAMADA, K., AND H. FUJIKAWA. 1957. The steady two-dimensional flow of viscous fluid at low Reynolds numbers passing through an infinite row of equal parallel circular cylinders. Q. J. Mech. Appl. Math. **10**: 425–432.

VOGEL, S., AND M. LABARBERA. 1978. Simple flow tanks for research and teaching. BioScience **28**: 638–643.

Submitted: 20 December 1988
Accepted: 27 July 1989
Revised: 10 January 1990