

EFFECTS OF MICROHABITAT SELECTION ON FEEDING RATES OF NET-SPINNING CADDISFLY LARVAE¹

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Abstract. Net-spinning caddisfly larvae of the family Hydropsychidae are known to prefer microhabitats with large, stable substrate and high water flow velocity. It is often assumed that net spinners in high-velocity microhabitats have higher feeding or growth rates than larvae in less preferred sites, but there is no direct evidence to support this assumption. We hypothesized that net-spinning caddisflies would select microhabitats that offered the greatest feeding rates. This hypothesis was tested by field experiments in which we determined if net-spinning caddisfly larvae preferred high-velocity sites even when substrate size and type were held constant. We then measured feeding rates of net spinners in microhabitats with different flow characteristics. High-flow positions were selected by 96% of hydropsychid larvae colonizing artificial moss substrates. *Artemia nauplii* released into the water column were captured by individual larvae in high-flow sites at a rate of 0.016%/m, significantly higher than the capture rate in low-flow sites. Combining this rate of prey capture with mean hydropsychid densities of 1125 individuals/m², we estimate that hydropsychid larvae in riffles remove drifting invertebrate prey at a rate of $\approx 18\%$ /m. Assuming exponential prey removal, a prey item in the drift would travel an average of only 5.5 m before being consumed. This study is one of the first to show that the distribution of a stream filter feeder is related to the feeding rates obtainable in different microhabitats.

Key words: artificial substrate; colonization; current velocity; feeding rates; invertebrate drift; microhabitat; net-spinning caddisflies; seston.

INTRODUCTION

Many streams are dominated, in terms of biomass and secondary production, by filter-feeding invertebrates. Immature insects such as larval black flies (Diptera, Simuliidae) and net-spinning caddisflies (Trichoptera, especially the Hydropsychidae and Philopotamidae) are generally the most important filter feeders in smaller streams, where they are found primarily on rocky substrata or on aquatic macrophytes. In larger rivers, filter-feeding insects are limited to scarce hard substrata such as woody snags (Cudney and Wallace 1980, Benke et al. 1984), and other invertebrates such as bivalves (Cohen et al. 1984) and protozoans (Carlough and Meyer 1990) become the more important filter feeders.

Substrate characteristics (size, stability, heterogeneity, and surface texture) are important determinants of the distributions of many stream invertebrates (Minshall 1984), while current velocity and flow patterns would be expected to have a direct influence on passive filter feeders such as net-spinning caddisfly larvae (cf. Edington 1965, 1968, Osborne and Herricks 1987). What are the relative importances of substrate and

velocity in determining the distributions of the net-spinning caddisflies? Caddisfly larvae with coarse-meshed nets (the Arctopsychinae and larger Hydropsychinae) are known to prefer sites on the tops and sides of large rocks in rapid flows (cf. Wallace 1975, Malas and Wallace 1977). Several studies (Williams and Hynes 1973, Wallace 1975, Haefner and Wallace 1981, McAuliffe 1983, 1984) have found positive associations between moss or riverweed (*Podostemum*) cover and the distributions of net-spinning caddisfly larvae. The three caddisfly species studied by Williams and Hynes (1973) showed higher association indices with moss cover than with velocity or substrate size; substrate size was significantly associated with current and moss cover. Distributions of both species of net-spinning caddisflies in Haefner and Wallace's (1981) study were significantly correlated with moss cover, while the correlation with current velocity was insignificant for one species and significant but weaker than the correlation with moss cover for the other. These studies suggest that net spinners may be directly selecting moss or *Podostemum* habitats, due to the support provided for their net/retreat structures, or because of the increased surface area and habitat heterogeneity provided by the plant cover (Minshall 1984).

The available data concerning microhabitat selection by net-spinning caddisflies fail to distinguish the

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effects of substrate type and current velocity. A confounding correlation between moss cover and current velocity may exist because large, stable substrata, which support the greatest moss cover, will predominate in erosional zones in streams due to the sediment-sorting effect of current (Leopold et al. 1964). This raises the question, do net-spinning caddisflies select the tops and sides of large rocks because these locations provide high-velocity microhabitats, or because of a preference for moss habitats? These confounding effects can only be disentangled by means of controlled experiments conducted in the natural stream environment (Hart 1983, Minshall 1984).

We hypothesized that net-spinning caddisflies, because they are passive filter feeders, would select microhabitats offering the greatest rate of seston flux into their nets. Stream filter feeders exhibit intra- and interspecific aggressiveness in both laboratory and field studies (Edington 1965, Glass and Bovbjerg 1969, Hemphill and Cooper 1983, Hart 1986, Gatley 1988, Hemphill 1988, Hershey and Hiltner 1988), and there exists indirect evidence that interspecific competition for suitable sites for nets may have driven the evolution of net-spinning caddisflies (Georgian and Wallace 1981, Alstad 1986, Thorp et al. 1986). Gut analyses (Benke and Wallace 1980) and behavioral studies (Petersen 1985) have shown that the larger hydropsychid larvae feed selectively on high-quality food items such as diatoms and drifting animals, despite the fact that these materials compose only a very small portion of the particulate organic matter (POM) transported by streams (e.g., Parker and Voshell 1983). A strong positive correlation exists between the proportion of animal material in the guts of hydropsychids and the velocity in which the larvae place their nets (Wallace 1979). This correlation suggests that a high filtration rate is required for hydropsychid caddisflies to specialize on rare food items (Georgian and Wallace 1981, Petersen et al. 1984), but there is no direct evidence that net spinners in high-velocity microhabitats have higher feeding or growth rates than larvae in less preferred sites.

We tested the hypothesis that net-spinning caddisflies preferred microhabitat sites offering greater access to suspended food by allowing net-spinning larvae to colonize artificial moss-like patches positioned in four different orientations with regard to current flow. In this way we created microhabitats in which substrate type was held constant while velocity was varied. We then released food particles into the water column and measured feeding rates of larvae in different microhabitats. Our study addressed three questions. (1) Would net-spinning caddisfly larvae colonize artificial substrates on the basis of current flow, when the confounding effects of substrate type, size, and stability were held constant? (2) Is substrate selection by net spinners related to feeding success? (3) Can suspension feeding by net-spinning caddisfly larvae influence the

type and quantity of organic matter in suspension in streams on a local or larger scale?

STUDY SITE

The study site is located within the Mianus River Gorge Preserve maintained by The Nature Conservancy. The Mianus River arises in mid-eastern Westchester County, New York, in the township of North Castle. It flows ≈ 70 km through New York and Connecticut to Long Island Sound. The river passes through a small (≈ 1.50 -ha) impoundment 1.5 km upstream of the study site. The reach studied is third order. It has typical summer discharges of 0.2–0.5 m³/s, widths of 5–10 m, and depths of 0.5 to 1.5 m in pools and <0.5 m in riffles. Composition of the stream bed ranges from gravels to large cobbles and boulders. Rocks with diameters of > 10–15 cm are covered with growths of aquatic mosses. At the study site the river flows between gorge walls of 40–50 m height, limiting direct penetration of sunlight to the stream bed to a period of 2–3 h around noon in the summer. Hemlock stands predominate on the gorge walls and large hemlock boles form many debris dams in the river.

During the summer study periods (June–August) the stream was warm, with temperatures ranging from 15.5° to 22.5°C. The water was circumneutral, with pH of 7.4, and two measures of positive charge concentration, alkalinity and hardness, with values of 1.2 and 0.82 mmol/L, respectively. The dry-mass concentration of suspended particulates (seston), determined in June 1986 by wet-seiving (cf. Gurtz et al. 1980 for methods), was 4.63 mg/L, of which 1.06 mg/L was organic material (the ash-free dry mass).

METHODS

Colonization experiments

Substrate patches consisting of synthetic grass carpet (hereafter, "artificial moss") were placed in the Mianus River for 21-d colonization periods. Previous workers (Philipson 1969, Hildrew and Edington 1979, Fuller et al. 1983, Smith-Cuffney 1987) have found that this artificial substratum is readily colonized by net-spinning species that normally occupy moss habitats. The carpet had a density of 12 tufts/cm²; each tuft consisted of ≈ 12 –15 thin plastic strips 1 cm in length and 0.6 mm in width. Substrate patches were attached to 6 cm high steps in plexiglass troughs in four orientations with respect to current flow (Fig. 1): upstream face, top, downstream face, and "valley" position, in the region of "dead water" on the base of the trough between two adjacent steps. (We will refer to these orientations as top, upstream, downstream, and valley positions, respectively.) Patches were 6.5 × 15.25 cm (100 cm²) and were attached with Velcro hook-and-loop fasteners (Fuller et al. 1983) to permit rapid removal without disturbing nearby patches.

We determined colonization curves of net-spinning

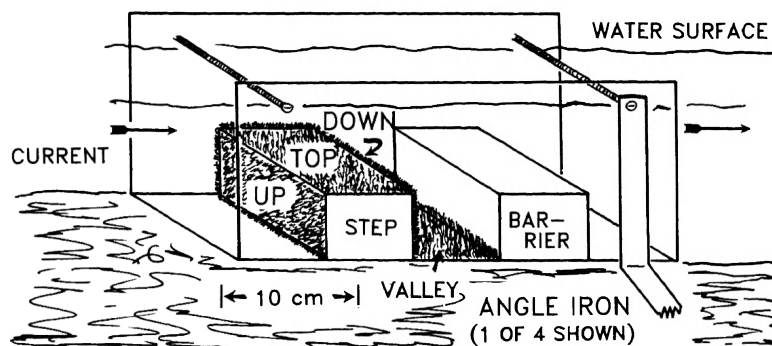


FIG. 1. Diagram of plexiglass troughs used in the colonization and feeding experiments. The steps are 6.5 cm wide, and the upstream step is covered by 6.5×15.25 cm patches of artificial grass carpet.

caddisfly larvae on these artificial substrates during June and July 1986. Substrate patches from each of the four microhabitat positions were collected at intervals of 3, 6, 9, and 16 d. Invertebrates were identified to species and instars were separated on the basis of head capsule width histograms (e.g., Mackay 1978). Accumulated sediment was characterized as inorganic (residual mass after ashing at 500°C) or organic (ash-free dry mass).

During the summer of 1987 we placed 24 replicate troughs in two riffles (12 troughs on 24 June and 12 on 2 July). The locations of the troughs were carefully standardized with respect to velocity, water depth, and substrate size distributions to reduce variability between treatments (Allan 1983, Walde and Davies 1984). We measured water depth and velocity over the downstream or barrier step (Fig. 1) of each trough on three dates. Velocity was measured ≈ 2 cm above the step with a bag meter designed by Gessner (Hynes 1970:6). Froude numbers (Fr) were calculated from depth and velocity measurements to assess whether flow over the steps in the troughs was subcritical ($Fr < 1$) or supercritical ($Fr > 1$) (Smith-Cuffney and Wallace 1987, Davis and Barmuta 1989).

After colonization for 21 d, the troughs were used for short-term feeding experiments (see *Feeding rate measurements*) and then the substrate patches were removed and preserved in Kahle's fluid (Pennak 1978: 780). Net-spinning caddisfly larvae were identified to instar and counted. Abundance data were transformed logarithmically to achieve normality and homogeneity of variance among treatments. Differences in distribution among the four patch positions were analyzed by ANOVA. Comparisons of means were based on Tukey's honestly significant difference (T) method (Sokal and Rohlf 1981:245).

We sampled net-spinning caddisfly larvae from natural moss habitats in the Mianus River on 10 July and 7 August 1987 in order to determine if the abundances on artificial substrate patches were similar to those on natural substrates. Nine samples were collected on each date, using a modified Hess sampler with a sample area

of 65 cm^2 , which permitted us to restrict samples to the moss-covered tops of single rocks.

Feeding rate measurements

Half of the troughs used for colonization experiments were randomly assigned at the end of the colonization period to receive high-quality animal food (laboratory-reared *Artemia salina* nauplii) as a food supplement. *Artemia* are of course not natural prey of Mianus River net spinners, but they were available in the large quantities required for these experiments, and preliminary observations showed that they were consumed readily by the net spinners. The fact that *Artemia* are not part of the stream's natural fauna insured that any appearing in caddisfly nets or guts were part of the experimental releases. Two-day-old nauplii were fed on a suspension of $6.3 \mu\text{m}$ diameter, red-dyed polystyrene microspheres (Polysciences, Warrington, Pennsylvania) for 30 min to mark them and then rinsed thoroughly to remove undigested microspheres and salt from their culture medium. A suspension of *Artemia* in 2.5 L of stream water was dispensed into the center of each trough, 10 cm upstream of the first step and at mid-water depth, over 20–30 min. Preliminary observations with food dye indicated that material released in this manner was thoroughly mixed in the water column, both laterally and vertically, before reaching the substrate patches. The *Artemia* mixture was stirred constantly while being dispensed to ensure homogeneity. Replicate, 10-mL subsamples of the *Artemia* suspension were collected to enable us to calculate the number of *Artemia* released into each trough. Food supplement releases began with troughs at the downstream end of each riffle and proceeded upstream to avoid unintended transport of the supplement to other troughs.

Artemia were released at a rate that produced a concentration of 0.66 ± 0.16 nauplii/L ($\bar{X} \pm \text{SE}$, $n = 10$) in the troughs. More *Artemia* were released during the second experimental period (23–24 July) than on the first date (15 July). As a result, the concentration of *Artemia* in the troughs was more than three times great-

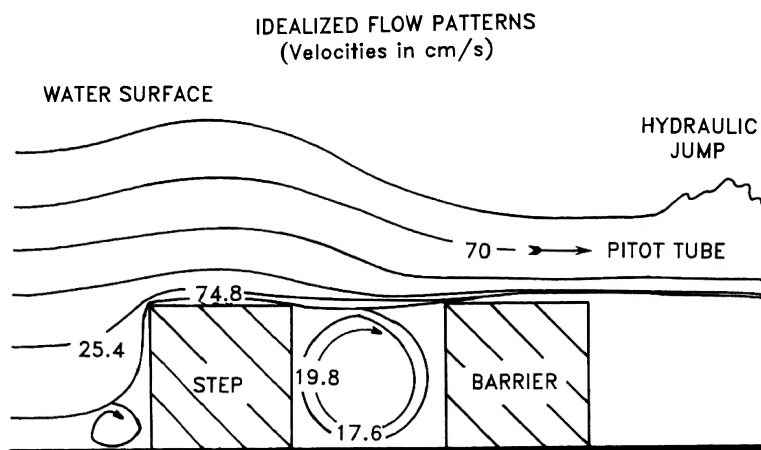


FIG. 2. Flow profiles through the experimental troughs, as visualized in a laboratory flume. The free-stream velocity (70 cm/s) was measured with a pitot tube in the location illustrated. The velocities indicated for each substrate position are means of 25 measurements.

er in the second set of experiments (mean = 1.03 nauplii/L vs. 0.30 nauplii/L on 15 July), a significant difference ($P = .012$, t test). We therefore expressed *Artemia* capture by caddisflies as a percentage of the total number released in each trough to permit comparisons between sample dates among troughs. Because these percentages were uniformly very small (all lying between 0 and 0.2%) and skewed strongly to the right, they were transformed logarithmically to remove dependence of the variance on the mean (linear regression, $P < .0001$ before transformation, $P > .50$ after transformation) and to ensure homogeneity of variances among treatment groups (Bartlett's test, $P < .0001$ before transformation, $P > .01$ after transformation). The arcsine transformation was not successful in normalizing these data because they were not distributed symmetrically (Sokal and Rohlf 1981).

Caddis larvae were given an additional 10 min to clear their nets and then the substrate patches were collected and placed in Kahle's fluid. We counted *Artemia* in caddisfly foreguts using light microscopes. Detecting the translucent *Artemia* was made easier by the presence of the red microspheres they had ingested.

Flow measurements

We measured flow through the experimental troughs in a laboratory flume. A pitot-static tube (cf. Vogel 1981:47) was used to determine water velocities in the main water column. Differential pressures generated by the pitot-static tube were read with a Gilmont micrometer manometer (Gilmont Instruments, Barrington, Illinois) using carbon tetrachloride (specific gravity = 1.60) as a manometer fluid. Flow profiles at heights of 3–10 mm over the substrate patches were analyzed using hydrogen bubbles as a means of flow visualization (Merzkirch 1974). Mean velocities over each substrate position and idealized flow patterns are shown in Fig. 2. Velocity differences among positions were highly significant (ANOVA, $P < .001$). The top posi-

tion had velocities significantly higher than the other positions ($P < .001$). Velocities over the upstream position were significantly faster than those over the valley positions ($P < .01$), but not different from the downstream position ($P = .068$). Two regions of flow occurred over the upstream patches (Fig. 2): rapidly flowing water moving over the step, and a much slower vortex formed in the corner between the base of the trough and the vertical wall of the step. Mean velocity may underestimate the high-velocity microhabitats that are present on the upstream patches. Overall flow patterns were very similar to the skimming flows described by Nowell and Jumars (1984:321), who pointed out that benthic depressions are areas of "reduced shear stress and enhanced deposition or residence time of suspended material." The flow in the depression between the steps was slow, and examination of individual particle tracks showed that many suspended particles were swept across the opening and did not enter the depression.

RESULTS

Rate of colonization

The preliminary colonization experiment in the summer of 1986 indicated that hydrosychid caddisfly larvae reached constant abundances on the substrate patches in 6–9 d (Fig. 3A). Abundances of nearly 50 larvae per patch occurred in top positions, higher than the average abundances that occurred on natural moss or on artificial patches in any position in the following summer. The preliminary experiment was not replicated, so the significance of these differences cannot be assessed, but it seems likely that the high abundances observed in 1986 were due to the low discharge that summer, which concentrated the river's flow into a narrow channel, with our troughs occupying as much as 20% of the width of the stream. In 1987 the river had a higher summer discharge, the riffles were much

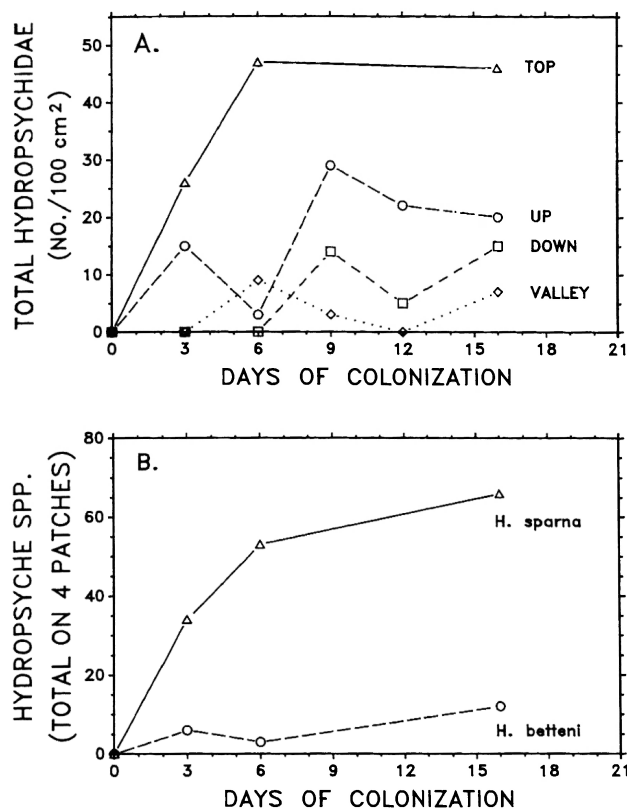


FIG. 3. Colonization of artificial substrates in the Mianus River, July 1986. (A) Abundances of all hydropsychid larvae, including *Hydropsyche* and *Cheumatopsyche*, on the four substrate positions on ridge transverse to the water flow (Upstream, Top, Downstream, and Valley). Samples from the Top positions were lost on days 9 and 12. (B) Colonization curves for *Hydropsyche betteni* and *H. sparna*, summed over all four substrate positions (total area 400 cm²). Days 9 and 12 are omitted because of the loss of samples from the Top position.

wider, and the experimental troughs occupied a negligible portion of the stream.

Colonization rate differed between the two most abundant net-spinning caddisflies, *Hydropsyche betteni* and *Hydropsyche sparna* (Fig. 3B). *H. sparna* colonized rapidly with individuals of late instars dominating. *H. betteni* arrived slowly, and 86% of colonizers were first and second instars. The difference in colonization patterns between these two species is probably due to their life cycles. At the study site in June–July, 56% of *H. betteni* larvae were in final (fifth) instar, and the remaining larvae were in first through third instar. Final-instar larvae undergo pupation in early August and show little tendency to drift at this stage of their life cycle. *H. sparna*, by contrast, was in the midst of a summer cohort, and larvae of all instars were present.

Organic and inorganic sediment collected on the artificial substrate patches during the 20-d preliminary colonization study. Organic sediments reached a plateau on all but the valley positions in 9 d (Fig. 4A), while inorganic sediments initially increased to high levels on the horizontal patches (top and valley posi-

tions) and then stabilized at similar levels for all but the valley positions, which again were still increasing at 9 d (Fig. 4B). Overall, the results of our preliminary colonization experiments agreed well with Smith-Cuffney (1987), who found that collector–filterers colonized artificial moss substrates rapidly, reaching maximum abundances in 7 d, and that sediment loads leveled off in 10–15 d.

Microhabitat selection

During our 21-d colonization periods in 1987, both hydropsychid and philopotamid larvae showed highly significant (ANOVA, $P < .001$) selection for the top and upstream substrate positions. Hydropsychid abundance was highest on the upstream positions (Fig. 5A), with densities very comparable to those in natural moss habitats. Abundances on top positions were lower but not significantly different than upstream substrate patches, while abundances on downstream and valley substrate patches were significantly lower than in other positions. Distributions of philopotamid larvae were similar (Fig. 5B). Densities on upstream substrate patches were higher than on natural moss, although the difference was not significant.

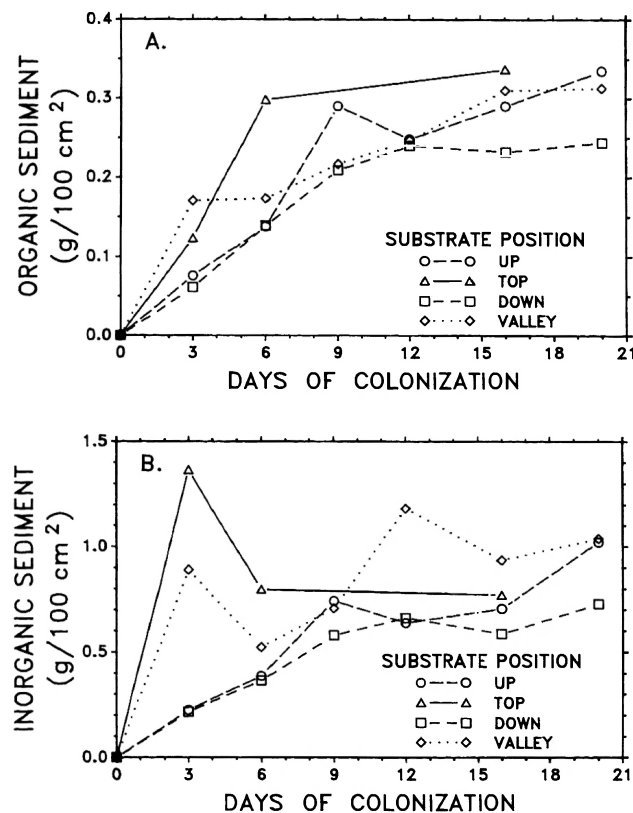


FIG. 4. Accumulation of (A) organic and (B) inorganic sediment in four positions (Upstream, Top, Downstream, and Valley) on artificial moss substrates on ridges transverse to the water flow in the Mianus River, July 1986. Samples were divided into organic and inorganic dry-mass fractions by ashing at 500°C. Samples from the Top positions were lost on days 9, 12, and 20.

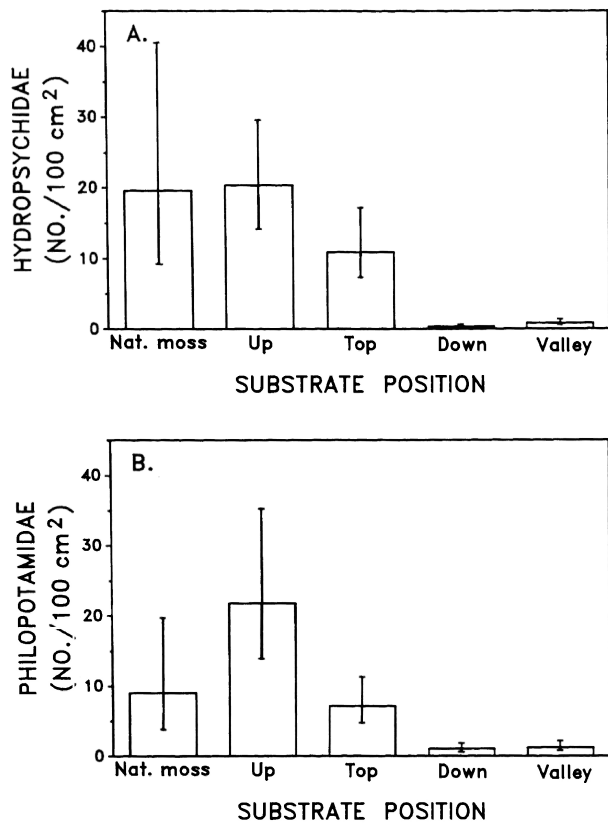


FIG. 5. Abundances of net-spinning caddisflies on natural and artificial substrates. The vertical bars represent 95% confidence intervals, which are asymmetric because they are based on log-transformed data. Differences among means were tested with ANOVA and Tukey's HSD. Positions whose means do not differ significantly ($P > .05$) are underlined in the lists below. (A) Densities of larval hydropsychids (*Hydropsyche betteni*, *H. sparna*, and *Cheumatopsyche* spp.); ANOVA: Nat.Moss Upstream Top Valley Downstream. (B) Densities of larval philopotamids (*Chimarra* sp. and *Dolophilodes* sp.); ANOVA: Upstream Nat.Moss Top Valley Downstream.

Feeding rates

Capture rates by net-spinning caddisfly larvae paralleled their microhabitat preferences. Sample sizes were large enough to permit estimation of feeding rates for only the last three instars of *H. sparna*, the most abundant net-spinning caddisfly on the substrate patches.

Despite high variances in the individual capture rates, substrate position had a significant effect on capture (ANOVA, $P < .05$). Capture was highest in upstream and top positions (Table 1), averaging 0.016% per individual. Average capture was nearly as high in the valley position (Table 1), but this value was strongly skewed by a single fifth-instar larva that consumed 11 nauplii. Excluding this individual, capture on valley patches average 0.006%, intermediate between upstream the top positions on the one hand and the downstream position (0.002%) on the other.

The relationship between microhabitat selection and feeding rate is illustrated in Fig. 6A, in which we use mean density in each of the four substrate positions as a measure of microhabitat preference. The single fifth-instar larva from the downstream position patch with an extreme capture rate, 0.234%, discussed previously, was omitted from this analysis. Linear regressions between density and feeding rate were calculated for each instar (Fig. 6A). Because the sample sizes were small, none of the regressions are statistically significant. The slopes of the regressions decrease from third to fifth instar, as might be expected, because older instars are found at lower absolute densities on both the colonized patches and natural moss habitat in the stream. We converted the absolute densities to relative densities by dividing the mean density for each instar on each patch type by the total density for that instar on all four patch types combined. This transformation permitted us to combine data for all instars. The results (Fig. 6B) indicated that all instars distributed themselves among the substrate positions in proportion to the mean rate of prey capture attainable on the patches. The relationship is highly significant ($r^2 = 0.81$, $P < .001$, $n = 10$) when, once again, the fifth-instar individual with an extreme capture rate is omitted. When this individual is included, the relationship is still significant for third and fourth instars ($r^2 = 0.79$, $P < .01$, $n = 7$), but not for fifth instars.

Rate of prey removal from the drift

When data on prey capture by individual larvae are combined with larval densities, it is possible to estimate the proportion of prey that would be captured

TABLE 1. Capture of *Artemia* by *Hydropsyche sparna* larvae, as a % of the total number released per trough, in 4 positions on ridges transverse to the water flow, Mianus River, 15 and 23–24 July 1987. (Values in parentheses are limits of 95% confidence intervals around the mean.)

Larval instar	Substrate position											
	Upstream			Top			Downstream			Valley		
	Mean	(95% CL)	<i>n</i>	Mean	(95% CL)	<i>n</i>	Mean	(95% CL)	<i>n</i>	Mean	(95% CL)	<i>n</i>
III	0.012	(.007, .024)	8	0.013	(.004, .038)	8	0.001	(0, .070)	4	0.003	(0, .064)	4
IV	0.028	(.016, .048)	8	0.010	(.000, .088)	3	0.006	(.006, .006)	2	...*		0
V	0.012	(0, .195)	3	0.025	(.004, .143)	6	...*		0	0.115	(0, 204.4)	2
III–V (combined)	0.017			0.016			0.002			0.012		

*No larvae of this instar were found in this position in the feeding experiments.

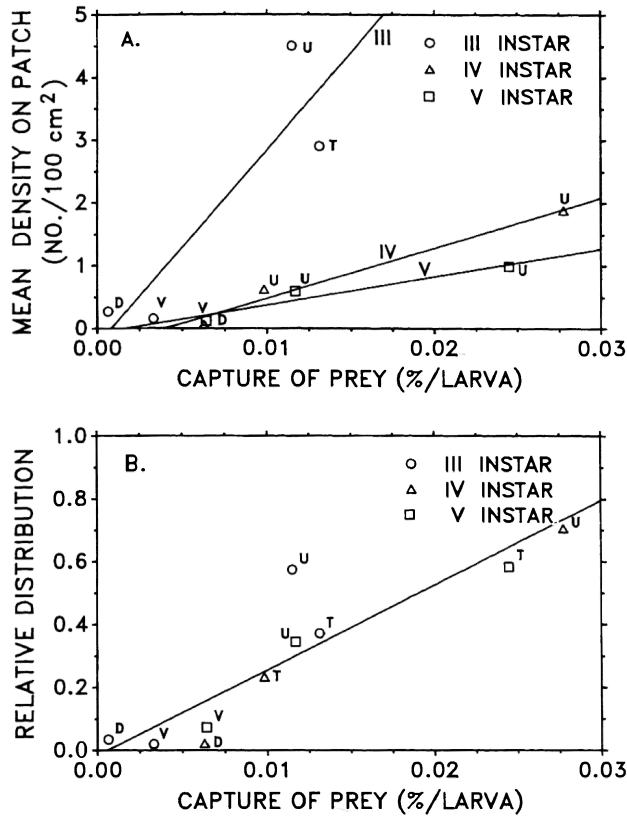


Fig. 6. Hydropsychid density as a function of the fraction of prey captured by larvae on different substrate patches. Each data point is labeled to indicate its substrate position: U = Upstream, T = Top, D = Downstream, V = Valley. (A) Mean density of hydropsychids on patches (no. per 100 cm²), by position. Regressions are: third instars, $r^2 = 0.80$, $P = .11$; fourth instars, $r^2 = 0.98$, $P = .10$; fifth instars, $r^2 = 0.69$, $P = .38$. (B) Relative distribution among patch positions (density in position/density summed over all positions). Regression: $r^2 = 0.81$, $P = .0004$.

and ingested while passing over each patch position (Table 2). Total capture by instars III–V is greatest for patches in the upstream position (57% of total capture) and lowest for the downstream position (0.3%). Capture by all three instars on all patch types totalled 0.19%. Because one “unit” of patches, consisting of two horizontal and two vertical patches (Fig. 1), occupies 0.13 m of longitudinal (upstream–downstream) distance, this capture rate equals 1.49% per longitudinal metre. Assuming exponential removal of *Artemia* from the water (cf. McLay 1970), half the drifting prey would be removed from the water column in 46 m, while the average distance traveled by a prey item would be 67 m.

These calculations apply directly only to the removal of *Artemia* from the experimental troughs. Using density data from natural habitats, however, we can calculate how rapidly drifting invertebrate prey might be removed from a riffle area of the river by natural caddisfly populations. We begin by assuming that *H. betteni* larvae are at least as efficient as *H. sparna* larvae at capturing drifting prey. This assumption seems reasonable, because *H. betteni* larvae are larger than *H. sparna* larvae of the same instar (Mackay 1979, T. Georgian, unpublished data), have larger nets that protrude farther into the water column, and are more carnivorous in their feeding habits (Fuller and Mackay 1980). Densities of *H. betteni* and *H. sparna* (third–fifth instars only) in natural moss habitats averaged 1701 larvae/m² (95% CL = 889–3149, $n = 8$) in July. If these larvae capture prey at the average rate of *H. sparna* larvae in upstream and top microhabitats (0.0162% per individual), total prey capture would be 27.2% per longitudinal metre. (We are assuming that the overwhelming majority of larvae in natural habitats select microhabitats equivalent to those preferred in

TABLE 2. Calculation of the rate of removal of *Artemia* from the water column by *Hydropsyche sparna* larvae, third to fifth instars, in four positions on ridges transverse to the water flow, in July 1987.

Larval instar	Substrate position							
	Upstream		Top		Downstream		Valley	
	Mean	<i>n</i>	Mean	<i>n</i>	Mean	<i>n</i>	Mean	<i>n</i>
A. Mean capture rate (% per individual)								
III	0.01151	8	0.01311	8	0.00064	4	0.00330	4
IV	0.02774	8	0.00982	3	0.00627	2	...*	0
V	0.01170	3	0.02446	6	...*	0	0.11479	2
III–V (combined)	0.01680		0.01558		0.00170		0.01189	
B. Mean density in experimental troughs (no. per 100 cm ²)								
T	4.50	24	2.90	24	0.27	24	0.16	24
	1.88	24	0.62	24	0.06	24	0.11	24
	0.59	24	0.99	24	0	24	0.12	24
	6.97		4.51		0.33		0.38	
C. Capture per patch (%)								
	0518		0.0380		0.0002		0.0005	
	0522		0.0061		0.0004		...*	
	0069		0.0242		0		0.0138	
	.1109 (57%)		0.0683 (35%)		0.0006 (0.3%)		0.0143 (7%)	

*this instar were found in this position in the feeding experiments.

our experiments, an assumption borne out by observation of the positions on rocks occupied by caddisfly larvae in the Mianus River.) This estimate of 27.2%/m is too high, because it assumes the entire riffle is covered with rocks large enough to have moss on their tops and upper sides. We do not have extensive data on densities of net-spinning caddisflies in all microhabitats within Mianus River riffles, but three Surber samples taken in mid-June gave average densities of 1125 caddisflies/m² (95% CL = 391–3500) for *H. betteni* and *H. sparna* third–fifth instars. This density and a capture rate of 0.0162% per individual yields a prey capture rate of 18.2%/m. Again assuming exponential prey removal, larvae of these two species could reduce drifting invertebrate concentrations in riffles by 50% in 3.8 m, and a prey item in the drift would travel a mean distance of only 5.5 m before being consumed.

DISCUSSION

Microhabitat selection and feeding rate

The results of our colonization experiments indicate unequivocally that net-spinning caddisfly larvae strongly prefer higher flow sites when substrate size, stability, and surface texture are controlled. Highest larval abundances occurred on the upstream and top positions, where the highest flows occurred. It seems likely that the larvae are responding to particle availability rather than current velocity itself (cf. Matczak and Mackay 1990). Feeding rates were generally as high on upstream as on top patches (Table 1). Apparently the flow patterns were such that nets on at least the upper part of upstream patches had as great an access to suspended particles as nets on top patches, even though the upstream position did not have as high a velocity as the top position (Fig. 2). The dramatic avoidance of downstream and valley patches may also relate more to particle flux than velocity itself. Calculations based on Davis and Barmuta (1989) indicate that flow through our troughs is subcritical (mean Froude number = 0.54, 95% CL = 0.44–0.64, $n = 24$) and skimming across the steps (see Fig. 2), with most of the flow passing over the space between steps. Not only will most small organic particles skim over the steps without entering the valleys (as observed by us in a laboratory flume), but the depression between the steps will suffer from increased sedimentation of denser inorganic particles (Nowell and Jumars 1984), which would tend to clog nets. Osborne and Herricks (1987) found that net spinners preferred regions of rapid vortices (which tended to trap particles) to slower, more even flows. The spaces between the steps in our troughs were too narrow and deep to permit such turbulent vortices to penetrate (Davis and Barmuta 1989; T. Georgian and J. H. Thorp, *personal observations*), making the downstream and valley positions inferior locations for FPOM capture.

Our results provide an evolutionary rationale for

distributional patterns that is lacking in more descriptive or even experimental studies that designate habitat in lotic environments as “available,” or “optimal” on the basis of occupancy alone (Power et al. 1988). Habitat selection should be considered optimal only when fitness components such as survival, growth, or fecundity have been measured (e.g., Pacala and Roughgarden 1985) or at least estimated indirectly, in terms of feeding rates (Colbo and Porter 1979, Hart 1986, this study).

In order to explain the results of our colonization studies in terms of the hypothesis that net-spinning caddisfly larvae select microhabitats offering the greatest access to suspended particles, we must assume that larvae colonizing new substrates actively search for acceptable sites for their nets. Hildrew and Townsend (1980, Townsend and Hildrew 1980) have shown that a predatory net-spinning caddisfly, *Plectrocnemia conspersa* (Polycentropodidae) has an aggregated distribution in the field because of larval response to areas of high prey availability. Larvae introduced to a new substrate tend to wander for 30–60 min, apparently to assay prey availability before investing time and energy in net construction, and will abandon their nets after 1–2 d if no food has been captured at a site. Williams and Levens (1988) found that net-spinning caddisfly larvae (both Philopotamidae and Hydropsychidae) in the drift had significantly more empty or half-full guts than those that remained on the substratum. Matczak and Mackay (1990) found that *Hydropsyche morosa* larvae on artificial substrates in a laboratory stream defended smaller territories when conditions were favorable (faster flows and/or higher food concentrations). We have made observations using identifiable fifth-instar *Hydropsyche betteni*; they indicate that caddisflies colonizing our artificial moss patches were moving freely between substrate positions over a 1–2 d period. Based on these results and the studies reviewed above, we feel justified in assuming that the larvae colonizing the artificial moss patches searched for acceptable microhabitats before beginning net construction, and therefore that the microhabitat distributions observed after 21 d of colonization represent selection of preferred microhabitats.

We would expect that colonizing larvae would “fill” a habitat by selecting the most favorable filtering sites first. When these become crowded the competitive inferiors (shown to be smaller individuals or those without existing retreats to defend: Jansson and Vuoristo 1979, Matczak and Mackay 1990) would be displaced into poorer microhabitats. The hydropsychid densities we observed on upstream and top substrate positions were much lower than previously reported for hydropsychid densities on natural substrates (Oswood 1979, Cudney and Wallace 1980), and under conditions of high food availability in laboratory streams (Matczak and Mackay 1990). It is not clear, then, that the larvae in preferred habitats in our experiment were

TABLE 3. Seston uptake by filter feeders from a variety of stream sizes. Uptake values were generated using an exponential model for the removal of seston from the water column (see McLay 1970).

A. Utilization of total POM			
Filter feeders	Method of measurement	Uptake (%/m)	Reference
First- to third-order streams			
<i>Hydropsyche occidentalis</i> , <i>Simulium</i> sp.	Consumption rates measured in laboratory	0.011	McCullough et al. 1979a, b
<i>Diplectrona</i> sp.	P ³² release in field	0.0027	Newbold et al. 1983
<i>D. modesta</i> , <i>Parapsyche cardis</i> , 2 sites	Estimated from secondary production	0.006 0.010	Haefner and Wallace 1981
Hydropsychids, 3 spp. and philopotamids, 3 spp.; 3 sites	Estimated from secondary production	0.010 0.0032 0.0010	Ross and Wallace 1983
Fourth- to sixth-order streams			
Hydropsychids, 5 spp. and philopotamids, 1 sp.	Estimated from secondary production	0.00015	Benke and Wallace 1980
Hydropsychids, 5 spp. and philopotamids, 1 sp.	Hydrodynamic model of net filtration	0.005	Georgian and Wallace 1981
Hydropsychids, 7 spp. and philopotamids, 1 sp., 3 sites	Estimated from secondary production	0.0003 0.00018 0.00015	Ross and Wallace 1983
Hydropsychids, 6 spp. and philopotamids, 2 spp., 4 sites	Estimated from secondary production	0.0245 0.0025 0.0007 0.0083	Parker and Voshell 1983
B. Utilization of drifting invertebrates			
Filter feeders	Method of measurement	Uptake (%/m)	Reference
First- to third-order streams			
<i>Diplectrona modesta</i> , <i>Parapsyche cardis</i> , 2 sites	Estimated from secondary production*	1.30 0.65	Haefner and Wallace 1981
Hydropsychids, 3 spp. and philopotamids, 3 spp., 3 sites	Estimated from secondary production*	0.044 0.011 0.006	Ross and Wallace 1983
<i>Cheumatopsyche</i> sp.	Change in zooplankton concentration	3.0	Brown et al. 1989
<i>Hydropsyche</i> , 3 spp.	Estimated from secondary production†	13.1	Petersen 1989
<i>Hydropsyche betteni</i> and <i>H. sparna</i>	In situ measurements of feeding rates	18.2	This study
Fourth- to sixth-order streams			
Hydropsychids, 5 spp. and philopotamids, 1 sp.	Estimated from secondary production*	0.0014 0.0005 0.0004	Ross and Wallace 1983
<i>Brachycentrus spinae</i> , 2 sites	Estimated from secondary production*	0.024 0.040	Ross and Wallace 1981

* Animal material assumed to be 0.04% of total seston.

† Only animal material passing within 1 cm of substrate included.

anywhere near saturation densities. We do not know if the small number of larvae we found in low-flow positions represent individuals displaced into inferior areas, or merely transients that had colonized the troughs too recently to have located the preferred sites. We could not determine if these individuals had constructed nets, which were destroyed by our sampling procedure, but 5 of 12 (41.7%) of the larvae on downstream and valley patches had no *Artemia* in their guts, as compared to 2 of 36 (5.6%) on upstream and top positions, a significant difference (two-way contingency

table with continuity correction, $\chi^2 = 6.8$, $P < .01$). This result suggests that individual larvae on downstream and valley patches were suffering under inferior conditions rather than having located isolated microhabitats within these locations with adequate filtering potential.

Seston capture

Filter feeders have been hypothesized to retard the downstream transport of suspended POM (Wallace et al. 1977). In so doing, they may significantly decrease

spiralling distances of ecosystem resources (Webster and Patten 1979, Newbold et al. 1981). Few actual measurements of the rates at which filter feeders remove seston from streams have been made. We summarize many of the existing estimates in Table 3. Two patterns stand out; first, filter feeders have little impact on total POM transport in streams. POM uptake ranged from 0.00015 to 0.025%/m in all size streams, with a mean of 0.00536%/m. The mean distance traveled by a seston particle in these streams (using an exponential model of loss from the water column: McLay 1970) would be 18.7 km. Second, by contrast, net-spinning caddisflies can remove high-quality food items such as drifting animals from the water column at a rapid rate. Removal of animal material from the drift (Table 2) averaged 2.8%/m. The effect is particularly dramatic in shallow headwater streams where the average removal rate is 4.6%, meaning that the average prey item moves only 22 m downstream before being captured by a net-spinning caddisfly. This distance is of the same order as the distances traveled by drifting invertebrates before returning (actively or passively) to the substratum (Elliott 1971), suggesting that drifting invertebrates in streams may be forced to settle back to the bottom rapidly to avoid predation. If one adds the effects of fish predation on the drift, it seems likely that drift is generated and removed in shallow riffle habitats over distances on the order of only 10 m.

The experiments of Smith-Cuffney and Wallace (1987) indicate that the effectiveness with which filter feeders remove prey from the water column depends on water depth and flow characteristics, which are combined in the Froude number (Fr). They found that net spinner abundances and utilization of drift were highest in shallow-water habitats with moderate (0.55) and high (1.59) Froude numbers. In a different system, a Massachusetts estuary, Wright et al. (1982) found that blue mussels (*Mytilus edulis*) removed algae from tidal flow at a maximum rate of 3.2%/m when depth was lowest (10 cm), and the removal rate decreased to 0.6%/m at the maximum depth of 44 cm. The average water depth in which our troughs were placed was 18.2 cm, resulting in water depths over the step tops of 12 cm and mean Fr of 0.54. Based on these measures, our troughs mimicked the habitat in riffles but not the deeper water habitats in pools and runs. As a consequence, the prey removal rate of 18%/m that we estimate would almost certainly not be as high for the entire river system. It should also be noted that our estimate is based on summer data only, while many of the studies summarized in Table 3 apply to the entire year, or at least to spring-fall. During the summer, high caddisfly abundances, rapid growth rates and low discharge would all tend to elevate prey capture above the annual average.

Estimates of seston removal by filter feeders in large rivers are rare, but they suggest that filter feeders exert less control over seston in these deeper systems. Cohen

et al. (1984) estimated that the Asiatic clam (*Corbicula fluminea*) can filter the entire volume of a study reach on the Potomac River in 3–4 d, but they do not provide enough information to calculate clearance per longitudinal metre. Carlough and Meyer (1990) measured filtration rates of Ogeechee River ciliates and flagellates and found that protozoan filter feeders can clear 47% of the water column of bacteria each day. If the average velocity in these rivers is on the order of 0.5 m/s, it may take 40–100 km for a 50% removal of sestonic bacteria to occur.

Our study shows that net-spinning caddisflies select microhabitats that provide them with greater access to drifting prey. Within the portions of the stream that provide such microhabitats, net spinners exert a major influence on the quantity and type of POM in suspension (Benke and Wallace 1980). Stream ecologists have implicitly assumed that placing a drift net in a stream permits measurement of drift for the entire stream reach. In shallow streams with large net-spinning caddisfly populations, predation may be holding drift at very low concentrations that do not at all reflect the number of organisms entering the water column within a reach. Total seston, by contrast, is removed so slowly that it must build in concentration downstream until a steady state between POM generation and its deposition is reached.

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LITERATURE CITED

- Allan, J. D. 1983. Hypothesis testing in ecological studies of aquatic insects. Pages 484–507 in V. H. Resh and D. M. Rosenberg, editors. *The ecology of aquatic insects*. Praeger, New York, New York, USA.
- Alstad, D. N. 1986. Dietary overlap and net-spinning caddisfly distributions. *Oikos* 47:251–253.
- Benke, A. C., T. C. Van Arsdall, Jr., D. M. Gillespie, and F. K. Parrish. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. *Ecological Monographs* 54:25–63.
- Benke, A. C., and J. B. Wallace. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. *Ecology* 61:108–118.
- Brown, A. V., R. L. Limbeck, and M. D. Schram. 1989. Trophic importance of zooplankton in streams with alluvial riffle and pool geomorphometry. *Archiv für Hydrobiologie* 114:349–367.
- Carlough, L. A., and J. L. Meyer. 1990. Rates of protozoan bacterivory in three habitats of a southeastern blackwater river. *Journal of the North American Benthological Society* 9:45–53.

- Cohen, R. R. H., P. V. Dresler, E. J. P. Phillips, and R. L. Cory. 1984. The effect of the Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. *Limnology and Oceanography* 29:170-180.
- Colbo, M. H., and G. N. Porter. 1979. Effects of food supply on the life history of Simuliidae. *Canadian Journal of Zoology* 57:301-306.
- Cudney, M. D., and J. B. Wallace. 1980. Life cycles, microdistribution, and production dynamics of six species of net-spinning caddisflies in a large southeastern (U.S.A.) river. *Holarctic Ecology* 3:169-182.
- Davis, J. A., and L. A. Barmuta. 1989. An ecologically useful classification of mean and near-bed flows in streams and rivers. *Freshwater Biology* 21:271-282.
- Edington, J. M. 1965. The effect of water flow on populations of net-spinning Trichoptera. *Internationale Vereinigung für theoretische und angewandte Limnologie, Mitteilungen* 13:40-48.
- . 1968. Habitat preferences in net-spinning caddisfly larvae with special reference to the influence of water velocity. *Journal of Animal Ecology* 37:675-692.
- Elliott, J. M. 1971. The distance travelled by drifting invertebrates in a Lake District stream. *Oecologia (Berlin)* 6:350-379.
- Fuller, R. L., and R. J. Mackay. 1980. Feeding ecology of three species of *Hydropsyche* (Trichoptera: Hydropsychidae) in southern Ontario. *Canadian Journal of Zoology* 58:2239-2251.
- Fuller, R. L., R. J. Mackay, and H. B. N. Hynes. 1983. Seston capture by *Hydropsyche betteni* nets (Trichoptera: Hydropsychidae). *Archiv für Hydrobiologie* 97:251-261.
- Gatley, G. K. 1988. Competition and the structure of hydropsychid guilds in southern Sweden. *Hydrobiologia* 164:23-32.
- Georgian, T. J., Jr., and J. B. Wallace. 1981. A model of seston capture by net-spinning caddisflies. *Oikos* 36:147-157.
- Glass, L. W., and R. V. Bovbjerg. 1969. Density and dispersion in laboratory populations of caddisfly larvae (*Cheumatopsyche*, Hydropsychidae). *Ecology* 50:1082-1084.
- Gurtz, M. E., J. R. Webster, and J. B. Wallace. 1980. Seston dynamics in southern Appalachian streams. *Canadian Journal of Fisheries and Aquatic Sciences* 37:624-631.
- Haefner, J. D., and J. B. Wallace. 1981. Production and potential seston utilization by *Parapsyche cardis* and *Diplectrona modesta* (Trichoptera: Hydropsychidae) in two streams draining contrasting southern Appalachian watersheds. *Environmental Entomology* 10:433-441.
- Hart, D. D. 1983. The importance of competitive interactions within stream populations and communities. Pages 99-136 in J. R. Barnes and G. W. Minshall, editors. *Stream ecology: applications and testing of general ecological theory*. Plenum, New York, New York, USA.
- . 1986. The adaptive significance of territoriality in filter-feeding larval black flies (Diptera: Simuliidae). *Oikos* 46:88-92.
- Hemphill, N. 1988. Competition between two stream dwelling filter-feeders, *Hydropsyche oslari* and *Simulium virgatum*. *Oecologia (Berlin)* 77:73-80.
- Hemphill, N., and S. D. Cooper. 1983. The effect of physical disturbance on the relative abundances of two filter-feeding insects in a small stream. *Oecologia (Berlin)* 58:378-382.
- Hershey, A. E., and A. L. Hiltner. 1988. Effect of a caddisfly on black fly density: interspecific interactions limit black flies in an arctic river. *Journal of the North American Benthological Society* 7:188-196.
- Hildrew, A. G., and J. M. Edington. 1979. Factors facilitating the coexistence of hydropsychid caddis larvae (Trichoptera) in the same river system. *Journal of Animal Ecology* 48:557-576.
- Hildrew, A. G., and C. R. Townsend. 1980. Aggregation, interference and foraging by larvae of *Plectrocnemia conspersa* (Trichoptera: Polycentropodidae). *Animal Behavior* 28:553-560.
- Hynes, H. B. N. 1970. *The ecology of running waters*. University of Toronto Press, Toronto, Ontario, Canada.
- Jansson, A., and T. Vuoristo. 1979. Significance of stridulation in larval Hydropsychidae (Trichoptera). *Behavior* 71:167-186.
- Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. *Fluvial processes in geomorphology*. W. H. Freeman, San Francisco, California, USA.
- Mackay, R. J. 1978. Larval identification and instar association in some species of *Hydropsyche* and *Cheumatopsyche* (Trichoptera: Hydropsychidae). *Annals of the Entomological Society of America* 71:499-509.
- . 1979. Life history patterns of some species of *Hydropsyche* (Trichoptera: Hydropsychidae) in southern Ontario. *Canadian Journal of Zoology* 57:963-975.
- Malas, D., and J. B. Wallace. 1977. Strategies for coexistence in three species of net-spinning caddisflies (Trichoptera) in second order southern Appalachian streams. *Canadian Journal of Zoology* 55:1829-1840.
- Matczak, T. Z., and R. J. Mackay. 1990. Territoriality in filter-feeding caddisfly larvae: laboratory experiments. *Journal of the North American Benthological Society* 9:26-34.
- McAuliffe, J. 1983. Competition, colonization patterns, and disturbance in stream benthic communities. Pages 137-156 in J. R. Barnes and G. W. Minshall, editors. *Stream ecology: applications and testing of general ecological theory*. Plenum, New York, New York, USA.
- . 1984. Competition for space, disturbance and the structure of a benthic stream community. *Ecology* 65:894-908.
- McCullough, D. A., G. W. Minshall, and C. E. Cushing. 1979a. Bioenergetics of lotic filter-feeding insects *Simulium* spp. (Diptera) and *Hydropsyche occidentalis* (Trichoptera) and their function in controlling organic transport in streams. *Ecology* 60:585-596.
- McCullough, D. A., G. W. Minshall, and C. E. Cushing. 1979b. Seston removal by filter feeders. *Ecology* 60:1075.
- McLay, C. L. 1970. A theory concerning the distance travelled by animals entering the drift of a stream. *Journal of the Fisheries Research Board of Canada* 27:359-370.
- Merzkirch, W. 1974. *Flow visualization*. Academic Press, New York, New York, USA.
- Minshall, G. W. 1984. Aquatic insect-substratum relationships. Pages 484-507 in V. H. Resh and D. M. Rosenberg, editors. *The ecology of aquatic insects*. Praeger, New York, New York, USA.
- Newbold, J. D., J. W. Elwood, R. V. O'Neill, and A. L. Sheldon. 1983. Phosphorus dynamics in a woodland stream ecosystem: a study of nutrient spiralling. *Ecology* 64:1249-1265.
- Newbold, J. D., J. W. Elwood, R. V. O'Neill, and W. Van Winkle. 1981. Measuring nutrient spiralling in streams. *Canadian Journal of Fisheries and Aquatic Sciences* 38:860-863.
- Nowell, A. R. M., and P. A. Jumars. 1984. Flow environments of aquatic benthos. *Annual Review of Ecology and Systematics* 15:303-328.
- Osborne, L. L., and E. E. Herricks. 1987. Microhabitat characteristics of *Hydropsyche* (Trichoptera: Hydropsychidae) and the importance of body size. *Journal of the North American Benthological Society* 6:115-124.
- Oswood, M. W. 1979. Abundance patterns of filter-feeding caddisflies (Trichoptera: Hydropsychidae) and seston in a Montana (U.S.A.) lake outlet. *Hydrobiologia* 68:177-183.
- Pacala, S. W., and J. Roughgarden. 1985. Population experiments with the *Anolis* lizards of St. Maarten and St. Eustatius. *Ecology* 66:129-141.

- Parker, C. R., and J. R. Voshell, Jr. 1983. Production of filter-feeding Trichoptera in an impounded and a free-flowing river. *Canadian Journal of Zoology* **61**:70-87.
- Pennak, R. W. 1978. *Freshwater invertebrates of the United States*. Second edition. John Wiley & Sons, New York, New York, USA.
- Petersen, L. B.-M. 1985. Food preferences in three species of *Hydropsyche* (Trichoptera). *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* **22**:3270-3274.
- . 1989. Resource utilization of coexisting species of Hydropsychidae (Trichoptera). *Archiv für Hydrobiologie/Supplement* **83**:83-119.
- Petersen, R. C., Jr., L. B.-M. Petersen, and J. B. Wallace. 1984. Influence of velocity and food availability on catch-net dimensions of *Neuroclipsis bimaculata* (Trichoptera: Polycentropodidae). *Holarctic Ecology* **7**:380-389.
- Philipson, G. N. 1969. Some factors affecting the net-spinning of the caddisfly *Hydropsyche instabilis* Curtis (Trichoptera: Hydropsychidae). *Hydrobiologia* **34**:369-377.
- Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. R. Hauer, W. J. Matthews, P. B. Moyle, B. Statzner, and I. R. Wais DeBadgen. 1988. Biotic and abiotic controls in river and stream communities. *Journal of the North American Benthological Society* **7**:456-479.
- Ross, D. H., and J. B. Wallace. 1981. Production of *Brachycentrus spinae* Ross (Trichoptera: Brachycentridae) and its role in seston dynamics of a southern Appalachian stream. *Environmental Entomology* **10**:240-246.
- Ross, D. H., and J. B. Wallace. 1983. Longitudinal patterns of production, food consumption and seston utilization by net-spinning caddisflies (Trichoptera) in a southern Appalachian stream (U.S.A.). *Holarctic Ecology* **6**:270-284.
- Smith-Cuffney, F. L. 1987. Ecological interactions in the moss habitat of streams draining a clearcut and a reference watershed. Dissertation. University of Georgia, Athens, Georgia, USA.
- Smith-Cuffney, F. L., and J. B. Wallace. 1987. The influence of microhabitat on availability of drifting invertebrate prey to a net-spinning caddisfly. *Freshwater Biology* **17**:91-98.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. Second edition. W. H. Freeman, New York, New York, USA.
- Thorpe, J. H., J. B. Wallace, and T. J. Georgian, Jr. 1986. Untangling the web of caddisfly evolution and distribution. *Oikos* **47**:253-256.
- Townsend, C. R., and A. G. Hildrew. 1980. Foraging in a patchy environment by a predatory net-spinning caddis larva: a test of optimal foraging theory. *Oecologia (Berlin)* **47**:219-221.
- Vogel, S. 1981. *Life in moving fluids: the physical biology of flow*. Willard Grant, Boston, Massachusetts, USA.
- Walde, S. J., and R. W. Davies. 1984. Invertebrate predation and lotic prey communities: evaluation of *in situ* enclosure/exclosure experiments. *Ecology* **65**:1206-1213.
- Wallace, J. B. 1975. Food partitioning in net-spinning Trichoptera larvae: *Hydropsyche venularis*, *Cheumatopsyche etrona*, and *Macronema zebratum* (Hydropsychidae). *Annals of the Entomological Society of America* **68**:463-472.
- . 1979. Some aspects of net-spinning trichopteran diversity. Pages 45-64 in *Occasional Papers, Department of Entomology, Research Report 82-1, Virginia Agricultural Experiment Station, College of Agriculture, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA*.
- Wallace, J. B., J. R. Webster, and W. R. Woodall. 1977. The role of filter-feeders in flowing waters. *Archiv für Hydrobiologie* **79**:506-532.
- Webster, J. R., and B. C. Patten. 1979. Effects of watershed perturbation on stream potassium and calcium dynamics. *Ecological Monographs* **19**:51-72.
- Williams, D. D., and G. P. Levens. 1988. Evidence that hunger and limb loss can contribute to stream invertebrate drift. *Journal of the North American Benthological Society* **7**:180-187.
- Williams, N. E., and H. B. N. Hynes. 1973. Microdistribution and feeding of the net-spinning caddisflies (Trichoptera) of a Canadian stream. *Oikos* **24**:73-84.
- Wright, R. T., R. B. Coffin, C. P. Ersing, and D. Pearson. 1982. Field and laboratory measurements of bivalve filtration of natural marine bacterioplankton. *Limnology and Oceanography* **27**:91-98.