located precisely in nerves supplying circular smooth muscle. Like ATP, VIP is present in large dense granules of the terminals of p-type nerves, is released by electrical stimulation of nonadrenergic inhibitory nerves, and can cause relaxation of circular smooth muscle (*3–8*). The profile of neurally stimulated relaxation is more closely mimicked by exogenous ATP than by VIP, but this is probably because of slower diffusion of VIP across muscle layers. The probability of neurotransmission by VIP need not preclude a role for ATP. The topographical and functional parallelism between VIP and ATP may reflect a modulatory, perhaps synergistic, interplay between these two substances.

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Current Speed and Filtration Rate Link Caddisfly Phylogeny and Distributional Patterns on a Stream Gradient

Abstract. *Patterns of body size and net construction suggest that current speed and food-particle concentration (not size) influence the distribution of suspension-feeding caddisflies on a downstream gradient. Large ancestral taxa with high filtration rates occur in resource-poor upstream habitats; more derived members of the phylogeny enter successively in downstream reaches with slower current and greater concentrations of particulate food.*

Larvae of the net-spinning caddisflies (Trichoptera: Hydropsychidae) capture suspended particulate food from stream water passing over their retreats (*1, 2*). Their abundance and worldwide distribution suggest that filtering net spinners play an important role in stream ecosystems. In Rocky Mountain and Appalachian streams, particulate concentration increases downstream on long altitudinal gradients; both the density of individuals and the number of net-spinning species show a correlated increase. In all thoroughly studied drainages, these community changes have a similar pattern; large ancestral hydropsychid species inhabit the most nutrient-poor upstream reaches, and more derived taxa of smaller body size are added to the community sequentially at lower elevation (*3, 4*).

Studies of distributional ecology and community structure have focused most often on two aspects of hydropsychid biology. First, the observation that coexisting species show differences in the mesh dimension of catch nets suggested that interspecific partitioning of food particle sizes is an important feature of community organization (*5*). According to this view, increasing particle availability influences the number of coexisting species by extending the range of potential particle size specialties or by permitting changes in the specialization or overlap of the taxa. This partitioning hypothesis is weakened by the occurrence of several instar classes and net sizes in each species and by recent quantitative studies demonstrating extremely broad overlap and little specialization in the particle sizes ingested by taxa with very different nets (*4, 6*). The second major focus of hydropsychid ecology has been microhabitat selection. Evidence suggests that the current speed requirements of net spinners are very precise (*7, 8*). Artificial diversions cause insects to abandon retreats and relocate (*9*), and active selection of current speed occurs in the laboratory (*10, 11*). Interspecific partitioning of microhabitat space has been demonstrated in the field with a nearest-neighbor analysis (*4*), and the patterns are associated with current speed preferences. Flow rate differences are related to the functional morphology of large and small catch nets, but current alone cannot explain the pattern of distributions on a stream gradient. For example, sheltered slow currents are available in even the most precipitous upstream reaches of a Rocky Mountain stream, yet species characteristic of this microhabitat at lower elevations are absent.

Data showing (i) a correlation of insect abundance and species diversity with increasing particle concentration, (ii) little specialization in the kinds of food items taken, and (iii) interspecific variation in current speed requirements are all consistent with a model of hydropsychid distributions based on resource availability and filtration rate. Particle capture must depend on the concentration of material in suspension and the volume of water filtered. Caddisfly taxa may compensate for low particle availability by adaptations that permit large amounts of water to pass through the net. A filtration rate model of hydropsychid distributions predicts that species found in the most resource-poor sites at high elevation will have large net structures and occupy fast-current microhabitats. Taxa with lower filtration rates should be restricted to downstream reaches with a higher concentration of particulate resources. Several types of data support this prediction.

1) Net structures must reflect the current speeds in which they function. Silk strands need sufficient thickness to withstand the current's force, and mesh cells must vary in size to adjust drag in different flow rates. Among most hydropsychids, these net properties are related to the insect's size and the dimension of mouthparts involved in the net spinning process. A distributional model based on filtration rate predicts that body size, silk strand thickness, and mesh dimension should all decline with downstream entry sequence on the resource concentration gradient. Rocky Mountain hydropsychids illustrate this pattern clearly (*4*). Average catch-net diameters also decline (Table 1). Thus net structures are consistent with the hypothesis that upstream taxa accommodate a low resource concentration by filtering more water than downstream species do.

2) Direct measurements of current speed around caddisfly nets and retreats decline in the same predicted sequence (*12*). Data taken by timing the dissolution of a salt pill show that large arctopsychines from resource-poor headwaters occupy the fastest microhabitats, and currents associated with species that enter downstream are successively slower

0036-8075/82/0430-0533$01.00/0

Table 1. Four hydropsychid species from Utah are listed in the order of their appearance on the downstream gradient. Current speed measurements, which were made with a 0.9-mm-bead thermistor at 2 mm and 10 mm above the rock surface beside each retreat, decline with entry sequence and differ significantly among species (Kruskal-Wallis one-way analysis of variance; $H = 47$, $P < .001$; and $H = 16$, $P < .01$, respectively). Water flow through the nets, which declines similarly in late-entry species, is given for the most common instars. Insects and their retreats were taken to the laboratory for measurement. Net area, calculated from net diameter, is multiplied by current speed through the net to approximate the filtration rate in milliliters per second. Values of current speed and net diameter are means ± standard deviation.

Species	N	Current speed			Net diameter (mm)	Net area times current speed (ml/sec)
		2 mm	10 mm	Net		
Arctopsyche grandis	34	28.8 ± 15.1	36.4 ± 16.6	25.4 ± 12.8 (4th instar)	6.2 ± 0.6 (4th instar)	7.7
Symphitopsyche cockerelli	10	20.6 ± 8.6	28.5 ± 13.3	17.7 ± 6.9 (5th instar)	5.2 ± 0.8 (5th instar)	3.8
Symphitopsyche oslari	11	16.0 ± 4.9	23.1 ± 9.6	14.4 ± 1.6 (4th instar)	3.4 ± 0.3 (4th instar)	1.3
Hydropsyche occidentalis	32	8.3 ± 6.1	22.9 ± 9.2	4.8 ± 4.7 (5th instar)	4.8 ± 0.4 (5th instar)	0.9

(*4*). More accurate measurements, made with a 0.9-mm-bead thermistor probe (*13*) held 10 mm above the rock surface chosen by individual caddisflies show that currents differ significantly among species and decline with entry sequence (Table 1). Rates of water passage through the net, and the product of net area and water passage (which approximates filtration rate), decline similarly. Dwelling sites chosen by young larvae are maintained through later development (*14*). Currents measured 2 mm above the rock surface adjacent to caddisfly retreats show that the stagnant boundary zone is compressed by rapid currents; this finding suggests that first-instar larvae experience an accurate correlate of the currents that will be available later in development as their nets reach above the rock surface into faster water. These data support the prediction that current microhabitat differences result in filtration rates that decline with the downstream entry sequence of taxa on the resource concentration gradient.

3) Food quality and availability influence caddisfly growth (*15*). If current speed affects the rate of particle capture, individuals of the same species sampled at a single locality and date should differ in size and growth rate according to the current speeds occupied. Insect sizes and current speeds were significantly associated in a sample of *Arctopsyche grandis* (Banks) from Utah (Fig. 1). These data suggest that caddisflies occupying faster currents have collected resources and grown more rapidly, or that during a protracted period of settlement, the first insects to take sites and begin feeding chose rapid-current positions.

In several respects, this model relating filtration rate and distribution remains oversimplified. Heavy particles fall from suspension in slow water, and resource concentration may vary among current speed microhabitats. Similarly, slow-current nets with fine mesh will retain more material than larger nets. Thus variations in filtration rate may be compounded or compensated by differences in capture efficiency and resource quality. These details are under continuing investigation, but the conclusions that water filtration rates influence the resource concentrations required by hydropsychid caddisflies and that current speed preferences are important determinants of their distributional ecology are unlikely to be altered.

Ancestral caddisflies lived in cool, montane streams. Within most of the modern trichopteran families, morphologically primitive taxa retain this habitat preference, and increasingly derived species are found in warmer, slower water (*16*). Among net-spinning Hydropsychidae, this phylogenetic sequence exactly parallels the distributional pattern of species in a single stream drainage. Large species of the primitive subfamily Arctopsychinae persist alone at resource-poor high-altitude sites, and increasingly derived Diplectroninae, Hydropsychinae, and Macronematinae, which spin successively smaller net mesh, are added sequentially as resource concentration increases downstream. Smaller body size and net mesh may reduce calorific requirements and increase capture efficiency, but appear unable to fully compensate changes in filtration rate. Taxa that have invaded slow water are limited to habitats with high particulate concentration. The functional morphology of the filtering process offers a proximate ecological mechanism linking patterns of distribution and evolutionary phylogeny among the net-spinning caddisflies.

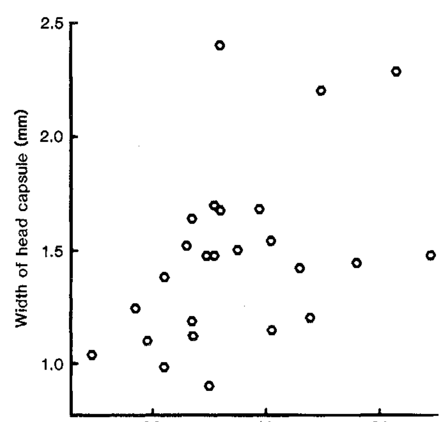

Fig. 1. *Arctopsyche grandis* sampled at the same locality and date show a significant association of head capsule width and current speed 10 mm above the dwelling site (Spearman rank correlation, $r_s = .49$; $P < .01$).

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