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The influence of microhabitat on availability of drifting invertebrate prey to a net-spinning caddisfly

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SUMMARY. 1. Invertebrate drift was sampled at both a rockface and a deep pebble riffle site in streams draining both a clearcut and a forested catchment.

2. A sampler was designed to separate the bottom 2 cm of flow, encompassing the effective range of caddisfly (Hydropsychidae: Trichoptera) catchnets, from upper flow.

3. No significant difference in drift density (numbers per cubic metre) was seen between sites within each stream. However, numbers per square centimetre intake area per day at the rockface sites were 4 times higher in the clearcut and 10 times higher in the forested stream than at the pebble–riffle site.

4. Rockface habitat which had highest drift availability was also the site of maximum secondary production of the predaceous collector-filterer *Parapsyche cardis* in both streams studied.

5. Increased sediment load in the clearcut stream may influence the efficiency of utilization of invertebrate drift by collector-filterers.

Introduction

The study of invertebrate drift in streams has most often been approached from the standpoint of its role as a behavioural response to such factors as food availability (Elliott, 1967; Hildebrand, 1974) and population density (Waters, 1961; Dimond, 1967; Ciborowski, 1983). The importance of physical factors, such as flow (Minshall & Winger, 1968) and substrate (Hall, Waters & Cook, 1980), have been recognized as both independent and as closely associated factors (Waters, 1969; Elliott, 1971). The above approaches emphasize drift as part of the animal's life history and its importance as such to individual species and benthic communities as a whole. The presence of macroinvertebrates in the water column of a stream can also be viewed as a food resource. This approach has been used primarily by fish ecologists (Allan, 1978; Fausch, 1984). Fish have been found to exhibit selectivity in utilization of drift (Griffith, 1974; Johnson & Johnson, 1982) as well as behavioural responses in relation to drift availability, primarily in their positioning within the stream (Everest & Chapman, 1972).

In small, high gradient, headwater streams, where fish are generally absent, drifting invertebrates are used as food by collector-filterer macroinvertebrates such as larvae of Hydropsychidae (Trichoptera). Animal material contributes significantly to the production

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of these insects (Benke & Wallace, 1980) which in turn may feed on the drift (Ross & Wallace, 1983). Furthermore, laboratory studies indicate that some hydropsychids selectively feed on animals as opposed to detritus particles captured in their nets (Petersen, 1985). As with fish, collector-filterers may be exploiting habitats which maximize drift yield.

Hydropsychid caddisflies are often associated with rockface habitat (Nelson & Scott, 1962; Freeman & Wallace, 1984; Gurtz & Wallace, 1984). Edington (1968) found that *Hydropsyche instabilis* Curtis colonized moss covered boulders in great numbers but only when water velocity was high. In high gradient headwater streams rockface substrates are typically high velocity environments. Production of *Parapsyche cardis* Ross in some small headwater streams may be 16–190 times higher on rockface than cobble–riffle and sandy reach substrates, respectively (Gurtz & Wallace, unpublished data). *Parapsyche* are primarily carnivorous (Benke & Wallace, 1980; Ross & Wallace, 1983) and their preferred habitat, rockface, may be a microhabitat which has higher invertebrate drift rates in comparison with other, less frequently colonized, habitats. Drift found only near the substrate surface, which is within range of hydropsychid catchnets, is probably especially important. Gradient and substrate influences on flow may result in very different drift patterns within the bottom layer of the water column over rockface substrates compared to other stream substrates.

Our objective was to examine differences in drift availability over rockface versus deep riffle habitat within the effective filtering depth of collector-filterers. Streams draining both a forested and a clearcut catchment were examined. These streams exhibit differences in both sediment transport and benthic production. It is hypothesized that preferences for rockface substrate of primarily carnivorous hydropsychids, such as *Parapsyche cardis*, are a response to greater availability of drifting organisms than are present in lower gradient reaches. Furthermore, this relationship should exist in both the forested and clearcut stream as *Parapsyche* production was highest on rockface substrates within both streams (Gurtz & Wallace, unpublished data) despite stream differences.

TABLE 1. Physical characteristics and substrate distribution of Hugh White Creek (HWC) and Big Hurricane Branch (BHB)*

	HWC	BHB
Catchment area (ha)	61.1	59.5
Maximium elevation (m)	996	1060
Minimum elevation (m)	708	720
Mean stream depth (cm)	6.4	10.5
Main channel gradient (mm^{-1})	0.17	0.19
Mean annual discharge ($l\ s^{-1}$)	19†	17.7‡
Substrate type (%)		
Rockface	23.1	11.5
Pebble–riffle	5.6	10.5

*For additional characteristics see Gurtz & Wallace (1984).

†Based on 40 year record.

‡Based on 29 year record; pre-clearcut.

Study sites

The study was conducted on two second order streams at the Coweeta Hydrologic Laboratory in the southern Appalachian Mountains near Franklin, North Carolina, U.S.A. Hugh White Creek (HWC) drains a forested catchment of mixed hardwood vegetation with *Rhododendron maximum* dominant along the streamside. Big Hurricane Branch (BHB) drains an experimental catchment clearcut in 1977, 8 years prior to the present study. Physical characteristics of these catchments are summarized in Table 1. Following clearcutting, discharge and seston transport increased in BHB (Gurtz, Webster & Wallace, 1980). More recent studies indicate that seston transport remains elevated (Webster & Golladay, 1984).

Proportions of various substrates within the two streams are also shown in Table 1. A rockface and a deep pebble riffle site were chosen in each stream. Characteristics of the sample sites are given in Table 2. The primary physical differences between the pebble–riffle and rockface sites for both streams were substrate, slope and water velocity. Substrate in the riffle sections was a coarse pebble–gravel while rockface sections provided a relatively smooth extensive bedrock (granite) surface. Froude number ($F=V/(gD)^{1/2}$; where V=velocity, D=depth and g=constant of gravity) is an indication of flow regime. Generally for $F<1$ the stream is in a tranquil or streaming flow, termed subcritical flow; while $F>1$ indicates rapid or shooting flow, termed criti-

TABLE 2. Drift sampling site (PR=pebble–riffle, RF=rockface) characteristics within Hugh White Creek (HWC) and Big Hurricane Branch (BHB)

	HWC		BHB	
	PR	RF	PR	RF
Width (cm)	40	120	115	50
Average depth (cm)	11.75	0.7	8.4	4.5
Slope (°)	<2	23	<2	18
Average velocity* (cm s^{-1})	8.57	41.73	8.9	36.81
Froude number	0.080	1.59	0.098	0.55
Metres above weir	80	290	105	350
Substrate	Pebble	Rock	Pebble	Rock

*Based on average velocity through drift device.

cal flow (Morisawa, 1968). *F* is greater for the rockface site on both watersheds indicating conditions of critical flow.

Materials and Methods

A sampler (Fig. 1) was devised which consisted of two 12 cm long interchangeable, stacked boxes of 1 mm thick stainless steel. The lower box had an opening of 20×2 cm and the upper box a 20×16 cm opening. A canvas bag 30 cm long was fixed to each box for attachment of 60 cm long nytex nets with 143 μm mesh. Nets were attached to the canvas with velcro strips which facilitated rapid replacement in the field. Flow through each box was measured with a 1 m long, flexible, mylar funnel which was also attached to the canvas by velcro strips. All flow passing through the mylar funnel was caught in large buckets for timed (stopwatch) intervals.

Rockface and riffle sites were sampled simultaneously within a stream. Sites were separated by at least 200 m to avoid interference. Three consecutive replicate samples were taken three times during the day. In HWC, nets at both the riffle and rockface sites were in place for 20 min. In BHB, nets at the riffle site and the rockface site were in place for only 15 and 10 min, respectively, to avoid clogging. Drift in BHB was sampled on 11 March 1985 and drift in HWC on 12 March 1985.

All netted materials were preserved in 5%

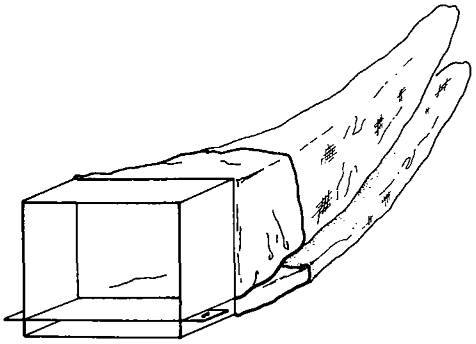

FIG. 1. Drift sampler used at rockface and pebble–riffle sites in Huge White Creek (HWC) and Big Hurricane Branch (BHB). The lower box sampled the bottom 2 cm of flow, representing the effective filtering range of net-spinning caddisflies.

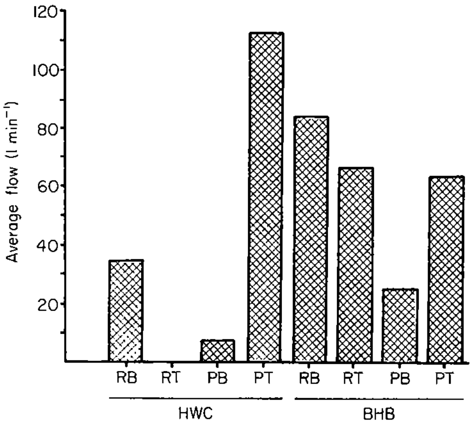

FIG. 2. Average flow (l min^{-1}) through bottom (B) and top (T) of samplers at rockface (R) and pebble–riffle (P) sites of Huge White Creek (HWC) and Big Hurricane Branch (BHB). Total depth of flow across the rockface of HWC was contained within the bottom 2 cm portion of the sampler; thus no flow is recorded for the top layer on rockface of HWC.

TABLE 3. Taxonomic composition of invertebrate drift by percentage of both abundance and weight. Total numbers and total weight of invertebrates collected at each site within each layer are given. Totals are the average of all samples taken in Huge White Creek (HWC) on 12 March 1985 and in Big Hurricane Branch (BHB) on 11 March 1985. (RF=Rockface, PR=Pebble–riffle.)

Site	Substrate	Layer	Total	Copepoda (%)	Misc. non-insect (%)	Collembola (%)	Ephemeroptera (%)	Plecoptera (%)	Trichoptera (%)	Chironomidae (%)	Simulidae (%)	Misc. insects (%)
Abundance			(no. m^{-3})									
HWC	RF	Bottom	107	35.51	11.58	4.35	2.89	9.42	4.34	20.29	9.42	2.16
HWC	PR	Bottom	47	27.69	16.92	3.08	9.23	1.54	1.54	29.23	9.23	1.54
HWC	PR	Top	11	31.00	13.54	12.23	11.79	7.42	3.49	16.59	1.75	2.18
BHB	RF	Bottom	127	38.64	8.33	5.30	13.64	2.27	1.52	20.45	6.82	3.03
BHB	RF	Top	113	41.57	14.61	11.24	4.49	2.25	3.37	15.73	1.12	5.62
BHB	PR	Bottom	110	17.02	27.66	4.26	25.53	2.13	2.13	14.89	6.38	0.00
BHB	PR	Top	115	32.30	9.32	0.00	31.36	1.69	1.69	16.10	5.08	2.54
Weight			(mg m^{-3})									
HWC	RF	Bottom	8.41	0.88	0.35	0.69	0.33	86.88	6.97	1.95	1.58	0.36
HWC	PR	Bottom	2.68	2.09	1.93	1.49	2.38	69.79	8.80	8.56	4.71	0.24
HWC	PR	Top	2.60	0.58	17.00	1.46	0.48	78.07	0.77	1.20	0.22	0.24
BHB	RF	Bottom	6.88	2.88	1.12	2.53	5.45	68.39	8.56	5.91	3.44	1.72
BHB	RF	Top	5.92	3.53	2.00	6.13	1.68	58.30	21.73	5.19	0.65	0.79
BHB	PR	Bottom	7.37	1.09	3.85	1.75	4.56	81.88	0.41	3.70	2.76	0.00
BHB	PR	Top	4.41	3.41	1.91	0.00	13.37	54.87	13.63	6.63	3.65	2.53

formalin with Phloxin B stain added in order to facilitate sorting of invertebrates. Invertebrates were picked at 12× magnification, and identified to genera when possible. In the clearcut watershed, where there was extensive sediment transport, a sample splitter (Waters, 1969) was used to split netted material into one-eighth subsamples prior to picking. Subsamples of each taxon were dried, ashed, and weighed for ash free dry mass (AFDM) estimates. Organic and inorganic contents of sediments were determined by oven drying, ashing, and weighing.

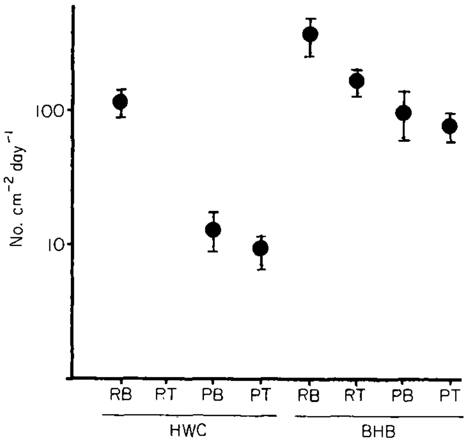

FIG. 3. Number of drifting invertebrates available per cm^2 intake area per day in bottom (B) and top (T) layers sampled at rockface (R) and pebble–riffle (P) sites of Huge White Creek (HWC) and Big Hurricane Branch (BHB). Note the use of log scale for vertical axis. Intake area is based on area of sampler opening and water depth. Bars indicate 95% confidence limits.

Results

Stream morphometry and substrate affected flow over the sample sites in the two streams. Flow through the bottom 2 cm layer was higher over rockface than pebble–riffle on both watersheds (Fig. 2). Overall, the volumes filtered by nets were higher on BHB, the clearcut watershed.

Drift densities (no. organisms m^{-3}) were significantly higher in BHB (mean=116.3 individuals m^{-3}) than in HWC (mean=31.0 individuals m^{-3}). Drift densities within each watershed did not differ significantly between rockface and riffle sites. In BHB, drift densities were 112.4 and 120.1 m^{-3} at riffle and rockface sites, respectively, while that in HWC was 29.1 at the riffle and 32.8 m^{-3} at the rockface. Taxa comprising the drift were also similar between sites. Percentage composition and mass indicate that a large number of very small organisms were predominant in the drift of both streams (Table 3).

The delivery rate (individuals cm^{-2} unit time^{-1}) of drifting organisms at each site is strongly influenced by differences in flow regime and position (top *v*. bottom). In the bottom layer of the water column, 4 (BHB) to 10 (HWC) times more organisms were delivered to rockface sites than to riffle areas (Fig. 3). These differences were significant ($P<0.01$, paired *t*-test).

The amounts of organics and inorganics were significantly greater ($P<0.01$, paired *t*-test) in rockface bottom layers than riffle bottom layers of BHB (Table 4). However, no significant differences existed between riffle and rockface bottom layers in HWC. Rockface sites had greater numbers of invertebrates per gram inorganic than riffle sites in HWC ($0.01<P<0.02$; paired *t*-test). Both organic

TABLE 4. Ash and organic content of drift in both layers at rockface and pool sites in Hugh White Creek (HWC) and Big Hurricane Branch (BHB). Units are mg cm^{-2} min^{-1} with 95% confidence interval in parentheses.

Stream	Substrate	Position	Ash	Organic	% Ash	Inverts/GmASH
HWC	RF	Bottom	1.095 (±0.038)	0.610 (±0.018)	64.22	115.83 (±33.35)
HWC	PR	Bottom	1.237 (±0.371)	0.051 (±0.007)	96.01	26.63 (±13.01)
HWC	PR	Top	0.105 (±0.027)	0.068 (±0.018)	60.53	91.45 (±39.90)
BHB	RF	Bottom	34.657 (±4.125)	14.987 (±0.859)	69.81	12.11 (±10.16)
BHB	RF	Top	6.517 (±0.627)	5.402 (±0.486)	54.67	21.40 (±7.69)
BHB	PR	Bottom	3.122 (±0.255)	1.997 (±0.163)	60.99	23.98 (±11.32)
BHB	PR	Top	2.365 (±0.180)	2.012 (±0.161)	54.03	26.49 (±9.13)

and inorganic sediments were much higher in BHB as seen in Table 4.

Discussion

Total drift over both rockface and pebble riffle of HWC and BHB are much higher than previously reported for HWC by O'Hop & Wallace (1983). In the previous study a drift net of 234 μm mesh was positioned near the weir and changed once every hour. The 143 μm mesh net used in this study, with sample times of 10–20 min, collected a greater number of very small organisms, primarily copepods and chironomids. More frequent net changes also resulted in smaller samples from which smaller invertebrates were more readily removed. Benke *et al.* (1979) also found that mesh size of drift nets profoundly influenced the results in a Southeastern (U.S.A.) Coastal Plain river. Drift densities in the present study are 5 times greater than that obtained by O'Hop & Wallace (1983) whereas biomass is only 3 times greater in the present study, indicating some underrepresentation of small organisms in the study by O'Hop & Wallace (1983). This pattern is similar for all samples regardless of position or site. Thus, the use of fine meshed nets as well as shorter sample intervals in drift studies may enhance efficiency of drift collection and processing.

In the present study, rockface and deep riffle sites exhibited very different flow regimes. Flow regime, as influenced by streambed morphometry, is an extremely important factor influencing invertebrate drift densities, organic debris and ash within the water column. Flows are generally faster and the water column's depth is compressed across rockface substrates which result in Froude numbers close to or greater than 1. In contrast, pools or deep riffles have slower flows and greater water depth, yielding Froude numbers much less than 1. On HWC, these differences were very obvious with Froude numbers of 1.59 for the rockface and 0.080 for the riffle site. Between-site differences were not as pronounced on BHB, although the rockface site had a Froude number of 0.55 which was 6 times higher than that of the pebble riffle site (0.098). Flow across the rockface site of HWC was critical ($F>1$), while that across the rockface site of BHB was subcritical. However, rockface flow in BHB was sufficient to provide a sharp contrast with the pebble riffle area.

These differences in flow regime and substrate produce conditions that provide a greater rate of food delivery, especially invertebrate drift, to collector-filterers on rockface habitats compared to that of riffles. The enhanced delivery rate is most pronounced in the bottom layer of the water column. While vertical variation of drift in large rivers appears to be species specific with no overall even distribution (Matter & Hopwood, 1980), in smaller streams the greatest density of drift has been found to be near the bottom of the stream (Eidt & Weaver, 1984). Our results support the idea of greater availability of invertebrate drift near the substrate, especially across rockfaces.

If only total flow were considered, or this bottom layer of flow not sampled, very different results would be obtained for drift availability to filtering collectors. In HWC, no significant difference in total invertebrates per minute is seen between rockface and deep riffle. Yet differences in the bottom layer of both BHB and HWC were significant, and it is this bottom layer of flow that encompasses the effective filtering range of net-spinning caddisflies such as *P. cardis*.

Based on *P. cardis* production estimates (Gurtz & Wallace, unpublished data), utilization of available drift was calculated employing the trophic distribution and assimilation efficiencies used by Benke & Wallace (1980). On rockface, habitat collector-filterer utilization of invertebrate drift was approximately 20% in HWC and 17% in BHB. In pool–riffle areas only 10% and 3% were used in HWC and BHB respectively. These may be overestimates of utilization as the drift measured by this technique is that remaining following upstream removal by filter feeders.

Although overall utilization of drift may appear low, two points should be emphasized. First, in regions of increased drift availability (rockface substrates), abundance and secondary production of *P. cardis* are significantly higher (Gurtz & Wallace, unpublished data). This indicates that these areas are more conducive to carnivorous filter feeding activity. Dense populations of net-spinning caddisflies often occur in outflows of lakes or impoundments (Cushing, 1963; Oswood, 1979; Parker & Voshell, 1983) and there is considerable evidence that the enhanced levels of secondary production of hydropsychids at such sites is attributable to higher food quality rather than quantity of the seston (Parker & Voshell, 1983; Voshell & Parker, 1985). Our results suggest that even in free-flowing streams some hydropsychids, e.g. *P. cardis,* may preferentially colonize microhabitats such as rockface substrates and thereby maximize the delivery rate of their food, i.e. invertebrate drift. Other net-spinning caddisflies have also been shown to aggregate in areas of high prey density; for example, *Plectrocnemia conspera* (Polycentropodidae) (Hildrew & Townsend, 1977, 1980).

Second, although drift densities are significantly higher in BHB than in HWC, a smaller percentage of the drift of BHB is used by filter feeders. This indicates a shift in factors controlling collector-filterer production and drift utilization between the streams draining clearcut (BHB) and undisturbed (HWC) catchments. Such factors as limited space and increased siltation may be affecting collector-filterers on BHB more than on HWC. Filter feeders such as *Dolophilodes distinctus* (Walker) (Trichoptera: Philopotamidae) were practically eliminated from BHB following road building and clearcutting of BHB watershed. Presumably their fine-meshed catchnets were inoperable under conditions of increased siltation and sediment transport (Gurtz & Wallace, 1984). The influence of siltation is evident in the low values of invertebrate per gram ash in drift on BHB. Compared to HWC, sediment and detritus appear to overwhelm the numbers of invertebrates in the water column. Thus, while drift is high in terms of numbers this advantage may be off-set by the deleterious influence of siltation. Species, such as *P. cardis,* that possess large-meshed catchnets which are less susceptible to clogging, may be favoured under such conditions.

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498