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A field study of the effects of water temperature, discharge and trout odour on the drift of stream invertebrates

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With 2 figures and 5 tables in the text

Abstract

Drift response varied according to the scale of changes in water temperature and discharge and also amongst taxa in a hardwater stream in Ontario. For example, during a period of wide-ranging discharge and water temperature, overall night-time drift density was positively related to both discharge and minimum temperature whereas during more constant conditions it was related to discharge alone. Analysis of catches of individual "replicate" drift nets showed considerable variance. No taxon showed a significant relationship with temperature or discharge during the day but some did at night. During the day, the overall density of drifting animals was greater in the presence of trout odour although density of some taxa was the same in both fish and fishless sections of the stream. At night, only three taxa drifted significantly more in the presence of trout. Mayflies, stoneflies and caddisflies drifting at night were larger in the presence of trout but amphipods were smaller.

Introduction

Much has been written about the drifting of stream invertebrates from perspectives of both the single species (e.g. OTTO, 1976) and benthic communities (e.g. SCULLION & SINTON, 1983). Field studies have been largely descriptive (see comments in TOWNSEND & HILDREW, 1976; STATZNER et al., 1984) but another study approach has been through laboratory experiments (e.g. CORKUM et al., 1977; WILLIAMS & MOORE, 1982). Although stream drift has been the subject of several reviews (e.g. WATERS, 1972; BRITTAIN & EIKELAND, 1988), there is still a great deal that we do not understand, particularly with respect to the complex array of factors, both abiotic and biotic, that govern the drifting process (STATZNER et al., 1984).

The purpose of this manipulative field study was to examine, in detail, over a relatively short period (September), the effects of three important environmental factors on a variety of drifting invertebrate taxa, to examine day/night differences, and to assess between catch-net variation. The factors chosen were: (1) water temperature — crucial in influencing the activity of poiki-

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lothermic animals; (2) discharge — a parameter fundamental in shaping running water communities; and (3) the presence of predatory fishes — recently, a number of experiments have examined the influence of predators on drifting invertebrates (e.g. Andersson et al., 1986; Culp, 1986) but the findings have been contradictory.

Materials and methods

The study site was a single, 15 m long, uniform riffle on the east branch of Duffin Creek, Durham County, Ontario (43 ° 58′ N; 79 ° 05′ W; 180 m elevation), some 3 km downstream from its source in several springs. This section of the stream is approximately 5 m wide and has a substrate of mixed limestone gravels with some sand and clay patches underlain by clay at a depth of 20 cm. Flat cobbles (up to 20 cm in diameter) occur at the surface and, in summer, these are heavily encrusted with calcium carbonate. During mid- to late summer, the water depth on the riffle averages 20 cm, dissolved oxygen is at or near saturation, and pH is normally around 7.5. The surrounding watershed is mostly rough pasture or woodland (mainly eastern white cedar *Thuja occidentalis* L.) with some mixed agriculture.

On August 10, 1981, the riffle was divided in half, lengthwise, using 60 cm high sheets of plywood joined end to end and held in place by iron stakes. Four 250 μm mesh nitex drift nets were positioned at the downstream end of the riffle, two on either side of the divider (Fig. 1). Each tapered net was 1 m long with an opening 45 cm wide × 30 cm high to which was affixed a galvanized metal funnel with a vertical slit opening measuring 30 cm high × 7.5 cm wide. This restricted opening was necessary to allow each net to fish for 12 h without clogging and has been used in other drift studies (e.g. Mundie, 1966). The uniformity of the riffle and net positions were such that water depth and current speed were the same for all nets at any one point in time (determined by a series of measurements prior to beginning drift collections; Table 1).

Starting on September 1, 1981, the nets were set at 20.00 h each day and emptied at 08.00 h the next day; this period was designated Night-drift. The nets were then reset and subsequently emptied at 20.00 h on that same day; this period was designated Day-drift. It was anticipated that Night-drift would include animals with crepuscular drifting activities as it encompassed both dawn (began at around 06.00 h) and dusk (began at 20.00 h). Drift samples were preserved in 10 % formalin solution containing rose bengal stain which facilitated later sorting into separate taxa (Williams & Williams, 1974). Drift collecting continued until 08.00 h on September 4 but then was discontinued (as, for the next two weeks, flow conditions were too constant thus frustrating attempts to

Table 1. Examples of measurements of physical factors recorded (3 times at each of the four nets over 24 h) to illustrate the uniformity of net positions.

Factors	Net 1			Net 2			Net 3			Net 4		
	0 h	12 h	24 h	0 h	12 h	24 h	0 h	12 h	24 h	0 h	12 h	24 h
Water depth (cm)	18.0	20.0	16.5	18.0	20.0	16.0	18.0	19.5	17.5	18.0	20.0	16.0
Velocity (cm/s)	60.0	75.0	60.0	60.0	76.0	59.0	60.0	76.0	60.0	60.0	76.0	60.0
Froude Number*	0.45	0.54	0.47	0.45	0.54	0.47	0.45	0.55	0.46	0.45	0.54	0.48
Discharge (m^3/s)	0.54	0.75	0.51	0.54	0.76	0.47	0.54	0.74	0.53	0.54	0.76	0.48

* Froude number < 1 indicate streaming flow, i.e. the ordinary turbulence found in most streams (Morisawa, 1968).

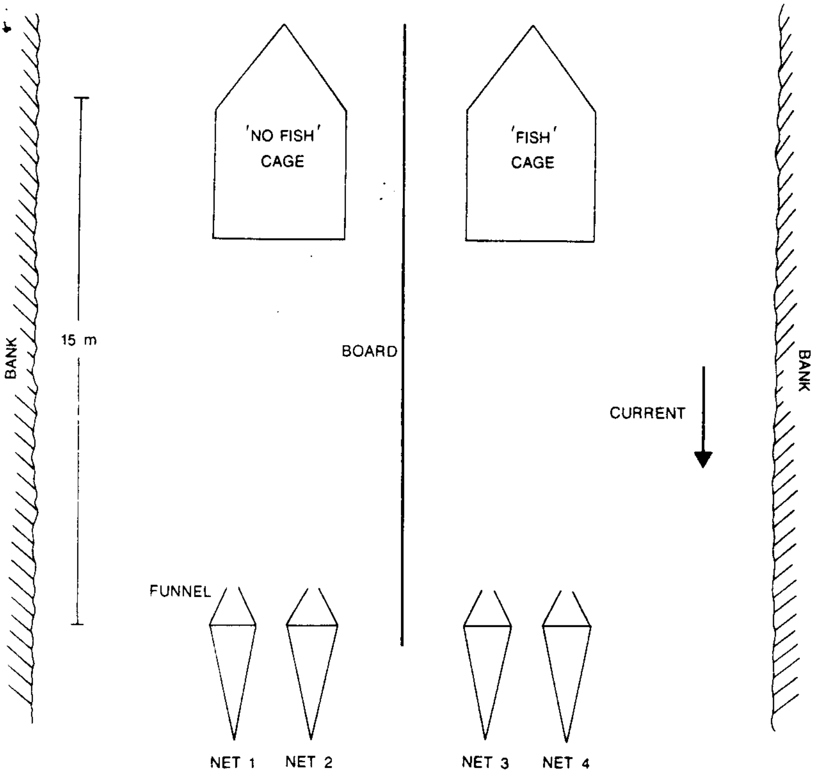

Fig. 1. Diagram showing the arrangement of the dividing board, the four drift nets and the trout cages on a riffle in Duffin Creek.

relate drift to discharge) until the nets were reset at 20.00 h on September 17, when discharge began to fluctuate again; collecting ceased at 08.00 h on September 22. One further set of Night-drift samples was taken from 20.00 h on September 24 to 08.00 h on September 25.

Maximum-minimum thermometers were attached to the frame of each of the four driftnets and were read each time the nets were emptied. Water depth and current speed (using a Gurley meter; Gurley Instruments, Troy, N.Y.) were determined in the opening of each net at these times by taking the average of three replicate readings; variance among replicates and between net opening readings and those made adjacent to the nets was less than 5 %. Spot-checks of waterlevel and current speed were made intermittently during the 12 h sampling periods, particularly when there was rain. Current speeds were converted to discharge (taking into account water depth and stream width) and were expressed as m^3/s. It was apparent that the readings of current taken when the nets were emptied were not always representative of the previous 12 h. This seemed only a problem during the heavy rain spanning the period 20.00 h, September 3 to 08.00 h, September 4 when discharge changed rapidly from 0.94 m^3/s to 2.28 m^3/s. During the first 3 h of this 12 h collecting period, the Froude Number (a scale measurement of turbulence; Morisawa, 1968) changed from 0.58 to 0.62 and then remained at the higher value. Thus even during this, the largest recorded change in discharge, the nets were collecting drift at a constant (measured) discharge for 75 % of the time.

To examine effects of predator odour on drift, a large galvanized metal cage (1.7 m long × 0.9 m wide × 0.3 m deep) of 1 cm mesh was placed at the upstream end of the riffle on each side of the dividing board on September 7 (Fig. 1). Each cage was anchored 5 cm off the substrate using iron stakes and was lined with 250 μm mesh nitex netting to prevent entry of larger drifting organisms and consumption by the fishes. Ten days after installation (20.00 h on September 17), 50 rainbow trout (*Salmo gairdneri* RICHARDSON) of mean length = 20 cm were added to the right-hand cage and covered with a fine net to prevent escape. The empty left-hand cage served as a control. The screens on both cages were brushed clean at the end of each drift collection period, prior to re-setting the driftnets. The trout remained in the stream until 08.00 h on September 22 (4.5 days).

In the laboratory, the drift samples were sorted using a dissecting microscope and the major taxa identified and enumerated. The numbers of animals caught in the drift nets were converted to densities, defined as catch/unit volume of water/unit time (ELLIOTT, 1970). Size measurements were made of individuals of species in the four taxa (Amphipoda, Ephemeroptera, Plecoptera and Trichoptera) containing the largest animals, as these were predicted (by virtue of their size, activity and predominance in salmonid guts, GIBSON & GALBRAITH, 1975) to be the most likely to be affected by the trout. Maximum head capsule width was the size variable measured for the insects, while total, stretched body length was measured for the amphipods.

Normality and homogeneity of variance tests on the data indicated that transformation was necessary (KOLMOGOROV-SMIRNOV Goodness of Fit, $p < 0.05$; F-max, $p > 0.05$). Transformation to ln x satisfied the assumptions for parametric statistical analysis.

Results

Effects of water temperature and discharge: Regression analyses of night samples (20.00 h to 08.00 h) over the period September 1—25 (when temperature and discharge varied widely) showed that the densities of animals collected in the driftnets (all taxa and all nets) increased significantly ($p < 0.05$) with increase in both minimum night-time water temperature and night-time discharge (Fig. 2 a, b) with temperature appearing to be the more important factor (Table 2). However, together they accounted for only 26.5 %

Table 2. Correlation coefficients (r) or coefficients of determination (R^2) of regression analyses, using ln x transformed data, of the densities of all animals collected in the drift nets at night versus the minimum night-time water temperature and night-time stream discharge during 9 nights over the period 1–25 September (composed of 3 nights from 1–4 Sept., 5 nights from 17–22 Sept. and 1 night from 24–25 Sept.).

	Discharge (r)	Min-water temp. (r)	Discharge and min-water temp. (R^2)
All nets (n = 36)	0.378*	0.509*	0.265**
Drift net 1 (n = 9)	0.521	0.580	0.342
Drift net 2 (n = 9)	0.649	0.901***	0.838**
Drift net 3 (n = 9)	0.374	0.711*	0.646*
Drift net 4 (n = 9)	0.161	0.116	0.026

Significance levels: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; Discharge vs. Min-water temp.: r = 0.823** in all cases.

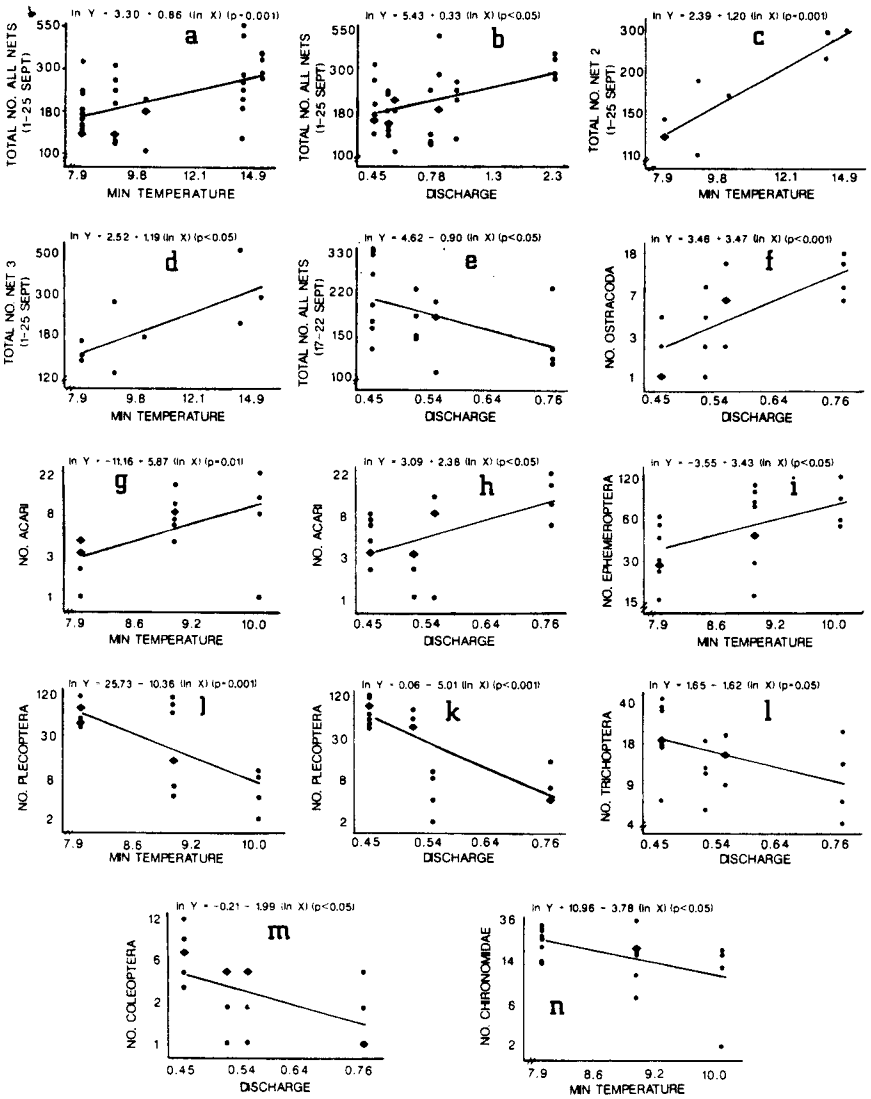

Fig. 2. Plots of the significant regressions between drift and minimum water temperature, and drift and night-time stream discharge, indicated in Table 2. Regression equation and significance of each regression are given; dependent and independent variables are back-calculated from ln units; diamonds indicate where 2 or more data points are superimposed; regressions a—d are based on the period September 1—25 when discharge and water temperature varied widely (range 0.45—2.3 m^3/s; 7.9—14.9 °C), while regressions e—n are based on the period September 17—22 when these factors were less variable (range 0.45—0.76 m^3/s; 7.9—10.0 °C).

of the variance in densities caught. Minimum water temperature and discharge were highly positively correlated at night ($p < 0.001$). Regression of change in density with change in discharge, to determine if drift catch was a function of increasing or decreasing discharge (sensu Ciborowski et al., 1977), was not significant ($R^2 = 0.149$; $p > 0.1$), and neither was change in density with change in minimum water temperature ($R^2 = 0.045$; $p > 0.1$).

Regression analyses on the densities of all animals collected during the day (08.00 to 20.00 h) and night (20.00 to 08.00 h) over the period September 17—22 (when temperature and discharge were less variable) showed no relationship with either temperature (maximum-day, minimum-night) or discharge during the day but there was a significant negative relationship with discharge at night ($p < 0.05$; Table 3; Fig. 2 e). There was a significant ($p < 0.05$) positive relationship between maximum water temperature and discharge during the day but none between minimum water temperature and discharge at night.

No individual taxon showed any significant relationship with either water temperature or discharge during the day (Table 3) though several associations were apparent at night. For example, there were significant relationships ($p < 0.05$) between minimum night-time water temperatures and the densities of chironomids (represented >90% by *Eukiefferiella* spp. and *Cricotopus* sp.; negative relationship; Fig. 2 n) and mayflies (represented entirely by *Baetis vag-*

Table 3. Correlation coefficients (r) or coefficients of determination (R^2) of regression analyses, using ln x transformed data, of the densities of animals in each taxon vs. the water temperature and stream discharge during the period 17–22 September (all nets pooled).

	Day (n = 16)			Night (n = 20)		
	Discharge (r)	Maximum water temp. (r)	Discharge and water temp. (R^2)	Discharge (r)	Minimum water temp. (r)	Discharge and water temp. (R^2)
All taxa						
Combined	0.075	0.048	0.005	−0.476*	−0.060	0.237
Oligochaeta	0.248	0.282	0.091	−0.012	−0.269	0.079
Copepoda	0.012	0.180	0.043	−0.269	−0.248	0.101
Ostracoda	−0.249	0.061	0.070	0.676**	0.315	0.467**
Amphipoda	−0.034	−0.038	0.001	−0.431	0.131	0.186
Acari	0.029	0.114	0.014	0.452*	0.473*	0.323*
Ephemeroptera	−0.021	0.003	0.000	0.242	0.494*	0.252
Plecoptera	−0.208	−0.025	0.055	−0.724***	−0.672**	0.735***
Trichoptera	0.046	0.060	0.003	−0.444*	0.174	0.311*
Coleoptera	0.036	0.147	0.024	−0.513*	−0.039	0.282
Chironomidae	0.071	0.040	0.005	−0.390	−0.507*	0.314*
Diptera (other)	−0.073	−0.008	0.007	−0.196	−0.036	0.039

Significance levels: $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$; Discharge vs. Water temp.: r = 0.558* in all cases; day-time water temp. was maximum while night-time water temp. was minimum in all cases.

ans Mc D. and *Ephemerella* sp.; positive relationship; Fig. 2 i) collected (all nets) but temperature accounted for only approximately 25 % of the variance in densities in each case. Densities of caddisflies (consisting of *Hydropsyche* sp., *Dolophilodes distinctus* [Walker] and *Brachycentrus* sp.), aquatic beetle larvae, *Promoresia* sp., and ostracods drifting were related significantly (the first two taxa negatively, the last positively; $p < 0.05$; Fig. 2 l, m, f) to night-time discharge and, in the case of the ostracods, discharge accounted for as much as 45 % of the variance. Densities of drifting stoneflies, *Brachyptera* sp., and mites, *Sperchon* sp., varied significantly (the first negatively, the second positively; Fig. 2 j, k and g, h) with both minimum night-time water temperature and discharge which together, in the case of the *Brachyptera* nymphs, accounted for 73.6 % of the variance in density. Density of amphipods, *Gammarus pseudolimnaeus* Bousfield, oligochaetes, *Nais simplex* Piquet, copepods and non-chironomid dipterans, *Antocha* sp. and *Dixa* sp., drifting were related neither to discharge nor water temperature, neither singly nor in combination.

Between net variation: Regression analyses for individual "replicate" drift nets over the period September 1—25 showed relationships that were somewhat different from the analysis performed on data from all nets combined. The densities of all animals caught in Net 1 and Net 4 were related to neither minimum night-time water temperature nor discharge (Table 2). In contrast, 83.8 % of the variance in density of animals caught in Net 2 was positively associated with temperature and discharge, with minimum night-time water temperature being the more significant factor (Table 2; Fig. 2 c). This was also the case for Net 3, where 64.6 % of the variance in animal density was associated with temperature and discharge (Table 2; Fig. 2 d).

Effects of trout: At night, there was no significant difference between the densities of all animals drifting in the fish and fishless (control) sides of the stream, however significantly more copepods, trichopterans and beetles drifted in the presence of fishes (Table 4). During the day, the overall density of animals drifting was greater ($p < 0.05$) in the fish section and this was primarily due to the chironomids, amphipods, non-chironomid dipterans, copepods and ostracods. Daytime densities of drifting stoneflies, caddisflies, mayflies, beetle larvae, mites and oligochaetes were the same in both fish and fishless sections.

Amphipods drifted significantly more at night ($p < 0.05$) in both the fish and fishless sections, while mayflies drifted more at night only in the fish section (Table 4). Mites, non-chironomid dipterans and ostracods drifted significantly less ($p < 0.05$) at night only in the fish section. Total numbers of animals drifting were greater at night in the fishless section but numbers were the same between day and night in the fish section (Table 4).

Baetis vagans and *G. pseudolimnaeus* drifting in the day were larger ($p < 0.05$) in the fish section than in the fishless section and this was also the

Table 4. Comparison of the densities of animals in each taxon caught in drift nets in the control (no fish; nets 1 and 2 combined) and experimental (fish; nets 3 and 4 combined) sections of the stream during the period 17–22 September (two-tailed, paired t-tests on ln x transformed data paired by date).

	Mean No. animals/section (± 1SE) (n = 4 for day; n = 5 for night)					
	Day		Prob. of sign. difference	Night		Prob. of sign. difference
	No Fish	Fish		No Fish	Fish	
All taxa	228.3±34.6*	477.8±70.4	<0.05	349.4±49.5*	416.0±56.1	NS
Oligochaeta	3.8± 0.6	6.3± 1.7	NS	7.6± 1.7	10.4± 2.0	NS
Copepoda	7.5± 1.9	21.0± 1.7	0.01	12.2± 0.4	22.6± 4.0	<0.05
Ostracoda	12.5± 5.1	90.5±21.1**	0.05	7.2± 2.4	13.6± 5.2**	NS
Amphipoda	1.8± 0.3*	8.5± 0.3**	<0.005	23.6± 2.7*	50.0±12.3**	NS
Acari	27.3± 6.4	54.5± 9.8**	NS	14.8± 5.2	13.2± 6.4**	NS
Ephemeroptera	51.8± 8.8	50.5± 7.7**	NS	123.6±25.2	102.0± 9.6**	NS
Plecoptera	38.5±10.1	57.8± 6.4	NS	85.4±33.3	103.4±38.9	NS
Trichoptera	34.0± 7.6	65.3±14.3	NS	29.2± 7.5	43.8± 8.5	0.01
Coleoptera	7.0± 2.2	10.3± 2.3	NS	4.4± 1.3	10.4± 3.7	<0.05
Chironomidae	39.8± 6.5	73.3± 9.3	<0.05	36.0± 6.2	37.2± 6.3	NS
Diptera (other)	6.0± 1.6	29.0± 6.9**	<0.01	5.8± 2.3	11.0± 1.6**	NS

* or ** indicate significant difference, at $p<0.05$, between pairs across the table, e.g. there were significantly more amphipods caught at night (50.0±12.3) than during the day (8.5±0.3) in the fish section; similarly, there were more caught at night (23.6±2.7) than in the day (1.8±0.3) in the fishless section.

case for *B. vagans*, *Brachyptera* sp. and *Hydropsyche* sp. at night (Table 5). *Gammarus pseudolimnaeus* drifting at night were significantly larger in the fishless section.

Analysis of the effects of trout by applying paired t-tests to the data was judged to be the most appropriate. However, by confining the analysis to the period when the fish were present (September 17—22) the assumption was made that there was no difference between the control (fishless) and the experimental (fish) sides of the stream. To address this I used a two-way ANOVA to compare the two sides of the stream before (September 1—4) and after the trout were added (September 17—22). There was no significant effect of position ($p > 0.1$) or of fish ($p > 0.1$) on the density of animals in the drift. Neither was there a significant interaction ($p > 0.8$) between position and fish which indicates that the total drift was not affected by the introduction of trout. The drawback in using this latter technique is that it suffers from temporal pseudoreplication (HURLBERT, 1984). However, it does substantiate the conclusions drawn from the paired t-test approach as to the lack of effect of fish on the total fauna, and also shows that there was no difference between the two sides of the stream.

Discussion

There is still debate as to the relative importance of endogenous circadian rhythms within a drifting animal and the influence of external, environmental

Table 5. Comparison of the size of a randomly-selected subset of animals (mm) in each of the four largest taxa caught in drift nets in the control (no fish) and experimental (fish) sections of the stream during the day and night (two-tailed, paired t-test on ln x transformed data from the period 17 – 22 September; there was no significant change in size of animals, within taxa, over this period).

	Mean head capsule width or length (± 1SE) (n)					
	Day		Prob. of sign. difference	Night		Prob. of sign. difference
	No Fish	Fish		No Fish	Fish	
Amphipoda (length) *Gammarus pseudolimnaeus*	1.81±0.07 (7)	2.95±0.08 (34)	<0.05	4.02±0.08 (90)	2.81±0.11 (111)	<0.001
Ephemeroptera (hcw)* *Baetis vagans*	0.39±0.07 (193)	0.43±0.07 (205)	0.01	0.40±0.07 (324)	0.44±0.07 (229)	0.005
Plecoptera (hcw) *Brachyptera* sp.	0.37±0.05 (152)	0.36±0.06 (236)	NS	0.33±0.06 (378)	0.37±0.06 (289)	<0.001
Trichoptera (hcw) *Hydropsyche* sp.	0.35±0.06 (133)	0.36±0.07 (261)	NS	0.33±0.07 (94)	0.38±0.07 (100)	<0.05

* head capsule width.

factors in controlling drift periodicities (e.g. WATERS, 1972; WILEY & KOHLER, 1984). Environmental factors that may influence drift were reviewed recently by STATZNER et al. (1984) and BRITTAIN & EIKELAND (1988). Observations in the present study all relate to exogenous factors though not for any lack of credence in endogenous control.

Clearly, over the period September 1—25, night-time drift densities (i.e. densities retained by the drift nets) of all taxa combined were positively related to water temperature and discharge. During this period, the range in night-time discharge was from 0.45 to 2.28 m^3/s and for minimum night-time temperature it was 8.0 to 15.0 °C. Presumably, increased drift was a consequence of an increase in overall activity resulting from a poikilothermic response to increasing water temperature, while increased drift in response to increasing discharge may have been the result of greater dislodgement of animals at higher flow. However, over the period September 17—22, when the ranges were smaller (0.45 to 0.75 m^3/s and 8.0 to 10.0 °C), the previously-noted positive relationships were replaced by a single, significant negative relationship with discharge. During the daytime there were no significant associations. These findings suggest that drifting response by the community considered as a whole may vary according to the scale of changes in certain environmental factors. It is known, for example, that the numbers of invertebrates drifting may increase both with increasing and decreasing discharge (BROOKER & HEMSWORTH, 1978; SCULLION & SINTON, 1983). CIBOROWSKI et al. (1977) showed that drift density in the mayfly *Ephemerella subvaria* McD. changed disproportionately while current velocities were increasing. A similar, hysteretic, analysis of the Duffin Creek data showed that changes in total drift density did not occur while discharge or temperature were in the process of changing.

Individual taxa showed no significant relationships with water temperature or discharge during the day but a wide spectrum of associations at night, some with temperature or discharge alone, others with both. For some taxa the relationships were positive, for others they were negative. Numbers drifting varied according to both taxon and factor, with some factors clearly accounting for most of the variance, e.g. 73.6 % in the stonefly *Brachyptera* sp. In some taxa there was no relationship between these physical environmental factors and drift density even though some, such as *Gammarus pseudolimnaeus*, are "classic" drifters. However, drift of *G. pseudolimnaeus* did not respond to experimental manipulation of water temperature (WOJTALIK & WATERS, 1970), thus its drift periodicity may be more strongly under endogenous control or the control of other exogenous factors such as light (WILLIAMS & MOORE, 1982). In contrast, drift of *G. pulex* (L.) in Europe has been positively related to stream temperatures (MÜLLER, 1963). Relationships of drift to water temperature in other taxa tend to be largely non-existent or positive (Table 1, page 321, STATZNER et al., 1984). Comparative field data for a variety of taxa indicate a mix of relationships of drift with discharge, i.e. some positive, some negative and some no relation (STATZNER et al., 1984).

Lack of association of drift density with temperature or discharge during the day may be a reflection of the strong nocturnal peak in drift activity recorded for many benthic lotic species (ELLIOTT, 1967; WATERS, 1972; BUTLER & HOBBS, 1982; DUDGEON, 1983). Individual animals may be less inclined to respond to changes in their environment during periods of reduced locomotor activity; the latter may be under either endogenous or exogenous (e.g. light) control depending on species. Not all benthic species are night active (ELLIOTT, 1967; GRAESSER & LAKE, 1984; DE MOOR et al., 1986).

Interestingly there was variation in drift catches between nets that had been deliberately positioned so as to represent as identical samplers as was practicably possible. It is known that drift rate (catch/unit time) varies both vertically in the water column (CRISP & GLEDHILL, 1970) and horizontally across the streambed (ELLIOTT, 1970), and this is related to the volume of water passing through each net. However, when this is corrected for by calculating catch/unit volume/unit time, as in the present study, then this drift density tends to remain fairly constant. ELLIOTT (1970) attributed any remaining variation in drift density between nets to random causes. In Duffin Creek, however, significant variation in drift densities in nets 2 and 3 were positively associated with minimum night-time temperature and discharge. Variation in drift density in nets 1 and 4 must have been due to factors not measured.

It is perhaps surprising that only in three taxa were there differences in the numbers of animals drifting in the presence or absence of trout at night. In all three cases (copepods, beetle larvae and caddisfly larvae) the drift densities increased in the presence of fishes. In the laboratory, activity level of the stonefly *Paragnetina media* (WALKER) increases when it is exposed to rainbow trout, however the activity of another stonefly, *Agnetina capitata* (Pictet), decreases (WILLIAMS, 1986). Depression of drift rates by predators or disturbance by other species has been noted also in chironomids, while increases in activity have been observed in *Baetis* sp., *Simulium* sp. and a few other mayflies and blackflies (STATZNER et al., 1984).

In Duffin Creek, *G. pseudolimnaeus* drifted more at night than in the day and, at night, the animals drifting in the fish section of the stream were significantly smaller than in the fishless section. This observation supports the finding that the presence of rainbow trout in laboratory stream tanks dramatically decreases the drift activity of adult *G. pseudolimnaeus* (WILLIAMS & MOORE, 1985). ANDERSSON et al. (1986) found that although the average size of drifting *G. pulex* was greater at night the presence of predaceous sculpins (*Cottus gobio* L.) did not alter the size distribution of drifting animals. Drifting *Baetis vagans*, *Brachyptera* sp. and *Hydropsyche* sp. in Duffin Creek were larger in the fish section at night and these observations agree with those of ALLAN (1978) on *Baetis* *bicaudatus* Dodds. Allan (1978) suggested that smaller instars or taxa, because they are at less risk from fish predators, are less constrained than larger forms which, presumably should drift more at night. However, during the day, *B. vagans* and, surprisingly, *G. pseudolimnaeus*, were larger in the fish section although their daytime drift densities were low. Perhaps these conflicting results may be explained in terms of relative risks of individual taxa and instars to predation by predators of different size and with different prey preferences and hunting behaviours. For example, densities of small benthic invertebrates in an intertidal saltmarsh community were highest in enclosures with large fishes (*Fundulus heteroclitus* [L.]) and lowest in closed controls and in enclosures with small fishes. Intermediate densities occurred in enclosures with medium-sized fishes. The effects of fish size were greater at high fish densities but fish density, by itself, had little effect on benthos abundance (Kneib & Stiven, 1982).

It is acknowledged that the trout density in the cage was greater than would be found in most natural settings but one of my aims was to look for significant gross effects of fishes on drift in a semi-natural setting (see Williams et al., 1977). If it proved that there was no effect at high density then I surmised that there would likely be no effect at low density. However, if the experiment had been done at low fish density and no effects found, the somewhat more academic question of any effect at all, even under artificial densities would have remained unanswered. Further, the population of rainbow trout in Duffin Creek is augmented each spring when anglers add hatchery-reared animals. Thus some sections of the stream do, periodically, contain high densities — though there is no solid quantification of levels attained. By midsummer (August) most of these fishes have been removed such that, in 1981, in pools upstream and downstream of the study site (a distance of 300 m) I did not find (via observation, spot seining and disturbing likely retreats with a pole) more than five trout; none of these was on the experimental riffle.

Statzner et al. (1984) advocated attempts to devise a hierarchy of factors governing stream drift. Within the confines of the present observations, I conclude the following generalities for the benthos of Duffin Creek in September:

(1) minimum water temperature was more influential than discharge over a period when both parameters varied widely;

(2) discharge was more influential during a period of more moderate change;

(3) both physical factors were more influential than the odour of predatory fishes.

At the level of the individual taxon, however, the data indicate mixed and/or conflicting relationships, many of which reflect the fact that the species that make up lotic benthic communities show evolved differences as a consequence of their different phylogenetic origins. As the exact qualitative and quantitative composition of benthic communities varies from stream to stream, we may expect different results between studies — particularly if the relationships are studied at the community level. Unravelling of the complexity of factors governing stream drift will proceed, optimally, through study of individual species (including various stages in the life cycle: see STATZNER et al., 1987) in both field and laboratory settings. Ultimately, it may prove impossible to devise a hierarchical system of factors governing drift for all but single species and it may not be biologically prudent to aim for narrower resolution than exists.

Summary

Drifting response to three environmental factors by the benthos of a hardwater stream in southern Ontario was studied through catches in four 250 μm mesh nets positioned at the downstream end of a riffle. Drift varied according to the scale of changes in water temperature and discharge and also between taxa. For example, during a period of wide-ranging stream discharge and water temperature, night-time drift density (all nets and all taxa combined) was positively related to both minimum water temperature and discharge. During more constant conditions, night-time drift density was negatively related to discharge alone. Analysis of catches of individual "replicate" nets showed that in two of the nets, total drift was related to neither temperature nor discharge. In the other two nets, these two environmental factors accounted for 64.6 and 83.8 % of the variance in animal densities caught over time with minimum water temperature being more important than discharge. No individual taxon showed any significant relationship with temperature or discharge during the day but, at night, several associations were evident. Chironomids (*Eukiefferiella* spp. and *Cricotopus* sp.) and mayflies (*Baetis vagans* and *Ephemerella* sp.) were associated with minimum night-time temperature only, while caddisflies (*Hydropsyche* sp., *Dolophilodes distinctus* and *Brachycentrus* sp.), beetles (*Promoresia* sp.) and ostracods were associated with discharge, stoneflies (*Brachyptera* sp.) and mites (*Sperchon* sp.) were associated with both factors, amphipods (*Gammarus pseudolimnaeus*), oligochaetes (*Nais simplex*), copepods and non-chironomid dipterans were not associated with either factor. The relationships were positive for some species, negative for others.

Responses of individual drifting taxa to the presence (odour) of predatory rainbow trout were varied also. During the day, taxa drifted significantly more in the presence of trout odour. During the night, only three taxa drifted significantly more in the presence of trout odour. Drift densities of mayflies and amphipods were greater at night but were not affected by the odour of predators at this time. Drift by chironomids, mites, other dipterans and ostracods was significantly less at night, in the presence of trout, compared with during the day. Mayflies and amphipods drifting during the day were larger when trout were present as were mayflies, stoneflies and caddisflies at night. In contrast, amphipods drifting at night were smaller when trout were present. The different relationships observed may reflect evolutionary differences between the diverse phylogenetic groups that make up typical lotic benthic communities.

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