

PRIVATE LIBRARY  
OF WILLIAM L. PETERS

4

Arch. Hydrobiol.	66	1	56—90	Stuttgart, April 1969
------------------	----	---	-------	-----------------------

**Downstream Drift of the Invertebrate Fauna  
in a Stream Ecosystem**

By J. E. Bishop and H. B. N. Hynes

Department of Biology, University of Waterloo, Waterloo, Ontario, Canada

With plates 1—2, 10 figures and 5 tables in the text

### Abstract

The density and biomass of the invertebrates in the Speed River drift vary temporally and with total discharge. Partial depression of nocturnal drift maxima by moonlight is evident. All benthic species (Pelecypoda excepted) occur, at least occasionally, in the drift, but the proportion of standing stock moving downstream at any time is low (0.0002—0.004 %). Such losses result primarily from current forces acting on insects present in stone-top forage areas after the release of negative phototactic control. Reattachment by thigmotactic and rheotactic responses is normally rapid. All Ephemeroptera and Plecoptera and some Trichoptera are night-active while *Helicopsyche* and the Hydracarina are predominantly day-active; the Diptera show no preference. The biomass drifting is sufficient to sustain the vertebrate population, but still accounts for only about 15 % of annual production.

### Introduction

In a lotic habitat the current is the dominant physical force controlling the maintenance of an organism in its niche. HUEFALT (1927) felt that organisms were found in running water not because of any predilection for current, but rather because they need a set of conditions (physical, chemical and nutritional) that exist only where water is flowing. This enforced conditioning of the fauna to a particular habitat has led to morphological and behavioural adaptations that reflect physical limitations of the biotope.

Theoretical laminar flow is rarely evident under natural conditions; turbulent and eddy flow predominate in most streams (RUTTNER 1963). Velocities throughout a channel are not uniform, but rather a decrease in current occurs wherever there is friction between water column and bank; this results in a layer, contiguous to the substrate, that is characterized by progressive reduction of flow as the distance to the solid phase is decreased.

Morphological adaptations of the fauna to current have been described by many authors; e. g. dorso-ventral flattening by STEINMANN (1907, 1913), streamlining and the plane morphometry of leg structures by DODDS and HISAW (1923) and the use of heavy materials by casebuilding forms by these authors (1924). HORA (1930) and NEAVE (1930) recorded size reduction, the use of spines and hairs to prevent slippage and the use of various attachment organs. The relationship between morphology and distribution, particularly of trichopteran larvae and pupae, has been well documented (PHILIPSON 1954, SCOTT 1958, CUMMINS 1964, EDINGTON 1965). However, many exceptions to these adaptations exist (NIELSEN

1950, 1951). The work of AMBÜHL (1959, 1961) and JAAG and AMBÜHL (1964), in which the boundary layer and dead water spaces in areas behind obstructions were described, suggests that perhaps modifications against current are of little consequence except in the torrential fauna and clearly showed that reophilic animals spend most of their lives in areas of only slightly turbulent water (ULFSTRAND 1967).

Observations on the drift of aquatic organisms are numerous; much of the early literature has been summarized by MÜLLER (1954 a, b), WATERS (1961, 1965) and ELLIOTT (1967 a). Additional references to drift as a natural and continuous phenomenon are OHGUSHI and SAITO (1963), HUNT (1965), BAILEY (1966), ANDERSON (1967), DIMOND (1967), MINSHALL (1967), TOBIAS and THOMAS (1967) and PEARSON and FRANKLIN (1968). The magnitude of non-catastrophic drift in both biomass and numbers is often significant in respect to the standing stock (WATERS 1966), but fluctuates seasonally depending upon the life histories of the insects involved (BERNER 1951, ELLIOTT 1965 a, b, 1967 a, b). This restricts its use as a source of food for fish and limits its effectiveness in recolonizing areas denuded by flood or pollution.

Repopulation of eroded areas and colonization of new channels is often initiated by the drifting of an invertebrate fauna from upstream (MOFFETT 1936, SURBER 1937, LAURIE and JONES 1938, LEONARD 1942, MÜLLER 1954 a, b, LARIMORE et al. 1959, PATRICK 1959). WATERS (1964) showed that the number of organisms drifting was sufficient to recolonize an empty habitat, to carrying capacity, in 10 to 14 days; this agreed with the times recorded by SURBER (1937) and MÜLLER (1954 b). However, DIMOND (1967) felt that although the density of the benthos is returned to an average level fairly rapidly, the originally denuded area does not contribute a normal level of drift for one or more seasons. Recolonization of intermittent streams (HYNES 1958, HARRISON 1966) in which the new fauna comes either from the subsurface in drought-resistant stages, or from adult fly-in and oviposition, emphasizes that normal productivity is not restored until life cycles are completed.

The "colonization cycle" concept expounded by MÜLLER (1954 a, b) to explain the lack of depopulation of upstream reaches by the drifting out of nymphal forms, assumes that adults consistently migrate upstream and oviposit in the headwaters (ROOS 1957, DORRIS and COPELAND 1962, THOMAS 1966, WATERS 1968). WATERS (1961) theorized that the drift of immature forms was the result of the excess of production over carrying capacity of the stream bed, resulting in displacement through physical competition for food and space, and he used this (1962 a, 1966) as the basis for estimating productivity from the rate of drift. The direct relationship between benthic density and volume of drift (DIMOND 1967, PEARSON and FRANKLIN 1968) and the dependence of drift on the absolute volume of water and the rate of flow are clear (MACIOLEK and NEEDHAM 1951, LOGAN 1963, BAILEY 1966, ELLIOTT 1967 a). Other workers (LENNON 1941, MÜLLER 1963 b, WATERS 1968) have shown temperature dependence in specific cases, but this has not been substantiated in most studies (ELLIOTT 1967 a), although WATERS (1962 b) felt that the magnitude of the drift might be temperature regulated.

Non-catastrophic drift exhibits a diurnal pattern, first documented by TANAKA (1960). WATERS 1962 a, b, 1965), MÜLLER (1963 a, b, 1966 a, b), OHGUSHI and SAITO (1963), LEVANIDOVA and LEVANIDOV (1965), ELLIOTT (1965 a, b, 1967 a, b), MADSEN (1966), ANDERSON (1967), KURECK (1967) and TOBIAS and THOMAS (1967) have also reported on this, and many stream species have been categorized as night or day drifters. This circadian rhythm in the drift is intimately connected to the state of activity of the invertebrate fauna. A low level of passive drift as a result of mechanical

factors in the stream bed (erosion, etc.) is to be expected, but the nocturnal peak observed in drift is largely the result of a behavioural change in activity of the benthic animals. This change increases the propensity for detachment and transport by the current. WODSEDALEK (1911, 1912) observed a positive thigmotaxis and a negative phototaxis in *Heptagenia interpunctata* nymphs. GROS (1923), BERNER (1959), SCHERER (1962), CHAPMAN and DEMORY (1963), HUGHES (1966), and ELLIOTT (1967 a) have found negative phototaxis in many genera, mostly Ephemeroptera. Positive phototaxis has been demonstrated, particularly in the Diptera (SCHERER 1962, HUGHES 1966, ELLIOTT 1967 a), but all the species which have been studied have been thigmotactically positive in a lotic situation. These taxes tend to maintain the benthos in an attached state beneath stones during daylight hours. MOON (1940) found the bottom fauna to be more active at night and HUBAULT (1927), HYNES (1941), BRINCK (1949), CHAPMAN and DEMORY (1963) and ELLIOTT (1967 a) observed the movement of nymphal forms onto the tops of stones at night to forage. In this exposed location, jostling for position and available food results in the dislodging of some individuals and their recruitment to the drift. Analogous vertical movements to and from the upper levels in large rivers have been observed (KLYUCHAREVA 1963, LEVANIDOVA and LEVANIDOV 1965). Diurnal periodicity of flight by insects is well documented and summarized by LEWIS and TAYLOR (1964). The emergence times of aquatic forms are known to be light dependent (SPRULES 1947, BRINDLE 1958, MORGAN and WADDELL 1961) and ecdysis has been shown to be under light control (TOBIAS and THOMAS 1967). There is evidence (MOON 1935, MACAN 1957, MÜLLER 1966 a) that the activity of nymphs increases with stage of development. However, HARKER (1953) and MÜLLER (1965 a) have demonstrated endogenous activity rhythms in *Baetis*, and HARTLAND-ROWE (1955) in *Povilla*, that are light independent, with natural activity cycles continuing in extended light or dark periods. The depressant effects of moonlight on the activity and periodicity of aquatic insects have been summarized by CASPERS (1951); effects on emergence by HORA (1927), HARTLAND-ROWE (1955) and TOBIAS (1967), on vertical migration (BEETON 1960) and on drift by WATERS (1962 b) and ANDERSON (1966). ELLIOTT (1965 a, 1967 a), MÜLLER (1965 a, 1966 b) and HOLT and WATERS (1967) reported significant responses in drift to light patterns artificially imposed on insect populations that agreed, in most part, with the negative phototactic suppression of activity.

Utilization of "drift" foods by fish has been extensively studied (BERNER 1951, MÜLLER 1954 a, b, KAWAI 1959, KARR 1963, HUNT 1965, MAITLAND 1965, BAILEY 1966). The ratio of aquatic to terrestrial food changes seasonally (STARRETT 1950, O'DONNELL and CHURCHILL 1954, HUNT 1965, ELLIOTT 1967 c) and this reflects the level of production in the benthos paralleled by the volume of drifting insects. Nocturnal feeding to take advantage of periodicity in the drift is not well described. HOAR (1942) reported that young salmonids did not feed at night owing to lack of food, but ALLEN (1951) found no diurnal variation in the amount of food in the stomachs of trout in the Horokiwi River. BRETT (1957), KALLEBERG (1958) and ELLIOTT (1967 c) observed salmonids feeding at night and STARRETT (1950) recorded a night-feeding pattern for omnivorous minnows. Availability (ALLEN 1941, 1942, MACIOLEK and NEEDHAM 1951) dictates the proportion of the rhithron lost to fish predation and as the availability index is often  $>1$  at night (ELLIOTT 1967 c), a correlation with drift and increased invertebrate activity is indicated. Selective use of drifting foods (FROST 1939 a, b, McCORMACK 1962, THOMAS 1962, MADSEN 1966), particularly by young salmonids, reflects the relative inaccessibility of the young instars of most insects as food, even when suspended in the water

column as drift, and explains why larger larvae and nymphs are not often reported in drift.

The purpose of this investigation was to estimate the significance of drift of invertebrates in the Speed River, Ontario, Canada by assessing the relationship between the benthos and the composition of the drift on a quantitative and temporal basis.

### The Study Area

The Speed River has been described in detail elsewhere (BISHOP and HYNES 1969) so only a resume will be given here. At the sampling site ( $43^{\circ} 43' 54''$  N.,  $80^{\circ} 16' 24''$  W.) (Plate 1) the river is small (5—10 m wide), shallow (8—15 cm modal depth) with a widely fluctuating discharge (0.1—20 m<sup>3</sup>/sec). The substrate is mixed glacial outwash gravels and sand with occasional dolomite boulders; there is little emergent vegetation although *Nasturtium* beds occur in areas of slow current. The watershed, composed of undulating hills, swampy depressions and drumlin fields (CHAPMAN and PUTNAM 1966), is used extensively for mixed agriculture. The clearing of woodland for this purpose results in fast run-off and rapid changes in discharge. Physical parameters for 1966—67 are summarized in Fig. 1. Chemically the water is moderately hard, pH 7.5—8.6, 90—200 ppm CaCO<sub>3</sub>. PO<sub>4</sub>—P, NO<sub>3</sub>—N and SiO<sub>2</sub> levels are low during the winter, which may be attributed to the considerable growth of diatoms that develops under the ice, but rise to 1, 5 and 25 ppm respectively in the late summer when allochthonous fertilizer and manure drainage is maximal and discharge low.

### Methods

Various techniques have been developed for capturing drifting organisms in running water (NEEDHAM 1928, WOLF 1950, MÜLLER 1954 b, 1958, 1963 a, b, c, 1965 b, TANAKA 1960, WATERS 1962 a, b, CUSHING 1964, MUNDIE 1964, 1966, ELLIOTT 1965 a, b, 1967 a). The apparatus of MÜLLER (1965 b) is ideal but not practical for a stream of any size. The technique used in this study was basically that of WATERS (1962 b).

Twenty-four hour drift samples were taken monthly on the Speed River, with the nets emptied every three hours. Sampling periods were arranged so that twilight coincided with the beginning of a three-hour period. The nets were made of terylene mesh with a pore size  $167 \times 560$  microns. Tapering square nets, 2 m long, were attached to aluminum-rod frames,  $30 \times 30$  cm, with light-weight canvas. These nets were sufficiently long to ensure that the standing wave caused by the resistance to flow was always more than one-third of the way down the net, even at the end of a 3 h sampling period. The only times that the nets became blocked were during periods of either freezing or thawing when pieces of ice filled them every half-hour or so. The nets were held in position by wires looped around steel rods driven into the substrate. Drift samples were taken in a fast

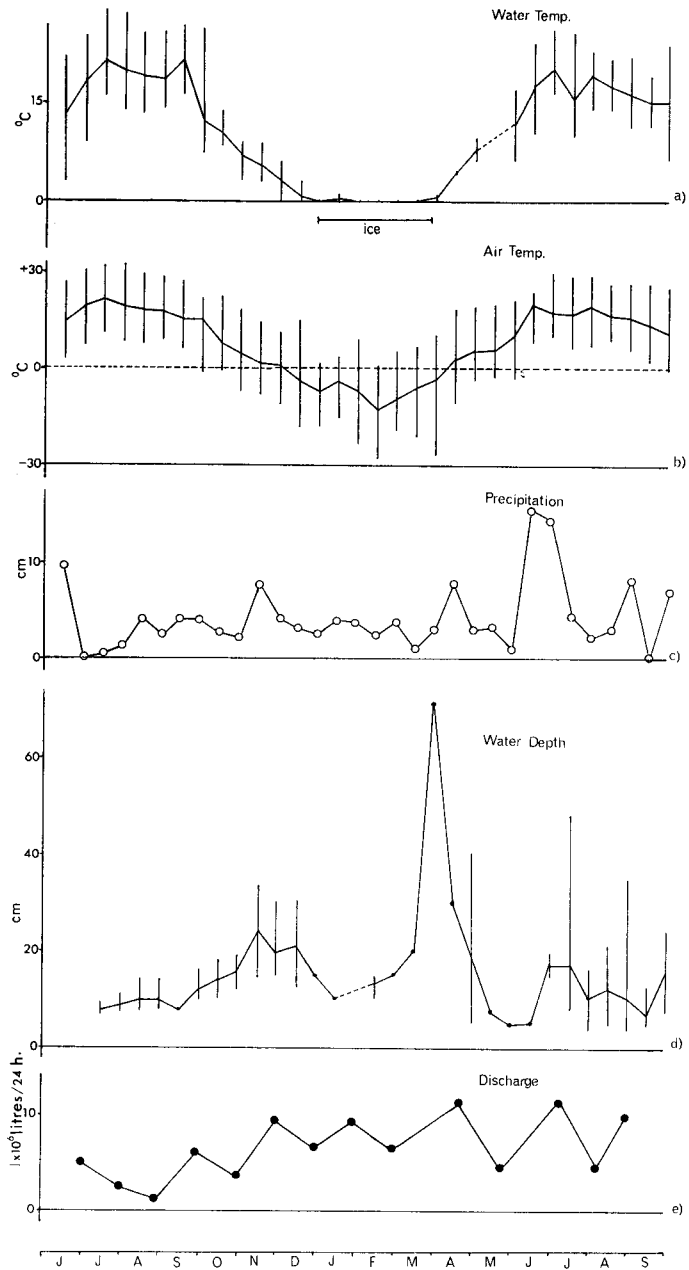


Fig. 1. Physical data for the Speed River (two week composites).  
 a) water temperatures; b) air temperatures; c) precipitation; d) water depth;  
 e) discharge.

section of the current from above a level board buried flush with the substrate across the stream (Plate 2). The volume of water passing through the net and the total flow in the stream were recorded at the beginning and end of each sampling run by measuring current velocities at nine points across the 5 m wide board transect, at the water surface and at the substrate level, with a portable water velocity meter modified from EDINGTON and MOLYNEUX (1960). The contents of the net were rinsed into a polyethylene bottle and preserved, in the field, with 5% formaldehyde. In the laboratory, the sample was washed in a  $167 \times 167$  micron sieve and the large pieces of plant material discarded. Depending on total volume, the sample was usually fractionized (HYNES 1961) and preserved in 70% ethanol. Counts, identification and measurements were made at X 20 magnification over a mm grid and the counts multiplied by the subsampling factor. For each month a drift factor was calculated taking into account the volume of water that passed through the net and the discharge of the stream. When the catch was multiplied by this factor, an estimate of total 24 h drift of the river past the sampling point was obtained. Samples were weighed as a 24 h composite after air drying in open dishes for a day.

#### The Standing Stock of Fish

Standing stock of fish in the riffle was estimated by the LIBOSVARSKY (1966) technique. The whole length of the riffle (93 m) above the drift sampling station, with both ends sealed off with one-quarter inch netting, was fished five times on 16 June, 1967, with a 400 volt A. C. electric fisher. An hour was allowed between sweeps. The fish were preserved in 20% formaldehyde.

### Results and observations

#### Composition of the Drift

Most species in the benthos were present in the drift at some stage in their life history, the notable exception being the Pelecypoda. A complete list of the genera taken, with relative frequencies, is given in Table 1. Young Limnephilidae were caught only during their early instars before they began to make stone cases, and the few Zygoptera nymphs captured were all less than 2 mm long. Terrestrial organisms were infrequent in the drift (3%); those taken were largely Collembola and Coccoidea, with a few adult Hemiptera and Thysanoptera. Other authors, particularly those working on fish nutrition (HUNT 1965, ELLIOTT 1967 c), have reported larger terrestrial components, but the large standing stock of fish in the Speed River may have cropped this extensively. In this regard, movement along the bank by cattle, researchers, etc. above the sampling site would result in large contributions to the drift and in this study these complications were avoided.

Table 1. Total drift with relative frequencies

A. = adults P. = pupae L. = larvae

		0—5 mm	>5 mm	Total	% of total drift
Coleoptera	<i>Stenelmis</i> spp.	125	0	125	0.08
	<i>Optioservis</i> spp.	88	0	88	0.05
	<i>Gonielmis</i> sp.	32	4	36	0.02
	<i>Dubiraphia</i> sp.	168	0	168	0.10
	Elmidae (L.)	352	0	352	0.21
	<i>Psephenus herriki</i>	76	0	76	0.05
	<i>Ectopria</i> sp.	288	4	292	0.18
	<i>Stenelmis</i> (A.)	152	0	152	0.09
	<i>Optioservus</i> (A.)	40	0	40	0.02
	Other (A.)	838	21	859	0.52
	Other (L.)	82	2	84	0.05
Other (P.)	32	0	32	0.02	
Total Coleoptera		2,273	31	2,304	1.41
Diptera	Chironominae	7,774	752	8,526	5.20
	Orthoclaadiinae	42,431	1,500	43,931	26.80
	Tanypodinae	3,443	244	3,687	2.25
	Chironomidae (P.)	7,085	0	7,085	4.32
	Chironomidae (A.)	14,581	32	14,613	8.91
Total Chironomids		75,314	2,528	77,842	47.49
	<i>Antocha-Limonia</i> spp.	1,514	46	1,560	0.95
	<i>Dicranota</i> sp.	16	4	20	0.01
	Other Tipulidae	32	16	48	0.03
	<i>Clinocera</i> sp.	92	0	92	0.06
	Other Empididae	72	0	72	0.04
	<i>Bezzia</i> group	4	81	85	0.05
	Other Ceratopogonidae	28	16	44	0.03
	<i>Simulium</i> spp. (L.)	3,985	100	4,085	2.49
	<i>Dixa</i> sp.	266	0	266	0.16
	Other Diptera (L.)	495	37	532	0.32
Total Diptera		81,818	2,828	84,646	51.64
Ephemeroptera	<i>Caenis</i> spp.	3,728	0	3,728	2.27
	<i>Leptophlebia cupida</i>	393	774	1,167	0.71
	<i>Paraleptophlebia</i> spp.	2,485	32	2,517	1.54
	Baetinae (all)	7,315	64	7,379	4.50
	<i>Stenonema</i> spp.	602	9	611	0.37
	<i>Ephemerella</i> spp.	2,069	65	2,134	1.30
	<i>Ephemera simulans</i>	52	2	54	0.03
	Other Ephemeroptera	776	0	776	0.47
	Ephemeroptera (A.)	228	45	273	0.17
Total Ephemeroptera		17,648	991	18,639	11.37
Plecoptera	<i>Allocapnia pygmaea</i>	1,579	920	2,499	1.52
	<i>Taeniopteryx</i> spp.	379	131	510	0.31
	<i>Nemoura completa</i>	608	128	736	0.45



Table 1. Continued

	0—5 mm	>5 mm	Total	% of total drift
<i>Amphinemura</i> spp.	1,264	0	1,264	0.77
Perlidae	73	2	75	0.05
Perlodidae	238	16	254	0.15
Other Plecoptera	32	0	32	0.02
Total Plecoptera	4,173	1,197	5,370	3.28
Trichoptera				
<i>Helicopsyche borealis</i>	1,430	0	1,430	0.87
<i>Hydropsyche</i> spp.	970	21	991	0.60
<i>Cheumatopsyche</i> spp.	1,505	34	1,539	0.94
<i>Rhyacophila</i> spp.	133	16	149	0.09
Other Rhyacophilidae	83	1	84	0.05
Philopotamidae	176	0	176	0.11
<i>Polycentropus</i> sp.	16	0	16	0.01
<i>Psychomyia</i> sp.	100	0	100	0.06
<i>Agraylea</i> spp.	80	0	80	0.05
<i>Ochrotrichia</i> sp.	664	0	664	0.41
Other Hydroptilidae	2,729	0	2,729	1.66
Limnephilidae	1,662	195	1,857	1.13
<i>Athripsodes</i> sp.	48	0	48	0.03
<i>Oecetis</i> spp.	256	0	256	0.16
<i>Mystacides sepulchralis</i>	96	0	96	0.06
Other Leptoceridae	2,013	0	2,013	1.23
Lepidostomatidae	16	0	16	0.01
Other Trichoptera	376	0	376	0.23
Total Trichoptera	12,353	267	12,620	7.70
Other groups				
<i>Nigronia</i> sp.	32	0	32	0.02
Hydracarina	7,210	0	7,210	4.40
Other mites	2,494	0	2,494	1.52
Copepoda	17,733	0	17,733	10.82
Ostracoda	2,256	0	2,256	1.38
Cladocera	1,640	0	1,640	1.00
Branchiobdellidae	512	0	512	0.31
Naididae	1,134	0	1,134	0.69
Other Oligochaeta	106	25	131	0.08
Nematoda	84	48	132	0.08
Tardigrada	64	0	64	0.04
<i>Chlorohydra viridissima</i>	18	0	18	0.01
<i>Hyalella azteca</i>	72	0	72	0.04
<i>Sphaerium</i> spp.	17	1	18	0.01
Others	2,023	39	2,062	1.26
Total Others	35,395	113	35,508	21.66
Total Aquatic Drift	153,660	5,427	159,087	97.05
Terrestrials				
Collembola			2,648	1.62
Others			2,188	1.33
Total Terrestrials			4,836	2.95
Total Drift			163,923	100.00

Overhanging vegetation and banks coupled with wind disturbance would also contribute to the terrestrial component and the Speed, by and large, flowed through open bottom pasture in the sampling area.

Thirteen 24 h sets of samples were taken during a fifteen month period from July, 1966 to September, 1967 at approximately monthly intervals, except in March and May when river conditions made this impossible; no consecutive sampling dates were more than six weeks apart.

A comparison of monthly drift samples (Fig. 2) shows some correlation between volume of water sampled (litres/24 h) and the number of organisms caught. The summer of 1966 was very dry and the drift results were correspondingly low. The slight increase in volume in September, due to rain, resulted in a peak in drift numbers in that month, scouring of the

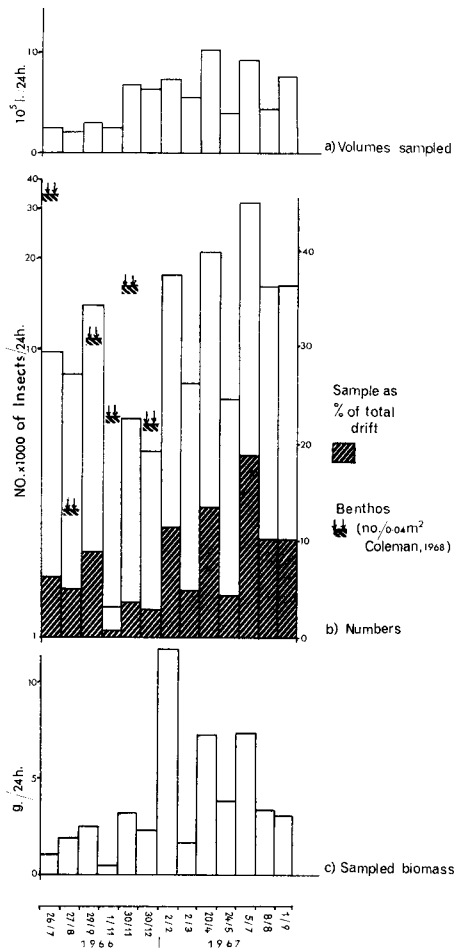


Fig. 2. Comparison of monthly drift samples. a) volumes sampled; b) drift/24 h; c) sampled biomass.

bottom and a very low drift catch in October, even though the total benthic numbers were not greatly reduced. The drift peak in February was caused by increased activity of *Allocapnia* and *Leptophlebia* and a concomitant high drift of copepods. Peaks in April and July, 1967, were caused by spates; the first resulting from the spring thaw and the second from the wettest June in 30 years. There was little correlation between benthic density and drift catches. Data from COLEMAN (1968) for the last six months of 1966 showed that the density of the bottom fauna was high, but comparatively little drift was caught (Fig. 2). The curvilinear function relating drift and density (DIMOND 1967) was never found, because bottom numbers fluctuated too widely. The biomass taken generally paralleled the total numbers caught; however, in both autumns when most insects were still in early instars, the weight/number ratios were low. The large peak in biomass taken in February was caused by *Allocapnia* and *Leptophlebia* which were almost mature with a relatively high weight/number ratio. Apart from this maximum there was no other period dominated by a stage in the life history of any component of the drifting fauna. Large numbers of emerging chironomids were taken throughout the spring and early summer, but neither emerging nor spent ephemeropteran imagines ever constituted as significant a proportion of the netted biomass as has been found by other investigators (ELLIOTT 1967 a).

The subdivision of drift into orders is given in Fig. 3. Results from April must be disregarded as ice break-up and severe flooding conditions prevailed. Maximum coleopteran drift occurred in late summer and corresponded to the hatching of the new elmids generations. Some elmids and hydrophilid adults were found in the April drift during the run-off period. The March peak in the number of Diptera reflected the emergence of many chironomid adults which continued as a major element in the drift until September. The winter maximum of midge-larval drift coincided with the peak development of diatoms on the stream-bed, and perhaps the greatest activity of gravel-dwelling forms feeding on them. Simuliidae contributed large numbers to the early spring drift (February—April). Maxima in ephemeropteran drift were seen in the September of both years, and corresponded to the hatching of *Baetis* spp. nymphs. The large numbers drifting in February have been discussed previously. Those taken in July and August were mainly *Paraleptophlebia* spp., *Caenis* spp., *Centroptilum* sp. and other Baetinae. *Allocapnia pygmaea* BURMEISTER dominated the Plecoptera, and nymphs, just after their period of diapause, were taken extensively in late autumn, and later instars from February to April, just prior to emergence. *Taeniopteryx* spp. nymphs appeared in small numbers in catches from November to March. *Nemoura completa* WALKER, *Amphinemura delosa* RICKER

and *A. wui* CLAASSEN were minor components of the drift in winter and early spring. Trichopteran drift was largely seasonal with low numbers moving downstream during winter. Hydroptilids, with short-interval contributions from *Helicopsyche* (July and August) and early instar Limnephilidae (September), were the principal forms involved. Significant groups encountered in the drift from the "Others" category were the Copepods, Ostracoda and Hydracarina throughout the year, with significant summer additions from the Naididae.

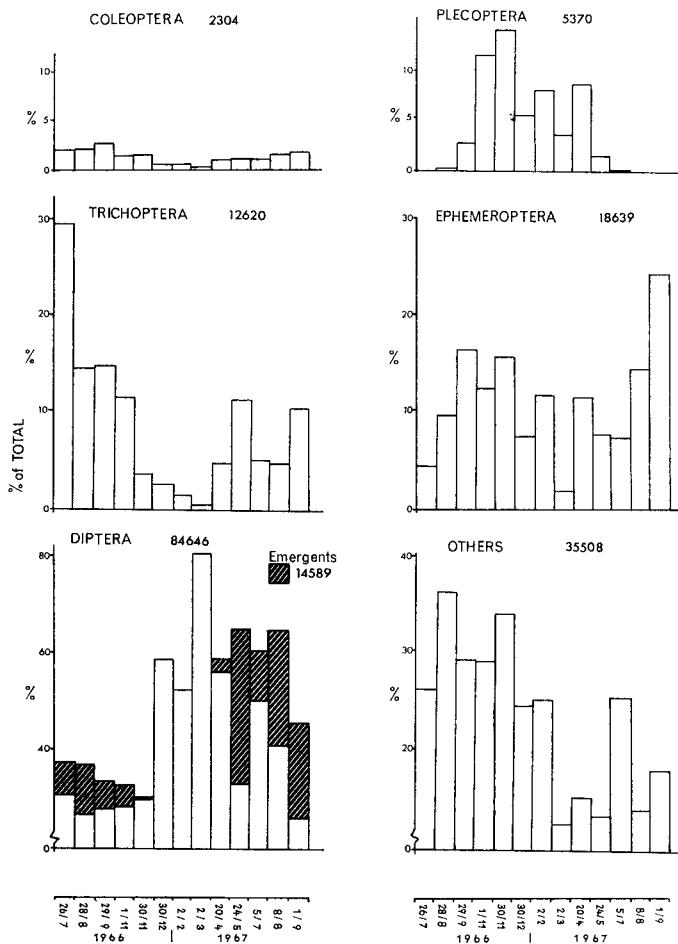


Fig. 3. Percentage composition of the drift.

### Diurnal Fluctuations of the Drift

Daily fluctuations in the quantity and composition of the drift were evident, but not uniform. Proportionately more aquatic invertebrates were taken during the dark periods in all samples except in May, 1967, when

large numbers of orthoclaidiine larvae were moving during the day (Fig. 4). The night maximum in drift activity reported by other authors (TANAKA 1960, WATERS 1962 b, MÜLLER 1963 a, b, c, ELLIOTT 1965 a, b, 1967 a) was seen in most months, and this reinforces the hypothesis that drift is largely light controlled. Of note are the pronounced effects of moonlight on these drift results. Full moon conditions occurred on six sampling dates. The depressant effects (cf. WATERS 1962 b, ANDERSON 1966) were clearly seen on 30 November, 1966, 30 December, 1966 and 24 May, 1967 when an initial post-

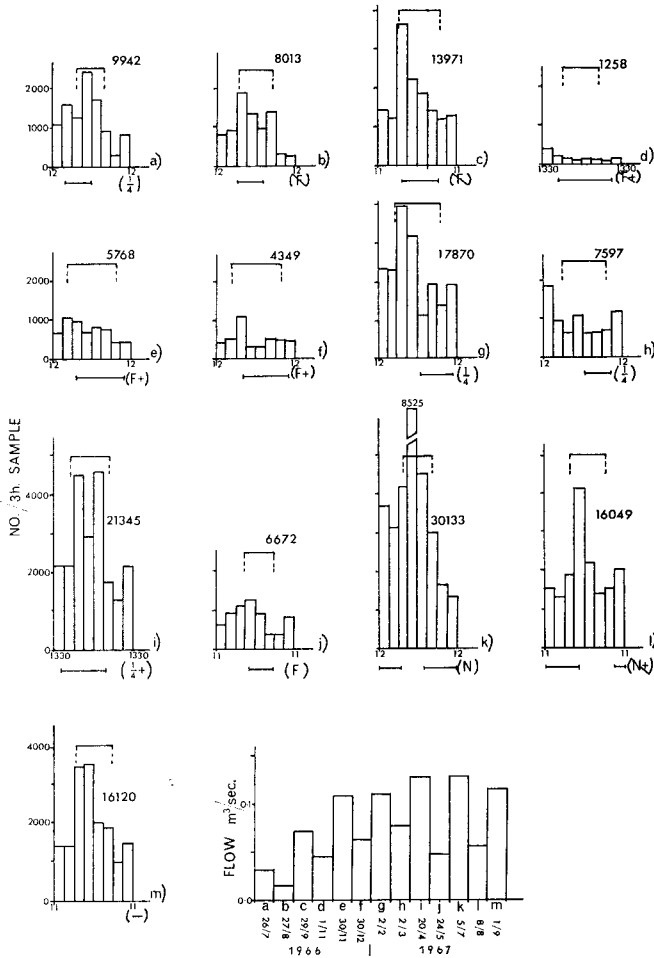


Fig. 4 Diurnal fluctuations in the drift — numbers of aquatic invertebrates per 3 h sample.

sunrise-sunset — top bar	E. S. T.
moonrise-moonset — lower bar	F = full
state of moon — ( )	N = new
moon occluded — ( \ )	1/4 = first quarter

sunset drift peak started to develop, but was suppressed as soon as the moon rose. On 27 August, and 29 September, 1966 a full moon was present, but occluded by heavy cloud cover, and the normal nocturnal drift pattern was undisturbed. Numbers taken on 1 November, 1966 after the spate, when a full moon was obscured, were too low to be significant.

Diurnal fluctuations by various components of the drift are summarized in Table 2 where the number drifting per hour and the overall day : night ratio are given. The principal members are listed except for the Chironomidae which showed no uniform pattern. Seasonal variations in the drift

Table 2. Day-night drift of selected invertebrate types.

	Av. no. drifting/h*		Overall ratio	
	Day	Night	Day	Night
<i>Antocha-Limonia</i> spp.	5.1	5.4	1	1.1
<i>Simulium</i> spp.	11.3	17.9	1	1.6
Baetinae	7.3	45.5	1	6.2
<i>Caenis</i> spp.	5.9	19.3	1	3.3
<i>Ephemerella</i> spp.	3.0	10.9	1	3.6
<i>Paraleptophlebia</i> spp.	1.8	13.1	1	7.3
<i>Allocapnia pygmaea</i>	2.7	10.5	1	3.9
<i>Amphinemura</i> spp.	0.7	7.6	1	10.8
<i>Nemoura</i> sp.	0.7	4.0	1	5.6
<i>Taeniopteryx</i> spp.	0.5	2.5	1	5
<i>Helicopsyche borealis</i>	7.2	0.3	24	1
Limnephilidae	6.9	5.5	1.3	1
<i>Ochrotrichia</i> sp.	1.8	2.7	1	1.5
Other Hydroptilidae	6.9	11.3	1	1.6
Copepoda	44.3	82.7	1	1.9
Ostracoda	11.6	5.0	2.3	1
Hydracarina	39.6	22.9	1.7	1

\*) Data for all samples 1966/67 were pooled to obtain this value.

ratio are seen in Figs. 5—10 in which total number netted for each day and night period (regardless of length) is plotted against the month. These figures also show the seasonal availability to the drift of the various components. The four mayfly groups were always more prevalent in the drift at night. *Helicopsyche borealis* HAGEN had a definite tendency to be a day drifter but only in its very early instars when the buoyancy of the larva balanced or exceeded the weight of the stone case. The other Trichoptera showed no consistent deviation from a 1:1 ratio, except for the greater drifting during the day of very early instar Limnephilidae in July and August (cf. WATERS 1968), even though the overall ratio for Hydroptilidae favoured night activity. The four plecopteran genera exhibited a dominant night

drifting pattern throughout their life cycles; the only exception was the day catch of emerging specimens of *Allocapnia pygmaea* in April during the spate. *Antocha-Limonia* spp. were taken with equal frequency both day and night. Although in spring months the numbers of *Simulium vittatum* ZETTERSTADT, *S. venustum* (SAY) and *Prosimulium fuscum* SYME and DAVIES drifting at night far exceeded the day catch, the overall ratio for this genus was less

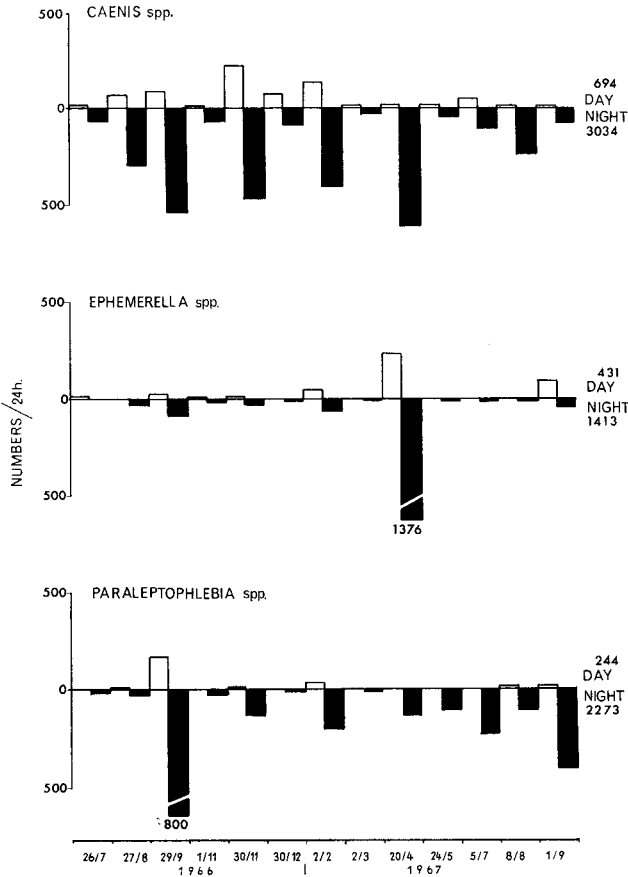


Fig. 5—10. Day-night drift of selected invertebrate types (total number per light or dark period).

Fig. 5. *Caenis* spp.; *Ephemerella* spp.; *Paraleptophlebia* spp.

than 1:2 in favour of night activity. The Copepoda were generally taken with higher frequency at night, while the Ostracoda were predominantly day drifters. No explanation can be given for this. With the exception of only two months in late autumn, the Hydracarina, excluding the Chironomidae, were the pre-eminent component of the day drift in terms of numbers.

Examples of daily fluctuations in the drift of selected types are given in Table 3 to show the characteristic responses to sunset and sunrise. Drift maxima immediately after sunset were seen for most of the night drifters. The Limnephilidae appears to be the only group that increased its drift in the period just after sunrise; the other day-drifters (*Helicopsyche*, Hydracarina and Ostracoda) were caught mainly in the afternoon.

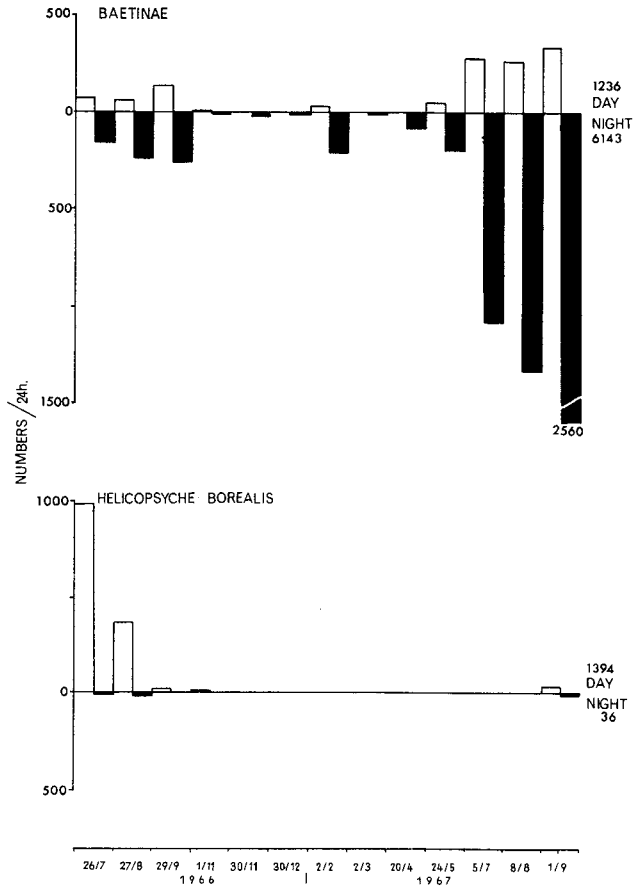


Fig. 6. Baetinae; *Helicopsyche borealis*.

The ratios listed in Table 2 are based on the number drifting per hour, and since monthly day-night observations were from a single date, the value correction (to numbers/1000 l.) of ELLIOTT (1967 b) is not necessary. The overall ratios are based on equal volumes sampled for each insect group and are therefore comparable. These ratios from the drift data indicate the following general divisions of the fauna:



Day Active  
*Helicopsyche borealis*  
 Hydracarina  
 Ostracoda

Night Active  
 Baetinae  
*Caenis* spp.  
*Ephemerella* spp.  
*Paraleptophlebia* spp.  
*Allocaenia pygmaea*  
*Amphinemura* spp.  
*Nemoura* sp.  
*Taeniopteryx* spp.  
 Copepoda

No Preference  
*Antocha-Limonia* spp.  
 Limnephilidae

?*Simulium* spp.  
 ?*Ochrotrichia* sp.  
 ?Other Hydroptilidae } Ratio 1 : < 2

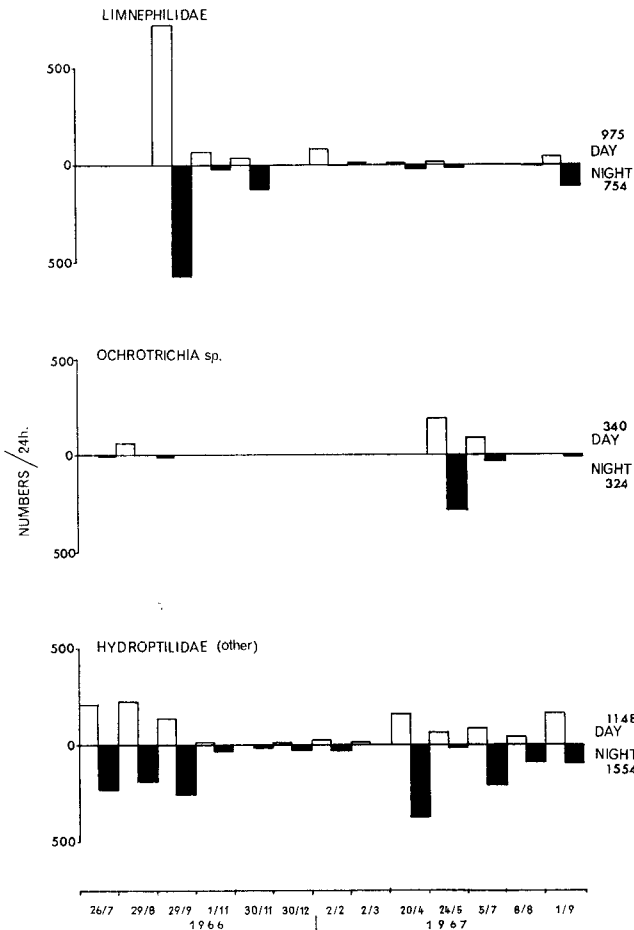


Fig. 7. Limnephilidae; *Ochrotrichia* sp.; Hydroptilidae (other).

Table 3. Examples of daily fluctuations in the drift of selected invertebrate types (numbers per 3 h catch).

	sunset			sunrise			Date
<i>Simulium</i> spp. (L.)	112	64	320	272	352	128	20/ 4/67
Baetinae	{ 80	16	560	496		288	8/ 8/67
	{ 64	304	1024	576		656	1/ 9/67
<i>Caenis</i> spp.	32	80	240	32	48	48	2/ 2/67
<i>Ephemera</i> spp.	32	32	352		320	624	20/ 4/67
<i>Paraleptophlebia</i> spp.	{ —	—	192	192	240	176	29/ 9/66
	{ —	—	144	16	48	—	2/ 2/67
<i>Allocapnia pugmaea</i>	{ —	—	112	256	112	64	30/11/66
	{ 32	32	688	176	160	80	2/ 2/67
<i>Amphinemura</i> spp.	16	—	224	160	528	80	20/ 4/67
<i>Nemoura</i> sp.	16	—	160	48	320	64	20/ 4/67
<i>Taeniopteryx</i> spp.	—	32	64	48	128	32	29/ 9/66
<i>Helicopsyche borealis</i>	64	272	16		—	—	27/ 8/66
Limnephilidae	96	192	160	176	96	144	29/ 9/66
<i>Ochrotrochia</i> sp.	48	—	112		128	32	24/ 5/67
Hydracarina	{ 256	336	80	—	64	80	20/ 4/67
Other mites	{ 112	320	112	—	—	32	1/ 9/67

These behavioural patterns essentially agree with those described by other authors: TANAKA (1960), MÜLLER (1966 a), ELLIOTT (1967 a, b) for Plecoptera; TANAKA (1960), WATERS (1962 a, b), SÖDERGREN (1963), ELLIOTT (1965 a, b, 1967 a, b), MÜLLER (1966 a) for Ephemeroptera; WATERS (1962 b, 1968), ANDERSON (1967) for Trichoptera; WATERS (1962 b), MÜLLER (1966 a) for *Dixa* and Simuliidae; and MOON (1940), MÜLLER (1966 a), BESCH (1967), ELLIOTT (1967 a) for Hydracarina.

Standing Stock of Fish

Table 4 indicates the numbers, size range and total weight per species from the five successive sweeps of the riffle on 16 June, 1967. The numbers of *Cottus* and *Etheostoma* were undoubtedly underestimated as these species were difficult to pick up after shocking, and very few 0 year fish were taken, probably because the riffle was not their habitat.

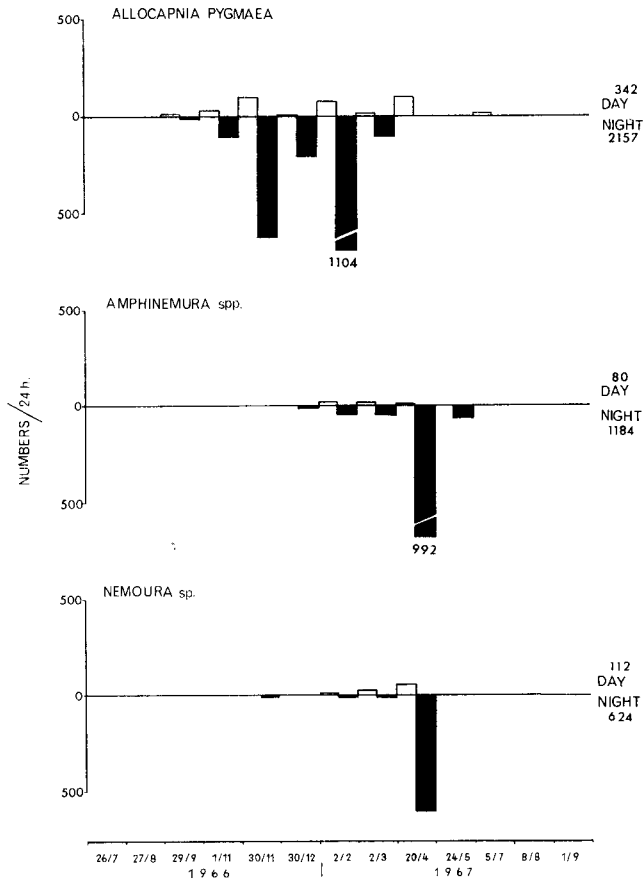


Fig. 8. *Allocapnia pygmaea*; *Amphinemura* spp.; *Nemoura* sp.

An estimate of total population, obtained by plotting the catch per sweep against accumulated catch for the five successive sweeps (LIBOSVARSKY 1966) gave a figure of 305. These data yield an average biomass of 3.82 g/m<sup>2</sup> for the riffle which compares reasonably well with the estimate of 1.95 g/m<sup>2</sup> of JOHNSON (1965) who worked on warm water streams in southern Ontario with less productive sand and silt substrates.

Table 4. Fish standing stock 16 June, 1967 on 92.5 m riffle section (5 sweeps 162, 81, 34, 13, 5 fish taken).

Species	No.	Fork length (cm)			Total wt. (g)	% no.	% wt.
		Max.	Mean	Min.			
<i>Catostomus commersoni</i> (LACÉPÈDE)	11	21.1	11.9	5.6	349.0	3.7	19.8
<i>Hypentelium nigricans</i> (LE SUEUR)	6	22.0	12.4	4.3	158.1	2.0	9.0
<i>Semotilus atromaculatus</i> (MITCHILL)	4	16.1	14.5	12.8	179.5	1.4	10.2
<i>Semotilus</i> sp.	62	10.0	7.2	5.0	408.2	21.0	23.1
<i>Notropis cornutus</i> (MITCHILL)	53	11.7	6.4	2.6	203.5	18.0	11.5
<i>Rhinichthys atratulus</i> (HERMANN)	2	5.4	5.1	4.7	3.8	0.7	0.2
<i>Rhinichthys cataractae</i> (VALENCIENNES)	1		7.5		6.5	0.3	0.4
<i>Rhinichthys</i> sp.	79	8.0	6.2	4.4	302.9	26.8	17.2
<i>Etheostoma flabellare</i> RAFINESQUE	63	5.5	4.2	1.5	55.7	21.4	3.2
<i>Cottus bairdii</i> GIRARD	11	6.8	6.2	4.2	38.7	3.7	2.2
<i>Salvelinus fontinalis</i> (MITCHILL)	2	18.5	16.6	14.6	56.9	0.7	3.2
<i>Eucalia inconstans</i> (KIRKLAND)	1		3.2		0.5	0.3	0.0
Total	295				1763.3	100.0	100.0

### Synthesis

Benthic production in the Speed River for 1966 was approximately 620 g/m<sup>2</sup> (COLEMAN 1968), calculated by using the method of HYNES (1961) modified by integrating the mass units present per year as the loss from the system. COLEMAN, unfortunately, did not measure biomass, but her estimated figures gave a standing stock for the year of 195 g/m<sup>2</sup>. Drift and benthos figures were recorded in Table 5 in corrected form to represent data for a single transect across the river. Drift loss per metre of stream width was 3.5 kg/yr and, if the average drift recruitment distance were 50 m (cf. WATERS 1965, ELLIOTT 1967 a), this would be equivalent to 70 g/m<sup>2</sup>/yr. The relationship between drift and production is obscure. WATERS (1961, 1962 a) measured the production of *Baetis vagans* McDUNNOUGH, but in his stream the diurnal drift exceeded the standing stock and was clearly density dependent, as was the drift described by MÜLLER (1954 b) and PEARSON and FRANKLIN (1968). In the Speed River, the same sort of situation existed as

was found by ELLIOTT (1967 a) in the Walla Brook, in which the proportion of the benthos in the drift at any time was very low. The calculations were made using the numerical benthic data from COLEMAN (1968) and were of the same magnitude as those found by ELLIOTT (cf. Table 5). The conclusion from this is that drifting in the Speed is not density dependent (as discussed earlier), and consequently the production of its fauna cannot be calculated

Table 5. Composite total data — all data represent samples taken for the complete stream width (5 m).

		Total drift past a point		Proportion of benthos in drift <sup>1)</sup>	Benthos (COLEMAN 1968)	
		No./day	mg/day		No./5 m <sup>2</sup>	mg/5 m <sup>2</sup>
1966	July	126263	13193.0	0.00031	4754959	496826.7
	Aug.	48078	11814.1	0.00368	380991	93619.3
	Sept.	257066	45205.1	0.00175	1504544	264574.0
	Oct.	20380	6947.1	0.00021	795867	271278.0
	Nov.	107862	60401.9	0.00025	2276309	1274740.9
	Dec.	42403	23657.4	0.00085	764738	426663.7
1967	Jan.					
	Feb.	226897	149026.9			
	Mar.	91164	2008.6			
	Apr.	226897	78547.2			
	May	71657	40665.9			
	June					
	July	366417	90290.4			
	Aug.	171403	36106.9			
	Sept.	204240	39206.2			
Total	1960779	615070.7				
Estimated total/year	55 × 10 <sup>6</sup>	17.3 kg				

<sup>1)</sup> Calculated from  $P = \frac{xD \cdot 100}{X - xD}$   
 (ELLIOTT 1965 b, 1967 a) where  
 x = no. drifting insects/m<sup>3</sup>  
 D = depth of water  
 X = no. benthos/m<sup>2</sup> of surface

from these data. The streams of WATERS and MÜLLER were both in uncleared, forested areas and not subject to severe flooding. In such streams, particularly with faunas dominated by amphipods and multivoltine mayflies, the "carrying capacity" (WATERS 1961) of the substrate is likely to be easily exceeded, with resultant density dependent drift of excess production (MÜLLER 1954 b, WATERS 1966). In Walla Brook and the Speed the situation is analogous to that in the insecticide-treated streams described by Dimond (1967), with severe seasonal spates, because of the open, cleared watersheds, having the same denuding effects on the benthos as D. D. T. In these two streams, density in the benthos probably rarely reached saturation, except in local niches following brood hatching, and most of the drift throughout the year was passive rather than the result of competition for space and food. The degree

of drift loss from the benthos was dependent on current and flow, as seen earlier, and was mediated by light control of the activity patterns of the invertebrates (BISHOP 1969).

The calculated hypothetical contribution of  $70 \text{ g/m}^2/\text{yr}$  to the water column is an underestimate, as no measurement of the degree of fish predation on the drift could be made and in no previous study has this

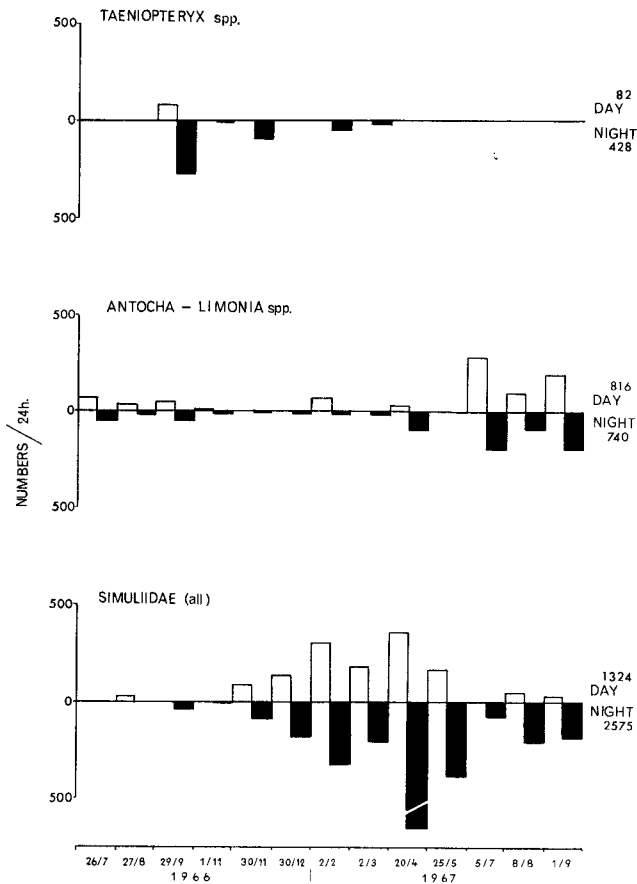


Fig. 9. *Taeniopteryx* spp.; *Antocha-Limonia* spp.; Simuliidae (all).

factor been quantitatively analysed. The considerable fish population on the riffle in this study, composed largely of omnivores and invertebrate feeders (STARRETT 1950, DAIBER 1956, KARR 1963, MINCKLEY 1963, GERALD 1966), would consume significant quantities of the drift. Preliminary stomach analysis of six fish of different sizes of each species substantiated these feeding patterns. If a factor of 6—8 (GERKING 1962, 1964, MANN 1964) is applied to the presumably stable standing stock as a maintenance and

growth parameter, a loss to the benthos of 25—30 g/m<sup>2</sup>/yr is calculated. The drift component lost to fish predation is probably not the same as that caught in the nets. ELLIOTT (1967 a) felt that the larger nymphs, particularly last and penultimate instars, were over-represented in the drift. From this study the opposite seems to be true as relatively few large invertebrates (> 5.0 mm, Table 1), and surprisingly low numbers of imagines or pupae (except in the

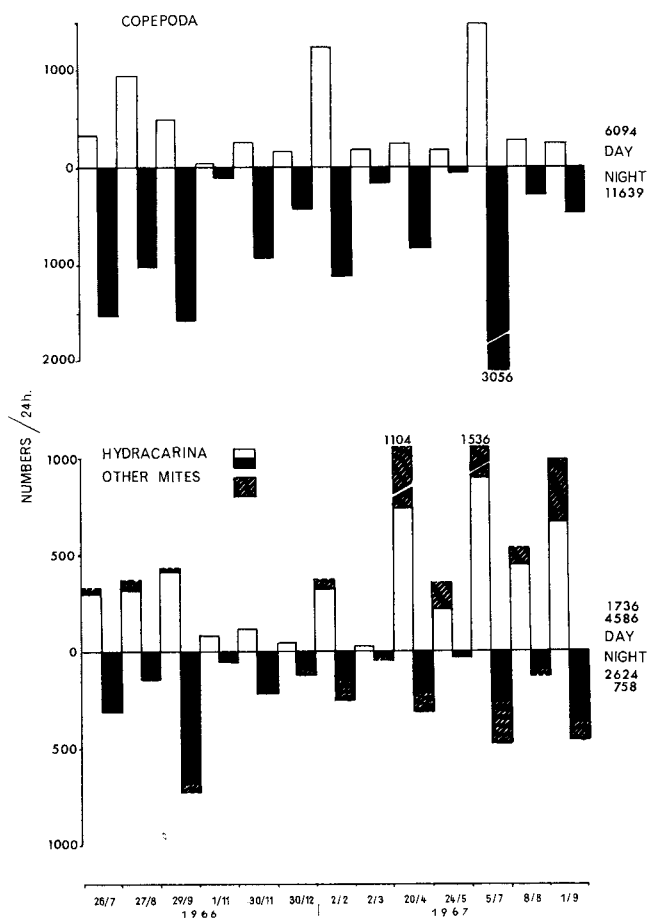


Fig. 10. Copepoda; Hydracarina.

Chironomidae) were taken in the drift. This apparent deficit was attributed to fish predation. Both *Semotilus* and *Rhinichthys* were observed feeding at the surface, particularly in the evening, and *Notropis*, *Cottus* and *Etheostoma* are known to feed from the water column. In addition, the lack of significant terrestrial drift points to an efficient utilization by the fish of all the floating components. Selective feeding by many species has been

recorded by various authors (STARRETT 1950, MÜLLER 1954 b, O'DONNELL and CHURCHILL 1954, NILSSON 1957, HORTON 1961, McCORMACK 1962, THOMAS 1962, WARREN et al. 1964, HUNT 1965, MAITLAND 1965, BAILEY 1966, MADSEN 1966, ELLIOTT 1967 c) and in almost all of these studies, the availability factor for small nymphs was less than one, even at night when the drift level was high. The obvious preference for large nymphs, emergents and terrestrial forms would cause a considerable underestimate of the drift biomass. Total loss to the benthos, including the estimates for fish consumption and total drift still only amounts to about one sixth of the production. Other losses may be attributed to natural mortality, invertebrate predation, perhaps significant in the Speed where Perlidae and Rhyacophilidae occur in quite high numbers, non-return of emerged forms to the water, definitely applicable to the Nemouridae that feed as adults and may live for six to eight weeks before oviposition, and loss of fauna by stranding on the floodplains following spates, observed both in May and July, 1967. Although these do not account for all the production, it is clear that there was more than enough food available in the drift to provide for the fish which were present. HORTON (1961) found almost enough drifting food to maintain her trout population in Walla Brook and this was netted after the fish had fed. WARREN et al. (1964) obtained similar results in a control stream section, but found that the fish fed primarily on benthic chironomids in a sucrose enriched section. Although many authors have determined fish feeding habits, the correlation between these and invertebrate activity peaks is not known for many of the common stream fish. Visual feeding in daylight and moonlight could deplete the drift, but the extent of feeding during dark periods remains conjectural.

### Discussion

Activity in aquatic invertebrates is largely controlled by two physical parameters, light and temperature, and it is activity patterns that dictate the extent of both upstream migration and drift. MÜLLER (1963 c) felt that drift resulted from a "periodic behavioural pattern" on the part of the invertebrates (i. e., a positive action leading to downstream movement), but the results of this study and those of ELLIOTT (1965 b, 1967 a) do not agree with this. The very small proportion of benthos in the water column at any time precludes there being some concerted mechanism releasing the insects from the substrate. Non-catastrophic drift is almost certainly the result of passive current forces that transport those insects that become exposed to their action through feeding or respiratory activities.

Light, specifically light intensity rather than wavelength (BISHOP 1969), is the most critical factor responsible for the circadian activity patterns recorded by several authors (see above). Negative phototaxis has been



recorded for many aquatic insects (cf. Introduction) and serves to maintain these organisms in areas of low intensity. Linked to this are the strong positive thigmotaxis observed in many benthic forms, the definite orthokinesis during periods of illumination and the positive skototaxis (directional response to areas of low light intensity) observed by HUGHES (1966). These mechanisms result in the firm attachment of most of the fauna to the undersides of stones during the daytime. The few phototactically positive insects such as *Simulium* (GRENIER 1949), *Odagmia* (SCHERER 1962), *Baetis* (HUGHES 1966), and *Rhithrogena* (ELLIOTT 1967 a) may not avoid the light, but are generally inactive once they have found a microniche in which suitable current conditions override orthokinetic responses (HUGHES 1966). Breakdown of the orthokinetic response of *Ephemerella* and heptagenid mayflies was frequently observed in an artificial stream (cf. MADSEN 1966). Once a nymph attained the upper layers of the water column, it became rigid and drifted passively with the current, perhaps as a defense mechanism against predation or as a result of complete disorientation. Observations in the field of nymphs forcibly detached from stones, confirmed a period of inactivity followed by active swimming and reattachment. The widely occurring dorsal light response, described for *Baetis* (HUGHES 1966), may be a mechanism common to swimming benthic fauna for maintaining orientation. Without this control, in darkness, nymphs become disequibrated and are unable to "land" properly after swimming. This may explain the higher night drift rate of this and other mayflies that are known to be more active at night (MOON 1940, HARKER 1953, ELLIOTT 1967 a). In sessile forms orientation is maintained by tarsal proprioceptors which override light effects, and locomotion is predominantly by walking, a method that preserves thigmotactic control at all times.

Increased activity during dark periods is accompanied, in most forms, by their presence in positions exposed to current forces. The breakdown of negative phototaxis results in the location of many more insects on the tops of rocks. Various authors (HUBAULT 1927, HYNES 1941, BRINCK 1949, CHAPMAN and DEMORY 1963, ELLIOTT 1967 a) have reported this phenomenon, and insects were always visible on the substrate surface if a light was directed onto it at night. Such movements are undoubtedly associated with foraging either for algal and microbial food (ULFSTRAND 1967) that is more abundant on the tops of stones, or, in the case of filter feeders, for the particulate material that is in greater supply up in the main current layers away from the "dead water" zone. The magnitude of the drift will depend on the amount of food available in a particular area, the degree of physical competition for it, and the tenacity of the individual (DORIER and VAILLANT 1954). A high density of foragers would result in considerable numbers being forced into marginal feeding areas and locations where increased propensity

for wash-off would increase drift. The distance drifted is also density dependent, as resettlement is a problem if all suitable feeding areas are occupied. WATERS (1965) found that drifters were present throughout the water column and that there was no uniformity in the distance drifted. Passage downstream of the unsettled fauna is likely to be in a series of short hops, the distance governed by velocity, length of dark period, and activity of the individual insect. The roiling, turbulent nature of the currents in most shallow streams, like the Speed, would allow the insects to return quickly to the substrate through contact with the bottom or attainment of a dead-water space.

Seasonal variations in the drift are related to the changes in age and density of the benthos and the physical parameters of the river. Increased drift with anchor-ice conditions (REIMERS 1957) would result from loss of the interstitial shelter zones. The decrease in drift observed in winter (WATERS 1962 a, 1966) and at low temperatures (MÜLLER 1954 a) may have been caused by a reinforcing of the dead water layers as the viscosity of the water increased (RUTTNER 1963), making escape from them by the fauna less likely. Conversely, with a rise in temperature, increases in drift (LENNON 1941, WATERS 1962 b, 1968, PEARSON and FRANKLIN 1968) would be expected, especially when coupled with increased invertebrate activity. However, in this study, flow and benthic density were the dominant factors determining the amount of drift.

The "availability" of the benthos to current forces has been studied very little. The assumption that the top substrate layers hold most of the fauna is probably unfounded (SCHWOERBEL 1961, 1964, ANGELIER 1962, CLIFFORD 1966, COLEMAN 1968). During peak discharge periods, many of the larger insects and some of the smaller are lost into the drift, as surface crevices and leaf and twig habitats are scoured and stones crushed and rolled. However, parts of the fauna are capable of moving down into the vacant interstitial areas created by the removal of silt and detritus (CORDONE and KELLEY 1961, BUSCEMI 1966). From field observations this zone may be 10—15 cm below the normal surface level after a flood. This hyporheal biotope at a dynamic depth may harbour the fauna for considerable periods after a spate and would account for the low drift and apparently denuded benthos often evident at such time. The fauna will only return to the "surface" layers as detritus and the microflora (BROWN 1961, EGGLISHAW 1964) are replenished in these areas, a process that may take the 6—8 weeks often labelled as recovery time. This would perhaps explain the recolonization of drought denuded areas. Interstitial flow through this deep habitat would probably be sufficient to maintain the fauna, which could quickly repopulate the upper strata when surface water became available (cf. HYNES 1958, HARRISON 1966). Drift will not become density dependent until benthic production

levels become greater than the carrying capacity (WATERS 1966, DIMOND 1967), and this was not seen in the Speed for reasons already discussed.

The hypothesis that drift is dependent on the stages of development of the organisms, rather than on their density in the benthos (MÜLLER 1966 a), is probably partially true as activity of the individuals depends to a large extent on their feeding requirements. In streams of restricted fauna, this dependence of drift on life stage could become the paramount factor as the drifting biomass would be dominated by a particular instar of one species. ELLIOTT (1967 a, b) partially substantiated this by showing that older nymphs were proportionately over-represented in the drift, but there was no evidence that such was the case in the Speed as all size groups were taken continuously. The low numbers of mature nymphs taken has been accounted for as fish predation.

Recolonization of headwater areas by ovipositing adults to compensate for the loss of immature forms in the drift was hypothesized by MÜLLER (1954 a, b) in his "colonization cycle". MÜLLER (1954 a), ROOS (1957), DORRIS and COPELAND (1962) and WATERS (1968) found that adults moved against the down-valley winds, but BRINDLE (1957) and ELLIOTT (1967 a) claimed that the direction of flight of imagines was with whatever wind was blowing. Empirical evidence in the Speed watercourse tends to agree with the latter, as no persistent upstream movement of swarming adults was seen on summer evenings. There may be no need for a cyclical repopulation mechanism if only small proportions of the benthos occur in the drift which was the case in this ecosystem. The definite and numerically significant upstream movements of amphipods (MACAN and MACKERETH 1957, MINCKLEY 1964, MÜLLER 1966 a, KURECK 1967) are probably a rheotactic and grazing phenomenon rather than a repopulation mechanism as drift of these invertebrates is usually that of excess population over carrying capacity (WATERS 1961, 1966).

The fate of drift moving into a polluted section of river has yet to be investigated. HYNES (1960) discussed the biological effects of chronic pollution and cited many instances of distinct zones of toxic water. Drift-borne insects may die quickly or they may actively escape the effects in two ways: by rapid reattachment and movement upstream out of the zone; or by allowing themselves to remain in the water column and be passively carried through the polluted area. ELLIOTT (1967 a) showed that most of the drift carried right through pool areas and this, along with the marked initial increase in drift caused by insecticide applications (before the onset of mortality) (cf. HOFFMAN and SURBER 1945, HOFFMAN and DROOZ 1953, HASTINGS et al. 1961, COUTANT 1964), may suggest that the invertebrates allow themselves to be carried by the current to avoid oxygen-depleted or poisoned water and unstable substrate areas. Whatever occurs, no invertebrates characteristic of the normal drifting fauna are found on the substrate

in heavily contaminated areas. Clarification of this problem would require a clean watercourse, with a single lethal effluent source, in which benthic density at the outflow and the linear extent and recovery of drift could be measured.

### Summary

Drift in the Speed River was sampled monthly from July, 1966 to September, 1967, for 24 h (with subsamples every 3 h) using nets of  $167 \times 560 \mu$  pore size. The predominantly aquatic insect catch was classified, measured and weighed, and the current, benthic density and temporal factors governing the displaced fauna investigated. Most species found in the benthos occurred in the drift at some stage in their life history, with the exception of the Pelecypoda.

The density and biomass of the invertebrates in the drift varied temporally (a nocturnal maximum in downstream movement generally occurred), with discharge in the river and with the volume passing through the net.

Various taxa were taken with sufficient frequency to enable their classification as day or night-active, and ratios of the number drifting per hour of light or darkness are given. Only the aquatic mites, *Helicopsyche* and perhaps the Ostracoda are day-active. All the Plecoptera, Ephemeroptera and some Trichoptera are night-active.

The depressant effects of moonlight on drift were evident on several sampling dates.

Only a small proportion of the benthos (0.0002—0.004 %) was present in the drift at any time, and this eliminated the hypothesis that some positive invertebrate activity leads to drifting. The minor part of the fauna lost to the drift is probably the result of activity by the insects, that exposes them to the current forces, and competition for space and food. These factors depend on the density of insects in the optimal stone-top forage areas, current velocity and total discharge.

Individual drifters do not remain in the water column for very long distances, except perhaps under polluted conditions, but reattach by thigmotactic and rheotactic responses to contact with the substrate and slow water zones. In most shallow streams, turbulent flow continually brings about this contact.

The standing stock of fish, predominantly omnivorous species that fed selectively on the terrestrial, emergent and larger aquatic drift components, was estimated at  $3.82 \text{ g/m}^2$  on a long riffle section. The benthic insect biomass taken in drift catches, which excluded that part already browsed off, was probably sufficient to sustain this vertebrate population.

An estimate of downstream faunal movement for the entire width of the river was made. Over the year, 17.5 kg of biomass drifted past the sampling point and this was equivalent to a loss of  $70 \text{ g/m}^2/\text{yr}$  from a hypothetical 50 m upstream section supplying the drift. Theoretical estimated production for 1966 (from COLEMAN 1968) for the same riffle area was  $620 \text{ g/m}^2$  and even with an estimate of 25—30  $\text{g/m}^2/\text{yr}$  for fish growth and maintenance, about 85 % of production was still unaccounted for. Loss of adults to the terrestrial habitat, invertebrate predation, flood stranding and natural mortality probably accounted for the rest of the lost production.

### Zusammenfassung

Von Juli 1966 bis September 1967 wurden jeden Monat einmal 24 Stunden lang (d. h. alle 3 Stunden eine Teilprobe) Proben der Drift im Speed River ge-

nommen, wobei Netze mit  $167 \times 560 \mu$  Maschenweite benutzt wurden. Der hauptsächlich aus Wasserinsekten bestehende Fang wurde klassifiziert, gemessen und gewogen. Strömung, benthische Populationsdichte und zeitliche Faktoren, welche die Drift beeinflussten, wurden festgestellt. Die meisten im Benthos gefundenen Spezies erschienen in der Drift in einem bestimmten Stadium ihrer Entwicklung, mit Ausnahme der Pelecypoden.

Der numerische Anteil und die Biomasse der Wirbellosen in der Drift schwankte zeitweilig (nachts war die Bewegung stromabwärts gewöhnlich maximal) infolge von Abwassereinlässen sowie mit dem Wasservolumen, welches das Netz passierte.

In hinreichender Häufigkeit wurden verschiedene Proben vorgenommen, um die Einteilung in tag- oder nachtaktive Arten zu ermöglichen. Dazu wird das Verhältnis der bei Licht respektive Dunkelheit pro Stunde driftenden Mengen von Tieren angegeben. Nur die Wassermilben, die *Helicopsychen* und vielleicht die Ostracoda sind tagaktiv. Alle Plecoptera, Ephemeroptera und einige Trichoptera sind nachtaktiv.

Der dämpfende Einfluß des Mondlichtes auf die Drift war aus mehreren Untersuchungsdaten ersichtlich.

Nur eine geringe Menge des Benthos (0,0002—0,004 %) war jeweils in der Drift enthalten. Dies widerlegte die Hypothese, daß die Drift durch eine spezielle Aktivität positiv hervorgerufen wird. Der kleinere Teil der in der Drift verlorengehenden Fauna ist vermutlich auf die Aktivität der Insekten selbst zurückzuführen, welche sie den Bedingungen der Strömung aussetzt, sowie auf die Suche nach Raum und Nahrung. Diese Faktoren hängen von der Dichte der Insekten in den optimal beschaffenen, steinigen Nahrungsplätzen sowie von der Strömungsgeschwindigkeit und von der totalen Abflußmenge ab.

Individuelle Drifter bleiben nicht über sehr große Entfernungen in der Wassersäule, es sei denn eventuell und unter sehr verunreinigten Wasserbedingungen, sondern setzen sich wieder fest durch thigmotaktische und rheotaktische Reaktionen auf den Kontakt mit dem Substrat, besonders in langsamen Wasserzonen. In den meisten flachen Wasserläufen fördert turbulente Strömung diesen Kontakt.

Die Menge der vorhandenen Fische, hauptsächlich Allesfresser, die sich wahlweise von Komponenten terrestrischen Ursprungs oder auf gestiegenen und größeren Bestandteilen der Drift ernährten, wurde in einem langen, mit geriffeltem Untergrund ausgestatteten Abschnitt auf  $3,82 \text{ g/m}^2$  geschätzt. Die benthische Insektenbiomasse, die bei Driftproben, welche den bereits abgeweideten Teil ausschlossen, gefunden wurde, war vermutlich ausreichend, diese Wirbeltierbevölkerung zu erhalten.

Die Driftmenge der Fauna flußabwärts wurde für die ganze Breite des Flusses geschätzt. Während des Jahres trieben  $17,5 \text{ kg}$  Biomasse am Versuchsort vorüber. Dies war gleichwertig mit einem Verlust von  $70 \text{ g/m}^2/\text{J}$  von einem hypothetischen Abschnitt  $50 \text{ m}$  stromaufwärts, der die Drift hergab. Die theoretisch geschätzte Produktion für 1966 (nach COLEMAN 1968) für denselben Abschnitt ergab  $620 \text{ g/m}^2$ , und sogar bei Annahme von  $25\text{—}30 \text{ g/m}^2/\text{J}$  für Fischzuwachs und Erhaltungenergie waren ungefähr  $85\%$  der Produktion noch nicht erfaßt. Der Verlust von Imagines an das Festland, Evertrebratenfraß, Strandung bei Flut, sowie natürliche Sterblichkeit machten vermutlich den Rest der verlorengegangenen Produktion aus.

### Acknowledgments

The assistance of the following is gratefully acknowledged. Mr. and Mrs. D. E. ROWAN for generous and unrestricted access to the Speed River on their property and their hospitality on numerous occasions, without which sampling during winter nights would have been intolerable: M. J. COLEMAN for the use of her unpublished benthos data: The Grand River Conservation Commission who supplied meteorological data from the Shand Dam: Miss J. VENN, J. GRIMALDI and B. GREIB for assistance in the field.

The work was supported by a Studentship to JOHN E. BISHOP and a Research Grant to H. B. N. HYNES. Both were awarded by the National Research Council of Canada to whom we express our thanks.

### References

- ALLEN, K. R. (1941): Studies on the biology of the early stages of the salmon (*Salmo salar*). 2. Feeding habits. — *J. Anim. Ecol.* **10**: 47—76.
- (1942): Comparison of bottom faunas as sources of available fish food. — *Trans. Amer. Fish. Soc.* **71**: 275—283.
- (1951): The Horokiwi Stream. A study of a trout population. — *N. Z. Mar. Dept. Fish. Bull. No.* **10**: 1—231.
- AMBÜHL, H. (1959): Die Bedeutung der Strömung als ökologischer Faktor. — *Schweiz. Z. Hydrol.* **21**: 133—264.
- (1961): Die Strömung als physiologischer und ökologischer Faktor. — *Verh. internat. Verein. theor. angew. Limnol.* **14**: 390—395.
- ANDERSON, N. H. (1966): Depressant effect of moonlight on activity of aquatic insects. — *Nature, Lond.* **209**: 319—320.
- (1967): Biology and downstream drift of some Oregon Trichoptera. — *Can. Ent.* **99**: 507—521.
- ANGELIER, E. (1962): Remarques sur la répartition de la faune dans le milieu interstitiel hyporhéique. — *Zool. Anz.* **168**: 351—356.
- BAILEY, R. G. (1966): Observations on the nature and importance of organic drift in a Devon River. — *Hydrobiologia* **27**: 353—367.
- BEETON, A. M. (1960): The vertical migration of *Mysis relicta* in Lakes Huron and Michigan. — *J. Fish. Res. Bd. Can.* **17**: 517—539.
- BERNER, L. M. (1951): Limnology of the Lower Missouri River. — *Ecology* **32**: 1—12.
- BESCH, W. (1967): Driftnetzmethode und biologische Fließwasseruntersuchung. — *Verh. internat. Verein. theor. angew. Limnol.* **16**: 669—678.
- BISHOP, J. E. (1969): Light control of aquatic insect activity and drift. (in press).
- BISHOP, J. E., & HYNES, H. B. N. (1969): Upstream movement of the benthic invertebrates in the Speed River. (in press).
- BRETT, J. R. (1957): Salmon research and hydroelectric power development. — *Bull. Fish. Res. Bd. Can.* **114**: (Referenced by ELLIOTT, 1967 c).
- BRINCK, P. (1949): Studies on Swedish stoneflies (Plecoptera). — *Opusc. ent. suppl.* **11**: 1—250.
- BRINDLE, A. (1957): Effect of temperature and humidity on the flight of Trichoptera. — *Entomologists' mon. Mag.* **93**: 63—67.
- (1958): Night activity of Trichoptera. — *Entomologists' mon. Mag.* **94**: 38—42.
- BROWN, D. S. (1961): The food of the larvae of *Chloen dipterum* L. and *Baetis rhodani* (Pict.) (Insecta; Ephemeroptera). — *J. Anim. Ecol.* **30**: 55—75.
- BUSCEMI, P. A. (1966): The importance of sedimentary organics in the distribution

- of benthic organisms. — Spec. Publ. Pymatuning Lab.Fld. Biol. **4**: 79—86.
- CASPERS, H. (1951): Rhythmische Erscheinungen in der Fortpflanzung von *Chunio marinus* (Dipt. Chiron.) und das Problem der lunaren Periodizität bei Organismen. — Arch. Hydrobiol. Suppl. **XVIII**: 415—594.
- CHAPMAN, D. W., & DEMORY, R. (1963): Seasonal changes in the food ingested by aquatic insect larvae and nymphs in two Oregon streams. — Ecology **44**: 140—146.
- CHAPMAN, L. J., & PUTNAM, D. F. (1966): The Physiography of Southern Ontario. — Univ. of Toronto Press, 386 pp.
- CLIFFORD, H. F. (1966): The ecology of invertebrates in an intermittent stream. — Invest. Indiana Lakes, Streams **7**: 57—98.
- COLEMAN, M. J. (1968): The Benthic Fauna of the Speed River, Wellington County, Ontario. — M. Sc. Thesis, University of Waterloo, Waterloo, Ont. 161 pp.
- CORDONE, A. J., & KELLEY, D. W. (1961): The influence of inorganic sediment on the aquatic life of streams. — Calif. Fish Game **47**: 189—228.
- COUTANT, C. C. (1964): Insecticide Sevin: effect of aerial spraying on drift of stream insects. — Science, N. Y. **146**: 420—421.
- CUMMINS, K. W. (1964): Factors limiting the microdistribution of larvae of the caddisflies *Pycnopsyche lepida* (HAGEN) and *Pycnopsyche guttifer* (WALKER) in a Michigan stream. — Ecol. Monogr. **34**: 271—295.
- CUSHING, C. E. (1964): An apparatus for sampling drifting organisms in streams. — J. Wildl. Mgmt. **28**: 592—594.
- DAIBER, F. C. (1956): A comparative analysis of the winter feeding habits of two benthic stream fishes. — Copeia 1956, 141—151.
- DIMOND, J. B. (1967): Evidence that drift of stream benthos is density related. — Ecology **48**: 855—857.
- DODDS, G. S., & HISAW, F. L. (1923): Ecological studies on aquatic insects. I. Adaptations of mayfly nymphs to swift streams. — Ecology **5**: 137—149.
- (1924): Ecological studies on aquatic insects. III. Adaptations of caddisfly larvae to swift streams. — Ecology **6**: 123—137.
- DORIER, A., & VAILLANT, F. (1954): Observations et expériences relatives à la résistance au courant de divers invertébrés aquatiques. — Trav. Lab. Hydrobiol. Piscic. Univ. Grenoble **45/46**: 9—31.
- DORRIS, T. C., & COPELAND, B. J. (1962): Limnology of the middle Mississippi River. III. Mayfly populations in relation to navigation water-level control. — Limnol. Oceanogr. **7**: 240—247.
- EDINGTON, J. M. (1965): The effect of water flow on population of net spinning Trichoptera. — Mitt. internat. Verein. theor. angew. Limnol. **13**: 40—48.
- EDINGTON, J. M., & MOLYNEUX, L. (1960): Portable water velocity meter. — J. scient. Instrum. **37**: 455—457.
- EGGLISHAW, H. J. (1964): The distributional relationship between the bottom fauna and plant detritus in streams. — J. Anim. Ecol. **33**: 463—476.
- ELLIOTT, J. M. (1965 a): Daily fluctuations of drift invertebrates in a Dartmoor stream. — Nature, Lond. **205**: 1127—1129.
- (1965 b): Invertebrate drift in a mountain stream in Norway. — Norsk ent. T. **13**: 97—99.
- (1967 a): Invertebrate drift in a Dartmoor stream. — Arch. Hydrobiol. **63**: 202—237.
- (1967 b): The life histories and drifting of the Plecoptera and Ephemeroptera in a Dartmoor stream. — J. Anim. Ecol. **36**: 343—362.

- ELLIOT, J. M. (1967 c): The food of trout (*Salmo trutta*) in a Dartmoor stream. — J. appl. Ecol. **4**: 59—71.
- FROST, W. E. (1939 a): River Liffey Survey II. The food consumed by the brown trout (*Salmo trutta* [L.]) in acid and alkaline waters. — Proc. R. Ir. Acad. **45**: 139—206.
- (1939 b): River Liffey Survey III. The growth and food of young salmon. — Proc. R. Ir. Acad. **46**: 53—80.
- GERALD, J. W. (1966): Food habits of the longnose dace, *Rhinichthys cataractae*. — Copeia 1966, 478—485.
- GERKING, S. D. (1962): Production and food utilization in a population of Bluegill Sunfish. — Ecol. Monogr. **32**: 31—78.
- (1964): Timing and magnitude of the production of a bluegill sunfish population and its food supply. — Verh. internat. Verein. theor. angew. Limnol. **15**: 496—503.
- GRENIER, P. (1949): Contribution à l'étude biologique des Simuliides de France. — Physiologia comp. Oecol. **1**: 165—330.
- GROS, A. (1923): Études sur les premières stades des Ephemeres du Jura français. — Ann. Biol. lacustre **12**: 49—74.
- HARKER, J. E. (1953): The diurnal rhythm of activity of mayfly nymphs. — J. exp. Biol. **30**: 525—533.
- HARRISON, A. D. (1966): Recolonization of a Rhodesian stream after drought. — Arch. Hydrobiol. **62**: 405—421.
- HARTLAND-ROWE, R. (1955): Lunar rhythm in the emergence of an Ephemeropteran. — Nature, Lond. **176**: 657.
- HASTINGS, E., KITTAMS, W. H., & PEPPER, J. H. (1961): Repopulation by aquatic insects in streams sprayed with D. D. T. — Ann. ent. Soc. Amer. **54**: 436—437.
- HOAR, W. S. (1942): Diurnal variations in feeding activity of young salmon and trout. — J. Fish. Res. Bd. Can. **6**: 90—101.
- HOFFMAN, C. H., & DROOZ, A. T. (1953): Effects of a C-47 airplane application of D. D. T. on fish-food organisms in two Pennsylvania watersheds. — Amer. Midl. Nat. **50**: 172—188.
- HOFFMAN, C. H., & SURBER, E. W. (1945): Effects of an aerial application of wettable D. D. T. on fish and fish-food organisms in Back Creek, West Virginia. — Trans. Amer. Fish. Soc. **75**: 48—58.
- HOLT, C. S., & WATERS, T. F. (1967): Effect of light intensity on the drift of stream invertebrates. — Ecology **48**: 225—234.
- HORA, S. L. (1927): Lunar periodicity in the reproduction of insects. — J. Proc. Asiat. Soc. Bengal N. S. **23**: 339—342.
- (1930): Ecology, bionomics and evolution of the torrential fauna, with special reference to the organs of attachment. — Phil. Trans. R. Soc. (B) **218**: 171—182.
- HORTON, P. A. (1961): The bionomics of brown trout in a Dartmoor stream. — J. Anim. Ecol. **30**: 311—338.
- HUBAULT, E. (1927): Contribution à l'étude des invertébrés torrenticoles. — Bull. biol. Fr. Belg. Suppl. **9**: 1—390.
- HUGHES, D. A. (1966): The role of responses to light in the selection and maintenance of microhabitat by the nymphs of two species of mayfly. — Anim. Behav. **14**: 17—33.



- HUNT, R. L. (1965): Surface-drift insects as trout food in the Brule River. — Trans. Wis. Acad. Sci. Arts Lett. **54**: 51—61.
- HYNES, H. B. N. (1941): The taxonomy and ecology of the nymphs of British Plecoptera with notes on the adults and eggs. — Trans. R. ent. Soc. London **91**: 459—557.
- (1958): The effect of drought on the fauna of a small mountain stream in Wales. — Verh. internat. Verein. theor. angew. Limnol. **13**: 826—833.
- (1960): The Biology of Polluted Waters. — Liverpool University Press. 202 pp.
- (1961): The invertebrate fauna of a Welsh mountain stream. — Arch. Hydrobiol. **57**: 344—388.
- JAAG, O., & AMBÜHL, H. (1964): The effect of current on the composition of biocoenoses in flowing water streams. — Adv. Int. Conf. Wat. Polln. Res. London. Pergamon Press, Oxford. pp. 31—49.
- JOHNSON, M. G. (1965): Estimates of fish populations in warm water streams by the removal method. — Trans. Amer. Fish. Soc. **94**: 350—357.
- KALLEBERG, H. (1958): Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). — Rep. Inst. Freshwat. Res. Drottningholm **39**: 55—98.
- KARR, J. R. (1963): Age, growth and food habits of Johnny, Slenderhead and Black-sided Darters of Boone County, Iowa. — Iowa Acad. Sci. **70**: 228—236.
- KAWAI, T. (1959): Foods of *Salvelinus pluvius* of the stream connecting with Lake Ōtori-ike. — Jap. J. Limnol. **20**: 167—173.
- KLYUCHAREVA, O. A. (1963): (Downstream and the diurnal vertical migrations of benthic invertebrates of the Amur River area.) (Russ.) — Zool. Z. **42**: 1601—1612.
- KURECK, A. (1967): Über die Tagesperiodische Ausdrift von *Niphargus aquilex schellenbergi* KARAMAN aus Quellen. — Z. Morph. Ökol. Tiere **58**: 247—262.
- LARIMORE, R. W., CHILDERS, W. F., & HECKROTTE, C. (1959): Destruction and re-establishment of stream fish and invertebrates affected by drought. — Trans. Amer. Fish. Soc. **88**: 261—285.
- LAURIE, R. D. & ERICHSEN JONES, J. R. (1938): The faunistic recovery of a lead polluted river in north Cardiganshire, Wales. — J. Anim. Ecol. **7**: 272—289.
- LENNON, R. E. (1941): Drift-borne organisms in Pond Brook, Passaconaway, N. Hamp. — Univ. N. H. Ext. Serv., Contrib. No. 2. Biol. Inst.
- LEONARD, J. W. (1942): Some observations on the winter feeding habits of brook trout fingerlings in relation to natural food organisms present. — Trans. Amer. Fish. Soc. **71**: 219—227.
- LEVANIDOVA, I. M., & LEVANIDOV, V. Y. (1965): (Diurnal migrations of benthic insect larvae in the river stream. I. Migration of Ephemeroptera larvae in the Khor River.) (Russ.) — Zool. Z. **44**: 373—385.
- LEWIS, T., & TAYLOR, L. R. (1964): Diurnal periodicity of flight by insects. — Trans. R. ent. Soc. London **116**: 393—476.
- LIBOSVARSKI, J. (1966): Successive removals with electrical fishing gear — a suitable method for making population estimates in small streams. — Verh. internat. Verein. theor. angew. Limnol. **16**: 1212—1216.
- LOGAN, S. M. (1963): Winter observations on bottom organisms and trout in Bridger Creek, Montana. — Trans. Amer. Fish. Soc. **92**, 140—145.
- MACAN, T. T. (1957): The life histories and migrations of the Ephemeroptera in a stony stream. — Trans. Soc. Br. Ent. **12**: 129—156.

- MACAN, T. T., & MACKERETH, J. C. (1957): Notes on *Gammarus pulex* in the English Lake District. — *Hydrobiologia* **9**: 1—12.
- MACIOLEK, J. A., & NEEDHAM, P. R. (1951): Ecological effects of winter conditions on trout and trout foods in Convict Creek, California, 1951. — *Trans. Amer. Fish. Soc.* **81**: 202—217.
- MAIDSEN, B. L. (1966): Om rytmisk aktivitet hos døgnfluenymfer. — *Flora Fauna* **72**: 148—154.
- MAITLAND, P. S. (1965): The distribution, life cycle and predators of *Ephemerella ignita* (PODA) in the River Endrick, Scotland. — *Oikos* **16**: 48—57.
- MANN, K. H. (1964): The pattern of energy flow in the fish and invertebrate fauna of the River Thames. — *Verh. internat. Verein. theor. angew. Limnol.* **15**: 485—495.
- MCCORMACK, J. C. (1962): The food of young trout (*Salmo trutta*) in two different becks. — *J. Anim. Ecol.* **31**: 305—316.
- MINCKLEY, W. L. (1963): The ecology of a spring stream, Doe Run, Meade County, Kentucky. — *Wildl. Monogr.* **11**: 1—124.
- (1964): Upstream movements of *Gammarus* (Amphipoda) in Doe Run, Meade County, Kentucky. — *Ecology* **45**: 195—197.
- MINSHALL, J. N. (1967): Life history and ecology of *Epeorus pleuralis* BANKS (Ephemeroptera: Heptageniidae). — *Amer. Midl. Nat.* **78**: 369—388.
- MOFFETT, J. W. (1936): A quantitative study of the bottom fauna of some Utah streams variously affected by erosion. — *Bull. Univ. Utah biol. Ser.* **26**: 1—33.
- MOON, H. P. (1935): Flood movements of the littoral fauna of Windermere. — *J. Anim. Ecol.* **4**: 216—228.
- (1940): An investigation of the movements of fresh-water invertebrate faunas. — *J. Anim. Ecol.* **9**: 76—83.
- MORGAN, N. C., and WADDELL, A. B. (1961): Diurnal variation in the emergence of some aquatic insects. — *Trans. R. ent. Soc. London* **113**: 123—137.
- MÜLLER, K. (1954 a): Die Drift in fließenden Gewässern. — *Arch. Hydrobiol.* **49**: 539—545.
- (1954 b): Investigations on the organic drift in North Swedish streams. — *Rep. Inst. Freshwat. Res. Drottningholm* **35**: 133—148.
- (1958): Beitrag zur Methodik der Untersuchung fließender Gewässer. — *Arch. Hydrobiol.* **54**: 567—570.
- (1963 a): Tag-Nachtrhythmus von Baetidenlarven in der „Organischen Drift“. — *Naturwissenschaften* **50**: 161.
- (1963 b): Temperatur und Tagesperiodik der „Organischen Drift“ von *Gammarus pulex*. — *Naturwissenschaften* **50**: 410—411.
- (1963 c): Diurnal rhythm in “Organic Drift” of *Gammarus pulex*. — *Nature, Lond.* **198**: 806—807.
- (1965 a): Field experiments on periodicity of freshwater invertebrates. — In *Circadian Clocks*, North-Holland Publ. Co., Amsterdam, pp. 314—317.
- (1965 b): An automatic stream drift sampler. — *Limnol. Oceanogr.* **10**: 483—485.
- (1966 a): Die Tagesperiodik von Fließwasserorganismen. — *Z. Morph. Ökol. Tiere* **56**: 93—142.
- (1966 b): Zur Periodik von *Gammarus pulex*. — *Oikos* **17**: 207—211.
- MUNDIE, J. H. (1964): A sampler for catching emerging insects and drifting materials in streams. — *Limnol. Oceanogr.* **9**: 456—459.

- MUNDIE, J. H. (1966): Sampling emerging insects and drifting materials in deep flowing water. — *Gewäss. Abwäss.* **41/42**: 159—162.
- NEAVE, F. (1930): Migratory habits of the mayfly, *Blasturus cupidus* SAY. — *Ecology* **11**: 568—576.
- NEEDHAM, P. R. (1928): A net for the capture of stream drift organisms. — *Ecology* **9**: 339—342.
- NIELSEN, A. (1950): The torrential invertebrate fauna. — *Oikos* **2**: 176—196.  
— (1951): Is dorsoventral flattening of the body an adaptation to torrential life? — *Verh. internat. Verein. theor. angew. Limnol.* **11**: 264—267.
- NILSSON, N.-A. (1957): On the feeding habits of trout in a stream in northern Sweden. — *Rep. Inst. Freshwat. Res. Drottningholm* **38**: 154—166.
- O'DONNELL, D. J., & CHURCHILL, W. S. (1954): Certain physical, chemical and biological aspects of the Brule River, Douglas County, Wisconsin. — *Trans. Wis. Acad. Sci. Arts Lett.* **43**: 201—255.
- OHGUSHI, R., & SAITO, Y. (1963): Ecological notes on the stream drifts in River Ukawa. — *Jap. J. Ecol.* **13**: 28—35.
- PATRICK, R. (1959): Aquatic life in a new stream. — *Wat. Sewage Wks.* December 1959. 5 pp.
- PEARSON, W. D., & FRANKLIN, D. R. (1968): Some factors affecting drift rates of *Baetis* and Simuliidae in a large river. — *Ecology* **49**: 75—81.
- PHILIPSON, G. N. (1954): The effect of water flow and oxygen concentration on six species of caddisfly (Trichoptera) larvae. — *Proc. zool. Soc. London* **124**: 547—564.
- REIMERS, N. (1957): Some aspects of the relation between fish foods and trout survival. — *Calif. Fish Game* **43**: 43—69.
- ROOS, T. (1957): Studies on upstream migration in adult stream-dwelling insects I. — *Rep. Inst. Freshwat. Res. Drottningholm* **38**: 167—192.
- RUTTNER, F. (1963): Fundamentals of Limnology. Trans.: FREY, O. G., and FRY, F. E. J. — University of Toronto Press. 3rd Ed. 293 pp.
- SCHERER, E. (1962): Phototaktisches Verhalten von Fließwasser-Insektenlarven. — *Naturwissenschaften* **49**: 477—478.
- SCHWOERBEL, J. (1961): Über die Lebensbedingungen und die Besiedlung des hyporheischen Lebensraumes. — *Arch. Hydrobiol. Suppl.* **XXV**: 182—214.  
— (1964): Die Bedeutung des Hyporheals für die benthische Lebensgemeinschaft der Fließgewässer. — *Verh. internat. Verein. theor. angew. Limnol.* **15**: 215—226.
- SCOTT, D. (1958): Ecological studies on the Trichoptera of the River Dean, Cheshire. — *Arch. Hydrobiol.* **54**: 340—392.
- SÖDERGREN, S. E. (1963): Undersökningar av driftfaunen i Rickleån. — *Laxforskningsinstitutet, Meddelande* **5**: 1—32.
- SPRULES, W. M. (1947): An ecological investigation of stream insects in Algonquin Park, Ont. — *Univ. Toronto Stud. biol. Ser.* **56**: 1—81.
- STARRETT, W. C. (1950): Food relationships of the minnows of the Des Moines River, Iowa. — *Ecology* **31**: 216—233.
- STEINMANN, P. (1907): Die Tierwelt der Gebirgsbäche. Eine faunistisch-biologische Studie. — *Ann. Biol. lacustre* **2**: 30—150.  
— (1913): Über Rheotaxis bei Tieren des fließenden Wassers. — *Verh. naturforsch. Ges. Basel* **24**: 136—158.
- SURBER, E. W. (1937): Rainbow trout and bottom fauna production in one mile of stream. — *Trans. Amer. Fish. Soc.* **66**: 193—202.

- TANAKA, H. (1960): On the daily change of the drifting of benthic animals in stream, especially on the types of daily change observed in taxonomic groups of insects. — Bull. Freshwat. Fish. Res. Lab., Tokyo **9**: 13—24.
- THOMAS, E. (1966): Orientierung der Imagines von *Capnia atra* MORTON (Plecoptera). — Oikos **17**: 278—280.
- THOMAS, J. D. (1962): The food and growth of brown trout (*Salmo trutta* L.) and its feeding relationships with the salmon parr (*Salmo salar* L.) and the eel (*Anguilla anguilla* L.) in the River Teify, West Wales. — J. Anim. Ecol. **31**: 175—205.
- TOBIAS, W. (1967): Zur Schlüpfrythmik von Köcherfliegen (Trichoptera). — Oikos **18**: 55—75.
- TOBIAS, W., & THOMAS, E. (1967): Die Oberflächendrift als Indikator periodischer Aktivitätsverläufe bei Insekten. — Ent. Z. **77**: 153—163.
- ULFSTRAND, S. (1967): Microdistribution of benthic species (Ephemeroptera, Plecoptera, Trichoptera, Diptera: Simuliidae) in Lapland streams. — Oikos **18**: 293—310.
- WARREN, C. E., WALES, J. H., DAVIS, G. E., & DOUDOROFF, P. (1964): Trout production in an experimental stream enriched with sucrose. — J. Wildl. Mgmt. **28**: 617—660.
- WATERS, T. F. (1961): Standing crop and drift of stream bottom organisms. — Ecology **42**: 532—537.
- (1962 a): A method to estimate the production rate of a stream bottom invertebrate. — Trans. Amer. Fish. Soc. **91**: 243—250.
- (1962 b): Diurnal periodicity in the drift of stream invertebrates. — Ecology **43**: 316—320.
- (1964): Recolonization of denuded stream bottom areas by drift. — Trans. Amer. Fish. Soc. **93**: 311—315.
- (1965): Interpretation of invertebrate drift in streams. — Ecology **46**: 327—334.
- (1966): Production rate, population density and drift of a stream invertebrate. — Ecology **47**: 595—604.
- (1968): Diurnal periodicity in the drift of a day-active stream invertebrate. — Ecology **49**: 152—153.
- WODSEDALEK, J. E. (1911): Phototactic reactions and their reversal in the mayfly nymphs *Heptagenia interpunctata* (SAY). — Biol. Bull. mar. biol. Lab., Woods Hole **21**: 265—271.
- (1912): Natural history and general behavior of the Ephemeridae nymphs *Heptagenia interpunctata* (SAY). — Ann. ent. Soc. Amer. **5**: 31—40.
- WOLF, PH. (1950): A trap for the capture of fish and other organisms moving downstream. — Trans. Amer. Fish. Soc. **80**: 41—45.

Address of the authors:

JOHN E. BISHOP, School of Biological Sciences University of Malaya, Kuala Lumpur, Malaysia.

Prof. H. B. N. HYNES, Department of Biology, Faculty of Science, University of Waterloo, Waterloo, Ontario, Canada.



a



b

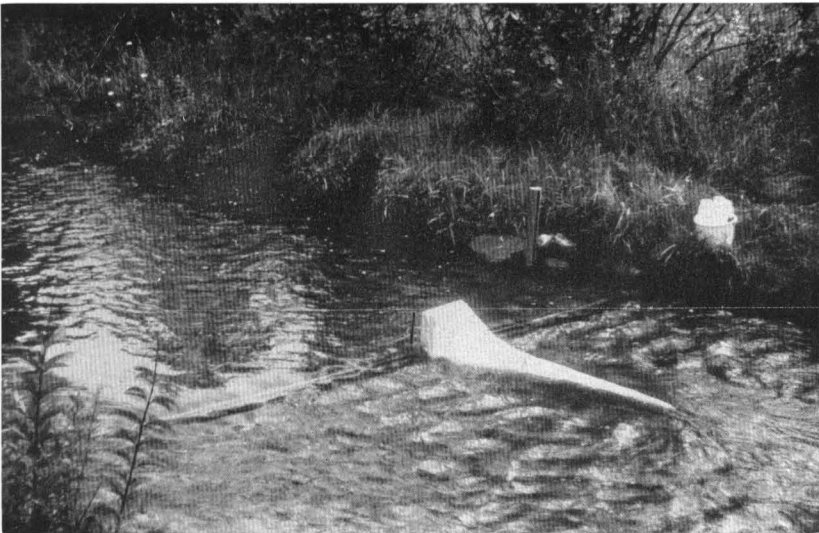


c

The Speed River at the sampling site.

a) modal flow; b) spring thaw condition; c) drought condition.

J. E. Bishop & H. B. N. Hynes: Downstream drift of stream insects.



a



b

Drift net in position over flow control board. a) summer; b) winter.

J. E. Bishop & H. B. N. Hynes: Downstream drift of stream insects.