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Invertebrate drift in a Dartmoor stream

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With plate 1, 12 figures and 10 tables in the text

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1. Introduction

There are many observations on aquatic organisms drifting in running water. This drift material can originate from both lenitic and lotic systems.

"Lake drift" is chiefly plankton which has been washed out via outflows (Woltereck, 1908; Chandler, 1937), and is often in sufficient quantity to be used as a food for salmonid fry (Kriegsmann, 1952; Geisler, 1953).

The biozone of the outflow usually consists of a dense community of filter and vortex feeders which are dependent on planktonic drift food from the lake (KNÖPP, 1952; MÜLLER, 1954 b, 1955, 1956; ILLIES, 1956), and are not found below regulated lakes (MÜLLER, 1955, 1962) except if supplied with plankton-rich surface water from above the dam (MÜLLER, 1962).

In lotic systems, a large proportion of the benthos can be removed as drift material in times of flood (NEEDHAM, 1929; BEAUCHAMP, 1932; MOFFETT, 1936; SURBER, 1937), or during break up of ice (MACIOLEK and NEEDHAM, 1952, BROWN et al., 1953; O'DONNELL and CHURCHILL, 1954), or after spraying with insecticide (HOFFMAN and SURBER, 1948; SCOTT, 1961; COUTANT, 1964).

In the absence of floods, ice, and insecticides, invertebrate drift is a normal feature of lotic systems, and is chiefly aquatic in origin (BORGH, 1927; IDE, 1942; DENDY, 1944; WOLF, 1946, 1951; BERNER, 1951; MACIOLEK and NEEDHAM, 1952; MÜLLER, 1954 a, c.; MACAN and MACKERETH, 1957; REIMERS, 1957; TANAKA, 1960; HORTON, 1961; WATERS, 1961, 1962 a; SÖDERGREN, 1963; WARREN et al., 1964), although terrestrial invertebrates may often dominate the surface drift (NEEDHAM, 1928).

Invertebrate drift from upstream facilitates the rapid colonisation of newly excavated stream channels (LEONARD, 1942; MÜLLER, 1954 a) and the repopulation of eroded areas (MOFFETT, 1936; SURBER, 1937; WATERS, 1964), except if insecticide has been applied up to the source of the stream (HITCHCOCK, 1965). Pools and lakes act as catching basins for invertebrate drift, the animals soon succombing to silt deposition, wave action in lakes, and unsuitable temperature (NEEDHAM, 1930; BEAUCHAMP, 1932; DENDY, 1944).

Both MÜLLER (1954 a) and ROOS (1957) assumed that the downstream drift of invertebrates must cause depopulation of the upper reaches of a stream, and they suggested that the chief compensating mechanism was the upstream flight of the female imagines for the purpose of oviposition. MÜLLER (1954 a) proposed the term "Colonisation Cycle" (Besiedlungskreislauf) for the whole process of adults migrating upstream, oviposition at the upper limit of habitat, and larvae drifting downstream.

The overall purpose of the present investigation was to assess the importance of invertebrate drift in a Dartmoor stream. It seemed necessary to determine:

(1) The qualitative and quantitative composition of the drift:
   a) At different sites;
   b) At different times of the year;
   c) At different times of the day.
(2) The extent of the drifting, and the proportion of the benthos in the drift.
(3) The validity of the "Colonisation Cycle" hypothesis.

(4) Why aquatic invertebrates drift in lotic systems.
(5) The utilisation of invertebrate drift as a food by salmonids (this will be dealt with in a separate paper).

2. Methods

2.1. Bottom samples

Quantitative sampling of the bottom fauna is subject to two main sources of error: inaccuracies in the sampler used (reviewed by Macan 1958), and the non-random distribution of the bottom fauna (Leonard, 1939; Mottley et al., 1939; Badcock, 1954; Needham and Usinger, 1956). These errors are inevitable unless a large number of samples can be taken and this is usually not possible.

Of the samplers available, the shovel sampler of Macan (1958) was thought to be most suitable for the present study. The shovel samples an area of bottom equal to 500 sq. cm. or 1/20 sq. m. Preliminary observations showed that there was little variation in the fauna along a site, but considerable variation across the site. Similar observations have been recorded by Mann (1964) for a reach of the River Thames. Four bottom samples were therefore taken in a diagonal transect from bank to bank. All samples were preserved in 70 % alcohol and hand sorted in the laboratory.

2.2. Drift samples

As terrestrial insects often dominate surface drift compared with mid-water drift, two methods of sampling were used, namely surface nets and modified high-speed plankton samplers.

A surface net has a rectangular mouth with a total surface area of 960 sq. cm. and an effective sampling area of 336 sq. cm., water being sampled to a depth of 7 cm. from the surface (Fig. 1 and Plate 1). The net hooks on to a brass frame and can be easily changed whilst frame and floats remain in the water.

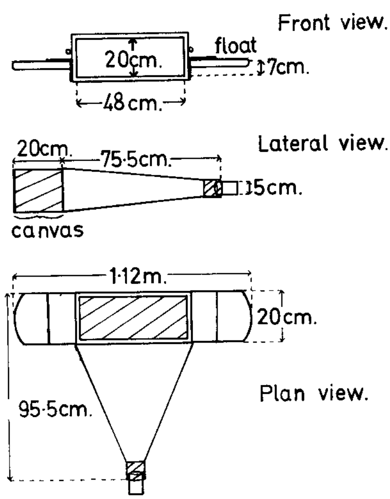

Fig. 1. Surface net.

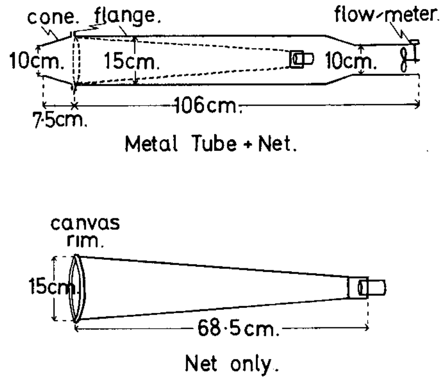

Fig. 2. Modified plankton sampler.

In the modified high-speed plankton sampler, the net is enclosed in a metal cylinder and a flow-meter fixed in the hind end of the tube records directly the volume of water passing through the net (Fig. 2. and Plate 1). Side brackets on the tube slide over iron rods driven into the stream bottom, and the apparatus remains rigid even in times of spate. The net is held in place by a detachable cone which reduces the effective sampling aperture to an area of 78.5 sq. cm. The original flow-meter was a copy of the CLARKE-BUMPUS model (1940), with an industrial counter recording the volume of water flowing through the net. An improved flow-meter was used from May 1964, this having a simple make and break with wires running to an electrical counter on the bank.

All nets were made of nylon sifting cloth with a mesh of 440 microns giving 15,5 meshes/cm. (=39.5/inch). This mesh trapped very small insect larvae (1—2 mm. long) but did not easily clog.

Sampling was for 24 hours, and the nets were emptied every 3 hours. All samples were preserved in 70 % alcohol and non-animal material was dried and weighed before disposal.

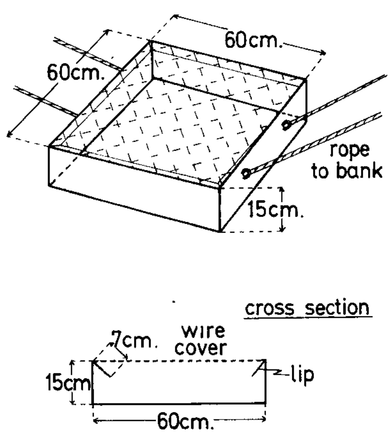

Fig. 3. Deep pool sampler.

2.3. Deep pool sampler

This consists of a tray with an overturned lip, a bottom of woven wire mesh and chicken wire over the top to prevent fish browsing on the material collected (Fig. 3). The tray proper rests on the woven wire mesh and consists of a wooden frame with nylon cloth (15.5 meshes/cm.) secured to it. The sampler was suspended in a deep pool and kept about 30 cm. from the bottom to prevent benthic animals crawling on to the tray.

2.4. Bilateral insect trap

The trap was a small version of that used by Roos (1957 after Malaise, 1937) and was fixed across the stream so that one entrance faced upstream and north whilst the other faced downstream and south. Each half of the trap functioned as a separate unit and had separate killing compartments. The entrance to each unit was 1.5 m. long by 0.7 m. high, the insects rising to the highest corner of the trap and then entering an upper compartment which led to the killing compartment. Each killing compartment was emptied every 12 hours at 5.30 h. and 17.30 h. (G. M.T.), and the catches were preserved in K.A.A.D. (Kerosene, alcohol, acetic, acid, and dioxan). In use the trap proved very effective, the only escapes being small Diptera (through the mesh of 1 sq. mm.), and the very manoeuvrable dragonfly *Cordulegaster boltonii.*

The following environmental readings were taken: air temperature and relative humidity (on a thermohygrograph); wind velocity (using a thermoelectric hot wire anemometer); general weather observations.

2.5. Laboratory experiments

In order to investigate the behaviour of the drift invertebrates, a simple experiment was set up in the laboratory utilising a tank with a waterfall. The depth of water in the tank was 7 cm. and the area of bottom 900 sq. cm., this area being increased by the addition of a large number of stones and roughened blocks for the animals to cling to or go under. A net at the lower end of the waterfall caught any animals washed over and was emptied every 3 hours, giving 8 samples per 24 hours. Temperature and rate of flow were kept constant, the latter at 360 litres per 3 hours. As the tank held 5 litres, there were at least 72 changes of water in 3 hours. All animals removed from the net were returned to the upper tank and allowed to re-establish themselves, which kept the numbers in the tank as high as possible. Illumination could be controlled by using artificial light in the normal night periods and a tank cover during normal daylight.

3. Description of the stream and sites

Field work was undertaken in the Walla Brook, a tributary of the East Dart, at monthly intervals from June 1963 to October 1964. This small stream is slightly acid (pH 6.4 to 6.8), has few tributaries and is only ocassionally in severe spate. There is a good population of *Salmo trutta* L., previously studied by Horton (1961).

The character of the stream changed abruptly about 2 km from the source. Above this point the predominant bottom type was large stones and a small amount of gravel, with bryophytes as the dominant plants. Below

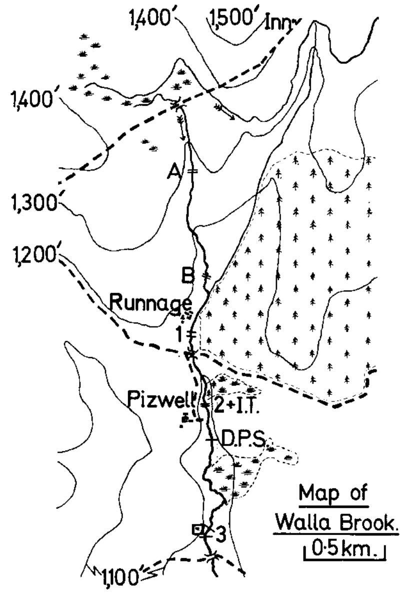

Fig. 4. Map of Walla Brook, showing position of sites (A, B, 1, 2, 3), deep pool sampler (D.P.S.) and insect trap (I.T.).

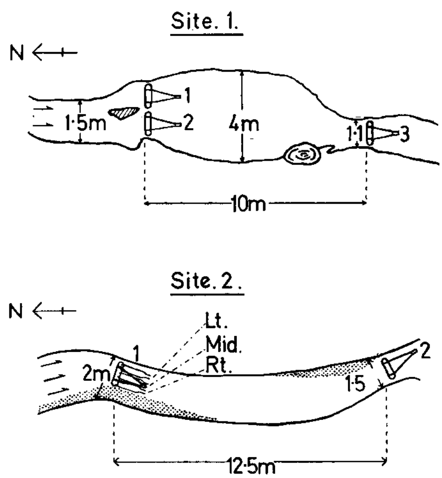

Fig. 5. Sites 1 and 2 showing position of surface nets (1, 2, 3) and left middle and right (Lt., Mid., Rt.) modified plankton samplers.

this point the bottom was chiefly gravel and small stones, with *Myriophyllum spicatum* L. and *Callitriche aquatica* SM. replacing bryophytes as the dominant plants. It was thought necessary to sample drift from both bottom types and these were represented by sites 1 and 2 (see Fig. 4 for map of area).

At site 1 (National grid reference SX 668790) the bottom was chiefly large stones and the dominant plants were the mosses *Fontinalis antipyretica* HEDW. and *Hygrohypnum ochraceum* TURN. Surface nets 1 and 2 were placed across the stream where a riffle changed to a wide run and surface net 3 was placed where the run changed to a second riffle (Fig. 5). Only surface nets were used as the average depth of water rarely exceeded 15 cm.

At site 2 (SX 669786) the bottom was chiefly gravel with *Myriophyllum spicatum* dominant. Samples were taken in a run where the average depth was rarely below 25 cm. Surface net 1 and three tubes were used, the tubes being referred to as left, middle and right according to their position athwart the stream (Fig. 5). Surface net 2 was placed 12.5 m. downstream of these and about 3 m. upstream from a deep pool.

Drift was sampled at site 1 from June 1963 to May 1964, and at site 2 from June 1963 to October 1964.

Site 3 (SX 669777) was about 1 km. below site 2 and was chosen because of the presence of a dam across the stream. Surface nets 1 and 2 were placed across the deep pool above the dam and net 3 was 23 m. below the dam. Sampling was from June to September 1963 and was discontinued after four months owing to the collapse of the dam.

In September 1964, drift was sampled simultaneously at site A (SX 668800), and site 2. As the distance between these sites was about 1.5 km., it was hoped that these results would indicate whether or not the drift changed in density towards the source. At site A the bottom was large

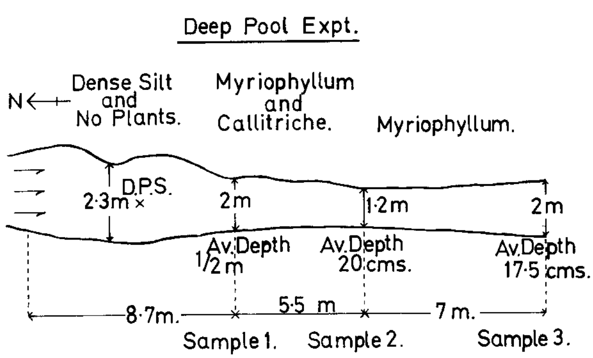

Fig. 6. Plan of deep pool experiment showing position of deep pool sampler (D.P.S.) and sampling points (1, 2, 3).

stones covered with a dense carpet of the liverwort *Scapania undulata* (L.) DUM. As the stream was only 1.2 m. wide at this site, only one surface net and tube were used. For a second 24 hours, the samplers were removed to site B (SX 669793), situated halfway between the source and site 2.

In July 1964, the site of the deep pool sampler (SX 669783) was utilised for an experiment. Drift samples were taken at three successive points downstream from the pool, the last site being at the upstream end of the next deep pool (Fig. 6). It was hoped that this experiment would indicate the amount of drift coming from and going into a deep pool.

4. Results

4.1. Bottom and drift samples

4.1.1. General considerations

Most of the aquatic invertebrates have been identified to species, the exceptions being the Chironomidae and Simuliidae from which *Pentaneura* spp. and *Simulium laetipes* have been separated in the bottom samples only. The complete list of fauna indicates presence or absence at all sites and in the drift (see appendix).

Associated with the different bottom types at sites 1 and 2 were quantitative and qualitative differences in the benthos. There were greater numbers of *Protonemura meyeri, Helmis maugei,* and Chironomidae at site 1 than at site 2, and greater numbers of *Amphinemura sulcicollis, Ephemerella ignita, Baetis* spp., and *Simulium* spp. at site 2 than at site 1. *Lepidostoma hirtum, Hydroptila* sp., *Deronectes latus* occurred only at site 1, and *Baetis pumilus, Sialis lutaria, Orectochilus villosus, Palpomyia flavipes* only at site 2. These qualitative differences were confined to the rarer members of the benthos, some of which were taken only in one month. *Brachyptera risi, Rhithrogena semicolorata, Leptophlebia vespertina,* and *Paraleptophlebia submarginata* were absent from the bottom samples at site 1. This was probably due to the inadequacy of the sampling technique as all four species frequently occurred in the drift samples at both sites.

A more detailed account of the benthos will be given in another paper.

4.1.2. Terrestrial and emerging components of the drift

Few drifting invertebrates of terrestrial origin have been identified to species, but a list of the principal groups involved appears in the appendix. Terrestrial invertebrates were taken in greatest numbers in the summer samples but their presence depended chiefly on the weather conditions prevailing at the time of sampling. On sunny days, large numbers of terrestrial insects were often taken in a 3 hour sample and under these

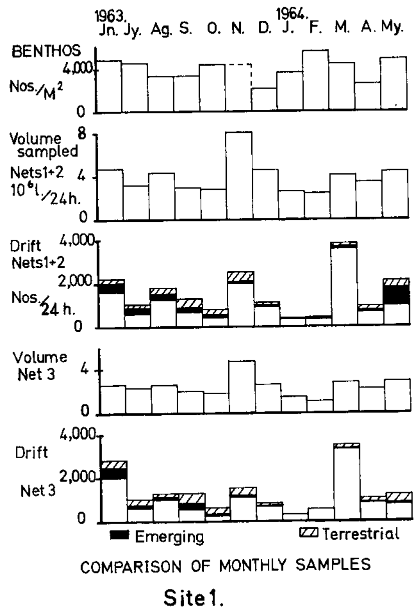

Fig. 7. Comparison of monthly samples at site I for surface nets 1 and 2.

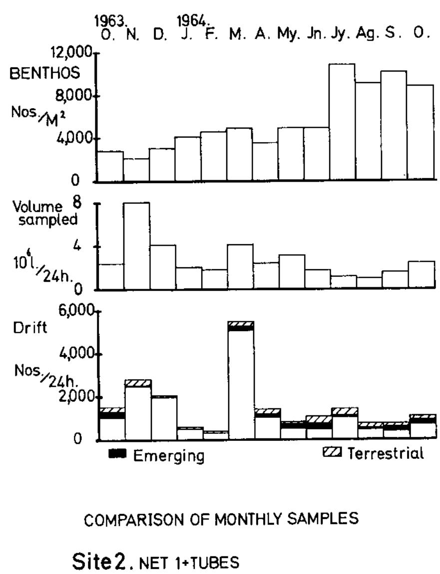

Fig. 8. Comparison of monthly samples at site 2 for surface net 1 and three modified plankton samplers.

optimum conditions the terrestrial component was temporarily dominant over the aquatic component.

The greatest numbers of emerging insects were taken in the drift samples of April to September (see Figs. 7 and 8). Most of the Plecoptera, Ephemeroptera and Trichoptera emerged during these months only, the exceptions being *Leuctra fusca* (July—December), *Chaetopteryx villosa* (August—December), and *Baetis rhodani* (all months). A few emerging adults of *Odontocerum albicorne* indicated that the larvae must have been present, although never taken in the bottom samples. Most of the Plecoptera, Trichoptera and Chironomidae emerged during the early hours of the night and this agrees with the observations of other workers (Brinck, 1949, on Plecoptera; Brindle, 1957 and 1958, on Trichoptera; Mundie, 1956; Williams and Davies, 1957; Morgan and Waddell, 1961, all on Diptera). The Ephemeroptera were the exceptions, emerging subimagines of *Ephemerella ignita, Baetis niger, B. scambus, B. rhodani* always being taken in the day samples.

4.1.3. Aquatic component of the drift

Nearly all species taken in the bottom samples were also taken in the drift, the exceptions being Tricladida and Trichoptera larvae with stony cases. Small limnephilid larvae (under 5 mm.) did occur in the drift and the absence of later instars appeared to be associated with the change from vegetable to stone cases. The only mollusc in the benthos was *Ancylastrum fluviatile* and this species was swept away only in a major spate (November 1963). Of the frequent members of the drift, only *Leuctra fusca* and *Dixa* sp. were absent from the bottom samples. Many rare members of the drift were absent from the bottom samples and are listed in the appendix. Most of these species were adult aquatic Coleoptera, many of which were probably occasional visitors rather than permanent members of the fauna. The three species of Odonata were all resident in the Walla Brook and their imagines were frequently seen in the summer months, although the nymphs were never taken in the bottom samples. The occurrence of *Hydra* sp. was of interest as this animal is not usually associated with an acid moorland stream.

In all months, the aquatic component of the drift predominated over both the terrestrial and emerging components when 24-hour samples were compared (Figs. 7 and 8). Catches were combined when nets sampled at the same cross-section of stream i.e. nets 1 and 2 at site 1, net 1 and three tubes at site 2. The 24hour drift samples were compared with the monthly bottom samples (numbers/sq. m.) and the amount of water flowing down the stream (expressed as litres sampled per 24 hours). Drought conditions were seen in January, February, June to September 1964 and were accompanied by heavy silting. A major spate occurred in November 1963 when the stream overflowed its banks, and there were minor spates in June, August, December 1963, March, May 1964. The remaining five months were classed as normal.

There was no correlation between the quantity of aquatic drift and the density of the benthos, but a strong correlation between the aquatic drift and the amount of water flowing down the stream (Figs. 7, 8). At site 2, this was especially evident in the summer of 1964, when a period of drought resulted in very low numbers in the drift, whilst the density of the benthos was at its maximum.

Although the amount of water flowing down the stream chiefly determined the number of aquatic invertebrates in the drift, a direct linear relationship was absent when different months were compared. This was not so when the same months were compared for surface nets at site 2 (Table 1). In June, July and September 1963 the amounts of water and drift were both twice those of the corresponding months in 1964. These two quantities were equal in the October of both years, and far greater in August 1963 than in August 1964. Therefore the density of aquatic drift appeared to be fairly constant for the same month but not for different months.

Table 1. Comparison of summer samples, surface net only at site 2.

		June	July	Aug.	Sept.	Oct.
Bottom samples	1963		5150	2895	2330	2780
(Nos./M².)	1964	4760	10815	9155	10230	8825
Volume sampled	1963	2144	1560	2768	1600	1592
(1000 l/24 h.)	1964	1048	720	624	984	1572
Aquatic drift	1963	763	1036	1998	770	477
(Nos/24 h.)	1964	267	619	261	217	443
Emerging	1963	406	187	174	134	179
(Nos/24 h.)	1964	263	59	84	123	148
Terrestrial	1963	111	409	297	198	125
(Nos/24 h.)	1964	326	261	169	185	173
Total drift	1963	1280	1632	2469	1102	781
(Nos/24 h.)	1964	856	939	514	525	764
Average temp.	1963	14.3	12.0	13.2	12.8	10.2
(° C)	1964	12.0	14.4	16.0	13.7	9.0

In the September experiment, drift was sampled upstream at sites A and B (Fig. 4) in turn and at site 2 at the same time. It was so arranged that the volumes of water sampled were approximately the same at all sites and therefore the drift figures could be compared (Table 2). The stream was wider at site 2 than at the upstream sites and the greater surface area of water over equal lengths probably accounted for the greater quantity of terrestrial drift at site 2. The differences in the emerging component of the drift were due to the far greater number of emerging Chironomidae taken at site 2 and this was due to the greater number of their larvae in the benthos. The number of aquatic invertebrates in the drift was similar at all three sites. This indicates that the aquatic drift did not change in density towards the source of the stream, in spite of a decrease in the density of the benthos. At site 2, the drift was fairly constant over three 24-hour periods (Table 2).

Table 2. Upstream experiment. — Sites A, B, and 2. September 1964

24-h. periods.		1		2		3
Volume sampled	S. A.	1440	S. B.	1304		
(1000 l/24 h.)	S. 2.	1416	S. 2.	1416	S. 2.	1416
Aquatic drift	S. A.	214	S. B.	248		
(Nos/24 h.)	S. 2.	310	S. 2.	230	S. 2.	369
Emerging	S. A.	25	S. B.	47		
(Nos/24 h.)	S. 2.	106	S. 2.	147	S. 2.	135
Terrestrial	S. A.	108	S. B.	74		
(Nos/24 h.)	S. 2.	223	S. 2.	182	S. 2.	191
Total drift	S. A.	372	S. B.	369		
(Nos/24 h.)	S. 2.	639	S. 2.	559	S. 2.	695
Benthos	S. A.	5780	S. B.	10330		
(Nos/sq. m.)	S. 2.	10230	S. 2.	10230		

In the July experiment, the catches at the three successive sampling points indicated that a direct linear relationship existed between aquatic drift and the amount of water passing the sampling point (Table 3). The ratio of both these quantities for the three 24-hour samples was 2:10:5 (sample 1 : sample 2 : sample 3). Therefore the density of aquatic drift was constant throughout the length of the run.

The density of aquatic invertebrates in the drift appears to be fairly constant for the same months (comparing summer samples), and at both single (September experiment) and different sites (September and July experiments) for a short period of time. Under these conditions, quantitative differences between 24-hour drift samples are a reflection of the different amounts of water passing the sampling points and a direct linear relationship exists between the two variables. This is not so when comparing drift samples from different months, and it is suggested that the density of aquatic invertebrates in the drift depends to some extent on the stages of their life histories. Although all instars were taken in the drift, the full-

Table 3. Deep pool expt.
Samples per 24 hours for surface net and 3 tubes.

	D. P. sample 1.	D. P. sample 2.	D. P. sample 3.
Cross section (M².)	1.0	0.2	0.33
Average velocity (M/sec.)	0.04	0.20	0.12
Volume sampled (1000 l/24 h.)	216	976	472
Aquatic invertebrates (Nos/24 h.)	484	2678	1221
Emerging (Nos/24 h.)	3	52	56
Terrestrial (Nos/24 h.)	44	374	65
Total drift (Nos/24 h.)	**531**	**3104**	**1342**

grown nymphs of Plecoptera and Ephemeroptera seemed particularly vulnerable to being swept away and this was especially evident in March. This month was just prior to the period of greatest emergence activity and full-grown nymphs of *Protonemura meyeri, Amphinemura sulcicollis, Leuctra inermis, L. hippopus, Baetis rhodani* and *Leptophlebia vespertina* were in the drift in large numbers. Therefore the number of late instars in the benthos was probably more important than the total numbers.

4.1.4. Daily fluctuations of the aquatic invertebrates in the drift

In all months, more aquatic invertebrates were taken at night than in the day, the greatest numbers being in the three-hour sample after sunset (Figs. 9, 10, 11 with sunset and sunrise marked as vertical broken lines). The numbers in the drift appeared to be related to fluctuations in light intensity, with fluctuations in water temperature as another possibility. In some months the gradual decrease in water temperature through the night could have explained the gradual fall in drift numbers, but in other months the temperature remained constant whilst the drift still decreased through the night. The relationship between drift and light intensity has already been reported for one month (Elliott, 1965 a) and for other streams (Waters, 1962 b; Müller, 1963 a—d; Södergren, 1963; Elliott, 1965 b).

In September 1964, drift was sampled continuously for 72 hours at site 2 (Table 4). Although samples taken at the same time showed large variations from day to day, the daily fluctuations of the drift followed a similar pattern for each 24-hour period.

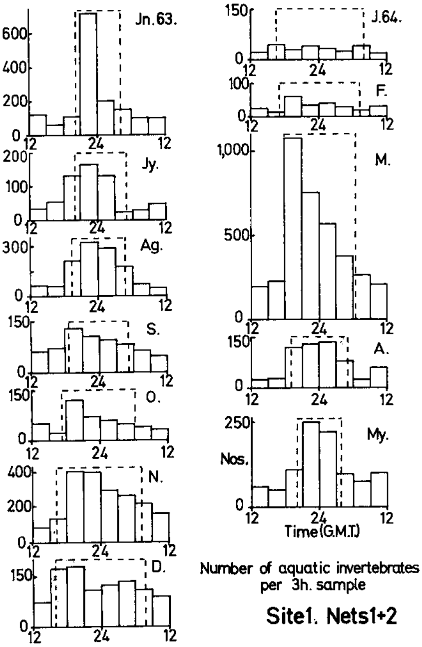

Fig. 9. Number of aquatic invertebrates taken in each 3 h. sample. Site 1, surface nets 1 and 2 (June 1963 to May 1964).

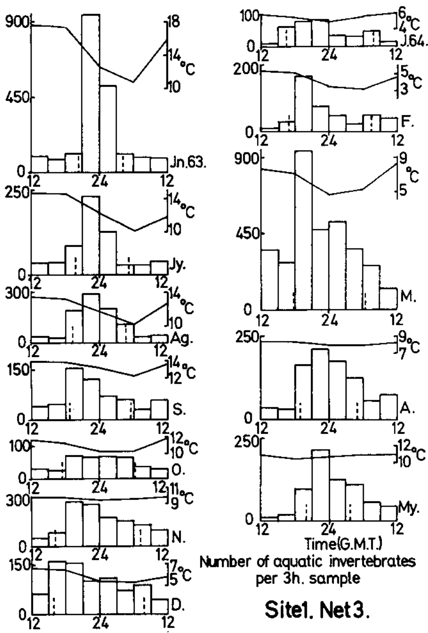

Fig. 10. Number of aquatic invertebrates taken in each 3 h. sample. Site 1, surface net 3 (June 1963 to May 1964).

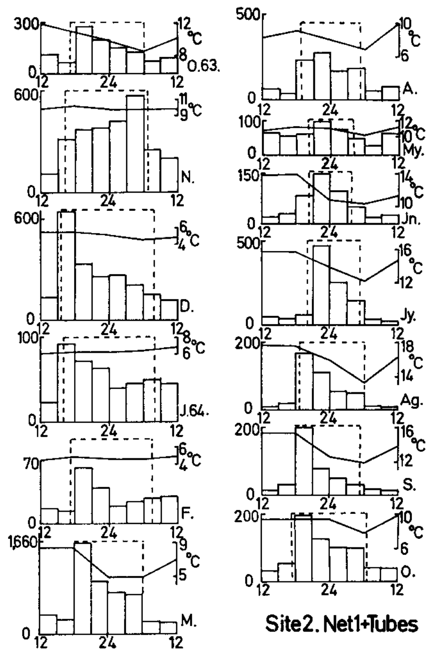

Fig. 11. Number of aquatic invertebrates taken in each 3 h. sample. Site 2, surface net 1 and three modified plankton samplers (October 1963 to October 1964).

Table 4. Numbers of aquatic invertebrates per 3 hour sample, September experiment.
Sunset 1800 h, sunrise 0530 h.

Sample number	1	2	3	4	5	6	7	8
Emptying time	15 h.	18 h.	21 h.	0 h.	3 h.	6 h.	9 h.	12 h.
1st period	24	14	125	44	28	38	14	23
2nd period	29	24	79	26	28	24	4	16
3rd period	7	21	168	67	44	30	17	15

The daily fluctuations of the aquatic species in the drift usually followed the pattern of the total numbers. Examples were abstracted from the complete tables (deposited in the library of the Freshwater Biological Association) and where possible, both December and March figures have been included to indicate the effect of different periods of darkness (Table 5). Of the principal members of the drift, only Chironomidae have been excluded as these were not identified to species. All four *Baetis* spp. followed the normal pattern and *Baetis rhodani* was the predominant member of the drift. These results agree with the recent finding on *Baetis* spp. (Tanaka, 1960; Södergren, 1963), *B. vagans* (Waters, 1962 b), *B. rhodani* and *B. vernus* (Müller, 1963 a), and *B. subalpinus* (Elliott, 1965 b).

Table 5. Examples of daily fluctuations of aquatic species in the drift. Number of animals per 3-hour sample.

Sample number Emptying time	1 15 h.	2 18 h.	3 21 h.	4 0 h.	5 3 h.	6 6 h.	7 9 h.	8 12 h.	Month
Protonemura meyeri	26	131	67	52	64	42	27	17	Dec. '63.
	16	6	98	59	44	28	11	4	Mar. '64.
Amphinemura sulcicollis	4	23	17	10	14	9	7	7	Dec. '63.
	41	15	268	116	54	48	20	13	Mar. '64.
Leuctra inermis	9	61	37	35	25	19	14	3	Dec. '63.
	15	5	100	62	46	35	14	6	Mar. '64.
L. hippopus	12	2	85	56	32	28	8	2	Mar. '64.
Isoperla grammatica	11	56	28	28	30	19	16	14	Dec. '63.
	20	1	64	57	45	51	15	8	Mar. '64.
Chloroperla torrentium	12	2	24	7	6	11	4	6	Mar. '64.
Leptophlebia vespertina	5	2	152	43	72	53	16	6	Mar. '64.
Baetis rhodani	28	181	79	61	76	43	35	24	Dec. '63.
	18	7	208	150	113	147	35	13	Mar. '64.
B. niger	2	0	1	477	269	130	1	0	Jy. expt.
B. pumilus	0	0	0	62	32	4	0	0	Jy. expt.
B. scambus	0	0	0	82	61	23	1	0	Jy. expt.
Ephemerella ignita	1	0	0	78	51	25	3	2	Jy. expt.
Polycentropus flavomaculatus	8	7	77	58	21	11	9	2	Mar. '64.
Hydropsyche instabilis	4	0	12	7	7	10	3	2	Mar. '64.
Limnephilidae (small)	31	38	62	31	58	51	13	28	Mar. '64.
	18	10	29	29	7	20	15	12	Oct. '63.
Helmis maugei L.	6	29	18	10	3	11	7	7	Dec. '63.
Helmis maugei A.	6	27	17	15	20	13	5	0	Dec. '63.
Simulium spp.	29	16	147	92	81	101	31	21	Mar. '64.
	5	2	3	76	49	29	8	12	Jy. '64.
Dixa sp.	0	0	20	5	5	4	1	0	Oct. '63.

	Sunset.	Sunrise.	Night samples.
October 1963	1715 h.	0620 h.	3—6
December 1963	1550 h.	0750 h.	2—7
March 1964	1800 h.	0610 h.	3—6
July 1964	2010 h.	0505 h.	4—6

Although the number of animals in the drift was always at a maximum in the first period after sunset, a second peak often occurred just before dawn. This has also been observed for *Gammarus limnaeus, Baetis vagans* (WATERS, 1962 b), *Baetis* spp., *Gammarus pulex, Niphargus aquilex schellenbergi* (MÜLLER, 1963 a—d). WATERS (1962 b) suggested that this second peak could be due to the occlusion of moonlight during the night, but this was certainly not the case in the Walla Brook as often the nights were overcast with no moon visible. MÜLLER (1963 b) found that the number of drift maxima (2 or 3) was determined by the length of the night, but this was not supported by the observations in the Walla Brook.

Small larvae (under 5 mm.) of Limnephilidae increased less in numbers in the drift at night than other species. When numbers were small there was often no apparent increase at night, but in March 1964 and October 1963 sufficient numbers were taken to indicate a slight increase at night (Table 5). The Hydrachnellae were the only exception to the general pattern. Although never in large numbers, the monthly totals have been separated into day and night samples from the collections at site 2 (Table 6). Over seventeen months, 75 % of the water mites were taken in the day samples and only 25 % at night. Hydrachnellae in lakes are known to be more active in the daytime than at night (Moon, 1940; Pieczynski, 1964).

Table 6. Hydrachnellae — Numbers taken during day and night samples — site 2.

		day	night
1963	June	14	1
	July	14	4
	August	21	6
	September	41	7
	October	11	1
	November	12	4
	December	2	4
1964	January	0	0
	February	18	4
	March	38	18
	April	23	8
	May	18	4
	June	24	1
	July	58	36
	August	4	3
	September	1	3
	October	9	0
	Total.	308 (75 %)	104 (25 %)

Although the frequency of severe spates was not known, local observers estimated 4—6 per year as typical of the Walla Brook. Although it was not intended to investigate the effect of spates on the drift, in November 1963 the monthly sampling coincided with a severe spate. For all other monthly samples the mean surface velocity was below 1 m./sec and the range was 0.66 to 0.90 m./sec for the five monthly samples taken in minor spates. During the November sampling at site 2, the mean depth of the stream increased from 40 to 90 cm. and the mean surface velocity from 1.35 to 2.50 m./sec. Associated with this increase in the amount of water flowing down the stream was an increase in the number of animals in the drift and both these quantities were at a maximum in sample 6 at 6 h.

Table 7. November 1963 — Spate conditions and number of animals in the drift at site 2.

	Sunset 1615 h.				Sunrise 0705 h.			
Sample no.	1	2	3	4	5	6	7	8
Emptying time	15 h.	18 h.	21 h.	0 h.	3 h.	6 h.	9 h.	12 h.
Temp. (° C)		10.2		9.8		9.8		9.8
Mean surface velocity (m./sec.)	1.35	1.50	1.64	1.85	2.25	2.50	1.85	1.40
Volume sampled × 1,000 l.	805	865	937	1040	1215	1405	1047	839
No. animals/3 h.	113	314	372	377	417	574	253	203
No./100,000 l.	14	36	40	36	34	41	24	24

(Table 7). The number of animals per 100,000 l. showed little variation through the night and therefore the rise in water velocity did not increase the density of animals in the drift. *Pyrrhosoma nymphula* (1 nymph), *Cordulegaster boltonii* (3 nymphs), *Sericostoma personatum* (1 larva), and *Ancylastrum fluviatile* (1) were taken in sample 6 at the height of the spate and this was the only time when these species occurred in the drift. As the number of animals per sq. m. of bottom was 2105 before the spate and 2890 in December, the November spate appeared to have no effect on the density of the benthos.

4.1.5. Extent of the drift and proportion of benthos in the drift

At site 1, the volume of water sampled by net 3 was always less than the total volume sampled by nets 1 and 2. The corresponding monthly drift totals were usually slightly less but showed an almost identical monthly pattern (Fig. 7). Except under conditions of severe spate (November 1963), most of the water entering the run from the riffle above was sampled by nets 1 and 2 with the consequent removal of nearly all the aquatic drift. The large amount of aquatic drift taken by net 3 must nearly all have originated from the 10 m. run between the two sampling points. As net 3 only sampled 60—70 % of the water leaving the run, the amount of aquatic drift taken was probably 30—40 % less than the total yield from the 10 m. run. The total yield would therefore approximate to the amount of aquatic drift entering the run from the riffles above. If this did not occur, the aquatic drift from the riffles would be added to that leaving the run and the net result would be depopulation of the run. Bottom samples indicated that there was no depopulation, and hence it was concluded that the aquatic drift was fairly local in origin with the slower current of the runs serving as a check to drift washed down from the riffles.

At site 3, most of the drift normally carried over the dam was removed by nets 1 and 2 whilst a large amount of aquatic drift was still taken in net 3. This drift nearly all originated from the 23 m. stretch of bottom below the dam and therefore reinforced the conclusions drawn from site 1.

The figures from the July experiment were used to estimate the total yield of aquatic drift from a known area of bottom. The bottom of the run was chiefly mud and *Callitriche aquatica* from sampling points 1 and 2 (area A), and chiefly gravel and *Myriophyllum spicatum* from sampling points 2 to 3 (area B). Comparing the bottom samples from these two areas: Chironomidae were far denser in area A (11,460 per sq. m.) than in area B (4,110 per sq. m.), whilst the four *Baetis* spp. and *Ephemerella ignita* were in denser numbers in area B (3,900 per sq. m.) than in area A (1,310 per sq. m.). In estimating the totals for drift and benthos, it was assumed that the samples were representative of the whole. The total amount of water flowing past each sampling point in 24 hours was 3456 cu. m. Benthic totals were 163,900 for area A and 157,320 for area B.

A total of 9,483 aquatic invertebrates drifted past sampling point 2 in 24 hours and this was equivalent to 5.8 % of the benthos in area A. The total number of aquatic invertebrates drifting past sampling point 1 and entering area A was 7,744 per 24 hours or 4.7 % of the benthos. These aquatic invertebrates either replaced the benthos removed as drift or formed a large proportion of the total drift passing sampling point 2. In either case the net loss was about 1 % of the benthos in 24 hours. Most of the aquatic invertebrates taken in sample 1 were species typical, not of the deep pool, but very much so of the run immediately upstream of the pool. The invertebrates must have been carried across the deep pool and therefore the latter was not a major check to drift.

The total number of aquatic invertebrates passing sampling point 3 and entering the second deep pool was 8,940 per 24 hours. These invertebrates were the daily yield from the whole run between the two deep pools. As the run gained 7,744 invertebrates from across the first deep pool, the net loss from the run was 1,196 invertebrates in 24 hours, or 0.37 % of the total benthos in the run. Therefore a very small percentage of the benthos was lost from the run in 24 hours.

As the total drift passing sampling point 3 was slightly less than the total drift passing sampling point 2, the latter drift must have either returned to the benthos in area B or formed the total drift leaving the run. The latter conclusion assumed that very little drift came from area B and this was not the case as known drift species were in far denser numbers in area B than in area A. This indicates that the invertebrate drift in the run was very local in origin, most of the aquatic invertebrates being returned to the benthos after travelling only a short distance. These findings

Table 8. Proportion of bottom fauna in the drift.

	Site 1		Site 2
	Nets 1 & 2	Net 3	Net 1 & tubes
1963 June	0.0010 %	0.0023 %	
July	0.0006 %	0.0004 %	
August	0.0012 %	0.0015 %	
September	0.0009 %	0.0012 %	
October	0.0005 %	0.0006 %	0.0041 %
November			0.0076 %
December	0.0014 %	0.0020 %	0.0043 %
1964 January	0.0003 %	0.0007 %	0.0012 %
February	0.0002 %	0.0007 %	0.0008 %
March	0.0028 %	0.0039 %	0.0086 %
April	0.0010 %	0.0024 %	0.0029 %
May	0.0006 %	0.0007 %	0.0008 %
June			0.0014 %
July			0.0019 %
August			0.0011 %
September			0.0007 %
October			0.0007 %

agree with those of Waters (1965) who estimated the distance of daily drift and concluded that "This seems a surprisingly short distance considering normal current velocities and the fact that organisms are well represented in the upper strata of water."

The above findings could explain the apparent paradox of *Leptophlebia vespertina.* Nymphs of this species were taken in the drift samples of October to May and during these months the nymphs were found at the sides of the stream in the bays with plenty of vegetation. Only in March and April were the nymphs taken in the bottom samples and this coincided with the largest numbers in the drift. At site 2 in March, the drift samplers took 349 nymphs in 24 hours and filtered only $^1/_7$ of the total volume of water passing the sampling point. With removal at this rate, nymphs would soon be absent from the main stream, but the density of nymphs on the bottom was 15 per sq. m. in April compared with 25 per sq. m. in March. Therefore the population of *Leptophlebia vespertina* had not been removed from the main stream in spite of the large numbers in the drift. This paradox could be explained in two ways. Either the nymphs removed from the main stream were replaced by their fellows from the sides, or they soon returned to the benthos after drifting a short distance. Both these explanations could be correct but only the latter is supported by the previous work. Emerging adults of *Leptophlebia vespertina* were never taken in the drift samples and this indicates that emergence took place close to the bank. A similar suggestion has been recently made for *Leptophlebia* in a tarn (Macan, 1966).

In order to estimate the proportion of the benthos in the drift at any instant in time, two assumptions were made:

(1) The sampling areas were representative of the cross section of stream;

(2) Equilibrium of the benthos existed, i.e. rate of settlement was approximately equal to rate of erosion.

Let the number of animals in the drift be x individuals per cu. m. and in the benthos X individuals per sq. m. If the average depth of the stream is D m, then the proportion of the benthos in the drift (P%) is given by the formula:

$$P = \frac{xD \cdot 100}{X - xD}$$

The percentages have been calculated for each month at sites 1 and 2 (Table 8). These percentages were all extremely low and indicated that there were very few invertebrates in a column of water above a square metre of bottom at any instant in time. The same conclusion was reached in a recent study on drift in a mountain stream in Norway (Elliott, 1965 b). Because a small percentage of the benthos was involved in the drift at any time and because the quantity of drift was not related to the density of the benthos, invertebrate drift in the Walla Brook could never be used to estimate the production rate of the benthos as suggested by Waters (1961, 1962 a).

4.2. Deep pool samples

Most of the more frequent aquatic members of the drift settled on the tray of the deep pool sampler. It was evident that the animals settling on the tray were those which were most abundant at the time of year, e.g. *Baetis rhodani* was taken during all months, whilst *Ephemerella ignita* was taken only from June to September. The monthly samples over three days were all extremely low in numbers when compared with the amount of drift taken at site 2. Little quantitative information came from these monthly samples, the low counts being probably due to the escape of the animals and the July experiment showed that large numbers of invertebrates drifted out of the deep pool.

4.3. Bilateral insect trap

The trap was used for 3 days each month from June 1963 to September 1964. Very few aquatic species emerged between November and March. Although this explained the low winter samples, climatic factors were also important, especially temperature and rainfall. Heavy rain coincided with the low numbers in August 1963 and very high numbers were usually

Table 9. Catches of Plecoptera, Ephemeroptera, and Trichoptera, compared with wind velocity and direction. South entrance to trap took upstream-moving imagines and north entrance downstream-moving imagines.

Month.		Wind velocity (m/sec)			Plecoptera catches				Ephemeroptera catches				Trichoptera calches			
					South end		North end		South end		North end		South end		North end	
		Max.	Min.	Av. Direction	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
1963.	Jn.	10	0.3	3.0 NNE	12	23	28	115	20	14	111	175	5	7	4	24
	Jy.	10	0.3	2.5 SW	4	37	3	18	10	35	1	2	8	19	2	1
	Ag.	12	0.3	4.5 W	1	6	0	1	0	2	11	18	5	14	4	4
	S.	1.5	0.3	0.6 SW-E	18	34	2	3	37	51	3	1	25	22	12	4
	O.	5	0.3	1.8 NW/SW	0/3	2/3	2/0	8/0	0/12	1/13	21/0	32/1	12/6	13/4	5/3	1/0
	N.	17.5	0.3	9.0 SW-SE	0	0	0	0	0	0	0	0	0	1	0	0
	D.	0.3	0.3	0.3 NNE	0	0	0	0	0	0	0	0	2	5	0	0
1964.	F.	1.4	0.3	0.7 NE	0	0	0	0	0	0	1	2	0	0	0	0
	A.	1.5	0.8	1.1 WNW	0	2	0	4	0	0	3	8	0	0	0	0
	My.	1.3	0.3	0.6 NNE	0	4	2	10	1	4	1	8	1	1	10	9
	Jn.	4	0.8	1.8 NNW	1	0	2	8	1	1	25	46	5	1	8	4
	Jy.	1.5	0.1	0.8 NW	0	0	0	0	3	4	20	30	8	8	5	5
	Ag.	2.5	0.3	1.0 NNW	0	0	1	5	0	0	35	37	7	6	0	0
	S.	3.6	0.1	1.7 SE-SW	2	11	0	0	71	146	0	0	10	13	2	1

associated with sunny periods and high temperatures. Low temperatures did not appear to affect the few imagines available in winter, *Chaetopteryx villosa* being taken at —5.0° C in December.

As the entrances to the trap faced north and south, downstream-moving imagines were taken in the north end whilst the south end took upstream-moving imagines. The Plecoptera and Ephemeroptera gave similar results, large numbers of both sexes moving downstream with predominantly downstream winds, and exactly the opposite occurring with upstream winds (Table 9). Both situations were seen in October, the wind blowing downstream for half the sampling time and upstream for the other period, with corresponding differences in the catches e.g. for Ephemeroptera, the ratio downstream to upstream-moving insects was 53 : 1 for the first period (wind from N. W.) and 1 : 25 for the second period (wind from S. W.). There appeared to be no definite upstream migration of imagines of Plecoptera and Ephemeroptera, their movements being determined by the direction of the wind. Recorded observations of upstream flight in Ephemeroptera (ULMER, 1927; SCHÖNEMUND, 1930; SAWYER, 1950; HARRIS, 1952) were probably made when the wind was in that direction, this situation occurring in the Walla Brook for 5 months out of 16.

Movements of the imagines of Trichoptera chiefly occurred at night and the effect of wind was not so obvious for 4 samples. In 3 months the downstream winds were strong at night and movements of Trichoptera were predominantly downstream, but for the four exceptions (October, December 1963, July, August 1964) the downstream winds were weak at night (0.3 m./sec. or less) and the imagines moved upstream (Table 9). It was not possible to explain these movements against weak downstream winds, but they support some of the observations of Roos (1957).

Roos found that 70—80 % of the females of lotic insects flew in an upstream direction, and he suggested that down-valley winds were the principal stimulus, as these winds occur in steep-sided valleys in the late evening and night (GEIGER, 1950). As the Walla Brook flows through open moorland, the geographical features necessary for down-valley winds are absent and the wind can come from any direction. The flight of the imagines was usually in whatever direction the wind was blowing. BRINDLE (1957) recorded similar observations for several species of Trichoptera.

As emerging adults were frequently seen near the source of the stream, full-grown nymphs and pupae must have been present. Both this observation and those on drift indicated that there was no extensive depopulation of the upper reaches of the Walla Brook, and therefore a "Colonisation Cycle" was unnecessary. Upstream migration of the aquatic stages may compensate for the small number of animals displaced downstream by drifting. These upstream movements have been recorded for ecdyonurid nymphs (HARKER, 1953 a; MACAN, 1957) and *Gammarus* (MINKLEY, 1964), but were not studied in the Walla Brook.

4.4. Laboratory experiments

It was hoped that these experiments would help to explain why aquatic invertebrates drift in lotic systems. The following members of the drift were used in the waterfall tank: *Protonemura meyeri, Amphinemura sulcicollis, Isoperla grammatica, Chloroperla torrentium, Leuctra inermis, L. hippopus, Baetis* spp., *Helmis maugei, Rhyacophila dorsalis, R. munda, Hydropsyche instabilis* and small larvae of Limnephilidae. Conditions in the tank were such that any detached animal was washed over the waterfall and caught in the net.

Experiments 1 and 2 showed that the daily fluctuations obtained in the field could also be obtained in the laboratory, and that the fluctuations were definitely correlated with changes in light intensity (ELLIOTT, 1965 a). In these experiments a maximum of 13—14 % of the available animals was removed in 3 hours from 360 l. of water. As the tank held 5 l., the maximum proportion of detached animals in the tank at any instant in time was about 0.2 %, this figure being comparable to those obtained in the field.

Experiments 1 and 2 did not indicate how light intensity was affecting the behaviour of the invertebrates and therefore further experiments

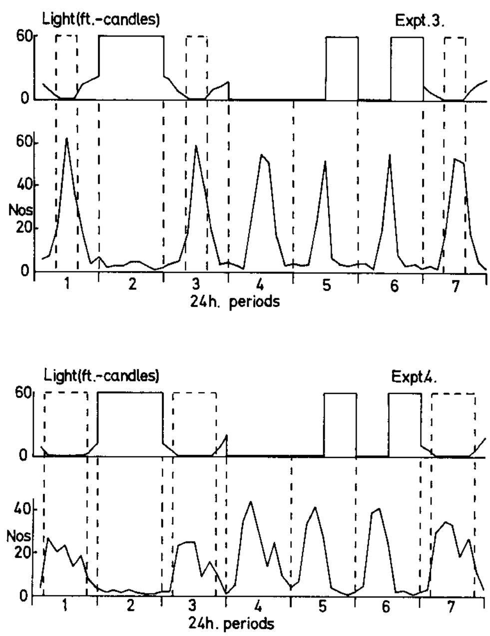

Fig. 12. Effect of modification of light over 7 days — experiment 3 in July 1964 and experiment 4 in December 1964.

were performed. Both experiments 3 and 4 were over seven periods of 24 hours, normal runs being in periods 1, 3 and 7 (Fig. 12). An artificial light was used during period 2 and the last half of periods 5 and 6, whilst the tank was covered for period 4 and the first half of periods 5 and 6. No small limnephilid larvae were used in experiment 3 but nymphs of *Ephemerella ignita* were added, and ecdyonurids were added in experiment 4. The length of the night differed in the two experiments, and was 8 hours in experiment 3 (July 1964), 16 hours in experiment 4 (December 1964). In the normal runs the number of detached animals increased at night, with one peak in the shorter nights of experiment 3 and at least two peaks in the longer nights of experiment 4. The effect of artificial light was to suppress the normal increase in numbers at night, even when used from 0 h. onwards in periods 5 and 6. Covering the tank seemed to have no effect, the pattern being identical to that of a normal run, complete with second peak in December.

In experiment 5 (May 1965), after a normal run the tank was covered for 3 days. The pattern of the normal run continued over the 3 days with no fall-off in numbers. This was followed by continuous illumination for 4 days, which suppressed the normal nocturnal pattern, this being re-established in the normal run on the ninth day.

In experiments 1—5, the animals washed over were always returned to the upper tank and so the effect of removal was not known. Experiment 5 was therefore continued for a further 7 days, the net being emptied at mid-day and the catch removed. In spite of the daily decrease in the number of animals in the tank, the proportion washed over was about 30 % for each of periods 1 to 3 and about 20 % for each of periods 4 and 5

Table 10. Expt. 5 continued. Removal of animals.

Periods —	Number removed after 24 hour period							Nr.
	1	2	3	4	5	6	7	left in tank
Protonemura	17	12	12	6	2	1		
Chloroperla	6	2	2					1
Isoperla	28	25	16	6	4	1	1	5
Limnephilidae								
small	10	10	6	9	1	1		9
large	3	1		1				32+8 p.
Hydropsyche	11	8	5	2	2			5
Polycentropus	8	6	7	1	1			10
Rhyacophila		1	1					3
Helmidae A.	42	35	10	4	6		1	1
Helmidae L.	10	8	5	2	4	3	1	3
Oxyethira	1							
Total/24. h.	**136**	**108**	**64**	**31**	**20**	**6**	**3**	**77**
% removed	31 %	35 %	32 %	23 %	19 %	7 %	4 %	

(Table 10). After period 5, only a small proportion of the available animals was washed over and the animals left in the tank were chiefly stone-cased and net-spinning Trichoptera.

In all the tank experiments, temperature was kept fairly constant (within 1° C) and therefore light intensity was the major variable. It was first thought that a decrease in light intensity at night brought about a corresponding decrease in the negative phototactic behaviour of the aquatic insects which form the drift. Although this hypothesis explained why artifical light suppressed the normal nocturnal increases in the number of detached animals, it did not explain why continuous darkness failed to increase the number of detached animals, nor why some positive phototactic animals (*Simulium* spp.) were present in the drift.

In the next section an attempt will be made to explain this incongruity.

5. Discussion

Müller (1963 b) stated "that the drift of organisms in a flowing body of water is not the result of their being passively carried along but rather constitutes a periodic behaviour pattern (change in activity) on the part of the animals". Exactly the opposite conclusions have been drawn from the present study. If drifting is an active process, a large proportion of the benthos would be in the drift at any instant in time and this was not the case either in the Walla Brook or in a mountain stream in Norway. The detached animals were in the drift for a short period of time and travelled only a short distance if conditions allowed a quick return to the benthos. This was best seen in the runs, with aquatic plants providing a natural sieve for the detached animals. The runs also served as a check to drift washed down from the riffles and only in the latter were the detached animals probably carried a long distance. It is therefore concluded that the animals in the drift are passively carried along and that the number of detached animals passing a sampling point in 24 hours depends upon the amount of water flowing past that point.

Variations in the density of animals in the drift suggest that the availability of the benthos for detachment changes with the time of year and the time of day. This availability will depend on the behaviour of the aquatic invertebrates. A strong negative phototaxis and a strong thigmotaxis have been observed in *Heptagenia interpunctata* (Wodsedalek, 1911, 1912), *Ecdyonurus forcipula* (Gros, 1923), *Leptophlebia, Baetis, Heptagenia* (Berner, 1959), *Baetis rhodani, Dinocras cephalotes* (Scherer, 1962), and *Paraleptophlebia* (Chapman and Demory, 1963). These taxes have been used for sorting samples (Britt, 1955). A strong positive phototaxis has been demonstrated in *Odagmia ornata* (Scherer, 1962) and this is probably true of all larvae of Simuliidae. Nearly all the species used in the waterfall tank showed a strong negative phototaxis, the exception being nymphs of *Rhithrogena semicolorata* which often remained motionless on the tops of stones in the daytime. All species in the tank showed a strong positive thigmotaxis, but if the flow of water ceased, the taxis was soon reversed and nymphs were seen swimming in the tank. Therefore most of the benthos in lotic systems is under the stones during the daytime and the aquatic insects never actively detach from the bottom, except when emerging.

The activity of the benthos will also affect its availability for detachment. Moon (1940) showed that the bottom fauna of lakes and rivers moved freely over the substratum and colonised bare areas. He recorded these as random movements and suggested that the animals were searching for food, as did Neave (1930) in explaining the annual migration of nymphs of *Blasturus cupidus* (= *Leptophlebia cupida*). Moon also found that the bottom fauna was more active at night. Harker (1953 a) found that upstream migration of *Ecdyonurus torrentis* occurred at night, and that in the laboratory the nymphs showed an inherent diurnal rhythm of activity with maximum activity at night (Harker 1953 b). Using an underwater light trap in a lake, Pieczynski (1964) took more Ephemeroptera nymphs at night than during the day, and Mundie (1959) caught Ephemeroptera nymphs in plankton nets which were towed during the night near the surface of a lake.

Associated with this increased activity at night is the presence of more animals on the tops of stones as the negative phototaxis no longer operates. Hubault (1927) observed ecdyonurids, *Baetis* spp., *Nemoura* spp., *Leuctra* spp., and *Taeniopteryx seticornis* on the tops of stones at night and suggested that these animals exhibited a definite "Rhythme Nycthéméral", being under the stones during the day and on the tops of stones at night. He also saw ecdyonurids slipping from the top to the underside of stones when he shone a torch on to them at night, and this observation has been frequently confirmed during the present study. In the waterfall tank the difference in behaviour was very evident, many animals being seen on the tops of stones and on the sides of the tank when suddenly illuminated at night, whilst only a few individuals were visible during the day. It is thought that the daily fluctuations in the drift numbers are a reflection of the numbers of animals moving across the tops of stones, the peaks in the drift coinciding with peaks in the activity pattern of the bottom fauna. There is some evidence which suggests that the nocturnal movements on to the tops of stones are associated with foraging. Hynes (1941) suggested that some Plecoptera move on to the tops of stones at night in order to feed on the algae, which were not abundant in the dark on the undersides. Chapman and Demory (1963) clearly showed that *Paraleptophlebia* sp. fed on detritus under rocks in the daytime, but moved onto the upper surface at night and fed on the algae. The competition for food would be greatest between full-grown nymphs and the foraging of both herbivores and carnivores would have to cover a larger area, including the more exposed parts of stones and aquatic plants. This would help to explain why these fullgrown nymphs were particularly vulnerable to being swept away, and therefore why the density of animals in the drift increased at certain times of the year.

From this discussion, the following tentative hypothesis is formulated. The bottom fauna shows an inherent activity pattern with greater activity at night and maximum activity just after sunset. As a result of this nocturnal activity the animals forage over both the upper and lower surfaces of stones, the negative phototaxis no longer operating in the dark. The density of detached animals in the drift reflects both the number of animals moving over the exposed parts of stones and aquatic plants, and the extent of competition between these animals for food and space. A very small proportion of the total bottom fauna is swept away, and this indicates that the animals lose their grip or are jostled by their fellows. The detached animals spend only a short time in the drift and re-attach as soon as possible.

The laboratory experiments did not contradict this hypothesis. When the tank was covered, the animals were detached in the normal night period because they were only active at this time of day and their inherent activity pattern persisted for the duration of the experiment. Although active at night, most of the animals were always negatively phototactic and therefore an artificial light kept them under the stones in the normal night period.

6. Appendix

Occurrence and list of fauna

Occurrence indicated at sites 1, 2, 3, A, B, and in the drift (D)

Plecoptera
Brachyptera risi (MORTON). 2, D.
Protonemura meyeri (PICTET). 1, 2, 3, A, B, D.
Amphinemura sulcicollis (STEPHENS). 1, 2, A. B, D.
Nemoura cambrica (STEPHENS). 1, 2, D.
Leuctra inermis (KEMPNY). 1, 2, 3, A, D.
Leuctra hippopus (KEMPNY). 1, 2, D.
Leuctra fusca (LINNÉ). D.
Perlodes microcephala (PICTET). 1, 2, A, D.
Isoperla grammatica (PODA). 1, 2, 3, D.
Dinocras cephalotes (CURTIS). 2, B, D.
Ephemeroptera
Ephemerella ignita (PODA). 1, 2, 3, D.
Ecdyonurus venosus (FABR.). 1, 2, 3, B, D.
Rhithrogena semicolorata (CURT.). 2, D.
Leptophlebia vespertina (L.) 2, D.
Paraleptophlebia submarginata (STEPH.). 2, D.
Baetis niger (L.). 1, 2, 3, B, D.

Baetis pumilus (BURM.). 2, D.
Baetis scambus (ETN.). 1, 2, 3, A, B. D.
Baetis rhodani PICT.). 1, 2, 3, A, B, D.
Megaloptera
Sialis lutaria (L.). 2, 3, D.
Trichoptera
Rhyacophila dorsalis (CURT.), 1, 2, 3, A, B, D.
Rhyacophila munda (MCLACH.). 1, 2, 3, A, B, D.
Hydropsyche instabilis (CURT.). 1, 2, 3, A, B, D.
Plectrocnemia conspersa (CURT.). 1, 2, D.
Polycentropus flavomaculatus (PICT.). 1, 2, 3, B, D.
Polycentropus kingi (MCLACH.). 1, 2, 3, D.
Sericostoma personatum (SPENCE). 1, 2, 3, B, D.
Silo pallipes (FABR.). 1, 2, 3, D.
Lepidostoma hirtum (FABR.). 1, 3, D.
Odontocerum albicorne (Scop.). D.
Hydroptila sp. (DALMAN). 1, D.
Oxyethira sagittifera (RIS.). 1, 2, 3, A, D.
Anabolia nervosa (CURT.). 1, 2, 3, D.
Limnephilidae — unknown species. 1, 2, 3, A, B, D.
Species taken in drift as emerging adults —
Chaetopteryx villosa (FABR.).
Drusus annulatus (STEPH.).
Limnephilus extricatus (MCLACH.).
Halesus radiatus (CURT.).
Coleoptera
Helmis maugei (BEDEL). 1, 2, 3, B, D.
Limnius tuberculatus (MÜLL.). 1, 2, 3, A, B, D.
Latelmis volkmari (PZ.). 1, 2, 3, D.
Deronectes latus (STEPHENS). 1, D.
Oreodytes rivalis (GYLLENHAL). 1, 2, D.
Hydroporini larvae 1, 2, 3, D.
Orectochilus villosus (MÜLLER). 2, D.
Hydraena riparia KUGELAN). 1, 2, 3, B, D.
Diptera
Dicranota bimaculata (SCHUMMEL). 1, 2, 3, A, B, D.
Limnophila sp. 1, 2, B, D.
G. Pentaneura (PHILIPPI). 1, 2, 3, A, B, D.
Other Chironomidae 1, 2, 3, A, B, D.
Palpomyia flavipes (MEIGEN). 3, 2, D.
Dixa sp. (MEIGAN). B, D.
Simulium laetipes (MEIGAN). 1, 2, 3, A, B, D.
Simulium spp. 1, 2, 3, A, B, D.
Platyhelminthes
Tricladida. 2, 3.
Annelida
Oligochaeta. 1, 2, 3, B, D.
Arachnida
Hydrachnellae. 1, 2, 3, D.
Mollusca

Ancylastrum fluviatile (MÜLL.). 1, 2, 3, D.

The following were taken occasionally in the drift samples alone: —

Odonata.

Agrion splendens (HARRIS). *Pyrrhosoma nymphula* (SULZER).

Cordulegaster boltonii (DONOVAN).

Trichoptera.

Philopotamidae.

Hemiptera

Corixa sp.

Coleoptera

Helodes sp. larva. *Gyrinus natator* (L.). *Haliplus lineatocollis* (MARSHAM).

Dryops. sp. *Deronectes 12-pustulatus* (OLIVER). *Oredytes septentrionalis* (GYLLENHAL).

Hydroporus erythrocephalus (L.). *Agabus bipustulatus* (L.).

Dytiscus marginalis (L.). Hydrophilid larvae. *Hydrobius fuscipes* (L.).

Berosus luridus (L.). *Helophorus brevipalpis* (BEDEL.).

Limnebius truncatellus (THUMBERG).

Diptera

Tubifera (= Eristalis) sp. larva. *Tipula lateralis* (MEIGAN) larva.

Coelenterata

Hydra sp.

Invertebrate drift of terrestrial origin

Very few invertebrates in this category have been identified to species.

The following were frequently taken in the drift samples: —

Hemiptera — Heteroptera

Velia caprai (TAMANINI). (Included here as it is not a strict aquatic species.)

Collembola

Hemiptera

Jassidae, Psyllidae, Aphididae.

Diptera

Tipulidae, Bibionidae, Tabanidae, Empidae, Syrphidae, Ephydridae, Calliphoridae, Muscidae.

Hymenoptera

Ichneumonidae, Braconidae, Cynipidae, Chalcidoida, Formicoidea, Vespidae, Sphecidae, Apidae.

Coleoptera

Carabidae, Staphylinidae, Coccinellidae, Cerambycidae, Chrysomelidae, Curculionidae.

The following were taken occasionally in the drift samples: —

Psocoptera, Thysanoptera, Lepidoptera.

Spent female imagines of Plecoptera, Ephemeroptera, Trichoptera.

Isopoda — *Oniscus asellus* (L.).

Myriapoda — Chilopoda.
Diplopoda — *Cylindrojulus punctatus* (LEACH).

Arachnida — Araneida.
Acarina.
Opiliones — *Leiobunum blackwalli* (MEADE).
Pseudoscorpionidae — *Neobisium muscorum* (LEACH).

Mollusca: Pulmonata — *Arion circumscriptus* (JOHNSTON).

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Sir Frederick S. Russell and Dr. A. J. Southward for their advice on the design of drift samplers. — Dr. J. Grindley for his help in the calibration of flowmeters. — Miss R. M. Badcock, Dr. J. M. Edington and Dr. T. T. Macan for checking some of the Ephemeroptera, Trichoptera and Coleoptera. — My colleague Dr. M. R. Rudge for his frequent assistance in the field, often under difficult conditions. — Dr. T. T. Macan for all his help in the preparation of this paper. — The work was supported by a grant from the Development Commission.

8. Summary

1. Monthly samples of invertebrate drift and benthos were taken at different sites in the Walla Brook over a period of 17 months.

2. A shovel sampler (Macan, 1958) was used for the bottom samples and both surface nets and modified plankton samplers for the drift samples. The drift samplers are described.

3. Aquatic, emerging, and terestrial invertebrates were present in the drift during all seasons of the year.

4. Aquatic invertebrates were the most important component of the drift and nearly all species taken in the bottom samples were also taken in the drift, the exceptions being Tricladida and Trichoptera larvae with stony cases.

5. The density of aquatic invertebrates in the drift appears to be fairly constant for the same months, and at both single and different sites for a short period of time. Under these conditions the numbers of animals in 24-hour drift samples are a reflection of the different amounts of water passing the sampling points.

6. The density of aquatic invertebrates in the drift varies in different months and at different times of the day.

7. In all months, more aquatic invertebrates were taken in the drift at night than in the day, the greatest numbers being in the three hour sample after sunset. The daily fluctuations were related to fluctuations in light intensity. The Hydrachnellae were the only exceptions to the general pattern and were taken in greater numbers in the day samples.

8. Only a small proportion of the benthos (under 0.01 %) was in the drift at any instant in time. The detached animals were in the drift for a short period of time and travelled only a short distance if conditions allowed a quick return to the benthos. Aquatic plants in the runs provided a natural sieve for the detached animals and the runs served as a check to drift washed down from the riffles.

9. The detached animals settling in the deep pools soon left, and large numbers of invertebrates drifted out of a deep pool in 24 hours.

10. There was no definite upstream flight of the female imagines and it was concluded that there was no extensive depopulation of the upper reaches of the Walla Brook.

11. The daily fluctuations in drift were also obtained in laboratory experiments. Artificial light suppressed the normal increase in numbers at night. Covering the tank seemed to have no effect, the pattern being identical to that of a normal run.

12. From the work on the Walla Brook and the observations of other workers, it is concluded that most aquatic invertebrates are negatively phototactic, po-

sitively thigmotactic, and more active at night. The nocturnal movements are probably associated with foraging and occur on both the upper and lower surfaces of stones. It is suggested that the density of detached animals in the drift reflects both the number of animals moving over the exposed parts of stones and aquatic plants, and the extent of the competition between these animals for food and space.

9. Zusammenfassung

Über einen Zeitraum von 17 Monaten wurden die Invertebratendrift und das Benthos untersucht. Für die Bodenfänge wurde ein „shovel sampler" nach MACAN (1958) benutzt, für die Driftfänge dienten ein Oberflächennetz (Plate 1) und modifizierte Planktonnetze (Plate 1).

Zu allen Jahreszeiten waren in der Drift aquatische, epipneustische und terrestische Invertebraten vorhanden, erstere weit überwiegend. Nahezu alle Benthos-Arten waren in den Driftfängen vertreten (Ausnahmen: Turbellarien und Trichopterenlarven mit Sandgehäuse). Die Häufigkeit der aquatischen Invertebraten in der Drift scheint für die einzelnen Monate jeweils ziemlich konstant zu sein. Die Tierdichte ist in einem 24-h-Driftfang abhängig von der Wassermenge, die die Probenstelle passiert, und ändert sich sowohl jahres- als auch tageszeitlich. Während des ganzen Jahres wurden in der Drift nachts mehr aquatische Wirbellose (Ausnahme: Hydrachnellae) festgestellt als tagsüber. Ihre größte Zahl erreichten sie in den Fängen 3 h nach Sonnenuntergang. Die tageszeitlichen Fluktuationen waren abhängig von den jeweiligen Lichtintensitäten.

In der Drift befand sich stets nur ein kleiner Teil der Benthosorganismen (weniger als 0,01 %). Die vom Substrat gelösten Tiere wurden nur über kurze Strecken verdriftet, um dann ziemlich schnell wieder auf den Boden zurückzugelangen. Die Wasserpflanzen bilden im fließenden Wasser natürliche Filter für die Driftorganismen, so daß hier die in den Bachschnellen abgewaschenen Tiere aufgefangen werden. Jedoch werden die Strudellöcher bald wieder verlassen, wie sich innerhalb 24 h feststellen ließ.

Ein spezifisch bachaufwärts gerichteter Flug der weiblichen Imagines wurde in keinem Fall festgestellt. Daraus wurde geschlossen, daß eine ausgeprägte Entvölkerung der oberen Bezirke des Walla Brook überhaupt nicht erfolgt.

Die tageszeitlichen Fluktuationen der Drift traten auch in Laborversuchen auf. Künstliches Licht unterdrückte die sonst in der Nacht auftretende Zunahme der Zahl an driftenden Tieren. Das Verdunkeln der Versuchsstrecke am Tage scheint keinen entsprechenden Einfluß auszuüben, wie auch aus den Beobachtungen am natürlichen Bach zu schließen ist. Aufgrund der Beobachtungen am Walla Brook und Literaturangaben wird angenommen, daß die Mehrzahl der aquatischen Invertebraten negativ phototaktisch, dabei positiv thigmotaktisch ist und nachts eine größere Aktivität entwickelt. Die nächtlichen Ortsveränderungen hängen wahrscheinlich mit der Nahrungsaufnahme zusammen und finden auf und unter den Steinen statt. Es wird angenommen, daß die Zahl der Tiere in der Drift abhängig ist von der Zahl der Tiere, die sich auf den exponierten Teilen der Steine und Wasserpflanzen bewegen sowie von der Konkurrenz zwischen diesen Tieren in bezug auf Nahrung und Raum.

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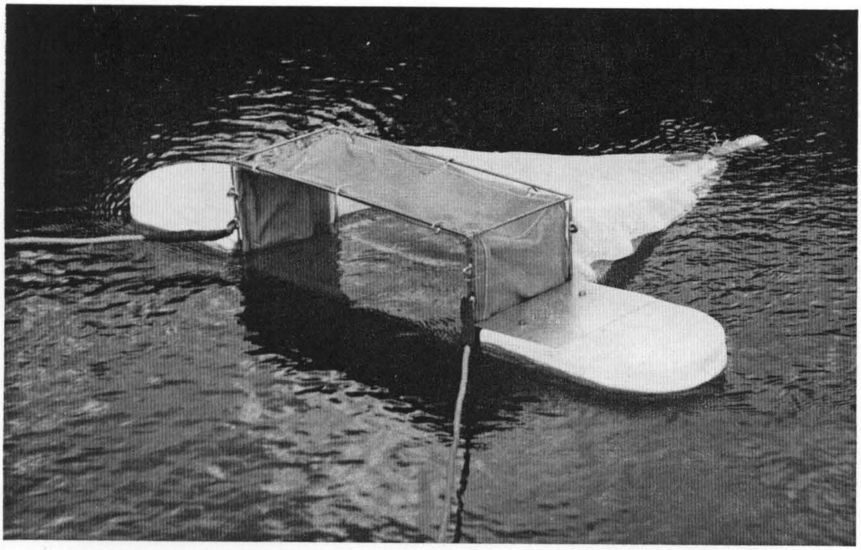

Fig. 1. Surface net.

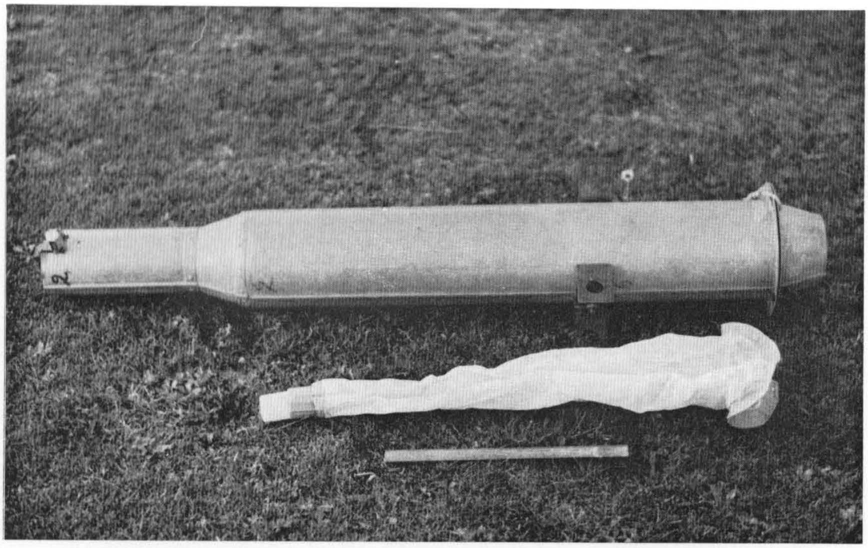

Fig. 2. Modified plankton sampler with net removed.

J. M. Elliott: Invertebrate drift in a Dartmoor stream.