

# MOVEMENT OF IMMATURE AQUATIC INSECTS IN A LOTIC HABITAT

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## Abstract

The movement of immature insects up down and across Salem Creek, Ontario, was measured with traps and nets at two week intervals from January to December 1977. Drift of most taxa was more strongly correlated with water velocity from August to December than it was over the whole year. That of *Baetis*, however, was not correlated with water velocity and it was significantly greater at the side of the stream than at the centre from May to July. Upstream movement, as measured in three different ways, was small compared with drift, being only 2.1, 7.3 and 15.2 percent respectively.

Upstream and across stream movements were not consistently different from one another, changes in their intensity apparently merely representing changes in numbers and behaviour of the animals. It is concluded therefore that upstream movement is only random movement.

Colonization of empty sediment in trays on and above the substratum confirmed that most reoccupation of denuded areas is by drift. This supports the finding that drift is far greater than random wandering of the insects.

## Introduction

The downstream drift of invertebrates is a normal feature of running water (references in Bishop & Hynes 1969a; Waters, 1969, 1972; Hynes 1970a, b) and compensatory adaptations are the upstream migration of larvae and flying adults. The active movement upstream of larval forms was found to be 5 to 30% of the drift by Bishop & Hynes (1969b), Brusven (1970), and Elliott (1971b) and it may serve to recolonize upstream stretches, Bishop & Hynes (1969b) showed that there was greater movement near the banks than at midstream during the winter, and at midstream during the summer. They also showed that the biomass moving into their traps increased in artificial darkness. Elliott (1971b) went further, to demonstrate a definite diel periodicity in upstream movement, with a distinct nocturnal peak for *Baetis rhodani* and *Gammarus pulex*. However, unlike Bishop & Hynes (1969b), he did

not observe seasonal differences in movement between the banks and midstream.

That upstream movement is an active process was clearly demonstrated by Hultin *et al.* (1969) as their animals had to ascend a trap 4 m long with a slope of 1 : 4. Their results also agree with those of Müller (1969) and Ulfstrand (1968) that the movements of many species occur only before pupation or emergence. Few studies have measured the distance or rate of travel upstream. Neave (1930) reported that *Leptophlebia cupida* nymphs travelled 1.6 km at a rate of 200 m per day, and similar observations were made by Hayden & Clifford (1974) on this species in Alberta, and by Olsson & Söderstrom (1978) on *Paramelitus chelifera* in Sweden. *Baetis pumilus* has been inferred to have travelled 2 km upstream into the tributaries of the River Allier after an exceptional drought (Verrier, 1953). Ball & Hooper (1963) investigated the addition of <sup>32</sup>P in bacteria to a stream, and found that 42 days later it occurred in invertebrates 300 yards upstream. In contrast, Bishop & Bishop (1968) found no upstream dispersal of <sup>32</sup>P labelled insects.

Other work also provides evidence of upstream movement. For example, Luedtke & Brusven (1976) showed that sandy reaches impeded the upstream movements of lotic insects, except for heavy cased caddisflies, *Dicosmoecus* sp. They also observed limited upstream migration in the laboratory, as have Mackay & Kalf (1973) and Mackay (1977). Mackay also reported upstream movements of larger *Pycnopsyche* larvae in the field when discharge was low, and Gore (1977) observed the invasion of a previously cold reach below a reservoir by insects from the warmer water downstream.

In a study of the colonization mechanisms of stream benthos Williams & Hynes (1976) found that 17.0% was by upstream movements, 38.7% by drift, 26.4% by air and 17.9% by movement from within the substrate. They concluded that all four directions are important in repopulat-

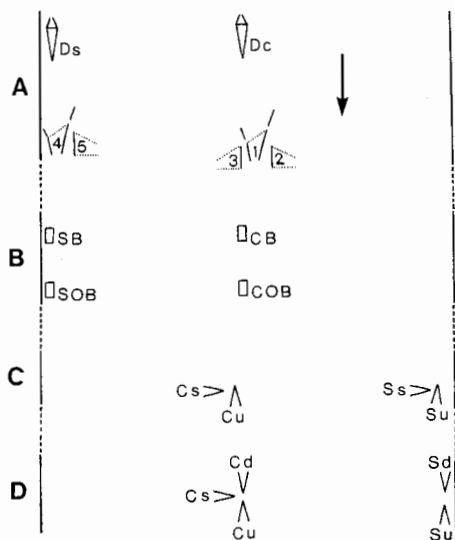


Fig. 1. The arrangement of the traps in the stream. A) the 72-hour study, B) the colonization trays, C) the 24-hour study, D) the buried nets study. Ds and Dc = drift centre and side. 1-5 = traps for upstream and lateral movement. SB and CB = trays side and centre, and SOB and COB = trays off the bottom. In C) and D) S and C denote side and centre, and s lateral movement, u upstream and d downstream (drift) movement.

ing denuded areas, and that, since many groups have preferred directions of movement, the establishment of distinct faunal assemblages could occur if any direction was excluded. In a study of the colonization of introduced substrate Townsend & Hildrew (1976) found that 82% was by drift; the remaining 18% was attributed to upstream and/or downstream movements on the bottom.

In recent years, drift has attracted much attention but active movement in other directions appears to have been overlooked (Hynes, 1970a). The purpose of this investigation was to assess further the significance of the upstream and other movements of immature aquatic insects.

### The study area

Salem Creek, a tributary of Canagagigue Creek, is a shallow, agriculturally enriched, hardwater stream 5 km east of Elmira, Ontario. It is about 7.5 km long and originates in a cedar swamp. The drainage basin is used primarily for cattle, with maize and hay as the principal crops, and only about 10% remains forested. The study site was in a forested area about 1.5 km above the confluence and 100 m downstream of pasture. A 15 m long, 6.7 m wide, and

shallow (0.35 m) riffle was used for the 72 hour random movement experiment. The others were done on riffles further downstream.

The substrate in the riffles was cobble, and boulders with sand and gravel. It was heavily colonized by diatoms during the colder ice-free months and by *Cladophora* in the warmer months. Sand accumulated during periods of low flow, but it and the *Cladophora* were frequently washed away by spates. Emergent vegetation was restricted to back-waters, and white cedar, *Thuja occidentalis*, and sugar maple, *Acer saccharum*, were the major trees bordering the stream, with some *Tilia americana* and *Crataegus*.

### Methods

Several independent series of samples were collected.

#### Random Movement and Drift, 72-hour study

Sampling extended from January to December 1977. Movement was monitored in four directions, up, down, and across the stream, at midstream and near the bank (Fig. 1a).

Downstream movements were monitored using drift traps, adapted from those of Dance *et al.* (1979), at midstream and near the bank. They sampled a narrow column of water from bed to surface which was led into a Nitex net of 505  $\mu\text{m}$  mesh which was 15 cm wide and tapered for 2 m.

The traps (Fig. 1a) for monitoring up and across stream movements consisted of one or two sides and a bottom of aluminum sheet with a 505  $\mu\text{m}$  Nitex screen upstream front, attached at an angle. The angle helped prevent clogging, while the rigidity of the structure allowed cleaning of the screens. Traps 2, 3 and 5 (across the stream) also had a second screen attached straight across the downstream end.

All the traps were 51 cm high, and thus emergent at all times, and all had an opening 22 cm wide. Upstream ones (1 and 4) had sides 64 cm and 36 cm long, with an upstream screen 51 cm wide. The others (2, 3 and 5) had one 46 cm long solid side with screens 46 and 41 cm long on the upstream and downstream sides.

Movable aluminum wings attached to the upstream traps, along with their tapering shape, allowed the adjustment of the flow so that the water left the traps at approximately the same velocity as upstream. No wings were attached to traps 2, 3 and 5 as this would have increased the outflow through the side entrance. Each trap thus monitored movement in one direction through a 22 cm wide

column of water. Traps Dc (drift centre), 1 (up), 2 and 3 (across) monitored movement in four directions at mid-stream while traps Ds (drift side), 4 (up) and 5 (across) monitored movement in three directions along the bank (Fig. 1a). Removal of the drift traps during the months of ice cover presented problems. On these occasions they were left in for longer periods and the results were calculated for a three day period.

The screens of traps 1 to 5 were cleaned each day in the morning and early evening during the 72 hour sampling period during the ice-free months, and more often if necessary because of high water. The traps were removed after 72 hours, and samples were collected at two week intervals throughout the year except during the spring runoff when they were taken weekly.

A bucket full of clean substrate, sand, gravel and stones up to 15 cm in length, was placed on the bottom of each trap making a layer about 5 cm deep. This had been collected at the site and dried for a month, and then cleaned of loose organic material. Upon removal from the stream the substrate was transferred to buckets and the organisms were removed by flotation with a saturated solution of calcium chloride, using a 505  $\mu\text{m}$  sieve, care being taken not to overlook stonecased trichopterans and molluscs. The floated material was preserved in 70% ethanol and the animals were picked out under a dissecting microscope. The substrate was rinsed to remove the salt and used again in the same trap.

The maximum and minimum water temperature was recorded when the traps were placed and removed, and water velocity was measured on each sampling date at the entrance of both drift samplers and above, in (traps 2, 3 and 5), and below (trap 1 and 4) the random movement traps. A portable electronic meter (Edington & Molyneux, 1960) was used until April, and a Pitot tube was used for later readings.

Analysis of the data for this and the other studies was by the Chi-square test. Values for traps Ds and Dc (mouth widths 1.0 and 1.3 cm) were multiplied by 22 and 16.9, respectively to allow comparison with values for traps 1 to 5 (mouth width 22 cm).

#### *Random Movement, 24 Hours*

A comparison of the pattern and quantity of movement during a shorter time period, and by another method, was desirable because the number of animals collected in the 72-hour study was low. Drift nets (20 x 20 cm mouth opening; 84 cm in length; 505  $\mu\text{m}$  netting) were used to monitor movement over the substrate, up and across the stream, at

midstream and near the bank (Fig. 1c) from May 26 to December 19 for 24 hours at 2 week intervals. A 3 to 5 cm layer of gravel and stones inside the nets provided a substrate for colonization, and together with a stake through the mouth frame it held the nets in position. At times of high discharge the nets were further secured by ropes. Values for downstream movement were obtained by expressing the data collected in the 72 hour drift monitors as values for 24 hours; values for traps Ds and Dc (mouth widths 1.0 and 1.3 cm) were multiplied by 20 and 15.4, respectively to allow comparison with the 24 hour traps (mouth width 20 cm).

#### *Random Movement, Buried Nets*

Elliott (1971b) found substantial upstream movements into nets buried to a depth of 12 cm in the substrate. On July 18 and August 29 similar studies were carried out in Salem Creek. Five of the nets used in the 24 hour study, were buried so that about 17 cm of the mouth was below the substrate and 3 cm above. Hence, animals could enter by moving either through or over the substrate. The nets were filled with substrate dug from this site and dried on the stream bank for one week. Movement up, down and across the stream at midstream, and up and down the stream near the bank was monitored (Fig. 1d). The other methods described above could, of course, measure movement through the substrate only to a maximum depth of 5 cm.

#### *Colonization of Trays*

Since the design of a trap may influence its catch a control was required for the random movement studies. Two trays, 35.6 cm x 17.5 cm x 2.5 cm, were filled with clean substrate and buried flush with the stream bottom, one at midstream the other near the bank. Two other trays were placed in similar positions 3 m downstream but suspended 5 cm off the bottom on metal stands (Fig. 1b). The bottom trays could be colonized by drift as well as by movement over the substrate. This was taken to represent 100% colonization. The suspended trays could be colonized only by drift, as climbing and swimming are considered insignificant. Using this technique, Townsend & Hildrew (1976) showed that movement over the substrate accounted for only 18% of the colonization in their study. In Salem Creek any differences in colonization by movement over the bottom seen in the trays, but not in the random movement traps, would indicate something that was not detected by the traps.

## Results and observations

### Physical Conditions

The temperature rose rapidly from near zero in mid-March to 10°C by mid-April, and then more slowly to 21°C in early August. It fell fairly steadily to 7°C by early December and to zero by the end of that month.

Water velocity showed much fluctuation (Table 2). Maxima occurred during the spring runoff and during a

spate on September 28 (87 cm/sec) when discharge reached nearly bankfull; low values occurred in June, July and August.

The pattern of flow through traps 1 to 5 was observed using fluorescein during the winter and spring. This showed that water passed freely through the screens maintaining currents inside the traps. There was, however, a small eddy near the mouth of trap 2 when it was ice-covered.

Table 1. Total number of insects, other than Chironomidae, collected in the 72-hour study. a = totals only from 28/04 to 19/12. b = nets from 24-hour study substituted for traps 1-5. \* =  $P < 0.05$ , \*\* =  $P < 0.005$ . P values in columns 1 and 4 denote significantly greater upstream than lateral movement; those in 2 and 5 denote significantly greater lateral than upstream movement.

1977	CENTRE				SIDE		
	1↑	2←	3→	Dc↓	4↑	5←	Ds↓
11/01	155**	80	25	42**	12	33**	-
23/01	50	112**	29	32	13	5	-
06/02	8	65**	11	32	27**	9	-
20/02	29	28	13	32	12	20	-
06/03	49	14	54	321	18	11	-
20/03	7	4	22	338	8	11	-
31/03	13	12	24	2282	17**	0	-
14/04	16	3**	39	1014	5	16*	-
28/04	8	10	10	524	4	7	638
12/05	5	11	7	811	10	45**	1342
26/05	9	3	-	3127	1	3	1628
09/06	14	19	19	1132	12	8	2310
23/06	25	35	19	389	14	9	770
07/07	15	6	6	1453	3	18**	1320
21/07	43**	27	13	254	8	28**	990
04/08	26**	14	7	642	14	15	330
18/08	13**	1	0	3110	5	3	374
01/09	15	22	9	372	3	25**	484
15/09	29	15	24	203	9	15	220
28/09	7	-	-	1437	15	11	902
13/10 <sup>b</sup>	2	9	-	575	5	6	88
26/10	1	12**	8	203	5	3	110
09/11	2	2	4	101	6	8	132
23/11	3	5	1	372	5	6	88
07/12	3	6	9	237	8	5	220
19/12	8	4	5	1132	6	7	176
Total	555	519	358	20,167	<sup>a</sup> 133	<sup>a</sup> 222	12,122
% of drift	2.7	2.5	1.7		<sup>a</sup> 1.1	<sup>a</sup> 1.9	

### Drift

The results for this and for most of the other studies considered here, apply only to insect groups other than the Chironomidae, because many of the latter could escape through the mesh sizes used.

Drift was almost always significantly greater ( $P < 0.005$ ) than movement in either of the other directions (Table 1). Only during January and February when difficulties were

experienced with ice, were the drift values lower than at least some of the other catches.

In general, higher drift rates corresponded with increased flow and with periods of emergence, and were greatest from April to September (Tables 1 and 2). Although drift of Ephemeroptera other than *Baetis*, Trichoptera and Elmidae (Table 2) did not show good correlations with water velocity over the whole sampling peri-

Table 2. Drift of several taxa relative to water velocity ( $v$ ) ( $r$  values) and comparisons of that at the centre and the side ( $t$  values). a = throughout the sampling period, b = from 04/08 to 19/12, c = from 12/05 to 21/07. n.s. = not significant, \* =  $P < 0.05$ , \*\* =  $p < 0.01$ .

	v cm s <sup>-1</sup>	CENTRE				SIDE				
		<i>Baetis</i> sp.	Other Ephemeroptera	Trichoptera	Elmidae larvae	v cm s <sup>-1</sup>	<i>Baetis</i> sp.	Other Ephemeroptera	Trichoptera	Elmidae larvae
1977										
20/03	79	68	0	34	0	-	-	-	-	-
31/03	60	135	811	51	862	-	-	-	-	-
14/04	32	355	253	101	237	-	-	-	-	-
28/04	40	186	152	51	34	22	308	286	0	22
12/05	27	389	169	17	34	16	1078	176	0	0
26/05	45	862	84	0	1724	24	1166	154	88	22
09/06	30	693	253	17	68	18	1842	292	0	22
23/06	11	169	169	0	0	8	506	22	22	88
07/07	25	237	33	34	642	11	924	44	110	110
21/07	11	101	17	51	51	8	484	66	132	22
04/08	29	287	186	68	17	12	176	22	44	0
18/08	25	2535	152	207	17	8	242	66	66	0
01/09	25	152	135	17	17	10	198	66	198	0
15/09	28	101	68	17	0	16	22	22	132	0
28/09	87	34	507	541	169	40	286	242	308	88
13/10	66	68	236	220	169	31	0	44	0	0
26/10	31	17	68	95	0	18	22	22	0	0
09/11	25	0	17	51	0	11	22	0	0	0
23/11	40	51	84	101	0	22	22	44	0	0
07/12	40	34	118	34	0	22	0	44	66	0
19/12	47	169	592	152	0	26	44	0	66	0
r values a		-0.203	0.452	0.591	0.182		-0.109	0.382	0.246	0.058
b		-0.280	0.691	0.858	0.872		-0.020	0.598	0.347	0.685
t values a							0.34 <sup>ns</sup>	1.84 <sup>ns</sup>	0.69 <sup>ns</sup>	1.44 <sup>ns</sup>
c							6.04**			

od (correlation coefficient,  $r = 0.452, 0.591$  and  $0.182$  at the centre and  $0.382, 0.246$  and  $0.058$  at the side) stronger correlations were obtained for the period from August to December (Table 2, b line of  $r$ -values). Lower correlations for the whole year may have been caused by the masking affect of behavioral drift during periods of emergence. For example, that for Ephemeroptera, mainly *Ephemerella subvaria*, *Stenonema vicarium*, and *Paraleptophlebia mollis*, increased in spring both under conditions of increased flow and of normal flow (Table 2). Their drift was also more strongly correlated ( $r = 0.691$ ) with water velocity from August to December, with early and half grown stages showing an increase with increased flow rates, i.e. on September 28 and October 13. However, drift of *Baetis*, mainly *B. intercalaris*, *B. vagans* and *B. rusticans*, showed no correlation with water velocity at the centre ( $r = -0.203$ ) or at the side ( $r = -0.109$ ) throughout the year, nor from August to December ( $r = -0.280$  at the centre, and  $-0.020$  at the side). Their drift was significantly greater ( $P < 0.01$ , student's test Table 2) at the side of the stream than the centre from May 12 to July 21, while their highest level of drift, on August 18, occurred during a period of low flow, and comprised both mature and newly hatched nymphs.

#### Random Movement, 72 hour study

The numbers of insects collected in the upstream traps were

low, with usually about twice as many in the trap at mid-stream as at the side (Table 1). Values for upstream movement were not significantly different ( $P < 0.05$ ) from those for across the stream throughout the year, although values for upstream movement were significantly greater ( $P < 0.005$ ) on four occasions at the centre and two at the side. However, across stream movement was also significantly greater ( $P < 0.005$ ) than upstream movement on four occasions at the centre and six at the side (Table 1). Such results can be regarded as random variations in a very variable system.

In total the values for upstream movement were equivalent to only 2.7% of drift at the centre and 1.1% at the side. That of Ephemeroptera, Trichoptera, Simuliidae and Elmidae was equivalent to 1.8, 5.4, 1.0 and 3.5% at the centre and 0.6, 2.0, 3.4 and 6.2% of drift at the side, respectively.

The pattern of movement across the stream showed significantly greater ( $P < 0.05$ ) numbers of insects entering trap 2 at the centre from January to February than trap 3, or 5 at the side (Table 1). This may have been caused by the small eddy of water observed at the mouth of this trap. Indeed, the ice sometimes reached the substrate near the bank, greatly reducing the flow and causing water to move towards midstream.

Although ice formed over all the traps in the winter, the

Table 3. Numbers of insects, other than Chironomidae, collected in the 24-hour study. \* =  $P < 0.05$ , \*\* =  $P < 0.01$ . In column Su a P value denotes a value greater than in Ss.

1977	SIDE			CENTRE		
	Ss→	Su↑	Ds↓	Cs→	Cu↑	Dc↓
26/05	4	23**	493	20	26	948
09/06	30	14	700	42	17	343
23/06	47	44	233	73	62	118
07/07	31	14	400	47	53	440
04/08	20	40*	100	46	37	195
18/08	17	14	113	27	40	942
15/09	5	5	67	20	29	62
28/09	5	3	273	8	8	435
26/10	4	4	33	7	9	62
09/11	3	2	40	1	3	31
23/11	4	10	27	5	6	113
19/12	6	1	53	8	13	343
Total	176	174	2532	304	303	4032
% of drift	7.0	6.9		7.5	7.5	

Table 4. Number of insects, other than Chironomidae, collected in the random movement buried net study.

1977	SIDE			CENTRE			
	Su+	Sd+	Ds+	Cu+	Cd+	Cs+	Dc+
18/07	62	65	900	150	175	95	231
29/08	68	70	440	11	48	31	338
Total	130	135	1340	161	223	126	569
% of drift	9.7	10.1		28.3	39.2	22.1	

flow through them was probably not much reduced, since the screens and entrance remained free, except near the surface and bordering the metal frame. In the warmer months clogging presented a problem during spates, but the numbers collected during low flow, when clogging was not a problem, were generally not much greater than when problems occurred.

#### Random Movement, 24 hours

Upstream movement was similar to that across stream throughout the sampling period, and the totals were almost identical. Only twice was upstream movement significantly greater (Table 3). Drift, however, was always significantly greater ( $P < 0.005$ ) than movement in the other two directions. Upstream movement was equivalent to 7.0% of drift at the side and to 7.5% at the centre. That for mayflies and caddisflies was 6.9 and 3.4%, and 8.1 and 13.3% of drift at the side and centre respectively.

The numbers of insects collected in the upstream and the across stream nets in 24 hours were generally larger than those caught in the other traps in 72 hours (compare Tables 1 and 3).

#### Random Movement, Buried Nets

The numbers of insects collected in the upstream buried nets at the centre (Cu) and at the side (Su) (Table 4) were almost equal to those collected in the downstream buried nets (Sd and Cd), but they were equivalent to 9.7% and 28.3% of drift at the side and centre, respectively. The higher value for upstream movement at the centre than across the stream on July 18 was partially because of 40 newly hatched *Baetis* nymphs which may have originated from an egg mass deposited near the net. Upstream movement of Ephemeroptera, Trichoptera and Elmidae was equivalent to 1.1%, 13.7% and 300% and 11.7%, 6.5% and 180% of drift at the side and centre, respectively. The relatively high ratios for elmid larvae indicates that they move mainly within the hyporheic zone.

#### Colonization of Trays

Colonization of the trays was generally greater during April and May (Table 5), but the pattern of colonization varied throughout the sampling period, being greater on the bottom trays on one occasion but not the next. That is, at the centre greater colonization took place into the tray on the bottom (CB) than into the one off the bottom (COB) on 14 of the 26 sampling intervals, 4 of these were significant ( $P < 0.005$ ) while on 6 occasions the COB count was significantly greater ( $P < 0.05$ ) than CB. At the side, colonization was greater into the bottom tray (SB) than into the one off the bottom (SOB) on 10 occasions; 3 of these were significant ( $P < 0.05$ ) while on 4 occasions the SOB count was significantly greater ( $P < 0.05$ ) than that in SB. The results showed that most of the colonization was by drift, i.e. the ratio of the totals COB/CB was 1.023 while that of SOB/SB was 1.037. Therefore being off the bottom, and hence not available to crawling specimens, had made no difference to the rate of movement. COB/CB and SOB/SB ratios for colonization of the trays by Ephemeroptera, Trichoptera, Simuliidae, Chironomidae and Elmidae were 0.944, 0.887, 2.415, 1.361 and 1.125, and 1.191, 1.133, 3.250, 0.846 and 0.527 respectively.

Table 5. Total numbers of insects, other than Chironomidae, collected in the colonization trays. a = from 31/03 to 19/12, \* =  $z = P < 0.05$ , \*\* =  $zz = P < 0.005$ .

In columns COB and SOB \* denotes a significant difference between values in columns CB and COB, and SB and SOB, respectively, z in columns SB and SOB denotes a significant difference between values in columns CB and SB, and SOB and COB.

1977	CB	COB	SB	SOB
11/01	39	78**	8 <sup>zz</sup>	37** <sup>zz</sup>
23/01	77	47**	-	105 <sup>zz</sup>
06/02	42	30	5 <sup>zz</sup>	25*
20/02	53	29	-	-
06/03	21	5**	-	-
31/03	29	63*	28	9* <sup>zz</sup>
14/04	46	146*	70	38* <sup>zz</sup>
28/04	55	44	23 <sup>z</sup>	10 <sup>zz</sup>
12/05	174	268**	170	274**
26/05	116	89	74 <sup>z</sup>	125* <sup>z</sup>
09/06	73	55	36 <sup>z</sup>	38
23/06	26	38	42	28
07/07	14	67**	56 <sup>zz</sup>	49
21/07	104	15**	16 <sup>zz</sup>	32
04/08	36	25	14 <sup>z</sup>	20
18/08	77	68	77	23** <sup>zz</sup>
01/09	97	18**	54 <sup>z</sup>	38
15/09	46	28	22 <sup>z</sup>	18
28/09	(30)	-	10 <sup>z</sup>	24
13/10	17	21	4	9
26/10	12	8	6	7
09/11	18	17	8	8
23/11	10	26*	5	8 <sup>z</sup>
07/12	11	19	16	9
19/12	34	51	21	13 <sup>zz</sup>
Total	1227	1255	752 <sup>a,zz</sup>	780 <sup>a,zz</sup>

The total colonization throughout the year was significantly greater at the centre than at the side; the SB/CB ratio was 0.745 for the ice free months, while the SOB/COB ratio was 0.709.

## Discussion

In the present study, drift was much greater than upstream or lateral movement, and was apparently influenced by both the life stages of the insects and increased water velocity. Stronger correlations between drift and water velocity were from August to December than for the whole year, probably because of a masking effect of behavioral drift during periods of emergence. That drift increases with water velocity is evident from catches during the severe spate on September 28, when the highest drift of Trichoptera, mainly Hydropschidae (*Hydropsyche betteni*, *H. bifida*, *H. slossonae* and *Cheumatopsyche*), and the mayfly *Stenonema vicarium* occurred. An increase in drift during spates is well documented (references in Bishop & Hynes, 1969a; others are McLay 1970, Mackay & Kalff 1973, Davies 1976, Zelinka 1976, Gore 1977, Siegfried & Knight 1977).

In general, our findings on drift are in agreement with those of other studies (Müller 1966, Anderson 1967, Elliott 1967a, b, 1971a, b, Ulfstrand 1968, Waters 1969, 1972) which have found drift to be related to the life cycle. Greater drift in warmer months is associated with later stages in the life cycle, the time of emergence, the number of generations per year, increasing population pressure at high growth rates, a search for suitable pupation or emergence sites, or a mechanism to distribute the species as widely as possible (Waters, 1969, 1972). Drift may also increase independently of water velocity with an increase in sediment input or turbidity (Gammon, 1970; Rosenberg & Snow, 1975; Ciborowski *et al.*, 1977). This, along with lower velocities and perhaps prior depopulation by the spate on September 28 are factors which may account for lower drift during the spate on October 13. Ciborowski *et al.* (1977) also found that changes in water velocity were more important in determining the magnitude of drift of *Ephemerella subvaria* nymphs than was the absolute velocity. This may account for a large increase in drift of *E. subvaria* observed on December 19 with only a moderate rise ( $7 \text{ cm s}^{-1}$ ) in water velocity.

The fact that higher values for the drift of some organisms were found at the side of the stream than at the centre supports the hypothesis that drift is an active pro-

cess (Walton *et al.*, 1977). This is because drift is proportional to the volume of water sampled (Elliott, 1970), and we know (Table 2) that the flow was lower at the side. For example, drift of *Baetis* was significantly greater near the banks than at midstream from May to July and showed no correlation with water velocity (Table 2). Also, the highest level of drift of *Baetis* occurred on August 18 during low flow. The presence of high numbers of *Baetis* in the drift during basal flow conditions in July to September, but their presence in fairly low numbers during the severe spate on September 28, not only supports the active drift theory, but indicates that perhaps very high discharges cause these species to seek shelter. This supports work done by Weninger (1968) who found little drift during a spate, and laboratory studies by Corkum *et al.* (1977), which showed that drift of *B. vagans* decreased with increasing current velocities and that more nymphs remained with the substrate at high water velocities than at low. Waters (1969) has also observed an increase in drift of *Baetis* at low current velocities.

On the other hand, the common observation of large numbers of insects on the upper surface of stones during the early hours of the night, their numbers decreasing thereafter, may lend support to the passive theory for drift. We agree with Ulfstrand (1968) that the active versus passive argument about drift is partly semantic, since they both result in increased drift caused by increased activity of the insects. However, we observed that nymphs released at the surface of the water column often initiate their return to the bottom by a somersault-like motion, and on rare occasions by swimming. This does not allow for total agreement with Ulfstrand's (1968) statement that the actual transport itself with the current is largely beyond the animals' control. Hence, both the beginning and the end of drift involve the active participation of the individual, whereas the movement itself is passive.

Our study has also confirmed that drift is much greater than upstream movement. The upstream component, in the random movement, 72 hour, 24 hour and buried net studies, was only equivalent to 2.1, 7.3 and 15.2% of the drift, respectively. These values are in general agreement with the 6.5% reported by Bishop & Hynes (1969b), but are much lower than the 25.2% reported by Elliott (1971b).

Of greater importance perhaps is our finding that in all our experiments the upstream and the lateral movements were not consistently different from one another (Tables 1, 3 and 4). One may conclude therefore that both are really random movements and that changes in their intensity merely represent changes in density and behaviour of the



benthos. For example an increased number of *S. vicarium* in the upstream trap at the centre on September 1 and 15 was also observed in the across stream traps.

Elliott (1971b), in a somewhat similar study found that upstream movement was always less than that across the stream and that it was predominantly by small individuals. Similarly, Bishop & Hynes (1969b) found that maximum upstream movement in summer corresponded to the July–August peak in benthic numbers, especially of newly hatched insects, while Hultin *et al.* (1969) found that it was restricted to the period before pupation or emergence in several species. In our study higher values in late February and early March corresponded to the late stages of *E. subvaria*, *S. vicarium*, *P. mollis* and *Baetis* nymphs, while a high value for upstream movement on January 11 was mainly of early instar *Ephemerella deficiens*. Higher values in September consisted mainly of early to mid-instar *S. vicarium* nymphs, while the high value on July 18 in the buried net study was caused mainly by newly hatched *Baetis*. Thus values found in upstream traps reflect values for the stream population and hence probably do not indicate directional movement, especially as none of the animals in this or the earlier studies was over-represented in the traps.

We also carried out a few mark and recapture experiments in the field, and movement observations in an experimental stream. These are not reported here, but they did confirm the observations of others (Commins, 1964; Brusven, 1970; Elliott, 1971b; Higler, 1975; Leudtke & Bruven, 1976; Mackay, 1977 and Arsuffi, 1977), that, at least under experimental conditions, many insects do not move far from the point of release, and that if they do move, they may go either up or downstream, with the latter predominating. Only Elliott (1971b) found a predominantly upstream movement, in large Plecoptera.

The numbers collected by our traps in 72 hours were generally less than were taken by the nets in 24 hours. We surmise that this was because the gravel was clean and so not a good habitat in which to remain. Egglshaw (1964) showed clearly that the amount of organic matter in the gravel is correlated with the invertebrate population. So we can suppose that specimens that wandered in also moved out when they found little food, and thus that the 72 hour findings possibly represent some sort of equilibrium. In any event, this discrepancy between the level of results obtained by the two studies does not invalidate the conclusions that may be drawn from them.

Indeed, the experiment with the buried nets (Table 4) confirms that movement is random in all directions, as

there was little difference between upstream, downstream and sideways movement where the downstream net was catching only a minimal amount of drift.

Finally, our experiment with trays of gravel on and 5 cm above the bottom confirm the findings of Townsend & Hildrew (1976) that most recolonization of empty areas is by drift. However, our results indicate an even greater importance for drift than theirs. Quite often, during our experiments, there were more insects in the upper than in the lower trays, a phenomenon that they did not observe, possibly because of their short experimental period of two weeks.

In our experiments the suspended – tray/bottom – tray ratios for Ephemeroptera and Trichoptera were 94% and 89% at midstream and 119% and 113% at the side, clearly showing the importance of drift for these groups. It was 242% and 325% for Simuliidae at the centre and the side, but this may reflect more the requirements of these larvae than their arrival by drift. They prefer shallow water and bare stones, and the suspended trays offered them shallower water and less silt, especially near the bank.

It seems undoubted then that, apart from special cases such as the Simuliidae, the tray experiments confirm that most colonization of denuded areas is by drift, and that random movement is so small a proportion of colonization in Salem Creek that it is hard to detect. Such a result confirms those of our trap and net studies that random upstream or lateral movement is equal to a very small proportion of the drift.

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