AN INVESTIGATION OF THE MOVEMENTS OF FRESH-WATER INVERTEBRATE FAUNAS

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1. Introduction

In a previous paper (Moon, 1935*b*) it was shown that in times of flood the invertebrate littoral fauna of Windermere moves on to parts of the shore recently covered by the rise in level of the lake. These flood movements are only a special case of the movements which are always taking place in the littoral region of lakes, and on the beds of streams. It is with these movements that the present paper is concerned.

2. Apparatus and methods

The movements were investigated by the use of trays covered with samples of the substratum from which the fauna had been removed (Moon, 1935*a*). The trays consisted of square iron frames laced across with wire netting and covered underneath with stramin or some other suitable material. The trays were covered with stones, sand or even weed in special cases, and left on the bottom of the lake or river for the desired length of time. By lifting the trays at various time intervals, and then counting the fauna which had moved on to them, an index of the amount of movement of the fauna was obtained.

In using these trays, precautions were taken against undue disturbance of the substratum, and the trays were left for at least 24 hr., free from stones, in the place they would occupy during the experiment. When the experiments were started the trays were lifted gently, washed free from any fauna which might have moved on to the bare stramin and netting, and then replaced in their position on the substratum covered with stones.

In the case of experiments on the diurnal variations of the fauna, the trays were lifted and the fauna removed at sunset and dawn, preferably at the equinoxes so that the hours of darkness equalled the hours of daylight. When it was impossible to carry out the experiment at the equinoxes, the trays were exposed during the day for a period of time equivalent to the hours of darkness. In the summer it was necessary to vary the periods of daytime exposure so that morning and afternoon periods were covered alternately. By this means was investigated the possibility that movement might be more active during the afternoon than in the morning. The same set of stones for each tray was used throughout the experiment.

3. Results

The first series of experiments was made in the stony littoral region of Windermere, using trays 1 sq. ft. in area. Table 1 gives the results of some of these experiments; it will be seen that considerable movement was taking place. In one case, for example, seven individuals representing five different species had colonized the trays in 12 hr. In another example fourteen individuals representing eight species moved on to the trays in 24 hr. If the trays are left on the bed of the lake for longer periods of time a fauna colonizes the trays approximately similar in number and composition to the undisturbed

Table 1. *Epley Head. Area of trays* 1 *sq. ft.*

Date (1932)	13 Sept.	13 Sept.	9 Sept.	9 Sept.
Time in lake (hr.)	12	12	24	24
Depth (ft.)	1	2	1	2
Ephemeroptera				
Ecdyonurus sp.	4	2	4	7
Centroptilum sp.	1	—	4	1
Caenis horaria (L.)	—	—	1	1
Plecoptera				
Nemura sp.	—	—	—	1
Trichoptera				
Limnophilus sp.	—	—	1	—
Agapetus sp.	—	1	—	1
Sericostoma personatum (McLachl.)	—	—	—	—
Stenophylax sp.	—	—	—	—
Lepidostoma hirtum (Fab.)	—	—	1	—
Mystacides nigra (L.)	—	—	—	—
Leptocerus aterrimus Steph.	—	—	—	6
Setodes sp.	—	2	—	—
Hemiptera				
Micronecta sp.	—	—	—	—
Diptera				
Chironomidae	1	1	—	—
Hydracarina				
Hygrobates sp.	—	—	—	1
Mollusca				
Limnaea pereger (Müll.)	—	—	1	—
Crustacea				
Gammarus pulex L.	1	—	1	1
Annelida				
Herpobdella atomaria Carena	—	1	—	—
Platyhelminthes				
Polycelis nigra Ehrenb.	—	—	—	—
Planaria lugubris O. Schm.	—	—	1	—
Total no. of individuals	7	7	14	19
No. of different species	4	5	8	8

areas around the trays. In Table 2 the difference between the 12 weeks and 4 weeks tray is due to the absence of *Agapetus* sp. on the former. Fluctuations such as this are fairly common in the littoral region during the autumn and early winter.

In Table 3 a number of other results have been summarized to show the amount of movement which takes place. Part of Table 3 is based on observations made from trays which were put down each month as far as possible, over a ten-month period. These trays showed that at all seasons of the year,

Table 2. *Epley Head. Area of tray* 4 *sq. ft.*

Time in lake (weeks)	4	12
Date	29 Nov. 1933	12 Nov. 1934
Depth (ft.)	1	—
EPHEMEROPTERA		
Ecdyonurus sp.	37	32
Centroptilum sp.	10	12
Leptophlebia sp.	6	19
Caenis horaria (L.)	—	23
PLECOPTERA		
Chloroperla sp.	22	—
Isoperla sp.	—	2
Nemura	5	2
TRICHOPTERA		
Leptocerus aterrimus Steph.	7	11
Oecetis sp.? furva (Ramb.)	—	1
Stenophylax sp.*	21	16
Sericostoma personatum (McLachl.)	1	—
Silo sp.	1	7
Agapetus sp.	58	—
Polycentropus flavomaculatus (Pict.)	1	—
COLEOPTERA		
Elmis (larvae and adult)	3	—
Gyrinus larva	1	2
DIPTERA		
Chironomidae	1	3
Ceratopogon sp.	1	—
MOLLUSCA		
Ancylastrum sp.	1	—
Pisidium sp.	6	—
Valvata piscinalis (Müll.)	3	—
HYDRACARINA		
Diplodontus despiciens (Müll.)	—	3
spp. indet.	—	4
CRUSTACEA		
Gammarus pulex L.	11	10
Total no. of individuals	196	147
No. of different species	19	15

* Larva resembles the continental *S. nigricornis* (Pictet).

Table 3. *Average of results from trays* on the Epley Head and Watbarrow Woods shoreline. Depths between* 6 *in. and* 4 *ft.*

Date	Time in lake hr.	No. of trays	Average no. of different species	Average of total no. of animals
14 Sept. 1932	6 hours	3	2	2
13 Sept. 1932	12 ,,	4	3	4
14 Sept. 1932	15 ,,	3	5	9
8–10 Sept. 1932	24 ,,	7	7	25
11 Sept. 1932	48 ,,	3	9	28
2 Nov. 1933	14 days	6	7	120
29 Nov. 1933	27 ,,	6	9	100
2 Jan. 1934	36 ,,	6	10	77
12 Feb. 1934	40 ,,	5	8	40
19 Mar. 1934	35 ,,	6	8	47
1 May 1934	42 ,,	6	8	78
18 June 1934	49 ,,	3	13	80
2 Aug. 1934	43 ,,	4	6	114

* 1932 trays = 1 sq.ft.; 1933–34 trays = 4 sq.ft.

down to a depth of 5 ft., there was movement. Below 5 ft. the stony littoral is usually replaced by *Litorella*, but, as was shown in a previous paper (Moon, 1935 *a*), movements also take place on the *Litorella*.

The comparison between the large and small trays in Table 3 is difficult. The small trays were used at the beginning of this work, and were put down in places selected for the richness of their fauna. The larger trays on the other hand were put down at two places where below 2 ft. there is a transition between the littoral and sublittoral, with a consequent reduction in fauna. Also there was a two-year interval between the experiments with large and small trays, and conditions may well have altered in this period.

Experiments similar to those described for lakes were made in the River Avon (Hampshire), and its tributaries. One set of experiments was carried out in Latchmore Brook, an acid New Forest tributary of the River Avon; the other in an irrigation channel leading water from the main river to a water meadow. The results are given in Table 4, and it is clear that fairly rapid currents of water do not prevent the fauna moving about and colonizing bare areas just as is the case in lakes. The much greater number of animals on the trays in the irrigation channel is due to two facts. First, the irrigation channel is to all intents a chalk stream, and therefore richer in animal life than the acid waters of Latchmore Brook. Secondly, the experiment was done at a time when *Limnaea pereger* (Müll.) and *Baetis* sp. were at a maximum, the former occurring extremely abundantly. In Latchmore the characteristic colonists were nymphs of *Nemura* sp., *Chloroperla* sp., *Leptophlebia* sp. and the amphipod *Gammarus pulex* L.

Table 4. *Results from trays in Latchmore Brook and an irrigation channel of the River Avon. Depth* 8 *in. Area of trays* 4 *sq. ft.*

Date (1938)		Time in stream days	Surface rate of flow (approx.) (ft. per sec.)	No. of trays	No. of different species	No. of individuals
			Latchmore			
8 Feb.		2	—	1	6	26
10 Feb.		4	—	1	4	6
12 Feb.		6	—	1	9	22
14 Feb.		8	—	1	8	22
25 Feb.		2	1·5	1	9	14
27 Feb.		4	1·0	1	8	84
1 Mar.		6	1·2	1	11	55
3 Mar.		8	1·5	1	11	117
			Irrigation channel			
Date (1938)	Depth					
27 July	2 in.	1	3·0	1	10	443
29 July	2 in.	2	0·3	1	11	1147
30 July	1 ft.	4	Negligible	1	12	1449

4. INDICATIONS OF DIURNAL VARIATIONS IN THE MOVEMENTS

By using trays it has been possible to show that although movement does take place during the daytime, the greatest activity for most of the aquatic invertebrates so far examined, is at night. Experiments were made in Windermere, and in the River Avon. The results of these experiments are given in Table 5, and the greater activity at night is apparent. Naturally the collections were dominated by the more abundant and active members of the fauna, and in these cases it was clear that they moved more at night than in the day. In the case of the less numerous and active forms, the numbers were too low for any statement to be made, beyond the fact that they showed a tendency to move more at night. In Windermere four insect nymphs, *Ecdyonurus* sp., *Centroptilum*, *Leptophlebia* sp. and *Chloroperla* sp., and a mite *Diplodontus despiciens* (Müll.) were more active at night. *Micronecta poweri* (D. & S.) however moved more during the day, while a mite *Hygrobates naicus* Johnst. moved equally in the night and in the day (Table 6). *H. naicus* however was peculiar in that it moved more during the afternoon than in the morning.

Table 5. *Diurnal variations in the movements of the fauna. Area of trays*, 4 *sq. ft.*

	Windermere		River Avon	
	Species	Total population	Species	Total population
D	17	140	—	—
N	*14*	*83*	*10*	*81*
D	13	53	9	45
N	*14*	*167*	*11*	*77*
D	11	139	9	25
N	*16*	*229*	*13*	*58*
D	11	108		
N	*10*	*148*		
D	10	60		
N	*16*	*254*		
D	10	52		
N	*12*	*230*		
D	12	73		
N	*15*	*260*		
No. of trays	9		4	
Depth (in.)	6		6	
Date	5–11 May 1935		6–9 Oct. 1938	
Exposure (hr.)	8		12	

D = day. N = night.

Table 6. *Variations in the movements of a mite* Hygrobates naicus *Johnst. from Windermere. Details as in Table* 5

Experiment no.	Night	Day	Morning	Afternoon
1	—	45	—	45
2	20	7	7	—
3	17	31	—	31
4	27	7	7	—
5	20	26	—	26
6	29	3	3	—
7	25	22	—	22
8	9	—	—	—

In the River Avon *Baetis* sp., *Asellus* sp. and *G. pulex* colonized the trays more at night than in the day, but *Sigara* sp., on the other hand, was more active in the day. This makes an interesting comparison with the results for the other Hemipteran *Micronecta poweri* (D. & S.), which also moved more in the day in the Windermere experiment. Tables 6 and 7 give the day and night movements of typical representatives from the two localities mentioned in Table 5. The experiments in the River Avon are of interest in that they yielded results under very unfavourable conditions. The only place at which they could be carried out had a limited population, the insect fauna still being depleted by the summer emergence of adult insects. Also the surface current at the places where the trays were set averaged rather more than a foot per second.

Table 7. *Diurnal variations in the movements of* Ecdyonurus *sp.* (*from Windermere*) *and* Baëtis *sp.* (*from the River Avon, Hampshire*). *Details of experiment as in Table* 5

Experiment no.	*Ecdyonurus* sp. Night	*Ecdyonurus* sp. Day	*Baëtis* sp. Night	*Baëtis* sp. Day
1	—	13	27	4
2	38	7	25	4
3	90	26	14	—
4	199	21		
5	80	21		
6	153	31		
7	121	10		
8	163	—		

In the case of those insect nymphs which show greater activity at night, it might be supposed that there was some relation between their stage of development, and their greater activity at night. The fact, however, that those forms showing greater activity at night were represented by mature and immature individuals, shows that the greater nocturnal activity is not directly connected with the stage of development.

5. Discussion

From these experiments two things are clear. First, the fauna moves about freely over the substratum and colonizes bare areas. Secondly, with one or two exceptions, the animals so far investigated tend to move more actively at night.

Movements of the bottom fauna have been observed by other workers. Wesenberg-Lund (1908) records movements of the bottom fauna on the shores of Baltic lakes in relation to change of water level in spring as a result of the melting snow. The same author (1912) describes the migration of the fauna to the warm southern shores of Baltic lakes in the spring. The shores with a southerly aspect become free from ice sooner than those facing north. Wodsedalek (1912) states that in American lakes the nymphs of *Heptagenia interpunctata* (Say) migrate away from the shore when the temperature falls in the autumn. Pauly (1917) working on the Müggelsee found that the fauna moved shorewards in the spring and out into deeper water in the winter. Pauly does not consider oxygen and temperature as important, in disagreement with Wesenberg-Lund who considers these two factors important. Lundbeck (1926) during his survey of the North German lakes found that many Chironomids, Tanytarsidae, Tanypodinae and the Mollusca, *Dreissensia* and *Valvata*, moved deeper in the winter and into shallower water in the summer. The factors responsible appear to be quite obscure, emergence movements, temperature and oxygen all being suggested as possibilities. Eggleton (1931) found a similar shoreward movement of the fauna in the summer and a retreat to deeper water in the winter. He correlated these movements with oxygen, and assumed that the shoreward movement of the fauna in summer was to avoid the stagnation in the deeper water.

The movements observed by these authors are different from those described in this paper, which seem to be purely random movements. The observations just referred to are evidently concerned with annually recurring movements associated with a definite set of factors. In the localities where the tray experiments were carried out there is no evidence for any annual regularity in the movements, probably because in Windermere there is never any oxygen shortage, nor does this lake freeze. The same applies to the River Avon and its tributaries.

The problem is complicated in the case of insect nymphs by an increase in activity as the nymph matures (Moon, 1935 *b*). It is suggested tentatively that the movements represent the wandering of the fauna in search of food. This agrees with the observations of Neave (1930) who found extensive migrations of the nymph of *Blasturus cupidus* Say. The nymphs migrated into temporary streams formed during the spring thaw in Manitoba. He correlated their movements with an abundant algal growth that appeared in these streams. Obviously these movements will be affected by external factors, e.g. change of water level in times of flood. The problem is greatly complicated by the fact that very little is known about taxes of the invertebrate fauna. Obviously, as with plankton movements, the reactions of the organism to light, temperature and food, and its physiological state, will influence its movements. The strong negative phototaxes of most freshwater invertebrates are well known. Wodsedalek (1912) records the negative phototaxis of *Heptagenia interpunctata* (Say). Gros (1923) noticed that after the fifth ecdysis the nymphs of *Ecdyonurus forcipula* (Pict.) avoided the light when not feeding, but while feeding they were very active. Gros also recorded that ecdysis usually took place at night.

One factor which might be assumed to influence the movements of the fauna is temperature. Although low temperature may limit the amount of movement, there is no evidence that low temperatures completely inhibit the activity of the fauna. For example in Table 4 the earlier set of trays at Latchmore were exposed to an average temperature of 6° C., while the large trays in Windermere were exposed in winter to an average temperature of 5° C. Yet in both these cases numerous animals colonized the trays.

6. Summary

1. A method is described for investigating the movements of the invertebrate fauna over the substratum.

2. Results from Windermere, and River Avon (Hampshire), show that artificially depopulated areas are re-colonized in a short space of time.

3. In the lakes and streams investigated there is much more movement at night than in the day, although a few insects, e.g. *Sigara* sp. and *Micronecta* sp. show the reverse. The mite *Hygrobates naicus* (Johnst.) showed equal activity in the day and night, but moved more in the afternoon than in the morning.

4. These movements are random movements, and distinct from the annually recurring movements described in certain European and American lakes. It is suggested that the movements are correlated with feeding activities.

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