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The Insects of the Stony Substratum of Windermere

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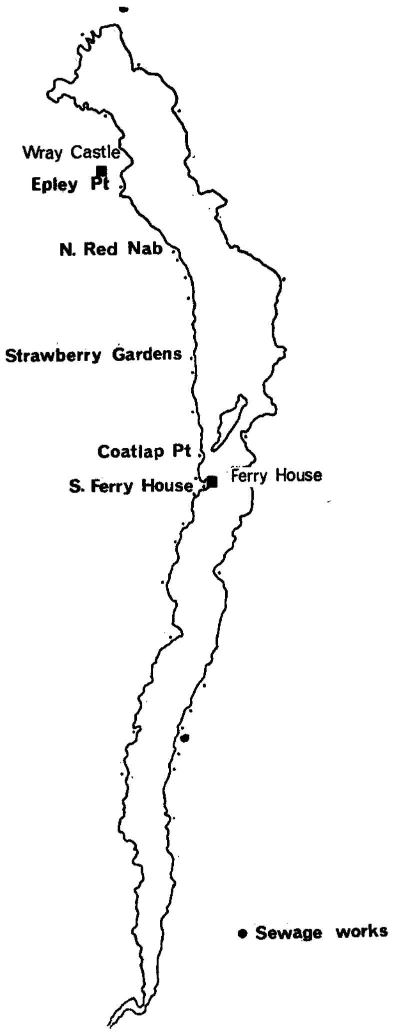
Trials in 1963 and 1964 showed that various species were not distributed uniformly on the stony substratum of Windermere, which indicated that a survey of the fauna of that biotope must be based on samples from as many different points as possible. The collections should also be close together in time because, during all but the winter months, hatching of all kinds of eggs, and emergence of insects whose adults are not aquatic, is altering the composition of the population. May and October 1965 were both dry months with the lake at a constant low level and as many stations as possible were visited during them.

It was decided to continue regular collections at five stations for a year in order to discover the life history of three species whose life history was not known. This yielded more information than was strictly relevant to a descriptive ecological study, and it seemed preferable to publish it separately. However, when the figures from which the life histories were deduced had been prepared, it was evident that they provided a basis for the discussion of other points also. It seemed a pity to defer this discussion to a later publication, in which the data would have to be repeated, and accordingly the scope of the article was enlarged. It now attempts, first to separate the true inhabitants of the stony substratum from invaders whose main centre is in an adjoining biotope. Then after the account of the life histories, variation in the samples is discussed, an essential preliminary to evaluating the significance of changes in numbers throughout the season. This also requires that something is known about the distribution with depth of each species throughout a year. Lastly, the marked differences in the communities at the different stations is pointed out, and a possible explanation of it is put forward.

A full account will be published elsewhere.

Most of the shallow water in Windermere is floored with stones. Moon (1934, 1936), whose work, unfortunately, was completed long before exact identification of many of the nymphs and larvae encountered was possible, studied a stretch of shore along which he could trace a series from flat rock face, through



1. Map of Windermere. The small dots show the positions of the collecting stations, those visited regularly being named.

stony bottom derived from rock and stony bottom derived from moraine, to sand in a bay sheltered from wave action. In fact, unwittingly, he had chosen a region where one of the most imposing outcrops of rock lies next to one of the largest moraine deposits to be found beside Windermere. Elsewhere the distinction is less clear, deposits of moraine lying between ridges of rock, with the result that stones from both sources are found on the lake bed. The nature of the substratum appears to be unimportant until, on moraine shores, there is sufficient shelter to permit the occurrence of finer particles on which plants, notably *Littorella,* can take root.

Collections have been made down most of the west side (fig. 1) and down part of the east, much of which, however, has not been visited because the construction of gardens and promenades and the building of boat-houses have altered its natural character.

The regular collections, monthly, or fortnightly at critical times of the year, were not made on fixed dates because it was desirable to avoid high lake level. The lake drops to 128 feet above sea level in dry weather and rises fairly quickly after rain. A rise of two feet is common and of three feet (1m.) far from rare; the highest level ever recorded was more than 6 feet above the lowest.

Methods

A station consists of 5 collections with a net, each lasting two minutes, the collector moving on 50 paces at the completion of each one. This technique was devised by Professor H. P. Moon during the course of an investigation of *Asellus*. Each stone is lifted with one hand and the net is swept underneath it to catch anything that has been exposed. The stone is rubbed with the hand in the mouth of the net before being returned. This method limits the collector to water whose depth is less than his arm. The net had 10 meshes/cm and therefore the smallest animals could pass through it.

Fauna of the stony substratum

It is not possible to know which species found on the stony substratum would not occur there if a barrier could be erected to prevent invasion from adjoining biotopes. It can only be supposed that a species distinctly more common and abundant on an adjoining biotope than on stones would not survive on stones but for continual immigration. This assumption leads to the following arrangement of the species recorded, the numbers quoted against each being the number taken in six of the winter collections, or in six of the summer collections, shown in table 1.

TABLE 1

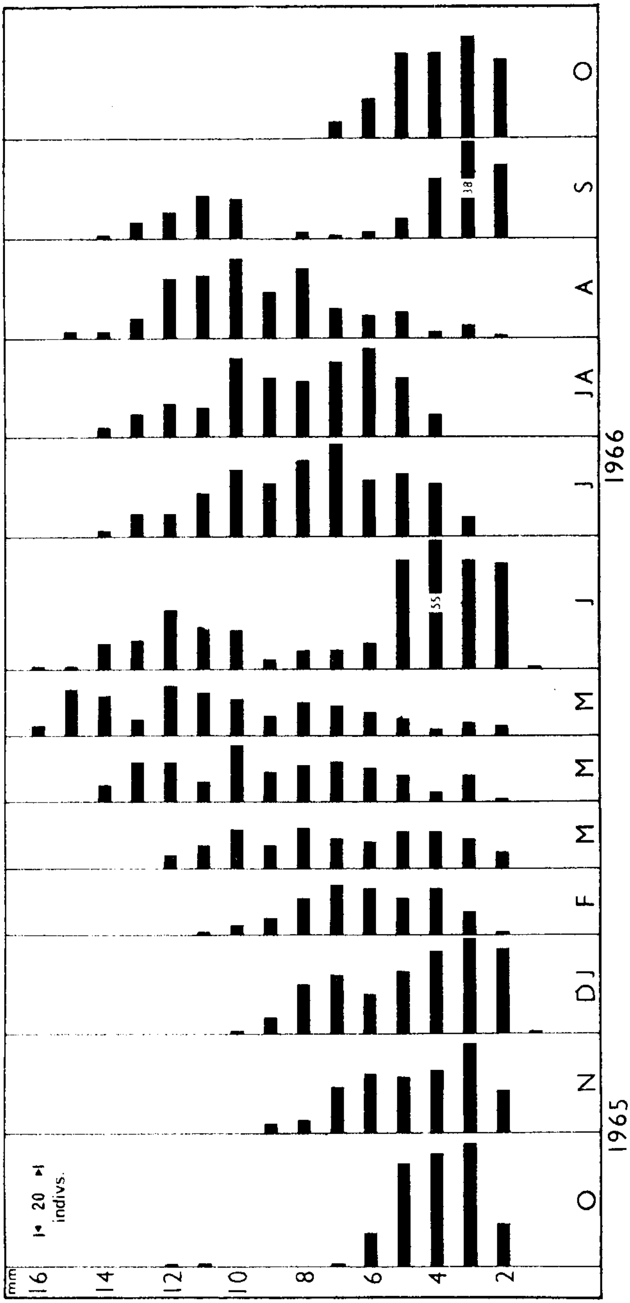
Numbers at five stations in Windermere during the course of a year. Each figure shows the numbers in 10 minutes collecting (2 minutes at 5 places, each 50 m. apart).

	←— 1965		—→	←—	
	Oct. 6-14	Nov. 16-19	Dec. 30-Jan. 4	Feb. 16-22	Mar. 15-17
Lake level in feet	128·6-129·6	128·3-·4	129·5-·9	128·8-129·5	129·0-·3
Lake level in metres	39·20-39·50	39·11-39·14	39·47-39·59	39·26-39·47	39·32-39·41
Ecdyonurus dispar					
Epley Point	61	29	66	68	43
N. Red Nab	87	82	82	14	34
Strawberry Gardens	1	1	1	2	2
Coatlap Point	—	—	—	—	—
S. Ferry House	—	3	1	—	—
Heptagenia lateralis					
Epley Point	27	6	4	29	6
N. Red Nab	35	20	1	8	37
Strawberry Gardens	3	19	—	7	12
Coatlap Point	—	—	—	—	—
S. Ferry House	1	8	—	7	11
Centroptilum luteolum					
Epley Point	17	12	2	6	13
N. Red Nab	3	6	4	5	7
Strawberry Gardens	—	1	—	1	—
Coatlap Point	—	1	4	—	5
S. Ferry House	—	—	—	—	—
Nemoura avicularis					
Epley Point	5	23	7	1	—
N. Red Nab	6	9	1	6	4
Strawberry Gardens	1	26	6	13	7
Coatlap Point	—	4	2	2	1
S. Ferry House	—	—	—	—	1
Diura bicaudata					
Epley Point	5	2	—	—	1
N. Red Nab	10	4	8	1	3
Strawberry Gardens	—	—	—	—	—
Coatlap Point	—	—	—	—	—
S. Ferry House	—	—	—	—	—
Chloroperla torrentium					
Epley Point	—	—	2	—	2
N. Red Nab	1	2	4	3	6
Strawberry Gardens	—	—	—	—	—
Coatlap Point	—	—	—	—	—
S. Ferry House	—	—	—	—	—
Capnia bifrons					
Epley Point	—	—	—	—	—
N. Red Nab	—	—	—	17	11
Strawberry Gardens	—	—	—	—	1
Coatlap Point	—	—	—	—	—
S. Ferry House	—	—	—	—	—
Poly. flavomaculatus					
Epley Point	27	26	21	22	11
N. Red Nab	4	24	6	1	9
Strawberry Gardens	2	5	—	3	2
Coatlap Point	5	5	1	—	2
S. Ferry House	3	43	3	39	41
Agapetus fuscipes					
Epley Point	877	420	513	306	334
N. Red Nab	1264	956	239	8	269
Strawberry Gardens	255	624	—	29	53
Coatlap Point	526	456	134	128	692
S. Ferry House	—	731	3	486	560

Lake levels—Figures in upper line are in feet and tenths of a foot. According to the Ordnance datum the surface of Windermere is 128·0 feet above sea-level; this must have been fixed near the end of a long dry spell.

1966 →							
May 2-4	May 17-30	June 20-21	Jul 13-15	Jul. 27-Aug. 1	Aug. 23-26	Sept. 20-23	Oct. 17-1[illegible]
128·7-·9	129·0-·9	129·0	128·4	128·2-·4	128·8-129·1	129·1-·6	128·8-·9
39·23-39·29	39·32-39·59	39·32	39·14	39·08-39·14	39·26-39·35	39·35-39·50	39·26-39·29
54	80	92	45	35	57	44	50
59	40	145	109	112	67	85	68
—	2	6	16	14	11	—	2
—	—	—	—	1	—	—	—
1	—	8	4	1	1	—	3
17	28	3	—	—	1	2	4
19	4	—	—	—	—	14	15
11	22	2	—	—	—	3	—
—	—	—	—	—	—	—	—
2	1	—	—	—	—	2	5
15	13	3	1	5	2	8	10
4	1	—	—	—	—	2	3
1	—	—	—	1	2	—	—
—	1	—	8	12	3	—	—
—	—	—	1	11	—	—	—
—	—	—	—	—	3	8	14
—	—	—	—	—	1	3	1
4	2	—	—	—	2	3	3
—	—	—	—	—	—	4	2
—	—	—	—	—	2	2	1
—	—	3	2	—	—	2	6
1	—	13	5	20	14	14	7
—	—	2	—	—	—	—	—
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
7	2	—	—	—	—	2	2
1	1	—	—	—	—	—	—
—	1	—	—	—	—	—	—
—	—	—	—	—	—	—	—
1	—	—	—	—	—	—	—
2	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
16	15	21	20	5	—	—	76
9	10	13	10	6	—	—	15
1	—	4	8	—	1	—	—
1	1	10	13	—	—	—	—
37	36	42	19	13	4	54	41
450	294	92	—	—	61‡	243	856
328	423	27	—	5	60‡	513	794‡
207	526	38	3	—	29‡	444	246
354	5	115	—	2	106‡	328‡	529
490	498	50	11	—	35‡	224‡	398

‡—only a few counted for each sample.



2. Number of specimens of *Ecdyonurus dispar* in mm. size-groups (length measured from front of head to tip of abdomen).

A + sign indicates that the species was not taken at any of these stations but was recorded somewhere else.

1. True inhabitants of the stony substratum

Nemoura avicularis (Morton)	(Plecopt.)	129
Platambus maculatus Linn.	(Coleopt.)	2
Stenelmis canaliculatus Gyll.	„	+
Ecdyonurus dispar (Curt.)	(Ephem.)	691
Heptagenia lateralis (Curt.)	„	290
Centroptilum luteolum (Müll.)	„	108
Diura bicaudata (Linn.)	(Plecopt.)	35
Polycentropus flavomaculatus (Pict.)	(Trichopt.)	369
Agapetus fuscipes (Curt.)	„	11,696
Chloroperla torrentium (Pict.)	(Plecopt.)	28
Leuctra fusca (Linn.)	„	4
Capnia bifrons (Newm.)	„	32
Cyrnus trimaculatus (Curt.)	(Trichopt.)	10
Tinodes waeneri Linn.	„	176

The first three are almost confined to this type of place. *N. avicularis* is found also occasionally in emergent vegetation in rivers (Hynes 1958). Balfour-Browne (1950) regards *P. maculatus* as a running-water species, but in the Lake District it has been found only in lakes and in two tarns, generally on a stony substratum (Macan 1940). *S. canaliculatus* is known only from Windermere where Claridge and Staddon (1961) recorded it for the first time.

E. dispar (Macan 1961), *P. flavomaculatus* (Edington 1964) and *C. luteolum* are found also in rivers, though the last is associated with sand and vegetation in the less rapid parts, not with stones. *D. bicaudata* occurs also in small streams high up, being apparently barred from the lower reaches by competition with *Perlodes microcephala* (Hynes 1952). Little is known about Trichoptera but the rest occur in small stony streams (Macan 1963).

The eggs of *Leuctra fusca* had not hatched when the first collections were made and many adults had emerged before the second. Specimens were taken at several stations visited in August. A decision whether a species of stonefly should be included in this section or the next has been based also on collections in other lakes and extensively on the remarks of Hynes (1941, 1958).

2. Species that would probably not maintain themselves on the stony substratum but for continual reinforcement from:—

i. streams

Ephemerella ignita (Poda)	(Ephem.)	3
Paraleptophlebia submarginata (Steph.)	„	5
Perlodes microcephala (Pictet.)	(Plecopt.)	+
Nemoura cambrica (Steph.)	„	8
Nemurella picteti Klap.	„	+
Amphinemura sulcicollis (Steph.)	„	1
Leuctra inermis Kempny	„	1
L. hippopus (Kempny)	„	7
L. mosleyi Morton	„	87

Plectrocnemia conspersa Curtis	(Trichopt.)	1
Elmis aenea (Mueller)	(Coleopt.)	+
Oulimnis tuberculatus Mueller.	,,	5
Hydraena gracilis Germar.	,,	22
Esolus parallelopipedus (Mueller)	,,	10
Oreodytes rivalis Gyll.	,,	1

ii. from below

Ephemera danica Müll.	(Ephem.)	1
Coenis moesta Bengts.	,,	38
C. horaria (Linn.)	,,	3
Sialis lutaria (Linn.)	(Megalopt.)	+

The first three live in sand, the last in mud, and occasionally, when loose stones lay on this kind of substratum, specimens turned up in the collections.

iii. from reed-beds

Siphlonurus lacustris Etn.	(Ephem.)	+
Sigara distincta (Fieb.)	(Hemipt.)	1
S. dorsalis Leach	,,	6
Deronectes assimilis Payk.	(Coleopt.)	+
D. depressus Fab.	,,	17
D. duodecimpustulatus Fab.	,,	+
Haliplus fulvus Fab.	,,	14
H. confinis Steph.	,,	1
H. lineolatus Marsh	,,	+
Coenagrion puella (Linn.)	(Odonata)	+
Enallagma cyathigerum (Charp.)	,,	+

A reed-bed was investigated by Moon (1936) and the Coleoptera by Macan (1940).

iv. from other places

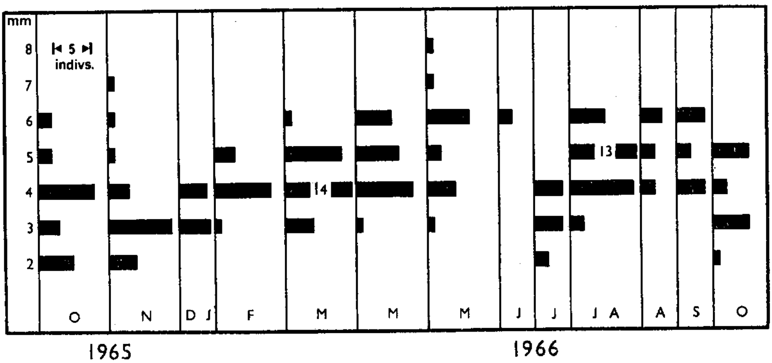
Leptophlebia marginata (Linn.)	(Ephem.)	23
L. vespertina (Linn.)	,,	+
Cloeon simile Eaton	,,	1
Micronecta poweri (D. & S.)	(Hemipt.)	+

Both species of *Leptophlebia* occur in the collections only at about the time of emergence, that is April and May. Work with an aqualung in March showed that they occurred at all depths on the stony substratum except the shallowest, being, in fact, the only species of which this was true. It is hoped to repeat this observation at other times of the year. The finding is unexpected, since Macan (1965a) records that *Leptophlebia* is scarce in the deeper parts of a small shallow fishpond but abundant in shallow water. It is also numerous in reed-beds in lakes (Moon 1936). *Cloeon simile* was not recorded by Humphries (1936), who studied the animals beyond the reach of the shore collector, but it is known elsewhere in weeds in comparatively deep water (Macan 1961, 1965a). *Micronecta poweri* is absent from many stations but abundant at a few. It appears to be associated with vegetation such as a tuft of *Fontinalis,* a plant of *Myriophyllum* or even a growth of filamentous algae, but its exact habitat has not been clearly defined.

These lists are incomplete because larvae of chironomids and other Diptera, and of some Trichoptera, cannot be named. That it has been possible to include some species of Trichoptera is thanks to the work of Mackereth (1956) and Edington (1964).

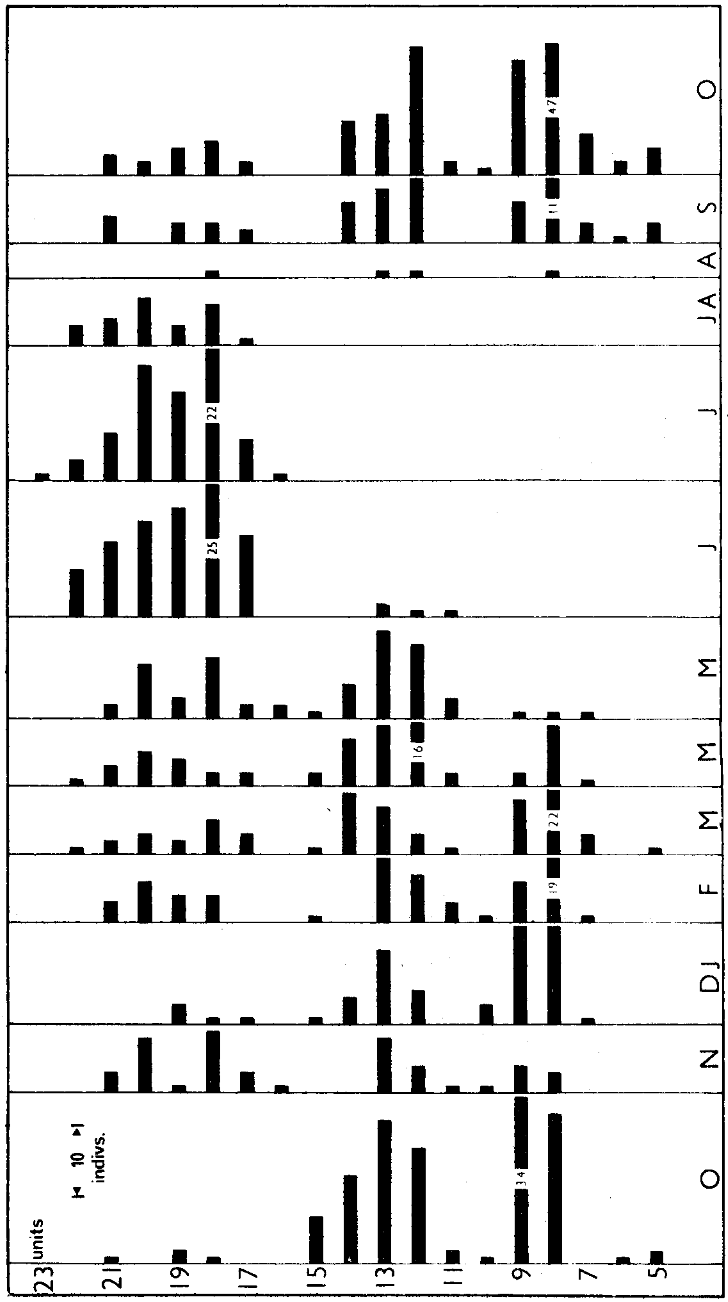
Life histories

The life histories of Plecoptera were studied by Hynes (1941) and the data gathered during the present work add nothing to what he records. Likewise the life history of *Heptagenia lateralis* is the same as in a stream (Macan 1961). *Agapetus fuscipes* was not measured, but the time of its disappearance (table 1) suggested that the life history was as described by Mackereth (1960). Catches in an emergence trap on the stream studied by Mackereth after she had ceased work on it have shown that in some summers there is a small emergence of *Agapetus* in the autumn, presumably the product of a quick summer generation. It is not known whether this may happen also in lakes. No information existed about the life histories in Britain of *Ecdyonurus dispar, Centroptilum luteolum* and *Polycentropus flavomaculatus,* and, accordingly, the data about these species in Table 1 are presented again in figs 2, 3 and 4 where they are broken down into mm. size-groups.



3. Numbers of specimens of *Centroptilum luteolum* in mm size-groups.

We have no observations on the time of emergence of the adults of *Ecdyonurus dispar.* Kimmins (1954) records that they are to be found from June to October. It is evident from a glance at fig 2 that there are two generations, one growing slowly in winter, the second, the beginning of which is clearly indicated by the large number of small specimens in June, growing rapidly in summer. The winter generation differs from the summer not only in slower growth but in the persistence of specimens 2 mm. long, which indicates either that the smallest specimens are not growing, or, more probably, that the hatching of the eggs is spread over a longer period. Also it means that an average of



4. Numbers of specimens of *Polycentropus flavomaculatus* in size-groups, according to the width of the head. The figures are the units of the micrometer eyepice used and 20 of them equal 1·25 mm.

the size each month is not a reliable measure of the rate of growth. The only, somewhat approximate, indication of this is the size of the largest specimen. In October (dates are given in Table 1) it is 7 mm. long, in November 9 mm. Thereafter the increment is only 1 mm. per month until May when 2 mm. are gained within the month. This suggests that, though more rapid in autumn and spring, growth continues throughout the winter. In the third week of June this winter generation is still emerging, but, as already noted, the summer generation, the progeny of the first to emerge of the winter one, has made its appearance. The new generation grows rapidly and there are no specimens 2 mm. long in July or at the beginning of August, and therefore small ones in late August are likely to be the off-spring of the summer generation. In September there is a gap between the generations, but the over-wintering generation is not separated by a gap from the one it produces. There is therefore a slight possibility that its smallest members become indistinguishable from the next generation and, with it, lay eggs that give rise to the overwintering specimens, without the intervention of the summer quick-growers If this does happen the numbers are small. The life history of *E. dispar* is similar to that of *E. venosus* described by Rawlinson (1939).

The life history of *Centroptilum* (fig. 3) is not as clear because fewer specimens were taken, and also because the size range is less, which means that the proportion of small ones lost through the net is greater. However, it is evident that there is a generation growing slowly all through the winter, and the following spring. By late June this generation has almost disappeared from the water and the smaller specimens in the collection three weeks later can safely be interpreted as the resulting progeny. This generation grows rapidly and specimens 6 mm. long, whose dark wings indicated that they were about to emerge, occurred in August. The offspring of this summer generation appeared in October and the life history is therefore like that of *Ecdyonurus dispar*. However, Kimmins records adults from April to November, and the histograms in fig. 3 suggest that there could have been emergence in November 1965. Such specimens are probably the last of the summer generation but it is possible that they are the product of a second quick summer generation, possibly one achieved by part of the population only. This species has been studied in detail by Bretschko (1965), who collected nymphs in a pond that was connected to a lake when the water level was high. In 1960 an overwintering generation emerged in May, which agrees well with what has been found in Windermere. In July and August only tiny nymphs were found, and Bretschko postulates an arrest of development due to high temperature, though the temperatures recorded are not particularly high, and the pond appears to be colder than Windermere. Not until September was there a distribution of size groups similar to that in Windermere in July. Imagines emerged in October but Bretschko refers to the possibility that only part of the generation

TABLE 2

Numbers during the winter 1965-66.

Each figure is the number in a collection of two minutes duration, except the sixth column in each month, which shows the total.

	October					Total	November					Total	December					Total
Ecdyonurus dispar																		
Epley Point	9	17	20	8	7	61	3	3	6	11	6	29	17	10	13	12	14	66
N. Red Nab	16	9	25	23	14	87	18	13	37	4	10	82	2	4	25	28	23	82
Heptagenia lateralis																		
Epley Point	3	2	9	13	—	27	1	—	—	1	4	6	2	2	—	—	—	4
N. Red Nab	20	6	2	5	2	35	2	5	5	3	5	20	1	—	—	—	—	1
Centroptilum luteolum																		
Epley Point	8	—	5	1	3	17	—	3	2	3	4	12	1	—	—	—	1	2
N. Red Nab	—	1	—	—	2	3	—	3	1	2	—	6	—	—	—	—	4	4
Leptophlebia marginata																		
Epley Point																		
N. Red Nab																		
Chloroperla torrentium																		
Epley Point													—	—	—	—	2	2
N. Red Nab	1	—	—	—	—	1	—	—	1	—	1	2	—	—	1	1	2	4
Diura bicaudata																		
Epley Point	2	—	2	—	1	5	1	1	—	—	—	2						
N. Red Nab	2	3	3	1	1	10	1	1	—	2	—	4	1	7	—	—	—	8
Nemoura avicularis																		
Epley Point	2	—	1	1	1	5	8	2	2	2	9	23	3	1	1	—	2	7
N. Red Nab	3	1	2	—	—	6	3	3	2	—	1	9	—	1	—	—	—	1
Capria bifrons																		
Epley Point																		
N. Red Nab																		
Agapetus fuscipes																		
Epley Point	91	142	314	314	16	877	95	76	128	64	57	420	243	109	64	78	19	513
N. Red Nab	407	117	420	166	154	1264	68	161	234	221	272	956	—	—	111	48	80	239
Polycentropus flavomaculatus																		
Epley Point	4	4	8	2	9	27	1	6	9	8	2	26	2	4	3	5	7	21
N. Red Nab	1	—	—	—	3	4	1	2	13	4	4	24	1	1	—	2	2	6
Cyrnus trimaculatus																		
Epley Point	—	—	—	—	1	1							—	—	—	1	—	1
N. Red Nab																		

TABLE 2 (continued)

	February					Total	March					Total	May					Total
Ecdyonurus dispar																		
Epley Point	5	15	14	15	19	68	9	8	10	7	9	43	12	16	7	10	9	54
N. Red Nab	3	4	3	2	2	14	6	11	6	6	5	34	7	15	16	8	13	59
Heptagenia lateralis																		
Epley Point	11	4	3	4	7	29	—	2	—	2	2	6	4	5	1	2	5	17
N. Red Nab	2	—	4	—	2	8	5	5	10	6	11	37	10	4	2	1	2	19
Centroptilum luteolum																		
Epley Point	1	1	—	3	1	6	1	1	3	3	7	15	3	1	4	3	4	15
N. Red Nab	2	—	—	2	1	5	—	1	—	2	4	7	2	1	—	—	1	4
Leptophlebia marginata																		
Epley Point													1	1	—	—	1	3
N. Red Nab													—	3	1	1	2	7
Chloroperla torrentium																		
Epley Point							1	—	1	—	—	2						
N. Red Nab	—	—	—	—	3	3	—	1	—	—	5	6	—	1	—	3	3	7
Diura bicaudata																		
Epley Point							1	—	—	—	—	1	—	—	1	—	—	1
N. Red Nab	—	—	1	—	—	1	—	—	1	—	2	3	—	1	—	—	—	1
Nemoura avicularis																		
Epley Point	—	—	1	—	—	1												
N. Red Nab	—	—	1	1	4	6	1	—	—	—	3	4						
Capnia bifrons																		
Epley Point																		
N. Red Nab	5	10	1	1	—	17	6	1	—	3	1	11	1	—	1	—	—	2
Agapetus fuscipes																		
Epley Point	142	33	43	70	18	306	92	78	59	37	68	334	65	94	146	92	53	450
N. Red Nab	1	—	7	—	—	8	4	66	116	65	18	269	4	28	130	56	110	328
Polycentropus flavomaculatus																		
Epley Point	6	4	4	6	2	22	4	1	4	1	1	11	3	—	4	9	—	16
N. Red Nab	—	—	1	—	—	1	—	2	2	1	4	9	1	1	3	2	2	9
Cyrnus trimaculatus																		
Epley Point	1	—	2	—	—	3	1	—	—	—	—	1	—	1	1	2	—	4
N. Red Nab																		

reaches this stage, the rest overwintering as nymphs, though concludes that the balance of the evidence is against this. The overwintering generation was growing in the same way as the one in Windermere, but emergence was later in 1961 than in 1960, taking place in June and July. As in the previous year the summer generation was later than in Windermere.

Unlike the preceding species, *Polycentropus flavomaculatus* belongs to a group in which the number of instars is small, a fact of importance in interpreting the histogram (fig. 4). A new generation appears in August and right at the beginning there are three size-groups, of which only the largest could be a relict of an earlier generation. In the following month there are three distinct size groups, which are likely to represent the last three instars. Fewer specimens had reached the last instar in October 1965 compared with October 1966, but by November 1965 the numbers in each of the three were in proportions that changed little until the following May. Evidently there is one generation a year, larvae appear in August and some grow extremely fast and reach the last instar quite soon. Throughout the winter there is no growth and a conspicuous shift of numbers from a smaller to a larger group is not apparent till the beginning of May.

Numbers

The figures in Table 1 are the totals of five collections. In Table 2 the number caught in each collection is shown and excessive size has been avoided by including only six winter months and only two of the five stations, the two at which the three species of Ephemeroptera were numerous. These figures, when not too small, are suitable for a statistical test of the probability that distribution was random. According to this *Ecdyonurus dispar* was randomly distributed in every month at Epley Point, though the result in October was only just significant. At N. Red Nab distribution was random only during the last three months. The distribution of *Heptagenia lateralis* was not random at either station in October but thereafter was generally very even. *Centroptilum luteolum* was similar. These results suggest that the collecting technique may be treated as a reliable quantitative one, yielding figures that are comparable though number per unit area remains unknown.

Since we could collect only near the edge, we could not know whether fluctuations were due to specimens migrating in or out of our reach and how far our collections were typical of the whole stony region. To obtain some information about this, we generally worked together in 1963 and 1964, one making a collection in water as deep as could be sampled with a bare arm, the other turning over those stones that were only just covered with water. The data in Table 3 are provided by these double collections. *Ecdyonurus* was always commoner in the shallow-water collection and *Centroptilum* in the deeper, with *Heptagenia* showing a more even distribution. These conclusions were confirmed, and data

TABLE 3

Results of a double collection at each place, one in water as deep as could be sampled, the other at the edge.

	Ecdyonorus dispar	*Heptagenia lateralis*	*Centroptilum luteolum*
Number of times commoner in shallow collection	7	4	0
Number of times commoner in deep collection	0	1	4
Total numbers in shallow collection	60	88	1
Total numbers in deep collection	14	69	17

for other species obtained, by the University of Newcastle-upon-Tyne Sub-aqua Club in March 1967. Their findings are shown in Table 4. *Leptophlebia marginata* was captured at all except the

TABLE 4

Numbers at five depths on stony substratum

(Fifteen 2-minute collections at 15 and 240 cm and twenty 2-minute collections at 60, 120 and 180 cm.)

	Depth				
	15	60	120	180	240 cm.
Ecdyonurus dispar (Ephem.)	77	5	1	—	—
Heptagenia lateralis (Ephem.)	9	2	1	1	—
Nemoura avicularis (Plecopt.)	15	3	4	2	—
Chloroperla torrentium (Plecopt.)	11	—	—	1	—
Capnia bifrons (Plecopt.)	11	1	—	—	—
Polycentropus flavomaculatus (Trichopt.)	3	2	3	—	—
Agapetus fuscipes (Trichopt.)	145	665	300	178	121
Centroptilum luteolum (Ephem.)	10	14	49	24	22
Leptophlebia marginata (Ephem.)	—	5	11	5	2

shallowest station. In the standard collections it was hardly ever taken except in May (Table 2) when it was presumably coming to the edge to emerge. At other times of year it inhabits water of such depth that it is not captured by collectors confined to shallow water. *Centroptilum* and *Agapetus* occurred at all depths but preponderated at the greater ones to an extent that would bias the figures of the standard collection against them. In contrast a standard collection would show *Capnia, Chloroperla,, Nemoura* and *Heptagenia* and *Ecdyonurns* to be more abundant on the stony substratum than they are. This statement assumes that the divers' findings in March (Table 4) hold for other places at other times. It is hoped that they will make more observations at other seasons.

The numbers of *Ecdyonurus* remained similar throughout the year (Table 1). When a low catch was made at one of the two stations where this species was abundant (Nov., Feb.) numbers were near the usual level at the other one, indicating that the low numbers were due to some chance. The highest figures at both stations were in June and coincided with the appearance of the new generation (fig. 2). There was no corresponding bulge when the next generation hatched, which confirms the idea that its hatching is spread out over a period of months. The present figures suggest that recruitment balances loss during the winter, though it will be necessary to establish whether part of the overwintering generation migrates into deeper water and keeps the shallow water population at a constant level by returning when gaps occur.

The numbers of both *Heptagenia* and *Centroptilum* also remain steady, though both show falls followed by recoveries which cannot at present be explained.

Macan (1966) has shown that the numbers of large specimens of certain species remain constant even though the rate of removal is increased, and has suggested that this is made possible by the maintenance of a reserve of small specimens, which do not grow unless they can take the place of a large one. Failure to grow may be due to failure to obtain a good vantage point for feeding or to the secretion of an inhibitor by larger members of the generation. Whether the steady population of *Ecdyonurus dispar* is due to a relationship of this kind is unkown.

Distribution

All but the last two species in Table 1 are abundant only at two of the five stations, the two most northerly on fig. 1. Collections all down the west side of Windermere revealed that this fauna persisted south from Epley Point nearly down to Strawberry Gardens. Further north and further south it was replaced by a community of which the most numerous members were *Polycelis nigra* (Müll) and *P. tenuis* (Ijima) and *Asellus* spp. These animals are particularly abundant near the outfall of the Bowness-Windermere sewage works, which supports the belief that they are favoured by enrichment from sewage. The works mentioned probably affect the whole of the south basin. The shallow region around the islands is enriched by houseboats and also by various shore establishments such as Ferry House, which has its own septic tank. The north end of the lake is under the influence of the Ambleside sewage works, which discharge into the main inflow.

The community in which Ephemeroptera and Plecoptera predominate occurs in that part of the lake most remote from sewage outfalls, and many of the species do not occur in the other community. It is unlikely that there is anything in the lake water harmful to them, and Macan (1965b) has postulated that they are unable to withstand the predation, possibly mainly a predation on their haphazardly laid eggs in which even scavengers and herbivores take part.

Agapetus fuscipes is widely distributed in the lake and can be assigned definitely to neither community, though its numbers are low in the immediate vicinity of the outfall from the Bowness-Windermere sewage works. *Polycentropus flavomaculatus* would appear to be similar from the figures in Table 1, but actually its affinities are clearly with the other insects, It is, however, particularly numerous at the station called South Ferry House, which is along a strip of shore at right angles to the long axis of the lake, and consequently exposed to severe wave action. It occurs at similar places in the South basin but not at the more sheltered stations in between. These exposed stations are also the ones where species such as *Heptagenia lateralis* and *Ecdyonurus dispar* occur among the flatworm — *Asellus* community. Why wave action should make this mixing of the two communities possible is not known.

Summary

1. Collections were made with a net on the stony substratum of Windermere. The collector worked for two minutes and then moved along 50 metres.

2. A list is given of what is thought to be the true inhabitants of this biotope. Other species are more abundant in adjoining biotopes and their presence is, it is tenatively suggested, due to immigration.

3. *Ecdyonurus dispar* and *Centroptilum luteolum* have an overwintering and a summer generation. *Polycentropus flavomaculatus* has one generation in the year. It appears in August and September and growth is evidently quick at first, as there are soon three size-groups, thought to represent three instars. After October there is little growth until the following May.

4. In most of the samples the species are randomly distributed horizontally. Most are more numerous in the shallowest water than further out, where divers collected, but the reverse was true of *Agapetus, Centroptilum luteolum* and *Leptophlebia marginata*. The last was the only species taken by the divers but not regularly by the shore collectors, who captured it only in May when emergence was imminent.

5. Numbers of species remained steady throughout a generation.

6. Insects predominated on the west shore of the central part of the North Basin of Windermere, giving place elsewhere to a community in which *Polycelis* and *Asellus* were the commonest members, apparently in regions influenced by sewage outfalls. How enrichment by sewage benefits these animals is not known. It is suggested that the absence of Ephemeroptera and Plecoptera among them is due to their consumption of the latter possibly particularly of their casually laid eggs. Their absence is general except where there is marked exposure to wave action, the reason for which is also unknown.

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