Verh. Internat. Verein. Limnol.	17	173—180	Stuttgart, November 1969

II. Lakes. 2. Europe

Fauna of the stony substratum in lakes in the English Lake District

T. T. MACAN and RACHEL MAUDSLEY

With 3 figures and 1 table in the text

The initial assumption that similar biocoenoses would be found on similar substrata in different parts of one lake was soon shown to be wrong. Evidently any statement about the composition of the communities must be based on as many samples as possible from as long a stretch of shoreline as possible. A survey of Windermere was carried out in accordance with these preliminary findings and the work was later extended to other lakes. The results are presented here.

Description of lakes

The English lakes lie in typical glacial basins. Windermere, 17 km long, is the largest. Reed-beds, if present at all, are generally confined to deeply indented bays, and most of the substratum in shallow water is stony. MOON (1934) distinguishes the substratum formed by the destruction of rock from that formed by the erosion of moraines; the former consists of slate-like fragments whose size tends to vary with the nature of the rock, the moraine or drift substratum consists of more rounded stones varying in size from pebbles to large boulders. MOON studied a stretch of shore where the contrast is particularly good. Elsewhere it is less distinct; deposits of boulder clay lie between ridges of rock and both contribute to the substratum of the lake.

The lakes form a series ranging from unproductive oligotrophic typical mountain lakes (Ennerdale, Wastwater, Buttermere) to Esthwaite, which is eutrophic (PEARSALL 1921).

Methods

The collector lifted stones with one hand and attempted to catch by means of a net held in the other any animal that did not remain clinging to the stones. This was continued for two minutes and then the process was repeated 50 m further on. Five such collections, that is 10 minutes activity, constituted a station.

Results

Fig. 1 shows the number of *Polycelis nigra* and *P. tenuis* at thirty-four stations in Windermere. Twenty-two of the stations are given numbers by which they are referred to later. Moderate numbers of *Polycelis* were taken at the north end of the lake (station 1 and 2), small numbers at station 3, and none at station 4. Numbers increased at subsequent stations and regained the initial level in the neighbourhood of the islands which divide Windermere into two basins. Flatworms were relatively numerous everywhere in the south basin of the lake.

Fig. 2 shows the other common species (for discussion see MACAN and

MAUDSLEY 1968) on the stony substratum. The numbers along the bottom indicate the stations, whose position is shown in Fig. 1, and the length of each histogram indicates how many specimens were caught in an average two minutes. Two more species of flatworms, *Asellus, Physa,* and the recent immigrant from America, *Crangonyx,* are distributed in a manner very like that of *Polycelis.* The remaining

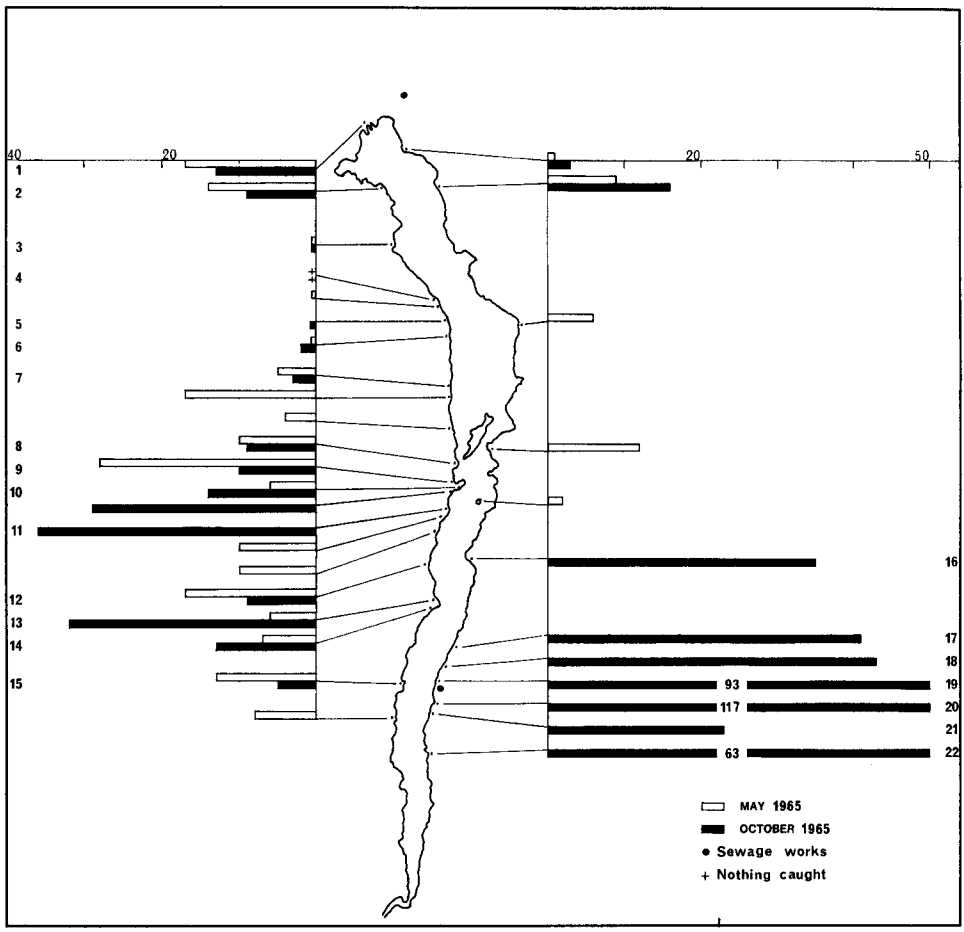

Fig. 1 Numbers of *Polycelis nigra* and *tenuis* caught at different stations in Windermere. (Figures are average number caught in two minutes. Each is the average of five or ten 2-minute collections.)

three species on the left-hand side are less similar. It will be noted that not one of these is an insect.

Diura bicaudata, the bottom species on the right-hand side of Fig. 2, occurs only at those stations at which *Polycelis* is scarce or absent. Two other stoneflies and three species of Ephemeroptera are distributed in the same way except that a few specimens occur in the south basin. *Polycentropus flavomaculatus,* a caddis

that spins a net, occurs in greatest numbers in the north basin where *Polycelis* is scarce, but is also present at several stations in the south basin and abundant at one. All these stations are on the south sides of promontories, that is on shores exposed to the waves driven by the prevailing south winds. It is here also that members of the "insect community" occur in small numbers among members of the "non-insect community".

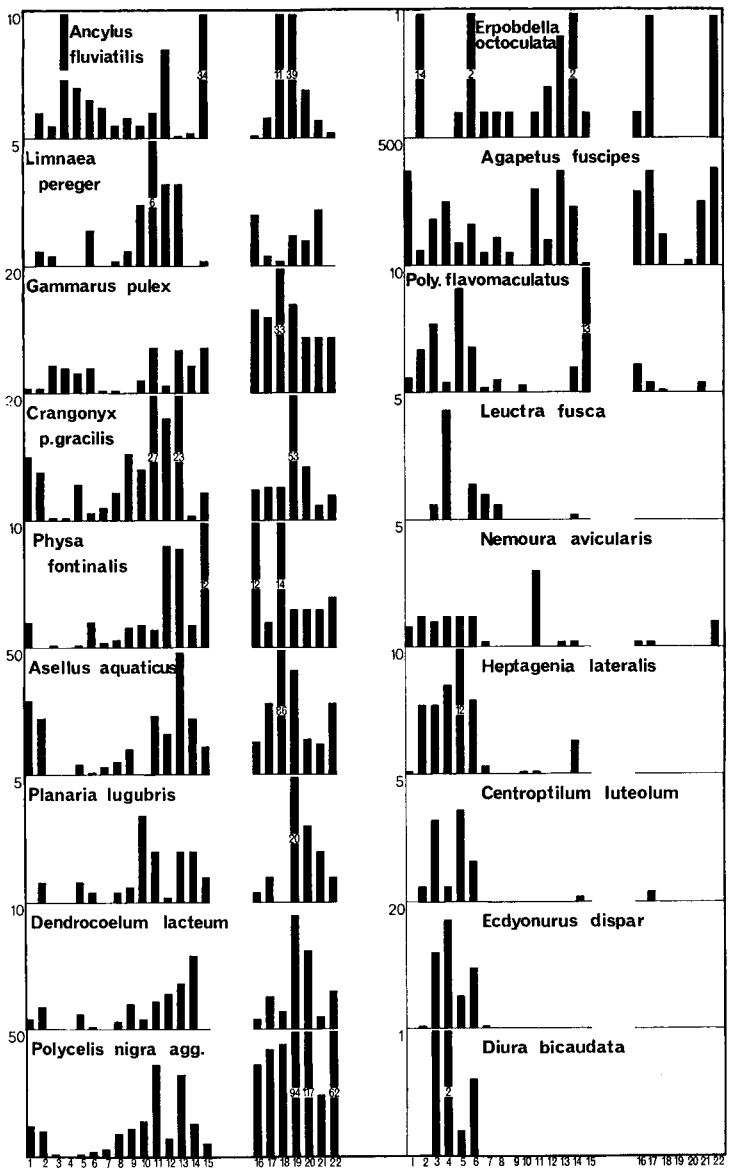

Fig. 2. Numbers of animals collected in two minutes in Windermere at stations numbered as in Fig. 1. (The numbers are the average of ten, sometimes five, collections.)

Agapetus fuscipes and *Erpobdella octoculata* are more uniformly distributed than any other species.

There are, therefore, two distinct communities or biocoenoses on the stony substratum of Windermere. As far as can be made out from the present data they merge gradually one into the other. Strong wave action appears to favour co-existence of the two.

One factor with which the occurrence of these two communities can be correlated is enrichment by sewage; the purification plants are too efficient and the dilution too great to warrant the use of the term "pollution". Ambleside sewage effluent enters the north end of the lake and is presumably generally blown back onto the north shore by the prevailing southerly wind. The rest of the north basin, being large and sparsely inhabited on the west side, is probably less influenced by sewage than any other part of the lake. Numerous houseboats enrich the water among the islands, and there are effluents from the Ferry House and, no doubt, other establishments. The south basin is affected by the large works treating the sewage from Bowness and Windermere. That several members of the "non-insect community" are particularly numerous on either side of the outfall from these works (stations 19 and 20 on Fig. 1) supports the view that the two are correlated. The nature of the connexion between enrichment by sewage and certain animals is unknown. Probably some small organism on which flatworms and other carnivores prey becomes more abundant in the richer waters influenced by sewage effluents, and this enables the flatworms to increase their numbers. This leads to greater predation on the insects and in due course to the disappearance of the species characteristic of unenriched waters. Possibly there is a great consumption of their eggs, in which omnivores and even herbivores play a significant part. It is noteworthy that the Plecoptera and Ephemeroptera scatter their eggs in a haphazard way, whereas the members of the non-insect community protect theirs, in tough cocoons (Hirudinea, Platyhelminthes), in masses of jelly (Mollusca) or in maternal brood-pouches (Amphipoda, Isopoda).

The results for other lakes are shown in Fig. 3. The arrangement is in descending order of productivity and the south (Wi S) and north (Wi N) basins of Windermere are treated separately. Thirlmere (Th) is now a reservoir with a rise and fall of the surface level which is five or six times greater than that in other lakes. Only in Coniston (Co) and Bassenthwaite (Ba) was the community of the stony substratum different in different parts of the lake, which is as expected because these are two lakes which, like Windermere, receive a sewage effluent of significant magnitude. Esthwaite (Es), also enriched, is uniformly populated probably because it is small. Most of Coniston and Bassenthwaite had a uniform biocoenosis and the few stations where it was distinctly different have been omitted. The histograms in Fig. 3 represent catch in 100 minutes.

The community in Esthwaite is like that in the richer parts of Windermere, but *Polycelis*, *Gammarus*, and *Erpobdella* are more numerous. There are fewer *Lymnaea* and *Physa*; possibly predation by leeches keeps numbers low. *Asellus*, surprisingly, is a comparatively recent immigrant into Esthwaite (Moon 1968). *Nemoura avicularis*, unexpectedly numerous in all the more productive lakes and scarce in the less productive ones, evidently has less ecological affinity with the

other Plecoptera and Ephemeroptera than was at first thought. Otherwise the scarcity or absence of species in these groups is as might have been forecast.

Numbers of the first five species in Fig. 3 fell with progress from productive to unproductive lakes, though not in the same way; the numbers of *Polycelis* drop

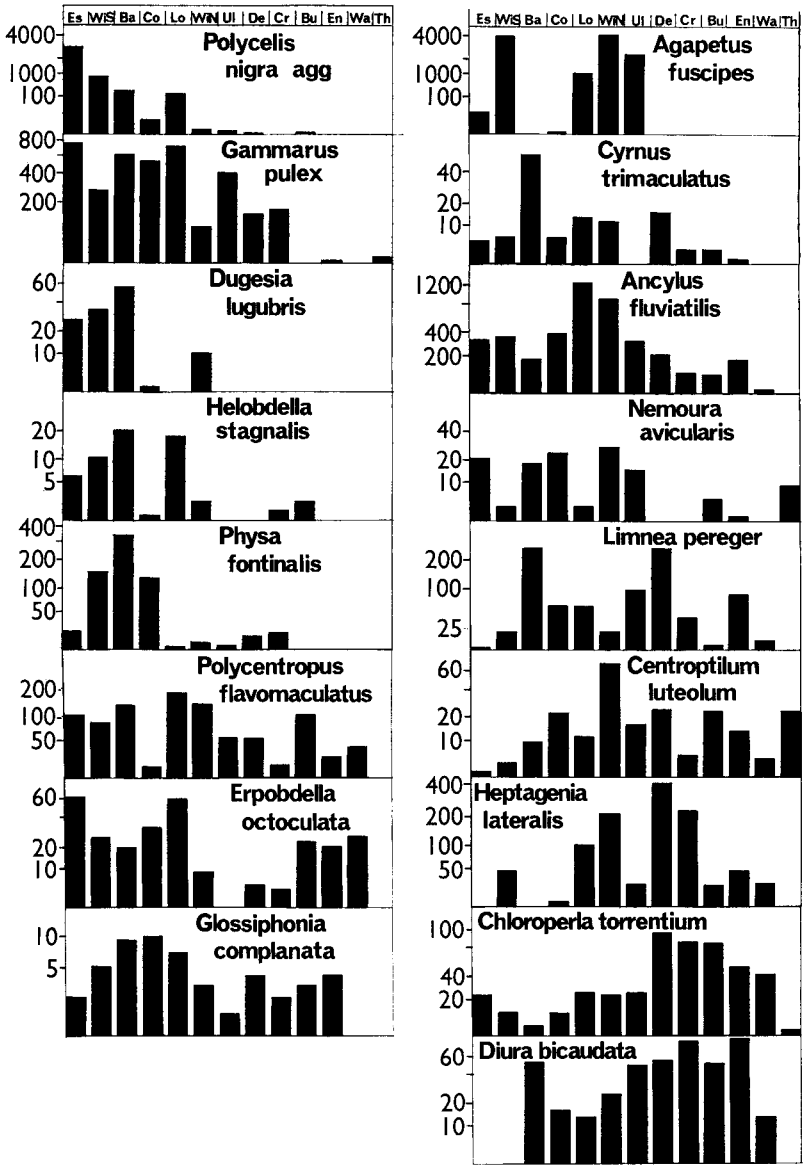

Fig. 3. Numbers of animals collected in each lake in 100 minutes. Contractions in the top line stand for the lakes: Esthwaite, Windermere (south basin), Bassenthwaite, Coniston, Loweswater, Windermere (north basin), Ullswater, Derwentwater, Crummock, Buttermere. Ennerdale, Wastwater, Thirlmere.

abruptly from the start, those of *Gammarus* more gradually till the last four lakes are reached, and *Physa* declines in three steps. All the flatworms have a similar distribution but *Dugesia lugubris* is less widespread than *Polycelis*, and *Dendrocoelum* less widespread still, occurring only on Windermere, Ullswater and Bassenthwaite. Its absence from Esthwaite may be due to the fact that *Asellus* has only recently arrived there. Apart from some anomalies discussed below, our observations in the Lake District lakes agree very closely with those described by REYNOLDSON (1966).

The next seven species, with the exception of *Agapetus*, occur in fair numbers throughout or nearly throughout the series. The last five, two Ephemeroptera, two Plecoptera and one mollusc, are scarce in the productive lakes, most abundant near the middle of the series and less numerous at the unproductive end. The serial arrangement is clear in the most and in the least productive lakes, less clear in the middle where there are some at present inexplicable anomalies, notably in Ullswater and Coniston. It may be significant that there has been extensive mining, mainly for lead or copper, in the drainage areas of these two lakes.

All the results are based on collections that extend no deeper than the length of the human arm. It would be desirable to know what lives on the stones at greater depths. The only information available (Tab. 1) was provided by the Newcastle University Sub-aqua Club who, in March 1967, made collections at three of our standard stations. The first five species in the table were confined to shallow water, the last ten were commoner in depths greater than those usually sampled. Of these only *Leptophlebia* was regularly absent from the standard collections, in which it was taken only in May, the month in which *L. marginata*

Tab. 1. Numbers at five depths on stony substratum. March 1967. (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	—	—	—
Ancylus fluviatilis (Moll.)	105	51	41	23	7
Crangonyx pseudogracilis (Crust.)	87	7	6	11	8
Polycentropus flavomaculatus (Trichopt.)	3	2	3	—	—
Physa fontinalis (Moll.)	19	20	22	11	25
Polycelis nigra (Triclad.)	25	3	12	15	24
Agapetus fuscipes (Trichopt.)	145	665	300	178	121
Centroptilum luteolum (Ephem.)	10	14	49	24	22
Leptophlebia marginata (Ephem.)	—	5	11	5	2
Valvata piscinalis (Moll.)	—	9	2	9	1
Gammarus pulex (Crust.)	34	13	22	31	50
Asellus aquaticus (Crust.)	16	14	51	71	76
Erpobdella octoculata (Hirud.)	1	9	11	26	26
Piscicola geometra (Hirud.)	4	4	—	9	1
Glossiphonia complanata (Hirud.)	1	1	5	11	9
Planaria lugubris (Triclad.)	—	—	4	10	7
Dendrocoelum lacteum (Triclad.)			2	17	2

emerges. It is evident that collections made in shallow water give a biased picture of the composition of the fauna, though how biased must remain unknown until many more collections under water have been made in many other places at different times of year.

Remarks on classification

At the north and south ends of the north basin of Windermere, there was a fauna characteristic of eutrophic conditions; in between one characteristic of oligotrophy. Evidently a lake or a lake basin cannot be taken as a unit. Since there appears to be no sharp division between the two biocoenoses, it is not possible to select units on which a scheme of classification involving division into rigid units can be based. Moreover, it is found that, when any attempt is made to divide the lakes into groups on discontinuities, the position of the dividing lines come between different lakes according to the group of animals used. It seems at present that a clearer understanding of why the composition of a community varies will come from a serial rather than a categorical approach, one community being selected as an arbitrary starting point and the modifications which it shows under varying conditions noted.

The observations in Windermere also make less tenable the ideas inherent in any kind of "Saprobiensystem". The community typical of the middle of the north basin of Windermere is presumably oligosaprobic, that in the south basin mesosaprobic. In a few places in the south basin the two communities are mixed. The places where this occurs are the south-facing shores exposed to the most intense pounding by waves. The distribution of the animals is evidently due to the interaction of several factors, but any rigid system relates it to one only.

Acknowledgments

We record with our best thanks the assistance of Miss SUZANNE HOPLEY, Mr. PETER BARNES and Mr. RICHARD SANDBROOK, and express our gratitude to the officers and men of the Newcastle University Subaqua Club.

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Discussion

BOUSFIELD: At the outflow of a lake, the shallow bottom fauna usually contains a higher percentage of plankton feeders (e. g. Hydropsychidae). Since your

stations did not cover the southernmost part of Windermere, and the outlet vicinity, would your comparative surveys between lakes (eutrophy or oligotrophy) not be more meaningful if the outflow area were included?

MACAN: Yes.

MORGAN: Do you think it would be better to classify lakes by the fauna of the sublittoral, which is not so greatly affected by wave action as the shoreline zone?

MACAN: No. You may remember the paper by VALOVIRTA at the Congress in Finland. He showed that the fauna in the mud of a lake changed with distance from the inflow.