THE COMMUNITIES OF RUNNING WATER IN CUMBRIA

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Early Work

Important studies of the communities in streams and rivers were made between the wars by F. T. K. Pentelow, R. W. Butcher and other members of the Ministry of Agriculture's team, and by E. Percival and H. Whitehead operating from Leeds. They were, however, handicapped by inadequate keys to the immature stages of Plecoptera, Ephemeroptera, Trichoptera and Diptera (notably Chironomidae), four groups whose larvae constitute a large proportion of the fauna of unproductive rapidly flowing water.

In 1937 H. B. N. Hynes arrived at Wray Castle as a research student and started work which resulted in a long paper on the taxonomy of nymphal Plecoptera (1941) and later a key in the *Scientific Publications* series (1967)*. This was followed by a similar key for the Ephemeroptera (Macan 1970).* When nymphs could be identified, work on life history and migration (Macan 1957a) started in Ford Wood Beck, a stony stream running through agricultural land. A comparison with other streams (1957b) followed, and Jean Mackereth, who was my assistant at the time, undertook a study of the Plecoptera (1957) and Trichoptera (1960). She also described and distinguished the larvae in two groups of caddis (1954, 1956). T. Gledhill succeeded Mrs Mackereth and studied the water mites (1971). He also climbed Helvellyn once a week to study the life history of the mayfly *Ameletus inopinatus* (1959) and to compare the emergence periods of various species in Whelpside Ghyll at 2000 ft and in Ford Wood Beck (1960). A further study of captures in emergence traps (Macan 1964) and a study of the amphipod *Gammarus* (Macan & Mackereth 1957) gave a comprehensive picture of the fauna of Ford Wood Beck.

There were 9 species of Ephemeroptera and 14 species of Plecoptera but the former were by far the more numerous. *Gammarus* was very abundant and maintained remarkably constant numbers, *Ancylus* (Mollusca) was numerous in places and a third characteristic species was *Agapetus fuscipes* (Trichoptera).

After the survey was complete the stream was enriched by effluent from an overloaded septic tank, which led to an enormous increase in the numbers of *Polycelis felina*. A simultaneous decrease in the number of some other species was probably due to predation by this flatworm (Macan 1962).

Temperature was recorded for several years (Macan 1958) and the effect of temperature on two species was observed (Macan 1960a, b).

* These are the dates of the most recent editions.

River Duddon

In 1965 Dr G. W. Minshall and Dr R. A. Kuehne, two visitors from America financed from U.S. funds, arrived for a year's work. The outcome (Minshall 1969, Minshall & Kuehne 1969) was a survey of the fauna of the River Duddon, which drains one of the few Lake District valleys without a lake. The highest point of origin is 735 m above sea level. In most of the upper basin of the Duddon they found a fauna consisting mainly of Plecoptera and some Trichoptera and Diptera. Ephemeroptera (except for an occasional specimen of *Baetis rhodani*), *Gammarus*, *Agapetus*, *Ancylus* and Elminthidae were absent. These groups, all well represented in Ford Wood Beck, occurred in much of the lower and parts of the upper basin, but Plecoptera retained numerical dominance at almost every station.

Later Dr D. W. Sutcliffe and Mr T. R. Carrick visited the Duddon Valley at intervals to study the effect of rainfall on the substances in water. They were able to recognize three classes of stream: (1) pH above 5·7, Ca above 3 mg l^{-1}; (2) pH about 5·0 and often below it, Ca below 3 mg l^{-1}; (3) values of both fluctuating between those in the other two classes, being depressed by rain and rising in fine weather. The regions where pH and calcium were low, either all the time or after heavy rain, were those in which so much of the typical stony-stream fauna was lacking (Sutcliffe & Carrick 1973).

In 1974 Dr Wayne Minshall returned on sabbatical leave to take the explanatory side of the work further, but he has not yet published his findings.

River Lune

Like the Duddon, the River Lune is fast enough throughout its length to be floored with stones, but it is larger, about 90 km long, and more diverse.

All the tributaries have names of their own, and 'Lune' first appears at Newbiggin, at the east end of a valley bounded by limestone to the north and a high ridge of Silurian age, the Howgills, to the south (Fig. 1). Numerous tributaries flow down from this area of Coniston Grits. Below Tebay the river turns towards the south and runs through this range in a gorge probably excavated by a glacier. It also receives tributaries from an area of Bannisdale slate that forms part of the Lake District. Below the gorge the river traverses a long alluvial plain on a bed of stones which are all relatively small and rounded. Eventually the river finds its way through a ridge of Millstone Grit (Fig. 2), making a spectacular loop known as Crook o' Lune. Millstone Grit forms a horizontal floor with few cavities or protuberances, and in the lower part of the passage much of it is dry during fine weather. The upper part, however, is always inundated because a dam, designed originally to deflect water to a mill, maintains a constant level. The rock in consequence is carpeted with moss, which

may also owe its luxuriance to the absence of bombardment by coarse sand and fine gravel during times of flood, a bombardment which keeps outcrops of Millstone Grit in other parts of the system clear of vegetation.

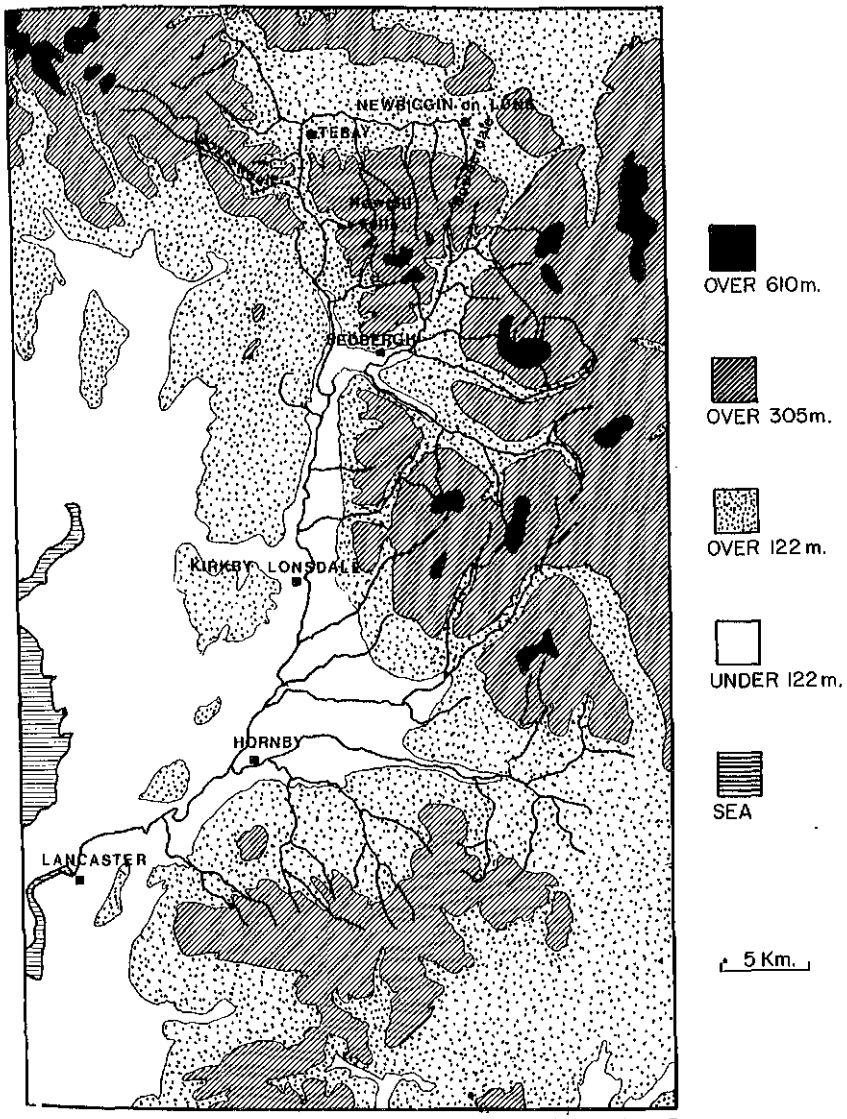

FIG. 1. Relief map of the drainage area of the River Lune.

Protection from this scouring is provided by the depth of water held up by the lower dam and more directly by another dam upstream. Long tributaries flow into the River Lune from the east, many bringing calcareous water from the limestone of the Pennines (Fig. 2).

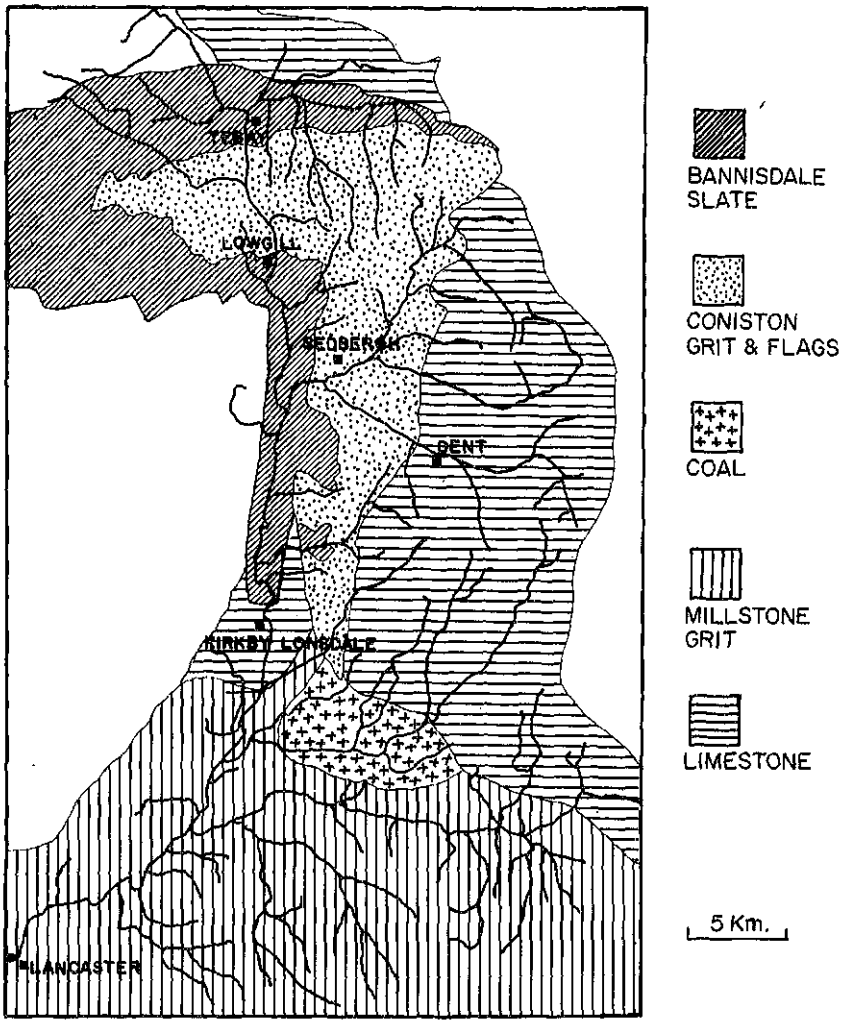

FIG. 2. Geology of the drainage area of the River Lune.

It is satisfactory to find in the Lune communities known from similar places elsewhere. This is particularly true of the headwater streams. In Borrow Beck, one of the Lake District tributaries, a two-minute collection yielded 74 specimens in 9 species, seven of which were Plecoptera. The other two were *Plectrocnemia conspersa* (Trichoptera) and, probably, *Simulium monticola*. The pH was 5·7 and there were 1·6 mg l^{-1} calcium. The fauna is similar to that of the Duddon in those parts where the calcium concentration was as low as this, though the pH in Borrow Beck is higher than usual in this type of water. Most Plecoptera grow throughout the winter and tide over the summer in the egg stage. Therefore, although streams of this type may be thickly populated in winter, they provide fish with little to eat in summer.

The highest station in Borrowdale (not to be confused with the better-known valley in which Derwentwater lies) was 420 m above sea level, the highest in the Howgills over 100 m higher than this. Calcium concentration in the latter region ranged from 5·8 to 8·6 mg l^{-1}, pH from 6·8 to 7·1 in summer, and species such as *Baetis rhodani*, *Gammarus pulex* and *Elmis aenea* (Coleoptera) extend up to the source. In addition there are two Ephemeroptera confined to high altitudes, *Ameletus inopinatus* and *Baetis tenax*. This community was not found in the Duddon system because water with high calcium and pH was nowhere found at high altitude therein, but it is known from Whelpside Ghyll. The same species were found in the calcareous tributaries in the Pennines, though total numbers were slightly higher and some species, notably *Gammarus pulex* and *Heptagenia lateralis* (Ephemeroptera) were relatively more numerous. This stands in sharp contrast with still water where the fauna in any given body varies greatly according to the amount of lime in it.

A series of stations down the length of the Borrow Beck was visited. Its waters soon became more calcareous as tributaries joined it and at an altitude of about 300 m there was evident enrichment from farming. Species typical of stony streams were added to the fauna at successive stations, *Baetis rhodani*, *Heptagenia lateralis* and *Polycentropus flavomaculatus* (Trichoptera) at the second, *Ancylus* at the third, *Rhithrogena semicolorata* (Ephemeroptera) at the fourth, *Gammarus pulex* and *Agapetus fuscipes* at the seventh.

In the gorge below Tebay large boulders that have rolled from the sides lie in the river and create a stability that must be rare on such a slope with so great a volume of water. This stability, combined with a productive water, much of it having by now traversed a long stretch of good agricultural land, results in a fauna richer in both individuals and species than that found anywhere else in the system. Net-spinning Trichoptera are abundant, *Hydropsyche siltalai* where the current is swift, *Polycentropus flavomaculatus* where it is not. *Ancylus fluviatilis* is numerous in sheltered patches and *Lymnaea peregra* and *Theodoxus fluviatilis* (Mollusca) occur. It is one of the few places in the system where not only will the bottom under these slow movers not shift, but where they are safe from stones rolling down from above.

In contrast, the unstable bottom of the alluvial plain is poor in species, though the few that are adapted to life on a shifting substratum occur in great numbers. The two most successful colonists are *Rhithrogena semicolorata* and *Baetis rhodani*. Near the edge, particularly if a shingle bed upstream projects towards the middle of the river and deflects the current, flow may be slight. Here *Ecdyonurus* tends to replace *Rhithrogena* and the number of species increases.

The community on the unstable bottom was described by Percival and Whitehead more than forty years ago, but the assemblage of species found in the Crook o' Lune among the moss appears not to have been described before. During the summer four species of Ephemeroptera are present in abundance: *Centroptilum luteolum*, *C. pennulatum*, *Procloeon pseudorufulum* (which must now revert to the name *bifidum*, which will be familiar to older workers), and *Baetis scambus*. A caddis, probably of the family Leptoceridae, and beetles of the genus *Deronectes* are fairly abundant, numbers of *Gammarus pulex*, *Lymnaea peregra* and *Theodoxus fluviatilis* are low and there is little else apart from an occasional stonefly nymph.

Elsewhere in the system these Ephemeroptera tend to occur in shallow water at the edge where there is little flow. J. M. Collins (1971) reports that *Centroptilum pennulatum* could not be found in the River Bela after engineers had straightened its banks. There appears to have been little activity of this kind in the Lune below Tebay, but between that town and Newbiggin the river bed has been modified extensively during the construction of a new road. The effect on the fauna has not been studied. Species diversity has no doubt been reduced but whether this is of importance to anyone except those interested in the groups affected is not known.

Collections in the Crook o' Lune were made once a fortnight and latterly once a week, almost without fail, from the spring of 1974 to the autumn of 1975. All but one of the four Ephemeroptera are summer species that probably undergo diapause development in the egg during the winter. The exception is *Centroptilum luteolum* which is present all the year round, though in small numbers in winter, and this, together with a sudden increase in spring, suggests that, of the last batch of eggs laid, some hatch soon but most not till the winter has passed. The fact that the nymphs which have overwintered are larger than their siblings which have just hatched makes interpretation of the life history difficult. The other species probably have between three and five generations during the summer, but other interpretations of the data are possible.

In October the last of the summer species emerges, and, apart from the few small *C. luteolum*, only eggs remain. At this time large numbers of *Baetis rhodani* appear and they persist until the spring, when their disappearance coincides with the reappearance in the active stage of the summer species. It is likely that they come from upstream. Emigration or passive transport downstream of *Gammarus* during winter has been observed in Germany by Meijering but this appeared to be a direct effect

of low temperature, whereas *B. rhodani* moves down before the water has cooled much. The phenomenon adds a further complication to measurements of productivity.

Discussion

That the Government supports an organization for the conservation of nature indicates an interest in living communities, for conservation cannot be effective until it is known what is to be conserved. Interest in rivers is heightened at the moment by plans to pump water from one bed to another, or to use a water-course as an aqueduct.

Descriptive biology has been out of vogue for some decades now and is not favoured by the Natural Environment Research Council at present (*NERC Report* for 1974-75, p. 93), but a descriptive phase in work of this kind is inevitable. In fact there is more than one: first the species then the communities must be described. The work of the FBA has embraced both phases and is still engaged on the first, mainly at the River Laboratory where the chironomids are being studied. Work on the taxonomy of Trichoptera larvae has been carried out elsewhere since Mrs Mackereth left.

In the study of the fauna, the recognition of communities is a convenience for the imparting of knowledge but open to the objection that it conveys a sense of rigidity that is not real. The communities described here in terms of species found and numbers of each are points in a continuum in three dimensions from which exploration to trace the modifications that follow alterations in the external conditions can be made. Such exploration frequently shows how one community merges into another. For example the community at the head of Borrow Beck is rendered distinctive by the absence of so many species typical of stony streams. These appear one by one down the length of the beck and the distinctive community gradually becomes a typical one. In the alluvial plain region changes can be observed by a collector passing from regions of swift current to those less exposed. In the gorge perhaps transition is more abrupt and the contrast between the fauna on loose stones between two boulders and the fauna under the lee of the boulders approaches more closely Marlier's idea of: 'une mosaique de petites synusies'.

In the process of delimiting the communities one starts the next process, that of explaining the differences; or at least one puts forward hypotheses that will require experimental verification later. It appears to be a safe deduction that the rich and varied fauna of the gorge region is due to the stability, a deduction confirmed lower down where, on the unstable bottom, only *Baetis rhodani*, a quick swimmer, and *Rhithrogena semicolorata*, adapted to cling to and move rapidly over the surface of a smooth stone, are able to thrive. Slow-moving snails must soon be crushed on stones that roll, and an animal that feeds on what it catches in a net requires a reasonably permanent support to attach its net to.

Substratum then is important, and so obviously is flow. The work of Minshall and Kuehne, followed by that of Sutcliffe and Carrick, has brought the importance of chemical differences much to the fore, and further advances in this field appear to be imminent. It is possible to establish that certain species occur only where the water is cold, others only where it is warm, but the assumption that a direct connection exists may be false. Confirmation from experiments is generally essential. Biotic factors have been somewhat neglected. J. C. Mackereth showed that the proportion of *Simulium* larvae devoured by *Perla bipunctata* is greater than the proportion in the living community. J. F. Wright (1975) has shown that another large carnivorous stonefly reduces the numbers of flatworms substantially. The scarcity of *Gammarus* throughout the system except in some headwaters is a notable feature of the Lune, and has been observed in other rivers. Predation has been thought to cause it. These, however, are isolated pieces of work and no extensive observations of the effects on each other of members of a community are on record.

It would have been possible to state that the fauna of the headwaters of the Lune was like that in most of the Duddon and Whelpside Ghyll, and that of the alluvial plain was like that described by Percival and Whitehead. The fauna of the gorge and of the Crook o' Lune would have required more detailed description as nothing exactly comparable had been described before. The time should come when it is possible to describe the fauna of a river in terms of communities already featuring in the literature. On the other hand, the search for explanations is likely to last for much longer.

The findings of the work on the River Lune were communicated to a seminar on the rivers of north-west Europe held at Amiens in November 1975. The proceedings of the seminar are to appear in special numbers of *Bulletin français de Pisciculture*. Statements in the publication are supported by the data from 19 of the 106 collections made. The full records will be lodged at the Windermere laboratory of the FBA and the Halton laboratory of the North West Water Authority.

References

Collins, J. M. (1971). The Ephemeroptera of the River Bela, Westmorland. *Freshwat. Biol.*, **1**, 405–9.

Gledhill, T. (1959). The life-history of *Ameletus inopinatus* (Siphlonuridae, Ephemeroptera). *Hydrobiologia*, **14**, 85–90.

Gledhill, T. (1960). The Ephemeroptera, Plecoptera and Trichoptera caught by emergence traps in two streams during 1958. *Hydrobiologia*, **15**, 179–88.

Gledhill, T. (1971). The water-mites (Hydrachnellae, Acari) of a stony stream. *Proc. 3rd int. Congr. Acarol.*, 159–67.

Hynes, H. B. N. (1941). The taxonomy and ecology of the nymphs of British Plecoptera with notes on the adults and eggs. *Trans. R. ent. Soc. Lond.*, **91**, 459–557.

Hynes, H. B. N. (1967). A key to the adults and nymphs of the British stoneflies (Plecoptera). *Scient. Publs Freshwat. biol. Ass.* No. 17, 91 pp.

Macan, T. T. (1957a). The life histories and migrations of the Ephemeroptera in a stony stream. *Trans. Soc. Br. Ent.*, **12**, 129–56.

Macan, T. T. (1957b). The Ephemeroptera of a stony stream. *J. Anim. Ecol.*, **26**, 317–42.

Macan, T. T. (1958). The temperature of a small stony stream. *Hydrobiologia*, **12**, 89–106.

Macan, T. T. (1960a). The effect of temperature on *Rhithrogena semicolorata* (Ephem.) *Int. Revue ges. Hydrobiol. Hydrogr.*, **45**, 197–201.

Macan, T. T. (1960b). The occurrence of *Heptagenia lateralis* (Ephem.) in streams in the English Lake District. *Wett. Leben*, **12**, 231–4.

Macan, T. T. (1962). Biotic factors in running water. *Schweiz. Z. Hydrol.*, 24, 386–407.

Macan, T. T. (1964). Emergence traps and the investigation of stream faunas. *Riv. Idrobiol.*, **3**, 75–92.

Macan, T. T. (1970). A key to the nymphs of the British species of Ephemeroptera. *Scient. Publs Freshwat. Biol. Ass.* No. 20, 68 pp.

Macan T. T. & Mackereth, J. C. (1957). Notes on *Gammarus pulex* in the English Lake District. *Hydrobiologia*, **9**, 1–11.

Mackereth, J. C. (1954). Taxonomy of the larvae of the British species of the genus *Rhyacophila* (Trichoptera). *Proc. R. ent. Soc. Lond.*, A, **29**, 147–152.

Mackereth, J. C. (1956). Taxonomy of the larvae of the British species of the sub-family Glossosomatinae (Trichoptera). *Proc. R. ent. Soc. Lond.*, A, **31**, 167–72.

Mackereth, J. C. (1957). Notes on the Plecoptera from a stony stream. *J. Anim. Ecol.*, **26**, 343–51.

Mackereth, J. C. (1960). Notes on the Trichoptera of a stony stream. *Proc. R. ent. Soc. Lond.*, A, **35**, 17–23.

Minshall, G. W. (1969). The Plecoptera of a headwater stream (Gaitscale Gill, English Lake District). *Arch. Hydrobiol.*, **65**, 494–514.

Minshall, G. W. & Kuehne, R. (1969). An ecological study of invertebrates of the Duddon, an English mountain stream. *Arch. Hydrobiol.*, **66**, 169–91.

Sutcliffe, D. W. & Carrick, T. R. (1973). Studies on mountain streams in the English Lake District. I. pH, calcium and the distribution of invertebrates in the River Duddon. *Freshwat. Biol.*, **3**, 437–62.

Wright, J. F. (1975). Observations on some predators of stream-dwelling triclads. *Freshwat. Biol.*, **5**, 41–50.