Dr W. L. Peters
with good wishes
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Running water

T. T. Macan

With 11 figures in the text

Any attempt to review work on running waters must start in 1967, the year reached by H. B. N. Hynes in his book *"The Ecology of Running Waters"* published in 1970. The time available must obviously preclude any attempt to bring that important work up-to-date, and my intention is to mention advances that appear to be highlights. I apologise in advance to those whose works are not mentioned. They have not been omitted for lack of merit but because they did not fit into a framework which within the space available must obviously be restricted. Moreover, the speaker invited to talk on a fixed date cannot pretend that he has searched the literature as diligently as the author of a book who is free to set his own deadline. No reference quoted by Hynes is also quoted here.

I shall not comment on the schemes of classification, to which Pennak (1971) has recently made an addition. It would be premature to assert which is likely to advance understanding most. Personally, I prefer to start with the animal community rather than with divisions based on physical and chemical variables in the environment. Before a community can be defined, taxonomic studies are indispensable, and this first stage is far from complete. Studies of the composition of communities, as I shall endeavour to show in a moment, make comparisons possible, and finally, in the third stage, tentative conclusions based on these comparisons must be tested experimentally.

Still water, or at least water that is still for long periods, must be rare, for temperature and wind set up and maintain slow currents wherever they reach water. In the slower stretches of a river, the R. Endrick (Maitland 1966) provides a good example, plants and animals that are found also in ponds may be common, and therefore it is expedient, at least in so far as it reduces the number of species that have to be discussed, to draw a line at a point where fine particles settle and rooted plants establish themselves. In reality, of course, there never is a hard and fast line, but a stretch, often long, in which the faster parts of the channel are floored with stones and the slower parts with fine material, or where silt settles when flow is slack and moves on in spates.

Almost all work on running water must start from a knowledge of what species are present and how numerous they are. Work of this kind on small streams, though not on rivers, has been popular in Britain in recent years (references up to that year in Arnold & Macan 1969; Jones & Howells 1969; Hawkes & Davies 1971; Langford & Bray 1969; Learner et al. 1971). In the present state of knowledge, it is preferable to restrict comparison to a small area. In Scandinavia (Ulfstrand 1967, 1968; Ulfstrand et al. 1971), the Pyrenees (Berthélemy 1967; Décamps 1967, 1968; Thibault 1971 a, b) or the Carpathians and the Danube basin (Kamler 1967; Kawecka, Kownacka & Kownacki 1971; Starmühlner 1969) the fauna is far from identical with that of the British Isles.

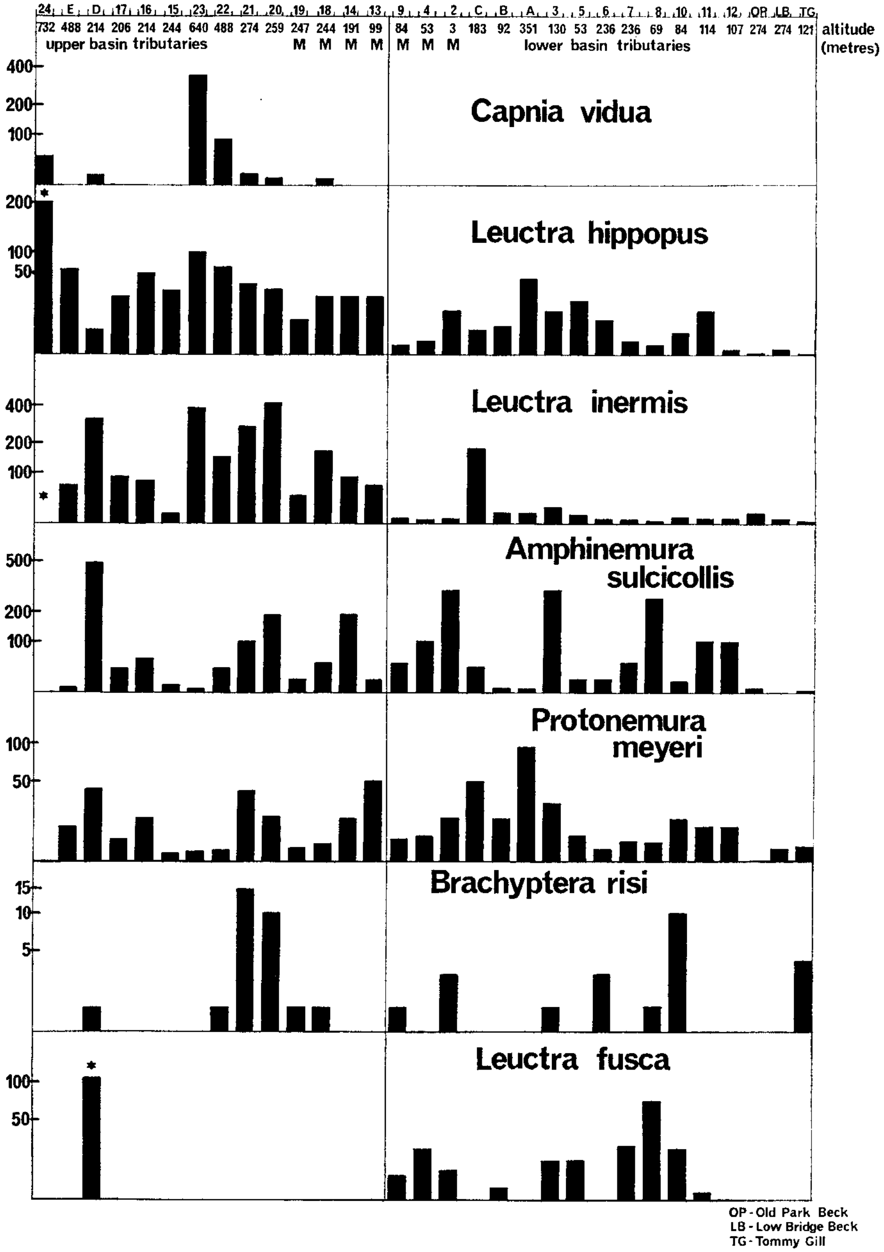


Fig. 1. Fauna of the R. Duddon system. The stations are roughly arranged so that those at the top lie to the left and those lower down to the right. M = stations in the main river. The vertical line separates the upper and the lower basin.

There are no doubt some exact vicariants among the species, but until one person has studied the fauna of two regions, satisfactory comparison will remain unlikely. What Illies (1966), who has contributed much to knowledge of it, designates region 14 in his (1967) Limnofauna Europaea is unusually rich in species, particularly in comparison with regions 17 and 18, the British Isles. Here too a comparison by one person who has worked in both regions is the ideal.

The River Duddon may be taken as the standard with which other British streams may be compared. It rises at an altitude of just over 700 m in the English Lake District mountains (or fells, to use the local Norse word, lest some object that mountains is a pretentious word for peaks that do not exceed 1,000 m), and flows 18 km to the sea in a bed that is stony all the way. The valley was broadened by a glacier and is separated into two basins by a stretch of harder rock that resisted glacial smoothing. Tributaries rise on the gentle slopes near

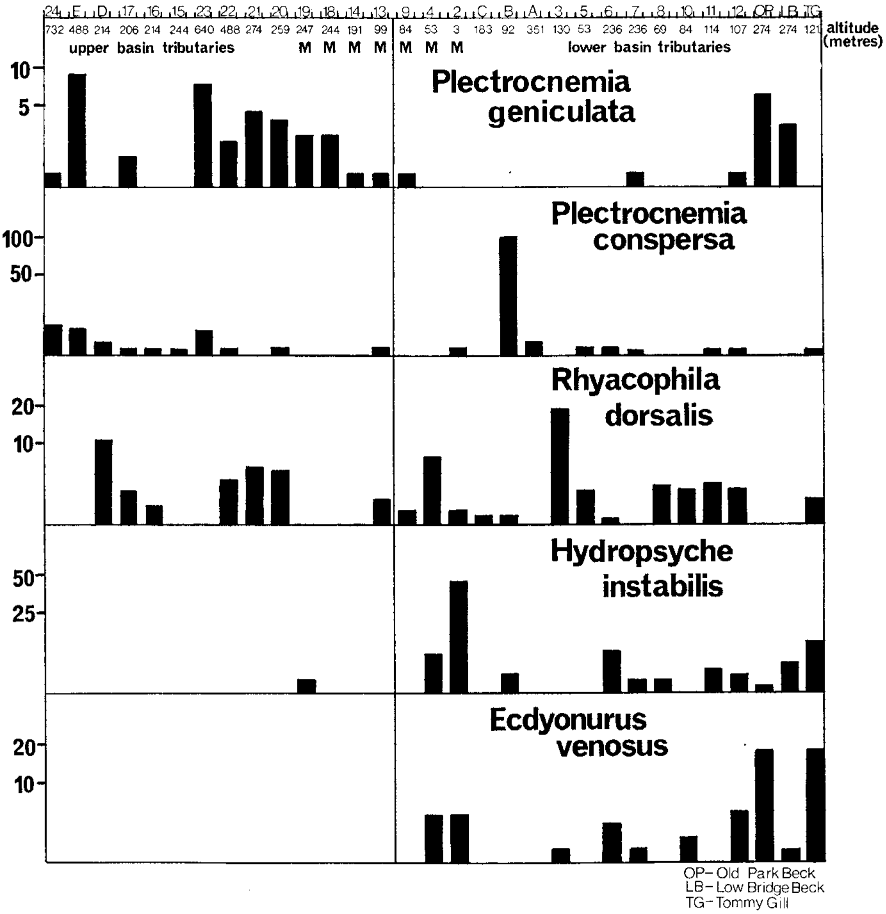


Fig. 2. Fauna of the River Duddon system (contd).

the tops of the fells, flow down the steep valley sides and then along a more gentle gradient in the valley floor. Summer temperature at 700 m is about 5° C cooler than in the lower basin. There are two farms in the upper valley and deciduous trees in the gorge of one valley only. Conifers have been planted recently in one area. In the lower valley there are twelve farms, two scattered villages and oakwood on the west side.

The system was surveyed by two American colleagues, Dr. G. W. Minshall and Dr. R. A. Kuehne who spent a year in England supported by fellowships.

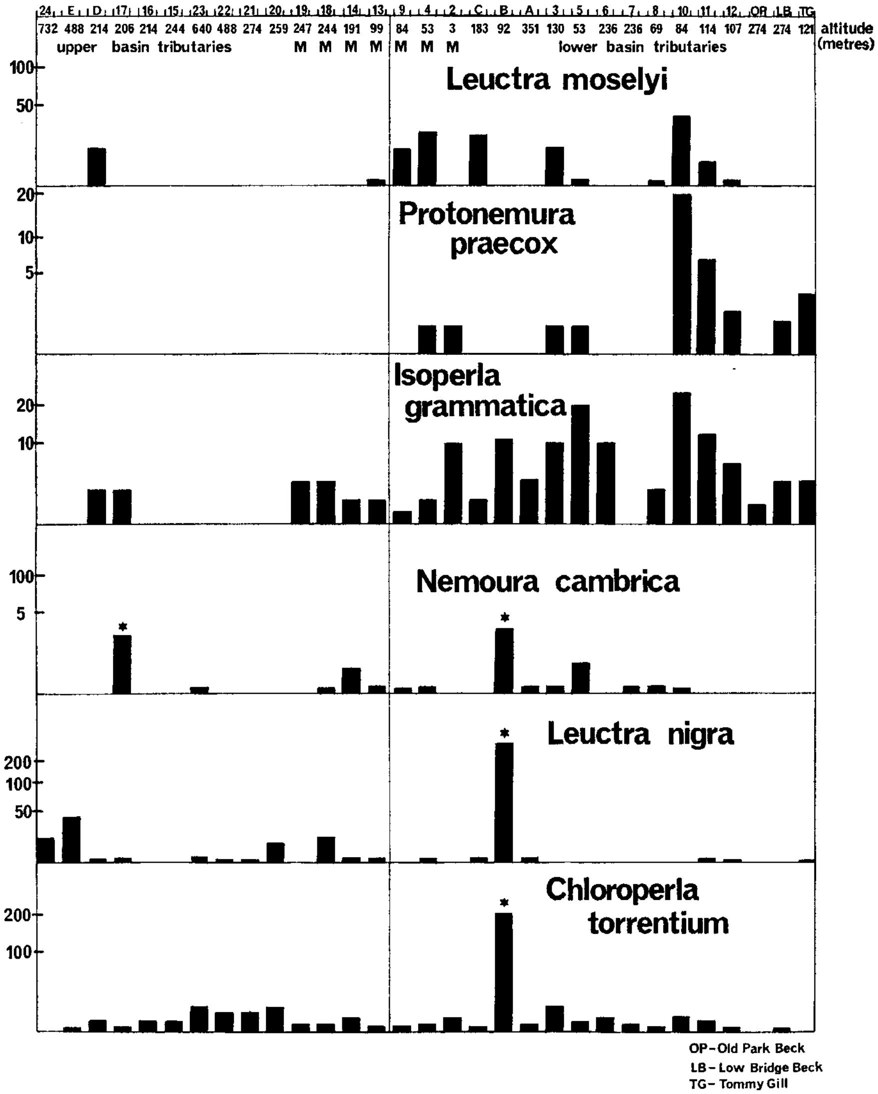


Fig. 3. Fauna of the River Duddon system (contd).

The occurrence of the fauna is shown in Figs. 1—5. Plecoptera predominate in the upper basin, the fauna of tributaries and main river being similar. Most of the species occur throughout the system and show a tendency to be less numerous in the lower basin. The striking feature of the upper basin is the absence or extreme scarcity of many familiar stream species: large carnivorous Plecoptera, Ephemeroptera, *Gammarus, Ancylus* and *Agapetus*. In studies of this kind absence is often more instructive than presence. The pioneer can only record what is present; statements about absence must await those who come later when enough work has been done to make comparisons possible. Most of the animals mentioned occur in the lower basin. In the last three stations, all tributaries on the east side, *Ancylus, Agapetus* and the large carnivorous *Dinocras cephalotes* are notably more abundant than elsewhere. There is, therefore, a distinct difference between the faunas of the upper and lower basins, and a less

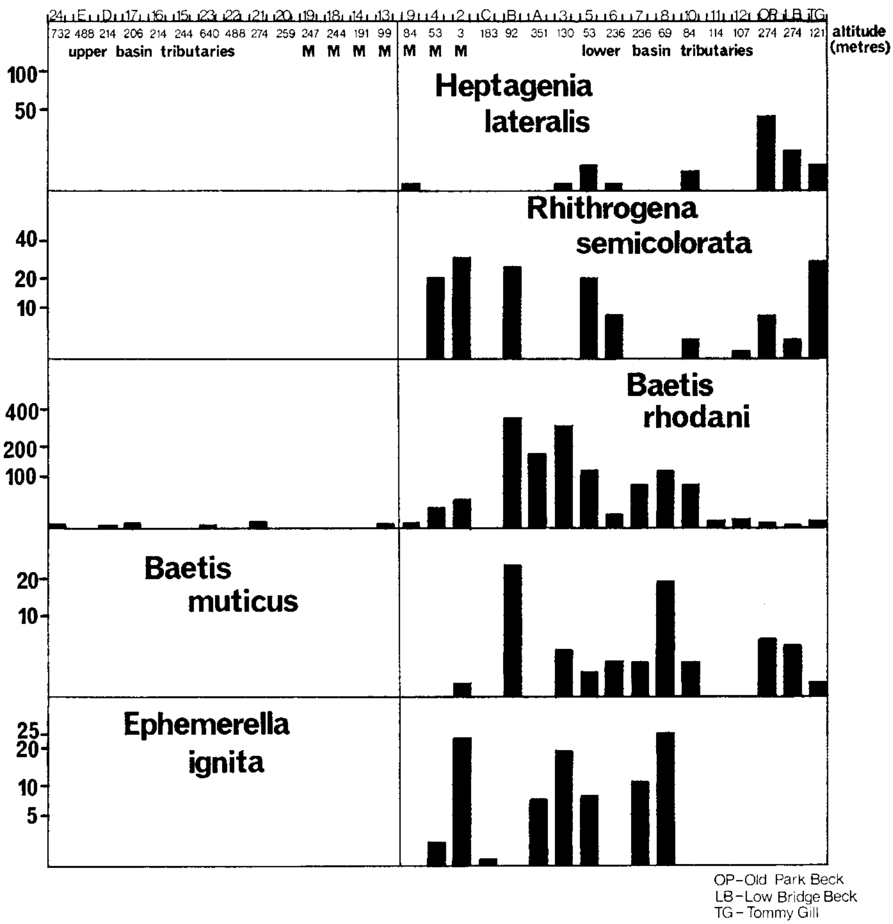


Fig. 4. Fauna of the River Duddon system (contd).

clearly marked one between that on the west side and that on the east side of the lower basin. These gross differences will be examined first and then attention will be directed to those irregularities of distribution which are marked with asterisks on the histograms.

If temperature were the factor responsible for this pattern of distribution, a similar fauna should be found in any other stream rising at the same altitude and having the same temperature. It is not. In Whelpside Ghyll, for example,

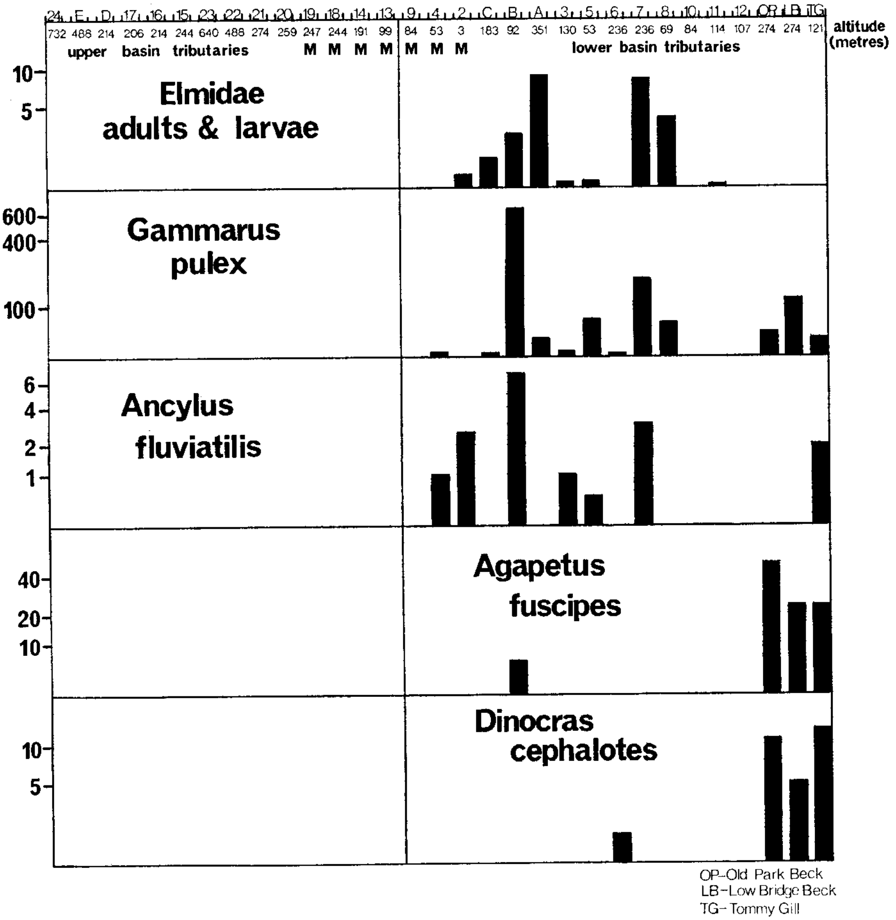
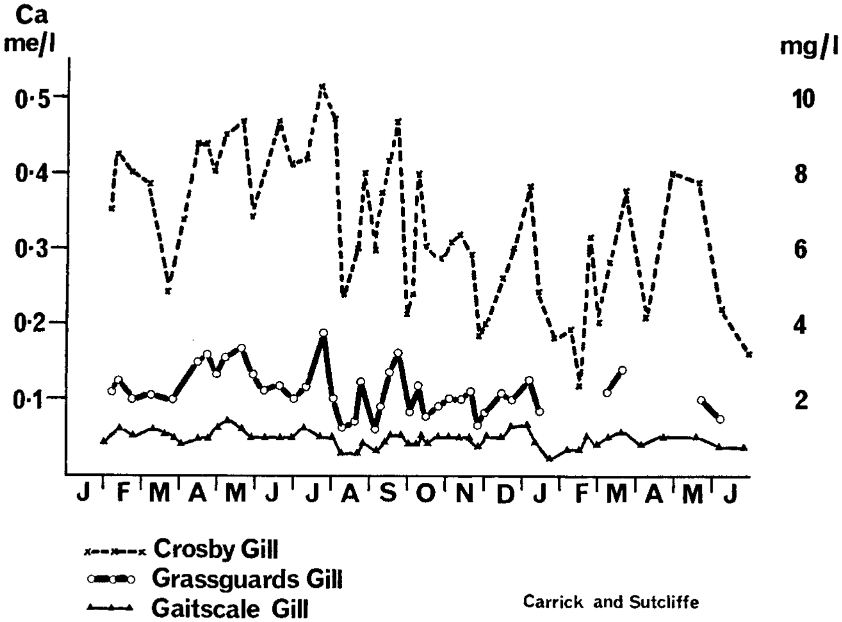


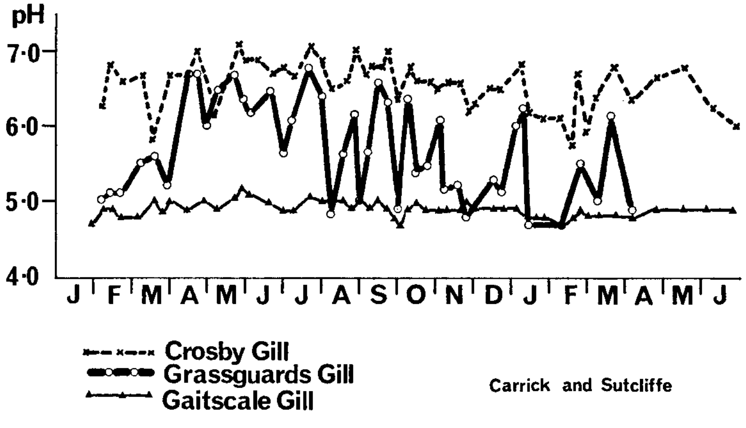
Fig. 5. Fauna of the River Duddon system (contd).

though the same preponderance of Plecoptera is found in the upper reaches, the common stream Ephemeroptera occur as well, and *Gammarus*, sparse in the stream, abounds in the spring from which it rises. Large carnivorous Plecoptera, *Diura bicaudata* at the top and *Dinocras cephalotes* lower down, are numerous and there are also two Ephemeroptera, *Ameletus inopinatus* and *Baetis tenax* which are found only at high altitudes in Britain.



Carrick and Sutcliffe

Fig. 6. Concentration of calcium in three tributaries of the River Duddon (from data kindly supplied by Mr. T. R. Carrick and Dr. D. W. Sutcliffe).



Carrick and Sutcliffe

Fig. 7. pH of three tributaries of the River Duddon (from data kindly supplied by Mr. T. R. Carrick and Dr. D. W. Sutcliffe).

Enrichment from farms and houses can also be ruled out, because the tributaries on the east side of the lower basin flow through land that is neither cultivated nor inhabited.

There does seem to be correlation with chemistry. Dr. Sutcliffe and Mr. Carrick who have been analysing a number of streams in the Duddon valley at frequent intervals in order to find out how concentration varies with rainfall, have kindly put their data at my disposal*. From their twenty-six stations three have been selected for presentation here in Fig. 6 and 7. Gaitscale Beck and Grassguards Beck are two tributaries in the upper basin. The former has one of the softest, most acid, waters in the basin, and calcium (Fig. 6) and pH (Fig. 7) remain consistently low. Grassguards has a higher pH (Fig. 7) except after heavy rain when there is a sharp drop. Calcium concentration drops too though less far. These two streams are typical of the upper basin. Both calcium and pH are consistently higher in the lower basin. Analyses made by Mr. J. HERON show that the calcium concentration near the source of the eastern tributaries is higher than in western tributaries. The calcium concentration of Whelpside Ghyll puts it into the same group as the lower basin of the Duddon system.

Another stream in the English Lake District, Ford Wood Beck is smaller, nearer sea level and bounded almost throughout its length by pasture which the farmer dresses with fertilizer. Ephemeroptera, *Gammarus, Ancylus, Agapetus,* and large carnivorous stoneflies, are all abundant, and the species of Plecoptera found in the R. Duddon, though present, contribute a smaller proportion to the total fauna. *Nemoura cambrica* is by far the most abundant stonefly, which may be attributed to the numerous packets of dead leaves in the stream, an association noted by HYNES in his pioneer taxonomic work on the group. When the stream was enriched by an overloaded septic tank, *Polycelis felina* and *Crenobia alpina,* previously scarce, became very numerous.

The other organisms are an important component of the environment of any species and cannot be ignored; on the other hand the community cannot be studied without detailed attention to individual species. Any unusual abundance or scarcity demands, therefore, a search for some factor with which there could be a correlation. Station 24 was the highest collecting point, and it is located at the top where the stream drains comparatively flat land in a channel in which grasses and sedges trail in the water and the bottom is of peat. MINSHALL & KUEHNE (1969) and MINSHALL (1969) record large numbers of *Nemoura cambrica* here, but re-examination of the material has shown it to be *N. cinerea,* a species which together with *Nemurella picteti,* occurs in similar places elsewhere in the fells. It also occurs in ponds. With the notable exception of *Leuctra hippopus,* most of the widespread species do not extend into this region of comparatively quiet flow. Station d is the only upper-basin tributary to be overhung with deciduous trees. The tributary in which station b lies flows into the lower basin from the west, but, in contrast to the others, which drain the flatter land beyond and reach the valley side with sufficient volume to have eroded deep gorges, it gathers only from the steep side. It has not volume enough to have eroded a well-marked channel, and flows between or under the boulders of the scree-covered slope, sometimes disappearing and reappearing in pools and seepages, many of which are slow enough to be filled with dead leaves from the oaks that cover the area. Allusion has already been made to the association between *Nemoura cambrica* and dead leaves. *Leuctra nigra* is frequently found in places where silt lies on the bottom.

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* now published, see SUTCLIFFE & CARRICK 1973.

Species may be grouped into those that are abundant everywhere in the system, those that are scarce everywhere, and those that are abundant at some stations only. Comparison with other water-courses reveals more about the habitats of the first two groups. For example, a single specimen of *Taeniopteryx nebulosa* was taken in the Duddon. Investigators of eight other British streams did not record it. MAITLAND (1966) found it in all parts of the River Endrick though never in abundance. BROWN et al. (1964) record that it is frequent in the streams in the Moorhouse Nature Reserve on the Pennines. The bedrock here is limestone though the calcium concentration in the water is not high. In contrast, in the calcareous streams of Lincolnshire, LANGFORD & BRAY (1969) encountered *T. nebulosa* more often than any other species and took it in numbers that were exceeded only by those of *Isoperla grammatica.*

This work has reached the second of the three stages mentioned earlier; the fauna has been described and environmental differences, chemical in the cases mentioned, which coincide with faunistic differences, have been uncovered. Until the third, the experimental, stage has been reached no more than speculation is possible. The explanation may lie in the field of physiology, the upper waters of the Duddon being so poor in ions that many common stream animals cannot take up from the water what they require. Another, in my view more likely, possibility is that the relationship is with food. Certain species feed extensively on algae and both ALBRECHT (1968) and THORUP (1970) have shown that in unshaded reaches both they and algae are more abundant. In most streams, however, allochthonous material is the main source of primary food. MINSHALL (1967) has provided figures for an American stream. EGGLISHAW (1969) has shown that animals are more numerous in places where detritus accumulates. In a swift stream there will, therefore, tend to be an increasing amount of food passing by with increasing distance from the source. HYNES and his Canadian school, whose work will be discussed in a moment, have, however, pointed out that stage of decomposition may be more important than total amount. EGGLISHAW (1968) has related decomposition with calcium concentration, showing that in a series of streams in Scotland the biomass of animals per gram of plant detritus increased as concentration of calcium increased. He also found that the disappearance of boiled rice in nylon sacks was the higher the more calcareous the stream in which it was tethered.

Much of the interpretation so far has been speculative. Passing from this to more firmly established facts, we approach work of this kind in yet another way, discussing ecological factors one by one. HYNES has followed the suggestions about food that he based on field observations with laboratory experiment in collaboration with KAUSHIK. They (1971) have shown that when leaves are first immersed in water they lose substances into solution. The residue is broken down by fungi. The rate of this process depends on temperature, and also on species, leaves of *Ulmus* and *Acer* decaying faster than those of *Quercus* and *Fagus.* An isopod and two species of amphipod, when offered a choice, preferred the species in an order which was the same as that based on rate of decay. The same animals consumed considerably more untreated leaf than leaf whose decomposition had been halted by heat or antibiotics (Fig. 8).

When leaves are immersed in water, the total dissolved organic carbon increases rapidly, reaches a peak after 30 hours, and then declines quickly (Fig. 9). Nitrogen is leached even sooner. The rise and fall of the bacteria in-

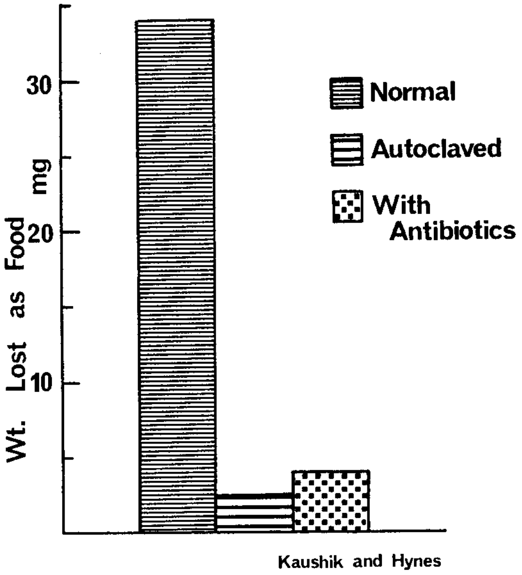

Fig. 8. Quantity of elm leaves consumed by *Gammarus* (Kaushik & Hynes 1971).

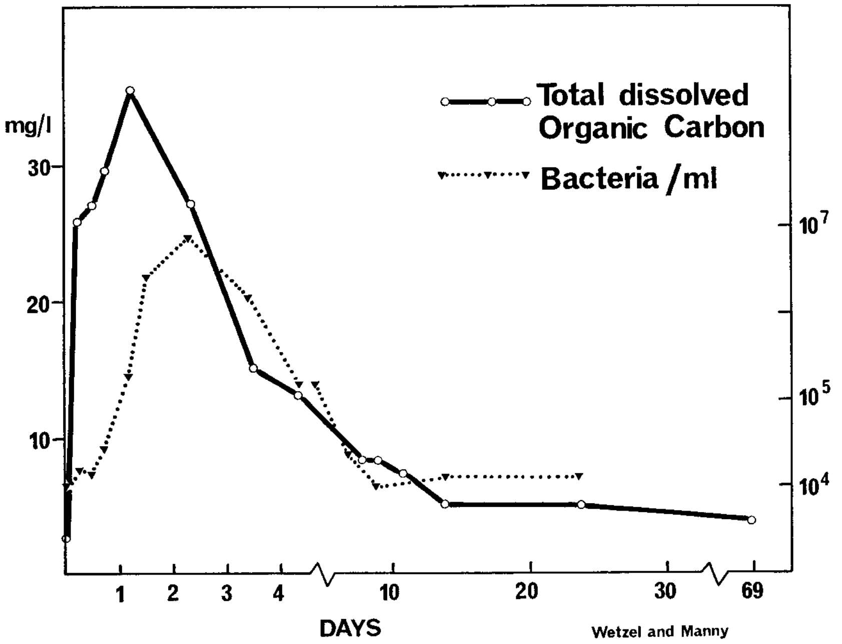

Fig. 9. Chemical and biological changes in an artificial stream after the addition of hickory and maple leaves (Wetzel & Manny 1972).

dicates that they are utilizing this dissolved matter which, through them, becomes available to filter feeders (WETZEL & MANNY 1972).

The chief filter-feeders are the net-spinning Trichoptera larvae and *Simulium*. The faster the current the more food passes a fixed point in unit time, but, above a certain speed, the greater the effort required to retain a foothold and the greater the difficulty of keeping a net in operation. EDINGTON (1968) mapped the rate of flow and the position of the nets of *Hydropsyche instabilis* in a suitable area of stream. He found very few in regions where the current was less than 15 cm/sec, and the upper limit, which was not established exactly, exceeded 100 cm/sec. In contrast most nets of *Plectrocnemia conspersa* were in regions where flow was less than 10 cm/sec, a few were found up to 20 cm/sec and none in faster flow.

EDINGTON confirmed experimentally that the larvae selected a place in a current by placing a baffle above the area in which they were numerous. Within a few days they had left the area of quiet water in the lee of the baffle to take up positions where the water flowed rapidly on either side of it.

Larvae of the Polycentropodidae occur in pools, whereas *Hydropsyche* inhabits rapids. EDINGTON finds that the riffle species are not found in pools, but that the pool species extend into riffles, where, no doubt, in spite of the fast flow overhead, they can always find a place between or under the stones where the current is suitable for their net-building. There seems no reason to doubt that other animals avoid current in this way, and that rate of flow has not the over-riding importance as an ecological factor that some earlier workers attributed to it. If it had, the disjunctions of the fauna of the River Duddon would have come where a tributary flowing torrentially down a valley side reached the flatter gradient of the valley floor, a type of distribution not observed.

AMBÜHL, in a classic study, showed that current is also reduced in the layers immediately above a flat surface, but DÉCAMPS, CAPBLANCQ & HIRIGOYEN (1972) have shown that the laminar flow observed by him becomes turbulent at velocities greater than any which he tested. TRIVELLATO & DÉCAMPS (1968) have studied the effect on flow of objects projecting from the substratum.

Current speed, oxygen concentration and temperature are related. Both DÉCAMPS (1967) and ULFSTRAND (1968) point out that some species occur in a slower flow at higher than at lower altitudes, but I have not seen any extension of the work in which AMBÜHL demonstrated an increase in oxygen consumption with increasing flow.

It may be expedient to discuss one factor only, when little is known of any other, but it can rarely offer a complete explanation of the range of a species because this is generally determined by several interacting factors. The one group whose ecology has been studied comprehensively is the planarians. Work started in the early days of our subject and there has been much contradiction and controversy since. PATTEE has recently made an important study of the points at issue. In much of western Europe *Crenobia (Planaria) alpina, Polycelis felina (cornuta)* and *Dugesia (Planaria) gonocephala* generally occur one above the other down the length of a stream, though, if flow is not fast, *P. felina* may extend to the spring with or without *C. alpina*. PATTEE (1966, 1968) established thermal death-points by means of a criterion more rigorous than any generally used. It is, according to him, the temperature at which births outnumber deaths, and the levels for the three species are:

C. alpina	12—14° C
P. felina	16—17° C
P. gonocephala	20—21° C

All can withstand much higher temperatures for a few days. These incipient limiting levels explain limitation downstream but not upstream. Pattee (1969a, 1970) investigated growth and reproduction, and his findings are presented in Fig. 10. If two species are subject to indiscriminate predation, whichever reproduces more rapidly is likely to be the only survivor. The differing rates of growth and reproduction, therefore, explain why *P. felina* and *D. gonocephala* do not extend further upstream, but it might be expected from these data that the temperature at which *P. felina* replaces *C. alpina* would be lower than it is commonly found to be. However, in further work (Pattee 1969b; Pattee & Bournaud 1970) it was shown that *C. alpina* is unaffected by current above the speed which *P. felina* tends to avoid and at which it is dislodged if it does not avoid it. The distribution of these three species can, therefore, be explained in

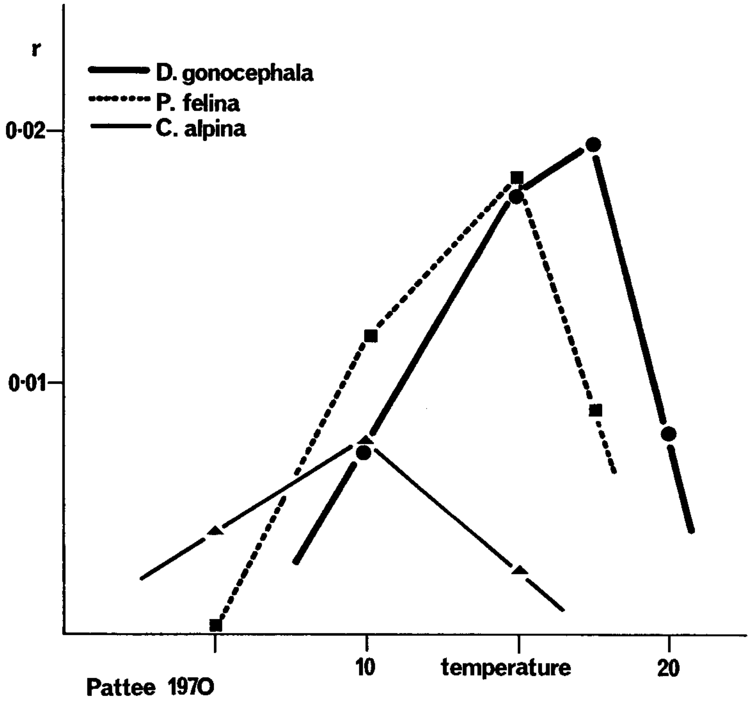

Fig. 10. Rate of growth at different temperatures of three species of planarian (Pattee 1970).

terms of lethal temperature, optimum temperature and competition with current speed playing some part. SCHLIEPER has shown that the rate of movement of *C. alpina* increases with rising temperature up to 15° C and then decreases, whereas *D. gonocephala* is moving fastest at 20° C. It may be surmised that different rates of activity of the three species at different temperatures influence the outcome of competition between them.

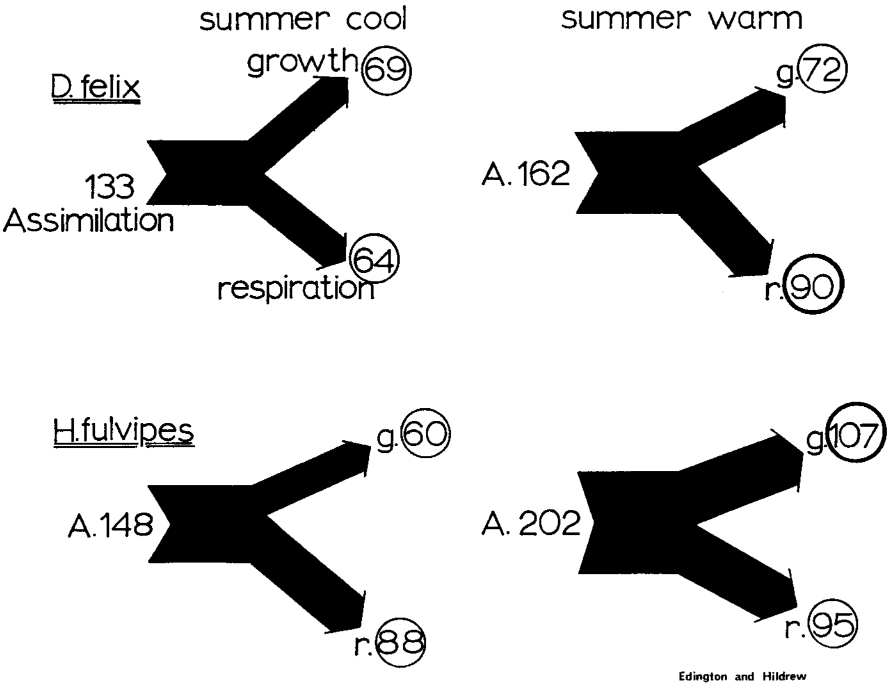

Fig. 11. Growth and respiration (in calories/g dry weight/24 hrs) of two hydropsychid larvae under different temperature regimes (EDINGTON & HILDREW in press).

This is the aspect which EDINGTON & HILDREW (in press) have investigated. They find six species of hydropsychid succeeding one another down the length of a river and they have studied particularly the top two, *Diplectrona felix*, which occurs in small tributaries, and *Hydropsyche fulvipes* which replaces it in slightly larger headwaters. When trees shading a small stream were felled and the water was warmed by the sun to which it was now exposed, *H. fulvipes* joined *D. felix*, which had been the only species up to then. The temperature lethal to both species was found to be well above that which they were likely to encounter in the field. Experiments on rate of respiration at different temperatures contributed more to an understanding of distribution. The consumption of oxygen by *H. fulvipes* was relatively independent of temperature over a range of 5—15° C but by *D. felix* only over one of 5—10° C. The experiments were repeated in temperatures which fluctuated in the same kind of way as those in natural waters, and results were similar. Rate of growth was also studied in the laboratory, where there was never shortage of food. Specimens were compared under "summer-warm" and "summer-cool" conditions, that is water in which the temperature frequently exceeded 15° C and water in which it rarely did so. The respiration rate of *H. fulvipes* was similar in the two regimes, but growth was less in the summer-cool water. Food was being utilized less efficiently. The same was true of *D. felix* in the summer-warm water, but it was growth that remained constant in the two conditions and oxygen consumption that rose (Fig. 11).

Three species in the genus *Gammarus* show a similar zonation in those parts of Europe where they all occur, *G. fossarum* being generally the commonest and sometimes the only species in the epirithron, *G. roeselii* being typical of the potamon, and *G. pulex* abounding in between in the metarhithron (KALLNBACH & MEIJERING 1970; MEIJERING 1971, 1972). The zonation is not as clear-cut as that of the flatworms and is all too often obscured by pollution. *G. pulex* appears to be most resistant to pollution, *G. roeselii* the least. *G. roeselii* tends to inhabit slower water than the other two. The main difference between *G. fossarum* and *G. pulex* is that, whereas both can maintain station in a fast stream in summer, when the temperature drops in winter *G. pulex* is carried downstream and *G. fossarum* is not. It is left in sole possession of the upper reaches while *G. pulex* is swept down to quieter regions. In the summer it regains the lost ground. Immediately below springs a temperature of some degrees above freezing may persist all through the winter, under which circumstances, if flow is not excessive, *G. pulex* may be able to maintain a fairly large population. MEIJERING concludes that the occurrence of these three species of *Gammarus* is to a great extent explicable in terms of their different powers of resisting the current. Competition must play a part too, for in Britain, where only *G. pulex* occurs, it extends from source to mouth in rivers where other conditions are suitable.

Various studies have revealed zonation which is likely to be due in part at least to temperature, though the experimental work to establish how temperature affects the organisms has not yet been done (BERTHÉLEMY 1967; DÉCAMPS 1967; MINSHALL 1968; SPENCE & HYNES 1971).

Drift is another topic that has been popular in recent years and around which controversy has centred but, as it has recently been reviewed by WATERS (1972), little need be added here. Important discussions of the subject may be found also in the papers of ELLIOTT (1967, 1971), BISHOP & HYNES (1969), HYNES (1970b) and ULFSTRAND (1968).

It is unthinkable that a review delivered in 1972 should ignore production. More than one worker since K. R. ALLEN has found that fish apparently eat more than is available (HYNES 1970a p. 420). HYNES (1968) explains this paradox by postulating that the collecting techniques used by these workers yielded no more than about 10 % of the fauna because it did not go deep enough. In collaboration with COLEMAN (1970) he experimented with a sampler consisting of two perforated tubes, one within the other, 30 cm deep. The outer was buried vertically in the substratum, and the inner was filled with a sample of the substratum, lowered into the outer and left to be colonized. A sock lying crumpled at the bottom of the outer tube could be pulled up around the inner one to prevent the escape of animals when the time came to examine the sample. The gravel in the inner tube was divided into four equal portions of which three were in sealed plastic bags that denied access to animals. The position of the quarter that was open for colonization varied, but, wherever it was, at the top, at the bottom, or in the middle, the number of animals that entered it was similar. The method is open to the criticism that the gap between the two tubes provides a route for vertical migration that is not available in a natural substratum. However, BISHOP (1973) has circumvented this objection by burying boxes at different depths. Each box is open back and front but the contents, substratum similar to that in which it lies, can be sealed by means of two shutters. These lie below the box when it is open but can be pulled up in grooves by means of two wires which end in handles at the surface. When the shutters have been raised to close the box, the whole contraption is dug out and removed for examination. BISHOP confirms the results of COLEMAN & HYNES, though he found a denser colonization near the top than lower down more often than they did.

It is clear that reliable measurements of production in streams can be obtained only by means of sampling techniques that penetrate much further into the substratum than those currently in general use. This is not the only development that is essential. Beds of substratum as loose as those studied by the authors named do not floor water-courses uniformly. In many parts of a stream studied by the author, the bottom a few centimetres below the superficial loose stones is either rock or what PERCIVAL and WHITEHEAD called cemented bottom, that is stones and gravel embedded in fine material that has settled and filled the interstices. On the other hand STUART has shown that beds of gravel loose enough for water to flow through freely are chosen by *Salmo trutta* as spawning beds. They must, therefore, be of fairly frequent occurrence. It would seem that a study of a stream bed to determine the extent of these different types of substratum will prove to be an essential preliminary to studies of production. The nature of the rock may be found to exert an influence on the fauna through the size and shape of the pieces into which it disintegrates.

COFFMAN, CUMMINS & WUYCHECK (1971) sampled a woodland stream at frequent intervals and worked out the amount of food of different kinds found inside the animals taken. The amount was converted to calories and it was found that 2—5 % was detritus, 17—21 % was of algal origin and 71—73 % was contributed by animal remains. As often to be noticed in studies of this kind, precise information about rate of intake and efficiency of digestion is lacking.

SCHWOERBEL (1972) is, it is deduced, summarizing the work of a team studying the Mettma Brook, work of which a full account is beginning to appear (see *Arch. Hydrobiol.* suppl. Bd. **41**, Heft 1, Sept. 1972). The brook is polluted and a reach is covered with *Sphaerotilus*, below which there is a zone densely colonized by *Simulium* larvae. These establish themselves in abundance at a distance from the *Sphaerotilus* such that dislodged fragments of this filament-forming bacterium have broken into particles small enough for them to catch and devour. The larvae may reach numbers of 120,000/m^2. Where the water is 50 cm deep this population secures only 1 % of the bacteria passing by, but, even so, it is space rather than food that is limiting numbers. The nutritive value of the bacteria drops with passage downstream. *Rhyacophila* preys on the *Simulium* larvae and as many as 800 pupal cases in a square metre have been counted, but mortality is high among pupae, possibly because of low oxygen concentration. There were no fish to prey on the *Rhyacophila.* Other work on consumption by algal grazers is mentioned.

SCHWOERBEL (1967) has made a study of the animals which inhabit the fine material below the superficial stones over which a stream flows. In a tenth of a cubic metre he records over 1000 tiny nymphs of Plecoptera and nearly 2000 similar specimens of Ephemeroptera and many other animals in an alpine stream with an unstable bottom in which the fauna was poor. In experiments he found most animals among particles whose diameter ranged from 0.5 to 2 mm, and a regular decrease in numbers with increasing and decreasing size of particle. Nematodes were the only group in which highest numbers were found in the finest particles, whereas nymphs of Plecoptera were most abundant in the coarsest. Where the grains were of various sizes there were more animals than where they were all of one size. Total numbers, particularly those of insect groups, fell with increasing distance from the water's edge up to 150 cm, the greatest distance tested. SCHWOERBEL stresses the importance of the stability of the hyporheal region, not only its physical stability but also its more equable temperature. It provides a refuge for cold-water stenotherms at times when the temperature of the open water is unfavourably high.

SCHWOERBEL and others who have studied this fauna are interested primarily in the true interstitial fauna and further study of those members of it that, when larger, are caught by conventional methods of collecting in running water is desirable. The present writer has observed that of a generation of pond-inhabiting Odonata some grow at a normal rate while others hardly grow at all. The number of large specimens was only very slightly less when they were being preyed upon by *Salmo trutta* than they had been when there were no fish in the pond. The suggestion put forward (MACAN 1974) is that the number of good feeding places is limited and that, when one is vacated because the occupier has been found by a fish, it is immediately taken over by a small specimen that had previously been living in a place where little food came its way. This specimen then grows rapidly. In other words there was a reserve from which losses of successful specimens could be made good. The question is whether the small specimens in the hyporheal constitute a comparable reserve; can they remain there for a long time, if necessary growing extremely slowly perhaps not at all, until there is a niche for them in the more open conditions above? The niche in this context may be a literal physical one. If they can, the calculations of any student of production who is collecting among the superficial stones and taking no account of possible replacement from below of specimens lost between two of his samplings, may be subject to large error.

The study by ILLIES (1971) of insects emerging from a stream is a contribution to production studies about which we shall learn more when we visit Schlitz.

Life histories, particularly of insects, are of intrinsic interest to the naturalist and to the physiologist. They are also of importance to the student of production, for delayed hatching of eggs, overlapping generations and diapause complicate his calculations. This, however, is a specialised topic for a general audience, and, as my time is running out, I must review it briefly. THIBAULT (1971 a, b) contrasts the Lissuraga, flowing from the Pyrenees, with streams in the north of England and in Scotland. Whereas the temperature of the latter may be below 5° C for up to 13 weeks in a year that of the stream in the south west corner of France never is. The number of weeks between 5° and 15° C is similar, and the French stream is above 15° C for longer than the British ones. THIBAULT compares emergence of Ephemeroptera, Plecoptera and Trichoptera with unpublished data from the north of England. The summer species, *Leuctra fusca* emerges later in France; the emergence period of the rest is longer in the south and starts earlier, often several months earlier. *Ephemerella ignita* has been attracting speculation for some years, because, obviously univoltine in some streams with up to ten months in the egg, rapid growth and emergence during a short period, it is to be found in all stages at all times of the year in others. THIBAULT (1971 c) trapped or netted subimagines in a cage from February to October and records a peak in April, May and June. He suggests that mature nymphs in late summer represent a partial quick summer generation, but this does not explain why the proportion in each size group remains almost the same with a maximum in the small ones throughout the summer. A steady influx of new nymphs could account for this. BOHLE (1972), in a painstaking study, demonstrates diapause development in *Ephemerella ignita,* and suggests that temperature alone operates. Diapause intervenes when the embryo reaches a certain stage, which it does in 40 days at 16° C and about 110 days at 7 · 2° C. Development takes much longer at higher and lower temperatures. Diapause development will proceed at comparatively high temperature as BOHLE showed by keeping eggs at constant temperature, but it is slow, eggs taking 400 days to hatch at 13 · 3° C, for example. At low temperature it proceeds more rapidly. Experiments suggest that it is completed in about 156 days at 7 · 2° C, 90 days at 5° C and probably less at lower temperatures. The optimum for post-diapause development lies between 19 · 2 and 24 · 1° C. The closely synchronized hatching and emergence recorded in northern England and Scotland is clearly related to the cold winters, during which all eggs complete diapause and start post-diapause development together when the temperature rises. The more scattered emergence recorded by THIBAULT is related to high winter temperature which does not bring all the larvae to the end of diapause development. High temperature cannot hasten development and it is possible that THIBAULT's postulate of two generations a year is incorrect. BOHLE's findings suggest that the irregularity is likely to be due to development taking more than a year rather than less. BOHLE (1969) has made a similar study of *Baetis vernus* and *B. rhodani.* The latter has no diapause but the former resembles *Ephemerella,* except that some eggs hatch in a relatively short time at comparatively high temperature. BENECH (1972 b, c) has studied the generations and the fecundity of *Baetis rhodani,* but it is not possible to do justice to his closely reasoned presentation in a few lines. He (1972 a) has also studied rate of development of eggs collected in the wild and reared at constant temperatures between 7 · 5° C and 27 · 5° C, length of day being constant. He calculates that at 3° C development would take about 130 days. Duration falls till it reaches its minimum of 8 days at 25° C, above which there is no hatching. Just below it too there is a high mortality which decreases down to about 15° C. BENECH also worked in southern France and it is interesting to find that ELLIOTT (1972) working in the English Lake District, and unaware that anybody else was exploring the field, obtained almost identical figures.

HUMPESCH (1971) finds that the emergence of *Baetis alpinus* is governed mainly by temperature and that light plays a part when temperature is constant.

BOHLE had to test many permutations and combinations of time and temperature and could examine specimens from a few sources only. Not all species are uniform. KHOO (1968), for example, finds that females of the large carnivorous stonefly *Diura bicaudata* from Lake Bala in Wales laid eggs of which some hatched after 2 or 3 months without diapause and others hatched after 9 or 11 months, having completed diapause development in the winter. In contrast all the eggs of specimens from the Afon Hirnant, a stream not far away, underwent diapause. KHOO also demonstrated diapause in summer in the nymphs of *Capnia bifrons* and in the eggs of *Brachyptera risi*. HARPER & HYNES (1972) report on types of life history in two families of the Plecoptera. *Brachyptera risi* is the only one at present known to undergo diapause in the egg, the nymphs appearing in late autumn and growing steadily to emerge in the following spring. *Capnia bifrons* is an example of those whose eggs hatch in spring and whose aestivating diapause is spent in the nymphal stage. After hatching in the autumn nymphs may achieve most of their growth in late autumn or early winter, grow steadily throughout the winter or pause in growth during the middle part of winter. These are the fast growers (F_1) of HYNES in contrast to the species which grow slowly (S_1) throughout the year without any diapause, though there may be a period when the final instar, awaiting conditions that trigger emergence, does not grow.

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