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THE ECOLOGY OF STREAM INSECTS

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When I was asked to write this review I had just completed a book on the ecology of running waters that surveys the literature to almost the end of 1966 (44). Citations of work earlier than this have therefore been kept to a minimum, and the bibliography given here should be regarded as supplemental to that of the book.

The subject encompassed by the title is enormous; there already exist many hundreds of often lengthy papers. It has thus been necessary to be selective of topics and to confine this review quite literally to streams as opposed to rivers. We are therefore considering only localities where the flow is fairly swift, the water shallow, and the substratum rock, stones or gravel, with only limited areas of sand or silt. This is a very loose definition of the habitat known as the rhithron, although it also includes spring brooks, sometimes called the crenon.

It is, however, a habitat which is usually dominated by insects except in very calcareous waters. Hydrida, Tricladida, Rotifera, Nematoda, Oligochaeta, Copepoda and Parasitengona are nearly always also present, and in hard water they are usually joined by Hirudinea, Isopoda, and Amphipoda and sometimes by Decapoda.

THE INSECT FAUNA OF STREAMS

Perhaps the most striking feature of the rheophile insect fauna is its world-wide uniformity. In this respect it falls short of the biotic uniformity of a few special habitats, such as hot springs or temporary pools but, in contrast to other biocoenoses that are dominated by a large variety of insects, it is remarkably similar on all the continents. Usually one finds many of the same families and life forms and often even the same genera wherever one looks on the planet, with the not unexpected additional fact that isolated land masses, such as New Zealand and Britain and recently glaciated areas, tend to have impoverished faunas. The Pleistocene glaciation of northwestern Europe, because it involved icecaps both to the north and on the Alps to the south, has resulted in some extra limitation of the variety of stream fauna there. There are, for instance, no European Corydalidae or Deuterophlebiidae, and Blepharoceridae are absent from the northern mountains. There is also some dichotomy between the northern and southern hemispheres, which differ almost completely in their families of Plecoptera (45)

and in that Leptophlebiidae in Australia and South America occupy some niches which in the north are inhabited by other families of mayflies.

Another particular feature of the stream fauna is that there are many families, or even larger groups, which are virtually confined to running water. These are to be found among the Ephemeroptera, Odonata, Plecoptera and Nematocera, together with some small taxa among the Heteroptera, Coleoptera, Lepidoptera and Brachycera.

These two features lead one to conclude that much of the insect fauna of streams is of ancient lineage, and that it has lived in the same type of environment for a long while. It is not surprising therefore that many genera display obvious adaptational modifications to their peculiar habitat.

Some of these modifications are morphological and involve such specializations as flattening, streamlining, friction discs, close application to the surface of stones and even the presence of hydraulic suckers. The adaptational significance of some of these features has been challenged on the ground that they are not confined to stream animals (72), but that is really a spurious argument. Similar modifications may occur in response to quite different conditions for the same or for different reasons. Even within the stream environment, flattening allows some animals to live on stones, e.g., *Psephenus* larvae, while the flattening of others, e.g., many Heptageniidae, permits them to creep under stones into shelter from the current.

Our understanding of the exact function of many of these morphological adaptations has been greatly clarified by Ambühl's (2) study of flowing water in relation to microhabitats, and his demonstration of a boundary layer of almost static water on stones, and of spaces filled with dead water downstream of and below them. Bournaud (10) has shown that most of the modifications enable animals to avoid many of the effects of flow by keeping their bodies down in the boundary layer away from the force of the current. He also stressed that behaviour is more important than morphology, and that cryptic habits are characteristic of most stream insects. These can also lead to morphological adaptations, such as the long narrow bodies of many Plecoptera and Ephemeroptera (Leuctridae, Capniidae, Chloroperlidae and some Gripopterygidae, Leptophlebiidae and Baetidae). These nymphs burrow into the gravel, and thus avoid any contact with the current. In fact the only insects which regularly expose themselves to fast water and swim against it are the streamlined Baetidae, such as most species of *Baetis* and *Centroptilum*.

Other important changes which are associated with stream life have occurred in respiratory physiology. Normal streams are always well oxygenated because of their turbulent flow; and they are usually cooler, during summer, than bodies of still water. Associated with this many stream insects, all of which must use dissolved oxygen as they cannot go to the surface to obtain gaseous air, are unable to tolerate low oxygen tensions. Moreover, many of them have lost the ability to ventilate, by flapping gills or undulating their abdomens, and have come to rely upon the current to renew the oxygen supply at their body surfaces. Some can still ventilate *in ex-*

tremis, but they are unable to keep it up for long; they are therefore tied to water movement, high oxygen content and low temperature, or at least to any two of these factors, and this confines them to running water (46). Only in the Arctic and at high altitudes does the distinction between stream and lakeshore faunas tend to become blurred because the lakes are very cold at all times (18, 92). But even there, there are some genera, e.g., *Rhyacophila*, which remain restricted to streams, probably because of their respiratory physiology, and others are so confined by their feeding habits, which are considered below.

These modifications, and differences in levels of adaptation between species, go some way toward explaining the close association with particular types of substratum which are so characteristic of many stream insects. For instance, water pennies can attach only to rocks or fairly large stones, the suckers of Blepharoceridae and the friction discs of many other insects can be applied only to fairly smooth surfaces and are rendered useless by a thick covering of silt or diatoms, and Leuctridae need gravel in which to burrow, and are eliminated by any considerable admixture of fine sand.

There are, however, also many unexplained associations with particular types of substratum, and certain species are always found in or on particles of a certain size for no clear reason. A recent study of this type of preference is that of Eriksen (33), who showed that nymphs of *Hexagenia limbata* burrow only into fine substrata, while *Ephemera simulans* chooses gravel, although these two mayflies are superficially fairly similar. The result is that, in the mozaic of types of substratum and areas of shelter on a stream bed, there is a corresponding faunal mozaic (90). This makes quantitative data extremely difficult to obtain, and the now almost classical example of this problem is the study of a single riffle in a Californian stream which demonstrated that an almost impossibly large number of samples is needed to determine the number and weight of animals present per unit area (71).

Differences in temperature tolerance, coupled undoubtedly with competition between allied species, also result in zonation along the lengths of streams, as species replace one another either wholly or in part. This has led to some controversy in recent years about the possibility of defining distinct zonal biocoenoses in terms of their invertebrate faunas. A general conclusion seems to be emerging that such a classification is not justifiable except in the most general way, because specific changes occur for different reasons at various points along a continuum. Nevertheless, the close association of particular species with definable microhabitats is well established, and it often results in a clear zonal distribution along streams within the limits of certain taxa. Several examples have been published during the past three years (18, 64, 65, 93-95).

Generally speaking, it is the most highly adapted insects which are the most abundant and important members of the stream fauna. Such are the Plecoptera, Baetidae, Rhyacophilidae, net-spinning Trichoptera (of which more will be said below), Simuliidae, and Elminthidae, the last of which are

remarkable among the water beetles in using plastron respiration. To these we should add many Diamesinae and Orthocladiinae of whose adaptations we know little, although the fact that many of them are confined to streams probably indicates at least respiratory adaptation. Ross (78) has stressed that the primitive families of Trichoptera are confined to streams, and it seems to be true that streams have become refuges for many primitive, but nonetheless highly adapted, types. One has only to consider the Plecoptera, Ephemeroptera, Corydalidae and several highly specialized families of Nematocera to appreciate this point. Most of the insects which live actually out in the current-swept areas are survivors of primitive groups, and they have been joined by a comparatively few more highly evolved insects. The latter include some Rhagionidae, Tabanidae (*Haematopota*) and a very few Schizophora (e.g., *Limnophora*), a few genera of Pyraustidae (e.g., *Cataclysta*) and Hemiptera (some Naucoridae and *Aphelocheirus*), and some beetles, among which only the Elminthidae are important. The widespread Hydræinidae spend only their adult lives out on the stream bed, and the majority of higher Diptera which are associated with streams (e.g., Dolichopodidae, Empidae and most Tabanidae) and Coleoptera (Dytiscidae and Gyrimidae) occur only in sheltered backwaters or at the extreme edge of the water. This perhaps indicates the difficulties presented by the stream environment and the problems faced by more highly evolved forms in replacing well-adapted primitives from niches in a severe habitat. A parallel example is the persistence of the ancient Phyllopora in temporary pools in the face of competition from the more modern Crustacea.

Particularly striking is the almost complete absence of Hymenoptera which are so common almost everywhere else. Only the genus *Agriotypus*, which parasitizes pupae of Goerinae, has actually succeeded in invading streams, although some stream insects are liable to parasitism by other Aculeata during stages that are not spent under water (11). The absence of parasitoids provides a great contrast with the terrestrial situation.

Among the important groups, the adults of Elminthidae alone are aquatic and long-lived. In nearly all the others adult life is terrestrial, short, and concerned only with breeding and dispersal, although even the latter is in some dispute. Many imagines fly weakly and live for a very short while, and some stoneflies do not fly at all. There is some evidence that black fly adults may move considerable distances (8), but set against this is the fact that at least some species show local chromosomal varieties (22) which indicates little gene exchange between populations. Similarly, many species of stonefly have very limited areas of distribution (76). We clearly need more investigation into the importance of the adult stages in dispersal.

Food

Many stream insects feed on the periphyton growing on stones, which is an unusual diet for insects; but it is available in large amounts only to those species, such as Psephenidae and Glossosomatinae, which spend all or much of their time on exposed, and therefore lighted, surfaces. Even they appear

to be not particularly selective as they also eat organic detritus trapped in periphyton, and a great many other insects feed primarily on dead organic matter lodged in the substratum. Egglisshaw (25) has demonstrated very elegantly that the micro-distribution of most of the fauna is correlated with the amounts of plant debris present and that the insects seek it out and concentrate upon it; and many studies [e.g. (13, 67, 92)] have emphasized that allochthonous plant material is the most important primary source of energy for the stream fauna, and is made available to higher trophic levels through the activities of detritus-feeding insects. The productive capacity of the valley is therefore more important than the primary production in the stream itself, which may, because of shading, be very low and yet apparently support a dense fauna.

Drifting detritus, plankton and washed-up benthic organisms are also an important source of food for many insects, and this has resulted in a number of specializations which are found only in stream dwellers. They range from the sticky strings of saliva hung between the arms of the hydra-like tubes of *Rheotanytarsus*, through the fringes of hairs on the forelegs, or even the mandibles, of some Ephemeroptera nymphs, to the elaborate nets and associated structures built by many campodeiform Trichoptera larvae. Perhaps the best known of these passive feeders are the larvae of Simuliidae, whose premandibles bear elaborate double fans (37). The fans are held open by the current, up into which the larvae thrust them from their shelter in the boundary layer, and this imposes a lower limit of rate of flow in which the larvae can feed. It is about 20 cm/sec for *Simulium ornatum* (39) and this alone restricts the species to certain types of locality. Feeding is apparently quite unselective, so the quality of the available food affects the population, and where large numbers of larvae are present they remove microseston from the water very rapidly (62). They also catch very tiny particles so, in contrast to most insects, they can complete their life cycles on suspensions of bacteria (34). It seems very probable that, in some situations, bacteria form the bulk of their food, thus giving the stream community almost direct access to organic matter coming from the watershed in solution.

The nets of Trichoptera have been described by many authors; two recent papers are those of Kaiser (48) and Sattler (80); and Gibbs (35) discusses the manner in which some of the more elaborate structures in which they occur may have evolved. In most of them the mesh apertures are quite large, measurable in tens of microns (24), so the food particles caught are large and varied, and the common Hydropsychidae are more or less omnivorous. But in at least one species, *Micrasema ulmeri*, the meshes are only $3 \times 19 \mu$ (80), so very small particles must be collected. We do not, however, know how common are such very finely meshed nets.

It has been shown that nets, like the fans of black fly larvae, are efficient only in a current, so it is not unexpected that Edington (23, 24) was able to show that when he interfered with the flow in field situations the larvae moved to new locations and constructed new nets. They, like *Simulium*, are

restricted to certain current speeds by their feeding mechanisms, and different species are tied to different ranges of speed by the varying structures of their nets (24). At least the genus *Hydropsyche* is also limited by temperature; two species which Kaiser (48) studied became inactive below 8° C. Edington also showed that where *Hydropsyche* is abundant the nets are very evenly spaced downstream of one another, although often closely side by side, in such a way that no net is fishing already filtered water. How this distribution is achieved is not certain, but it may be relevant that the larvae are known to stridulate, an ability which is rather rare among larval insects (47).

Clearly, also, these passive feeders are benefited by conditions which make the water particularly rich in food particles. Several studies have shown that they are often very abundant just below lakes, which are a source of plankton; recent ones are those of Cushing (16) and Ulfstrand (92). It can also readily be observed in Canada that beaver dams and pestilential swarms of black flies go together. As might be expected from our knowledge of seasonal changes in lake plankton, the effect is more noticeable in the summer than at other times, Ulfstrand found that the fauna of lake outflows in arctic Sweden was always much denser by a factor of ten or more, than that of other streams during July and August, but that this did not apply earlier or later in the year. In Sweden, the increase was caused by Simuliidae, and in Canada Cushing recorded a similar, but longer, summertime maximum of campodeiform Trichoptera. It is also interesting to note that some species of black fly seem to occur only near lake outlets. Possibly this restriction is not universal and it may have nothing to do with food. Some mayflies are similarly confined in Swedish Lapland but not elsewhere in their geographical ranges, and others are not found below lakes there although they occur in other streams (92). This indicates that temperature is the operative factor, as lakes warm up more slowly, become warmer and remain warm longer than streams. Possibly the same factors influence some of the species of Simuliidae.

LIFE HISTORIES

Stream temperatures near springs or ground-water seepages are often remarkably stable, and even far downstream of such sources they are much more uniform than they are on land. This is partly because evaporation and, very often, shade from riparian trees keep temperatures down in hot weather, and partly because, even during severe winters, the water continues to flow under an insulating layer of ice and snow. The habitat of benthic insects therefore never freezes, and Schwoerbel (83) has shown that the winter temperature a few centimetres down in the substratum may be several degrees higher than that of the overlying water. Even during the Canadian winter, after many weeks of freezing weather resulting in 0° C in the water and tens of centimetres of surface ice, we have recorded temperatures as high as 1.3° C 60 cm below the gravel surface.

This lack of frost, coupled with the fact that autumn leaf-fall provides a readily available and abundant supply of food to the biota, has allowed the evolution of many species which are active throughout the winter. These do much of their growing when they are least likely to fall prey to fishes which are rendered sluggish by the cold.

Many investigators, during the last two decades, have demonstrated that there are species of Plecoptera and Ephemeroptera that grow actively during the winter, and Raušer (76) concludes that the threshold temperature for many Plecoptera must be very near 0° C. Ulfstrand (91) found that *Ameletus inopinatus* and *Leuctra hippopus* undergo most of their nymphal development while the streams are iced over in northern Sweden and, although the growth of many species is slowed down or even stopped for a while by intense cold (29, 86), many others continue to grow through the winter. In the mild climate of West Virginia the wing pads of *Epeorus* grow fastest in the coldest weather (66), and in Scotland, which also has mild winters, differences in the severity of different years have apparently little influence on the rates of growth of several stonefly and mayfly species (26). It is clear therefore that in these two orders there are a number of genuine winter species, the adults of which emerge in the early spring. These are extreme examples, but there does seem to be a general tendency towards cold stenothermy among many stream insects. Macan (61) found that *Heptagenia lateralis* is restricted to streams that do not exceed 18° C, because it needs a sufficiently long time between its rather high temperature threshold for growth and its fairly low lethal temperature. So, although the eggs are known to tolerate high temperatures on lake shores, warm streams heat up too fast to allow the species to complete its nymphal development. There are other species whose distribution is probably controlled in a similar manner, and it is becoming clear that in many instances it is the pattern of temperature change rather than the absolute temperature attained that is the important factor.

Most of the cold-water insects are univoltine, but in extreme environments some species which are not able to grow adequately at the lowest temperatures have become opportunistic, and make the most of such short slightly warmer periods as occur. Thus, *Diamesa valkanovi* in a Norwegian glacier brook appears to have a two-year life cycle near the glacier but to be univoltine in the lower reaches (79); and *Rhyacophila evoluta* is able to go into cold-induced diapause at any stage of its life history, and so take one, two or three years to develop. This allows it to inhabit a wide variety of streams in the Pyrenees, in contrast to less adaptable animals (18). At the other end of the scale, the cool-water, as opposed to cold-water, bivoltine species of *Baetis* can avoid the effects of very warm water in southern or low-altitude streams by increasing the gap between successive generations and spanning it by remaining in their eggs (75).

Diapausing eggs that avoid the consequences of high temperature seem to be a common device among stream insects, and they are found in many

species of Ephemeroptera, Plecoptera and Simuliidae, especially *Prosimulium*. Sometimes indeed the diapause is so long that it allows the nymphs to hatch at the most favourable season for early growth, nearly a year after oviposition. Khoo (52) has shown that this applies to the northern holarctic stonefly *Diura bicaudata*, and that, very interestingly, it seems to be losing this peculiar characteristic in lowland lakes where it is not necessary.

Khoo (50, 51) also showed that *Capnia bifrons*, a winter stonefly, has a nymphal diapause which is induced by temperatures above 9° C, or by increasing day-length at lower temperatures, and that the nymphs avoid the warm weather by remaining deeply buried in the substratum in this condition. We now know that other Capniidae, e.g., *Allocapnia*, behave similarly, and it is a small addition to such aestivation that permits many insects to avoid the consequences of drought. Thus, many cold-water species, such as *Prosimulium gibsoni*, *Allocapnia pygmaea* and *A. vivipara*, which inhabit temporary streams [(3, 15) and personal observation] survive the dry season as eggs or diapausing nymphs, and some Trichoptera aestivate as prepupae (15). Where, however, drought is very severe and prolonged, as in Rhodesia, it seems that only the last mechanism is possible, and the faunas of temporary and permanent streams differ little because of rapid recolonization (38). This can, however, occur in a warm climate in a way that it could not where the end of a long summer dry period is also the end of the flying season for adults.

In addition to the peculiar cold-water species, there is also a corresponding population of warm-water insects that avoid the winter season as eggs, pupae or very small nongrowing nymphs. The majority of such species are Simuliidae (3, 12), but they include some Trichoptera and Ephemeroptera. Such are *Glossosoma intermedium* in northern Sweden (91) and *Chitonophora* sp. (larvulae) and *Ephemerella ignita* (eggs) in Austria (75). Generally speaking, the number of species of these summer insects is lower than that of the winter species, a fact which often results in the greatest biomass being present in the spring at the end of the growth of the latter (26, 97). There are, however, often two peaks in numbers of individuals, in early winter and early summer, respectively, as the two groups begin their periods of growth. It is also often possible to observe the apparently direct temporal vicarious occurrence of similar species, as did Egglisshaw & Mackay (26) between *Leuctra fusca* and *L. inermis*, and *Rhithrogena semicolorata* and *Ecdyonurus* in Scottish Highland streams.

An interesting fact in association with the existence of closely related cold-water, cool-water and warm-water species is that in the Elminthidae there is a decrease in size from the first to the last. Steffan (85) has shown that this applies to several genera in central Europe, and he has suggested that it may be connected with better oxygen relations or longer larval life at the lower temperatures. An analogous situation is known to occur in several species of mayfly in which early-emerging individuals are larger than later-emerging ones of the same or of a subsequent generation. This is probably

connected with the temperature at which the nymphs have grown, but there may be complicating factors associated with photoperiod. Khoo (50, 51) found that the adults of *Capnia bifrons*, which emerge from February to May in Wales, become progressively smaller as the season advances, and that exposure of the nymphs to long photoperiods hastens the appearance of adult characters in immature nymphs. The smaller adults also have relatively shorter wings than the larger ones, and this may provide an explanation for the occurrence of short-winged specimens of many insects at high altitudes (79). Presumably, the cold does not permit them to grow as fast as their lowland relatives, but the onset of summer hastens development to the point of emergence before they are large enough to have large wings. It has often been shown that early emerging species emerge later at higher latitudes and altitudes (9, 32, 88); and it is also known that species with long emergence periods at low altitudes have shorter ones at high altitudes, and that altitude makes little difference to the times of emergence of autumnal species (17). These findings would fit with the assumption that emergence times are under the dual control of temperature and day-length, and presumably their relative importance varies from place to place. For example, Minshall (69) concluded that the time of emergence of *Epeorus pleuralis* from near the source of a spring stream in Kentucky must be controlled by photoperiod as the temperature of the water varies very little; and photoperiod is almost certainly the over-riding factor for the winter stoneflies which emerge through small thaw holes in ice-covered streams.

Photoperiod also seems to be important in controlling the rate of maturation of eggs, and in synchronizing the timing of life cycles of species which inhabit varied water bodies. There are two well-worked examples among the Trichoptera. In southern England, *Limnephilus lunatus* inhabits both spring-fed watercress beds and nearby streams. The relatively high winter temperature of the spring water permits earlier emergence from the watercress beds than from the streams. But the females from both types of locality mature their eggs slowly on land in such a way that both groups are ready to oviposit in the autumn (36). In the Pyrenees, *Allogamus auricollis* occurs over a wide range of altitude and, as is usual in such situations, the low-altitude specimens emerge earlier than the high-altitude ones. They then mature their eggs away from the water. The high-altitude specimens are much smaller than their downstream sisters, probably because they spend less time in the fifth larval instar, and they have fewer eggs. But their eggs are mature at the time of emergence, so oviposition is more or less synchronized at all altitudes (18). Control of oogenesis by photoperiod would appear to be the most reasonable hypothesis in both these instances.

Differences in temperature tolerance with particular reference to life histories therefore account in large measure for the altitudinal, longitudinal, and seasonal distribution of species in streams as well as for the often reported relatively great importance of Plecoptera at high altitudes and latitudes (9, 18, 19, 49, 84, 92). They also explain the frequently observed coex-

istence of closely allied species in the same habitat, as it is possible to avoid direct competitive exclusion by having life cycles out of step with one another. This can occur even when emergence and oviposition times coincide or overlap, because of different eclosion and growth patterns related to different seasons. Such temporal succession may occur even among coexisting multivoltine summer species, as was shown by Obeng (73) among *Simulium* species in Wales. She found, for example, that succeeding generations of *S. reptans* and *S. variegatum* were out of phase, so that small larvae of one accompanied large larvae of the other throughout the summer. This, presumably, reduces competition between the two species and allows them to occur together.

One must, however, be cautious about regarding differences in life history as the only explanation for coexistence of allied species. Often there are differences in preference of microhabitat which are difficult to detect in the fine mosaics of stream beds. A good example is Madsen's recent careful study of *Heptagenia sulphurea* and *H. fuscogrisea* in Denmark (63). These two species look very similar and often occur together, but *H. sulphurea* is more flattened, swims little when detached from the substratum, and takes hold of the bottom as soon as it touches it, settling in the boundary layer. *H. fuscogrisea* swims when released into free water, does not reattach so readily, and seeks out dead water. The two species therefore live only centimetres apart but in quite different microhabitats. Interestingly, Madsen was able to find small morphological differences between them, involving the positions of hair fringes on the legs and the teeth on tarsal claws, which he was able to relate clearly to the habits and habitats of the species. It is pleasant to think that perhaps some day we shall understand the significance of at least some of the trivial morphological characters which we use for distinguishing the young stages of stream insects.

DRIFT

During the past few years many investigators have concerned themselves with the downstream drift of stream animals as revealed by nets left stationary in the water. It is well established that most stream insects face into the current, and indeed many of them have little option in this as their long tails (Ephemeroptera and Plecoptera) or tapering cases (Trichoptera) sweep them round to face the local direction of flow. Thus, any voluntary move they do make tends to take them upstream. However, any loss of hold sweeps them downstream, and the numbers carried past a given point seem far in excess of any possibility of compensation by merely walking upstream.

When Roos (77) showed that he caught more adult insects flying upstream than were flying downstream in central Sweden the problem seemed to be solved, and the idea of the "colonization cycle" resulted. This postulates that adults fly upstream to oviposit, the young stages drift down and emerge, and the adults again fly upstream. Support was given to this by the finding that even the winter stonefly, *Capnia atra*, which emerges onto the

snow when it is too cold to fly in northern Sweden, walks about 100 m directly from the stream and then turns upstream and goes on walking (89). Other workers have also reported upstream flights [e.g. (98)]. Unfortunately for this theory, Elliott (28, 30) was not able to confirm Roos' results in England, where wind direction seems more important than stream direction in controlling movement. And, in Ontario, while we have been able to observe the initial march away from the stream by a winter stonefly, *Allocapnia pygmaea*, the upstream part of the journey is not as clear-cut as reported for *Capnia*. Moreover, about a month elapses in the Capniidae between emergence and oviposition, so unless the females remain close to where they arrive on their initial journey and retain knowledge of the local geography, it is difficult to see how a net upstream movement can result.

Several species of mayfly nymph are known to be negatively phototropic or to be more active in brighter light, and these responses tend to keep them in sheltered places during the day (30, 42, 81, 82). When night falls they wander out of the shelter and are more readily dislodged by the current. As a result, the drifting of mayflies, and also stoneflies, campodeiform Trichoptera and many other insects, is greatest at night, and the same applies in large rivers as in small streams (4, 5, 27, 28, 54, 57, 70, 99). The drift rate of Chironomidae seems, however, not to vary over the 24 hours (4) and some species of Limnephilidae drift by day but not by night (5, 98).

As light is clearly involved in much of this behaviour it is understandable that it has been reported that nocturnal illumination, or even a full moon, reduces the amount of drift, and that artificial darkening before nightfall brings it forward (4, 27). Holt & Waters (41) showed that the critical level of illumination for *Baetis vagans* is about 1 lux, while Elliott (30) reports levels of 5 to 20 lux for the start of activity and 2 to 60 lux for its cessation in a number of other mayflies. These differences may account for some discrepancy in the findings of Anderson (4) and Elliott & Minshall (32) on the effect of moonlight. It seems, indeed, that the effective level of illumination must vary from place to place, or from species to species, as Ulfstrand (92) found that the midnight sun in the Arctic does not totally suppress the diurnal rhythm.

Drift may also be enhanced by freshets, as they increase the flushing effect of the stream. This so-called catastrophic drift has been studied by Anderson & Lehmkuhl (6) and Elliott (28) who found that the diurnal rhythm persisted even where the numbers were greatly increased, and by Weninger (99) who observed little drifting at times of very high water, indicating perhaps that very high discharges cause the animals to seek shelter.

The rhythm, however, is more complex than a simple nocturnal maximum. Usually, the maximum follows soon after sunset, and there is often a later one, or even two, before dawn on long nights (28, 70). A probable explanation for this is provided by a recent study by Chaston (14) who showed that *Simulium*, *Isoperla* and *Ephemerella* have fluctuating innate rhythms of activity which are suppressed by light. The onset of darkness releases the rhythm and the animals drift most readily at their times of peak

activity, of which there may be one or more depending upon the length of the cycle and the duration of the night.

A further complication is that not all size groups of any one species drift in the same proportions as they occur in the population. Anderson (4) found that the drift of larger individuals was more depressed by moonlight than that of smaller ones, and that the early caseless instars of *Hydroptila rono* drift less readily than larger case-bearing ones (5). There are thus indications that drifting is associated with life history (99), and Elliott (29, 31) concludes that in most species the maximum amount of drifting occurs at seasons of maximum growth.

Other studies indicate that temperature may affect the drift rate (74) and that this may be the major controlling factor for daytime drifters (98); that riffles and runs produce more drift than do pools which may indicate a decreasing importance of drift in lower reaches (7); that reductions in flow cause increases in drift (68); and that there is some correlation between the density of the population and the amount of drift (21, 74).

The last point appears to indicate that drift is at least partly an outcome of competition for space, and that it causes the loss of excess production to downstream areas. But in the present state of our knowledge the significance of drift is far from clear. It is even uncertain how far the animals move, and whether there is any significant downstream displacement of the population as a whole. Some earlier studies indicated that individuals travel tens of metres each night, and Carlsson (12) mentions movement of some hundreds of metres by *Simulium* larvae marked with ^{32}P . On the other hand, ^{32}P has been shown to move similar distances upstream, with at least circumstantial evidence that it had been carried by aquatic insects. Recent studies have stressed that only a very small proportion of the population is in the water column at any one time, and that the size composition of the drifting insects varies irregularly (28, 57, 92). This seems to indicate that the distances moved may be quite short and, despite the large numbers caught in drift nets, Elliott (28) has calculated that the loss to the fauna, if it is one, is only 0.37 per cent per day in an English stream. The corresponding figure for an arctic Swedish stream is about 1 per cent (92). These low figures, together with our lack of knowledge of how much upstream movement occurs, possibly indicate that the importance of drift has been overstressed. It certainly remains in need of further study, with particular reference to upstream movement and distances moved, before its ecological importance can be fully assessed.

AVOIDANCE OF DISASTER

Catastrophic drift caused by high rates of discharge is only one symptom of the difficulties faced by insects in the essentially unstable habitat of the stream bed. Severe floods with their attendant scour, wash-out and abrasion may occur at any time, and only those species which can survive them can successfully inhabit streams. It has been known for a long time that spates reduce the fauna; recent reports of this phenomenon are those of Maitland

& Penney (64) on Simuliidae in Scotland, and Hynes (43) on the insects of a Welsh stream.

One way in which such effects are minimised is the very close attachment of eggs to the substratum, so that even if stones are rolled and abraded some survive. The elaborate attachment mechanisms of the eggs of stoneflies and mayflies have often been described and reports on them continue to appear (20, 53, 55, 56). Moreover, in many insects the eggs continue to hatch over a very long period, often far exceeding the flight period of the adults. Macan (59) has discussed the importance of this phenomenon, and it has been subsequently observed, or inferred from the continued appearance of very small specimens, by many authors. Long hatching periods, coupled with firmly attached eggs, of course ensure that there is a long period during which a spate severe enough to remove nymphs or larvae will not eliminate the species.

Another disaster which may, regularly or infrequently, overtake stream insects is drought, and here again there is evidence that many species survive as eggs, and again the long eclosion period is an insurance. Some invertebrates can burrow deeply into the substratum and escape the dryness, but among insects this ability is confined to Coleoptera and some Diptera. Mayflies and stoneflies, apart from the diapausing nymphs of Capniidae, normally survive only as eggs.

It is not, however, generally appreciated that even when water is present great numbers of the small stages of stream insects, and some large ones also, burrow deeply into the gravel. Schwoerbel (83) has written extensively on this "hyporheic" habitat, and has shown that the insects spread out laterally from the edges of streams and can be collected some distance from the water's edge. Work in my laboratory has confirmed that a dense fauna extends downwards for tens of centimetres below the substratum/water interface in a stream in southern Ontario, and it seems probable that the hyporheal has considerable ecological significance. It seems, for instance, the only reasonable explanation for the steady return of the fauna to a Welsh mountain stream which had been devastated by an unusual flood, because most of the species returned before they had had time to recolonize as flying adults and their size-distribution was the same as it would have been had the flood not occurred (43). The last point indicates that at least most of the recolonization had not resulted from unhatched eggs.

QUANTITATIVE STUDIES

The fashionable trend in modern ecology is towards the study of production and measurement of energy transfer between trophic levels. This is very difficult in streams not only because much of the primary source of energy is allochthonous and irregularly transient and thus very difficult to measure, but because we have no effective methods for quantitative sampling.

We have already seen that very large numbers of samples have to be collected because of the mosaic nature of the stream bed. Those results were

based on collections made with a Surber sampler which is, for various reasons, rather inefficient despite its general usefulness. Better samplers are available and have been discussed by Macan (60) and Albrecht (1). None, however, penetrates very deeply into the substratum so, quite apart from any other failings they may have, they do not collect a great deal of the hyporheal. They also all involve the use of some kind of screen, which causes the loss of small specimens if it is too coarse and large ones if it is too fine (60, 87).

Moreover, there are indications that insects move laterally across the beds of streams as they pass through various stages of their life histories (58, 92). In high mountains, the fauna becomes concentrated toward the centre of the bed under the ice (18), and this probably applies in all severe climates, and at least one species of mayfly, *Habroleptoides modesta*, seems to leave the stream altogether for part of its life history, wandering far out into the hyporheal under the banks (83).

It will be clear therefore that all the quantitative data so far obtained are very unsatisfactory, and that even our estimates of standing biomass are almost certainly far too low. This accounts for the paradoxical finding of some fishery workers that fishes seem to eat many times the numbers of insects present at any one time, even though most of those insects are univoltine.

FUTURE PROSPECTS

It will be apparent from this survey of recent work that study of the ecology of stream insects is still largely exploratory and descriptive. We are beginning to understand some of the reasons for particular distributions in relation to substratum and temperature, and also some of the relationships of life cycles to seasonal changes. We suffer, however, very much from our inability to identify immature insects. Wiggins (100) has stressed that only a very small percentage of the species is known and that this type of study is unfashionable. The situation is particularly bad with very early stages, which are often of considerable ecological importance, and the universal and abundant Chironomidae are almost impossible to identify. This lack of taxonomical work is one of the most serious barriers to further progress.

Another serious barrier is the inadequacy of our sampling methods, especially in view of the depth to which many insects apparently penetrate. Until this problem is solved all quantitative work, unless it is strictly comparative, must be accepted with great reservation.

We also need to know much more about the adult stages and what influence their habits and requirements may have on the distribution of species. Van Someren (96) has suggested that the absence of some stream insects at high altitudes on Mount Kenya may be because nightly frosts eliminate adults, and Hartland-Rowe (40) proposes that the distribution of *Rhythrogena* in the Canadian Rockies may be controlled by the oviposition habits of the adults; and the same sort of consideration has been applied to Simuliidae and damselflies (12, 101). The reverse situation may apply to *Hy-*

draena which has aquatic adults but semiterrestrial larvae. It occurs up to only about 1000 m in the Pyrenees, whereas at least some Elminthidae, in which both adults and larvae are aquatic, are found at much higher altitudes (9). Much of this is, however, merely speculation and there is an obvious need for further study.

Finally, there is the almost uninvestigated field of the role of allochthonous organic matter and its associated microflora in the nutrition of the primary consumers in streams. Insects comprise the majority of the species which feed on this organic detritus.

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