# THE EFFECT OF THE CURRENT ON THE COMPOSITION OF BIOCOENOSES IN FLOWING WATER STREAMS

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## 1. THE DISTRIBUTION OF LIVING FORMS IN FLOWING WATER

IN MANY respects, great and even fundamental differences exist between those animals and plants which live in standing water and those in flowing water. This has long been common knowledge among technologists concerned with waste water as among others. As an example, one has only to recall the "sewage fungus" *Sphaerotilus natans* which lives in large amounts only where the water is flowing. Such differences in population are not, however, limited to the extreme cases of "standing" and "flowing" water; they extend over the whole range from waters which are stagnant through those which are moving slowly to those which are flowing or even running. The differences are perceptible not only as between long stretches of a stream but also within small and minimal sections of the same. In those, as for instance in the outlets from lakes or in brooks of which the beds are not homogeneous in composition, it is normal that all the chemical and physical conditions remain the same except the current, whence it follows that all biological differences must be attributable to the latter alone. When considering the composition of the living world as a whole the current is not, indeed, the only governing factor; there are other variants such as the temperature, the oxygen content and the chemical interplay which play specific roles also. These, however, affect the general character of a large section of water more than they affect any small area within it.

The biocoenoses in a river change with the elevation and with alterations in its gradient. Recognition of this fact has attained practical significance in what are known as "fishing regions", used for classifying the flowing waters of the central European region in accordance with the types of fish they characteristically contain. This division, which is based on practice and for the existence of which a justification has long been sought, was analysed further by HUET.[2] In his "gradient rule" and "gradient diagram" he has formulated and has circumscribed numerically the relationship which exists between the physiographical data for a given section of a watercourse and its population. The fact that such a division, which other authors have carried still further, should be possible in practice at all provides support for the correctness of the gradient rule, described by leading specialists as a great step forward in the biocoenosis of flowing waters. The rule may be stated as follows: "Within any given biogeographical region, flowing streams that have the same width and depth as well as similar gradients possess analogous biological properties especially as regards fishing." It is true that this rule is based particularly on fish as being the leading organisms in the biocoenosis, but in fact it applies to the whole of it. In the gradient diagram, the relations between physiography and biocoenosis are represented as curves which relate to concrete cases. This form of diagram is an excellent tool for the practician, but its application in its present form is limited to the temperate zone of western Europe.

A universally applicable classification of the biocoenoses that occur in flowing waters was first published in 1961. ILLIES was impressed with the fact that in other parts of the world, zoogeographically quite isolated from one another, flowing streams maintain almost similar living communities even though these are made up of animal species which systematically are quite different, and he established a general biocoenotic classification of flowing streams.[4] For central Europe his classification approximates to that of the fishing regions, whereas in other areas the elevations of the various regions vary according to their geographical latitude. For this purpose the distinctions were drawn not between the *same* coenoses—for that would be possible only within a relatively small area—but between *comparable* coenoses, those composed of similar living types but not of identical species.

It is clear that here the current of the stream (or its gradient, as the case may be) plays an important role, but that it is primarily the elevation and temperature which determine the general character of actual biocoenoses under consideration. The fact that temperature should be counted among the most important factors governing the composition of flowing water biocoenoses was one of the first to be established in the whole ecology of flowing water, thoroughly examined in many earlier works. The conclusion reached by HUET and ILLIES that many flowing-water species (among which *Ephemeroptera* was the example actually taken) are everywhere distributed, geographically and in elevation, according to temperature, is agreed. Another indication of the significance of temperature is the fact that a great many species existing in mountain streams are stenothermal whereas the fauna in rivers of the plains is largely composed of eurythermal elements.

As regards flowing-water fauna, considerable significance has always been attributed to the oxygen content also. Recognition of the fact that the inhabitants of streams and rivers normally appear in water which is rich in oxygen has led to their being designated without any further investigation as "oxyphile", "oxybiontic" or even "stenoxybiontic". In this context more recent invesigations have shown that, for rheophilic organisms breathe and which require oxygen, the oxygen content and the movement of the water are closeley connected factors. This means that the actual demand for oxygen, or the ecological significance of the oxygen content, required to be examined separately for each species. In any case, as will here be brought out in greater detail later, the exhaustive investigations of WINGFIELD[8] and PHILIPSON[5] as well as the present authors' work have shown that as regards the physiology of breathing the movement of the water may be of greater importance than its oxygen content. This, however, is not a correct way of stating the problem; for, since the movement and the oxygen content of the water are closely connected factors from the physiological standpoint and in a sense are components of one and the same system, it is fundamentally impossible to discuss the significance of one component without at the same time taking account of the other. The connections between them were first formulated by RUTTNER.[6] According to him it is not the oxygen content of the flowing water in itself that governs the situation but its "respiratory value", a concept which embraces "rate of flow" along with oxygen as its second component. In postulating this, though without carrying out any further investigations, RUTTNER foreshadowed the outcome



of the present-day research at least qualitatively, and the pertinent work carried out in the last few years confirm his thesis in every respect.

It is indeed the temperature and also the chemistry of the water that exert the greatest influence on the composition of living communities considered over large areas and it is indeed possible to tell, from the places those communities occupy in the spectrum of biogeographical data as a whole, which are the organisms that have any chance of occurring at all; but going beyond this it is largely the current that determines how the living communities actually are composed. The ecological scope of most organisms which inhabit flowing water, at least as regards all those of them which are rheophilic, is strictly limited by the current. In the case of certain specialist organisms—namely

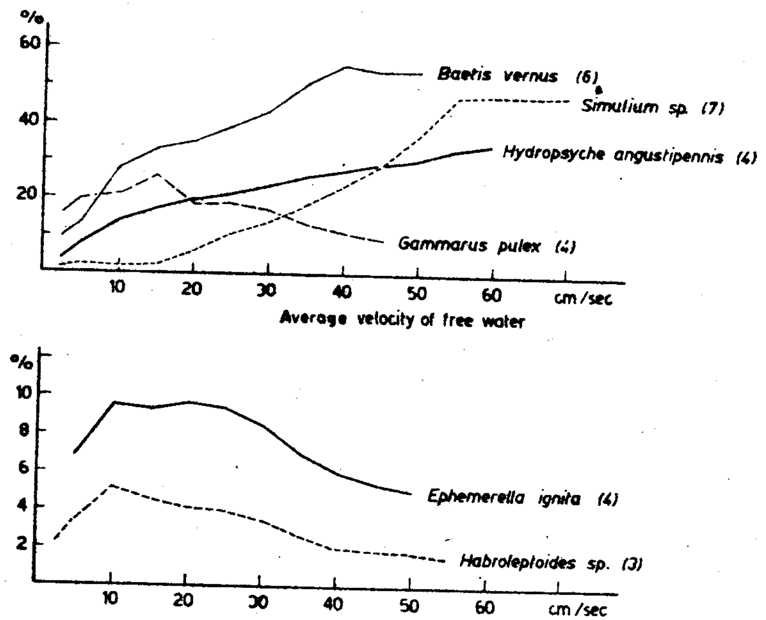


FIG. 1. Effect of the current on the frequency of certain animals living in streams within the local zoocoenosis. The velocity was measured in open water, and the indications of percentage frequency values relate to the total numbers of these animals counted in the area of investigation. The number following each specified name indicates from how many separate investigations the curves were established.

the net-building larvae of the *Trichopterans Plectrocnemia conspersa, Neureclipsis bimaculata* and *Wormaldia subnigra*—it has been established that their nets require a quite definite velocity of current in order to function properly. Relatively little is known, however, of the special physiological and biological demands made by individual inhabitants of flowing water, and in this respect further surprises may be expected. Ultimately it is such peculiarities of particular species as these which account for the fact that, not only as between large areas but also within the same bodies of water or within minimal length of stream and tiny areas, the differences in frequency of occurrence of particular animals and plants are so clearly marked. If, for instance, comparisons are made between the animal populations of small narrowly delimited areas which lie very close together—even within a few metres of square metres—and which exhibit no differences except as regards the velocity of the water current, then it is found that differences in the frequency with which any given species occur depend quite definitely on its behaviour in relation to the current, corresponding to the particular requirements of that species. Under these conditions, where temperature and chemistry remain constant throughout each series of observations, the only differences between points of observation are those which can be traced back primarily to the different current.

In FIG. 1 the results of such investigations are evaluated graphically. The velocity of the current was measured in the open water. Since the individual species react very differently to the current, some exposing themselves to it directly whereas others disappear into the mud or under stones in the bed of the stream and so forth, these data as they stand tell us nothing about the speed of the current to which the animals are in fact subjected; that is, which effectively acts upon their bodies. However, for the purpose of our present problem no exact understanding of the rheophilic behaviour is necessary. We shall return to this point later, and may content ourselves for the present

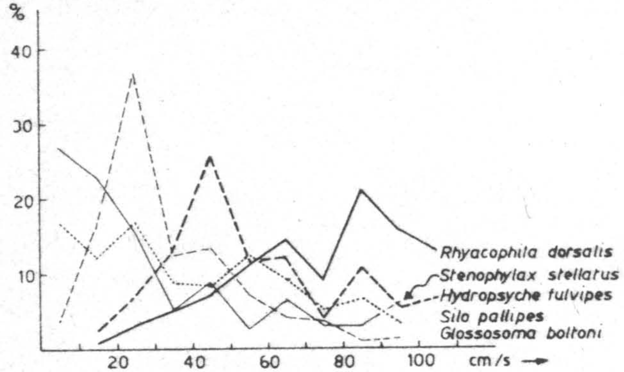


FIG. 2. Effect of the current on the distribution of certain *Trichoptera* larvae. The indications of percentage frequency values refer to the total number of samples found belonging to each species. Adapted from SCOTT.[7]

with recognizing that typical species of animals react quite differently from one another to the flowing water. There are unmistakable current specialists (*Baetis vernus*, *Simulium* sp., *Hydropsyche angustipennis*, for instance) but there are also species which find their optimum at a definite and relatively low velocity (e.g. *Gammarus pulex*, *Ephemerella ignita*, *Habroleptoides* sp. Investigations by SCOTT[7] of the relative frequencies with which certain *Trichoptera* larvae occur in a stream further go to confirm that each species prefers a certain range of velocity (FIG. 2).

This general conclusion, which presumably applies also to plants in the flowing water, is by no means new. It has for instance been implicit in the literature of indentification for a long time past even though none of the older literature contained any numerical indications of the demands made by the species in question as regards current.

Thus it is definitely established that the water current exerts a decisive influence on the composition of flowing water biocoenoses. This indeed is so far true that it determines the satisfaction of the major demands of plants and animals within every small and minimal community, so that within every partial and microbiotope those

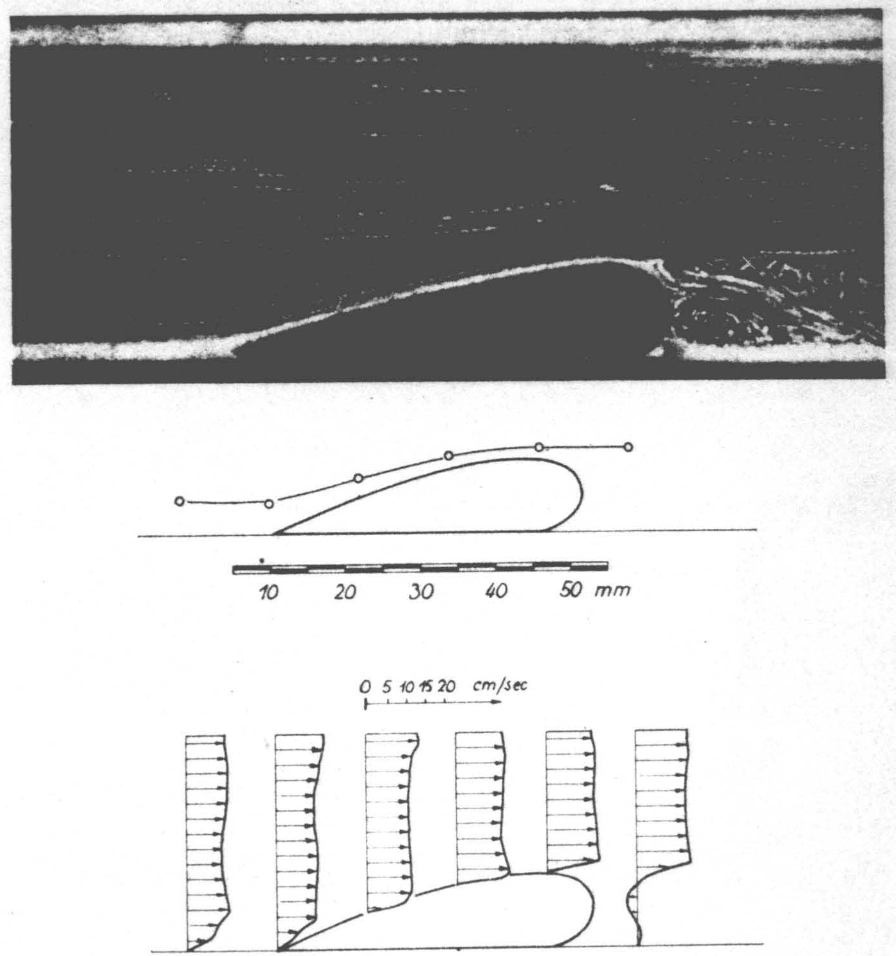


FIG. 3. Course of Prandtl's boundary layer in the passage over an obstacle: (a) Photograph of the flow; (b) Graphical interpretation of this; (c) Course of the boundary layer.

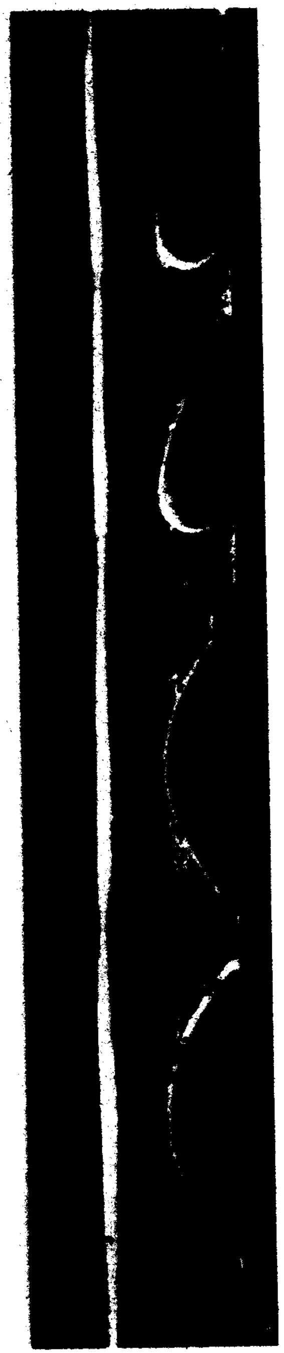

FIG. 4. Composite picture of a current model (flowing water aquarium) in action.

forms exist which find their particular requirements satisfied there. Consequently a stream with its heterogeneous hydraulic conditions harbours a population which qualitatively—that is to say specifically—is to some extent homogeneous, but which is divided into a mosaic of partial biocoenoses within which the individual species occur with varying frequencies. The differences brought about by the current lie, therefore, primarily in the quantitative composition of the biocoenoses.

Admittedly it is impossible, from the knowledge available up to now, to make any pronouncement as to the multiple *causes* which lead to this dependence of the distribution on the strength of the current. The basis for all further work in this direction must be, above all, the fullest possible understanding of the physical phenomena that occur in flowing water and of the properties of rheophilic organisms as regards their physiology of behaviour and of respiration.

## 2. THE PHYSICAL PHENOMENA OF CURRENT

Let us now briefly consider the movement of water from the purely physical aspect. Here we need not enter into detail regarding the peculiarities of laminar and turbulent flow, but may confine ourselves to the essential points.

Laminar flow would appear, superficially, to resemble in some respects the very slow movements of water such as occur for instance in lowland canals or at river dams. It can, however, be confirmed by physical means that such movement hardly ever occurs in nature, at least in surface waters. Since a mass of water in laminar movement undergoes no mixing action, no oxygen exchange is possible in it except by diffusion; hence laminar flow must almost be regarded as inimical to life. It may be said that all current phenomena occurring in waters above ground are *turbulent*. Turbulence implies that after the passage of certain geometrical limits which depend on the prevailing conditions the moving mass of water behaves as if it were split into separate packets or small packets, each of which has its individual velocity and direction superimposed on the motion of the water as a whole. This interpenetration of movements is induced by marginal effects and by those due to fixed obstacles in the bed and on the banks of the stream which break up the current. It must not, however, be confused with a mere formation of eddies. Whereas it is well known that any exchange of matter which is dependent on diffusion takes place very slowly, the exchanges occurring in the water of streams and rivers and also in those of lakes and oceans do so rapidly. The reason is turbulence. It is entirely due to this phenomenon that such waters constitute inhabitable living space. Without it, only the most limited kind of life would be possible under water.

In every turbulently flowing system, marginal effects develop in what are called boundary layers, named after their discoverer as Prandtl's layers. Close to the substratum, movement of the water gradually ceases owing to friction and a boundary layer is constituted in which the flow is strongly retarded, until ultimately, it is stagnant. Moreover, zones of dead water are formed in cracks, fissures and spaces between the individual stones of the stream bed and the like, as well as behind every protrusion into the stream, so that to a great extent the dead water is separated from the freely moving water. As can be observed in the streams themselves as well as by experiment, it is in such dead waters and in sediments that the greater part of rheophilic life is spent. Hydraulically speaking the inside of plant clusters, moss and algae as well as fragments of roots, rotting leaves, etc., are to be classed with the dead water. What remains, namely, lithophile fauna with its characteristic species, (i.e. *Epeorus*, various species of *Baetis*, *Rhithrogena*, *Rhyacophila*, *Simulium*, *Liponeura*, etc.), exposes itself directly to the current. At least externally this appears to be the case, though in fact these forms make use of the boundary layer action to reduce the strength of the current.

It has been shown by model experiments that under the conditions existing in natural streams the thickness of the boundary layer is in the same order of magnitude as the shoulder-height of most animals living in streams; that is to say, up to several millimetres.

For the purpose of these experiments the current flowing through a channel-shaped aquarium, and tracer material floating therein, were made visible by intermittent slit lighting and in this way were photographed and measured (FIG. 3).

Both phenomena, the existence of boundary layer and that of dead water, have great biological significance as regards colonization in flowing waters. In all biological and ecological investigations of flowing waters they should duly be taken into account as important and integrating components of the system as a whole. Without a thorough knowledge of them it is impossible adequately to survey and understand that

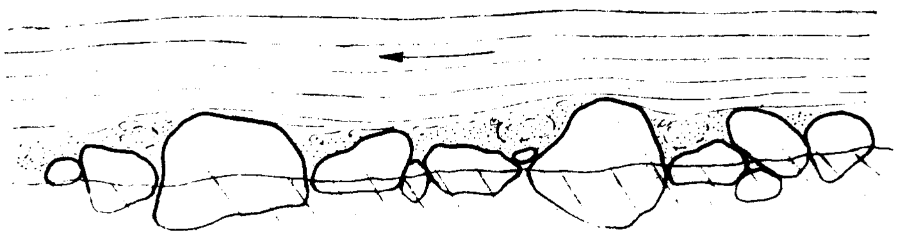

FIG. 5. Schematic representation of the bed of a mountain stream: development of dead waters which divert the flowing wave away from the bottom layer.

system. Further, it must be borne in mind that flowing water of whatever kind is far from constituting a homogeneous uniformly conditioned living space, being in fact made up of multiple and very miscellaneous current zones which include dead waters as well as places flowed over at greater or less velocity, etc. In FIG. 4 the photograph taken of a model gives some idea of this. When the impressions gained from this model are transferred to a natural stream bed we find that most of the latter consists not of parts over which water is flowing but of dead water pockets (FIG. 5), in which there is indeed some movement of the water but its impact is broken. It is entirely because of this that the stream bed has become a living space for the extraordinarily rich colonization which we know.

## 3. THE RHEOTACTIC BEHAVIOUR OF SOME ANIMALS THAT INHABIT FLOWING WATER

At the beginning of this paper attention was drawn to the fact that the ecological optima for particular animals which live in flowing water correspond to quite different velocities of current. Since however the conditions which prevail in the flowing stream differ notably from those of the "micro-climate" close to the substratum, and since



direct comparison is further complicated by the existence of boundary layers and of dead water, there can be no doubt that the range of velocities which each animal in fact has to endure is not the same as its own optimal range. As regards the physiology of sensation it is just this effective velocity which is of interest, for it is just this which

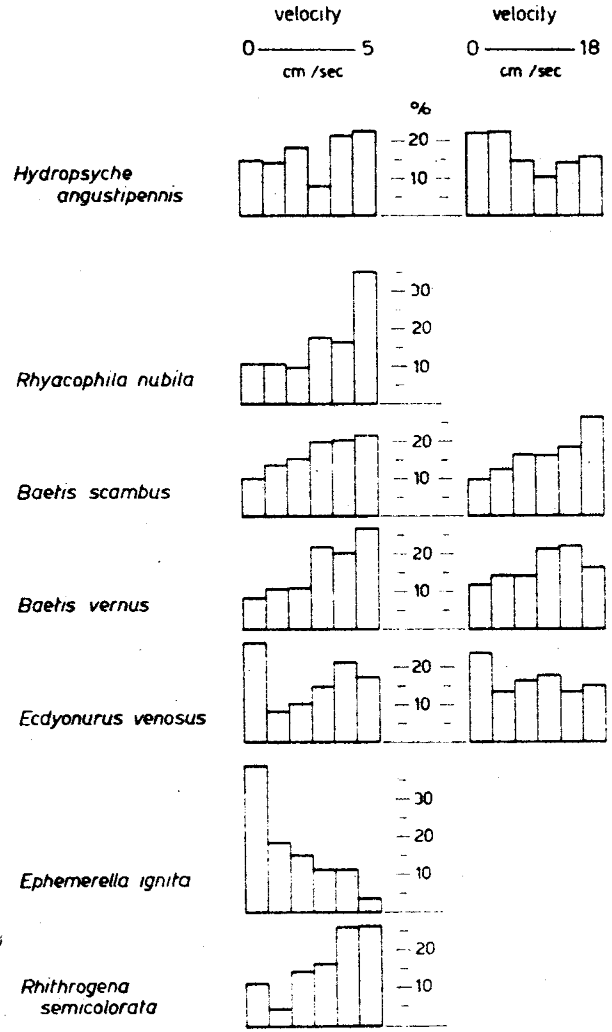


FIG. 6. Rheotactic distributions taken up by various animals living in running streams within certain ranges of velocity: the results of measurements carried out in the experimental channels. In each diagram the total height of the columns adds up to 100 per cent and the velocity scale is absolute, indicating the effective current which prevails in the immediate vicinity of the animal.

can tell us something about how the animal reacts to the stimuli afforded by the current.

We have subjected this question to experiments upon certain insect larvae. The animals in question were kept in channel-shaped running water aquaria (FIG. 4) and their positions from time to time were recorded. The hydraulic conditions prevailing in these aquaria were accurately known from optical registrations. This made it possible to divide the channel beds, which were covered with model stones, into definite regions overflowed by currents at different known velocities, and finally to draw conclusions as to the rheotactic reactions of the animals from the relative frequencies with which they remained in the respective regions. Crude as the experiments may appear to have been, they nonetheless confirm from technically valid measurements the more qualitative observations which have been made in natural waters. The results are interpreted graphically in FIG. 6.

This represents the behaviour of species already known, from observations on streams, to prefer living in a current (*Rhyacophila*, *Baetis*, *Rhithrogena*) and which the experiment too shows to be positively rheotactic: they are animals which seek a current to move into. The Ephemerid larva *Ephemerella ignita*, which is a typical dead water form, moves resolutely out of the current whilst *Ecdyonurus* (FIG. 7), a flat mayfly nymph behaves more or less indifferently. *Hydropsyche*, a caddis fly larva which does not build a case and which chooses places in the flowing stream at which to erect nets from which to suck out its food, likewise seems to be indifferent. Since however, other explicitly biological factors play a part here, further experiments are necessary for interpretation. Taken as a whole the rheotactic behaviour which emerges from these experiments, considered along with the remaining biological peculiarities of each form examined, can be explained without difficulty.

Quantitative investigations of natural conditions reflect, to some extent, the integrated action of all the natural influences at work; but the experiments made it possible to examine the effects of the current alone, all other disturbing agencies being excluded. The question of what it is which ultimately induces or compels the animals to behave in these ways and not in others has yet, however, been answered. In further experiments we have endeavoured to make a first contribution towards answering that.

## 4. CURRENT AND RESPIRATION

Many animals which live in flowing water can be maintained only in such water; in stationary water they suffocate. This is a long-established fact, theoretically easy to explain. Most of the species which live in standing water possess organs with which they can themselves procure their breathing water. In this context it is only necessary to recall the many species of crustacea, the *Trichoptera* which have cases or the nymphs of mayflies which live in ponds or in mud.

Such animals are found also in flowing water; characteristically they keep in still zones such as dead water or in sediment, or they belong to the forms known as rheophile which are more or less indifferent to the current, such as *Ecdyonurus*. All these species, however, either possess no ventilating organs or have changed or lost the function of those in the course of their evolutionary history: they are extremely sensitive to still water and quickly die in it. These are the same forms as react the most positively in the channel experiments, which seems to point to one of the reasons for the rheophilic behaviour of the species in question. We, therefore, tested in a further series of experiments the extent that a correlation exists between the current and the intensity of breathing in rheophilic animals.

In an apparatus designated a "circulating pipe"[3, 1] we measured, by an electrochemical method, the oxygen consumption of rheophilic insect larvae under different

FIG. 7. *Ecdyonurus venosus* at rather great velocity of the current. The front part of the flat head is only some tenths of a millimeter from the substratum and within the boundary layer. The current flows above the animal.

but temporarily constant velocities of current (Fig. 8). We cannot here enter into details of the measuring technique and basis of calibration, for which the reader is referred to the original work.[1]

It has already been established, from a whole series of publications already listed,[1] that many species of animals which live in flowing water exhibit higher rates of oxygen consumption—that is, they breathe with higher intensity—than comparable and closely related species which live in standing water. On the other hand, only very few works are available comparing the respiration of one and the same species in moving and stagnant media. Philipson[5] established for trichopteran larvae kept in water containing little oxygen that an increase of the oxygen content in stagnant water had the same effect as imparting motion to water poor in oxygen, a phenomenon which he explained

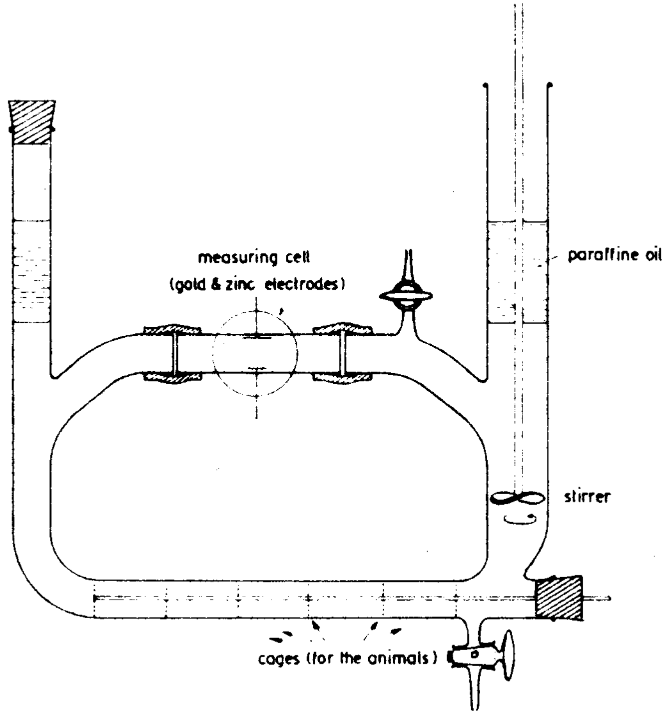


Fig. 8. 'Circulating pipe' for the measurement of the oxygen consumption of small animals living in flowing water.

on the ground that movement of the water shortens the diffusion path for the oxygen in immediate proximity to the body of the animal. Fundamentally this is nothing else than a more exact formulation of Ruttner's[6] conception, already generally accepted, of "respiratory value". It is fully consistent with Zahner's[9] establishment of the fact that for the nymphs of the odonatan genus *Calopteryx*, putting the water in motion increases the intensity of respiration to the same extent as doubling the existing oxygen content.

The results of our own preliminary experiments likewise all pointed in this direction. We felt urged to test quantitatively these relations which were already to some extent known qualitatively, in order to obtain a basis for comparing the individual species with one another.

Measurement of the oxygen in the circulation pipe was accomplished by the dynamic system. That is to say, the oxygen consumption of the animals was not ascertained in water having a constant oxygen content, but the variation time of the oxygen content was measured for the water in the circulation pipe. With the aid of graphical interpretation, this enabled the oxygen consumption to be followed down to the point at which the concentration was low enough to become lethal. In FIG. 9 the consumption values are represented graphically though only for an oxygen concentration of 8mg/l. $O_2$. For the results as a whole reference should be made to the original work.[1]

It can be seen from this illustration that the oxygen consumption is related to the

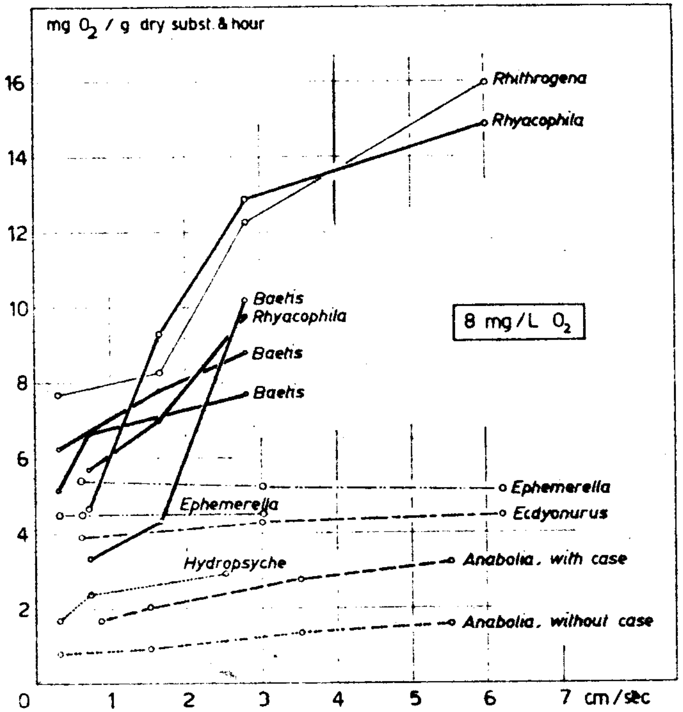


FIG. 9. Effect of the velocity of the current on the oxygen consumption of certain fresh-water animals. Measured values at 8 mg/l. $O_2$ and 18° C.

current quite differently for each species. It is the *Ephemeropterans Rhithrogena semicolorata*, *Baetis vernus* and the *Trichopteran Rhyacophila nubila*, all of which are definitely rheophilic species, that have the greatest absolute and also the most strongly current-dependent rates of metabolism, whereas the other species do not show this dependence or do so only slightly. The reasons are obvious. *Rhithrogena*, *Baetis* and *Rhyacophila* belong to those species which, by reason of their construction, and probably also by reasons of secondary morphological or functional changes or reductions in their breathing apparatus, are no longer in a position to maintain a breathing current for themselves. They are adapted to living in a current which relieves them of the mechanical part of respiratory action: namely, the water supply. A similar though not so marked dependence is also to be found in the trichopteran pupae, *Hydropsyche*



*angustipennis* and *Anabolia nervosa*. By far the most sensitive and most oxygen-requiring species is *Rhithrogena semicolorata*.

The faster the water flows the lower in general is the "lethal" oxygen content, meaning the content just insufficient to support life, though here again the peculiarities of each individual species express themselves (FIG. 10.) This shows with particular clarity

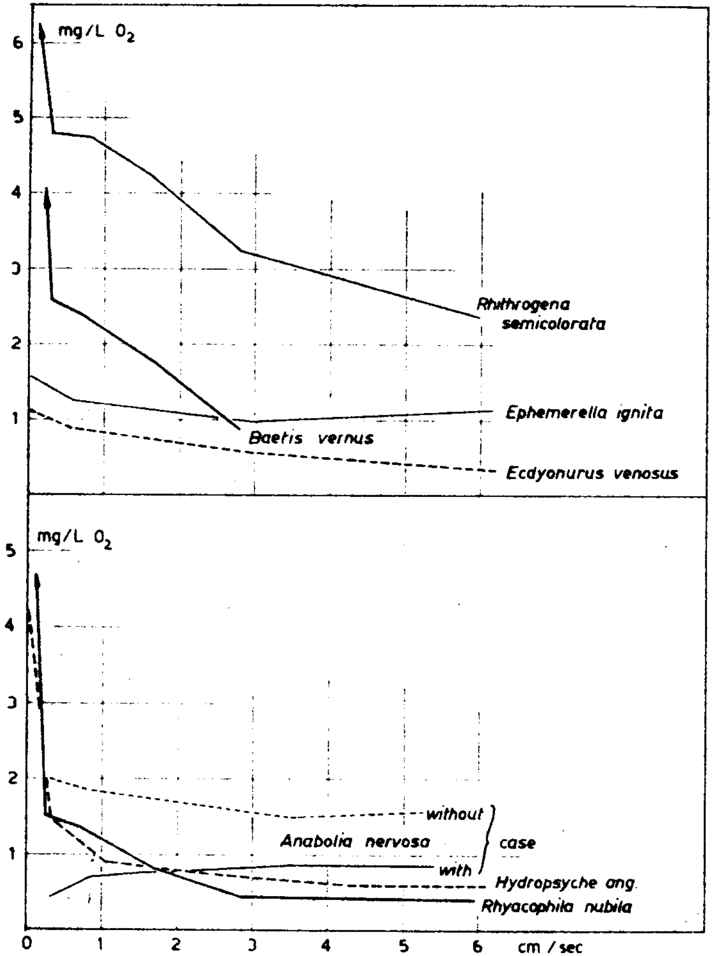


FIG. 10. Oxygen concentration just too low to be acceptable by the experimental animals (lethal concentration) measured at different velocities of current.
Upper diagram: mayfly nymphs.
Lower diagram: caddisfly larvae.

how closely dependent on the movement of the water are those species which have no ventilating mechanism of their own.

The evidence that the metabolism depends on the velocity of the current has a fundamental significance, at least for those insect larvae or nymphs which possess no ventilating organs of their own. As a corollary to the explanation given by PHILIPSON[5] this can be expressed as follows: the movement of the water shortens the diffusion path for the oxygen. Since the intensity of respiration in animals which have no respiration pigment—including the insect larvae here examined—depends on the oxygen content of the medium immediately surrounding them, the critical content for the support of metabolism is not to be looked for either in the surrounding water or directly on the surface of the body, but in the Prandtl boundary layer which forms itself around the animal. This oxygen content is the outcome of various influences:

(i) Oxygen consumption by the animal (breathing).
(ii) Oxygen content of the surrounding water.
(iii) The rate at which the boundary layer is renewed, which the velocity of the current plays a decisive role in determining. The latter also helps to determine the thickness of the boundary layer, which is significant for the diffusive component of the gas exchange.

It is the interplay between these several components that finally determines the oxygen content with which the animal in fact has to satisfy its needs. If any one of them

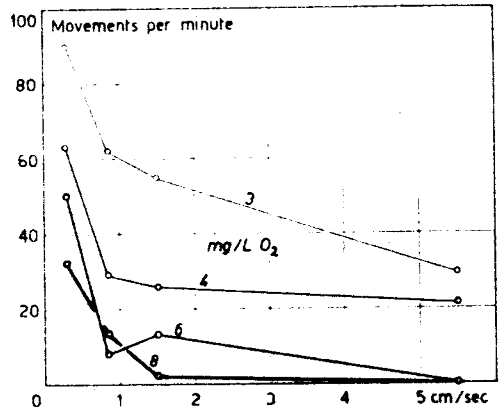


FIG. 11. Frequency of the ventilating movements performed by *Hydropsyche angustipennis* at various oxygen contents, in relation to the current.

is insufficient within the system as a whole it must, in principle, be compensated by the other components. Otherwise the theory will not hold. It is, however, only those species of animals which are able to ensure their own ventilation that have this possibility. The breathing experiments on *Trichoptera* offered a chance to confirm this, for in accordance with the oxygen content and the current the larvae of those animals execute more or less frequent undulating movements of their abdomen. In the case of *Hydropsyche angustipennis* and *Halesus digitatus* we measured the frequency of these movements and were able to establish a very clear and definite dependence of them on the oxygen content and strength of the current, as shown in FIGS. 11 and 12.

This work suggests one of the possible reasons which induces animals inhabiting running water to behave in quite definite ways in relation to the current. It shows also, though again only suggestively, that the current has primary and direct significance in determining the fauna which lives in flowing water.

We would not wish, however, to end this paper without referring to a new and recently published work by P. ZIMMERMANN[10] which deals with the effect of the current



on the composition of living communities, determined experimentally in large-scale tests.

Whereas, in the experiments here described, we ourselves tested the direct effect of the current on individual organisms, Zimmermann made large-scale model experiments to find out how the current influences the composition of newly developing societies of organisms. A system of canals 74 m long, 20 cm wide and 15 cm deep, adjustable at will, was set up as part of the equipment in the experimental plant at Tüffenwies belonging to the Federal Institute for Water Supply, Sewage Purification and Water Pollution Control in Zürich. This made it possible to create biotopes which differ in no respect except the average velocity of the current, all other components being identical at least at the beginning of the experiment.

The experiment as a whole was carried out in three channels having different gradients, and lasted for four years. At the end of each year the quality of the water, which initially was pure ground-water, was worsened by an admixture of waste water so as to be able to try out also the working of chemical effects. In this way twelve communities of organisms were observed and examined in the course of four experi-

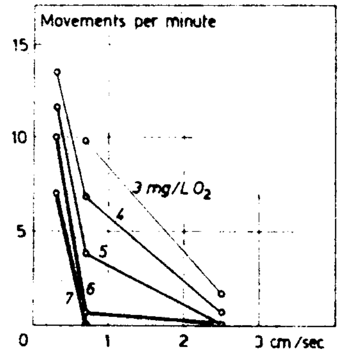


FIG. 12. Frequency of the ventilation movements of *Haleus digitatus* larvae without cases under the same conditions as FIG. 11.

ments, during which each community was enabled to develop freely under known conditions. In what follows below, only the essential final results from this important piece of work are mentioned.

Under different velocities of current, but with the other conditions completely identical, the associations of organisms evolved with strong differentiation between them in respect of their specific compositions and populations. On the basis of an accurate analysis of the individual species it was found that, in the case of about one-half the species, the current exercised a stronger ecological effect than could be ascribed to the loading with polluted water or to the chemical composition. If now the saprobian system, which is more and more being used in Europe for the biological assessment of waters despite its known deficiencies, is applied to these communities, it is found that the three experimental channels subjected to the same chemical conditions belong to different saprobian or pollution degrees. According to ZIMMERMANN, a high velocity of current favours those organisms which have lower saprobic values whereas a low velocity favours those life communities which come higher on the saprobian scale. With the saprobian system in its present form, therefore, the faster a body of water is flowing the better will it be rated, and indeed the difference may amount in some cases to a whole saprobian step.

This shows on the one hand that the saprobian system is not a simple tool which can be applied uncritically but is something which should be used by the specialist alone. It shows on the other hand that, equally from the aspect here under consideration, the current velocity of the water plays a significant role in determining the development and the qualitative and the quantitative composition of living communities.

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## DISCUSSION

T. W. Beak (*Canada*): My approach to the task of discussing this important contribution to our knowledge of the effects of the environment on the composition of the freshwater community, is that of the applied biologist who is principally concerned with the measurement of water pollution using biological assessment.

Like many biologists working in this field in North America, and unlike many of our counterparts in Europe, my methods have been strongly influenced by the vastness of the waters in which I must work. Except for a few areas of Canada, I am seldom concerned with restricted areas of intense pollution. Many of our rivers are fifty to one hundred times as large as the River Thames and a few even larger than this. They flow into lakes which are comparable in size with the English Channel and many flow thousands of miles before they reach the sea.

These physical factors of size have undoubtedly influenced us in our quest for methods of pollution measurement which are extensive, rather than intensive, in conception. We have tended to develop systems for evaluating the data we collect in large surveys, rather than study the ecology of the organisms we encounter. Many of these systems depend of such broad conceptions as numbers of species without regard to the biology of these species, or to numbers of individuals within broad biological groupings such as genera or even families.

These systems have been necessary because we had a job to do with inadequate tools and insufficient numbers of workers. Due to their development and use a great deal of valuable work has been done which would not have been done had we failed to develop methods—inadequate though they may be—which enabled us to work with the knowledge and facilities we possessed.



I consider we have reached a plateau in the progress we can make with this type of approach. I think that many North American research workers, like many Europeans, are turning their attention increasingly back from the extensive concept of biological evaluation to the more intensive concept, which requires a thorough knowledge of the relationship between the species of animals in any environment and the physical, chemical and biological parameters of the environment. The paper we have just heard is an important contribution in this field.

Very few pollution surveys have taken current velocity into account at all and fewer still have considered it as a quantitative factor. We have taken it into account indirectly when we have used the type of bottom deposit as a classification for composition of the communities, but we have very seldom measured it as a separate factor of the environment. The authors have demonstrated, however, that a variation of current, within the limits which we might encounter within one survey, certainly in our continent, can have an influence equivalent to the difference of one stage of the saprobian system.

I should first like to examine the application of some of the ideas and results given in this paper to a field situation with which I am familiar in Canada. The river is the St. Clair River. It is this part of the Great Lakes system which connects Lake Huron with Lake St. Clair, which in turn empties through the Detroit River to Lake Erie.

It is a large river with a volume in the region of eighty to one hundred thousand million gallons per day. It forms the international boundary between the United States and Canada. Near its outfall from Lake Huron there are medium-sized towns on both banks with the usual association of mixed industries. In addition, on the Canadian side there is a complex of oil refineries, chemical and petro-chemical industries.

In its upper part the river is rapid with a midstream current velocity of the order of 80 cm/sec. It decreases in velocity as it proceeds downstream and just before entering Lake St. Clair is probably of the order of 10 cm/sec.

In addition to the longitudinal gradient in velocity there is a transverse gradient. I have not measured these velocities, but I have noted the bottom deposits in the course of biological studies carried out in 1957.[1]

On the Canadian side of the river, close to the bank, the bottom is of a silty nature, even near the upper end. In the centre of the river it consists of very coarse sand on a clay substrate and on the American side it consists mostly of large algal-covered stones on a clay substrate. Proceeding downstream, the silty type of bottom extends farther into the river and at one point where there are large islands in the river extends to these. This is, of course, a very broad description and there are many local variations.

Above all the pollution sources, the macro-invertebrate fauna is rich in both numbers of species and numbers of individuals in the silty bottom on the Canadian side. It includes small numbers of *Hydropsyche* sp., fairly large numbers of *Hexagenia* sp. and *Ephemera* sp., some *Stenonema* sp. and *Baetisca* sp., several species of *Chironomidae*, *Gammarus* sp., six species of *Gastropoda*, two species of *Sphaerodae* and some *Oligochaetes*. In the faster current in the centre of the river, with the coarse sandy bottom, the fauna is very restricted both as to numbers of species and of individuals. There are a few specimens of *Hydropsyche* and *Hexagenia*, a few *Chironomids*, some *Sphaeridae* and very few *Gastropoda*. On the American side, in the fast current with the stony bottom, the fauna consists of large members of *Hydropsyche* sp. and the related *Cheumatopsyche* sp., a small number of *Ephemera* sp. and *Hexagenia* sp., some *Gammarus* sp. and a few *Gastropoda*.

On re-examination of this data in the light of the paper we have just heard, it is clear to me that we could, with advantage, have taken more account of current velocity in evaluation of the data than we did. I want, therefore, to re-evaluate some of the results in the light of this paper.

The first pollution source on the Canadian side was domestic sewage from the town of Sarnia. At the time this was untreated, but a treatment plant has since been built. The effect of this was to reduce the fauna on the silty bottom so that only occasional specimens of *Hydropsyche* sp. and *Ephemera* sp. could be found, but the *Chironomidae*, *Gastropoda* and *Oligochaeta* were little affected.

This pollution did not extend to the swifter current on the American side, but it is possible that there was some pollution present from the American city of Port Huron. The population of *Hydropsyche* sp. and *Cheumatopsyche* sp. in this faster current was unaffected and we took this to indicate that there was no pollution effect on this side. In the light of Dr. Jaag's paper, it is possible that the lack of effect was the result of the fast current and that there was in fact some pollution on this side too. This interpretation is favoured by the fact that at one point on the Canadian side at which there is a faster current and stony bottom there is a similar fauna dominated by *Hydropsyche* sp. and *Cheumatopsyche* sp., but very few *Ephemeroptera*.

Immediately below the main sources of industrial pollution on the Canadian side most of the fauna except *Tubificidae* were eliminated, both in the slacker current and on the stony bottom. At the same point on the American side the bottom was silty and the fauna, dominated by *Hexagenia* sp., *Chironomidae* and *Gastropoda*, was similar to the silt bottom fauna on the Canadian side upstream.

Below the pollution sources the fauna recovered relatively quickly. This was attributed to the high dilution and I do not doubt that this was an important factor. However, in the light of Dr. Jaag's paper it seems likely that the high current velocity contributed more to this faunistic recovery than was conceded at the time.

In this connection it is interesting to consider what happened at a point farther downstream at which there are large islands in midstream. The current at this point is of medium velocity, with a silty bottom on the Canadian side; of medium-swift velocity with a bottom of stone, silt and mixed weed beds on the Canadian side of the islands; of medium velocity with a sand bottom on the U.S. side of the islands and of medium velocity with a bottom of sand and stones on the U.S. bank.

The silty area in the slacker current had a pollution-tolerant fauna dominated by *Tubificidae*, *Lymnae* sp. and *Physa* sp. The medium-swift current on the Canadian side of the island had a clean water fauna dominated by *Hydropsyche* and *Cheumatopsyche* with a few *Stenonema* and *Baetisca*, *Gammarus* and *Goniobasis*. On the American side of the island there was a poor fauna with few species and on the American side of the river a few *Hydropsyche* associated with the weed, but generally a rather poor fauna.

Again on re-examining the data I think that insufficient emphasis was placed on the effect of current velocity in the evaluation. It is clear that, given sufficient current, the weed suffices as adequately as the stony bottom as an attachment for the nets of *Hydropsyche* and, due to its greater vertical distribution, favours even larger numbers of individuals than the stony bottom.



Over one hundred samples were taken in this survey and I could multiply severalfold the examples I have given. I hope that I have given enough to illustrate the application of the data given in Drs. Jaag and Ambuhl's paper to a field situation in a large river in North America.

It is clear that in applying it to a field situation it is essential to take into account not only the direct effects of current, but also the associated effects of bottom deposits. This becomes particularly important in the intermediate current velocities which are associated with a coarse sandy bottom. This is a very harsh environment in which few macro-invertebrates can live.

There is one other aspect of the application of the results given in this paper which I want to mention before I leave the question of field application. The authors have shown that increased current has the same effect on the biocoenoses as decreased pollution. If, therefore, the effect due to decrease in current velocity, in a field situation such as I have described in the St. Clair River, should be of the same magnitude and opposite in direction to that due to recovery, one might have a situation in which, judging from the biocoenoses, there was no recovery taking place proceeding downstream from the pollution source. This could be confusing unless proper allowance were made in the evaluation for change in current velocity.

I should like now to look at another aspect of the effect of current velocity on the measurement of pollution by biological assessment.

The authors have drawn attention to the important effect which current velocity has on "threshold" or "lethal limits" of dissolved oxygen and the difference of these effects on organisms which have provision for producing an artificial respiratory current and those which do not.

Lloyd[2], in a recent paper in which he was discussing the effect of dissolved oxygen on toxicity of several poisons to fish, suggested that the reason a given concentration of poison is increased in toxicity by reduction in dissolved oxygen is that the concentration of poison at the gill surface is controlled by velocity of respiratory flow as well as by concentration of poison in the bulk solution, and that respiratory flow increases with reduced oxygen. Similarly Amberg and Cormack[3] have shown that the development of *Sphaerotilis natans* is dependent not merely on concentration of assimilatable organic material in the water, but on the product of concentration and current velocity.

Taking these three observations together it seems to me that the measurement of toxicity levels for macro-invertebrate fauna must take into account not merely concentration of toxic substance, but also oxygen tension and current velocity. An animal which requires a high current velocity to ensure it an adequate oxygen supply will also be exposing itself to a higher concentration of toxic material at the respiratory surface than one which requires a lower oxygen uptake. If this be the case—and I do not know of anyone who has investigated it experimentally—it will have an important bearing on the relative effects of toxicity and reduced oxygen tension—a problem with which we are frequently confronted in the field.

I want to pursue this line of thought one step farther. Neil[4] has shown that sublethal levels of potassium cyanide adversely affect the ability of fish to maintain themselves against a current. It seems to me from the authors' work that it is essential to certain organisms that they maintain themselves in strong currents, because they are not otherwise able to obtain an adequate supply of oxygen. If, however, there should be a sub-lethal concentration of toxic material and if the effect on macro-invertebrate is the same as on fish, it seems that these organisms may be unable to exist in the field in a concentration of toxic material which would not be lethal under experimental conditions in which they were not dependent on maintenance of their position against a current to obtain adequate oxygen. In the case of animals which exhibit respiratory movements, it is possible that these might also be affected by sub-lethal concentrations of toxic substances.

These considerations are of interest to me. I am hoping, shortly, to engage in a research programme which has as its aim the investigation of the environmental and biotic factors which bring about changes in the macro-invertebrate fauna in the various stages of recovery from pollution. My approach to this research programme and the design of the experiments I shall conduct will be significantly affected by the paper we have heard today. This paper also contains a great deal of information which is of value to those of us who are concerned with the practical problem of measuring water pollution and it is a significant step forward in the important research field of investigating the manner in which changes in the environment, such as a result from pollution, bring about changes in the biocoenoses.

PROFESSOR O. JAAG: I thank Dr. Beak for his tribute to the work we have done. The fact that in his practical investigations in large rivers he has arrived at a point of view similar to ours is for us a confirmation of our own observations made in experiments and in small watercourses. The extremely various significance of the current in the biology of flowing waterways naturally has effects in many fields which have been only slightly studied up to now, and it is more than conceivable that the toxicity of much poisonous matter in waterways depends on the current, just as the oxygen content and the temperature exert their special influences (cf. investigations by Wuhrmann and Woker).

In fact, then, the current is an important factor in the over-all combination of ecologically operative factors in flowing water. It is not the only one, however. Biotic factors, the differential behaviour of the individual animal species in the face of chemical influences, competition with regard to nourishment, environment and habitat, subjection to predators, etc., appreciably complicate the situation. Thus the investigator who probes more deeply into these problems comes again and again upon the most surprising facts. An example may elucidate this; though it does not come from flowing water, it is no less germane.

In the late summer of 1961 there came simultaneously from two neighbouring lakes in the Canton of Zurich (Switzerland) alarming announcements that the surface of the water was suddenly covered with a thick green layer of algae, which were being driven in masses against a shore embankment and were there decaying, giving off a strong stench. It turned out that this was the sudden mass development of a blue alga, namely, *Alphanizomenon flos-aquae*, an alga which had long been known, of course, but not in this region and only in ponds of standing water. What, or to speak in ecological terms, which combination of factors can have caused this alga to appear suddenly in masses, when it had never before been noted in these lakes? We do not know the answer. A contrary phenomenon occurred in another lake, the Lake of Hallwil. Here since the turn of the century the predominant species in the plankton had been the "Burgundian blood alga", *Oscillatoria rubescens*. After the hot autumn of 1961 with a pronounced oxygen deficiency and a catastrophic fish mortality, *Oscillatoria rubescens* suddenly vanished from the plankton of the lake and has never appeared again to this day. Cause: unknown.



Thus we repeatedly find ourselves faced with surprising occurrences that are at the moment inexplicable, and the same thing probably applies as well to the field of flowing-water biology. In the present discussions we have broached the whole complex of problems concerning the effect of the current on the organisms in the water; we have analysed a number of special questions and come by and large to the conclusion that this vast, manifold and intricate field still remains very largely uninvestigated.

A SPEAKER commented that he had often found in large rivers, in floating debris, currents which would support the same or similar species as would riffles in a small stream. He had noted that *Simulid* larvae, which usually lived only in very rapidly flowing water, where most other species cannot live, will nevertheless live in less rapid currents if there is no predation by other species.

PROFESSOR O. JAAG agreed. Beside current speed, other factors operate and in particular biological factors. Competition of different species plays an especially important role.

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