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PRESENT TRENDS IN RIVER STUDIES

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SUMMARY

A review of recent studies on river ecology is presented. Emphasis is laid on the importance of basin processes which are key factors in defining the structure and function of river communities. At present rivers are viewed as parts of ecosystems where disturbance and spatial heterogeneity play a central role. Biotic interactions (predation, competition) do not seem to be important at the ecosystem level because of the frequency and intensity of disturbances in the rivers. In some of them, however (the lower part of the largest rivers), or during short periods of time, herbivores and predators (especially fish) may have great involvement in the production and structure of the community.

On the other hand, much recent work has been done in the temperate zone, and some of the more recent ideas may well have to be re-examined in the future, when more comprehensive studies of small streams in tropical areas become available. The lack of knowledge about Mediterranean rivers is also emphasized.

Many of the recent ideas in river ecology have emerged in discussions at meetings. Those of the North American Benthological Society and the Regulated Rivers Symposia deserve special mention as forums for the exchange of fruitful ideas. Finally, tribute is paid to Prof. Margalef for his pioneer studies on river ecology and his always stimulating and iconoclastic ideas on the general rules of science.

KEY WORDS: River ecology, basin, disturbance, spatial heterogeneity, biotic interactions, regulated rivers, Mediterranean rivers.

INTRODUCTION

The last twenty years have seen a spectacular development in the ecology of rivers. Constant repetition of the same type of descriptive studies has given way to synthetic studies which are based on previous hypotheses. One of the results of this is an increase in the number of books about river ecology over the last few years. A large part of ecology theory that had only just been introduced in the study of rivers has been applied to them on a large scale, especially by means of *in situ* experiments and studies carried out in the laboratory. Biotic interactions, hardly considered as determining factors in population dynamics until the mid-seventies, have gathered importance as one of the aspects that may sometimes be crucial to the organization of communities of organisims living in rivers. Nowadays the ecology of rivers is one of the most thrilling areas of ecology, and the number of studies published increases year by year. For this reason, it is both easy and difficult to synthesize them.

MARGALEF (1960) was one of the first to focus upon a few valid ideas which would place river ecology within the conceptual framework of general ecology. Even today, his paper is still compulsory reading for those who wish to view rivers within a wider context. These original ideas, corrected in the light of new discoveries, were later developed in his book *Limnología* (MARGALEF, 1983). In this book and in many other papers, we can appreciate Professor Margalef's wide knowledge of the subject, set within the more general framework of limnology and ecology, as he himself has emphasized recently (MARGALEF, 1990). It is indeed in this latter publication that Margalef complains of the scant attention that general ecology has paid to river ecology.

A LITTLE HISTORY

There were very few books available on river ecology until the beginning of the seventies. Those by HYNES (1960, 1970) deserve mention, as his research team was one of those that worked most intensely on the subject. Articles of synthesis from those years dealt especially with the subject of zonation (HUET, 1959; ILLIES & BOTOSENEANU, 1963) and almost completely ignored the dependence of a river on its basin. One of the first books to bring together the ideas of many authors is a good example of this kind of omission and of the state of the subject at that time (WHITTON, 1975). MARGALEF (1960) had already argued the importance of considering the river within the wider framework of its basin and studying the longitudinal organisation of the river within the context of ecological succession, a subject that was later broached by FISHER (1983). Without doubt the holistic approach to the study of hydrographic catchment areas (LIKENS & BORMANN, 1985) was responsible for the main subject of study in the seventies being the dependence of the river on its basin (FISHER & LIKENS, 1973; PETERSEN & CUMMINS, 1974). Hynes' Baldi lecture at the SIL Conference in Canada (HYNES, 1975) had a very thought-provoking title in this respect. Some years later, the subject was approached again, but now with a more precise development, at another SIL conference (again as the central communication). It was possible to see what had been produced by a decade of research focused on the idea of the basin as an ecological unit, especially in headwater rivers (LIKENS, 1984). At this point we should pay a special tribute to the limnology conferences of the SIL (*Societatis Internationalis Limnologicae*), which has been a meeting place for ideas and experiences in limnology every three years since 1922. The *Verhandlungen* (Proceedings) that are published after every conference, although often criticised for their bulk and sometimes for their lack of "quality", are a reflection of the development of world limnology over the preceding three years, and have thus a testimonial value which transcends their scientific value.

Studies by various North American groups at the end of the seventies have produced, as their most outstanding consequence, the emergence of a hypothesis which was applauded without reserve by some and criticized by others (especially the Europeans): the hypothesis of the river as a continuum (VANOTTE *et al.*, 1981). This had the virtue of recognizing the work of some of the pioneers (among them Margalef) and of provoking a few years of intense study of rivers, together with various controversies on the subject (WINTERBOURN *et al.*, 1981; BARMUTA & LAKE, 1982; STATZNER & HIGHLER, 1985; RYDER & SCOTT, 1988). This frenzy is reflected in numerous publications and more than a dozen books, some of which are monographs which integrate data to one specific river, or to a determinate geographical area (BARNES & MINSHALL, 1983; FONTAINE & BARTELL, 1983; WHITTON, 1984; WELCOME, 1985; DAVIES & WALKER, 1987). New ideas and methodologies have emerged from this, which situate the study of rivers in its optimum moment at present. Studies published in the *Journal of the North American Benthological Society* (JNABS) bear witness to this moment, from among which we draw special attention to a recent monograph (STANFORD & COVICH, 1988), or the conferences on regulated rivers and studies published in the journal that specializes in this subject, *Regulated rivers.*

River ecology is, however, still the ecology of rivers from temperate zones, and for that reason it is only part of our understanding of a much wider topic. The present state of knowledge of the great African and Latin American rivèrs is still poor, but some of these rivers have merited their own more or less recent monographs, like the Amazon (SIOLI, 1984). As for the Mediterranean rivers, we could say that we have hardly past the descriptive stage, with the exception of a few studies which have recently been done on Californian rivers (RESH, in press).

THE HYDROGRAPHIC BASIN AS AN ECOLOGICAL UNIT

Nowadays nobody would dispute the importance of the processes which occur in the basin in determining how the energy flow is structured in a river. For certain basins, the integration of data from many years allows us a comprehensive view of the processes in the basin, and of how these connect with those of the river, which are of extraordinary interest (e.g. SWANK & CROSSLEY, 1987). This is particularly clear in the case of headwater rivers when the river flows through forest regions. The Hubbard Brook experiments have provided a solid set of data which show the dependence of energy flux in these rivers on the input of alochthonous material, and how plant leaves cannot be processed by animals without first being colonised by bacteria and fungi (KAUSHIK & HYNES, 1971; CUMMINS *et al*., 1973; PETERSEN & CUMMINS, 1974; ROUNICK & WINTERBOURN, 1983). The nutrient flow in the river is closely related to this process (MEYER *et al*., 1981). The movement of the nutrients in the river is affected by their transport downstream and by the retention they may undergo if they are used by organisms, or in the sediments. This has led to the interesting concept of nutrient spiralling (NEWBOLD *et al*., 1982), which although highly attractive from the theoretical point of view is hardly applicable to natural rivers.

This point of view has recently come in for criticism, as all the experiments are normally carried out on dry leaves, whereas in areas where willows and elders are abundant the input of leaves is mainly in the form of fresh material. This does not decompose so rapidly, and may have a different nutritional value (GESSNER & SCHWOERBEL, 1989). In the same way the study of the decomposition of tropical forest leaves that are poor in nutrients also shows the importance of other factors. Thus, the leaves of certain trees that are rich in tannins take much longer to decompose than those that live in nutritive soils and are poor in these compounds. Experimental transfer of the leaves of tropical rivers to temperate rivers demonstrates the importance of the characteristic flora of each river in the decomposition, as the leaves that have been transferred always decompose with greater difficulty (STOUT, 1989). These experiments open very interesting new perspectives in a subject which could have been considered exhausted.

However, even in highly shaded rivers, primary production can be important and may explain the permanence of certain species in the river (MEYER & LIKENS, 1987). On the other hand, when there is no forest cover, or when light can penetrate at certain times of the year, primary production can also be important. The energy flux may then become dominated by the incorporation of carbon by the plants and not by alochthonous inputs or by transport from the upper parts of the river (MINSHALL, 1978). The dependence of primary production on the river gradient and the importance of this in the seston transported by the current were thoroughly studied by NAIMAN (1983 a, b).

Regularities in the organisation of the energy flux along the length of the river and the change from coarse materials in the upper reaches to fine materials in the lower parts form one of the central axes of the hypothesis of the river as a continuum. The comparison between different rivers (in near natural conditions or without important disturbances by man) has led to one of the arguments that most support this hypothesis (MINSHALL *et al*., 1983, 1985), in spite of the criticisms it received.

THE RIVER: AN ECOSYSTEM WITH DISTURBANCE AND HETEROGENEITY

It may sound like a cliché to say that a river is a system organized along a horizontal axis. This is doubtless the reason that sets it apart from lakes, which have always been aquatic ecosystems *par excellence*; UNESCO even defines limnology as the study of lakes in its fields of knowledge.

The factor that generates the river identity is the existence of a current. The possibility of carrying materials and organisms downstream (and thus, the possibility that communities might disappear) has been counteracted by a multitude of adaptations on the part of organisms, from morphological changes to behavioural attitudes which have been studied convincingly in laboratory rivers and using microphotography (STATZNER & HOM, 1982; STATZNER *et al*., 1989; EYMAN, 1988).

For the same reason, the substrate recolonisation in a river after disturbance is relatively fast, and in little more than two weeks an abundant, well-structured population can be found. This is very clearly evidenced in experiments of artificial colonisation of rivers (LAMBERTI & RESH, 1985; PRAT *et al*., 1986). A general model of colonisation and extinction has been put forward for the colonisation of rivers (MINSHALL & PETRERSEN, 1985). In the first few days of colonisation, the model seems to fit well with the process, but afterwards the situation can evolve in many different ways, in response to external changes, or the importance of biotic interactions, especially as a response to herbivore or predator pressures.

Changes that exceed the limit of resistance of any organism to the water flow (floods), or those related to the disappearance of water (drought) are extremes in the face of which we must wonder how communities respond. Thus, when faced by great floods, many organisms possess different adaptations (like taking refuge in the interstitial zone), the importance of which has recently been pointed out (HYNES, 1983; WILLIAMS, 1981; DANIELOPOL, 1988; STANFORD & WARD, 1988). After a strong disturbance (excessive flow, drought), the river regenerates in a short time a community similar to the previous one (WILLIAMS & HYNES, 1976, 1977). Thus, thanks to their adaptability to extreme changes, rivers as ecosystems recover easily, unless these changes (disturbances) are either very strong or too frequent. The hypothesis of the mean disturbance (CONNELL, 1978) has been suggested as one of the keys to understanding the changes in specific richness and diversity in rivers (WARD & STANFORD, 1983a). Some studies have provided convincing data on the importance of disturbance in community structure in different types of rivers (FISHER & GRIMM, 1988; WALLACE *et al*., 1986; ROBINSON & MINSHALL, 1986), although in other cases the effect of disturbances does not appear to be so determinant (HAWKINS, 1988). A recent study by GRIMM & FISHER (1989) clearly shows the concepts of resistance and resilience may be applied to rivers in the study of a long series of disturbance events, thus placing rivers inside the framework of general ecological theory.

The greatest complexity of a river cannot be understood, however, unless its enormous spatial variability is considered, both in the longitudinal course and also within a specific zone. The difficulties involved in the estimation of the population density of the species inhabiting rivers are well known. Even with standard errors of 40%, it is necessary to take more than 20 samples to estimate the density of a given species (RESH, 1979). The use of transects clearly reveals the importance of this spatial heterogeneity and the problem of estimating populations (MILLET *et al.*, 1987; MUÑOZ *et al.*, 1985), for which solutions have been attempted with stratified sampling or grids of random samples (IVERSEN *et al.*, 1985). The microdistributions produced in algal populations related to the microtopography of the substrates are also interesting (KREJCI & LONG, 1986). The action of the animals, like the presence of tubes of chironomids (WARD, 1985), and the importance of the size of individuals (OSBORNE & HERRICKS, 1987) has been also emphasized as being responsible for spatial heterogeneity.

Therefore, the most promising models in river communities studies are the combination of changes due to disturbances with structuration in space. The model of TOWNSEND (1989) is a good starting point in this respect, and may well replace the classical models of zonation. This model contemplates the entire range of systems, from the simplest system describable in terms of the Lotka-Volterra equations, to the most complex system, which would be one with great spatial heterogeneity and intermediate disturbances. The hypothesis of mean disturbance is again emphasised in this model.

The most generalised conclusion for the majority of rivers is that the frequency the intensities of disturbances produced at random falls within a range that does not permit its internalisation by the organisms. Gradual assimilation of these disturbances by life is not possible (in the sense of MARGALEF, 1986; Fig. 3). Thus the organisation of the system in rivers has little to do, in general, with biotic interactions, but rather with the type, frequency and intensity of random disturbances.

THE ROLE OF BIOTIC INTERACTIONS

Some of the most thought-provoking ideas in river ecology in the last few years have come from laboratory experiments. In many cases, an attempt has been made to show the importance of biological interactions (competition, predation, herbivory) in the structure and complexity of communities; thus in the experiments the density of predators or of possible competing species was manipulated. Most of the experiments carried out to date (both in the laboratory and *in situ*) show the real importance of herbivors for the algae or macrophytes on which they feed and also the key effect of the presence of predators. On the other hand it appears that competition does not has a particularly outstanding role in rivers of the temperate zone (ALLEN, 1984). The possible importance of parasitism in the regulation of some insect populations has recently been suggested (CUMMINS & WILZBACH, 1988). Although it is probably of limited importance, the presence of symbionts or of mutualism has also been pointed out in certain cases, like that observed between *Nostoc* and a species of chironomid growing in their interior (*Nostococladius*). The *Nostoc* colonies with chironomids have a different morphology and grow much more than those that do not have them (PRINGLE, 1985).

In the case of the interaction between herbivores and the communities on which they feed, changes have been described both in the specific composition (which results in the dominance of small diatoms if the herbivore density is high), and in the production and biomass of plant communities (e.g. HILL & KNIGHT, 1987; COLLETTI *et al*., 1987; LAMBERTI *et al*., 1987; LOWE & HUNTER, 1988; OGILVIE, 1988; STEINMAN *et al*., 1987a, 1987b; RICHARDS *et al*., 1988). A general model of the effect of herbivores on production of algal communities was suggested by LAMBERTI & MOORE (1984). This model assumes a decrease in biomass with an increase in pressure from herbivores and greater productivity at intermediate densities. The model seems to fit well to many of the experimental results reported to date. The possible influence of differences in periphyton composition on the animal communities that feed on them has also been pointed out (DUDLEY, 1988).

The effect of predators in artificial rivers and its importance for the macroinvertebrate communities has been emphasised on many occasions in river ecology (PECKARSKY, 1984; MERRIT & WOTTON, 1988; RUTHERFORD & MACKAY, 1986). In some cases data are available on their effect on the microdistribution and behaviour of the prey (MICHAEL & CULVER, 1987). As has been mentioned above, it has been more difficult to find evidence that competition is a key factor in rivers (ALLEN, 1984), although some examples have been presented from laboratory studies (LAMBERTI *et al*., 1987). Only in cases of competition for space, at moments when population density is high, it can be assumed that competition may be an important factor. One of the most frequently cited cases is the intraspecific competition among trichoptera to spin their webs (*Hydropsyche*), or interspecific competition between simuliidae and hydropsychidae (HERSHEY & HILTER, 1988).

Nevertheless, as RESH (in press) has shown, densities that appear to be critical for herbivores, predators or competition to act, deduced from laboratory studies, are rarely reached in rivers. Thus in rivers of the temperate zone that are subject to considerable thermal and hydrological fluctuations, biotic interactions appear to be relatively unimportant (except the herbivores in some cases or the predators, especially fish) in modelling the community, whereas external factors (which we have referred to as disturbances) and heterogeneity in space appear to be the key to the organisation of communities in rivers (LAKE, 1985; LAKE *et al*., 1988; GRIMM & FISHER, 1989).

Studies on the importance of behaviour in the interactions between organisms has not received much attention in rivers. Some data on the interactions between *Baetis* and the chironomids that form their tubes in the zones in which these are grazing (recorded on film), show that this aspect deserves much greater attention (HERSHEY, 1987).

REGULATED RIVERS

An important factor in the development of river ecology in recent years has been the boost given to the general understanding of it by limnologists who have studied the effects of river regulation by dams. The model of the river as a continuum has always assumed a river with gradual transformations along its whole length; most of the rivers in the world, however have been dammed (WARD & STANFORD, 1979), hence the presence of reservoirs has a clear incidence on the characteristics of the river downstream.

Depending on the type of dam and the depth at which the water flows into the river, the effects on the communities are predictable according to a relatively simple scheme (WARD & STANFORD, 1984). The river can be viewed not as a continuum, but rather as a series of discontinuities and WARD & STANFORD (1938b) and STANFORD *et al.*, (1989) have proposed a measure of this discontinuity. A similar idea has been applied in some Catalan rivers and yields positive results in simple parameters such as conductivity (SABATER & ARMENGOL, 1989). In fact the changes produced by the dams could be classified as disturbances, which would allow us to place regulated rivers within the framework of the more general ecological context.

The various conferences on regulated rivers have been a good forum for the debate of these and other aspects of rivers, and have contributed in a significant way to the recent advances in river ecology (WARD & STANFORD, 1979; LILLEHAMMER & SALVEIT, 1984; CRAIG & KEMPER, 1987; PETTS, 1989). There is also a monographic book on the subject (PETTS, 1984).

LONGITUDINAL ORGANIZATION

Longitudinal organization has always been one of the classic subjects within the study of rivers. Words like rhython and potamon became common currency in the sixties. The study by ILLIES & BOTOSENEANU (1963) cited above is the best example of this research line. Here we should also remember some of the pioneering work done by MARGALEF (1958) in this field.

Longitudinal zonation, which assumes the change from some communities to others along the length of the river, was heavily criticised in some cases (HAWKES, 1975) and the idea of the river as a continuum seemed to relegate the application of zonation to those cases where serious alterations in the characteristics of the environment were produced, such as pollution. More recently, however, the subject has drawn new interest, especially because of a better application to rivers of the concept of hydraulics.

In effect, changes in gradient may occur in certain rivers in relatively short stretches within their length. This may lead to important differences in shear stress at the bottom of the river, and consequently limit the presence of many species belonging to higher or lower stretches of the river. The sites at which the gradients of the rivers change would be where species from both zones would be found, and thus these will be zones of higher specific richness. STATZNER (1981) and STATZNER & HIGLER (1986) are the most ardent defenders of this idea, which allows a somewhat different interpretation of the change in species richness along the river, which derived from the idea of the river as a continuum (VANOTTE *et al.*, 1981).

The study of the lower parts of rivers has brought to light the importance of alluvial plains in determining the characteristics of the river, and their interest as filters between zones adjacent to the river and the river itself (CHAUVET & DECAMPS, 1989). These studies confirm the importance of ecological processes in flood plains and in the lower stretches, as they are known in large rivers (SIOLI, 1984), and open up possibilities for the study of processes of succession, as proposed by MARGALEF (1990).

APPLICATION OF ECOLOGICAL THEORY TO MEDITERRANEAN RIVERS

Most of the studies carried out to date have been in the temperate zone. The rivers that we could include within the regions of

Mediterranean climate have not received equal treatment until recently (GIUDICELLI *et al.*, 1985), if the studies carried out in California and in Australia are excepted; even in the latter case only very recent attention has been paid to them (BUNN & BOUGHTON, in press). The rivers situated around the Mediterranean Sea, with a typically torrential hydraulic regime, have been predominantly descriptive. They have not been placed explicitly within the comprehensive scheme of river ecology (PRAT *et al.*, 1986). Furthermore, most of these rivers have been greatly transformed by the action of man, and so there are very few left to compare as a model. Moreover, only long-term research can provide us with complete ideas on their behaviour, and it is rarely possible to go on with the same type of research for 20 years or more. The only data of this kind appear to be those of RESH *et al.* (in press), for Californian rivers that may dry up in some years, or be subjected to sharp increases in their volume.

Severe disturbances that are repeated annually (floods and droughts) with varying intensity are key factors in Mediterranean rivers. However, the intensity of the floods and the severity of the droughts vary from one year to the next and from one river to another. This is linked to a thermal regime that permits the development of the majority of the species in the river with relatively short cycles if we compare them with the same species living at higher latitudes.

As a result of this, and of the ease of dispersion of the species, Mediterranean rivers undergo spectacular changes in their community similar to those of rivers from desert zones such as those studied by FISHER *et al.* (1983). But in some years, or in some rivers, there is no period of drought and the bed of the river does not dry up. Also, in many years the floods are not great enough to eliminate all the community from the river.

As a consequence, the Mediterranean rivers offer a much greater diversity and a much higher complexity than rivers of temperate zones, although the species with a fast life cycle (particularly Diptera) appear to dominate over those with a more long and complex life cycle (for example, Trichoptera and Ephemeroptera).

LOOKING TO THE FUTURE

In the next few years river ecology should devote more attention to large and small rivers in the tropical zones, both on the plains and at higher altitudes, in order to determine whether it is really in terms of disturbances and spatial heterogeneity that the structure and evolution of communities are to be explained. Particularly the alluvial plains of the great rivers should attract our attention, as on the one hand they are threatened with extinction, and on the other they promise great scientific interest, especially in ecotones. A broad perspective on the progress and questions for the future can be found in the special volume of the *JNABS* mentioned above (STANFORD & COVICH, 1988) and in a recent book (NAIMAN & DÉCAMPS, 1990).

Another area which promises to be of interest is the in-depth study of the importance of biochemical factors and related subjects at the molecular level, including population genetics by means of the use of enzymes (ARSUFFI & SUBERKROPP, 1988; BARLOCHER & PORTER, 1986; FINDLAY *et al.*, 1986).

Studies in which the sampling unit is the stone are also of interest, and this may be related to the colonised area, an aspect with a certain tradition in river ecology (STOUT & VANDERMEER, 1975), which has recently been developed in a more complex way (WRONA *et al.*, 1986).

Without doubt laboratory studies of rivers will continue to be important, especially as far as they are able to reflect and lay down the rules of the possible signification of certain processes and interactions (e.g. CIBOROWSKI & CRAIG, 1989; REITER, 1989).

But we must not forget those overall views that remind us that the tree should not be allowed to interrupt our perception of the wood. The ideas developed by Margalef, his view on this or any other subject, always as critical as they are passionate, are a stimulus and a perennial reminder of the insatisfaction that is so characteristic of scientists. This paper is heartily devoted to him.

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