COMMENTS ON RIVERS AND MODELS

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Introduction

The epicontinental aquatic ecosystems have been and are traditionally the object of study of Limnology. This science has been inordinately fond of lakes. seen as miniature oceans, able to provide much stimulation combined with a relatively easy access and conditions of work. They were supposed to provide at a small scale, appropriate for study, the same basic phenomena associated with aquatic life generally. Flowing waters have attracted less attention that they deserve, as their study posed serious problems, conceptual and otherwise, but now it is time to reverse this tradition, and think of the epicontinental waters mainly as a transport and accumulation system, functioning as a bridge or link between continental and oceanic ecosystems. From the point of view of the practical problems of everyday life, water supply and water quality, flowing waters are without doubt the most important. Think only of cultural water distribution systems, and of sewers, two subjects of study that biologically have been almost neglected.

Limnologists have been biaised against rivers and in favour of lakes and one deep reason for this, was the conceptual difficulties associated with the modelling of rivers, and even of how to conceive rivers in the frame of traditional ecology. The problems concern the physical nature of rivers and other flowing waters connected to them, and ways to possible quantitative descriptions, the regime of the flow of waters through the whole system, and a reasonable attempt at modelling.

An epicontinental transport system

The epicontinental (freshwater or limnic) part of the biosphere is not only a section of the global water cycle, but a most important part of it. The disproportion between the surfaces covered by oceans and by land, and the easier evaporation over water, means that land receives a relative excess of rain, so that annually 30000 km" must flow through the rivers from the continents to the sea. This water carries a load of very diverse materials, in part as a result of chemical and physical erosion, in part as a result of the activity of organisms. We know that the amount of organic carbon carried from the continents to the sea through the rivers. amounts to the one por cent of the net primary production of the continental part of the biosphere. Rivers themselves are in a large fraction heterotrophic. This «vocation» for heterotrophy has been abused by mankind that has always found it expeditive to drop organic residues from itself and from its civilization into the water.

As the influence and transport works one way, the oceans are heterotrophic to a degree that has surely changed through geologic times. As the carbon compounds of terrestrial organisms —plants— are often notably recalcitrant to decomposition as a result of the biochemical evolution for resistence of their system of transport and support (wood), one could suspect that a considerable fraction, above that expected, of the organic matter dissolved in the ocean water may ultimately be of terrestrial or continental origin. In fact, in freshwater. macrophytes (with the associated action of terrestrial fungi) are relatively more important than algae, as suppliers of the dissolved dark organic matter that characterizes several bodies of continental water (black water rivers, etc.).

The epicontinental aquatic system should be studied in all its extension. From the drop of rainwater, that stays or glides over the surface of a leaf, to the wetlands joining the sea. Now there are supplementary motives of interest that originate in recent human action; for instance. the changes in the composition of rain-water as it washes an altered atmosphere and comes out with more acid ions, or with varied neutral substances of very diverse effects compared with former times. Rain not only clears air of noxious substances, but also takes out pheromones and other materials with potential biological significance. On the surface of leaves, rain-water provides a substratum for bacterial growth, disperses diaspores of fungi and other organisms and supports the development of small animals, including species of ciliates that are very typical of such situations *(Colpodu)*. In adaptation to the short period of presence of liquid water, after excystation and feeding for a few hours on bacteria, they encyst again and experience cell division inside the cysts in preparation of the next rain. In areas in which water remains more time, a higher number of species find access and a more diverse fauna develops, as in the sheats of leaves of grass, in the small pools on the leaves of *Dipsacus* and on the tropical *Bromeliaceue.* Part of the same system is the water flowing over the trunks of the trees, which at pre-

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sent attracts a considerable amount of attention, also because it is enriched in the leaves by particular ions —specially potassium—, which are then transported down.

Runoff is an important part of the cycle. In deep, mature soils, runoff water tends to be poor in ions and with a rather uniform composition over large areas —eventually a characteristic of climax—. There are other regularities in runoff, related to successional or otherwise time-ordered microbial activities in soils, being shown. for instance, in the initial peak of nitrogen enrichment of water. In areas or situations of less regular rain, poor vegetal cover. or with heterogeneous soils or geological substrata, runoff is less uniform over large surfaces and. in general. comes out more mineralized. This is important and would justify closer examination, because it is one of the main effects of man on water quality. On humanized landscape, runoff and flowing water are, on average, more concentrated in all sorts of dissolved —and suspended— materials, and locally more heterogeneous. Particular effects, coming from concrete, asphalt, or salt used in fighting ice accumulation on the roads, contribute to the same properties in ways that can be easily traced. Considering other anthropic effects, perhaps not so generally negative, that might be important in the future, we might remember the possible injection into the ground of solutions contributed through desalinized seawater. In the same chapter we must consider the dangers of water transfers between different watersheds and among them the effects of dilution, washing, or, on the contrary, salinization. as a result of changing the correspondence between water amount and quality, quality of the soils and response of vegetation.

Underground waters are important reservoirs and parts of a circulation system, but the total amount of ground and deep water is not well known and information about their persistence and flow is scarce. Piezometric readings, inferences based on chemical analysis, including isotopes, and general geophysical surveys provide only partial information. It is an extremely important subject, in relation with the increasing intensity with which such reserves of water are tapped. The consideration of such reserves and any forecast about them has to take into account the circumstances of a world in which human action is increasing. Man pumps out deep water and accelerates its flow towards the oceans; this acceleration often means replacement of part of the water by other water of dubious quality, that can have a considerable charge of pollutants derived from human action. The acceleration is paid for by the energy invested in pumping water —and in planning and constructing such exosomatic expansions of our civilization—.

The action of mankind on rivers is quite complex. Rivers become simplified, converted into regular channels and flow is made more direct and uniform; this is accompanied by a loss of biotic and biospheric diversity. Think only of the destruction of most of the very diverse water bodies in the alluvial plains that were associated with meandering courses of water, in America (madrejones, pantanales), Australia (billaboongs) and elsewhere. In Europe most of them had dissapeared a long time ago. From the point of view of ecology this is regrettable, and it also means the disappearance of aquatic ecosystems characterized by supply of nutrients in the surface, encouraging development of surface communities —neuston, pleuston—, as well as the dismise of an important mechanism of interplay between water ecosystems and terrestrial ecosystems, linked by processes of succession that maintain, from the point of view of the evolution, the interaction between the river and the forest.

Through the construction of dams, man slows down tluxes and, in a certain way, the result of this operation may be considered as opposed to the pumping out of water from aquifers. One question to be asked is to what point the energy obtained through dams (hydroelectric power) compensates the energy used in pumping waters from the aquifers.

Morphology of drainage systems

The evacuation system develops in association with the morphology of the earth's surface and in relation with the erosional activity of the water courses. Some regularities in the resulting structures are expected and are indeed common, like the distribution of altitudes along the water courses as a function of erosion and transport and in relation with the materials of the surface drained. The old idea about the equilibrium profile of a river is an example of the (dynamic) regularities involved and is still worthy of further study. In the upper stretches of the river, the fluvial system is made by a succession of convergences of separate segments; below, on the aluvial plain, the work of the river is expressed in the formation of meanders. In this active process the river erodes along one shore, intercepting terrestrial communities in different stages of ecological succession, and, on the opposite shore the river opens an area to terrestrial invasion and colonization, and over this area successive stages develop in the form of bands parallel to the receding shore. The contrast between cutting a banded pattern of communities at a right angle, and allowing the addition of a paralel new area to the preceding complex is a paradigm of succession, and can be appropriately described by an asymmetrical matrix.

Close to the sea, the interaction between dynamics of the river and tidal dynamics may generate wetlands with very complicated drainage systems. The trend observed in the upper reaches of the river appears reversed, now the river tends to be divided in different outlets. Otherwise, the main stream becomes a large estuary. All this is strongly dependent on the geological characteristics of the coast and on the local tidal regime.

The structure, profile and expansion through convergence, meandering and divergence of the main draining veins shows many regularities, appropriate for quantitative or numerical expression, a number of laws or regularities have been suggested, in relation with convergence of affluents, morphological regularities of meanders that accept a simple geometrical explanation, and also development and characteristics of deltas. It is easy to understand that relations between flows, development of water courses and drained surfaces often allow to allometric or fractal expressions. Today these relations provide a testing ground for the now fashionable approaches. Replication of definite trends and motives at different scales lend themselves to a comparison with fractals. This area of study is open to fascinating developments, and from the beginning we face problems that go very deep and that might bc worth following. This all adds to the attractiveness of the subject.

As an example I refer only to the difficulties in combining two complementary, hut independent, fractal approaches to the description of the landscape. Television has made us familiar with artificial fractal landscapes. Their construction is now of no direct concern: In general we start with certain hypsographic curve (distribution of surfaces according to their altitude) and some randomness is injected in the distribution of the altitude of the different points, with some restrictions imposed for neighborhood, etc.

Assume that rain falls on such a landscape and also that each drop of rain flows down through the steepest slope locally available and in doing so produces a certain amount of erosion, taking away some solid material. Making some assumptions about the rain — amount, degree of periodicity, uniformity or regularity of the differences between neighboring places, etc. — we may ask the following question: If the first landscape could be generated by some fractal expression, can we expect that the second or final landscape can also be fitted to some fractal expression, or subjected to fractal interpretation? The problem also concerns the relation between surface morphology and the properties of the drainage system.

From an ecological point of view, the system of converging affluents is also interesting because the convergence and union of different flows can make the resulting common flow more uniform (or else exaggerate the peaks in cases of strong rainfall hitting neighboring valleys simultaneously). This system also favours chemical homogenization, through mixing, of waters that might have slightly different composition. Finally, the mixing of population~drifting through by the respective affluents, combines different genotypes into a new environmental system in which strong selection may be expected.

We often imagine that the underwater systems and aquifers in general are a projection and continuation of the same river below the surface, with the same, if slower, role in transportation, all related to the permeability and texture of the bed materials. The domain of underground waters is, in fact, much larger and may be associated with deeper geological features of the country.

Speeding up the features of succession and change

Life combines relatively slow (sometimes programmed, sometimes just allowed) processes of selforganization. and the response to unpredictable disturbances that, more often than not, destroy a proportion of the organization achieved. The expected or more general result is that the system, as a result of the disturbance. is changed or reconstructed acquiring some characteristics that approaches it to some former state that was already passed through and that was considered as a younger stage in ecological succession. This is only an example of very general rules of change that also include growth and death, and, in ecological terms, it is manifested in inevitable succession and in the repeated resetting or reinitializing the process at a given stage. As a very important corollary, once ecological succession is accepted it cannot be accepted that ecosystems exist without being coinvolved in successional processes (It is like in evolution, where, once accepted, no biologist can imagine that a string of generations can exist without evolution, external or internal).

Ecology is full of appropriate examples, but if we were in need of more, we could be served with largesse considering the distribution of flow in the rivers: here the disturbances are associated with the distribution of rainfall in the respective hydrographic basins. Much worry and ingenuity has gone into the examination of temporal distribution of rainfall and river flow, over different scales of time. Randomness is tantalizing, and effects like the distribution of extreme values, the «adherence» between neighboring values, suggesting short cycles or particular interactions over time, never find a satisfactory explanation. but remain a source of stimulus for research.

The following model may be of more general application in ecology: Assume a standard system of development, selforganizative or successional, subjected to a spectrum of disturbances, from which it can be said only that the most strongest — measured, if convenient, in terms of external energy involved — are less frequent than the less strong. This general view of a spectrum of disturbance is not pure. but contains some difficulty born in biology and evolution, because very common disturbances become conditions for life and must be internalized by the organisms, like daylnight {{disturbance., seasonal change, no matter how important they are in terms of energy. In fact the daylnight cycle is ***also very important*** in terms of the energy involved. To assign a given frequency, ***a posteriori***, to a given class of disturbances does not mean that we have to expect a regular distribution over time of the events to which it refers. The events may cluster, like glacial periods at their scale, or rainy and dry years, which may be associated in a row, from pairs to groups of seven. An interesting question that can be approached through simulation is: Given such circumstances, what is the probability of being right in attempting some prediction, which we can simplify asking only for the probable lenght of time in which we can expect disturbances of an even sign or of a decreasing sign, or at less, not interrupted by major disturbances. Some exercises of simulation show how difficult it is to find encouraging answers, that is, answers that make some success at prediction likely. This is very discouraging if one tends to believe or to expect that one of the roles of ecology in society is prediction, even if understanding is not complete.

The alternative interplay between «regular» development and disturbance informs change in ecology, but is not exclusive to life. It can also be recognized in the sediment deposited in river beds and elsewhere. Regular cycles (cycles of Bouma, etc.) begin suddenly with coarse materials, as a result of a rapid increase in the transport capacity of the system, in our case of a river, and then follow with materials of decreasing size, eventually reaching sands and muds. What is important, as a paradigm of change that compares favorably with ecological succession, is the gradual change from coarse to fine materials, as opposed to the suddeness of the change in the contrary sense. From the point of view of river ecology this is important for the distribution of boulders and other materials on the bottom of a river. River biologists usually used to relate the motility of boulders, according to their size, with definite speeds of water. In this connection also, there is relation between populations and the past history of flows.

Approaches to modeling river populations and ecosystems

It is difficult to study in detail biotic populations in flowing waters and to conceptualize in their ensemble. This probably contributes to explaining the traditional unwillingness to include rivers in general ecological approaches to limnology. Many approaches have been attempted in the line of description of communities, developed as a function of properties of local substrata, and organized in mosaic-like fashion. When limnologists have been more aware of the strong relations between local communities. as associated with other flowing with the water, they have felt that this should be hailed as progress, under the name of the continuum concept. The real position of the epicontinental aquatic part of the biosphere as a transport system, enhances its unique position and perhaps opens the way to a more realistic approach to its biology. As a preamble we might recognize that downstream there is a steady colonization pressure from populations living upstream, which must be countered by selection going another way. Populations living in the upper stretches can influence populations living below, through different sorts of chemical influence, whereas the converse action upwards does not exist. Simply, populations in upper stretches exist and are maintained through steady adaptation to local conditions and brute force in multiplication. But in the lower stretches very subtle relations become more important. It is possible to say that lower stretches exploit upper stretches of the river. And this would be reason enough to explain the fact that biotic diversity usually increases downstream. In general, systems exploited from outside have their biotic diversity depressed. In relation with the model of «random walk» to be commented below, biotic diversity is usually negatively correlated with the power k that characterizes the random walk regime.

We should proceed through a number of steps:

1) Flow cultures. Difficulties in adopting an exclusively Eulerian or Lagrangian approach.

2) A more flexible approach and a guide to the evolution of riverine life.

3) Turbulence and its equivalents.

The simplest model of a river is a chemostat or flow culture. In it natural growth of a population tends to move to a balance with the amount of the population driven away by the flow. If r is the rate of increase of populations —no deaths considered now—, N the quantitative expression of the population, x a length measured along the axis of the «river», positively in the downstream direction, and V the speed of the water or culture medium, and t is time, in one point of the river we should have

$$dN/dt = rN - V\,(dN/dx)$$

an expression that can be compared to that one used in plankton biology, with reference to a vertical dimension z, and to which a term referring to turbulence (A) is added, in the form:

$$+\ A\,(d^2N)/dz^2).$$

If organisms were to develop suspended as plankton in water moving in a laminar flow, it is obvious that they would be rapidly washed out of the system. There is an aphorism by Ambühl that goes as follows: «No life is possible without water, and no life in water is possible without turbulence». This is easy to understand, and the practical realization of a persistent flow culture consists in joining a number of small reservoirs in each of which a separate mixing is achieved. This is properly what happens in a river, with the difference that the intensity and the length of mixing are not constant in any given section. Indeed, mixing intensity and modality changes continuously according to the place. For this reason it does not make much sense to dwell on the traditional discussion between the Eulerian or the Lagrangian approach, if one should consider what happens in one point of the environment —not including the important question of how big the point is— when it is a fixed point with reference to an exterior space, or when it is considered that the point drifts with the water. It becomes a purely «academic» question.

Actually there is continuous change in speeds and trajectories, all combined together, that forces us to a statistical approach, which would be difficult to qualify as either Eulerian or Lagrangian, Biological factors make the model more complicated. In simple flow systems. in the form of reactors for the production of bacteria or algae, or of their metabolites, some sort of turbulence is striven for, but organisms that attach to the walls, if genetically different, often gain preeminence. The capacity for holding the position is an asset in evolution. In other words, not only a wide range in the conditions of flow. but also in the characteristics of the organisms, is important in associating them with given flow situations, or linking their probabilities of survival to the size of the solid materials, from grains of sand to boulders, to which they attach.

This is extremely important in discussing life in rivers. In the preceding expression, a sort of trade-off between r and V is implicit, in the sense that species that reduce the effective speed of drift can slow down rate of reproduction and this is the most obvious advantage in selection. This has represented a constant pressure in the evolution of what have been considered as adaptations to life in streams: attachement to stones, life among the sediments, and other forms to oppose to unavoidable drift of at least a fraction of the populations, like the tendency to swimm against the current through mechanisms that allow optical clues in relation to the environment, or forms of behaviour like the tendency of aquatic insects in their adult and aerial life to crawl or fly in a direction opposite to the flow of the river in whose waters they were born. Of course. the simplest distinction is between potamoplankton, moving with the water. and potamobenthos, fixed to the bottom, but the distinction is never neat, as can be deduced from the discussion about the appropiateness of Eulerian and Lagrangian approaches to the description.

The drift of one part of the benthic populations can be quantified, supported by the catches of nets extended normally to the current and a net speed of movement downwater assigned to each species. Such speed is not constant, being subjected to circadian and seasonal cycles, and to other factors. Persistence of populations requires that the net drift has to be compensated by multiplication of the populations and other eventual inputs. As the speed of water changes, often catastrophically, it is obvious that the aerial life stage in insects is very important for the persistence of their population~and this form of life —which we could call schizophrenic— is expectably very common among the aquatic fauna.

Different approaches to an enlarged concept of turbulence

One simple approach that may have some advantages is based on the concept of «random walk». In moving from a to b, over a distance of L, expressed as the number N of steps, one can follow steps strictly in the «convenient» direction, where $L = N$, or $L = N^k$, for $k = 1$, or else wander continuously around a point without making any advance in relation to some exterior fixed system of coordinates, in which case one step is the maximal distance from the initial point. The same expression is valid with $k = 0$. The values of k characterize the system. Along one dimension, for instance, along the axis of the river, the population behaves like a Marathon course. After a while some individuals are ahead, the bulk follows, and some lag behind. If we assume a normal distribution —which cannot be, as the causes are not completely symmetrical, its variance σ^2 would be proportional to the elapsed time —from the starting line— multiplied by a coefficient of diffusion (A).

Whereas in modelling plankton systems over the z axis, turbulence (A) and sinking speed (V,) can be considered separately, in general, the speed of water (V,) is seen as a main factor in flowing water, and the turbulence begins to be considered rather as a modifying factor. This is not completely appropriate, however, because of the existence of environments in proximity, with quite different regimes, and the organisms can move from one to the other easily, as in sediment, or in the margins of rivers. Of course small eddies can be observed in the sluggish large streams where the generally downwards motion of water is locally reversed. There is another aspect which shows the complexity of the problems involved and the interest of a certain uniformity in their modeling. The rivers of a water-course are a true bank of germs of potential colonizers of the water. Diaspores are left on the banks under quite different situations. It is clear that colonization by species of algae —*Hydrurus* and many others— at the time of high water comes from germs left over the banks. As water level falls and other species develop, most of them leave some resting stages on the banks. It is amazing how many alive organisms. in suspended animation, or as cysts and various resilient forms (coccons of *Aeolosoma*, rotifers, nematodes, tardigrada) are found in the soils in the vicinity of water, in winter frozen but alive, apt to recolonize the river. This bank of germs at several different stages offers ample possibilities for the recolonization of the river. but scarce attention has been given to it. The point here is that its persistence is equivalent to a form of turbulence for the whole population, and to this persistence should be added the preservation of population in the interstitial water at the different levels.

We end with a concept of turbulence that surpasses the consideration of a criss-cross of trajectories at random, and directed to draw a statistical spectrum. The physical or more random part of it becomes mixed with the results of the behavior of a number of organisms that impose arbitrarieness and biaised trajectories, in directions and speeds, and in the interaction between velocity and trajectories, as well as changes subjected to circadian rhythms. Natural selection works against a background that is not simple, and exposed to continuous change. in relation with the fluctuations in the speed of water.

Irreversibility of natural change

The uncritical use of simple regressions can be very misleading. Suppose we are interested in the relation between phosphorus load and chlorophyll in the surface of lakes. Such relation is standard in the consideration of eutrophication. The line that describes the change in a diagram in which both descriptors (phosphate load an chlorophyll) in the photic zone, are entered, is different during the ordinary processes of eutrophication and back, if and when contemplated protective action is successful. The way down is not like the way up taken in the opposite direction. A simple solution would be to postulate that the function depends which way one goes, if increasing eutrophication or going away from it, and perhaps, in a general way we should not write $y = f(x)$, but $y = f(x, dx/dy)$ or, probably better, try some expression involving complex numbers.

In our example of eutrophication followed by success in remedial action, the surface comprised inside the loop that describes the process is very likely proportional to the economic cost of the whole operation. A large lake, and still more a sea. takes a long time to be impaired. but it is very costly to clean. On the contrary, a river is rapidly spoilt but, theoretically, with the same ease can be cleaned. Its storage capacity is not great. This is a non usual approach and it would be interesting to examine how the study of the consequences of accelerations and decelerations in the flow, always asymmetrical, could be studied in an analogous frame.