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Some critical remarks on the usual approaches to ecological modelling

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INTRODUCTION

A model is an intellectual construct purporting to reflect the structure and working of some system, and, in the present context, of some ecosystem. The literature about models of ecosystems is heavily redundant. Little real progress has been done since VOLTERRA (1926), LOTKA (1925) and RILEY, STOMMEL and BUMPUS (1949). Mathematical models are indispensable, but they must help to grow ideas and not just to feed computers. I argue that models apparently sophisticated, but inexact in the basic assumptions, can hinder progress and even impair the ability or the pretence to understand nature. This, of course, can be interpreted as the envious remarks of somebody unable to follow or even to understand the mathematical approach, expecting to arouse some sympathy from fellow field ecologists. But I insist that nature can be seen in different ways and that usual model building translates into mathematical terms only a small and biased part of what is known about the workings of ecosystems.

My comments will be limited to the sort of models described in following lines, but I think that the same sort of criticism can be applied to most, if not to all, models. In the models to which I refer specially, the system is split down in boxes, with inputs and outputs, and the particular input of one box may be the output of another box. Inputs

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and outputs are made dependent of the amount or of the properties of the contents of the different boxes or compartments, and often from some other general and pervasive property, as the temperature. Such sort of models can refer to matter, to energy or to organisms. Matter is conserved, and what is lost in one point appears somewhere else, and it is possible to draw a nice symmetrical transition matrix. Not so with energy, ecosystems being dissipative systems, and in every change a certain amount of energy is not recovered for the ecosystem. Dealing with organisms is more difficult, because it is customary to refer to individuals, that are parcels of matter and energy; they do not come in the same size, they are wasteful of energy in different degree, and through sedimentation or active movement they transport matter in a way completely different from physical diffusion. Organisms imply some strategy and modelling at this level has to be done in the context of game theory.

The ecologists coming from the field of biology are most familiar with the models associated with the names of LOTKA and VOLTERRA. Here the model consists of a set of differential equations, and each of them expresses the rate of change of the number of individuals of one species, component of the system. Changes depend on a number of interactions among the components of the ecosystem, and it is assumed that the frequency of interactions is proportional to the product of the densities of the interacting species. In the LOTKA-VOLTERRA approach it is possible, of course, to write equations not only for species, but also for the concentrations, outside the organisms, of some selected nutrients.

TWO INCONVENIENTS OF THE USUAL MODELS

Discussion and criticism concerns frequently linearity or non linearity, time lags and heterogeneity of the environment. Such criticism is well founded, but here I want to consider only two features of the usual models that have to do with space. Space is neglected from the start, in writing down the basic equations. Then the system is assumed to be closed. I tend to believe that both assumptions invalidate much that is expected from models.

Dismissal of space in the basic equations

In the usual LOTKA-VOLTERRA approach, the starting point is to write equations of the form

$$dN/dt = \sum_{j=1} a_{ij} N_i N_j$$

One or several N 's can stand for nutrients and eventually made constant. The so called kinetics approach in phytoplankton nutrition comes naturally from LOTKA-VOLTERRA formulation.

In such expression it is not stated if reference is made to a single point in space—in which case at most only one element of one kind could be considered—, or to an indefinite extension of space—hopefully to be defined later—, in which case one assumes that everything has the same probability of interacting with everything and everywhere, which is obviously false. The importance of space and transportation has been, of course, recognized. PATTEN (1968) distributes the models of plankton in two groups (dN/dt)-models and (dN/dz)-models ; but we need models considering simultaneously time and space. Sometimes, the consequences of advection (V) and turbulence (A), in one (z) or more dimensions are included

$$(dN_i/dt) + V(dN_i/dz) - A(d^2N_i/dz^2) = \sum a_{ij}N_iN_j$$

But this does not remove the ecological problem of how to figure out the product N_iN_j . Neither solves the problem the introduction of migration rates, or the subdivision of space, because every species, and perhaps every interaction, would require a slightly different procedure.

Surely one has to consider partial derivatives, in relation with space and time, starting with

$$\partial^2 N_i / \partial t \partial z = \sum_{j=1} f(N_i, N_j)$$

or, better, including more than one dimension of space, and returning later, if needed, to the expression of dN_i/dt . It is obvious that then, instead of the simple products N_iN_j as a measure of the interaction we will have some sort of integral describing the interaction as a function of the peculiar distribution in space of the interacting individuals and of some properties of their respective behaviours. A motile animal can interact successively with many organisms distributed over a rather large space, but many other species, or the same species under different conditions, are more dependent on actual local density. Large animals of the highest trophic level interact over large distances, and competition can keep their number of species relatively lower than in the case of other ensembles of potential competitors belonging to lower trophic levels. This is a factor of upward reduction of diversity in the communities, meaning that diversity in the higher trophic levels is less than in the levels of primary producers or of herbivores.

An adequate formulation is a problem for the mathematicians to

solve. Intuitively and from the point of view of the ecologist, it seems that the expression of the interactions will come closer to

$$a_{ij}N_i^{k_{ij}}N_j^{k_{ji}} \text{ than to } a_{ij}\bar{N}_i\bar{N}_j$$

using \bar{N}_i as the average density of the species i over a space to be defined. The exponents k_{ij} would give a measure of the intensity of the interaction; in the case of $k = 0$, the result of the interaction is independent of the concentration of the reactant, and this may be the case when N stands for some selected environmental factor. The way that biological species interact makes impossible to accept that interaction could be adequately expressed by a simple coefficient a_{ij} .

The problem that I am discussing has an interesting counterpart: the organization of space by the activity of the (organismic components of the ecosystem). It is pressumible that every species contributes to a certain size of the grain of the whole pattern.

Closed versus open systems, and an ecological analogue of Gödel's theorem

The usual models assume a conservative material system, linked to a dissipative system of energy. They are closed in what concerns matter and open in what concerns energy. Their description takes the form of a set of equations, that admit a common solution, representative of the state of the system. Starting with a large set of possible different initial stages, the equations purport to describe the changes of the system, until it reaches one of a small set of final states, or even a single final state. Among the possible final states are the disruption and disparition of the system, or the occurrence of regular fluctuations. Not much is changed if stochastic formulation is substituted for the deterministic one, because as soon as probability laws are stated, the model becomes for most purposes deterministic.

The generalized equations, including random or non density dependent effects, may have the form

$$dN/dt = \sum_{j=1} a_{ij}N_iN_j + \sum_{j=1} b_{ij}R_j$$

where R_j are independent stochastic functions. Thus, the set of independent values of R_j 's become stabilizing (as in a model of diversified industry or holding companies); it is easy to see that a similar stabilizing effect has to occur in space.

Such a model is used to predict what will happen if some components, or some constants describing interaction, are changed arbitrarily, so to speak from outside the system. The functions R_j may be considered also

generated outside the system. We can consider, or simulate, a change in incoming radiation, the inflow of some substance, mixing, immigration or emigration of individuals of some species, sedimentation, etc. It can be assumed that all the variables that are not considered, are conceptually cast out to the exterior of the modelled system; and every input that is *really* random is equally exterior.

The usual way of representing an ecosystem by a mathematical model leads us to a very curious situation: If the system has the properties expressed by the set of equations, it reaches a fixed final state, as fatally as in thermodynamics a closed system approaches a state of «maximal entropy». Now, what is important, what drives the system to new states, and what awakes the reactivity of the system, has to be considered as an unpredictable external input, or perhaps some unpredictable internal event, as a mutation in the genetic system of some individual.

From a practical point of view, the model, then, becomes uninteresting, and could be substituted by a description of the final states to which it leads. On the contrary, what is really important comes from outside the model, and has to be considered in the frame of a larger system in which the particular system that we are modelling is embedded. The random functions R_j become determined in the frame of an enlarged system. An interesting system cannot be closed; even the universe to keep going has to be open, or expanding. The same considerations can be repeated as we step up the ladder in any hierarchy of compounded systems. Such considerations represent an unmistakable parallel or analogue of Gödel's theorem. What can be studied and tested in the frame of the model of the ecosystem, is not necessarily important in its regulation, and there are causes and factors, important in the future of the system, that cannot be predicted or proved in the context of the model. They ask for some larger model or metamodel.

I do not believe that this is simple hair splitting and every ecologist is aware of the sort of problems implied. Limited models can be proposed and are used in the treatment of probability of extinction, of competition, of effectivity of defence mechanisms: all of them lead to predict a simplification of nature, species become extinct, but no new species appear; there should be a rigorous mutual exclusion among ecologically similar species; defense is expected to evolve and become effective. But, actually, the same phenomena have led to the diversification and richness of biota and ecosystems. All models look suspiciously asymmetric: they accept extinction, but do not allow for new species.

USE OF CURRENT MODELS AND FURTHER PROBLEMS

Such sort of criticism is never intended to discourage modelling. Actually, the task of writing down the equations of the model, visualizes or emphasizes a number of relations that matter, and leads to consider and to evaluate a number of functions, transfer efficiencies, and other elements necessary for the understanding of the workings of an ecosystem. Moreover the system must hold, and this is the most basic contribution of ecology to the understanding of the organic world. If it is meant seriously to model the system, for the purpose of writing properly the equations, it is necessary to estimate or to invent reasonable values for many constants that appear in the equations. But it is not safe to assume that because the system holds, the value of the model is proved and the particular values assigned to the constants are correct.

People feel happy if the construction of the model is such that the predictable future states are not so much sensitive to the particular values assigned to the constants, because such final states are more dependent on the whole set of relations, or of the structure of the model. Such models are called robust. But this quality is hard to evaluate. It is not altogether excluded that one robust system could be dethroned by another equally robust system, the cause being a single mutation appearing in a population.

Parameters concerning populations of organisms are extremely difficult to evaluate. We encounter this problem in any demographical approach. Extremely small differences in the net rate of increase mean the success of one population over another, but such small differences cannot be identified in the usual computation and presentation of life tables, being lost in the process of integrating age classes and time periods.

Most models, and specially robust models, are conceived as expressing the workings of a mechanism as fixed as it were made of cogs, levers, wheels, etc. There is a set of inputs and a set of corresponding outputs, assuming a rigid or almost deterministic linkage between them. This is accepted as a matter of course even by people that keep in contact with nature, as fisheries biologists are, and much more by speculative ecologists. But in fact the whole structure of the machine, the array of its parts, changes according to the inputs from outside the system and to the outputs. That is, any stress, understanding as such something that is not given in the expression of the model, changes the model, and not just something being processed by a persistent modelable system. Then, of course, the model has to be enlarged and include some hint on how the machinery changes according to inputs or driving functions.

The precedent criticisms apply only to very general models. But usually models are not proposed, so to speak, in the void, but with a certain purpose, commensurate with its potentialities. Motivations, objectives, results, the whole strategy of research has to be considered and evaluated in order to select or to build some model from an infinite set of possible models. It does not pay to build a complicated model for its own sake, and, in order to implement it go through a wild chase after data that are often inexistent and even unobtainable and that, after all, may turn to be irrelevant. Perhaps this expression reflects the frustration of the ecologist, unable to provide data to fit the holes of almost any model. Anyways many an ecologist believes that a better prediction can be obtained by rapid intellectual appraisal and elaboration of a complex situation, than after a tiresome computation based on unreliable measurements and on constants that may be only «uneducated guesses».

To develop a critical attitude is a gain, but moreover it would be desirable to explore the possibility of combining a series of open models into larger models, is a way appropriate to answer the needs for description (eventually for cartography) and for prediction, and much better if the implementation of such models is commensurate with the kind and amount of information that actually can be obtained.

SOME SUGGESTIONS FOR COMPLEMENTARY APPROACHES

Following comments are based on very simple considerations. Assume that almost closed systems exist, and that closed models are fit on them. Such models have to lead to a final state of maximal maturity, if one accepts this term as the expression of an asymptotic situation. No matter how the model is constructed, it can be substituted practically by a statement of the final state, that is, by a simple description of the system. Now, many systems in the whole set of the systems, may be more open than others, and in this case there are inputs and outputs unpredictable in the context of the model. Any model may be then useful to explain why the final state is different, and often the explanation will have the following form: the model is basically the same, but as there is a continuous or irregular inflow of something, or the sedimentation or emigration of something, the reactions are prevented to attain the same steady state as expected. Ecologists would say perhaps that the system is prevented to attain maturity and remains in an immature state; in engineering and applied science circles, people would perhaps prefer to speak of a stress applied to the system. In any case it is possible to devise some measures of such stress, considered to be proportio-

nal to the difference between the actual state and the predictable final state if the model were closed—can be gathered from other areas where the system is not stressed—. As the said stress can have the form of upwelling and mixing, and of the usual forms of impact of man in nature—exploitation, fertilization, transportation—, the whole approach may be useful in terms of practical ecology. The complementary aspect of this approach is that a closed or almost closed system can be considered surrounded either by an impassable boundary, or by a boundary across which the exchange is symmetrical and for practical purposes cancels itself, whereas an immature or *stressed* system is not closed, implying a boundary across which exchange is asymmetrical. In the marine environment it is possible to take small vertical prisms, from the surface to the bottom, as elementary systems, look for a correspondence between the degree of stress or lack of stress, and the importance of horizontal exchange between neighboring prisms, and then combine such elementary systems—and their corresponding models— into a larger system—respectively, a larger model.

In following paragraphs, different aspects of the proposed dissection—or construction of models—are discussed briefly.

The elementary models and stratification

The aquatic space cannot be divided in reasonably closed systems by an horizontal boundary, because the photic layers and the dark deep ones are complementary and linked in the cycles of matter and energy characteristic of the system. On the contrary, vertical boundaries can separate practically autonomous elementary systems. There is much horizontal change, of course, but as gradients are small, they cancel themselves as far as the composition of the system is concerned; only when different layers of water move steadily in relative opposite directions there is a different situation to model.

The usual set of differential equations leads to a final state—steady or with regular fluctuations—. If, then, it is assumed that, for every species, or every component, $dN_i/dt = 0$, it is possible to divide all the terms of the right side of the equations by N_i , and a series of static regression equations is obtained, in which the abundance or density of every species, or of every component, is related to the density of all the other components. But it must be added that relations are never so simple; assuming that such regressions are adequate, and computing them on samples collected over a certain space, contagious distributions become evident in organisms (MARGALEF, 1967), implying the influence of past events and of distributions in neighbor areas.

The final situation would be much simpler and predictable in the

case of chemical substances, where the final state can be deduced from the equilibrium constants in a set of chemical reactions. Such constants are influenced, of course, by the temperature and pressure, that are variables depending from outside the system. But in dealing with organisms, relations are much more complex, because organisms behave as units, and some approach more related to game theory than to the mass action law would be appropriated. Anyway some equilibrium is eventually approached. As well in the case of chemical compounds as in the case of organisms, the equilibrium conditions being expressed by ratios, it is not to wonder that the result of the combination of multiple equilibrium equations leads to a regular distribution in the amounts of the different chemical species, and in the distribution of individuals into species; such regular distributions have been much discussed in relation with the concept of diversity. Now, it is easy to see that, always, the addition or subtraction of reactants, or of individuals of key species, puts in motion the system, that tends to regain a sort of equilibrium like the initial one, and that in such process, numbers or concentrations come apart, and diversity drops all the time when there is some stress or lag in the readjustment of the system.

But now we are interested in quasisteady state. In their natural development, ecosystems tend to differentiate in the vertical direction. In the marine environment, assuming a low or moderate degree of turbulence, utilization of inorganic nutrients is a function of penetration of light; the average depth of return of the limiting nutrients to the water is below the average level of their utilization, the distance between such depths being dependent on the transport system made up by the living community and the sinking of particulate material. Somehow a regulatory mechanism develops, an essential part of which is the upward slow diffusion of nutrients, associated to an important gradient in their distribution. The result is a well stratified community that is almost closed in what concerns matter —no loss to the sediments—. It is important to note that in the process of building such stratification, there is a slowing down of general turnover. Vertical distributions of light, nutrients and primary producers take such form and combine in such a way, that primary production goes down. The process can be modelled, although it is perhaps difficult to get an appropriate estimation of the effectivity of the transport system constituted by the organisms. Anyway, the average vertical profiles in open seas areas, not subjected to strong mixing, provide an idea of the final state to which such model would lead. Incoming energy —light and heat— may determine the precise form of the model. Annual fluctuations in light and heat cause the system not to go to an extreme low productivity: its degree of maturity remains lower.

Maturity, stress and divisibility of systems

In fact, the predictable final state is rarely realized, by the action of factors which origin is exterior to the system and, in consequence, are not described by a limited model. Turbulence and vertical mixing tend to uniformize the vertical distributions of nutrients and of organisms within a vertical distribution of light that remains essentially the same as before. The extra energy coming from outside and doing the work of mixing causes a better utilization of the energy provided by light. It has been said that part of the energy we get with our food comes actually, for all practical purposes, from oil (ODUM); in the same way it can be stated that part of the energy fixed in chemical form by the primary producers is contributed through the termic energy in the interaction between atmosphere and hydrosphere. Upwelling is another manifestation of the same kind of phenomena. In our model it can be visualized as a vertical prism being cut in two, the upper part being translated aside, making place for the rising lower half. This exposes nutrient rich and organism poor water to the light, and a process of organization that can be described by the model starts again, and eventually will lead to the development of stratification. In this case, if the model was too specific it must be substituted by another, and perhaps a whole hierarchy of models has to be envisaged, with a broad and general model splitting down in a set of more specified models, according to which kind of interactions we can take out or forget. The general model provides the frame into which the particular models converge or are replaced.

Any input or influence not included in the description of an almost closed system can be considered as a stress, and, in very general terms, it hinders the system to attain maturity, that is, to follow up to the limit the results of the interactions reflected hopefully by the equations of the model.

If the agents of stress are external to the small or elementary system under consideration, they can be internalized and conceptually assimilated enlarging the system—and its model—. This process can be followed until the boundaries of the system under consideration, that under the effects of stress become asymmetrical in what concerns exchange, are again symmetrical or indifferent. An upwelling area, thus, can be combined with the neighboring areas, from which the first one receives nutrients—with deep water—and to which exports organisms—with surface water—. All such areas combined form again an almost closed system, that can be compared to a vertical prism of offshore water, only being larger in horizontal section. The same regularity applies everywhere: an oligotrophic lake can be studied almost by itself, as a reason-

ably closed system ; but it is not possible to understand an eutrophic lake—under stress— without taking into consideration the surrounding farmland, human populations, and so on. The concept of functional divisibility is very important in ecology.

The size of the frame of reference needed to provide a similar degree of description or of explanation, gives a measure of the degree of immaturity caused by stress, and also a measure of stress. This is most obvious in the case of pollution ; it represents a stress on natural systems, and is clearly associated to the linking of far away systems by the human transportation system : collecting resources over a large area—exploiting it— and afterwards concentrating and dumping the half used materials in a single spot.

Stability and succession

Stability is a controversial term. I will use it here as the property of a system to return to a state similar to a previous one, if it is led away from it by some agent or force, external to the system as described or not included in its model. Stress activates the stability of a system, the system under stress does not change as much as it would change if it were not stable and slowly regains a state similar to the primitive one. This is usually successful, if stress is retired. Under persistent stress, the redressing mechanisms continue to be active, are recognizable and constitute notorious characteristics of the stressed system.

In current speech, as persistence with or without stress, stability makes sense only in relation with the character that is considered : species composition, energy flow, etc., and the different kinds of stability are not necessarily coincident. This is the source of much confusion.

A most general concept of stability is implicit in the set of equations that are used to describe a system. Many initial states, inside a reasonable domain, should converge towards a few final states. Indeed it would be unrealistic as well as difficult, to propose a model with a different outcome. With certain provisos concerning the preservation of certain structural elements—reflected on the model in the non vanishing equations—, it can be anticipated that random inputs are ironed out, and the same trend towards a final steady state is regained.

Such stability is associated with the constants of equilibria in the many reactions and interactions going on in the system, and with the general net of relations ; the regulatory behavior is more effective in the interactions that are markedly non linear. Several of the regulatory mechanisms can be clearly presented in plain language, as following : Any extraordinary development of primary producers leads to the development of organisms of higher trophic levels, with a certain time lag ; in the process, the ratio producers/consumers, momentarily distorted

in favour of the producers, tends to regain its primitive value. If an extraordinary inflow of nutrients allows an uncommonly high primary production, the surface layers become oversaturated with oxygen, part of the gas escapes to the atmosphere, and the way back is hindered by the persistence of a strong gradient of oxygen. More oxygen than the leftover amount is necessary to oxydize all the organic matter produced, and a deficit of oxygen develops in deeper layers. As a result, part of the produced organic matter cannot be oxydized and is taken off the cycle, to the sediments, retaining variable proportions of biogenetic elements. If phosphate concentration in water exceeds a certain limit, part of it is precipitated and retained in the sediments, in form of phosphorites or apatite. An excess of nitrate can be decomposed, and the resulting nitrogen transferred to the compartment of atmospheric nitrogen. These are a few mechanisms by virtue of which any extra addition of nutrients (eutrophication) sets in action some sort of brake on the cycle, with the result that a fraction of the added elements is taken out of circulation. The percentage of the element that is retired is higher for more important additions of the element; this is clearly a regulatory device. Many other homeostatic mechanisms can be recognized in the community: Grazing pressure in deep water consumes a percentage of the sinking particles that is higher in rich than in poor areas, with the result that the final concentration of suspended particles tends to be uniformized.

The ensemble of such kind of relations form a complex homeostatic or cybernetic system. If the composition of the ecosystem is represented by a point in a multivariate space—the dimensions standing for the variables of state, numbers of individuals of such and such species, and so on—it could be assumed that a field of forces exist driving any point along optimal paths and towards some steady final state. This state should be implicit in the set of equations purporting to describe the system. It seems intuitiv to suppose that the activity or the effect of the forces driving the system—or redressing it after a perturbation—and the speed of the changes they produce, has to be proportional to the distance between the point representing the present state of the system, and the point representing the final or asymptotic state, that stands for the reference value in the operation of the cybernetic system. This reference value is not a reality at hand, but simply the extrapolation of the combined activity of a set of mechanisms.

For certain purposes of description it may be allowed to dispense with all the details of the workings of such mechanisms, and try to describe the path followed using some simple variable of state. This would mean a reduction in the number of necessary variables, allowable if the functions are linked. As the new selected variables, few in

number, or even single, purport to give a general picture of the system, they can be qualified as synthetic or macroscopic. In more practical terms, it is possible to look for some measurable function, choosing it so, that its value changes monotonically with the progressive operation of all the interactions described by the model, from any initial situation. Such function can be selected by convenience (MESAROVIĆ, 1972), but there is always the *risk* of associate with it some idea of finality, or discover in it formal analogies with other fields of science.

A function of this sort may have general properties that make it really useful for prediction. This would happen if the function is «larger than the model» and able to predict not only changes in the model—in the sense that any change is linked to every input in such a way that the function is maximized or minimized—but also the substitution of a model by another. Then it would improve over the description provided by a set of equations dealing with fixed variables, because the function could serve then to recognize and predict trends following important changes in the structure of the system—requiring a reconstruction of the set of equations of the model—. For instance, it would be possible to predict the likelihood that some alien species, or a mutant, will be accepted or rejected in the process of selforganization of the ecosystem. The criterium would be if acceptance or rejection changes the value of the selected function along the accepted trend. To use other words of the ecological terminology, the value of the selected variable becomes a measure of the degree of maturity or of the advancement of the succession, with the possibility of quantifying such elusive concepts. In this frame, succession appears as an extrapolation or further manifestation of the same mechanisms implicit in the notion of stability, as developed before.

Several functions have been proposed, although in imprecise form. Following could be further tested as for their applicability to serve as the required guide or macroscopic functions: 1) The ratio between primary production and the total biomass. 2) The ratio between primary production and total respiration. 3) The ratio between living parts, and dead organic matter that is retained by its structural properties (shells, wood in terrestrial ecosystems). 4) The degree of stratification, measured as some index of the steepness and lack of coincidence in the vertical profiles of distribution of selected substances and organisms. 5) Accumulation of transition products (nitrite, for instance) as a result of differential acceleration in interconnected cycles. 6) Diversity or, better, steepness of the spectra of diversity. 7) The Q index proposed by MAC ARTUR (1972), which is minimized as the ordinary result of interspecific competition. It would be wise to select a number of such functions, if possible to be measured through independent methods, study their

statistical association and, if possible, to find principal components for their common expression, as a further step in the reduction of the number of state variables used. But such reduction could go on in different directions. Here it is clear that my personal bias is to give paramount importance to some variable trying to express concepts of organization or maturity (MARGALEF, 1967 b).

In the context of development and use of models of ecosystems, state variables as advocated might have some usefulness. They could give a measure of the difference between the present state of an ecosystem and the final state predictable from within in the frame of a rather small and closed model, and advise on the need of enlarging the model, to internalize the inputs that I have included in the concept of stress. By mapping the values of the selected state function over a large area it is possible to have an idea of the necessary hierarchy of models to build; in this connection it can be remembered that surfaces connecting points with the same degree of maturity or of stress, separate adjacent spaces with an asymmetric exchange between them,

AN EXAMPLE OF THE IMPORTANCE OF SIZE IN THE PRODUCTIVITY MODELS

Problems are treated not according to their interest and relevance, but according to their accessibility, and one has to try to make accessible what is relevant, or what one believes that is relevant. I want to discuss further the need for a careful consideration of the possibility of developing some principle of constructivity of a whole hierarchy of models, or some principle of putting ones inside of others, in relation with one of the most important properties of marine systems, their productivity.

We should start with a model of the type dN/dz . There exists considerable information about the vertical organization and vertical dynamics of the pelagic ecosystem. It is a system that brakes itself and the braking mechanism is simple. Assume the usual vertical distributions of light, nutrients and plankton. Organisms, or, at least, part of the primary producers, are passive and denser than water, and anyways nutrients trapped in particles on the average travel faster down than in solution. If there is light and nutrients, nutrients are passed from solution to particles, and some net transport down is achieved. The final distributions will be defined by the physical upward diffusion of nutrients and also by some properties of the organisms. In fact a part of the solar energy can be used in keeping swimming producers at selected levels, and even in pushing up nutrients, assuming such consumers so

well behaved (the superprudent predators!) as to feed down, preferably on dead organisms, and to excrete in the illuminated levels.

Such a model is unrealistic, because *we know* there are several ways for the nutrients dissolved in deeper layers to go back to the photic zone. But here we hit head on with the discussed difficulties. It is impossible to enlarge the model to accommodate the return of nutrients if we do not enlarge its horizontal cross section. Dealing with photons, dissolved nutrients and phytoplankton does not require a large section, and one can visualize quite well a model of only one square cm cross section, and reduce it to a single (vertical) dimension in relation with distributions, that then are reduced to vertical gradients. But we need a larger cross section to accommodate such phenomena as turbulence or the movement of animals. The *z*-model has to be substituted by a *xyz*-model.

The second problem is that some extra energy is needed to pay for the return of nutrients. In textbooks of Ecology it is often assumed that the energy «entering the ecosystem» is only electromagnetic energy trapped in the process of photosynthesis. But human ecology has taught the importance of ancillary energy that is used in transportation, heating, fertilizing, irrigation, harvesting, etc. In fact, the degree at which light energy is used in primary production, is dependent on the availability of other forms of energy (although of ultimate solar origin as well) that is dissipated in producing turbulence, mixing layers of water, and pushing water up in upwelling areas. In terrestrial ecosystems, such energy is the cause of wind, that enhances diffusion of CO₂, and brings water and nutrients into the cycle through rain, erosion and transport. This is not new, but its general ecological implications have been badly neglected.

The relative amount of the available radiation that is used in photosynthesis is variable, and usually small. It is much smaller in the center of the large Oceans in comparison with the upwelling systems. It depends on the amount of auxiliary energy, that can be considered as a stress that enhances production. Actually the energy effectively used in making more effective the utilization of light is only a small fraction of the total energy that is continuously dissipated in the marine circulation and as a result of interaction between atmosphere and sea. Nevertheless, some idea of the order of magnitude of the energy involved in different processes as turbulent mixing, or upwelling, can be gathered from different sources. This has been expressed tentatively in fig. 1. Migration of animals can use 0.1 to 0.2 mW m⁻². This means energy from primary production reinvested to keep mechanically alive the system, and could be made inutile by a too high input of other forms of energy (strong mixing turns inoperative any regular migration of animals).

Actual primary production, thus, is a composite function of light, nutrients, etc., *and* of some stressing function, measurable as a vertical transport and using a certain amount of ancillary energy. The appropriate consideration of such auxiliary energy emphasizes the need for considering space and, simultaneously, offers a paradigma of some of the ways of constructing a hierarchical set of models in space.

Considering only primary production and light, the system has been modelled just as a vertical line; but the consideration of an auxiliary

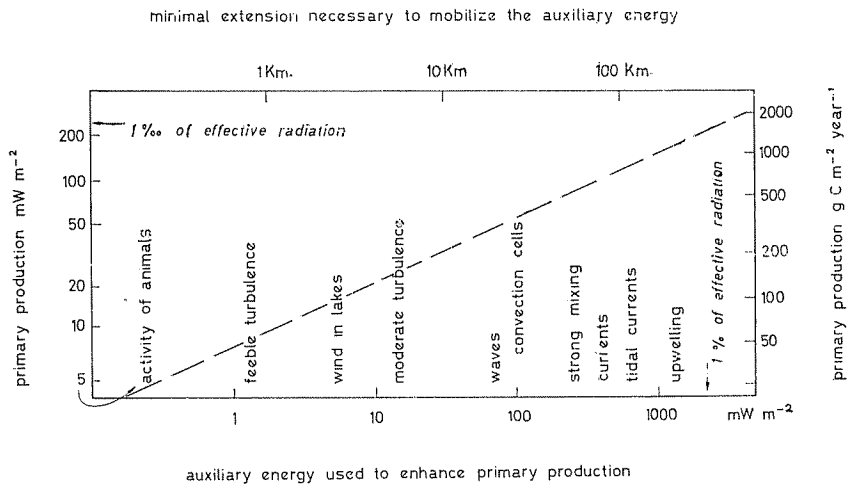


FIG. 1. — A qualitative and semiquantitative sketch of the dependency of primary production on the availability of sources of mechanical energy in the marine environment.

energy makes necessary to enlarge horizontally the model. And so more as the involved forces are available only if they have leverage, if they can do work over a large extension. Upwelling can be conceived only in extensions of the order of 100 Km, and perhaps the roots of some upwelling processes have to be sought in phenomena affecting much larger surfaces; tidal currents may be effective in smaller extensions; in lakes and in the sea some fetch is necessary to get some positive action from wind. Any model purporting to describe an area of very high primary production, has to be a geographically large model, because it has to include, as an essential part of the model, the structures through which the energy of the wind is used in some way to enhance or optimize the utilization of light and nutrients. One can perhaps visualize such kind of relations, as a set of funnels of different sizes concentrating in small areas the impact of phenomena than have to be understood

over much larger extensions. In other words, the mobilization of a certain intensity of energy can succeed only through some funneling over a large area, draining part of the available energy, that is effective in a small part of the whole area involved; an upwelling area is smaller than the larger region from which it depends for exchange. Part of the rest of the energy available in the large area can be drained again not in one, but in several selected secondary spots, and so on, and in some places of the large system, it can be accepted that narrow columns of water receive a very small amount of auxiliary energy, even inside or close to the ranges of an upwelling area. Surely, a large and compound model of this type should have a lot of asymmetric boundaries, between ascending and sinking portions, between productive and less productive ones, and so on. In practice it would be very difficult to propose a sensible dissection of the space, but perhaps it could be possible to associate a certain dimension to every point: a small dimension for a profile near equilibrium (with nutrients used and plankton down), a large dimensions for a stressed point (an upwelling spot).

The attractive of such way of thinking about systems is the possibility of finding some links with the more general theories about the relations between the energy dissipated in the production of work (turbulence, mixing, currents, upwelling) and the size of the structures (waves, eddies) in which such work is manifested. In the theory and observation about the distribution of energy along the spectra of turbulence, it is accepted that the fraction of energy is related to the $5/3$ power of the size of the corresponding structures (KOLMOGOROFF, and others). It is difficult to make estimates of the auxiliary energy actually involved in promoting primary production, and much more to discuss this in the frame of some hypothesis relating energy and size of hydraulic structures, but perhaps some new and useful starting point for future work lies here.

Going back to the initial criticisms of the models in use, it can be added that a model must be a divisible model, because its parts are not equivalent. The relevant rules of composition in this case mean that some extra energy has to be added at every step of enlarging the system, as a sort of «cement», but in fact to pay for the implementation of exchange.

The consideration of space emphasizes the need for linking vertical and horizontal distributions. One interesting question is how some available energy is partitioned among the different components (vertical and horizontal) of movements, and if there is some optimal distribution from the point of view of primary production. Upwelling is patchy, just as a cumulus field is patchy, and the hierarchy or the organization of the discontinuity, of the patchiness, may be important.

Auxiliary energy is important also in benthic communities. Flow of water enhances availability of nutrients to fixed organisms. RIEDL (1973) points out how tidal energy (through the tidal pump) connects vertically the layers of the interstitial system, forcing water between the deep anoxic layers and the more superficial and oxydized ones. This happens through an «energy window» extended along all the shores.

Any plot of a function of correlation between nutrients and phytoplankton (or chlorophyll concentration), or any mesure of diversity, in function of the horizontal extension of the space over which the correlation or the diversity has been computed, is a spectrum that summarizes structures and rules of composition of structures, and probably can be related to the supply of energy.

A rectangular or flat spectrum of diversity, as well as a constantly positive correlation between nutrients and chlorophyll, implies a rather strong horizontal mixing and, in consequence, an important dissipation of energy. In these situations, more available energy is usable to enhance primary production. The opposite situation, with a lower amount of usable energy, has typically a diagonal diversity spectrum, and the correlation between nutrients and chlorophyll may be negative if small spots are considered, passing to a positive correlation as area increases. Anyways, the association of high values of nutrients with low pigment concentration is transitory, since nutrients cannot persist or accumulate at light without being used.

The type of structure and the size of its elements has to be taken into account in any sampling program, and has to do with the dimensions upon which interpolation is justified, or averaging is allowed for definite purposes.

RESUMEN

ALGUNOS COMENTARIOS CRÍTICOS A LA FORMA USUAL DE MODELAR ECOSISTEMAS. — Si se supone que un modelo refleja de manera apropiada un ecosistema, tiene poco interés, porque el sistema debiera hallarse entonces en cierta forma de estado estacionario y cualquier modelo muy complicado puede ser sustituido por una descripción más breve del estado final o de los estados posibles, que no serán muchos. En realidad no es así, porque los ecosistemas son entidades que varían continuamente; las variaciones importantes son resultado de la reacción del sistema a impactos procedentes del exterior y no previstos en el modelo. Todo lo que se puede pedir a un modelo es que identifique y exprese mecanismos homeostáticos y permita prever de alguna manera la transformación, y verosímil atenuación, de cualquier impacto nuevo. La razón de esto es que los modelos tratan de sistemas cerrados. Otro inconveniente es que, prácticamente, todos los modelos ignoran la organización espacial de los componentes vivos del sistema.

Si los modelos son complicados, cerrados y poco prácticos, tal vez se pueden reemplazar por algunas afirmaciones sobre los estados finales o de equilibrio que son más verosímiles. Cualquier desviación de dichos estados implica algún impacto no previsible en el modelo que utilizamos, significa que el sistema no está cerrado y, en realidad, nos obliga a considerar el modelo incluido en otro modelo más amplio. Cuando un modelo cerrado y pequeño (en relación con el espacio) resulta apropiado, ello significa que el sistema al que se aplica es autónomo, o sea, no hay tensiones (stress) procedentes de fuera. Pero la mayor parte de los fenómenos cuyo estudio resulta más interesante o más útil, como afloramiento, polución, fertilización, eutrofización, explotación, transporte, se han de considerar como tensiones (stresses) que mueven al ecosistema hacia un estado más o menos alejado del previsible por cualquier modelo local. Por esto requieren construir un modelo más amplio en el cual se incluya el modelo inicial junto con los agentes causantes de la tensión.

De esta forma nos vemos conducidos a formular o a adoptar ciertos principios de construcción jerárquica de modelos. Se pueden proponer diversas funciones de estado que midan la desviación de cualquier sistema en relación con alguna de las situaciones de equilibrio implícitas en la adopción de determinados modelos. Muy frecuentemente, la necesidad de ampliar modelos para poder abarcar adecuadamente los fenómenos, se debe a la operación de formas de energía que sólo pueden ser efectivas si afectan a una extensión geográfica mínima. Esta extensión, entonces, nos fija la dimensión mínima del modelo. Así, por ejemplo, podríamos construir un modelo aceptable de un sistema planctónico de alta mar referido a una columna vertical de agua de 1 m², o de 1 km² de sección; pero si se trata de un sistema de afloramiento dicho modelo resulta inapropiado por existir cambios asimétricos con sistemas limítrofes —el agua nutritiva viene de alguna parte—, y entonces dicho modelo elemental ha de integrarse en un modelo más amplio, cuya extensión mínima será la necesaria para que en ella se manifiesten los efectos de la interacción atmósfera/hidrosfera que producen el afloramiento.

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