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SPATIAL MODELLING OF CORAL REEFS

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INTRODUCTION

Most existing approaches to ecosystem modelling concentrate on the flows of energy or materials between various components or compartments of the system. Compartments are generally functionally defined relative to the basic system processes producing inputs, outputs, and transformations of energy or materials (Dahl et al., 1974). Any such model must be highly simplified or generalized to keep it within workable dimensions, and it thus becomes an abstraction from which many significant aspects of the system must be excluded.

One aspect that becomes increasingly significant in a more highly developed ecosystem is its physical structure--the spatial arrangement of its component parts. In a higher organism, structure is often as significant as physiology in determining its characteristics; similarly in an ecosystem such as a coral reef, spatial relationships determine many parameters and control mechanisms that are fundamental to system functions. Methods of modelling are therefore needed to treat spatial relationships, structure, and form, and to link them with energy and material flows for a more complete understanding of the system. This paper thus presents a preliminary conceptual framework for spatial modelling as applied to the coral reef ecosystem.

CHARACTERISTICS OF SPACE

A coral reef, like any object, has a well-defined situation in space. It is fixed in its relationships to the underlying substratum and to the air-water interface, although these may be subject to alteration over geologic time. Depending on the nature of the substrata, the reef may have a predominantly linear form if following a coastline or atoll rim; or it may form patches in a lagoon or on an irregular shallow bottom. Each reef develops in relation to a particular pattern of waves and currents, and the reef may trap and accumulate nutrients from the surrounding sea or receive inputs from adjacent land areas. The principal energy source is sunlight, which always follows cyclical patterns of directional input. In addition, a coral reef is distinguished from many other ecosystems by its ability to construct and thereby to alter the form of its own substratum. This ability gives the system a certain evolutionary control over its form and its utilization of space.

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In considering the need to model the spatial relationships of the reef and of its component parts, one must first define the characteristics that objects have in space then determine how these characteristics can be quantified, measured, and modelled.

Objects, of course, have SUBSTANCE, which may be a simple material or a complex combination. With the many standard analytical methods available, there is no conceptual problem in determining the nature of the substance and the quantity present. It may be more difficult to decide what level of substance determination is appropriate to the model situation. These substance measures can provide the principal link between spatial models and energy or material models.

Substances are bounded by SURFACE. Every object or organism can be considered as some complex of surfaces with various characteristics. The surfaces provide the interfaces across which various transfers can take place. Since surfaces form the boundaries between substances, or "compartments," the surfaces are the defined limits across which energy or material transfers are determined, and between which (in most models) processes are lumped or generalized. Life itself is surface-oriented; witness the importance of membranes in fundamental biological processes. The quantification and characterization of surface can therefore provide powerful tools for the understanding of ecosystem processes (Dahl, 1973; in press). Surface may be measured directly or estimated using theoretical constructs. Surface may be expressed directly in area or by using a surface index (SI), a dimensionless number for the increased amount of surface relative to a similarly-bounded plane (Dahl, 1973).

The space enclosed by surfaces has VOLUME, which can be expressed in standard volumetric units. A complete surface always defines two volumes, that inside the surface and that outside. Both are important in the spatial evaluation of an ecosystem.

Surfaces or surface-bounded objects also have FORM, some type of shape or configuration that may be characteristic of the object and have great functional significance (Neushul, 1972). Form is not readily quantified and is therefore difficult to model. It is probably simplest to develop a system of classification capable of distinguishing between the principal forms of interest. Many forms can also be generated using simple growth computations, and thus can be characterized by the features of those computations (Cohen, 1967; Lindenmayer, 1968a,b; Dahl, 1971).

Forms may well have ORIENTATION relative to surrounding features. That orientation is often expressed as a polarity. A spatial model thus needs some type of fixed reference grid to which such orientations can be referred.

There is also the question of SIZE or SCALE, generally most significant as a relative measure and therefore arbitrarily defined to suit the needs of the system or model. Often a series of scales can be used to provide the necessary scope and detail. Usually the comparability of sizes is important in determining significant interactions.

To establish the relationships between objects, there need to be measures of DISTANCE and DISTRIBUTION. In the field, one can use simple measurements or standard ecological techniques for determining spacing and pattern. In a spatial model, the plotting of all data points relative to a set of coordinates can permit the construction and analysis of spatial relationships such as the attenuation of a feature with distance, the mechanisms for fitting large numbers of organisms into a limited space, or the role and extent of competition.

Finally there is the TEMPORAL DIMENSION which affects all aspects of the system. There are some elements and phenomena which can be considered static while others are dynamic; some organisms are attached, others highly mobile; forms may be rigid or flexible; growth and mortality, as well as other kinds of increase and decrease, can be included. Temporal changes can also be considered at different scales: seconds, days, years, or millenia; each will reveal a different set of significant aspects of the system. Repeated measurement or sampling, analysis of certain system features or the geological record, and projection from known data points can all be used to develop the different scales of variation over time.

MODEL ELEMENTS

One possible approach to spatial modelling is to use a three-dimensional point matrix stored in and manipulated by a computer system. The resolution of the model would depend on the number of points used. Devices could be developed or existing programs used to provide visual or graphic readout from the data.

Each point would be coded for the following multiple characteristics:

a. three coordinates to indicate position in the model;

b. a polarity indicator for directional phenomena;

c. a substance code for whatever substances are distinguished by the model (water, calcium carbonate, photosynthetic plant, etc);

d. quantity indications for the substances, if needed;

e. a surface or non-surface indication (showing whether or not the point occurs at or defines a surface);

f. an organism, entity, or compartment code for distinguishing the separate units of the model, linked with subroutines governing temporal changes in the entity; and

g. additional or subsidiary material and phenomena codes, when these can coexist at a particular point, and proximity codes where reactions are to be triggered before actual contact.

Characteristics that are not directly coded, such as form, volume, orientation, size, and distribution, would be shown by the arrangement and number of coded points and their positions in the matrix.

The points are then coded in groups to indicate the elements of the model. A volume of water would be designated by points coded water; those points defining the air-water interface would additionally be coded surface, the rest non-surface. Water is translucent, so additional codes could illustrate the presence of light, its intensity, and direction. Current or wave direction would be indicated by the polarity code (force or speed are basically temporal, and would show as changes in the entity code as the model operates). Dissolved materials would appear as subsidiary material codes and amounts.

Each organism would be described by points coded for the particular species and individual, to the extent that these need to be distinguished in the model. The arrangement of points would give the form of the organism, and the exterior points would be labeled as the organism surface. The cluster of points for each organism would be programmed to behave as a unit for purposes of movement, growth, mortality, etc. The substance(s) of the organism and any subsidiary materials distinguished would also be coded, as well as a polarity if this is involved in growth or movement. The total of all the substance values would give the biomass of the organism.

These point codes would be manipulated by a variety of programs and subroutines, depending on what aspect of the system was being modelled. Growth would involve points coded surface transferring to the next point away from the organism, either uniformly in the case of general growth, or at specific points designated by the polarity indicators. Changes in form would occur similarly. Movement would involve the transposition of the complete set of points designating an organism or entity. Where the resolution of the points is not adequate to indicate an essential feature, an amplifying subroutine, like a magnifying glass, can provide a submodel with greater resolution from which to generalize to the coarser model.

Special routines would be used for light, nutrients, etc. A light direction would be designated relative to the coordinates and the initial points at that side of the model field would be coded "light," perhaps with intensity indicated. The "light" coding would then be transferred in that direction through the model to all points for which the substance code indicated translucency. Absorption would occur at any point of opaque material, leaving "shadows" beyond. Attenuation could be indicated by a loss of intensity at each transfer. Additional refinements could incorporate wavelengths, reflectance, and so forth, if these were needed.

Nutrients could be similarly introduced into the model, transported by water currents until "uptake" at an absorptive surface (so indicated by a combination of surface and organism or substance codes). Nutrient presence, accumulation, depletion, or other change would be shown by appropriate subsidiary codes.

A series of time programs would link the operation of the various routines controlling the dynamics of the system at the temporal scales of interest.

THE SPATIAL MODEL

With these elements, it should be possible to construct in three dimensions a spatial model of an ecosystem such as a coral reef or some part thereof. To keep within present computer limitations, a series of submodels of different reef zones and at different scales could be combined to produce a generalized reef model. Data could be drawn from an actual reef area, or be based on theoretical constructions of typical situations (Dahl, 1973). The constraining substratum would be indicated and benthic organisms situated, followed by mobile organisms and external inputs. Much of the initial construction could be completed by computer using appropriate subroutines and the data points provided.

The initial data block would then be manipulated using the appropriate programs, and the resulting ecosystem parameters or characteristics read out. Values such as biomass, area coverage, frequency, abundance, and distribution could be readily obtained by tabulating or plotting the appropriately-coded points. The amount of illuminated photosynthetic surface under specified conditions, and its diurnal or seasonal variation, would be easy to determine, as would the potential for uptake of specified nutrients. This could then lead to studies of the comparative efficiency of different reef structures or communities under defined conditions of load or stress. Quantitative measures of carrying capacity, competition, or feeding potential could also be derived from the model, as could the results of growth or even the evolution of reef structures over geological time. It would be possible, using a spatial model, to apply theories of island biogeography (MacArthur and Wilson, 1967) to the community level by defining "islands" of substratum or habitat within the reef system and then analyzing rates of colonization and extinction.

One particularly interesting application would be to develop paired spatial and material flow models, with each exercising controls over the other. Compartment values could be linked with the appropriate organism biomasses and materials pools in the spatial model, and the flows between compartments related to appropriate transfers or events. It would thus be possible to tie together primary productivity and illuminated photosynthetic surface, or skeletal deposition and structural changes in the reef framework. This linkage would provide a more flexible and realistic set of control mechanisms for the flow model and give an output that would lend itself more readily to validation in actual reef situations. It should also produce significant advances in understanding the functional significance of reef forms, structures, and other spatial elements.

With further development, additional complexities could be added, such as the multiple layers of organisms found in many reef habitats. Analyses could be made of alternative evolutionary strategies for reef ecosystems, and of the effects on such systems of various human impacts that might alter the reef structure, eliminate certain organisms, or change inputs of light or materials.

CONCLUSION

The author is not in a position to pursue the development of spatial models at the present time. He therefore offers this conceptual framework in the hope that it will stimulate projects elsewhere. There are still questions as to the capacity of present computer systems to manipulate models of this sort with large numbers of data points. It may be that more simplified special-purpose spatial models will be necessary initially.

However, even the conceptual development of spatial models may help to depict the coral reef ecosystem as a dynamic living "veneer," constantly changing in detail, but maintaining a surprising consistency in the processes of construction, erosion, and community evolution. Such models can also lead to an increasing understanding of the functional and ecological significance of form, structure, behavior, and the use of space.

REFERENCES

Cohen, D. 1967. Computer simulation of biological pattern generation processes. Nature 216:246-248.

Dahl, A. L. 1971. Development, form and environment in the brown alga _Zonaria farlowii_ (Dictyotales). Bot. Mar. 14:76-112.

__________ 1973. Surface area in ecological analysis: Quantification of benthic coral reef algae. Mar. Biol. 23:239-249.

__________ 1976 (in press). Generation of photosynthetic surface area by coral reef algae. Micronesica 12(1).

Dahl, A. L., Patten, B. C., Smith, S. V., and Zieman, J. C. Jr. eds. 1974. A preliminary coral reef ecosystem model. Atoll Res. Bull. 172:6-36.

Lindenmayer, A. 1968a. Mathematical models for cellular interactions in development. I. Filaments with one-sided inputs. J. Theoret. Biol. 18:280-299.

______________ 1968b. Mathematical models for cellular interactions in development. II. Simple and branching filaments with two-sided inputs. J. Theoret. Biol. 18:300-315.

MacArthur, R. H., and Wilson, E. O. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, New Jersey. 203 p.

Neushul, M. 1972. Functional interpretation of benthic marine algal morphology, p. 47-70, in: I. A. Abbott and M. Kurogi, eds., Contributions to the systematics of benthic marine algae of the North Pacific. Japanese Society of Phycology, Kobe, Japan.