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MODEL OF THE SPATIAL STRUCTURE OF ROCKY SHORE COMMUNITIES[1]

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Abstract. A mathematical model is constructed for the spatial distribution of rocky shore communities, taking as an example the community of Ancon beach, Lima, Peru, and using the algebraic theory of lattices. The resultant model is displayed algebraically and graphically. Advantages over taxonomical zonation patterns are described. An ignored property of nature, the inanimate property of living nature, is identified by the model.

Introduction

Rocky shore communities show a characteristic zonation pattern in the spatial distribution of organisms. This has been observed by many researchers (*e.g.*, Ricketts and Calvin 1968, Hiscock 1985, Norton 1985). The representation of this pattern has been attempted by different authors (Stephenson and Stephenson 1949, Womersly and Edmonds 1952, Southward 1958, Lewis 1964, Ricketts and Calvin 1968, Paredes 1974, Newell 1979), but they rely upon a taxonomical approach as Hiscock and Mitchell (1980) point out. Here I develop a mathematical model which represents this zonation pattern with the algebraic theory of lattices. The model is time static, but incorporates a property ignored up until now. I call this the inanimate property of living nature, because although it is reflected in living organisms (*e.g.*, Mytilids), it is inert, and is also performed by stones.

Taxonomical zonation pattern

A rocky shore community is an assemblage of organisms distributed according to elevation. The distribution has a characteristic zonation pattern, with some overlap between zones. Although the species assemblages of this environment change with locality, the general pattern remains the same. The zonation described by Paredes (1974) is an example:

a) Supralitoral fringe from the upper level of *Littorina peruviana* to the higher level of *Chthamalus cirratus*.

b) midlitoral zone from the lower limit of supralitoral fringe to the upper level of *Megabalanus psittacus*; and

c) infralitoral fringe from the lower limit of the midlitoral zone to the mean height of ordinary low spring tides. In Paredes' (1974) scheme, however, the overlap of zones is not elucidated, and from it, it is difficult to make inferences about essential properties of nature.

The mathematical model

The model uses the algebraic theory of lattices, considers the abundant species, and is related to spatial distributions. Distinct litoral zones are recognized, a metric is imposed, and an *ad hoc* conceptualization of population is proposed. A "population" is considered to be a group of organisms of the same species that occupy the same litoral zone, confined by a specific upper limit. Accordingly, species are grouped as shown in Fig. 1. A 'lattice' is a partially ordered set in which every pair of elements has a join (or least upper bound) and a meet (or greatest lower bound) (Birkhoff, 1940, and Crawley and Dilworth, 1973). The partial order relation is $\leq$. It can be equivalent to set inclusion ($\subseteq$), such as in the condition, $a \subseteq b$, implying that a is nearer to sea level than b. With the above in mind, the following definition is established:

Definition 1

Lattice R is the set of all subsets of R, with the condition that every subset should have at least one element (population) of a determined level and all the elements (populations) that are below that level (nearer to sea). R is thus partially ordered by set-inclusion. The representation of the lattice R in Fig. 2 is displayed in Hasse's diagram and some symbols are added to each node to show its algebraic development, which is displayed in Table 1. Lattice R is complete, modular and distributive; and if one species population is eliminated, or added, the same properties remain. Biologically, this implies that the general zonation pattern remains constant. The number of species and the densities of each can be changed, but the general zonation

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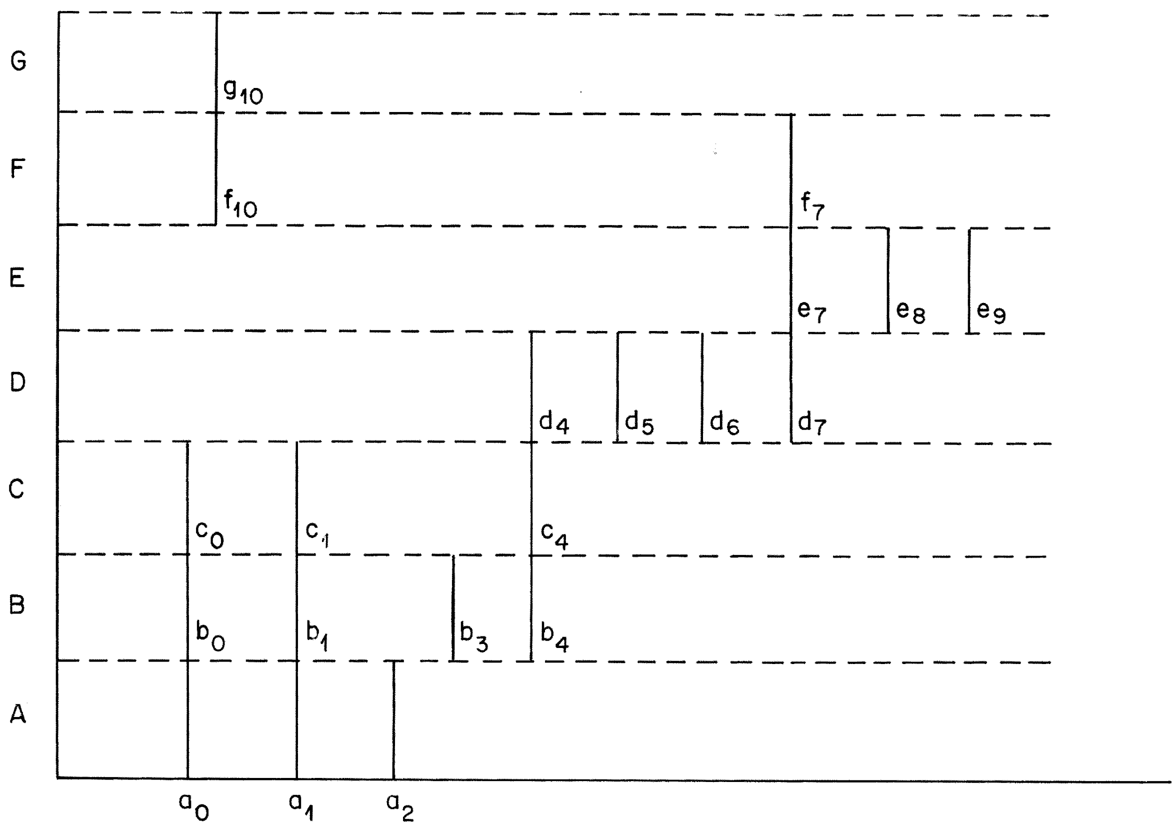

Fig. 1. Levels of spatial distribution. Each litoral level is represented by a capital letter. A subscript identifies a species population. A lower case letter indicates 'population' of a given level.

pattern persists.

A property of nature

On rocky shores there are depressions, and where there is a cover of Mytilids, sand accumulates and Amphipods and Lumbrinerids gain a goothold. The same two types of organisms exist also in other parts of the shore where sand is covered by stones (Fig. 3).

Using the same metric and characterizations used in the construction of lattice R, the lattice M for the part covered by Mytilids and S for the part covered by stones are constructed. In this case the relation $x \subseteq y$ means that x is lower down than y. The following definitions are established:

Definition 2

The lattice M is the set of all subsets of M, with the condition that every subset should have at least one element (population) of a determined level and all the elements (populations) that are beneath that level. M is partially ordered by set-inclusion.

Definition 3

The lattice S is defined in the same way as the lattice M. The new distribution, lattices M and S, and their Hasse's diagrams are shown in Fig. 4. These lattices are mathematically isomorphic and they are complete, modular and distributive. This leads me to identify a property as the 'inanimate property of living nature'. In other words, Mytilids are performing the same function as stones, *i.e.*, protecting the organisms under them from waves and tides. This has been proved experimentally, R. Paine (pers. comm. 1988).

Discussion

The present model can be used to represent organismal zonation of any rocky shore community. Because, it may be developed with any number of species and levels. Based on the Hasse's diagram, it is easy to recognize the zonal boundaries at any level, since they are represented by single nodes.

It is necessary to point out that the apparent symmetry might be an artefact, owing to the use of abundant species only. This simplification makes the model more tractable mathematically and clearer to a non-

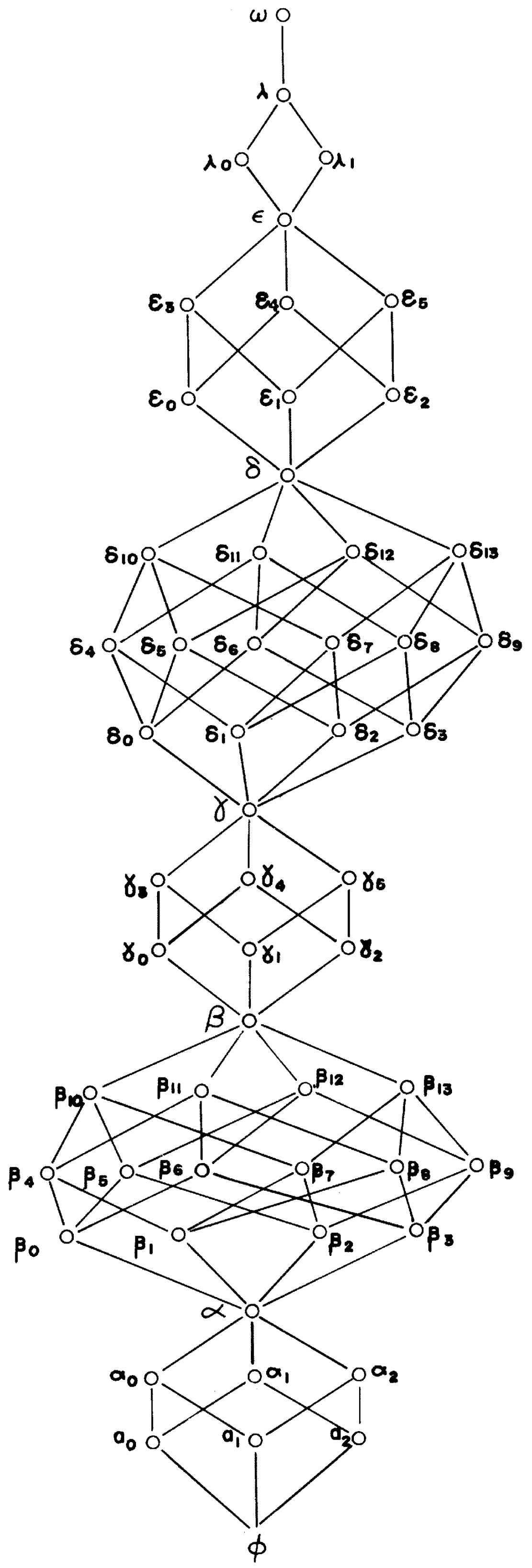

Fig. 2. Hasse's diagram of lattice R, where a single node is the upper limit of a level, and it is marked by a Greek letter. The other nodes are marked by a Greek letter with a subindex, to show its algebraic development in Table 1.

Table 1. Algebraic development of lattice R.

			(continuation)
α_0	$=\{a_0, a_1\}$	δ_0	$=\{\sigma, d_4\}$
α_1	$=\{a_0, a_2\}$	δ_1	$=\{\sigma, d_5\}$
α_2	$=\{a_1, a_2\}$	δ_2	$=\{\sigma, d_6\}$
α	$=\{a_0, a_1, a_2\}$	δ_3	$=\{\sigma, d_7\}$
β_0	$=\{\alpha, b_0\}$	δ_4	$=\{\sigma, d_4, d_5\}$
β_1	$=\{\alpha, b_1\}$	δ_5	$=\{\sigma, d_4, d_6\}$
β_2	$=\{\alpha, b_3\}$	δ_6	$=\{\sigma, d_4, d_7\}$
β_3	$=\{\alpha, b_4\}$	δ_7	$=\{\sigma, d_5, d_6\}$
β_4	$=\{\alpha, b_0, b_1\}$	δ_8	$=\{\sigma, d_5, d_7\}$
β_5	$=\{\alpha, b_0, b_3\}$	δ_9	$=\{\sigma, d_6, d_7\}$
β_6	$=\{\alpha, b_0, b_4\}$	δ_{10}	$=\{\sigma, d_4, d_5, d_6\}$
β_7	$=\{\alpha, b_1, b_3\}$	δ_{11}	$=\{\sigma, d_4, d_5, d_7\}$
β_8	$=\{\alpha, b_1, b_4\}$	δ_{12}	$=\{\sigma, d_4, d_6, d_7\}$
β_9	$=\{\alpha, b_3, b_4\}$	δ_{13}	$=\{\sigma, d_5, d_6, d_7\}$
β_{10}	$=\{\alpha, b_0, b_1, b_3\}$	δ	$=\{\sigma, d_4, d_5, d_6, d_7\}$
β_{11}	$=\{\alpha, b_0, b_1, b_4\}$	ε_0	$=\{\delta, e_7\}$
β_{12}	$=\{\alpha, b_0, b_3, b_4\}$	ε_1	$=\{\delta, e_8\}$
β_{13}	$=\{\alpha, b_1, b_3, b_4\}$	ε_2	$=\{\delta, e_9\}$
β	$=\{\alpha, b_0, b_1, b_3, b_4\}$	ε_3	$=\{\delta, e_7, e_8\}$
σ_0	$=\{\beta, c_0\}$	ε_4	$=\{\delta, e_7, e_9\}$
σ_1	$=\{\beta, c_1\}$	ε_5	$=\{\delta, e_8, e_9\}$
σ_2	$=\{\beta, c_4\}$	ε	$=\{\delta, e_7, e_8, e_9\}$
σ_3	$=\{\beta, c_0, c_1\}$	λ_0	$=\{\varepsilon, f_7\}$
σ_4	$=\{\beta, c_0, c_4\}$	λ_1	$=\{\varepsilon, f_{10}\}$
σ_5	$=\{\beta, c_1, c_4\}$	λ	$=\{\varepsilon, f_7, f_{10}\}$
σ	$=\{\beta, c_0, c_1, c_4\}$	ω	$=\{\lambda, g_{10}\}$

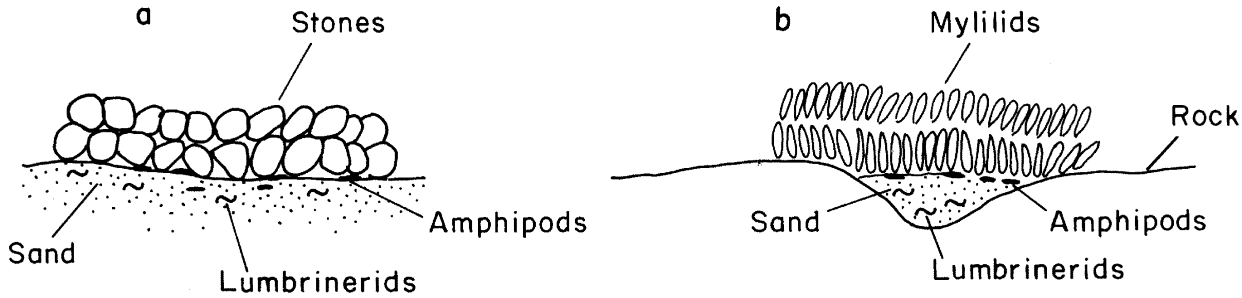

Fig. 3. The inanimate property of living nature. a. Bottom sand with stones, supporting the organisms that inhabit the sand. b. Depressions with sand accumulation under Mytilids, supporting similar organisms as the conditions in a.

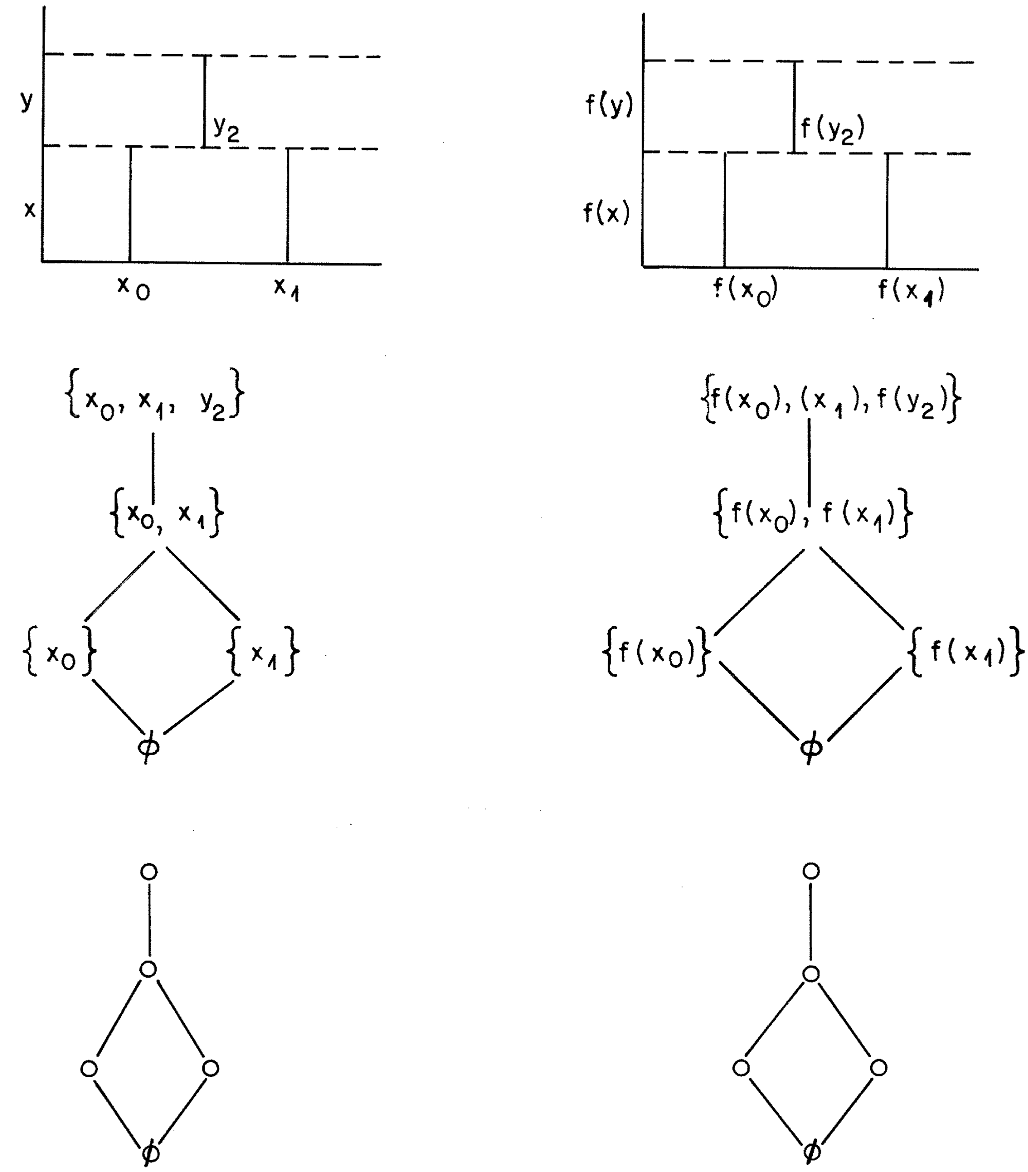

Fig. 4. Levels of the spatial distribution in the two areas of Fig. 3. Each level is represented by a capital letter (X, Y) and a function (f) of these. A subscript signifies a species or stone. Lower case letters represent population or stones on a defined level. Also shown is the algebraic display and the Hasse's diagrams of lattices M and S. Single nodes indicate the upper limit of a level.

mathematician. Possible, if the entire community is considered the symmetry may disappear.

Southward (1958) asserts that it would really be astonishing to detect a static condition given the variability of environmental factors on the sea shore. Yet, the model clearly shows that the general zonation pattern remains invariant. Since structural properties influence the dynamics, it is important to take into account that different individual elements may produce the same structure. So focussing on species composition (*i.e.*, the taxonomic aspect), could lead one to neglect structural equivalences, and fail to observe how similar processes may result from different structural elements. The living Mytilids, substituted for stones, is an example. The inanimate property of living nature may be extended to the condition of organisms acting as simple substrates, such as beds of seaweed (Norton 1985), and in general to any organism serving as substrate to epiphytic and epizoic organisms. The use of the algebraic theory of lattices may permit representation of other types of spatial distributions and patterns. Extension of the model to combine it with fuzzy set theory is contemplated.

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REFERENCES

BRIRKHOFF, G. 1940. *Lattice Theory*. American Mathematical Society, Colloqium Publications 25, New York.

CRAWLEY, P. and R.P. DILWORTH. 1973. *Algebraic Theory of Lattices*. Prentice Hall, Inc., New Jersey.

HISCOCK, K. 1985. Aspects of the ecology of rocky sublitoral area. *In:* P.G. Moore and R. Seed, (eds.). *The Ecology of Rocky Coasts*. p. 23-34. Hodder and Stoughton, London.

HISCOCK, K. and R. MITCHELL. 1980. The description and classification of sublitoral epibenthic ecosystems. *In:* J.H. Price, D.E.G. Irvine and W.F. Farnham, (eds.). *The Shore Environment, Vol. 2: Ecosystems*. p. 323-370. Academic Press, London.

LEWIS, J.R. 1964. *The Ecology of Rocky Shores*. The English Univ. Press, London.

NEWELL, R.C. 1979. *Biology of Intertidal Animals*. Marine Ecology Surveys Ltd., Kent.

NORTON, T.A. 1985. The zonation of seaweeds on rocky shores. *In:* P.G. Moore and R. Seed (eds.). *The Ecology of Rocky Coasts*. p. 7-21. Hooder and Stoughton, London.

PAREDES, C. 1974. El Modelo de zonación en la orilla rocosa del departamento de Lima. Rev. Per. Biol. 1: 168-191.

RICKETTS, E. and J. CALVIN. 1968. *Between Pacific Tides*. Stanford Univ. Press, Stanford.

SOUTHWARD, A.J. 1958. The zonation of plants and animals on rocky sea shores. Biol. Rev. 33: 137-177.

STEPHENSON, T.A. and A. STEPHENSON. 1949. The universal features of zonation between tide marks on rocky coasts. J. Ecology 37: 289-305.

WOMERSLEY, H.B. and S. EDMONDS. 1952. Marine coastal zonation in Southern Australia in relation to ageneral scheme of classification. J. Ecol. 40: 84-90.

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