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CHTHAMALUS BISSINUATUS (CIRRIPEDIA) AND BRACHIDONTES SOLISIANUS (BIVALVIA) SPATIAL INTERACTIONS: A STOCHASTIC MODEL

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This paper is dedicated to the memory of Jorge A. Petersen, beginner of this study, who died tragically while at field work.

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ABSTRACT

Chthamalus bissinuatus and *Brachidontes solisianus* are two solitary species with a sessile mode of life, coexisting in high densities in the mid-intertidal. Our aim was to show that spatial interactions between both species on a rocky shore could be described by means of a stochastic model, in our case a Markovian system with an infinite number of components interacting locally. To check the model, simulations were compared to the real data through a family of functions which discriminate between different spatial chaotic configurations.

Introduction

Chthamalus bissinuatus and *Brachidontes solisianus* are the two dominant mid-intertidal space-occupants of the rocky shores of São Paulo state. Both are solitary suspension-feeders with a sessile mode of life. Dispersion is assured by a great number of planktonic larvae, a reproductive strategy common for tropical marine organisms (Crisp, 1974). These larvae will eventually settle and metamorphose on suitable empty spaces. Barnacles are able to colonize almost any hard substratum, and are among the first organisms to settle on primary space (Crisp and Barnes, 1954, Crisp, 1961). Mussels, on the other hand, attach preferentially to filamentous structures and rough surfaces (Penchaszadeh, 1973), arriving in a later successional stage.

Both species are potentially able to populate heavily a great extension of the coast. However, they coexist in a patchy distribution due to important temporal and spatial fluctuations in the density of both populations, which can even lead to the numerical dominance of one or the other alternately. Patches are common features of the intertidal landscape and are the consequence of different successional stages in nearby areas (Paine and Levin, 1981). It is quite possible that the *Chthamalus* -*Brachidontes* patchy configuration could be explained merely by factors such as recruitment and mortality patterns, and especially spatial interaction between adjacent individuals of the two species.

Our starting point was a series of observations carried out by Jorge A. Petersen, John P. Sutherland and Sonia Ortega from 1979 to 1982. Our purpose was to define a simple mathematical model, more precisely a Markovian system with an infinite number of components interacting locally, that could throw light on the primary rules responsible for the C. *bissinuatus* and B. *solisianus* community development.

Study site and photographic records

The model was based on photographic records taken by J.A. Petersen from the rocky shore at the Marine Biological Center (CEBIMar) of the University of São Paulo, at São Sebastião, state of São Paulo (Fig. 1).

Sets of 100 cm^2 fixed quadrats were photographed bimonthly over a period of 3 years (Nov. 1979 to Dec. 1982) on protected and moderately exposed areas. Each set consisted of several control and experimental quadrats positioned on nearly horizontal mid-intertidal rocky surfaces. Experimental quadrats were scraped and burnt, and the observation of new sets was initiated in April and November of each year in order to analyse the recruitment patterns of each species.

We restricted our study to a series of sets totaling 20 pairs of control-experimental quadrats, which belonged to the moderately exposed site, distributed over an area of approximately 13 m^2.

The model

Our model is a Markov chain, non-homogeneous in time, assuming values in the set of the functions from $\mathbb{Z}^2$ to $\{0,1,1.1\}$. The following conventions were established: the rocky coast was represented by the $\mathbb{Z}^2$ grid; each point of intersection of $\mathbb{Z}^2$ could be empty or occupied by no more than one individual of any of the two species considered. Each species had a particular pattern of behaviour, all individuals of the same species behaving in the same way. Thus a configuration of organisms was represented by a function $x: \mathbb{Z}^2 \rightarrow \{0,1,1.1\}$, 0 indicating an empty space, 1 representing *C. bissinuatus* and 1.1 *B. solisianus* (1). Therefore, the occupation of a generic point (i,j) of $\mathbb{Z}^2$ is expressed by $x(i,j)$, which is the value of the function x at the point of intersection (i,j). Each temporal unit of this Markov chain corresponds to 3 months and only interactions between adults of the two populations are taken into account.

Let the Markov chain be represented by $(X_t)_{t=0,1,2,\ldots}$. Thus, if $X_t(i,j) = 1$, for instance, at the end of trimester t the point (i,j) of the rocky coast is occupied by a barnacle. The transition probabilities of the chain are thus defined: given k integer $(i_1,j_1),\ldots,(i_k,j_k)$ in $\mathbb{Z}^2$, and $a_1,a_2,\ldots,a_k$ in $\{0,1,1.1\}$

$$P(X_{t+1}(i_1,j_1) = a_1,\ldots,X_{t+1}(1_k,j_k)=a_k \mid X_t=x) =$$

$$= \prod_{\ell=1}^{k} P(X_{t+1}(i_\ell,j_\ell)=a_\ell \mid X_t=x).$$

for any configuration x and instant t. Furthermore

$$P(X_{t+1}(i,j) = a \mid X_t = x)$$

will be a function of the remainder of $t/4$, a, the $x(i,j)$ value, and the number of C. *bissinuatus* and B. *solisianus* at the 4 nearest positions of (i,j). Let $R_n(.,.,.)$ be the function in which n is the remainder of $t/4$ (e.g., R_0 defines the particular rules of the model during the first trimester considered, an so on), that is

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(1) - This is an interesting convention for working with the total number of individuals of both species inside a sufficiently small area. For instance, if the sum obtained is 4.1, the total number of individuals is 4, 1 being B. *solisianus* and 3 C. *bissinuatus*.

$$P(X_{t+1}(i,j) = a \mid X_t = x) =$$

$$= R_n(a, x(i,j),\ x(i+1,j) + x(i-1,j) + x(i,j+1) + x(i,j-1))$$

The functions R_n are therefore defined in the following way

$$\left.\begin{array}{l} R_0(1.1,0,z) = p_1 \\ R_0(0,0,z) = 1-p_1 \end{array}\right\} \quad \text{if } z \geq 2$$

$$\left.\begin{array}{l} R_0(1,0,z) = p_2 \\ R_0(0,0,z) = 1-p_2 \end{array}\right\} \quad \text{if } z \leq 1.1$$

$$\left.\begin{array}{l} R_0(0,1,z) = q_2 \\ R_0(1,1,z) = 1-q_2 \end{array}\right\} \quad \text{if } \mathrm{dec}(z)^{(2)} \leq 2$$

$$\left.\begin{array}{l} R_0(0,1,z) = q_1 \\ R_0(1,1,z) = 1-q_1 \end{array}\right\} \quad \text{if } \mathrm{dec}(z) \geq 3$$

$$R_0(0,1.1,0) = 1$$

$$R_0(1.1,1.1,z) = 1 \quad \text{if } z \neq 0$$

$$\left.\begin{array}{l} R_1(1,0,z) = p_2 \\ R_1(0,0,z) = 1-p_2 \end{array}\right\} \quad \text{if } \mathrm{dec}(z) < 3$$

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(2) - dec(z) is the decimal part of the number z: dec(4.3) = 3

$$R_1(0,0,z) = 1 \qquad \text{if } \mathrm{dec}(z) \geq 3$$

$$\begin{array}{ll} R_1(0,1,z) = q_2 & \\ & \text{if } \mathrm{dec}(z) \leq 2 \\ R_1(1,1,z) = 1-q_2 & \end{array}$$

$$\begin{array}{ll} R_1(0\,,1,z) = q_1 & \\ & \text{if } \mathrm{dec}(z) \geq 3 \\ R_1(1,1,z) = 1-q_1 & \end{array}$$

$$R_1(0,1.1,0) = 1$$

$$\begin{array}{ll} R_1(0,1.1,z) = q_1 & \\ & \text{if } \mathrm{dec}(z) = \mathrm{int}(z)^{(3)} \text{ and } z \neq 0 \\ R_1(1.1,1.1,z) = 1-q_1 & \end{array}$$

$$\begin{array}{ll} R_1(0,1.1,z) = q_3 & \\ & \text{if } \mathrm{dec}(z) \neq \mathrm{int}(z) \text{ and } z \neq 0 \\ R_1(1.1,1.1,z) = 1-q_3 & \end{array}$$

$$\begin{array}{ll} R_2(1,0,z) = p_2 & \\ & \text{if } \mathrm{dec}(z) \leq 2 \\ R_2(0,0,z) = 1-p_2 & \end{array}$$

$$R_2(0,0,z) = 1 \qquad \text{if } \mathrm{dec}(z) \geq 3$$

$$\begin{array}{ll} R_2(0,1,z) = q_2 & \\ & \text{if } \mathrm{dec}(z) \leq 2 \\ R_2(1,1,z) = 1-q_2 & \end{array}$$

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(3) - int(z) is the integer part of the number z: int(4.3) = 4

$$\begin{array}{ll} R_2(0,1,z) = q_1 & \\ & \text{if } \mathrm{dec}(z) \geq 3 \\ R_2(1,1,z) = 1-q_1 & \end{array}$$

$$\begin{array}{ll} R_2(0,1.1,0) = 1 & \\ R_2(1.1,1.1,z) = 1 & \text{if } z \neq 0 \end{array}$$

$$\begin{array}{ll} R_3(1,0,z) = p_2 & \\ & \text{if } \mathrm{dec}(z) \leq 2 \\ R_3(0,0,z) = 1-p_2 & \end{array}$$

$$\begin{array}{ll} R_3(0,0,z) = 1 & \text{if } \mathrm{dec}(z) \geq 3 \end{array}$$

$$\begin{array}{ll} R_3(0,1,z) = q_2 & \\ & \text{if } \mathrm{dec}(z) \leq 2 \\ R_3(1,1,z) = 1-q_2 & \end{array}$$

$$\begin{array}{ll} R_3(0,1,z) = q_1 & \\ & \text{if } \mathrm{dec}(z) \geq 3 \\ R_3(1,1,z) = 1-q_1 & \end{array}$$

$$\begin{array}{ll} R_3(0,1.1,0) = 1 & \\ R_3(1.1,1.1,z) = 1 & \text{if } z \neq 0 \end{array}$$

Justifying the model

Initially the use of a countable set of numbers, $\mathbb{Z}^2$, to represent the continuous surface of the rocky coast may seem improper. Nevertheless, our choice is justified by the well defined shape and size of C. *bissinuatus* and B. *solisianus*. Configurations of individuals of these two species have strong geometric constraints and are essentially discrete. There are also a limited number of individuals that can occupy a circunscribed surface, thus making reasonable the utilization of $\mathbb{Z}^2$ instead of $\mathbb{R}^2$ to represent configurations of organisms by punctual processes. This is easier to understand if we think of a box full of black and white buttons, of similar or dissimilar diameters, without superposition.

The grid $\mathbb{Z}^2$ is not the only possible choice to represent the base of the configuration. Grids of other geometries (hexagonal, for example) would adjust better to the shape of the individual. As we consider this to be of minor importance, the computational simplification of $\mathbb{Z}^2$ was preferred.

In order to account for the large number of factors affecting the evolution of the community, it was natural to use a stochastic model. Since Boltzmann's work (see Cohen and Thirring, 1973) we know this is the right manner to deal with deterministic systems which have a great number of components. Being a Markov chain, our model does not take into account the age of the organisms, and it is assumed that the state of one point at a given instant reflects all its past evolution. The choice of a Markov chain was based on the absence of empirical evidence as to the longevity of the two species and on photographic observations leading to the belief that the organisms were predominantly killed instead of dying of old age.

In our model, each individual interacts only with its 4 nearest neighbours, such that

$$P(X_{t+1}(i,j) = a \mid X_t = x)$$

is only a function of a, n, $x(i,j)$, $x(i\pm1,j)$ and $x(i,j\pm1)$. This was decided after verifying that the effects of the reproductive strategies, larval settlement, or mechanisms of disappearance acting on a given individual were restricted to its adjacent organisms. These kinds of models are called in the literature Markovian systems with an infinite number of components interacting locally (Spitzer, 1970, Ligget, in press).

Our model is spatially homogeneous (there is no reason for a greater number of grooves to be clustered in a particular area of the rock), so if x and y are two configurations such that

$$\begin{aligned} &y(0,0) = x(i,j). \\ &y(\pm1,0) = x(i\pm1,j), \\ &y(0,\pm1) = x(0,j\pm1) \text{ then} \\ &P(X_t(i,j) = a \mid X_t = x) = \\ &= P(X_t(0,0) = a \mid X_t = y) \end{aligned}$$

We chose a temporal unit so that it would denote meaningful changes in the configuration of the organisms without overlapping two important effects. The division in quarters of the year distinguished, for example, the heavy recruitment of

B. *solisianus*, visible from mid-spring to mid-summer, from the period of significant mortality of this species, which occurs from mid-summer to mid-autumn. Due to the temporal unit chosen, it became reasonable to represent only the interaction among adults.

The biological parameters taken into account were:

1. recruitment of *Chthamalus bissinuatus*: barnacles are able to settle on primary space and we have indications that C. *bissinuatus* recruitment occurs during the whole year (J. A. Petersen, personal communication). Therefore, individuals of this species can occupy any bare space of the grid. In our model we will let the barnacles recruit all year round on empty intersections with less than 3 B. *solisianus* as neighbours. This rule accounts for the death of C. *bissinuatus* due to overgrowth caused by the mussels, while it also counts indirectly the age of the barnacles, since only the old ones can have 3 or 4 mussels as neighbours.

2. recruitment of *Brachidontes solisianus*: this species has maximal recruitment in late spring and early summer and attaches preferentially to irregular surfaces. As the quadrats were not established over cracks, and settlement on algae was not common, the first B. *solisianus* recruited on or between the barnacles. In our model each individual of this species recruits only during one quarter of the year, if it will be surrounded by at least 2 organisms of any species.

3. death of C. *bissinuatus*: it seems to be caused especially by overgrowth of adjacent B. *solisianus*. Therefore, we will let the barnacles vanish every quarter of the year with different probabilities depending on the number of neighbouring mussels.

4. death of B. *solisianus*: during late summer there is a significant mortality of the mussels due to desiccation and high temperatures (J.A. Petersen, personal communication). This species is more susceptible to these abiotic factors than C. *bissinuatus* partly owing to differences in shell anatomy and body colour. Also B. *solisianus* individuals cannot remain isolated. In our model, mussels left without neighbours are eliminated from the array, and during one quarter of the year they disappear, each one independently of the others, with different probabilities depending on the number of neighbouring barnacles.

Dead barnacles in the photographic records were considered empty spaces in the simulations, since they do not remain attached for a long period. C. *bissinuatus* and B. *solisianus* can be found piled up on the rocky coast, although this is not frequent; therefore, this type of situation was excluded from the model.

The simulations

As C. *bissinuatus* and B. *solisianus* have a covering area of roughly 0.5 cm in diameter, the simulations were plotted on a torus of 20 x 20 intersections in order to resemble the approximate density of elements on a 100 cm² quadrat. The simulation records were compared to the control quadrats using the same 100-point reticulate applied to the latter.

Each one of the 4 temporal units (or cycles) represented: mid-spring to mid-summer (R_0), mid-summer to mid-autumn(R_1), mid-autumn to mid-winter (R_2), and mid-winter to mid-spring (R_3). Simulations of 40, 100 and 500 cycles were run corresponding to 10, 25 and 125 years respectively.

We adjusted the probabilities of the model in order to picture an average quadrat of either all the quadrats placed near each other at the same level of the shore or of only one quadrat throughout the period of observations (spatial and temporal variation).

The combined effects of minimal variations in wave shock, insolation, winds and other factors we did not consider may cause individual quadrats to correspond to different parameters in spite of their proximity and tidal level. This suggested the use of random probabilities independently chosen before each cycle which would, up to a certain point, compensate for the short observation period of the data (3 years).

Evaluation of the model

To evaluate the accuracy of our model we needed criteria to allow us to compare the results of the simulations with the real data. An intuitive comparison would not lead us too far because the images of both distributions gave a chaotic impression.

A point-by-point comparison would be as absurd as comparing in the same way two configurations of heads and tails obtained by throwing a hundred coins on a grid: the probability of a given point of the grid showing the same configuration (head or tail) is one half in both experiments.

Therefore, to compare these two configurations in which chance was involved we used the following criteria:

1) We first compared the empirical densities of each species. Let

$$d_{c,p,y} = \frac{\text{points of the grid occupied by species c}}{\text{total number of points}}$$

were p is the period considered in the year y.

By analogy $d_{b,p,y}$ is the density of species b in the period p and in the year y.

We have used the adjective empirical to refer to the result of one simulation. While the model does not specify deterministically what will happen in each point of the grid, a computer simulation does so since it describes a function of the sample, $X_t(\omega)$, instead of describing a family of random variables, X_t.

When y tends to infinity these densities do not converge to a limit; they pulsate in a chaotic way because the total number of points taken into account is small. To stabilize this chaotic behaviour we have calculated averages at longer and longer intervals of time (Cesaro mean, in Choquet, 1964): if the limit exists

$$d_{c,p} = \lim \frac{1}{N} \sum_{y=1}^{N} d_{c,p,y} \quad \text{for species c.}$$

In the same way we have $d_{b,p}$ for species b.

We obtained 8 limit average densities (for *C. bissinuatus*, *B. solisianus*, in the simulation periods 0 to 3), strongly correlated, therefore not enough to ascertain the 5 parameters of our model (p_1, p_2, q_1, q_2, q_3).

2) The second step of our analysis took into account the geometric shape of the configurations. Intuitively a very homogeneous configuration as mussels on the black squares of a chess-board and barnacles on the white ones is very different from filling one half of the board with mussels and the other with barnacles, the densities of the two species being equal in both cases (see Fig. 2).

One of the simplest ways to distinguish two functions with the same average is to consider the square differences between them. Unfortunately we could not apply this procedure to the indicatrix function of each species because the two indicatrix functions ϕ_1 and ϕ_2, leading to the same density d, would take the values one or zero exactly the same number of times. Therefore, the square deviations of ϕ_1 and ϕ_2 are equal:

$$\int |\phi_1 - d|^2 = \int |\phi_2 - d|^2 .$$

This situation changes when the function takes more than two values. So we decided to consider functions on the discrete segment $(1,\dots,10)$, cutting a square Q by vertical and horizontal lines. This idea came from integral geometry (see appendix).

Let $f^{v}_{c,p,y}(j)$ be the number of individuals of species c, placed in the j-th column at period p of the year y, and $f^{h}_{c,p,y}(j)$ the number in the j-th row. In the same way we can define $f^{v}_{b,p,y}(j)$ and $f^{h}_{b,p,y}(j)$ for species b. Thus

$$d_{c,p,y} = \frac{\sum_{j=1}^{10} f^{v}_{c,p,y}(j)}{100} = \frac{\sum_{j=1}^{10} f^{h}_{c,p,y}(j)}{100} \quad \text{and}$$

$$d_{b,p,y} = \frac{\sum_{j=1}^{10} f^{v}_{b,p,y}(j)}{100} = \frac{\sum_{j=1}^{10} f^{h}_{b,p,y}(j)}{100}$$

To compare each function to its mean we consider

$$\sigma(f) = \sum_{j=1}^{10} (f(j) - \bar{f})^2$$

$$\text{where } \bar{f} = \frac{1}{10} \sum_{j=1}^{10} f(j) .$$

Therefore we obtain the square deviations

$$\sigma^{\cdot}_{\cdot,p,y} = \sum_{j=1}^{10} (f^{\cdot}_{\cdot,p,y}(j) - \bar{f}^{\cdot}_{\cdot,p,y})^2 .$$

These values oscillate considerably due to p and to y. The p represents seasonal fluctuations to which the distribution of the two populations is sensitive. To eliminate fluctuations in time we use the Cesaro mean once again. The values

$$\frac{1}{N} \sum_{y=1}^{N} \sigma^{\cdot}_{\cdot,p,y}$$

of the simulation seemed to converge afterwards, although in a slow way.

The integer y can be substituted by the label of different sites at approximately the same tidal height of the seashore. Therefore, working with Petersen's data we have obtained an estimate of the spatial square deviations. That is, exchanging j and y allows us to measure spatial oscillations. Nevertheless, that would make sense if the number of years of observations taken into account have been on the order of 10.

We defined a family of functions discriminating between various values of the parameters. To estimate the error of those functions, a precise computation of the real data was compared with a less time consuming procedure which caused a minimal counting error (±1) dues misplacing C. *bissinuatus*, B. *solisianus* and bare space. The little difference between both counting procedures gave us an indication of the confidence interval we should adopt for the function d when comparing the simulations with the real data (Table I).

There was a difference between the values calculated for the σ functions of lines and columns for both the simulations and the real data. This difference in the real data could be a consequence of factors such as gravity and inclination of the surface. However the size of the quadrats ($100cm^2$) is certainly not enough to cause such a difference. Furthermore, the simulations show these same deviations which were reduced with a longer simulation time. This led us to believe that the difference observed in both cases is just an effect of statistical deviations which are expected in samples of small size. Nevertheless, the values of this difference gave us an indication of what should be the order of magnitude of the confidence interval for σ (Table I).

Finally we looked for the probabilities that set the functions d and σ within the confidence interval established by the parameters of the real data.

Simulations X reality

With an appropriate choice of probabilities $(p_1, \dots, q_3)$, the simulations emulated reasonably well the density variations of both species inside the quadrats as well as variation of these densities along rows or columns ($\sigma(f)$) (Fig. 3). Values for d functions obtained from the simulations seemed to converge reasonably after 40 cycles (10 years) while the σ values fell within intervals of size 0.4 and 0.2 after 100 and 500 cycles respectively.

We analysed the results of simulations combining a wide range of different probability values to check for the ones which fell within the confidence interval based on the real data. We verified that the former matched with the real data for only a limited interval of q_1,q_2 and q_3 values. Therefore, we fixed q_1,q_2 and q_3 within that class of matching values ($q_1=0.75$, $q_2=0.15$, $q_3=0.25$) and ran simulations combining only the p_1 and p_2 values (0.2 to 0.8, interval of 0.05). We obtained practically a segment of a line, as far as the functions d and σ are concerned (Fig. 4). As this curve is almost a line of positive inclination, to compensate for any increase of p_1 we should proportionally increase p_2($0.4 \leq p_1 \leq 0.65$, $0.5 \leq p_2 \leq 0.75$).

As far as the functions d and σ are concerned, it is possible to find probabilities p_1^0, p_2^0, q_1^0, q_2^0, q_3^0 such that the values of the empirical d and σ are close to the values obtained with random probabilities. But if we computed the temporal quadratic dispersion τ, this new function would probably distinguish the model with random probabilities from the model considered in this paper. However as Petersen's data covered only a period of 3 years, to calculate the observed quadratic dispersion τ would not be statistically significant. Thus we stuck to the model with fixed probabilities.

Discussion

Stochastic models have already been proposed to describe ecological processes such as competition for a limited resource and succession (Clifford and Sudbury, 1973, Horn, 1975, Usher, 1979, Greene and Schoener, 1982). An interesting aspect about working with stochastic models is that they can, up to a certain extent, predict the evolutionary trend of the process observed. Also, they are useful to discriminate among the factors involved, thus giving a clearer image of the role of those factors in the process.

Patterns of recruitment and death were considered to be of major importance in our model because both species considered were solitary with a sessile mode of life. The arrival of larvae of both species can occur, independently form one another, wherever there is bare space. Therefore, we have a system composed of infinite boundaries where interactions occur, these being restricted to the nearest neighbours. Within the same given area the total interacting perimeter of the boundaries is much greater in the case of solitary than colonial species.

Mytilids are dominant competitors for space and can even be found as extensive monocultures (Dean, 1981, Paine and Levin, 1981, Harms and Anger, 1983). However, *B.solisianus* never completely dominated the community at São Sebastião. The absence of competitive exclusion of C. *bissinuatus* by B. *solisianus* seemed to be a consequence of: 1) recruitment of the mussels within a limited period of time; 2) barnacle recruitment all year round and 3) mass mortality of the mussels during the hot period of the year. Considering the situations where both species are present in a heavily occupied space, any increase in the recruitment of one species should be accompanied by a proportional increase in the recruitment of the other. If not, coexistence of both species is compromised.

Predation is frequently mentioned as a major factor preventing monopolization of space (Dayton, 1971, Paine and Levin, 1981). Top predators found at São Sebastião were the gastropods *Thais haemastoma*, *Leucozonia nassa* and the crab *Eriphia gonagra*. However their density was very low at the level where *C. bissinuatus* and *B. solisianus* coexist. Thus the effect of these carnivores was considered of slight importance.

Herbivores frequently observed at that tidal level were *Acmaea subrugosa*, *Littorina flava* and *Littorina zic-zac*. Of these the bull-dozer *Acmaea subrugosa* is the major herbivore to affect the community. As it scrapes the substratum (Steneck and Watling, 1982) *Acmaea* affects the earlier stages of colonization by removing newly settled larvae. Since our model deals with interactions among adults the aspect of herbivory considered was the delay of the rate of occupation of bare space and not its effect on survival of the larvae.

The main cause for space clearance, with the consequent patchy structure within the community, was mass mortality of the mussels. Patchy configurations were distinguished through the σ functions. Patchiness could also be measured, defining for each point of the grid occupied by species s a function for the number of neighbours of the same species s. The integral of this function on the torus would be: 1) zero, if species s was positioned on the black squares of a chess-board; 2) close to the area of the board (Q) if s was filling every second column and 3) close to twice this area Q if s was clustered on one half of the board (Fig. 2A, B and C).

Although the model describes reasonably well the development of the configuration of the *Chthamalus bissinuatus*-*Brachidontes solisianus* community on a rocky coast, a longer observation period or else a greater number of quadrats would have been more appropriate for the confidence intervals of the real data to be shortened and the probabilities of the model better defined.

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Appendix

The Radon transformation(Gel'fand et al, 1966):

Let f be a function from the plane to $\mathbb{R}$. From f we will obtain a new function $\hat{f}$.

Let A be the space of all lines contained in the plane. This space A is a surface as a line can be moved in two essentially different ways: translation and rotation around a given point of the line.

We can now calculate on each line D the integral

$$\int_D f = f(D)$$

When f is zero outside a disk of $\mathbb{R}^2$ whatever its size, and it is both limited and measurable, $\hat{f}$ will be defined for all lines. We used a small part of the information contained in the function f, precisely the restriction of $\hat{f}$ to two curves of A.

By substituting f by $\hat{f}$ information is not lost, because f can be recovered out of $\hat{f}$. Such an inverse Radon transform is computed by scanning. This explains why a measurement along a sufficient number of lines allows a scanner to reconstitute a 3-dimensional object.

In relation to our square deviations (σ) it is not a surprise it allows us to distinguish between different types of configurations. If the σ functions are different, so must be the Radon transforms of $\hat{f}$. Thus the inverse Radon transforms of $\hat{f}$, which are the initial functions f, should be also different.

Table I - Confidence intervals established for comparison of the simulation with the real data.

cycles	function d		function σ	
	$d_{c,p,y}$ (a)	$d_{b,p,y}$ (b)	$\sigma_{c,p,y}$ (a)	$\sigma_{b,p,y}$ (b)
R_0	$5.0 \leq x_{i,j} \leq 6.0$	$2.0 \leq x_{i,j} \leq 3.0$	$1.0 \leq x_{i,j} \leq 5.0$	$1.6 \leq x_{i,j} \leq 3.4$
R_1	$5.1 \leq x_{i,j} \leq 6.1$	$1.6 \leq x_{i,j} \leq 2.6$	$0.5 \leq x_{i,j} \leq 6.0$	$0.7 \leq x_{i,j} \leq 2.0$
R_2	$5.3 \leq x_{i,j} \leq 6.3$	$1.25 \leq x_{i,j} \leq 2.25$	$1.2 \leq x_{i,j} \leq 3.5$	$0.7 \leq x_{i,j} \leq 2.1$
R_3	$5.95 \leq x_{i,j} \leq 6.95$	$1.2 \leq x_{i,j} \leq 2.2$	$1.3 \leq x_{i,j} \leq 3.1$	$0.6 \leq x_{i,j} \leq 2.5$

(a) $d_{c,p,y}$ and $\sigma_{c,p,y}$ refer to C. *bissinuatus*

(b) $d_{b,p,y}$ and $\sigma_{b,p,y}$ refer to B. *solisianus*

Fig. 1 - Study site: São Sebastião, state of São Paulo.

Fig. 2 - Different types of configurations for the theoretical position of mussels and barnacles on a board.

Fig. 3 - Comparison of simulation cycle nº 499 (R_3), p_1=0,55, p_2=0.65, q_1=0.75, q_2=0.15 and q_3=0.25 (A) with control quadrat nº 9 photographed in October 1981 (B); example chosen by chance .

Fig. 4 - Range of recruitment probabilities (0.2 to 0.8, 0.05 intervals) and death fixed values (q_1=0.75, q_2=0.15 and q_3=0.25) for the simulation functions comprised within the confidence interval established.

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70°
62°
54°
46°
38°
0°
0°
8°
8°
BRAZIL
16°
16°
24°
24°
32°
32°
ATLANTIC OCEAN
70°
62°
54°
46°
38°

FIGURE 1

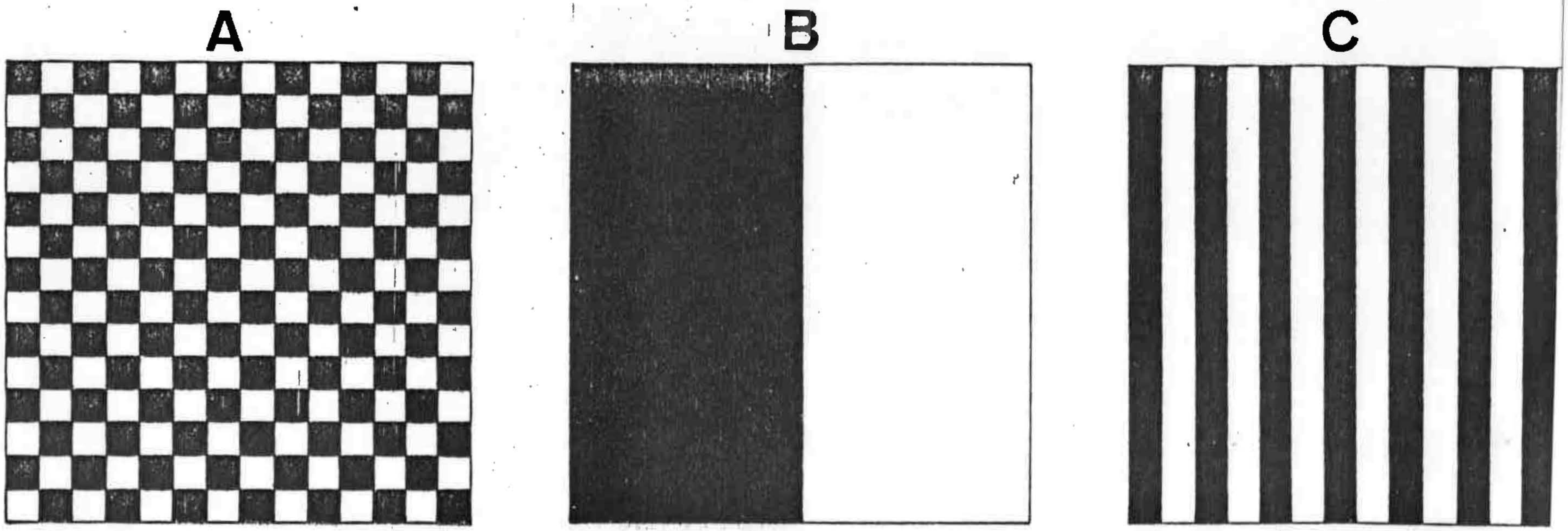

FIGURE 2

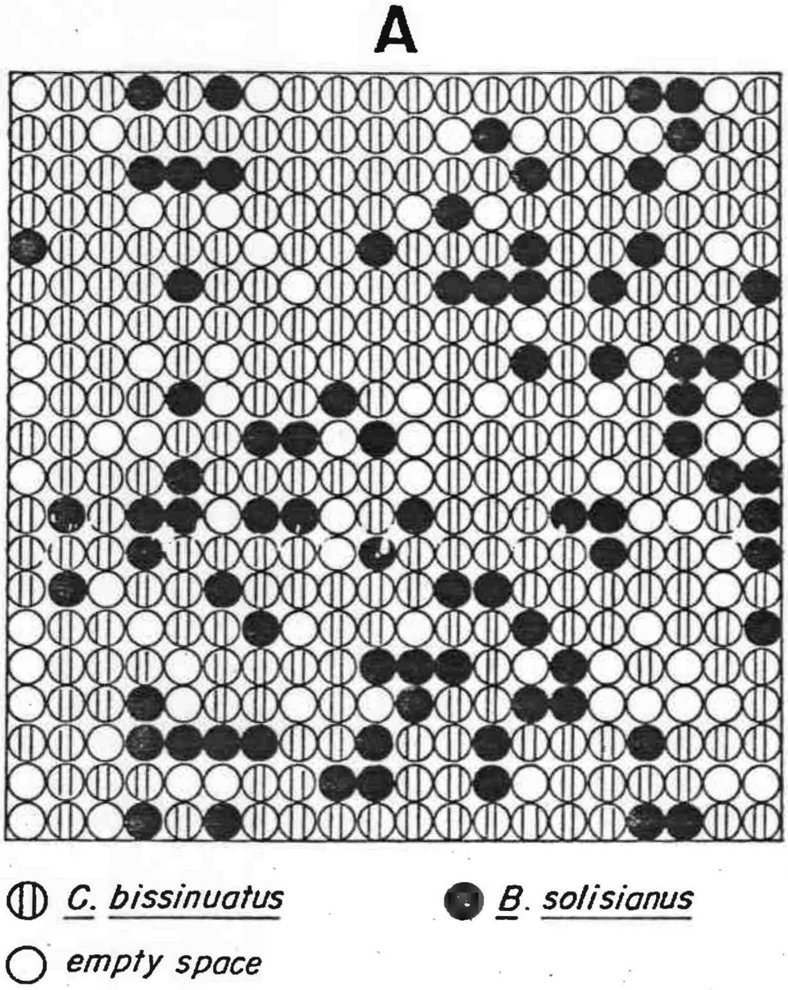

FIGURE 3A

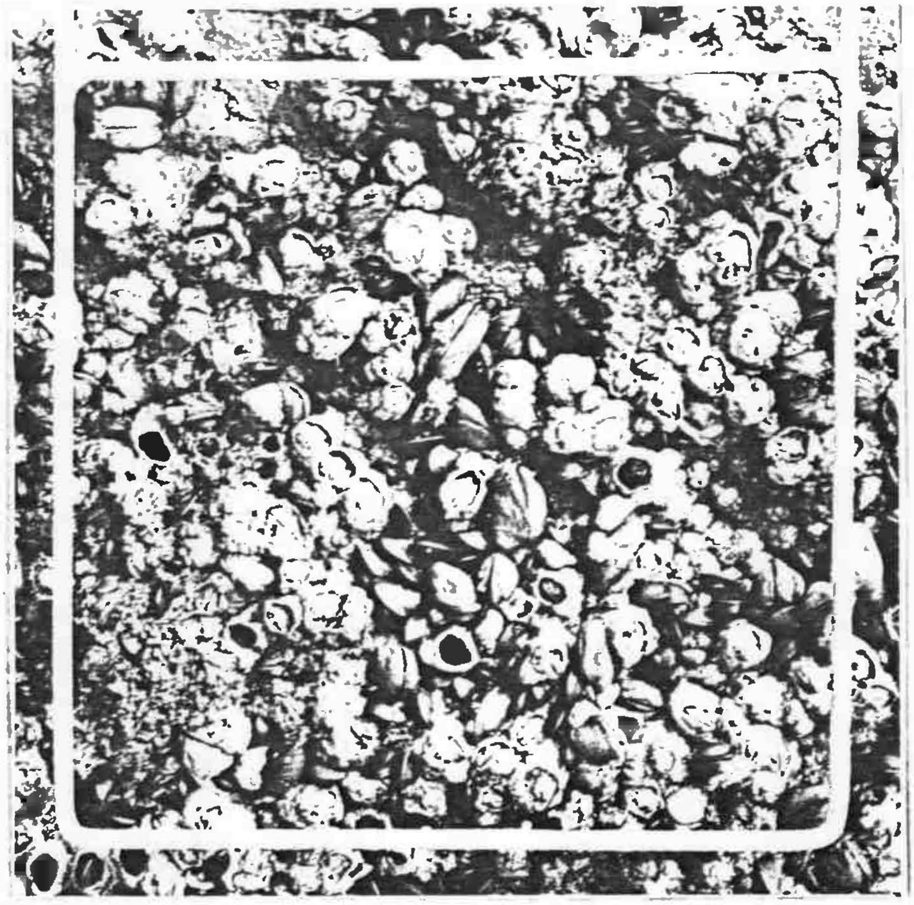

FIGURE 3B

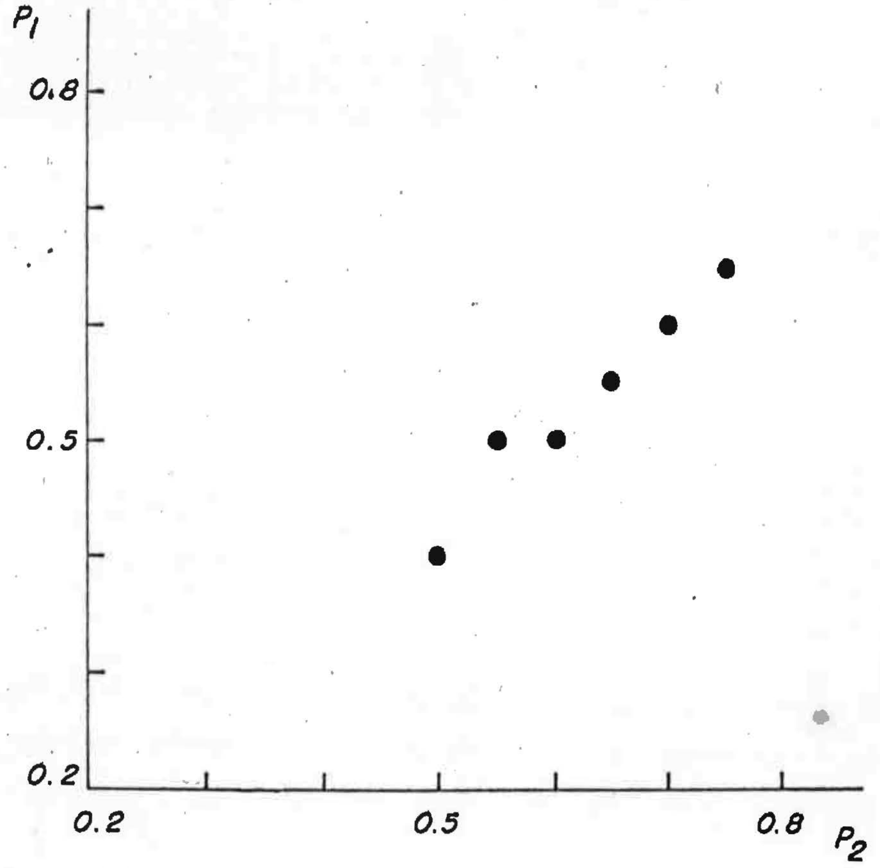

FIGURE 4