

Detection of Non-Random Zonation Patterns in Sandy Intertidal Communities

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ABSTRACT

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The issue of zonation patterns has historically received special attention from ecologists of rocky and sandy intertidal systems. Nowadays, the question of whether generalizable zonation patterns exist is still a focus of controversy, especially among sandy beach ecologists. Many procedures have been employed to detect zonation patterns, from graphical (kite diagram) to multivariate methods. These traditional techniques are not suitable, since neither of them allow an objective test of the non-randomness of the patterns detected. Determining whether the pattern observed differs from what is expected by chance is very important from the ecological point of view, since it would imply the existence of any underlying deterministic process. In this paper, I advocate the use of two techniques to analyze zonation patterns, randomized cluster analysis and gradient analysis, which solve the objectivity problem. These methods provide the risk (probability) of detecting spurious patterns, *i.e.*, those that do not differ from what is expected by chance. In other words, the statistical significance of the pattern could be tested. I describe the procedures using data from a sandy intertidal system, and discuss their attributes and limitations.

ADDITIONAL INDEX WORDS: *Cluster analysis, gradient analysis, intertidal, non-randomness, randomization, sandy beach, zonation pattern.*

INTRODUCTION

When we observe an intertidal community, especially in rocky systems, the first phenomenon that calls our attention is the way in which the organisms occupy the space. The different species are not equally distributed but occupy specific portions of the intertidal zone, producing different faunal-floral belts in the intertidal. Description of zonation patterns has historically received special attention from intertidal ecologists. Several general classification schemes have been proposed, both for sandy (e.g., DAHL, 1952; PICHON, 1967; TREVALLION *et al.*, 1972; for a review see McLACHLAN and JARAMILLO, 1995) and rocky systems (e.g., STEPHENSON and STEPHENSON, 1949; LEWIS, 1964). The question of whether generalizable zonation patterns exist is still a focus of controversy among sandy beach ecologists (e.g., RAFFAELLI *et al.*, 1991; BRAZEIRO and DEFEO, 1996).

The analysis of zonation patterns seeks to identify discrete spatial belts with homogeneous composition of species. Traditionally, the detection of zones has been done on the basis of simple graphical methods, namely kite diagrams (e.g., DAHL, 1952; TREVALLION *et al.*, 1972; JARAMILLO, 1978; BALLEY, 1983). Recently, more sophisticated techniques have been employed, such as numerical classification (e.g., SANCHEZ *et al.*, 1982; BORZONE *et al.*, 1996; BRAZEIRO and DEFEO, 1996; McLACHLAN *et al.*, 1996) and ordination methods

(e.g., RAFFAELLI *et al.*, 1991; DEFEO *et al.*, 1992; BORZONE *et al.*, 1997).

RAFFAELLI *et al.* (1991) recognized that "few investigations have employed appropriate numerical methods to analyze species distribution patterns" in sandy beaches. However, their use of cluster, correspondence and detrended correspondence analysis, and nonmetric multidimensional scaling to analyze species distributions fail to test the non-randomness of the patterns detected. In a recent paper, McLACHLAN and JARAMILLO (1995) reviewed almost all studies on zonation on sandy beaches around the world; although a variety of methods have been employed to describe zonation, [none] of them [considers] the evaluation of the nonrandomness.

Determining whether the observed pattern differs from what is expected by chance is very important from the ecological point of view, since it would imply the existence of an underlying deterministic process. Ergo, the non-randomness is an essential trait of a pattern, which must be appropriately tested. The traditional methods of analyzing zonation assessed non-randomness in a subjective way ("by eye") (see McLACHLAN and JARAMILLO, 1995). This is evident in the case of the kite diagram, but subjectivity also occurs in the use of multivariate methods. For instance, in a cluster analysis, the selection of the cut off-level (*i.e.*, the level used to cut the phenogram) is generally subjective.

Two techniques are available that allow the detection of non-random zonation patterns with a substantial reduction

of subjectivity, randomized cluster analysis and gradient analysis. The first method is a modification of the general randomization technique (MANLY, 1991) applied to cluster analysis, and the second one was described by DALE (1988). These techniques provide the probability of detecting spurious patterns (*i.e.*, in the context of this paper, patterns that are not different from what is expected by chance), and thus enable the statistical significance of the patterns to be tested.

In this paper, I describe the methods mentioned above and illustrate their application in sandy beach communities, also discussing their advantages and limitations.

METHODS

To exemplify the use of the randomized cluster and gradient analyses, data from the macrofaunal community of Barra del Chuy beach (33°45'S, 53°20'W), on the Atlantic coast of Uruguay, were employed.

Sampling Designs

The macrofauna of Barra del Chuy was sampled along three transects perpendicular to the shore line and spaced 8 m apart. The transects extended between a fixed point located at the base of the dunes, and 12 m below the low tide level. Sampling stations were located along each transect at 4 m intervals. A metal cylinder of 1/16 m² area and 40 cm depth was employed to obtain the samples. Sand was sieved through a 0.5 mm mesh and the retained fauna was then identified and quantified in the laboratory. The mean density per tidal level (average of three replicates) was calculated for each species. This sampling was carried out monthly from February 1988 to January 1989. A full analysis of this information is contained in BRAZEIRO and DEFEO (1996), and in this paper I only used annual averages (Table 1).

Randomized Cluster Analysis

The Spearman rank-order correlation coefficient was calculated between all pairs of sampling stations. In this way, a diagonal matrix of correlations was generated (Table 2). The use of the Spearman coefficient is not a requisite; any other statistic (*e.g.*, product-moment correlation, similarity or dissimilarity coefficients) can be used. On the basis of this matrix, a cluster analysis was carried out using the Unweighted Pair-Group Method (UPGMA). The UPGMA clustering algorithm is also not a requisite.

The randomized cluster procedure is based on the general randomization method described by MANLY (1991), which consists of the generation of a null model by the random reallocation of the original data to test the hypothesis under investigation. This general method can be modified in order to be applied to the detection of objective cut-off levels of phenograms. The modified procedure is as follows: (1) randomize (100 times) the original data (Table 1); (2) calculate the Spearman rank correlation between all pairs of sampling stations, for each of the 100 matrices generated; (3) build the cumulative frequency distribution of the Spearman correlation values that were generated (pseudovalues) (Figure 1); (4) obtain the Spearman rank correlation value that corresponds

to the probability levels of 5% and 1% as a two-tailed test; and (5) use the values obtained as cut-off levels in the phenogram (Figure 2).

The above description required several previous steps. First, a randomization method must be selected. This is an important point, since the way in which data are randomized determines the pertinence of the null hypothesis generated. LAWLOR (1980) defined four basic algorithms (*RAs* in his paper), which vary in the degree of restriction imposed to the rearrangement of data. The *RA1* algorithm retains the minimum of the original structure of the data matrix, all values are randomly moved. The *RA4* retains the maximum of the original structure, zero values are retained in their original position and only non-zero values are re-assigned. In the case of species distributions, the adequate null model must allow that species have the opportunity to occur everywhere, hence the *RA1* algorithm is preferred.

Second, an adequate number of iterations (data matrix randomization) must be carried out. MANLY (1991) stated that at least 1000 iterations are required to test the hypothesis at the significance level of 5%, and at least 5000 at the 1% level. In this example, 100 iterations were carried out that generated 15,300 pseudovalues. Each iteration generated a matrix of 153 pseudovalues of Spearman rank correlation (as in Table 2). Third, the choice of the significance level, as in any other statistical test, is the responsibility of the investigator. In this example, the significance levels of 5% and 1% were selected (Figure 1). The critical levels were selected considering a two-tail test, because improbable large negative correlation between stations, as well as improbable large positive correlations, suggest non-random spatial patterns.

Gradient Analysis

Several methods have been developed to detect non-random patterns in environmental gradients (PIELOU, 1975; UNDERWOOD, 1978; DALE, 1986; DALE, 1988). In this study I consider the technique of gradient analysis described by DALE (1988), because it has some improvements in relation to prior methods.

I describe the procedure in brief (for details see DALE, 1988). The method is as follows: (1) locate in the gradient (standardized to length 1) the distribution boundaries of all species (Figure 3); (2) calculate the statistic h_m :

$$h_m = \sum_{i=1}^m u_i \cdot u_{i+1},$$

where m is the total number of boundaries excluding the extremes, and u_i the length of the segment i between two adjacent boundaries (see Figure 3); (3) compare h_m with the considered critical level (Table 2 of DALE, 1988), if it is greater, the hypothesis that there are clumps of boundaries in the gradient is supported; (4) in order to detect the location of the clumps, for each pair of boundaries calculate the binomial probability, $p(i,j)$, that the interval between them contains at least as many boundaries as it does. The probability $p(i,j)$ is calculated as follow:

$$p(i,j) = 1 - \sum_{k=0}^{i-1} \sum_{k=0}^{j-1} C_{i-k}^{i-1} (x_i - x_i)^k \cdot (1 - x_i + x_i)^{m-k},$$

Table 1. Annual average values of species density (ind. m⁻²) per sampling station of the macrofauna community of Barra del Chuy, Uruguay. Data used to exemplify the randomized cluster and gradient analysis.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
Sampling Stations	4	8	12	16	20	24	28	32	36	40	44	48	52	56	60	64	68	72	
Distance from Dunes (m)																			
<i>Baccinops daartei</i>								0.6	8.9	7.7	20.7	1.8	8.9	12.4	12.4	1.8	1.8	26.7	
<i>Bathyporeiapus ruffoi</i>							2.2	0.4				17.2	13.6	7.7	3.0	13.0	14.7		
Carabidae	8.4	11.6	10.2	12.0	14.2	15.1	2.2												
Cicindelidae	1.3		1.3	2.7	1.3														
Coleoptera 1	4.0	4.0	1.3	2.7	12.0														
Curculionidae	2.7	10.7			8.0														
<i>Donax hanleyanus</i>							9.8	11.7	9.5	17.5	61.9	40.2	73.6	50.0	33.5	44.4	49.8	10.6	
<i>Exirolana armata</i>	2.2	10.7	31.6	122.2	213.3	224.4	227.6	414.2	470.7	420.4	317.8	216.0	168.4	96.0	27.6	52.4			
<i>Euzonus furciferus</i>						1.8	3.6	5.3	13.3										
<i>Emerita brasiliensis</i>									4.0	4.0	7.8	21.5	95.2	32.9	121.0	38.9	56.5	15.1	
<i>Exirolana brasiliensis</i>	2.0	0.7	2.0	0.7			0.7	1.3	0.7	0.7	0.7	2.0							
<i>Hemipodius olivieri</i>										0.9	3.6	2.7	3.6	1.8		2.7			
<i>Macrochiridotea giambiagiae</i>											9.5	10.1	6.5	14.8	7.1	21.3	12.7	9.8	
<i>Macrochiridotea lillanae</i>									3.6	0.9	9.8	8.9	3.6	6.2		2.7			
<i>Mesodesma mactroides</i>							47.6	96.9	81.9	71.6	47.2	60.6	220.2	255.6	86.4	127.8	50.3	30.4	
<i>Metaripita</i> sp							3.6	1.8	0.9	2.7	10.7	6.2	37.3	10.7	3.6	13.3			
<i>Orchestoidea brasiliensis</i>	1.2	1.2	4.1	3.6	1.2	2.4													
<i>Olivella formicacorsii</i>											2.0	2.7	2.7	10.7	11.3	4.7	12.4	10.7	
<i>Olivancillaria teaguei</i>												2.7		2.7	2.7				
<i>Olivancillaria vesica-auriculata</i>														1.3	5.3			2.7	
<i>Phoxocephalopsis zimmeri</i>								65.0	107.6	153.2	199.8	156.6	138.2	103.3	116.4	140.6	37.3	11.4	
<i>Spio gaucha</i>	2.4	5.3	11.9	8.9	2.4									1.8	1.8				
Staphilinidae	6	2	0	0	4	2	3	3	3	1	2	3	0	2	2	4	2	8	
No. of distributional boundaries																			

Table 2. Spearman rank correlation matrix among stations sampled in Barra del Chuy beach.

Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	1																	
2	0.61	1																
3	0.78	0.87	1															
4	0.84	0.73	0.83	1														
5	0.6	0.78	0.86	0.76	1													
6	0.33	0.31	0.3	0.44	0.3	1												
7	0.24	0.14	0.18	0.38	0.2	0.44	1											
8	0.18	0.07	0.12	0.31	0.12	0.5	0.95	1										
9	0.09	-0.06	-0.06	0.11	-0.09	0.29	0.72	0.8	1									
10	0.16	0.08	0.01	0.2	0.04	0.24	0.63	0.69	0.72	1								
11	0.0	-0.12	0.17	0	-0.13	0.11	0.57	0.64	0.8	0.91	1							
12	-0.2	-0.02	-0.15	0.08	-0.02	0.06	0.43	0.49	0.62	0.76	0.85	1						
13	0.2	-0.22	0.27	0.07	-0.18	0.1	0.5	0.54	0.67	0.84	0.89	0.82	1					
14	-0.2	-0.28	-0.38	-0.16	-0.31	-0.02	0.46	0.48	0.6	0.74	0.82	0.78	0.92	1				
15	-0.3	-0.28	-0.34	-0.15	-0.29	-0.08	0.39	0.41	0.48	0.56	0.64	0.64	0.79	0.9	1			
16	-0.1	-0.22	-0.23	-0.01	-0.1	0.03	0.47	0.51	0.67	0.81	0.89	0.79	0.93	0.86	0.75	1		
17	-0.3	-0.22	-0.32	-0.13	-0.2	0.05	0.28	0.36	0.51	0.61	0.66	0.66	0.78	0.83	0.85	0.78	1	
18	-0.3	-0.2	-0.27	-0.08	-0.19	-0.08	0.29	0.24	0.36	0.4	0.47	0.52	0.7	0.79	0.88	0.67	0.8	1

where x_i and x_j are the position of the boundaries i and j respectively, with $j > i$, and k is the number of boundaries observed in the interval $x_i - x_j$. In the case of overlapped or included intervals with improbably large number of boundaries in them, DALE (1988) recommended to chose the one with the lowest probability as the one most likely to indicate a critical level on the gradient.

RESULTS

Randomized Cluster Analysis

This technique allows the use of cut-off levels of phenograms which have an associated significance level. This

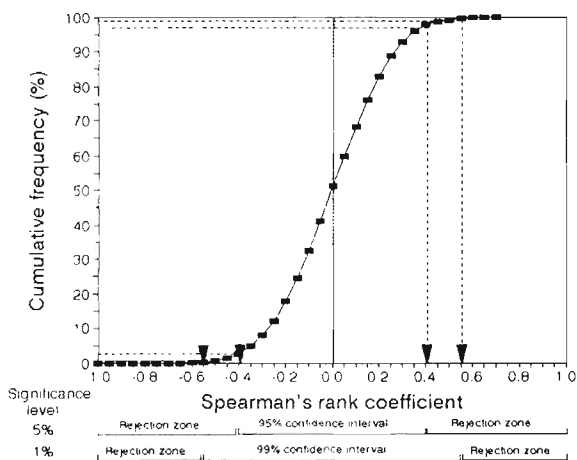


Figure 1. Randomized cluster analysis: Determination of cut-off levels for the phenograms of the spatial distribution of Barra del Chuy macrofauna. Cumulative distribution of 15,300 pseudovalues of Spearman rank correlation generated by 100 randomizations (see text for details). Two cut-off levels are selected, ± 0.40 and ± 0.55 , that correspond to probability levels of 5% and 1% respectively. The acceptance and rejection zones of the null hypothesis of randomness are indicated for each of the two significance levels considered.

means that the correlation values that are higher or smaller than these levels have very low probability (0.05 or 0.01 in the example) to occur by chance, and therefore they could be considered as non-random. In the example, I estimated the critical correlation values associated to the significance levels of 5% and 1%, ± 0.40 and ± 0.55 respectively (Figure 1). Using the right critical value of $+0.40$ as a cut-off level, two groups of significantly correlated stations emerged, an “upper zone” group that included sampling stations 1 to 5, and a “mid-lower zone” group that included the rest of the beach levels sampled (7 to 18), whereas station 6 remained apart (Figure 2). But if we consider a cut-off level of $+0.55$, the “mid-lower zone” group may be divided in to a “middle zone” group that includes levels 7 to 9, and a “lower zone” group that includes levels 10 to 18. There were not correlations lower than the critical values of the left tail (i.e., -0.40 and -0.55), which means that there was no group of significantly negatively correlated stations.

Gradient Analysis

The result of gradient analysis is presented in Table 3. The estimated value of h_m was significantly ($p < 0.001$) lower than the expected value, which suggests that the distribution of boundaries follows a regular rather than a clumped pattern. However, a zone of clumping of boundaries was detected between the 0.24 and 0.48 of the gradient, which corresponded to stations 5 to 9 (Figure 3). The clump was associated with a turnover of species.

DISCUSSION

Strengths and Capabilities of the Methods

The two methods described are based on different principles, however both provide the capability of detecting non-random distribution patterns. These approaches for recognizing zonation patterns represent a clear improvement in relation to traditional methods because they provide an estimation of the risk of identifying spurious patterns.

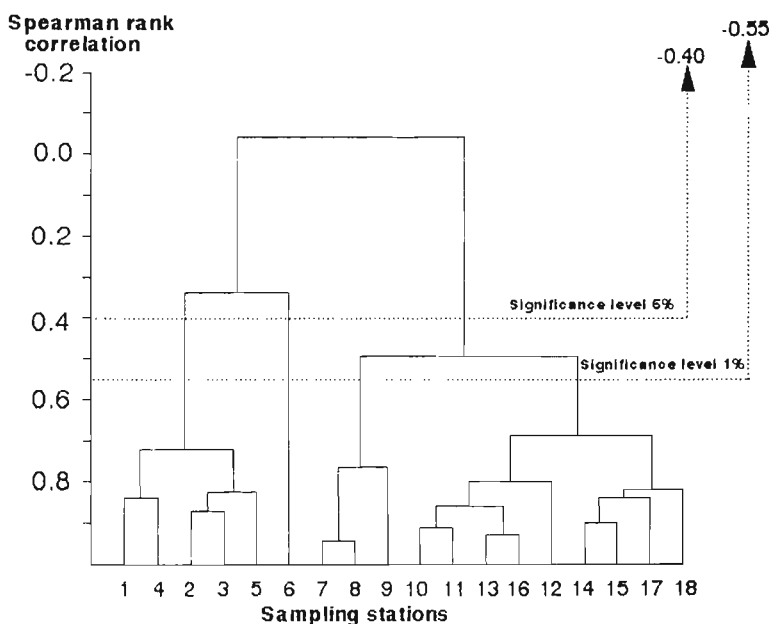


Figure 2. Randomized cluster analysis: Phenogram of Spearman rank correlation among sampling stations of Barra del Chuy. The cut-off levels of 5% (± 0.40) and 1% (± 0.55) of significance are indicated.

While the subjectivity in the identification of faunal-floral zones is reduced by the use of these tests, it is not completely eliminated. As in any statistical test, the significance level or probability of rejecting the null hypothesis of randomness when it is correct, must be selected by the investigator. Significance levels other than the traditional 5% and 1% could be utilized.

The methods described here deal with zonation patterns from different perspectives. While gradient analysis focuses on the detection of zones where many species start or finish their distribution, randomized cluster analysis is centered in the identification of groupings with homogeneous species

composition. Thus, both methods could be employed as complementary descriptors of the community distribution.

The results obtained by random cluster (Figure 2) and gradient analysis (Figure 3), revealed interesting patterns in the spatial distribution of the macrofaunal community at Barra del Chuy. The "middle-zone" group (stations 7 to 9) detected by randomized cluster analysis coincides with a zone where a clump of boundaries occurs (stations 5 to 9). This suggests that the "middle-zone" group is in fact a boundary zone, where typical species of the adjacent areas end their ranges of distribution. Thus, the community of Barra del Chuy could be divided in only two assemblages, not in three as was suggested by cluster analysis when a cut off level of 1% was employed. In this sense, this result agrees with WENDT and MCLACHLAN (1985), who recognized two well-defined assemblages, the air-breathers (upper zone) and the water-breathers (lower-zone).

Furthermore, the gradient analysis technique allows the use of three zonation traits to describe and compare the com-

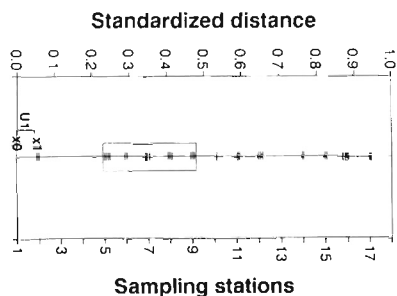


Figure 3. Gradient analysis: Location of boundaries of spatial distribution of the Barra del Chuy macrofauna. X0 and X1 indicate the position of the first and second boundaries of distribution, and U1 the distance between them. The portion of the gradient where a significantly higher number of boundaries were detected is enclosed in a rectangle (See also Table 3).

Table 3. Results of gradient analysis of Barra del Chuy data.

m	h_m	p_1	Position of Clump	p_2	Amplitude of Clump
33	0.0114	<0.001 (-)	0.24-0.48	0.023	0.24

"m" is the number of boundaries excluding extremes; " h_m " is a statistic (see text); " p_1 " indicates the probability of h_m , "-" indicates that h_m is smaller than the expected value; "Position of clumps" refers to the part in the gradient in which there were more boundaries than expected by chance and " p_2 " is the associated probability; and "Amplitude of clump" refers to the length of the interval in which the clump was detected.

munity distribution patterns; the number of clumps, their position in the intertidal and their amplitude or extent (see Table 3). Traditionally, comparison of zonation patterns among different sandy shores have been qualitative (*i.e.*, comparison of species composition per zone between sites). However, the gradient analysis method brings the opportunity to compare zonation patterns in a quantitative way. Since these traits are expressed as standardized measures, comparison could be done between intertidal systems of different geographical regions with dissimilar intertidal extent, and also with different species composition.

Moreover, gradient analysis allows us to study species distributions along dimensions other than space. In the case of sandy beaches, sediment water content seems to be a key factor in explaining zonation patterns (see also SALVAT, 1964). The technique of gradient analysis is a suitable statistical tool to analyze this hypothesis. For instance, SALVAT'S (1964) zonation scheme, based on sediment water content, could be appropriately tested by analyzing the species distribution along the moisture gradient.

Weaknesses of the Methods

The randomized cluster analysis method has some problems, as discussed by JAKSIC and MEDEL (1990). The problems arise when the cut-off level, selected from the frequency distribution of pairwise correlation values, is directly used to cut the whole phenogram. On the one hand, the significance level obtained applies correctly to paired comparisons, but in cluster analysis multiple comparisons are made. Thus, the probability level would have to be adjusted for multiple comparisons. Also the critical value obtained should be applied directly to a phenogram only if the clustering algorithm does not distort the correlation scale. However, almost all clustering algorithms (including UPGMA) produce distortion, which means that the critical value for a single-pair comparison might not exactly correspond to the critical value for the whole phenogram. JAKSIC and MEDEL (1990), based on personal comments of R. Strauss, proposed a method to solve these problems, which include the following steps: (1) randomize the original data matrix, (2) calculate the pairwise correlation matrix, (3) produce a phenogram, (4) record node values (*i.e.*, linkage levels), (5) accumulate node values in a frequency distribution, and (6) select cut off-levels. Selecting the cut-off levels from the frequency distribution of nodes (as pseudovalues), rather than of pairwise correlation values, allow to solve the problems of multiple comparisons and distortion, but imply an excessive amount of time and computational work.

In relation to gradient analysis, DALE (1988) noted that there is a problem in the detection of clumps of boundaries (step 4 of the procedure). Since the probability of all possible intervals must be estimated, there are cases of included or overlapped intervals. In these cases, the probabilities $p(i,j)$ are not independent of each other because the intervals share some distributional boundaries. Since the estimation of the $p(i,j)$ values are not independent, the method does not provide an accurate statistical test of whether the boundaries are significantly clumped in a certain portion of the gradient. To

solve this problem, DALE (1988) recommended to use a given hypothesis derived from other information, which defines an interval in which clumping is suspected. For example, physical data reveal that around the effluent and drift lines there are important environmental (*e.g.*, sediment moisture) variations, therefore, it could be hypothesized that at these zones there are clumps of distributional boundaries associated with species turnovers.

Comparing Results

The example data of the intertidal community of Barra del Chuy were previously analyzed by BRAZEIRO and DEFEO (1996). In the prior study the community distribution was analyzed using a common cluster analysis and the Bray-Curtis dissimilarity index. Using an arbitrary cut-off level, we detected a pattern with three zones (Figure 2, BRAZEIRO and DEFEO, 1996), which resembles the pattern obtained here using the cut-off level of 1% significance (Figure 2). Thus, the present results support those reported by BRAZEIRO and DEFEO (1996), suggesting that the arbitrary cut-off level used in the prior study was conservative enough to assure the non-randomness of the pattern detected. In this case, the non-randomness of the zonation pattern detected was confirmed, but the generality of this result requires confirmation.

CONCLUSIONS

The zonation patterns of many sandy intertidal communities have been described, however the non-randomness of the patterns detected has never been properly tested (see the review of McLACHLAN and JARAMILLO, 1995). Patterns that statistically seem to be random (*e.g.*, chaotic population dynamics) can also be generated by deterministic processes (see MAY, 1976), however, the most parsimonious hypotheses to explain them are purely stochastic models. On the other hand, the non-randomness of a pattern strongly suggests the existence of an underlying deterministic process. Therefore, if the final goal of studying the distribution of organisms is to find the biological processes underlying the patterns, we must focus our attention on those in which deterministic factors are suspected, *i.e.*, non-random patterns. Randomized cluster analysis and gradient analysis bring us the capability to test the randomness of our patterns, for this I believe they are very useful tools in the study of spatial distribution of sandy intertidal species.

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