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Zonation patterns in tideless environments (Northwestern Mediterranean): looking for discontinuities in species distributions*

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SUMMARY: Distribution of macrobenthic marine organisms was studied along the air-water interphase in a transect made on a rocky coast near Cap de Creus (Northwestern Mediterranean). The transect consisted of 34 contiguous samples that were quantitatively and qualitatively analyzed using different numerical methods (diversity spectra, similarity indexes, multivariate analysis .) to detect discontinuities in species distribution. Results were compared with a visual description of the zonation in order to test the agreement between ecotones detected with numerical methods and visual changes in zonation. Qualitative results showed that, although some discontinuities were detected, they do not always correspond to those predicted from direct observation. On the other hand, quantitative discontinuities corresponded well with the observed ecotones. We conclude that apparent zonation is mainly a result of the distribution of the biomass of dominant species. No evidence is found supporting the existence of zones of coincidentally distributed species.

RESUMEN: MODELO DE ZONACIÓN EN UN MAR SIN MAREAS (MEDITERRÁNEO NOROCCIDENTAL): ¿HAY DISCONTINUIDADES EN LA DISTRIBUCIÓN DE LAS ESPECIES?. — Se ha estudiado la distribución de las especies a lo largo de un transecto constituido por 34 muestras contiguas en la interfase aire-agua, en un punto costero del Mediterráneo noroccidental. Los datos obtenidos se han analizado cualitativa y cuantitativamente mediante el uso de metodologías diversas (espectros de diversidad, índices de similitud, análisis multivariante .). Los resultados se comparan con una descripción naturalista de la zonación, con la intención de comprobar si la transición entre comunidades corresponde a discontinuidades en la distribución de las especies. Los resultados cualitativos muestran que, pese a que se detectan algunas discontinuidades, no siempre corresponden con las descritas en una observación directa. Por otro lado, las discontinuidades cuantitativas se corresponden con los ecotonos observados. Se concluye que la zonación es principalmente el resultado de la distribución de la biomasa de las especies dominantes. No existe ninguna evidencia sobre la presencia de especies con una distribución coincidente.

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INTRODUCTION

The description of the Biosphere needs a classification system in which the different assemblages can be enclosed. This classification involves the description of discrete units (termed communities or associations) which possess determined and relatively constant species pools and more or less discontinuous spatial distributions. The real existence of such communities has been strongly discussed by different authors who accepted the Curtis-continuum theory (CURTIS, 1959; CURTIS and MC INTOSH, 1961). Nevertheless, nowadays there is a sensible trend to accept more unifying concepts. Communities are considered as relatively homogenous areas (or volumes) (continuities) situated between other more heterogenous areas (or volumes) (discontinuities) (EGLER, 1968). The term community agrees well with the concept of *noda* (POORE, 1962). In fact, although deeply rooted in the human mind, the opposition between ordination and classification is not as strong as it appears (MARGALEF, 1984).

These topics have also been studied in intertidal systems (see a review in BALLESTEROS *et al.*, 1984). In particular, a regular distribution of species and communities is quite obvious in rocky shores. The strong physical gradients across the air-water interface account for the distribution of communities into horizontal, apparently homogenous fringes with sharp boundaries (zonation). These striped landscapes are very well developed in intertidal systems, and have been extensively studied on many shores of the world (DOTY, 1946; STEPHENSON and STEPHENSON, 1949; EVANS, 1957; LEWIS, 1964). The idea that critical tidal levels determine zonation patterns has gained considerable acceptance (e.g. LEWIS, *op. cit.*, NEWELL, 1970). Since it was first proposed by COLMAN (1933), this hypothesis postulates that the lower and upper limits of species distributions coincide with notable points of the emersion curve (see UNDERWOOD, 1978). Consequently, the zonation pattern would be physically determined. Recent works have refuted the existence of critical tidal levels and even the existence of zones of coincidentally distributed species (UNDERWOOD, *op. cit.*).

There is a spatially-reduced but well defined zonation in the Northwestern Mediterranean, described in detail in the early work of FELDMANN (1937). Most early works dealing with Mediterranean benthic biocoenology accept the existence of critical levels without any criticism or experimental evidence (see PÉRÈS and PICARD, 1964). Furthermore, although there are many papers describing zonation patterns in different Mediterranean areas (PÉRÈS and PICARD, *op. cit.*; BOUDOURESQUE, 1971; ROS *et al.*, 1985), little effort has been devoted to an accurate investigation of the zonation patterns and small-scale distribution of species (e.g. BOUDOURESQUE, 1970).

The aim of this work is to present a detailed examination of species distribution pattern along the air-water interface based upon a systematic

sampling that disregards traditional phytosociological distinctions between homogenous and non homogenous zones. Our purpose is to answer the following basic question: are there any qualitative or quantitative discontinuities in species distributions?

MATERIAL AND METHODS

Sampling

The study site was Cap de Creus (NE Iberian Peninsula, Spain, UTM 31T EG28, fig. 1). A single transect was made during spring on an homogenous rocky wall, NNE oriented, with a constant slope of 30 degrees, perpendicular to shore. The place was carefully selected to minimize sources of variation that could modify zonation on a small scale (rock discontinuities and crevices, different orientations or inclinations along the transect). A series of contiguous quadrats of 10 cm (height) \times 20 cm (width) was sampled from 1 m above mean water level to 0.6 m below mean water level. Sampling was performed by scraping off all organisms within each quadrat (BOUDOURESQUE, 1971). The area of the samples is sufficient to quantitatively represent the communities of the upper part of the transect but is small for the Cystoseira community (see BALLESTEROS, 1988). Nevertheless this sampling size was chosen taking into account the relation gain of information additional work based on the studies of one of us (BALLESTEROS, 1984) about the structure and minimal areas of littoral Western Mediterranean communities. Replication was not possible because of the large amount of work involved in sampling, separation, identification and quantification of species.

Samples were fixed (4 % neutralized formaline) and taken to the laboratory where the animals and plants were identified to species and then quantified in terms of cover (surface of thallus or body) and biomass (dry weight). See BALLESTEROS (1986) for details.

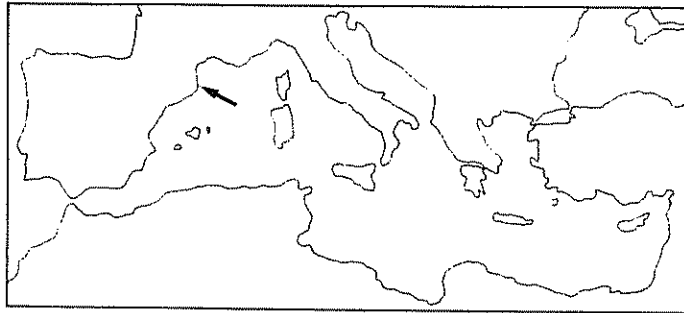


FIG. 1 — Situation of the sampling site (Cap de Creus, NE of the Iberian Peninsula).

Numerical methods

The data collected were subject to a series of analyses. First a qualitative approach was made using three kinds of methods:

a) Study of the upper and lower boundaries of the species distributions. The upper boundary is considered to correspond to the first sample where the species involved appears, while the lower is the last sample in which the species appears. The existence of discontinuities (i.e. critical levels) implies an aggregated distribution of such boundaries (PIELOU, 1975). Nevertheless, our samples showed an obvious increase in species richness from the upper to the lower part of the transect, which also produces an increase in the number of upper boundaries along the transect. So, we have represented the relative number of boundaries per quadrat, that is, the number of boundaries (upper or lower) present in the quadrat divided by the total number of species within the quadrat.

b) The Jaccard qualitative similarity index (LEGENDRE and LEGENDRE, 1979) was computed between each pair of contiguous quadrats:

$$s_{i,j} = \frac{c}{a + b - c}$$

where $s_{i,j}$ = qualitative similarity between samples i and j

a = number of species in sample i

b = number of species in sample j

c = number of common species in samples i and j

c) The same similarity index was computed for all the possible pairs of samples; a principal coordinate analysis (GOWER, 1966) was performed with the similarity matrix.

The quantitative approach was made following three methods:

a) The Kulczynsky similarity index (GOUNOI, 1969) was computed between each pair of contiguous quadrats:

$$S_{i,j} = \frac{2 \left[\sum_{p=T}^{p=I} \inf (B_{pi}, B_{pj}) \right]}{\sum_{p=1}^{p=T} B_{pi} + \sum_{p=1}^{p=T} B_{pj}}$$

where $s_{i,j}$ = quantitative similarity between samples i and j

B_{pi} = biomass (or coverage) of species p in sample i

B_{pj} = biomass (or coverage) of species p in sample j

T = total number of species

b) Diversity spectra. The diversity of each sample was computed using Shannon's formula (MARGALEF, 1957):

$$H' = - \sum_{i=1}^{i=T} p_i \log_2 p_i$$

where p_i is the ratio between the biomass (or coverage) of the species i and the total biomass (or coverage) of all the species of the sample. Smoothed diversity spectra were calculated by computing the diversity of five consecutive samples as a whole, to minimize small variations in order to observe where the greater changes occur. The effects on diversity spectra of transition between communities have been discussed by MARGALEF (1974) and NIELL (1974). According to these authors, diversity values should reach relative maxima in the transitional samples (ecotones).

c) Multivariate analysis. Some multivariate techniques were applied to our data (LEGENDRE and LEGENDRE, 1979; CUADRAS, 1981). The highest resolution between groups was obtained using correspondance or R-Q analysis (CORDIER, 1965; BENZECRI, 1973); further discussion about the adequacy of this method to biocoenology can be found in CHARDY *et al.* (1976).

Nomenclature

For species nomenclature see BALLESTEROS (1984).

RESULTS

DESCRIPTION OF THE TRANSECT

Results in the form of a species/samples matrix are given extensively in table I.

Samples 1 to 7 were collected in the supralittoral zone, in a community dominated by *Chthamalus stellatus* (Poli), *C. montagui* Southward (Cirripeda) and the lichen *Verrucaria symbalana* Nylander. This association is similar to that described by FELDMANN (1937) but *Mesospora macrocarpa* (Phaeophyta) and some characteristic Cyanophyta were absent. In sample 8 we found the first macroalgae, with increasing biomass in samples 9 and 10. These three samples corresponded well with the *Porphyra leucosticta* mediolittoral community (FELDMANN, *op. cit.*) although its development was scarce due to the season in which we sampled. Transition to the *Rissoella verruculosa* community took place in sample 11, while sample 15 marked the substitution of *Rissoella* by the *Lithophyllum tortuosum* community, which extended until sample 18, always showing a great abundance of *Mytilus galloprovinciale*. *Lithophyllum tortuosum* became less important from sample 19, and samples 19 to 22 could be attributed to the mediolittoral band of *Corallina elongata*. The mean water level was located in sample 23, where the communi-

15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
01								01											
1								1											
01	01		01	01	01	01	01	01											
1	1		1	1	1	1	1	1											
01			01	01				01											
1			1	1				1											
01																			
1																			
01	01	01				01	01	01	01		01			01				0.2	0.1
1	1	1				1	1	1	1		1			1				2	1
01																			
1																			
0.4	01	4.7	7.5	25.3	0.7	29.5	42.0	33.1	0.1		0.1	0.1	2.1		3.4	1.3	1.2	0.7	
4	1	47	140	293	7	315	380	321	1		1	1	21		36	13	12	7	
11	01		0.8																
6	1		4																
	1.4		0.1		0.1													0.1	
	1.4		1		1													1	
	0.1	0.7	1.7	11.0	3.7	0.6	1.6	7.0		2.1	3.2	5.7	4.0		0.4	15.1			
	1	7	17	120	70	6	16	143		21	32	93	72		4	209			
	17					0.5	1.4	70.3	13.8	1.8	5.3	40.2	96.1	18.7	178.5	64.6	11.6	9.8	
	17					5	14	639	152	18	93	346	909	209	2270	876	109	102	
	30.1	3.0	8.0	15.1	9.3	3.8	63.0	80.0	40.0	20.0	20.0	12.0	9.0	5.0	14.0	40.0	65.0	85.0	
	9219	1361	2232	3584	2991	997	20262	26547	12865	6433	6433	3860	2895	1608	4503	12865	20906	27338	
			0.1						0.1				2.3	0.1				0.1	
			1						1				7	1				1	
			0.1																
			1																
			0.1		0.1	0.1	0.1	0.1	4.0				0.1	0.1	1.1		18.0		
			1		1	1	1	1	40				1	1	11		180		
				4.5	9.2		17.3												
				45	95		137												
				0.1	0.1	0.1	0.1	1.7	0.1	0.1	0.1	8.0	0.6		0.1				
				1	1	1	1	17	1	1	1	80	6		1				
				3.0	0.1														
				30	1														
				0.1	46.3	37.5	86.7	150.1	94.6			2.6							
				1	393	400	1174	2002	971			26							
				0.1	0.1		0.1												
				1	1		1												
				0.7				0.3		0.1			1.2	16.1	3.8	0.6	3.6	0.1	
				7				3		1			12	149	48	6	36	1	
						0.1													
						1													
						0.1			0.1										
						11.3			1										
						585				8.3			2.0	0.4		6.5		1.8	
						0.1				433			105	80		279		106	
						1				0.1									
							0.1			1									
							1												
							18.6	23.5	56.7	20.0	54.0	45.1	8.1	7.0					
							372	470	1134	400	1080	902	162	140					

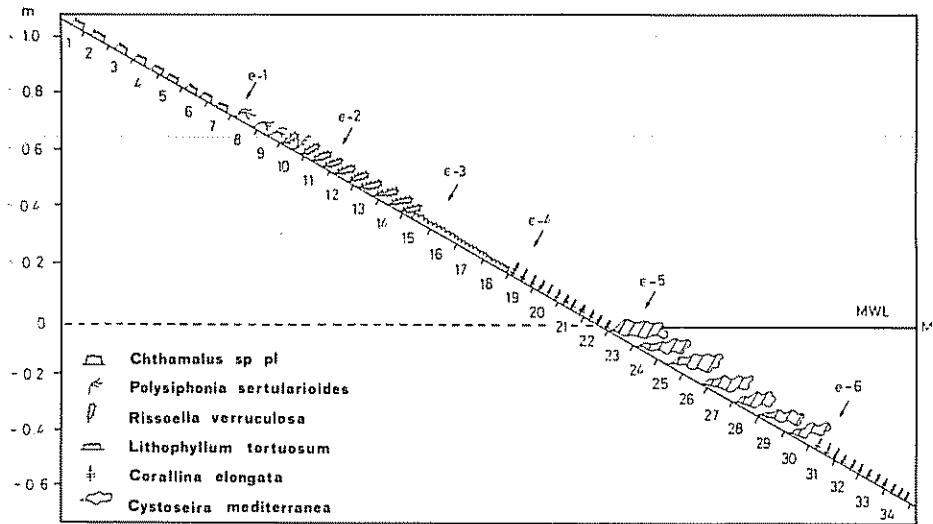


FIG. 2 — Diagrammatic representation of the transect showing the position of each sample, the dominant species and the ecotones (e1...e6).

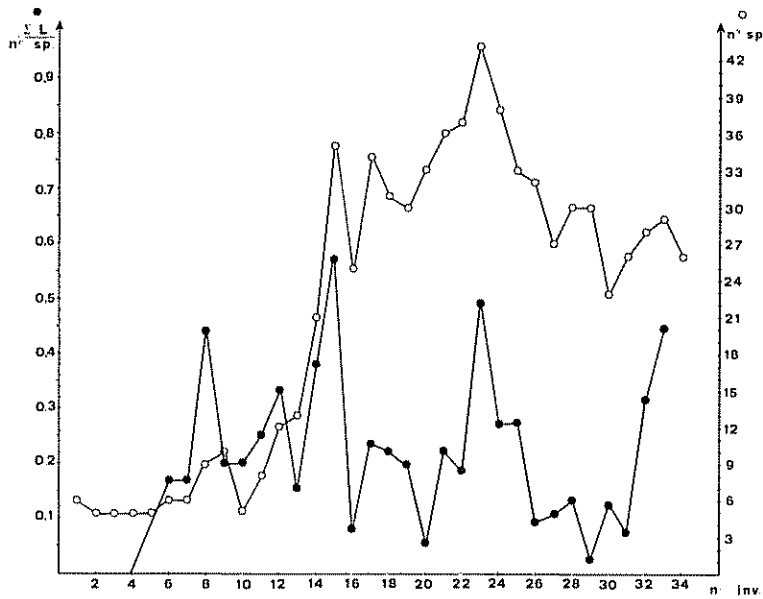


FIG. 3 — Number of species per quadrat along the transect (open symbols) and relative number of boundaries (black symbols).

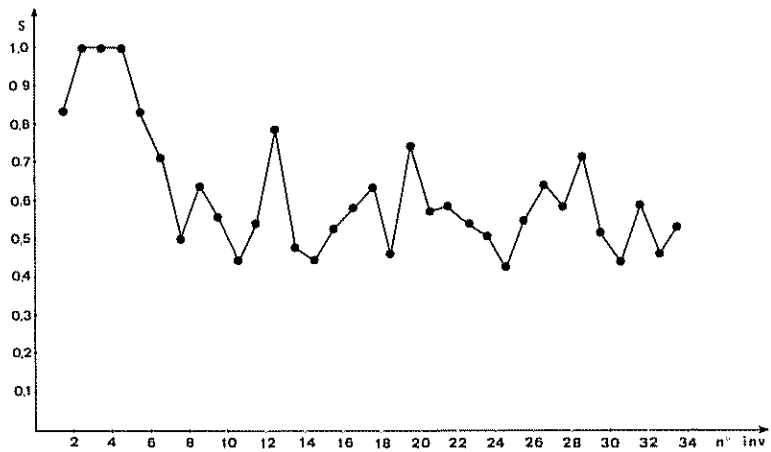


FIG. 4 — Qualitative homogeneity in terms of similarities (Jaccard index) between contiguous samples.

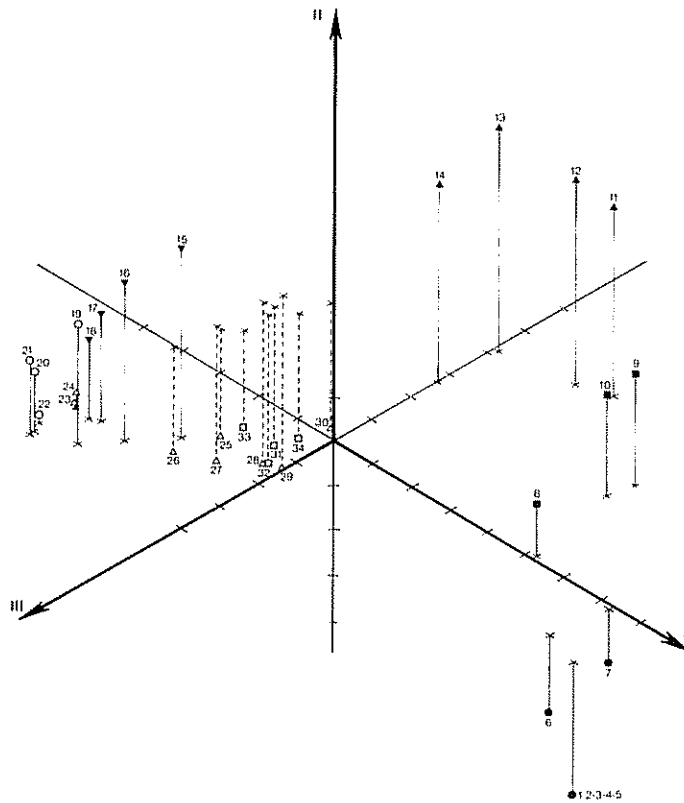


FIG. 5 — Sample representation in the first three axis derived from principal coordinate analysis. ● *Chthamalus stellatus* community; ■ *Polysiphonia sertularioides* community; ▲ *Rissoella verruculosa* community; ▼ *Lithophyllum tortuosum* community; ○ *Corallina elongata* community (mediolittoral); △ *Cystoseira mediterranea* community; □ *Corallina elongata* community (infralittoral).

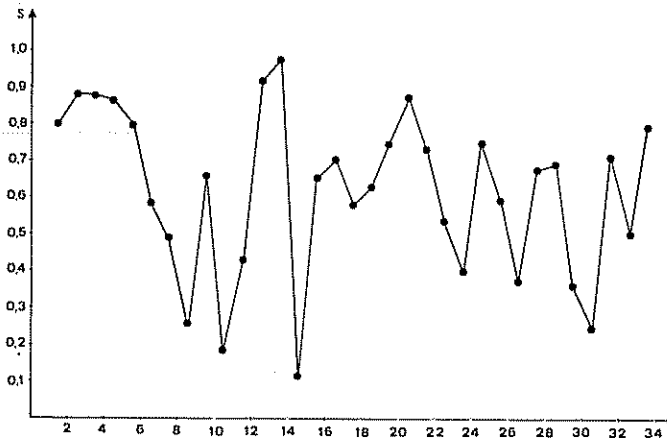


FIG. 6. — Quantitative homogeneity in terms of similarities (Kulczynski index) between contiguous samples. Data computed from coverage values.

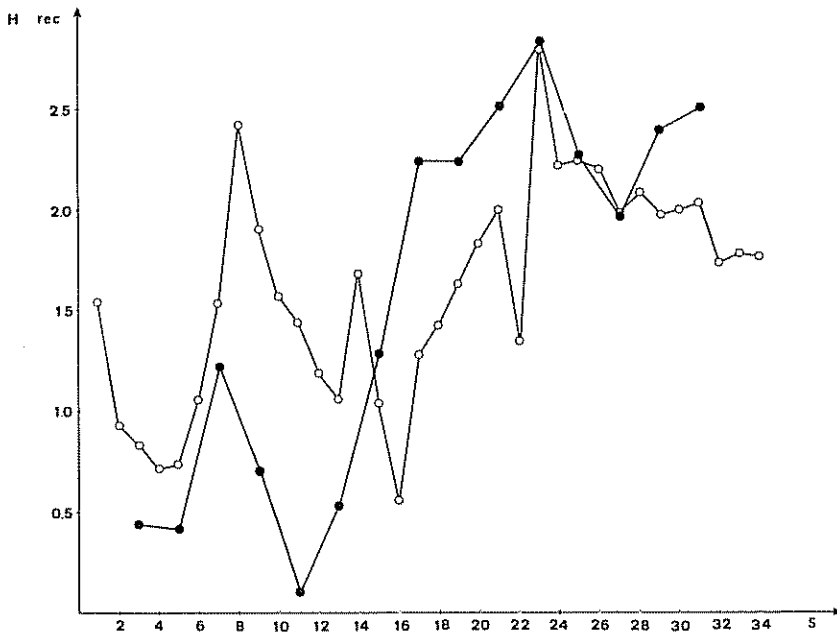


FIG. 7. — Diversity spectra: diversity of each sample (open symbols) and smoothed curve (diversity of five contiguous quadrats; black symbols). Data computed from biomass values.

ty of *Cystoseira mediterranea* appeared. *C. mediterranea* disappeared in sample number 30. Samples 31-34 were dominated by *Corallina elongata* (infra-littoral band) and *Asparagopsis armata*.

This summarized description is based only upon *in situ* observation and an overview of results presented in table I. A diagrammatic representation of the transect is given in figure 2.

QUALITATIVE RESULTS

Qualitative results are given in figures 3 and 4. Some ecotones are well defined by an increase in both species number and relative number of

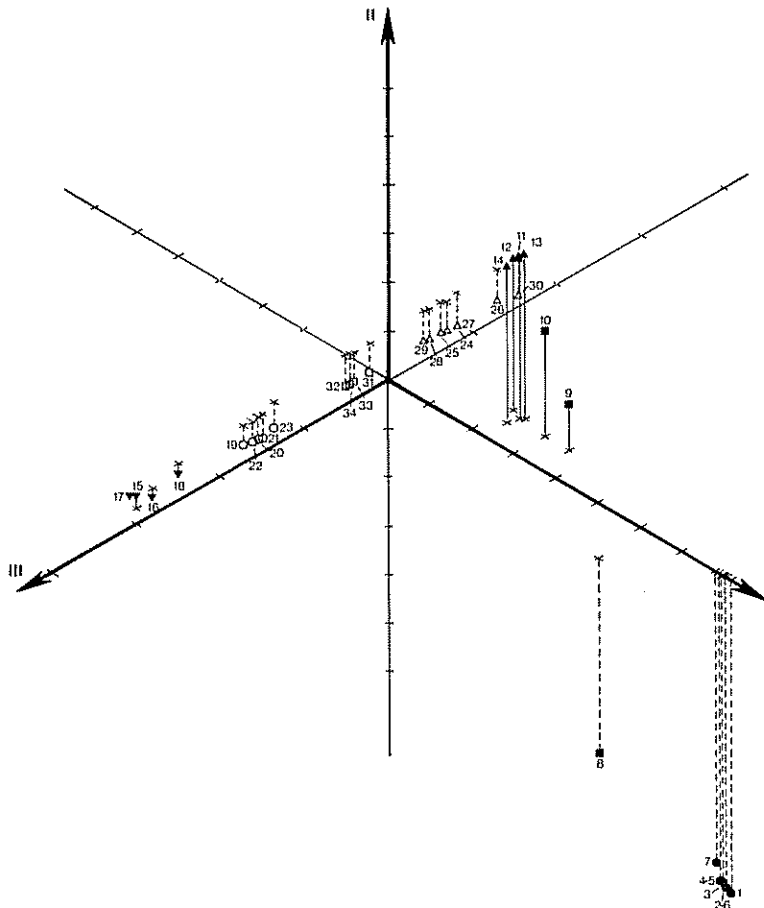


FIG. 8. — Sample representation in the first three axis derived from an R-Q analysis; symbols as in figure 5. Analysis computed from coverage values.

boundaries, as well as by a decrease in the qualitative homogeneity (for example, ecotones 1 and 3). But in other cases such maxima and minima do not appear. Principal coordinate analysis (fig. 5; axis 1, 2 and 3, explaining 44 % of total variance) is quite illustrative. A Guttman effect (HILL, 1973) is obvious; discontinuities corresponding to the first three ecotones are also clear. But the other ecotones are less well reflected, or not reflected at all. Note, for example that no discontinuity associated with the mean water level (sample 23) is detected with this analysis. We attribute this fact to the presence of infralittoral species in the *Lithophyllum tortuosum* community, as well as to the presence of mediolittoral species in the *Cystoseira* community, although these species have no quantitative significance at all. Consequently, we can state that there are some wide more or less homogeneous zones separated by

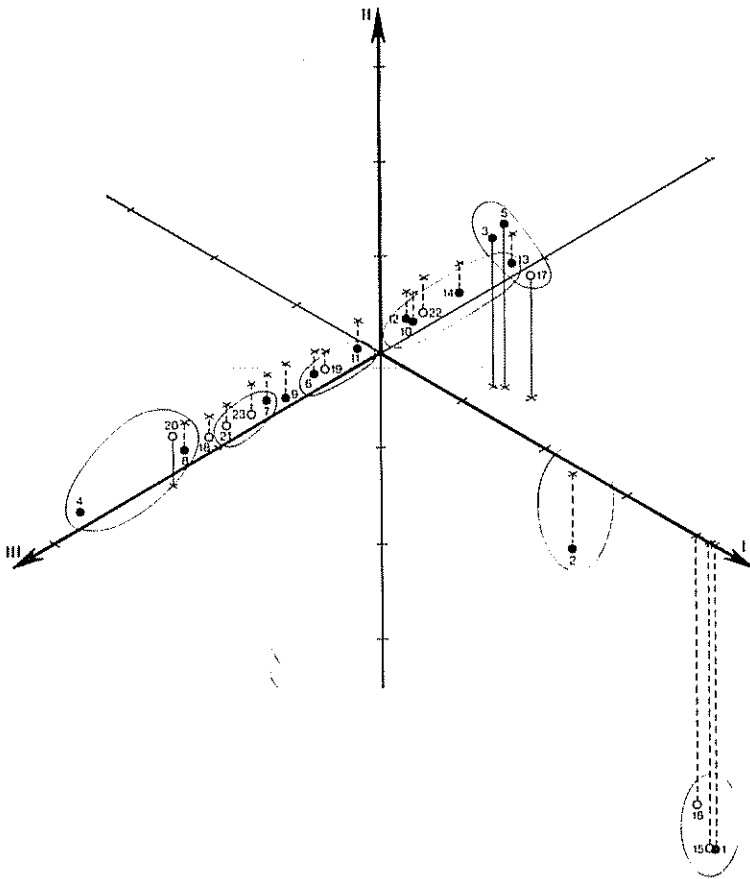


FIG 9 — Species representation in the first three axis derived from an R-Q analysis; open symbols, animals; black symbols, vegetals. Numbers refer to table I. Analysis computed from coverage values.

narrower ones, that could be termed discontinuities. But these discontinuities do not ever correspond with the ones described previously by direct observation and viceversa.

QUANTITATIVE RESULTS

The results of quantitative homogeneity are represented in figure 6. All the ecotones described in figure 2 are evident as relative minima. The minima between samples 26-27 is due to the uneven *Cystoseira* distribution, reflecting the fact that the sample size of 200 cm² is not enough to absorb the variance of the spatial distribution of this species, as we stressed before.

Diversity spectra are represented in figure 7. Again, all the ecotones are clearly shown, except ecotone 2, due to the lack of a well-developed community of *Porphyra leucosticta*. The uneven distribution of *Cystoseira* is again reflected in relative diversity maxima in the samples where this species is scarce. In the smoothed spectrum, most of the diversity maxima disappear, but the two major ecotones (1 and 5) are stressed. Remember that ecotone 1 coincides with the appearance of macroalgae, and ecotone 5 coincides with the mean water level (MWL).

Finally, figure 8 presents the first three axes obtained from an R-Q analysis (65 % of total variance explained). The first axis is clearly related to water availability, discriminating between the communities of the supralittoral and upper midlittoral; the second axis is a quadratic function of the first (Guttman effect), while the third one discriminates between lower mediolittoral and infralittoral communities. This analysis reveals the existence of discontinuities, since the points are not distributed continuously but in clusters with large separations (with occasional intermediate points, which mean transitional samples, like sample 8) between clusters. The species representation (fig. 9) is also illustrative: some species are «characteristic» of a given community, while others show an overlapped distribution.

The major conclusion arising from these data is, undoubtedly, that the species quantification allows us to detect discontinuities between the different communities.

DISCUSSION

The ecotones between the different zones defined by direct observation have a good correspondence with quantitative discontinuities; this fact is not surprising, since the zones are intuitively defined following the abundance of one or a few dominant species. From the abundance curves of the dominant species (fig. 10-11) it is shown that quantitative discontinuities arise from the sudden appearance of the dominant species of each level (for example *Chthamalus stellatus*, *Rissoella verruculosa*, *Cystoseira mediterranea*). Their disap-

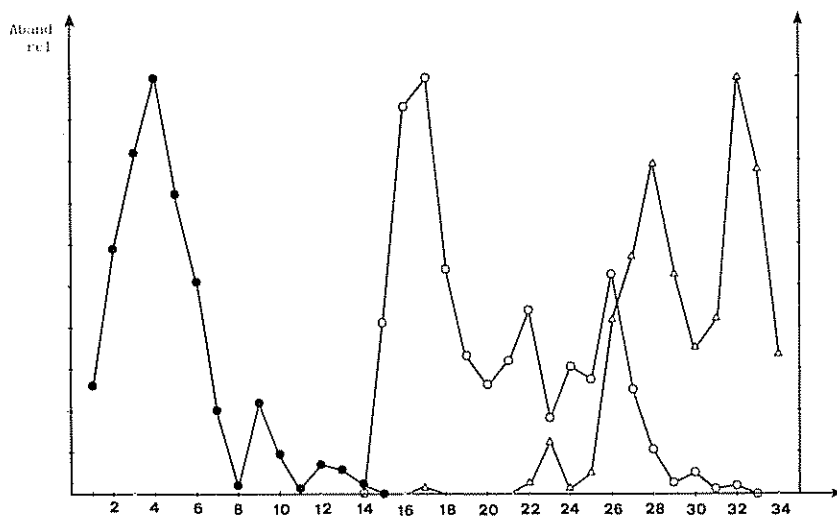


FIG. 10. — Relative abundance (computed from biomass values) of some dominant animal species (black symbols: *Chthamalus stellatus*; open symbols: *Mytilus galloprovinciale*; triangles: *Balanus perforatus*).

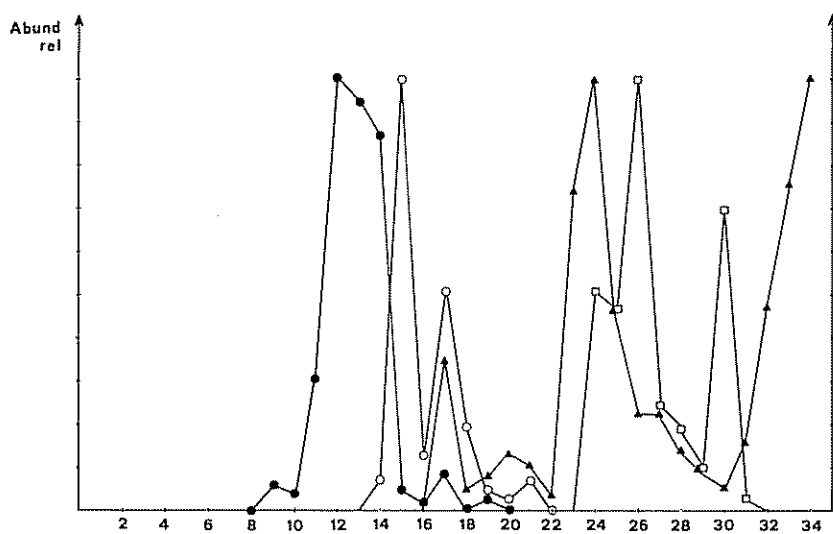


FIG. 11 — Relative abundance (computed from biomass values) of some dominant plant species (black symbols: *Rissoella verruculosa*; open symbols: *Lithophyllum tortuosum*, triangles: *Lithophyllum incrustans*; squares: *Cystoseira mediterranea*)

pearance is much more progressive; the distribution pattern seems to be in accordance with the imbricate ecological groups hypothesis (GODRON, 1967).

Qualitative discontinuities are not easy to explain. In some cases, they are associated to the quantitative ones, since the dominant species may provide a suitable microhabitat for small species or offer substrates for epiphytes: for example, in sample 15 the massive structure of *Lithophyllum tortuosum* allows the presence of many infralittoral species.

In conclusion, we find different communities that are well characterized from a quantitative (and sometimes also qualitative) point of view. Between these communities, distinct boundaries termed quantitative (and sometimes qualitative) discontinuities appear. The existence of critical «water availability» levels has not been investigated, but from the investigation of the pattern no evidence arises to support the concept of zone (sensu COLMAN, 1933 or PÉRÈS and PICARD, 1964). No conclusions can be drawn about factors and/or processes underlying the observed pattern. The asymmetrical shapes of the curves in figures 10 and 11 suggest that different processes could be involved. Further experimental work is needed to elucidate dynamical aspects of zonation in Mediterranean shores.

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