

Small-scale Structure of Infaunal Polychaete Communities in an Estuarine Environment: Methodological Approach

D. Martin^a, E. Ballesteros^a, J. M. Gili^b and C. Palacín^b

^aCentre d'Estudis Avançats de Blanes (C.S.I.C.), Camí de Santa Bàrbara s/n, 17300-Blanes (Girona), Spain and ^bInstitut de Ciències del Mar (C.S.I.C.), Passeig Nacional s/n, 08003-Barcelona, Spain

Received 27 September 1991 and in revised form 1 May 1992

Keywords: community structure; small-scale; sampling-area; shallow-water; Polychaeta; NW Mediterranean

This study compares different methods for the estimation of minimal areas (*viz.* species/area curves, diversity/area curves, similarity/area curves, variance/mean ratio *vs.* area curves) as community structure descriptors. The comparisons are based upon two polychaete taxocoenoses from muddy and sandy habitats, located in a semienclosed shallow-water Mediterranean bay (Alfacs Bay, Ebro Delta, NW Mediterranean).

The mud community appeared to be very homogeneous, with very low diversity. This community displayed high structural simplicity (related to various stress factors), and therefore, qualifies as a physically controlled community). The diversity index was stabilized for areas of 37 cm², quantitative similarity (Kulczynski index) was higher than 0.7 for areas of 90 cm², and density of individuals was stabilized for areas of 120 cm². Therefore, an area of 120 cm² is suggested as being representative of the community structure. However, it was impossible to define a qualitatively adequate sampling area (> 300 cm²).

The sand community displayed high structural complexity, with high species richness and high diversity. This community was characterized by high environmental stability and high variability of microhabitats, as is frequent in biologically accommodated communities. The number of individuals became homogeneous for areas of 600–1000 cm², diversity was stabilized around 300 cm² and a Kulczynski similarity index of 0.7 was already attained at areas of 1000 cm². Thus, a quantitatively representative sampling area of between 700 and 1000 cm² was suggested. Moreover, the more general pattern of species distribution (with an important set of common species) was directly related to the relatively low qualitative minimal area (400 cm²).

Introduction

The description of patterns in the distribution and abundance of organisms is an essential goal in ecology. Observed patterns are the basis on which models are built, and hypotheses formed and tested by experiments. Thus, observed patterns usually provide the context within which the results of experiments are interpreted.

In turn, suitable descriptions are strictly dependent on adequate methodology. Therefore, samples must represent qualitatively and quantitatively the community or communities to be studied. At the same time, sampling effort must also be cost-effective with regard to the information obtained (Ballesteros, 1986).

The balance between representativeness and cost-effectiveness constitutes the axis around which the philosophy of minimal areas rotates, particularly in certain studies on marine benthic ecology. The finding of a minimal area (to justify sampling adequacy) should always be a primary step in the planning of any community study. Unfortunately, these kinds of studies are seldom carried out and, if so, tend to be inaccessible. On the contrary, studies proceeding by standardized sampling methods (even intuitive methods) are habitually and quite uncritically accepted. Adequacy of sampling methods is seldom demonstrated, with custom or tradition guiding the planning, instead of previously evaluating the possibilities of adequate sampling designs (Andrew & Mapstone, 1987). However, one must point out that the different minimal area methods (*viz.* species/area curves, qualitative similarity/area curves, variance-mean ratio *vs.* area curves, diversity/area curves, qualitative similarity/area curves) provide, at the same time, excellent descriptors of community structure.

Estimates of an adequate sampling area are of less importance when one considers the additional information generated by the minimal area methods (Ballesteros, 1986). Although the value of these methods has been demonstrated in phytobenthic studies (Boudouresque, 1971; Boudouresque & Luck, 1972; Niell, 1977; Ballesteros, 1984), they have seldom been used in the study of animal communities (Weinberg, 1978; Hawkins & Hartnoll, 1980; Laborda, 1984; Gili & Ros, 1985; Kronberg, 1987; Gili & Ballesteros, 1991). Moreover their application to soft-bottom communities has been virtually nil.

The present study focusses on a comparison between the different minimal area methods when applied to the taxocoenosis of Polychaeta inhabiting a semi-enclosed shallow-water Mediterranean bay (Palacin *et al.*, 1991). In particular, this study investigates (a) the structure of the polychaeta taxocoenosis, (b) the usefulness of the information furnished by the different minimal methods in interpreting community structure and, (c) the relationships between community structure and environment.

Material and methods

Study area

Alfacs Bay (Ebro Delta), located on the North-East coast of the Iberian Peninsula (North-Western Mediterranean, 40°33'–38'N, 0°32'–44'E) (Figure 1), is a semi-enclosed shallow-water area, which can be characterized as a 'paralic' environment (*sensu* Geulorguet & Pertuisot, 1983). Muddy and sandy regions have been previously identified in the inner part of the Bay (Figure 1, Table 1) (Palacin *et al.*, 1991).

The sediment of the muddy region was very compact, with high organic matter, silt and clay contents, and a strongly negative Redox potential (Table 1). There were scattered shoots of the marine seagrasses *Ruppia cirrhosa* (Petagna) Grande and *Cymodocea nodosa* (Ucria) Ascherson in the area (Pérez & Camp, 1986). Moreover, large aggregates of floating sheet-like algae (mainly *Ulva* spp.) were occasionally accumulated on the shore, depending on the dominant currents (Martinez, 1990). The water column, though variable in height, was deep enough to keep the sediment submerged at all times (Table 1).

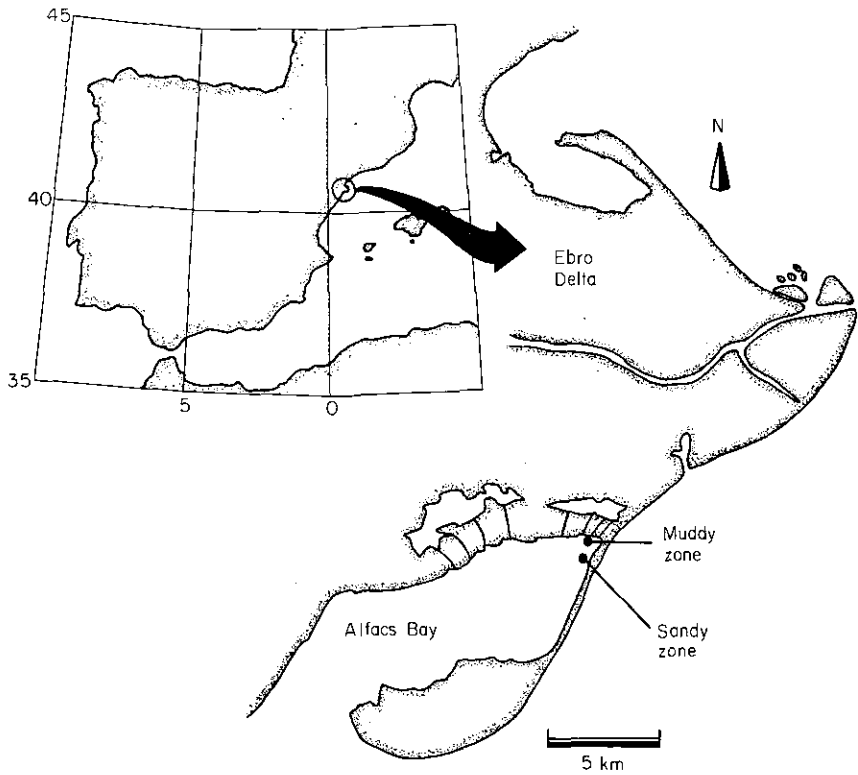


Figure 1. Location of sampling stations.

TABLE 1. Environmental factors in mud and sand communities. %SC: Silt and clay contents. %OM: Organic matter contents. REDOX: Surface Redox potential of the sediment. DEPTH: Depth range of the water column on the sediment

Factors	Mud	Sand
%SC	15.56	0.06
%OM	1.82	0.78
REDOX (mV)	-103.00	-8.30
DEPTH (cm)	20-50	50-100

The sandy region showed coarse sediments, with very low organic matter, silt and clay contents, together with a rather high Redox potential (Table 1). Shoots of *C. nodosa* were distributed in patches, denser than in the muddy region (Pérez, 1989; Duarte & Sand-Jensen, 1990). Changes in the water column depth were more noticeable than in the muddy region but, again, the sediment was never exposed (Table 1).

Sampling methods

A series of ten samples were collected at random from each region under study by means of manual cores.

Based upon previous studies on the polychaete fauna of both communities (Martin, 1991; Palacin *et al.*, 1991), sample size was 30 cm² in the muddy region and 200 cm² in the sandy region.

Each sample was filtered and fauna collected on a 500 µm sieve. Afterwards, all the polychaete species were separated, identified and quantified using a stereomicroscope (Wild Heerbrug M-8). The collected specimens were preserved in buffered 10% seawater formalin.

Qualitative and quantitative data were used to plot all the descriptors/area curves. Mean values of each descriptor for successively larger areas were calculated considering all the possible combinations of samples and plotted *vs.* their respective areas to obtain the curves.

To obtain the similarity/area curves, non-repeating combinations of samples had to be used in order to not artificially increase the similarity.

Studied parameters

Dominance and frequency

Dominance index (D) was calculated as follows:

$$D = n \times 100/N$$

where 'n' is the total number of individuals of a given species and 'N' is the total number of individuals (Soyer, 1970).

Frequency index (F) was calculated as:

$$F = m \times 100/M$$

where 'm' is the number of samples in which a given species was recorded and 'M' is the total number of samples (Soyer, 1970).

Species were considered rare species when they had a low dominance ($D < 1\%$) and a low frequency ($F \leq 50\%$) (Soyer, 1970).

Species/area curves

The observed species/area curves were fitted to a semilogarithmic function (Gleason, 1925):

$$y = a \times \ln x + b$$

where 'x' is the area in cm² and 'y' is the species number. The adjusted function can be expressed as a potential curve:

$$x = k \times e^{\lambda y}$$

$$\text{with 'k' } = e^{-b/a} \text{ and ' } \lambda \text{ ' } = 1/a.$$

Estimates of the Molinier points have been frequently used to determine qualitative minimal areas (Boudouresque & Belsher, 1979; Ballesteros, 1984, 1986). A Molinier point (M x/y) corresponds to a point from the species/area curve in which an x% of area increase is related to a y% increase in species number. These points can be found solving the equations

$$\begin{aligned} x &= k \times e^{\lambda y} \\ x + dx &= k \times e^{\lambda(y+d'y)} \end{aligned}$$

where dx and $d'y$ are, respectively, the relative increments of surface and species number (expressed as percentages). The solution can be expressed as:

$$x = k \times e^{[\ln(1 + dx)/d'y]}$$

Therefore, the Molinier point (x/y) depends on the relative increments of surface (dx) and species number ($d'y$) chosen, the k value being characteristic of each curve. Moreover, k is considered to be a good descriptor of the curve shape, providing useful information about the qualitative distribution of species inside the community (Ballesteros, 1986). A Molinier point $M 20/4 (= 95.4 k)$ (Ballesteros, 1986), has been chosen as representative in the present study.

Qualitative similarity/area curves

The Sorensen index (Sorensen, 1948) has been used to calculate qualitative similarity/area curves. The I_s index has been calculated as:

$$I_s = 2C_{pq}/(n_p + n_q)$$

where C_{pq} is the number of species common to the samples p and q , and n_p and n_q are, respectively, the total number of species in the samples p and q . The value of I_s ranges from 0 (total dissimilarity) to 1 (total similarity or identity). For the definition of a qualitative minimal area, a similarity index of 0.85 is deemed satisfactory (Weinberg, 1978).

Variance/mean ratio of the number of individuals vs. area

Changes in the variance/mean ratio (estimated on the basis of abundance values) *vs.* area are related to the aggregation level of individuals and, consequently, information about density patchiness can be directly inferred (Ballesteros, 1986). Maximum values in the curve indicate areas in which density differences are higher, while absolute values of the quotient point out the magnitude of the aggregation level.

Diversity/area curves

The Shannon index (Shannon, 1948), widely used as a diversity index, can be expressed as:

$$H' = - \sum_{i=1}^n p_i \lg_2 p_i$$

where H' is the diversity of the sample, p_i the proportion of individuals found in the i th species, and n the species number.

The Shannon index/area curves can be fitted by least squares to a Michaelis-Menten function:

$$y = Ax/(B + x)$$

after transformation to:

$$1/y = B/A \times 1/x + 1/A$$

If the sampling area is increased to infinity, then

$$\lim_{x \rightarrow \infty} [Ax/(B + x)] = A$$

so, the A values are good estimates of the community's global diversity, referred to as alpha-diversity or species diversity (Ballesteros, 1986).

Values of the slope, for each area size, characterize each curve. Niell (1974) assumed that stabilization of diversity/area curves is attained when the slope is not significantly distinct from zero. In the case of the fitted diversity/area curves, the value of area x corresponding to a z slope can be calculated by deriving the Michaelis–Menten function:

$$y' = AB/(B^2 + 2Bx + x^2)$$

Naming y , as z , the surface at which the curve will have a z slope is:

$$x = -B + \sqrt{AB/z}$$

Diversity stabilization can be assumed when the slope reaches a value of 1×10^{-3} (Ballesteros, 1986). In which case, the x value of area can be regarded as a structural minimal area (Ballesteros, 1986, 1991), as well as providing a good estimate of the pattern diversity.

Quantitative similarity/area curves

The Kulczynski index (Kulczynski, 1927) has been chosen to calculate quantitative similarity/area curves. The I_k index has been calculated according to:

$$I_k = \frac{2 \sum_{i=1}^n \inf(R_{ip}, R_{iq})}{\sum_{i=1}^n (R_{ip} + R_{iq})}$$

where R_{ip} and R_{iq} are the number of individuals per surface unit of species i respectively in samples p and q , and $\inf(R_{ip}, R_{iq})$ is the value of R_{ip} or R_{iq} whichever is smaller. The value of I_k ranges from 0 (total dissimilarity) to 1 (total similarity or identity). In that case, a similarity of 0.7 seems to be satisfactory for the definition of a quantitative minimal area (Weinberg, 1978; Ballesteros, 1986).

Results

The species (together with their respective abundances) of the 10 samples from both muddy and sandy stations are summarized in Table 2.

The muddy polychaete taxocoenosis was characterized by a low number of species. Moreover, rare species were relatively more important qualitatively (71.4% of the total species number) than quantitatively (1.1% of the total number of individuals). On the other hand, the sandy taxocoenosis showed higher species number, with a proportionally low frequency of rare species (29.4% of the total) showing a higher number of individuals (3% of the total number of individuals).

Species/area curves

Species/area curves showed different trends in mud and sand communities [Figure 2(a)]. Curves were fitted as:

$$\text{Mud community: } x = 10.403 \times e^{-0.496y}, r^2 = 0.973 \quad (\text{F1})$$

TABLE 2. Number of polychaete specimens per sample in mud and sand communities

Species of the mud community	1	2	3	4	5	6	7	8	9	10	DOM	FREQ	TROF
<i>Streblospio shrubsoli</i> (Buchanan 1890)	238	11	133	136	145	196	15	67	44	146	97.8	100	SDT
<i>Capitella capitata</i> (Fabricius 1870)	3	0	0	2	0	2	0	5	1	1	1.2	60	BMX
<i>Spio decoratus</i> Bobretzky 1871	2	0	2	0	1	0	0	0	0	0	0.4	30	SDT
<i>Hydroides elegans</i> (Haswell 1883)	0	0	0	0	0	0	0	0	0	3	0.3	10	FST
<i>Hediste diversicolor</i> (Müller 1776)	0	0	1	0	0	0	0	1	0	0	0.2	20	FDP
<i>Heteromastus filiformis</i> (Claparède 1864)	1	0	0	0	0	0	0	0	0	0	0.1	10	BMX
<i>Scoletopsis fuliginosa</i> (Claparède 1870)	0	0	0	0	1	0	0	0	0	0	0.1	10	SDT
Species of the sand community													
<i>Mediomastus fragilis</i> Rasmussen 1973	9	4	5	27	11	12	21	17	3	2	21.8	100	BMX
<i>Neanthes caudata</i> (Delle Chiaje 1828)	9	6	13	13	5	10	8	23	12	9	21.2	100	OMN
<i>Spio decoratus</i> Bobretzky 1871	4	6	12	5	11	21	9	3	1	5	15.1	100	SDT
<i>Scolaricia typica</i> Eisig 1914	8	11	5	2	4	1	1	2	2	5	8.0	100	BMX
<i>Capitella capitata</i> (Fabricius 1870)	1	2	3	2	5	6	7	7	2	1	7.1	100	BMX
<i>Phylo footidus adjimensis</i> (Fauvel 1925)	3	8	1	3	2	4	3	2	2	1	5.7	100	BMX
<i>Notomastus latericetus</i> Sars 1871	5	2	3	3	1	4	3	3	1	1	5.1	100	BMX
<i>Mastobrancheus trincheti</i> Eisig 1887	0	0	0	4	2	1	5	3	3	2	3.9	70	BMX
<i>Paraonis fulgens</i> (Levinsen 1883)	2	3	1	3	2	0	2	0	0	5	3.5	70	SMX
<i>Scoletopsis fuliginosa</i> (Claparède 1870)	2	0	4	0	1	0	0	2	1	1	2.2	60	SDT
<i>Glycera capitata</i> Oersted 1843	1	2	0	2	2	1	1	0	1	0	2.0	70	CDJ
<i>Hydroides elegans</i> (Haswell 1883)	0	0	1	1	0	1	1	0	1	4	1.6	50	FDT
<i>Exogone verugera</i> Claparède 1868	1	0	1	0	1	0	1	0	0	0	0.8	40	OMN
<i>Heteromastus filiformis</i> (Claparède 1864)	0	0	0	0	0	0	1	2	1	0	0.8	30	BMX
<i>Magelona equitamelae</i> Harmelin 1964	0	1	1	0	0	0	0	0	0	1	0.6	30	SDT
<i>Glycera trydactyla</i> Schmarda 1861	0	0	0	0	0	1	1	1	0	0	0.6	30	CDJ
<i>Cirrophorus furcatus</i> Hartman 1957	0	0	0	0	0	0	0	1	0	0	0.2	10	SMX
1 2 3 4 5 6 7 8 9 10 AVG STD													
Mud totals	244	11	136	138	147	198	15	73	45	150	116	74	
Specimens	4	1	3	2	3	2	1	3	2	3	2.4	0.9	
Species	45	45	50	65	47	61	64	66	30	37	51	12	
Sand totals	11	10	12	11	12	10	14	12	12	12	11.6	1.1	
Specimens													
Species													

DOM: Dominance. FREQ: Frequency. TROF: Trophic category (*sensu* Fauchald & Jumars, 1979, modified by Gambi & Giangrande, 1985). SDT: surface deposit-feeders, discretely motile, tentaculate. SMX: surface deposit-feeders, motile, sac-like pharynges. BMX: subsurface deposit-feeders, motile, sac-like pharynges. FST: filter-feeders, sessile, tentaculate. FDP: filter-feeders, discretely motile, pumping. OMN: Omnivores. CDJ: Carnivores, discretely motile, jawed.

$$\text{Sand community: } x = 1.0053 \times e^{-0.438y}, r^2 = 0.961 \quad (\text{F2})$$

The Molinier point M 20/4 was attained at areas of 992.5 cm² (muddy) and 95.9 cm² (sandy), respectively. Thus, both communities were clearly distinguishable: while the sandy minimal area would be lower than 100 cm² (the size of one sample), the muddy minimal area would be higher than the surface represented by all the collected samples. Moreover, estimates of *k* were higher in the mud community (F1) than in the sand community (F2), highlighting a more scattered qualitative species distribution in the former.

Qualitative similarity (Sorensen index)/area

Qualitative similarity was always lower in the mud community than in the sand community [Figure 2(b)]. A similarity value of 0.85 was already exceeded when combining two samples in the sand community (400 cm²), while it was never reached in the mud community (> 150 cm²).

Variations of the variance/mean ratio of the number of individuals vs. area

No significant peaks were observed in the curve of variance/mean ratio *vs.* area, suggesting that there were no intermediate patch sizes inside the communities.

Dispersion of individuals (expressed by the variance/mean quotient) becomes very low at areas of 120 cm² (mud) and of 600–1000 cm² (sand), respectively [Figure 3(a)]. Density of individuals can be considered to remain constant for larger areas.

Diversity/area curves

Differences between the two studied polychaete populations were also evident in the Shannon diversity index. The high dominance of *S. shrubsolei* caused low diversity values (hardly 0.2 bits for an area of 10 samples) in the mud community, whilst the sand community reached a rather higher value (3.2 bits also for 10 samples) [Figure 3(b)].

The fitted Michaelis–Menten curves obtained for the muddy and sandy communities were:

$$\text{Mud community: } y = 0.211 x / (10.764 + x), r^2 = 0.813 \quad (\text{F3})$$

$$\text{Sand community: } y = 3.299 x / (23.816 + x), r^2 = 0.972 \quad (\text{F4})$$

The alpha-diversity values, 0.211 (F3) and 3.299 (F4), characterized, respectively, the different complexities of mud and sand communities.

Slope values of 1×10^{-3} were reached for areas of 37 cm² (mud) and of 256 cm² (sand), respectively (both sizes exceeded when combining more than 1 sample). Thus, the two taxocoenoses studied were structurally quite well represented by the above mentioned area sizes.

Quantitative similarity (Kulczynski index) vs. area

Muddy samples proved to be very uniform [Figure 3(c)], with a 0.70 value of the Kulczynski index being exceeded when the sampling area reached 90 cm². On the other hand, in the sand community, this value was scarcely attained for a sampling area of 1000 cm².

Discussion

The dominant species in the mud community were small-sized opportunistic deposit-feeders (Grassle & Grassle, 1979) (Table 2). They usually display high turnover ratios

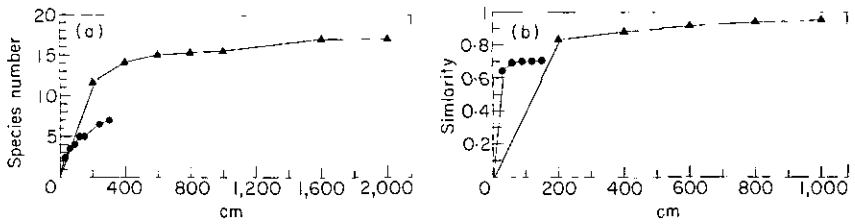


Figure 2. (a) Species/area curves. (b) Sorensen index/area curves. —●—, Silty; —▲—, sandy.

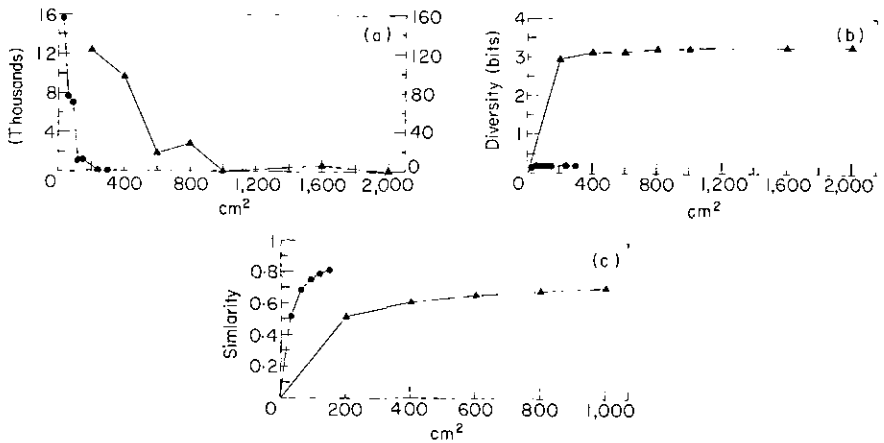


Figure 3. (a) Curves of variance/mean ratio *vs.* area. (b) Diversity/area curves. (c) Kulczynski index/area curves. —●—, silty; —▲—, sandy.

and their reproductive periods extend practically all year round (Martin, 1991). Their burrowing ability is poor or non-existent. In consequence, these species usually have low bioturbation power (at least vertically in the sediment), but they have the ability to process the resources available in the first few millimeters of sediment. The sponiid *S. shrubsoli*, a surface deposit-feeder (Gambi & Giangrande, 1985), shows the highest dominance values, but the dominance of *C. capitata*, a subsurface deposit-feeder (Gambi & Giangrande, 1985), was also of importance.

Species of the mud community were scattered in such a way that the species number did not become stable for the considered area ranges, and new species probably would still appear for larger areas. This was clearly reflected by the species/area curve, unstabilized for areas of 300 cm² [Figure 2(a)], but also by the high values of *k* and the Molinier point M 20/4 (F1) and by the low Sorensen index values [Figure 2(b)].

Quantitatively, the mud community showed strong small-scale differences in density (for areas lower than 90 cm²) [Figure 3(a)], demonstrating a pronounced patchiness of distribution of individuals at this level. Nevertheless, density differences quickly decreased as surface area increased. Moreover, the high dominance of a single species, *S. shrubsoli*, caused low species diversity values, together with practically no increase in the diversity index related to the sampling area increments (low pattern diversity) [Figure

3(b)]. This structural simplicity was also reflected by the quantitative homogeneity, the Kulczynski index value of 0.7 being reached at sampling areas of 90 cm² [Figure 3(c)].

In short, the mud community appeared as a very homogeneous community, with extraordinarily low diversity. Diversity stabilization for areas of 37 cm², quantitative homogeneity higher than 0.7 for areas of 90 cm², and density stabilization for areas of 120 cm², suggest an area of 120 cm² (four samples) as being representative of the community structure. However, new species would still appear for successively larger areas (> 300 cm²), as it was impossible to define a qualitatively adequate sampling area.

Structural simplicity of the mud community may be related to one or various stress factors, limiting diversification possibilities: hypoxia practically at a zero level, dense compactness of sediment, high organic matter contents, etc. (Pearson & Rosenberg, 1978). Thus, the mud community may be considered a physically-controlled community (*sensu* Sanders, 1969), where more resistant species (e.g. *S. shrubsoli*) are favoured, occupying all the space available. Environmental spatial homogeneity may also be a contributing factor in maintaining low levels of species heterogeneity. The relatively high number of rare species (always represented by a few individuals) could be directly related to chance. The absence of complex competence networks in physically-controlled communities may allow the presence of transient species which would not necessarily be well adapted to the particular environmental conditions.

The sandy polychaete taxocoenosis is characterized by the presence of species with a wide range of sizes and trophic strategies (Table 2). Most of the species reproduce annually and often have a lifespan of over a year. These species are able to burrow (and to modify) deep into the sediment, the majority being large subsurface deposit-feeders, such as the capitellids *Notomastus latericius* and *Mastobranthus trinchesi*.

The sand community was richer in species than the mud community. Moreover, its species distribution pattern became more general, with a group of common species and few rare species [Figure 2(a)]. This high small-scale species richness was directly related to the low *k* and *M* 20/4 values (*F*₂) and to the high qualitative homogeneity reached for low area sizes [Figure 2(b)].

The spatial pattern of the sand community was clearly defined by the evolution of the different quantitative parameters *vs.* area: the number of individuals becoming homogeneous for areas of 600–1000 cm², diversity stabilizing around 300 cm² and Kulczynski similarity index of 0.7 already attained at areas of 1000 cm². Thus, the structural pattern of the sand community was quite different from the mud one, with a number of species of equal dominance and a representative sampling area being between 700–1000 cm² (four to five samples).

The highest structural complexity of the sandy polychaete taxocoenosis may be directly related to the higher environmental stability and to the higher diversity of microhabitats (coarse sand, deeper oxygenated sediments, enough available food, etc.). Because of this, resources had to be widely distributed, especially through the sediment column, thus leading to the existence of a high number of species. In this way, a high specific coexistence together with an intense, but well distributed, interaction between species competing for the same food resource should be maintained. Therefore, the sandy community may be considered a biologically accommodated community, *sensu* Sanders (1969).

Species diversity decreases when organisms are exposed to severe physical stress (physically-controlled communities), as in the muddy polychaete taxocoenosis. Nevertheless, that is not the sole effect. In fact, each measured structural parameter seems to be affected by stress, resulting in a reduced number of species, a low pattern diversity, and

high homogeneity. On the contrary, whether environmental factors are more suitable for maintaining several species and the architecture of the habitat permits the coexistence of different microhabitats—as in the sandy polychaete taxocoenosis—both species diversity and pattern diversity increase and there is higher heterogeneity and species number.

The different minimal area methods that have been used in the present study have all provided valuable information depending on their qualitative or quantitative character and on their species-discriminant capability. A detailed interpretation of the curves of the proposed descriptors *vs.* areas, together with the parameters inferred from the curves, have provided clear community descriptions. Moreover, reasonable estimates of minimal areas have been proposed to facilitate the design of future seasonality or population dynamics studies.

Our study provides two different levels of interpretation using the curves of the different indexes *vs.* area: the sampling-design-methodology level and the community-structure-descriptor level. We propose that a minimum of two methods, one quantitative and the other qualitative, should be used when dealing with the former level. On the other hand, we recommend the use of several qualitative and quantitative methods when interested in the latter level, taking into account that, in this way, non redundant, complimentary information can be inferred.

The sandy and muddy polychete taxocoenosis studied in the shallow-water bay of the Ebro Delta greatly differ in their structure. Environmental factors and architectural features of the sediment seemed to be the main contributors to community patch-size, which increases in more stable communities (e.g. the sand community) and decreases in communities affected by environmental stress (e.g. the mud community). Our results provide new evidence supporting the theory that stress may be an important cause of structural simplification in natural communities.

References

- Andrew, N. L. & Mapstone, B. D. 1987 Sampling and the description of spatial pattern in marine ecology. *Oceanography and Marine Biology an Annual Review* **25**, 39–90.
- Ballesteros, E. 1984 *Els vegetals y la zonació litoral: espècies, comunitats i factors que influeixen en la seva distribució*. Ph.D. thesis, Universitat de Barcelona.
- Ballesteros, E. 1986 Métodos de análisis estructural en comunidades naturales, en particular del fitobentos. *Oecologia Aquatica* **8**, 117–131.
- Ballesteros, E. 1991 Structure and dynamics of North-Western Mediterranean marine communities: a conceptual model. *Oecologia Aquatica* **10**, 223–242.
- Boudouresque, C. F. 1971 Méthodes d'étude qualitative et quantitative du benthos (en particulier du phytobenthos). *Téthys* **3**, 83–184.
- Boudouresque, C. F. & Belsher, T. 1979 Le peuplement algal du port de Port-Vendrés: recherches sur l'aire minimal qualitative. *Cahiers de Biologie Marine* **20**, 259–268.
- Boudouresque, C. F. & Luck, H. B. 1972 Recherches de bionomie structurale au niveau d'un peuplement benthique sciaphile. *Journal of Experimental Marine Biology and Ecology* **8**, 133–144.
- Duarte, C. M. & Sand-Jensen, K. 1990 Seagrass colonization: patch function and patch growth in *Cymodocea nodosa*. *Marine Ecology Progress Series* **65**, 193–200.
- Fauchald, K. & Jumars, P. A. 1979 The diet of worms: A study of Polychaete feeding guilds. *Oceanography and Marine Biology an Annual Review* **17**, 193–284.
- Gambi, M. C. & Giangrande, A. 1985 Caratterizzazione e distribuzione delle categorie trofiche dei Policheti nei fondi mobili del golfo di Salerno. *Oebalia* **11**, 223–240.
- Gili, J. M. & Ballesteros, E. 1991 Structure of Cnidarian populations in Mediterranean sublittoral benthic communities. *Oecologia Aquatica* **10**, 243–254.
- Gili, J. M. & Ros, J. D. 1985 Estudio cuantitativo de tres poblaciones circalitorales de Cnidarios bentónicos. *Investigación Pesquera* **49**, 323–352.
- Gleason, H. A. 1925 Species and area. *Ecology* **6**, 66–74.
- Grassle, J. F. & Grassle, L. S. 1974 Opportunistic life histories and genetic systems in marine benthic polychaetes. *Journal of Marine Research* **32**, 253–284.

- Guelorget, O. & Perthuisot, J. P. 1983 Le domaine paralique: Expressions géologiques, biologiques et économiques du confinement. *Travaux du Laboratoire de Géologie, Ecole Normale Supérieure, Paris* **16**, 1–136.
- Hawkins, S. J. & Hartnoll, R. G. 1980 A study of the small-scale relationships between species number and area on a rocky shore. *Estuarine and Coastal Marine Science* **10**, 201–214.
- Kronberg, I. 1987 Accuracy of species and abundance minimal areas determined by similarity area curves. *Marine Biology* **96**, 555–561.
- Kulczynski, S. 1927 Die Pflanzenassoziationen der Pieninen. *Bulletin International Académie Tchèque des Sciences* **3**, 57–203.
- Laborda, A. J. 1984 *Estudio de la macrofauna bentónica sobre sustrato blando del piso intermareal de la playa de covas (o de El Grallal), Ría de Viveiro, Lugo*. Ph.D. thesis, Universidad de León.
- Martín, D. 1991 *Macroinfauna de una bahía Mediterránea. Estudio de los niveles de organización de las poblaciones de Anélidos Poliquetos*. Ph.D. thesis, Universitat de Barcelona.
- Martínez, M. A. 1990 *Estudio ecológico de las algas Efemerofíceas: Papel en los flujos de materia y energía en un sistema estuárico (Bahía de los Alfaques, Delta del Ebro)*. Ph.D. thesis, Universitat de Barcelona.
- Niell, F. X. 1974 Les applications de l'index de Shannon à l'étude de la végétation intertidale. *Bulletin. Société Phycologique de France* **19**, 238–254.
- Niell, F. X. 1977 Método de recolección y área mínima de muestreo en estudios estructurales del macrofitobentos rocoso intermareal de la ría de Vigo. *Investigación Pesquera* **41**, 506–521.
- Palacín, C., Martín, D. & Gili, J. M. 1991 Features of benthic infauna in a Mediterranean shallow-water bay. *Marine Biology* **106**, 101–107.
- Pearson, T. H. & Rosenberg, R. 1978 Macrobenthic succession in relation to organic enrichment and pollution in marine environment. *Oceanography and Marine Biology an Annual Review* **16**, 229–311.
- Pérez, M. & Camp, J. 1986 Distribución espacial y biomasa de las fanerógamas marinas de las bahías del Delta del Ebro. *Investigaciones Pesqueras* **50**, 519–530.
- Sanders, H. L. 1969 Benthic marine diversity and the stability-time hypothesis. *Brookhaven Symposium Biology* **22**, 71–80.
- Shannon, C. E. 1948 A mathematical theory of communication. *Belgium Systems and technics furnishing* **27**, 379–423, 623–656.
- Sorensen, T. 1948 A method of establishing groups of equal amplitude in plant sociology based on similar species content and its application to analyses of vegetation on Danish commons. *Biologiske Skrifter* **5**, 1–34.
- Soyer, J. 1970 Bionomie benthique du plateau continental de la côte catalane française. III. Les peuplements de Copépodes harpacticoides (Crustacea). *Vie et Milieu* **21**, 337–511.
- Weinberg, S. 1978 The minimal area problem in invertebrate communities of Mediterranean rocky substrata. *Marine Biology* **49**, 33–40.