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Spatial and Temporal Variation of a Nearshore Benthic Community in Southern Brazil: Implications for the Design of Monitoring Programs

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Patterns of spatial variation in a soft bottom benthic assemblage were assessed throughout a year in a 10 m deep nearshore area of southern Brazil. At three different scales every 2 months, five replicate corer samples (0·008 m^2) were taken at three random points (7 m^2) within two sites (2000 m^2). Spatial variation of the community was assessed by mixed ANOVA with two factors (Site and Time) crossed and one nested (Plot in Site). Variation presented a complex pattern indicating that even at such small scales, benthic community parameters (e.g. density, diversity, evenness) and dominant species differ in space and time. Results show the risk of pseudoreplication errors to which many monitoring programs and oceanographic surveys are subject whenever natural spatial variation of soft bottom benthic communities and vessel positioning precision are disregarded in designing a sampling program based on standard remote sampling methods.

Keywords: spatial variation; temporal variation; benthic fauna; oceanographic surveys; multiscale analysis; Brazilian coast

Introduction

Owing to their wide amplitude and low resolution (Jumars, 1993), oceanographic benthic surveys are often concerned with large scale processes, such as physical-chemical properties of water masses, oceanic fronts, and large sedimentary patterns. Many patterns observed in benthic communities are frequently interpreted in the light of such large scale processes (Jumars *op. cit.*), even though many small scale events, not addressed in the survey design, could give rise to strong variations in species or community responses, owing to e.g. differential larval settlement (Trueblood, 1991) or to biotic and physical interactions in the bottom boundary layer (Eckman, 1979; Thrush *et al.*, 1989). These small scale variations are well documented for many benthic environments and are responsible for complex patterns of benthic patchiness (Thrush, 1991; Morrisey *et al.*, 1992*a*; Aberg & Pavia, 1997; Li *et al.*, 1997) that can potentially confound the interpretation of results of the oceanographic survey.

One common solution to avoid sampling problems related to small scale spatial variation, when studying the relationship of large scale processes to macrobenthic patterns, is to disregard mapping patterns, and to treat each sampling station as a single unit of biotic and abiotic data, generating an association matrix of species supplemented by a set of environmental variables. Cause-effect relationships are then suggested by multivariate methods giving rise to exploratory analysis or even hypothesis tests through analysis such as Canonical Correspondence (ter Braak, 1986) or Multiple Regression Models. Nevertheless, these procedures are still open to sampling errors imposed by remote sampling methodologies, i.e. the acquisition of biotic and environmental data with different gears at a variety of depths and under different weather conditions (Somerfield & Clarke, 1997). In this way, the station area where environmental data were obtained is much larger than the area sampled by the benthic gear (Kendall & Widdicombe, 1999). Patterns of benthic parameters can be over- or underestimated owing to faunistic patches that could be present in such larger station areas. This would invalidate the interpretation of observations in the light of the environmental variables unless the benthic community parameter is estimated for the whole area with good precision (Green, 1979; Andrew & Mapstone, 1987).

The total area of the bottom within which samples were taken and represents the statistical populations

to be estimated, is herein referred to as the *station area* to avoid misunderstandings related to the concept of *sample area* (=the area of the sampling gear). The station area in a benthic survey changes according to (1) the sampling gear, (2) depth, (3) vessel size, (4) wind direction and so on. Ignoring such uncertainties may lead to pseudoreplication errors (Hulbert, 1984). In this case, observed variations would be interpreted in the light of temporal process when they actually reflect spatial differences, a common error with an apparent statistical background but devoid of any real significance. Likewise, environmental monitoring programs based on changes in macrobenthic parameters in a spatial and temporal framework (e.g. Before/After-Control/Impact—BACI, Green, 1979), are also subjected to many of the sampling drawbacks considered above, mainly when data are obtained by means of remote sampling.

In this paper I evaluate the variation of some community parameters (e.g. density of dominant groups, diversity, richness) and multivariate descriptors in different sampling areas in a soft-bottom tropical macrobenthic biocenosis with time. This permits an assessment of the risk of misinterpretation of community parameters in marine benthic surveys based on remote sampling methodologies. The null hypotheses of no variation in these parameters was tested at three spatial scales (7, 2000 and 50 000 m^2). These scales were chosen since they represent the standard ' station areas ' used in many oceanographic and benthic monitoring surveys. The relative roles of spatial and temporal variations were addressed and a possible environmental explanation for the most consistent pattern is also presented.

Material and methods

Study area

Sampling was done in the middle of Picinguaba Inlet (Figure 1), on the coast of São Paulo State, southern Brazil (23°22′S–44°52′W). Although located between two of the main ports of South America (i.e. Santos and Rio de Janeiro), it constitutes a well preserved site, far from intense human occupation, owing to its contiguity to a state park.

The gently sloping bottom of the bay is covered mainly by moderately to poorly sorted fine and very fine sand (>70%) (Rodrigues, pers. comm.). Given its south-western orientation, Picinguaba Inlet is periodically subjected to wave disturbance generated by frontal systems (Mahiques, 1995).

Three main water masses have been recognized in the area (Castro Filho *et al.*, 1987): Coastal Water (CW), with high temperatures and low salinities (*ca.* 24° and 35·4 respectively), Tropical Water (TW) with high temperatures and salinities (*ca.* 24° and 37) and the South Atlantic Central Water (SACW) with low temperatures and salinities (*ca.* 13·5° and 35·4). The CW covers shallow areas (<20 m) and is the predominant water mass in the bay. Nevertheless the SACW, which covers the outer continental shelf (>50 m) all year round, usually flows in to the inner shelf in summer, where it has a strong influence on the structure of benthic communities (Pires, 1992). The influence of TW is restricted to offshore surface waters.

Sampling

Macrobenthic samples were taken with diver-operated cores (diameter=10 cm, 25 cm depth, *ca.* 0·008 m^2) sieved in a 0·5 mm mesh-size and fixed in 10% formalin. A nested sampling design (Green, 1979; Underwood, 1997) was employed at two sites (A and B), 200 m apart (Figure 2), 10 m deep. Within each site, inside an area of *ca.* 2000 m^2 (50 m ϕ), five replicate samples were taken at three random plots (3 m ϕ, 7 m^2). Temporal variation was assessed by repeating the surveys, every 2 months, from May 1993 to March 1994. The total number of samples was 180 (5 replicates × 3 plots × 2 sites × 6 surveys). The survey sites were chosen for bathymetric and sedimentary homogeneity to permit the recognition of biotic variations. Positioning of sites was obtained by use of the Global Positioning System (GPS). Spatial scales used were chosen in order to represent potential station area from differently designed oceanographic surveys according to the sampling gear employed, positioning system, ship drift, etc. Hence each scale chosen in this study, represents the station area of the following methodologies normally used in other macrobenthic surveys:

(a) **Total area** (*ca.* 50 000 m^2)—*Positioning system*: compass; *sampling gear*: remote sampling with grabs.
(b) **Site** (*ca.* 2000 m^2)—*Positioning system*: GPS; *sampling gear*: remote sampling with grabs.
(c) **Plot** (*ca.* 7 m^2)—*Positioning system*: fixed buoys; *sampling gear*: diver-operated cores.

A sediment sample was collected at each plot (three per site) for grain-size analysis using the dry-sieve and pipette method described in Holme and McIntyre (1984) and obtaining Folk and Ward (1957) statistical parameters. Calcium carbonate content was determined by dry weight difference after HCl 10% attack. Differences between sites for sediment parameters were assessed by Wilcoxon non-parametric test (Zar,

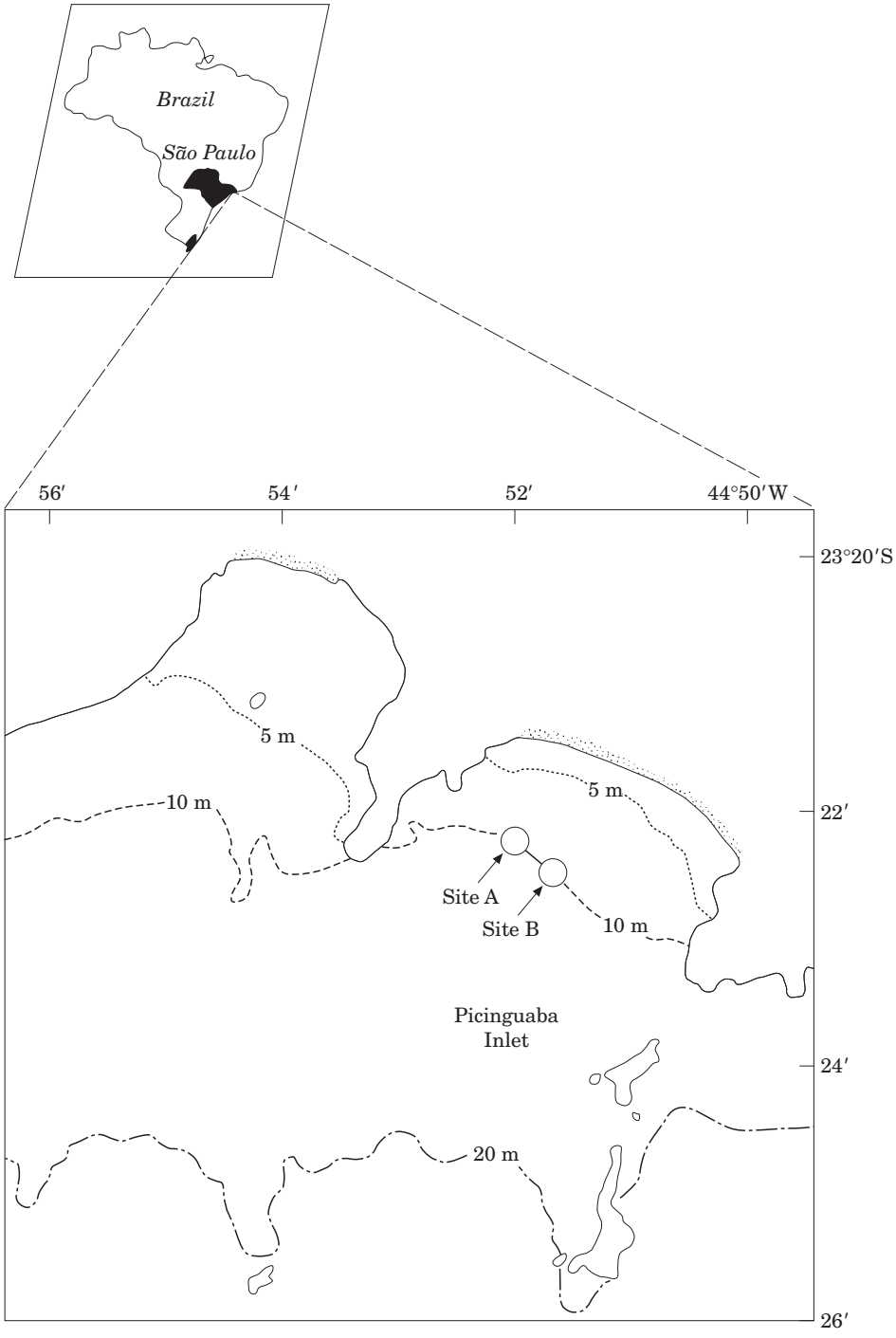

FIGURE 1. Map of the study area with location of the two sites (A and B).

1996). Temperature and salinity were also measured for the whole area in the six surveys.

Data analysis

Spatial and temporal variation of macrofauna was evaluated by mixed-model ANOVA with two fixed orthogonal factors (Site and Time) and one random nested (Plot in Site) factor. For each replicate, the following community descriptors were calculated: density of taxonomic groups, number of individuals (N), richness (S=number of species), diversity (Shannon's H′ index) and evenness (Pielou's J index, i.e. H′/Hmax). To assess the effect of sample size in

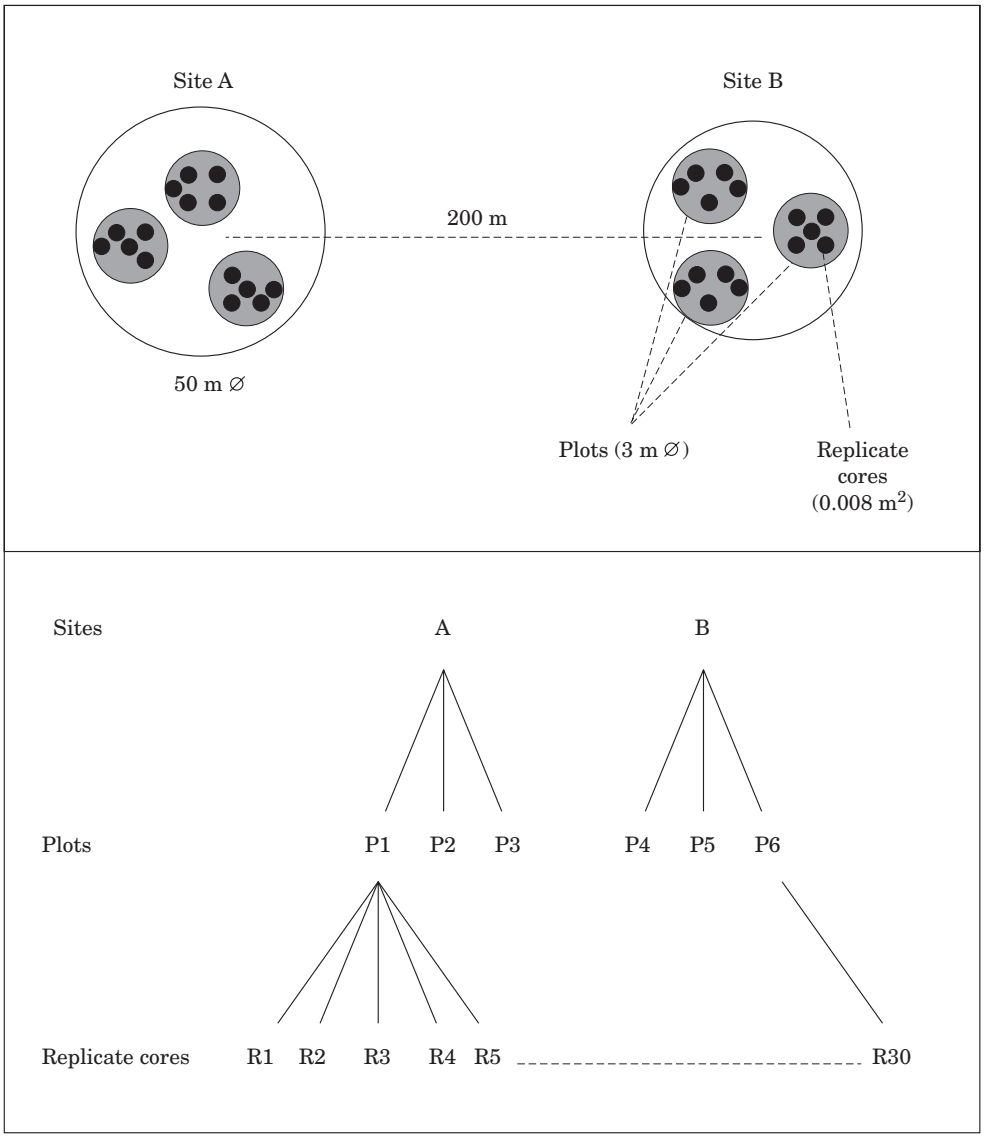

FIGURE 2. Sampling design used to assess spatial variation. The same design was repeated every 2 months.

community descriptors estimation, these were calculated for different sampling areas, i.e. sampling area of replicates (0·008 m^2), replicates pooled in plots (0·04 m^2) and replicates pooled in sites (0·12 m^2).

Before analysis, density of species, density of groups and richness data were square root transformed ($\sqrt{x+1}$). The transformation was chosen after applying Taylor's power law (Green, 1979). The results of the transformations were tested for homogeneity of variance using Cochran's test (Underwood, 1997) before performing ANOVA.

Since the observed patterns in macrobenthic surveys are usually based on multivariate responses in a species association matrix, a PCA (Principal Components Analysis) was applied, reducing the dimensionality of 53 species (rarer species excluded from the analysis) to a smaller number of components of variation. PCA scores obtained for each replicate were analyzed by ANOVA, this procedure improves the agreement of data to ANOVA assumptions of homoscedasticity and normality (Jassby & Powell, 1990).

Results

Environment

The bottom was gently sloping with ripple marks less than 10 mm high. Sediment was mainly very fine sand, poorly sorted, with 15 to 20% calcium

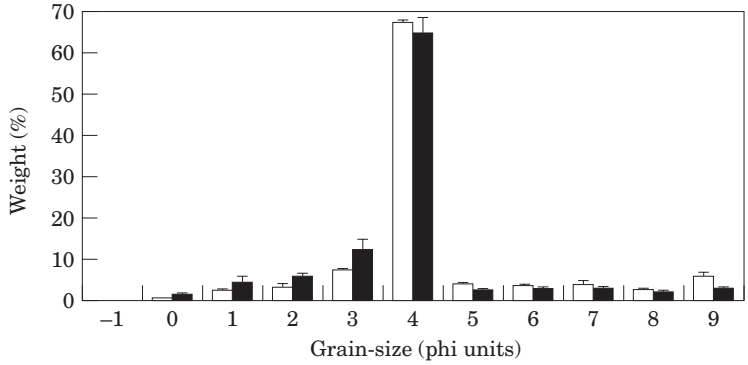

FIGURE 3. Grain-size distribution (phi units) in both sites. Site A: open bars; site B: closed bars.

carbonate content. A comparison between sediment parameters in the two sampling sites (A and B) showed subtle (Figure 3) but significant differences (Wilcoxon non-parametric test, $P<0{\cdot}05$) in mud content (more mud in A), grain-size (coarser in B) and skewness (> in A). No significant differences were found for kurtosis, sorting and calcium carbonate content. Temperature was stable during the whole survey (maximum 26·6° C) except in November 1993 (4th survey), when, under the influence of the cold SACW, the temperature dropped to 18·2 °C. Salinity varied from 32·2 to 35·5.

Community composition

Overall, 147 species were identified. Polychaetes were dominant (39% of the total number of species), followed by amphipods (16%) and molluscs (bivalves and gastropods, 9% each). A total of 3610 specimens was collected: 64% were polychaetes, 13% bivalves, 7% ophiuroids, 4% gastropods and 3% amphipods. Density ranged from 0 to 49 individuals per core (0·008 m^2), with a mean of 19. The mean number of species per core was 10, and ranged from 0 to 19. Of the 147 species found during the study, 23% were recorded in all surveys and 27% occurred in only one of the six surveys. The number of species/survey (0·24 m^2 of area) ranged from 70 to 94, and the density of individuals varied from 363 to 905. The most frequent (>5% of occurrences) or abundant (>10 ind m^{-2}) species are shown in Table 1.

Spatial and temporal variation of taxonomic groups

Significant differences in the abundance of dominant taxonomic groups were found in both space and time (Table 2). Bivalves showed only temporal variation while gastropods presented temporal variation and spatial variation at the scale of Site. Spatially, gastropods showed a preference for site A (Figure 4) with a decline in density through the sampling period, while bivalves increased in number. Polychaetes presented a rather complex pattern, with significant interaction (Site × Time), i.e. differences between sites were not the same with time. Ophiuroids did not present significant temporal and spatial patterns at any scale indicating a homogeneous distribution inside the study area and no temporal variation. The amphipod data were not submitted to ANOVA, since many null values were recorded through time. They were rare in all surveys, except for a peak recorded in the 4th survey (November 1993), due to the gammarid *Batea catharinensis*.

Community parameters

Community parameter variation was assessed for two different sampling areas, i.e., replicate corer area = 0·008 m^2 and plot area = 0·04 m^2. In this case, replicate cores for each plot were pooled for index measurements to assess the role of sample size in the interpretation of spatial and temporal patterns. The complex pattern is noticeable when one considers that diversity and richness presented significant interaction (Site × Time) in both scales (Table 2). Density and evenness did not present interaction but showed significant temporal and spatial variation at the scale of Site (2000 m^2) with density higher in Site A and evenness lower. Nevertheless, evenness did not present any significant pattern when measured at 0·008 m^2.

The sample size effect is also noteworthy when one attempts to discriminate between the two sites by means of these parameters calculated for replicates from all surveys, considering different times as replicates for spatial analysis. These results (Figure 5)

TABLE 1. Most frequent (>5% of frequency of occurrences) or abundant (>10 ind m^{-2}) species

	Main species	Taxonomic group	Ind m^{-2}	Occurrences (%)
1	*Lumbrineris curtolobata*	Polychaeta	392	64
2	*Spiochaetopterus costarum*	Polychaeta	188	58
3	*Owenia fusiformis*	Polychaeta	135	49
4	*Magelona variolamellata*	Polychaeta	131	44
5	*Magelona papillicornis*	Polychaeta	115	44
6	*Pholoididae* gen. sp.	Polychaeta	110	28
7	*Corbula cariboea*	Bivalvia	84	37
8	*Amphiodia atra*	Ophiuroidea	75	45
9	*Nucula puelcha*	Bivalvia	74	32
10	*Magelona posterolongata*	Polychaeta	56	29
11	*Amphiodia riisei*	Ophiuroidea	48	31
12	*Terebellides anguicomus*	Polychaeta	44	21
13	*Neanthes bruaca*	Polychaeta	39	24
14	*Hemipholis elongata*	Ophiuroidea	38	23
15	*Eunoe papillosa*	Polychaeta	35	22
16	*Eunice prayensis*	Polychaeta	31	19
17	*Diplodonta danieli*	Bivalvia	28	19
18	*Pectinaria* (*Pectinaria*) *laelia*	Polychaeta	26	16
19	*Clymenella* sp.	Polychaeta	26	15
20	*Melaniella* sp.	Gastropoda	24	14
21	*Batea catharinensis*	Amphipoda	24	2
22	*Tellina* sp.	Bivalvia	23	17
23	*Abra lioica*	Bivalvia	23	14
24	*Entodesma* sp.	Bivalvia	22	13
25	*Fimbriosthenelais marianae*	Polychaeta	22	16
26	*Ctena pectinella*	Bivalvia	21	14
27	*Dosinia concentrica*	Bivalvia	21	14
28	*Felaniella* cf. *candena*	Gastropoda	21	12
29	*Amphitalamus vallei*	Gastropoda	20	13
30	*Mooreonuphis lineata*	Polychaeta	20	11
31	*Parandalia tricuspis*	Polychaeta	18	12
32	*Amphicteis gunneri*	Polychaeta	17	8
33	*Ceratocephale oculata*	Polychaeta	17	8
34	*Finella dubia*	Gastropoda	17	7
35	*Scoloplos* (*Leodamas*) sp.	Polychaeta	13	9
36	*Tharyx* sp.	Polychaeta	13	8
37	*Voluvella* sp.	Gastropoda	13	9
38	*Sthenolepis grubei*	Polychaeta	12	8
39	*Tiburonella viscana*	Amphipoda	11	7
40	*Axiothella brasiliensis*	Polychaeta	10	6

indicate that it is possible to discriminate the two sites only when diversity is calculated for replicate cores pooled in Plots (0·04 m^2), i.e., when comparing two different places, different dominance and diversity patterns are obtained, depending on the sample size. When all surveys are taken together, the diversity and evenness measured for Plots (0·04 m^2) are not sensitive to temporal variations (Figure 5), i.e. they showed differences between Sites, but when measured for smaller (0·008 m^2) or greater (0·012 m^2) samples the two Sites are not distinguishable, indicating that the pattern of temporal variation was quite different when both indices were measured for different sample sizes.

Biocenosis descriptors

To evaluate the variation of species combination as used in standard community surveys, an ANOVA was also applied for the scores obtained in the PCA. The first principal component which accounts for the largest variation of the species data matrix showed significant interaction (Site × Time), so indicating the complex spatial to temporal pattern for the

TABLE 2. Results of the ANOVA for the factors Plot, Site, Time and Interaction (Site × Time); *P*=probability of type I error; %V=contribution of each factor to total variance. Significant values are in italics

	Error	Plot		Site		Time		Time × Site	
	%V	*P*	%V	*P*	%V	*P*	%V	*P*	%V
Taxonomic groups									
Polychaeta	30	0·729	0	*<0·001*	33	*<0·001*	33	*0·013*	4
Gastropoda	47	0·329	1	*0·020*	18	*<0·001*	34	0·622	0
Bivalvia	74	0·749	0	0·363	0	*<0·001*	24	0·221	2
Ophiuroidea	86	0·096	8	0·459	0	0·178	6	0·573	0
Community Parameters									
Density	35	0·281	1	*<0·001*	36	*<0·001*	26	0·134	2
Diversity (0·008 m^2)	51	0·169	3	0·778	0	*<0·001*	34	*0·014*	12
Evenness (0·008 m^2)	87	0·131	6	0·194	6	0·465	1	0·769	0
Richness (0·008 m^2)	50	0·763	0	*0·025*	12	*<0·001*	32	*0·018*	6
Diversity (0·04 m^2)			20	*0·004*	60	0·178	5	*0·019*	15
Evenness (0·04 m^2)			9	*<0·001*	77	*0·005*	10	0·081	4
Richness (0·04 m^2)			6	0·106	11	*<0·001*	61	*0·005*	21
1st Principal component	22	0·473	0	*<0·001*	32	*<0·001*	42	*0·006*	5
2nd Principal component	16	0·247	1	*<0·001*	81	0·053	2	0·783	0
3rd Principal component	79	*<0·001*	20	0·713	0	0·832	0	0·652	0

macrobenthic assemblages, i.e. differences between sites were not the same along time. The remaining amount of variation was due to Site differences (second principal component) and variations in the scale of Plots or Error term (third principal component).

Discussion

Patterns of spatial variation

The effect of scale on the analysis of patterns of distribution has recently received much attention in ecological studies (Schneider, 1994). Spatial heterogeneity is no longer regarded as an unwelcome complication, but as a central factor in ecological systems (Pickett & Cadenasso, 1995). The application of multiscale analysis in benthic studies is worthwhile not only when considering the influence of spatial patterns on sampling methodology (Morrisey *et al.*, 1992*a*) but also when attempting to relate the scale of abiotic and biotic processes to structural patterns observed in benthic communities (Kendall & Widdicombe, 1999).

The homogeneity of many abiotic conditions within Sites (i.e. among Plots) in this study did not allow a straightforward explanation for the observed significant biotic differences at the scale of Plots (*ca.* 7 m^2) when the third principal component was submitted to the ANOVA. Biological interactions and small-scale hydrodynamic processes not assessed herein could be responsible for such patterns. Trueblood (1991) attributed patches of this same magnitude in tropical polychaetes to differential larval settlement rates. Bioturbation effects, mainly by pit-digging crabs and fishes, can also be responsible for macrobenthic patches on a scale of metres and centimetres owing to reductions in abundance by predation, displacement and emigration of the local fauna (Van Blaricom, 1982; Hall *et al.*, 1991). Patchiness on even smaller scales is likely to occur if one considers the high contribution of statistical error to total variance (i.e. variance within Plots). This might be related also to bioturbation effects and to microscale topographic features like ripple marks, considered as the main cause of patchiness for amphipods and nematodes at centimetre scales (Sameoto, 1969; Hogue & Miller, 1981).

At larger scales, Thrush *et al.* (1989), Volckaert (1987) and Kendall and Widdicombe (1999) recognized patches of sizes very similar to the scale of Sites (*ca.* 50 m in diameter) for some intertidal and subtidal polychaetes, crustaceans and bivalves. Nevertheless, variation between the two Sites could also represent a gradient between two much larger faunistic patches (Morrisey *et al.*, 1992*a*). Despite attempts in survey design to control environmental heterogeneity by choosing an area of homogeneous topography, there were small but significant differences in sediment mud content between Sites (10% more mud in Site A). Since both Sites are, however, classified as very fine sand, it is not easy to draw conclusions on community

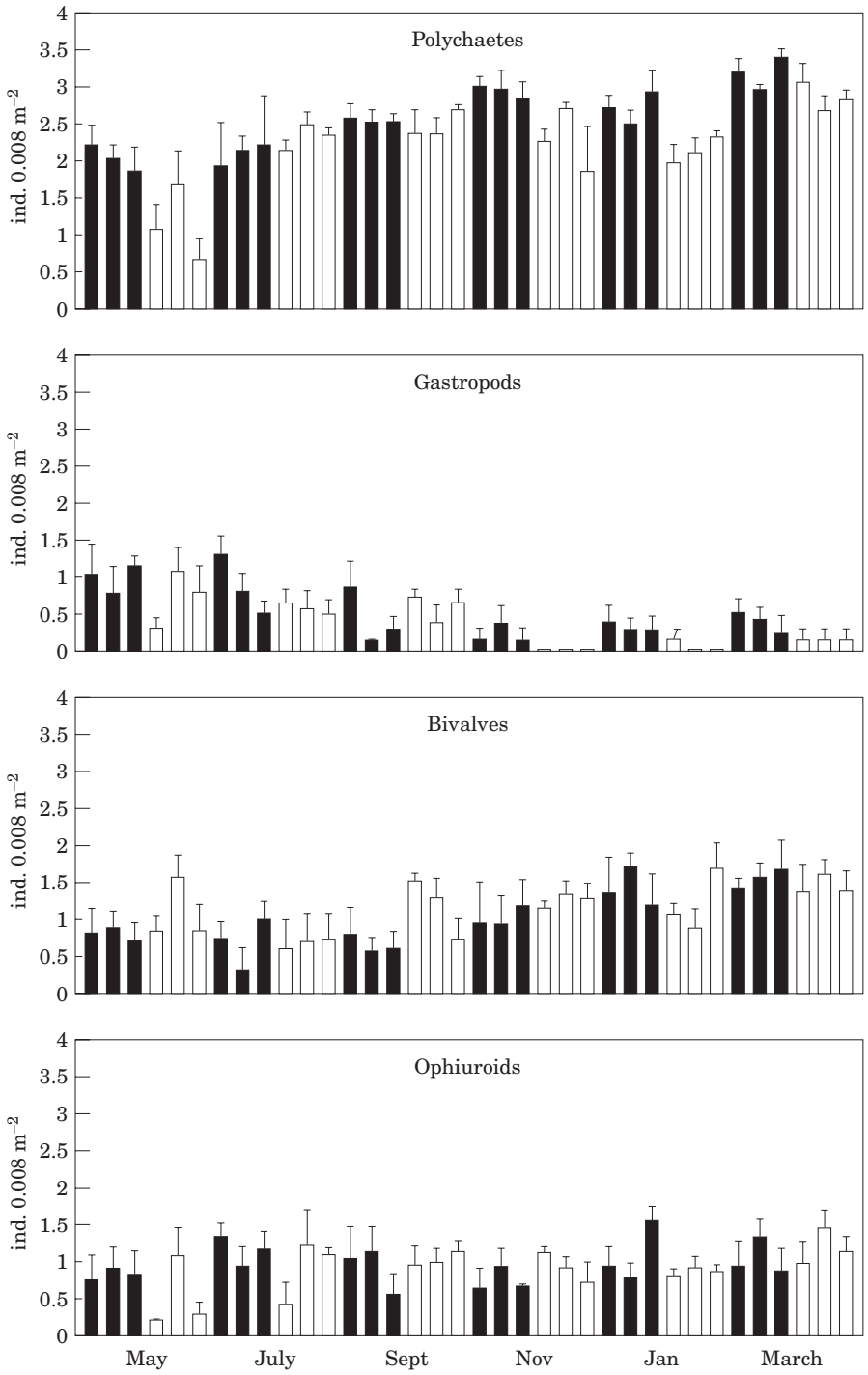

FIGURE 4. Mean density (natural logarithm of x+1) plus standard error of main taxonomic groups for each Plot in Site A (closed bars) and B (open bars).

variation on the basis of classical animal-sediment relationship theories, i.e. those that consider sediment as a super-parameter for the macrobenthic fauna (Janson, 1967; Gray, 1981). It is likely that the same hydrodynamic conditions that allow a greater deposition of mud in Site A could also be responsible for facilitation of passive larval settlement, since fine sediments present sinking velocities similar to those of many macrobenthic larvae (Butman, 1987). Larval settlement driven by hydrodynamic processes has

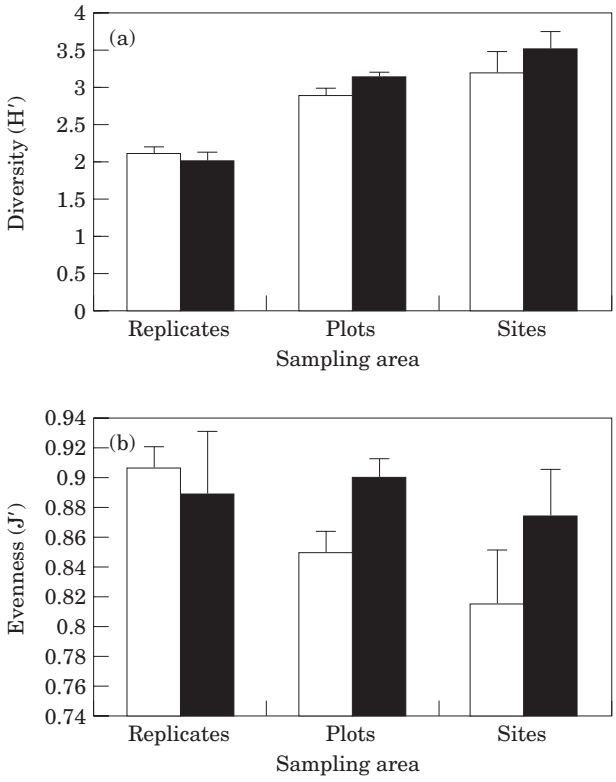

FIGURE 5. Shannon index (a) and Pielou's evenness index (b) calculated for replicates from all surveys in each site in three spatial scales: Replicates=index calculated for replicates; Plots=index calculated for replicates pooled in plots; Sites=index calculated for replicates pooled in sites. Site A: open bars; site B: closed bars.

been considered as the main factor in controlling adult populations of shallow water ophiuroids (Tyler & Banner, 1977) and of the polychaete *Owenia fusiformis* (Fager, 1964, Thiébaut *et al.*, 1992), the dominant species in Site A. Hence in the shallow waters of Picinguaba Inlet, the combination of larval settlement rates, post-settlement processes and hydrodynamic conditions in the sediment boundary layer may have generated a macrobenthic mosaic at small scales which are not determined primarily by sedimentation patterns.

Scales of variation and marine benthic monitoring sampling design

Despite our spatially restricted sampling area, variation in benthic community parameters were common at all scales assessed. This has some practical effect on sampling design of benthic studies. For instance, observed variation at smaller scales such as among Plots (*ca.* 7 m ϕ), inside the ' station area ' normally used in benthic surveys, leads to the need to increase the sampling effort in order to estimate variables (e.g. species abundance) with better precision and so discriminate actual spatial and temporal variations (Thrush *et al.*, 1994). Variation at larger spatial scales (e.g. among Sites, *ca.* 50 m ϕ) with the occurrence of interaction (Site × Time) for several parameters can give rise to pseudoreplication problems (Hulbert, 1984) if the ' station area ' in a sampling program is larger or encompass a gradient between two larger patches, so that replicates in different surveys may not be sampling the same area. In such a case, an increase in sampling effort (replication) for each survey could lead to over- or underestimation of any community variable, when comparing different temporal surveys. This kind of error is particularly dangerous in studies over time because the results obtained will present a high statistical significance, even though they are devoid of any actual meaning. In fact, they could be the result of failure to relocate the station precisely in sequential sampling. Hence, replication by means of remote sampling (e.g. grabs) requires scattering replicates over an area larger than the repositioning precision area assessed, thus increasing the oceanographic ' station area ', allowing sampling of the same statistical population over time and diminishing the risk of pseudoreplication errors.

Diversity and evenness indexes are still widely used in community description in marine surveys despite some drawbacks to their use in benthic studies such as ambiguous or late responses to disturbances (Gray, 1981; Bernstein & Zalinski, 1983) and their well known dependence on sample size (Magurran, 1988). In the present study, this dependence was not restricted to an underestimation of diversity when calculated for few samples pooled, but was also reflected in a complex pattern where differences in species dominance between Sites A and B depended on how many replicates were pooled, i.e., the sampling area used for calculating the indexes. Furthermore, the interaction term (Site × Time) in the analysis was significant, indicating that each Site, showed different diversity patterns in time, despite its proximity to the other site. Hence, observed patterns of diversity and evenness using data from small sampling areas (e.g. grabs and cores) cannot be analysed, even though they are widely used in many marine monitoring programs. The same pattern observed for diversity and evenness was also observed when analysing the multivariate responses of several species by means of PCA. The null hypothesis of the same community composition among different areas and surveys was tested against the alternative hypothesis of spatial and temporal variation (Clarke & Green, 1988). The rejection of the null hypothesis, owing to

the significance of the Interaction term (Site × Time), shows how variable the community is and how large the risk of pseudoreplication is when the sampling location cannot be relocated with a precision greater than 50 m, since similar sites only 50 m far apart can present rather different patterns. This scale of variation is within the ' station area ' normally used in oceanographic surveys, producing misleading results since it is likely that different statistical populations are being sampled in different times. Even with correct positioning, observation of shifts in biotic responses through time will depend on the choice of the site to be sampled (Morrisey *et al.*, 1992*b*). Unless all processes are correctly scaled and experimentally controlled (not so easy in environmental monitoring programs), no observed variation can be interpreted as temporal variation. This is the case for BACI experimental designs (Green, 1979), a procedure which has already been strongly criticized (Stewart-Oaten *et al.*, 1986; Underwood, 1997) although it is still in use in several monitoring programs, mainly in Third World countries.

The patterns described here were observed in a restricted nearshore site. Nonetheless, coastal environments at such a scale may be subjected to impacts from several types of development, such as maintenance dredging, marinas and breakwater construction, as well as by local discharge of untreated sewage. The effects of these activities are rarely monitored (Smith, 1991) and the natural variability of local communities must be assessed in order to avoid future misinterpretation when environmental monitoring is required.

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