Short-term stability of estuarine benthic assemblages: are storms pattern-defining events?

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ABSTRACT. Storms, associated with strong winds and heavy rains, are often the most severe physical disturbances in shallow coastal areas causing instability to sedimentary environments. We hypothesized herein that if storms influence short-term assemblage structure of macrofauna, then assemblages should change after storms, while remaining relatively stable over calm weather conditions. The study was conducted at the subtropical Paranaguá Bay, in southern Brazil. We selected four 700 m^2 sites, at the estuarine outlet, to monitor changes in number of species, number of individuals and Shannon diversity. Sampling was arranged considering the weather forecast so that both before and after conditions could be recorded. Data of each site was tested separately to access the significance of specific (before/after) comparisons using *t* tests. There were no clear effects of storms on macrofaunal species richness, abundance and diversity at the four sampled sites. Conversely, we showed that short-term variation in abundances occurred regardless of weather conditions. Increased dispersal may be the most common process associated with storms instead of mortality. Storms that intermittently affect the southern coast of Brazil can be thus seen as minor driving forces of shallow-water estuarine macrofauna. Effects of extreme meteorological events remain to be assessed.

KEY WORDS. Benthos; ecosystem disturbance; Paranaguá Bay; sedimentary environments; storms.

Unconsolidated soft sediments, ranging from intertidal shores and estuaries to oceanic abyssal depths, are the most extensive environments on the planet (MURRAY *et al.* 2002). Despite their apparent homogeneity, shallow coastal areas are in fact a mosaic of benthic patches where sediment properties and faunal components vary considerably (THRUSH 1991, HEWITT *et al.* 2008).

Shallow-water surface sediments are constantly under the influence of currents and waves, which cause transport and deposition of particles (KNEBEL *et al.* 1999). On a landscape scale the distribution of patches of sedimentary environments is particularly complex at the outlet of estuaries, due to a combination of geographic and hydrodynamic features (GREEN *et al.* 1997, ZAJAC 2008).

Natural physical disturbances may cause destabilization and subsequent mobilization of sediments with direct implications to macrofaunal population dynamics (PROBERT 1984, HALL 1994). Shallow-water benthic species may be, to a degree, adapted to erosion or deposition (BOCK & MILLER 1995), but tolerance to disturbance varies considerably among taxa and recovery to pre-disturbance conditions may not occur, especially after large scale physical disturbances (UNDERWOOD 1999). Recovery depends upon the active dispersal of adults or upon the transport and redistribution of juveniles and adults in the water column (ARMONIES 1999, COMMITO 1995, NEGRELLO FILHO *et al.* 2006, TURNER *et al.* 1997) and subsequent resettlement and colonization.

Storms are often presumed to be the most severe physical disturbances in shallow coastal and estuarine environments (DOBBS & VOZARICK 1983, HALL 1994). Ressuspension and transport of sediments and organisms presumably increase under storm conditions (REES *et al.* 1976). The survival rate of ressuspended organisms is uncertain, as either mortality or active/passive dispersal may occur (DERNIE *et al.* 2003). The role played by such storms in structuring benthic associations in the inner platform shelf and other shallow coastal areas remains to be assessed (GALLUCCI & NETTO 2004).

The subtropical southern Brazilian coast has two predominant weather states. The prevalence of eastern-northeastern winds leads to calmer weather, whereas southern-southeastern winds provoke greater swells and storminess with increased bottom sediment disturbance (PARISE *et al.* 2009). Storms are herein referred to the latter weather condition.

In this study, we hypothesized that if storms influence short-term assemblage structure of macrofauna, then assemblages should change after storms, while remaining relatively stable over periods of calm weather conditions. We carried out short-term monitoring surveys at four shallow-water sites before and after storms and over equivalent periods of calm weather.

MATERIAL AND METHODS

Our study was carried out at the outlet of the estuarine complex of Paranaguá Bay in southern Brazil (25°S, 48°W). Four sedimentary environments were selected for sampling: two intertidal and two sublittoral (8 m deep) sites (Fig. 1).
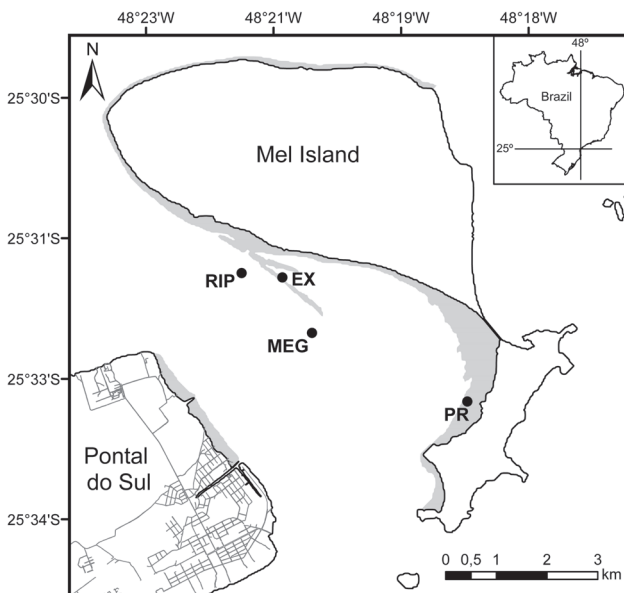

Figure 1. Map of study area showing the location of the different sedimentary environments sampled. (RIP) Rippled sublittoral, (EX) exposed intertidal sand bar, (PR) protected intertidal sand flat, (MEG) sublittoral with conspicuous megafauna.

The sites were classified as exposed sand bar (EX), protected sand flat (PR), rippled sublittoral (RIP) and sublittoral with conspicuous megafauna (MEG). The exposed sand bar, made up mostly by well sorted fine sand, is formed by local current dynamics with occasional disturbance by wave action. The protected sand flat is protected from the southern and southeastern winds by a land mass (Mel Island), and has compacted and moderately sorted sediments, including shells of *Anomalocardia brasiliana* (Gmelin, 1791), a dominant venerid bivalve on the upper part of the sand flat, and few patches of the seagrass *Halodule* sp. The rippled sublittoral site is a sand transport environment with megaripples (~5 m long, ≤ 40 cm in height), with mostly well sorted fine sand. The sublittoral megafaunal site is mostly poorly sorted sand, apparently stable with no sign of erosion, with many holothurians and the sand-dollar *Mellita quinquesperforata* (Leske, 1778).

Surveys were conducted at each site from October 2002 to November 2004, over storm and calm (non-storm) conditions, herein considered as statistical treatments. A storm can be understood as a disturbance variable, in the sense that they

summon up a series of changes in atmospheric and oceanographic variables (wind speed, pluviosity, wave height, bottom sheer stress, turbidity, salinity). In the study area they can be characterized by wind shifting to a southerly direction, as well as the persistence of southerly winds for at least one day (RODRIGUES *et al.* 2004) (Fig. 2).
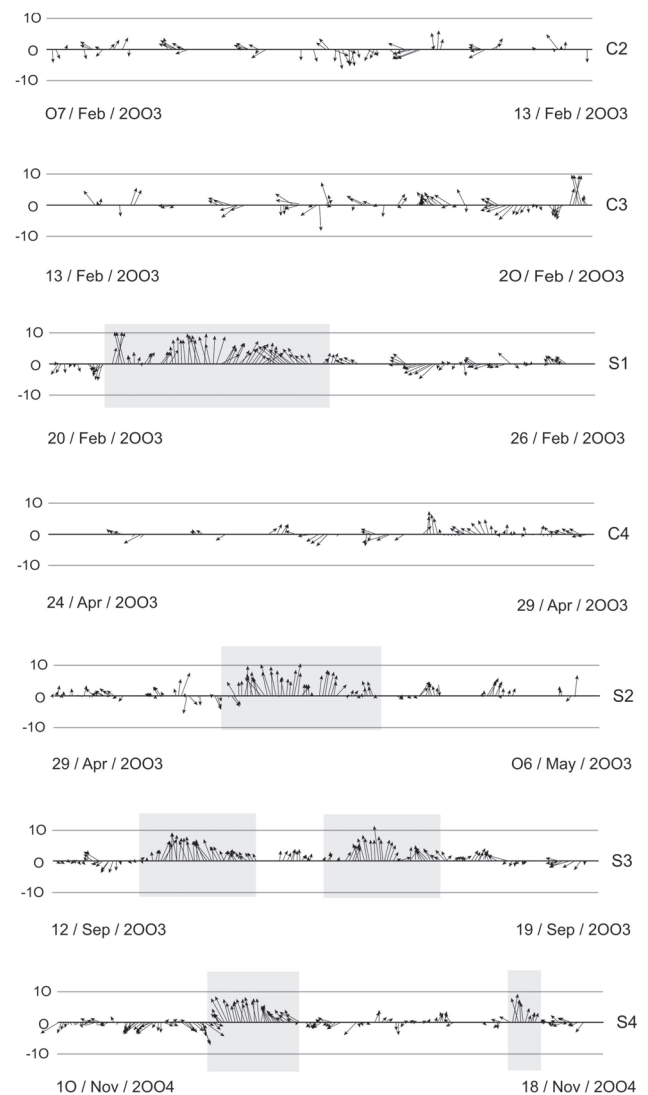

Figure 2. Graph showing wind velocity and directions during periods (5-8 days) between surveys. These periods are considered treatments depending on the presence or absence of wind shifts to a southerly direction (grey area), as well as the persistence of stronger southerly winds for at least one day. S (1-4) represents periods in which storm occurred and C (1-4) controls, or no storm condition. C1 (the only survey that took place in 2002) is not represented because the weather station was operational only by January 2003.

Storms are not predictable with precision so to choose the best sampling dates, we used weather forecasting available at the National Institute of Spatial Research (Instituto Nacional de Pesquisas Espaciais – INPE/CPTEC, www.cptec.inpe.br). Local atmospheric data were provided by the Physical Oceanography Lab at the Center for Marine Studies, Universidade Federal do Paraná. Once a storm prediction was reliably at hand, we quickly carried out a sampling survey prior to the storm, with subsequent sampling carried out 5-8 days later, as soon as navigation and diving conditions were reestablished (S1-4). Calm conditions were sampled using the same protocol, and over similar time intervals (C1-4).

Samples collected in February 20/Feb/2003 on stations PR and EX were lost due to poor preservation of specimens. In this case only we considered a grater time span for comparisons from 13 to 26/Feb/2003 (S1') and sampled another storm (S4) exclusively on these stations.

Three components of scale are important in ecological studies: grain, lag and extent (HEWITT *et al.* 1997, RAFFAELLI & MOLLER 2000). Thus, at each site sampling by scuba diving was conducted within a 15 m radius circle (aprox. 700 m²) that was positioned with permanent markers so that samples could be taken at exactly the same location. Within this area, 10 random replicates were taken, at each sampling event, at a distance greater than 1 m from one another to attempt to maintain spatial independence (SKILLETER 1996). Once sampled, depressions due to taking the sample were seldom visible (and then only at the protected sand flat and the subllitoral megafaunal sites) at a subsequent sampling time.

Since the physical disturbance caused by storms is restricted to the top few sediment surface centimeters (POSEY *et al.* 1996, GALLUCCI & NETTO 2004), in which most macrofauna is found, we used a circular corer of 15 cm wide x 5 cm height to sample. Samples were sieved through a 0.5 mm mesh and macrofauna were counted and identified under a dissecting microscope to the lowest possible taxonomic level.

We compared species richness, number of individuals and diversity (H') separately for each of the four locations, with *t* tests between consecutive (before/after) sampling dates. Multivariate comparisons of assemblage composition between consecutive dates were carried out using statistical routines in PRIMER version 5.0 (CLARKE & WARWICK 1994). Bray-Curtis index of similarity was calculated from square root transformed abundance data. An analysis of similarity (ANOSIM) was used to test the prediction that storms are associated with large changes in the macrofauna composition, while there is no or less changes in composition over similar time intervals during calm conditions. Multidimensional scaling (MDS) was used to illustrate changes in assemblage structure over time for each of the four locations.

We focused our attention on how each studied area, individually, responded to passing weather events. Statistical comparisons among sedimentary environments were not pursued because there was no point in testing for differences that were already apparent *a priori*. Moreover, such comparisons would demand another level of within site replication.

RESULTS

General community composition at locations

Macrofauna totaled 11,031 individual organisms in 176 taxa. Locations differed in composition, each with its own, mostly unshared assemblage of species. The protected sand flat (PR) had 61 taxa, the most common of which were the polychaetes *Terebellides anguicomus* Müller in Grube, 1858, *Ninoe* sp., *Heteromastus* sp. and one mollusk, *Bulla striata* Bruguière, 1792 (mostly juveniles). The exposed sand bar location (EX) had the fewest taxa (n = 20), the most common of which were the polychaetes *Armandia* sp. and *Scolelepis* sp. The rippled sublittoral location (RIP) had 51 taxa, with *Branchiostoma caribaeum* Sandevall, 1853, the amphipod *Eudevenopus* sp. and *Armandia* sp. being the most common. The sublittoral with megafauna location (MEG) had 97 taxa, dominated by *B. caribaeum*, *Laonice branchiata* Nonato, Bolivar & Lana, 1986 and *Magelona papilicornis* Müller, 1858.

Before/after comparisons

Macrofaunal richness, abundance and diversity varied over the duration of the study at all locations (Table I). Both intertidal and subtidal sites showed some significant differences on calm as well as storm treatments. There were significant differences in number of individuals in C4, S2, S3, S4 and diversity in S2 in the exposed sand bar site (EX). The protected sand flat (PR) showed significant results in number of species (C4 and S2), number of individuals (C1, C2, S1', C4, S2) and diversity (C4, S2).

The megarippled site (RIP) showed the most extreme result with no significant variation at all in storm periods. Significant differences were observed in number of species (C2, C3 and C4), number of individuals (C3 and C4) and diversity (C3). The subtidal site with megafauna (MEG) showed significant variations on all parameters during C1, for diversity in C2 and number of species in S1.

Most variation was clearly not influenced by storms (Table I). That is, changes in species richness, abundance and diversity in three locations between sampling occasions were more often observed for calm than storm treatments.

Multivariate analysis revealed that community structure did not change as hypothesized, with the results of ANOSIM test indicating that overall differences in structure were similar (if not slightly greater) between sampling occasions during calm periods and after storms (Table II). Significant differences were identified in all temporal comparisons at the protected sand flat and sublittoral with megafauna sites, but R values were over similar ranges in both treatments, and on average similar (PR: 0.27 for calm v 0.22 for storm) or the same (MEG: 0.31) (Table II). Significant differences in community structure be-

Table I. Results of t tests between sampling occasions for calm (C1-4) and storm (S1-4) treatments for all four sedimentary environments. Values are shown in bold when p is significant (p < 0.05). Samples collected in 20/Feb/2003 on stations PR and EX were lost due to poor preservation of specimens. In this case only we considered a grater time span for comparisons from 13 to 26/Feb/2003 (S1').

| | Exposed sand bar | | | | | | Protected sand flat | | | | | |
| | S | | N | | H' | | S | | N | | H' | |
	t	p	t	p	t	p	t	p	t	p	t	P
C1	-2.057	0.064	0.974	0,351	0.936	0.363	-1.902	0.073	-2.807	**0.012**	-0.798	0.435
C2	1.659	0.115	0.891	0,384	0.738	0.470	-1.745	0.100	-2.137	**0.048**	-0.934	0.364
C4	-0.553	0.587	-2.239	**0,038**	0.814	0.426	2.382	**0.028**	2.397	**0.028**	2.312	**0.033**
S1'	0.192	0.850	0.992	0,335	0.374	0.712	1.007	0.327	2.350	**0.030**	0.036	0.972
S2	0.198	0.845	2.118	**0,048**	-2.497	**0.022**	-2.984	**0.008**	-2.252	**0.037**	-2.639	**0.017**
S3	1.138	0.270	3.084	**0,006**	-0.609	0.550	-0.490	0.630	0.911	0.375	-0.350	0.730
S4	1.949	0.067	4.316	**0,000**	-1.953	0.067	-0.297	0.770	-0.576	0.572	-0.199	0.845

| | Rippled sublittoral | | | | | | Sublittoral with conspicuous megafauna | | | | | |
| | S | | N | | H' | | S | | N | | H' | |
	t	p	t	p	t	p	t	p	t	p	t	P
C1	1.584	0.134	-1.733	0.104	1.982	0.066	-2.830	**0.014**	2.919	**0.012**	-6.089	**0.000**
C2	-2.902	**0.010**	-1.579	0.132	-1.410	0.175	-2.106	0.049	-0.039	0.969	-3.663	**0.002**
C3	4.309	**0.000**	2.957	**0.009**	2.486	**0.024**	1.861	0.079	1.126	0.275	2.092	0.051
C4	-2.744	**0.013**	-3.267	**0.004**	-0.814	0.427	1.052	0.308	1.155	0.265	-0.115	0.910
S1	-0.658	0.519	-0.895	0.383	-0.047	0.963	-1.988	0.062	-2.238	**0.038**	-1.112	0.281
S2	0.726	0.477	1.782	0.092	-0.315	0.757	0.179	0.860	-0.901	0.380	1.603	0.127
S3	-0.779	0.447	-0.743	0.468	-0.563	0.580	0.122	0.904	1.771	0.097	-0.558	0.585

Table II. Results of ANOSIM pair-wise comparisons of assemblage similarity between sampling occasions for calm (C1-4) and storm (S1-4) treatments for all four sedimentary environments (PR = protected sand flat, EX = exposed sand bar, RIP = rippled sublittoral, MEG = sublittoral with conspicuous megafauna). R values are shown in bold when p is significant (p < 0.05). Samples collected in 20/Feb/2003 on stations PR and EX were lost due to poor preservation of specimens. In this case only we considered a grater time span for comparisons from 13 to 26/Feb/2003 (S1').

		PR	EX	RIP	MEG
C1	03/Oct/2002-08/Oct/2002	**0.373**	**0.690**	-0.039	**0.431**
C2	07/Feb/2003-13/Feb/2003	**0.318**	**0.140**	0.111	**0.485**
C3	13/Feb/2003-20/Feb/2003	–	–	0.063	**0.137**
C4	24/Apr/2003-29/Apr/2003	**0.132**	-0.008	**0.330**	0.171
S1	20/Feb/2003-26/Feb/2003	–	–	0.049	**0.128**
S1'	13/Feb/2003-26/Feb/2003	**0.288**	0.041	–	–
S2	29/Apr/2003-06/May/2003	**0.183**	0.000	**0.158**	**0.551**
S3	12/Sep/2003-19/Sep/2003	**0.199**	0.084	**0.123**	**0.241**
S4	10/Nov/2004-18/Nov/2004	**0.211**	**0.404**	–	–

tween treatments were found less frequently on exposed sand bar and rippled sublittoral, and on average R values were small, similar between treatments and the observed changes seemingly unrelated to storms.

The MDS ordination plots (Fig. 3) illustrate that ANOSIM results, showing that the magnitude of change in community structure between sampling occasions is similar for both calm and storm treatments for all sites. The MDS plots also show that there was no general pattern of grouping of samples by treatment or any general tendency for the post storm samples to illustrate any recovery towards the community structure observed during calm periods.
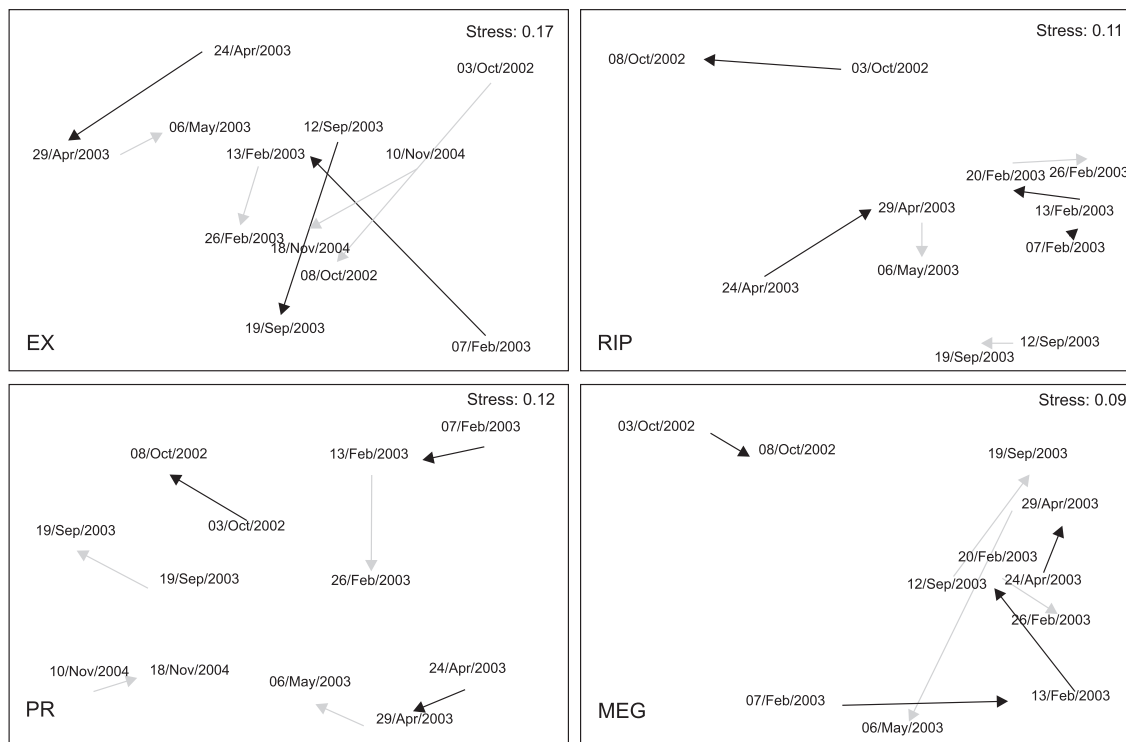
Figure 3. Non-metric multidimensional scaling plots of sampling dates at the four locations: exposed sand bar (EX),protected sand flat (PR), rippled sublittoral (RIP) and sublittoral with conspicuous megafauna (MEG). Dates represent the centroids of ten sampling units. Arrowed lines connect consecutive dates for storm (light grey lines) and calm (solid lines) treatments.

DISCUSSION

Our study tested for the presumed effect of storms on macrofaunal assemblages at four sites of Paranaguá Estuarine Complex. These events are the most common, and sometimes most intense, natural disturbance along the southern Brazilian coast, hence their potential to regulate macrobenthic dynamics (Rodrigues *et al.* 2004, Parise *et al.* 2009). For this reason, we expected to get results with a consistent pattern of changing numbers of species and individuals after such events and relative stability during calm weather periods.

Actual results refuted this working hypothesis. There were no clear short-term (5-8 days) effects of storms on the species richness, abundance and diversity of estuarine macrofauna. Results showed that fluctuation in numbers is the norm, but there were no temporal recurring pattern after storms (S1, S2, S3 and S4) in each site. Conversely, spatial differences were equally variable, with changes occurring regardless of weather conditions.

The variable temporal response in all measured assemblage parameters at all four sites, both during calm and storm conditions can be interpreted as a constant rearrangement of macrofaunal community structure. Multivariate analyses

showed that time periods before and after storms had no tendency to form groups (pre-disturbance vs. post-disturbance). What seems to be the case in all four studied sites is an ongoing modification in species composition and number of individuals.

Changes can occur as animals arrive or leave a site, either by dispersal or mortality. Instead of the negative effects of increased mortality associated with disturbance events, increased dispersal may be the most common process at the study sites as suggested by the significant differences more often observed in the number of individuals than in number of species (Palmer *et al.* 1996). Fluctuating numbers of individuals and an uneven pattern of change in the number of species suggested that dispersal and new colonization could account for observed changes in the composition and abundance of local assemblages (Günther 1992).

It can be argued that the time lag between sampling occasions (which was determined mainly by logistical constraints) may have been too long to detect a short term effect of the storms on the macrofauna assemblages at the study sites. Storm events typically lasted 48 hours at most (Fig. 2), and it is possible that any significant changes in assemblage structure may have only been detectable shortly after, and that recovery had

already begun by the time samples were taken 5-8 days after the storm. Working at a sandy beach, where sampling during storms was viable, Gallucci & Netto (2004) reported a decrease in numbers of species, abundance and diversity, that lasted for the day of the disturbance only, with fast recovery to previous conditions soon after.

The question of scale is the key to sum up our current findings, or at least to put them into context, even in the absence of better long-term meteorological information. The fact that ecological descriptors showed no clear variation patterns and oscillated in an uneven way, mostly during calm periods, refuted our initial hypotheses that storms cause decreases in the number of species and individuals. Even on mobile sands, both at intertidal and subtidal areas, recurring and consistent changing patterns were not observed.

We were able to show that "regular" subtropical storms are not major driving forces of the composition and abundance of shallow-water estuarine macrofauna in different sedimentary estuarine environments. However, we do not discard the possibility that extreme meteorological events over the Western South Atlantic Ocean, such as the Catarina subtropical hurricane (McTaggart-Cowan *et al.* 2004), may be proven relevant to affect benthic assemblages (Davis *et al.* 2004). Moreover, factors such as the role of cyclical oscillations such as tidal currents and flooding (Grilo *et al.* 2011) must be taken into account.

ACKNOWLEDGMENTS

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