IMPACT OF PLANT COVER REMOVAL ON MACROBENTHIC COMMUNITY STRUCTURE OF A SUBTROPICAL SALT MARSH

Paulo Roberto Pagliosa and Paulo da Cunha Lana

ABSTRACT

A short-term field experiment was conducted to investigate the effects of plant cover removal on temporal trends of species richness and abundance of the macrobenthic community in a subtropical salt marsh in Paranaguá Bay (southeastern Brazil). Plant cover was removed to test the hypothesis that habitat complexity plays an important role in structuring infaunal and epifaunal assemblages. Habitat complexity for the macrofauna assemblages, above and below the sediment surface, was greatly influenced by *Spartina alterniflora* Loisel, 1807 leaves, culms, roots, and rhizomes. The response of infaunal or epifaunal species depended on their ability to discriminate between vegetated or unvegetated habitats. Habitat specialists from the epifauna —forms closely associated with plant structures, such as the gastropod *Neritina virginea* (Linnaeus, 1758), the isopod *Sphaeromopsis mourei* (Loyola and Silva, 1960), and an unidentified gammarid species— were clearly affected by plant removal, whereas the habitat generalist epifaunal *Kalliapseudes schubarti* Mañé-Garzon, 1969 (Tanaidacea) did not respond to it. Relative abundances of habitat specialist infauna, such as the polychaetes *Isolda pulchella* Müller, 1858 and *Ne-reis oligohalina* Rioja, 1946, and habitat generalist infauna, such as the polychaetes *Laeonereis acuta* Treadwell, 1923 and *Capitella* sp., did not change significantly after plant removal. Abundance of local macrobenthic species was significantly correlated to rainfall and tended to be reduced after intense freshwater inputs in the summer. Changes in local macrobenthic associations were the result of interactive effects of plant biomass and sediment changes on small spatial scales, and physical impacts of summer freshwater runoff on large spatial scales.

Habitat complexity regulates plant and animal communities at different spatial and temporal scales. Plant cover is one of the main sources of spatial heterogeneity in tropical and subtropical tidal flats, since the distribution, density, and architecture of mangrove and saltmarsh plants can heavily influence the abundance and diversity of benthic invertebrates (Costa and Davis, 1992; Lana et al., 1997). Both grasses and shrubs from salt marshes or trees from mangrove stands are presumed to stabilize sediments and to provide food and shelter from predators for the benthic fauna (Micheli, 1996; Sardá et al., 1998; Schrijvers et al., 1998). Conversely, unvegetated tidal flats are presumed to sustain less diversified and abundant macrobenthic associations. However, even those apparently homogeneous intertidal areas are full of biogenic structures and microtopographical features, which can introduce spatial heterogeneity (Levin et al., 1998; Blanchard and Bourget, 1999).

Wetlands are a source of coastal protection and are frequently advocated for practical environmental restoration. The potential value of salt marshes for conservation is generally recognized, at least in terms of the diversity of plants and animals associated with them (Boorman, 1999). However, both natural and manmade disturbances may lead to vegetation loss in salt marshes. Natural disturbance can result from wrack deposition, grazing, and storms; whereas cultivation, restoration, reclamation, landfill, embankment, earthwork, and clipping for fishing activities are the more evident human impacts on the salt marshes. The effects of aquatic vegetation...
losses on invertebrates are better known in seagrass habitats but still poorly understood in salt marshes.

There is an impressive literature on the fauna of salt marshes, mainly in the northern hemisphere. This is not the case, however, for the fauna of tropical or subtropical marshes associated with or out-competed by mangrove woodland. Studies on macrobenthic species from intertidal flats of Paranaguá Bay (southeastern Brazil) have indicated that plant architecture, detrital input, and predation pressure play a major role in structuring epifaunal communities (Lana and Guiss, 1992). Infaunal abundance is related to below-ground plant biomass, which provides refuge to organisms or physical support to tubes. Seasonal changes in *Spartina alterniflora* Louisel, 1807 biomass, with typical cycles of below-ground storage in late winter and spring followed by aerial translocation in summer, influence both the abundance (Lana and Guiss, 1991) and reproductive strategies (Pagliosa and Lana, 2000) of local macrofauna. The more exposed the tidal flats, the more faunal numbers differ between vegetated and unvegetated sediments (Netto and Lana, 1996, 1999; Lana et al., 1997). These complex plant-animal relationships are also affected by freshwater runoff during spring and summer months (Pagliosa, 1997).

Experimental approaches are an useful tool to quantitatively and qualitatively assess the influence of environmental disturbance on benthic fauna. Field experiments are widely used to assess the role of habitat complexity in influencing the structure and function of soft-sediment communities. Experimental removal of plant cover, followed by the analysis of faunal trends, has provided insight on the putative importance of such regulating mechanisms. However, the effects of artifacts arising from experimental investigations in soft-sediments should not be minimized (Peterson and Black, 1994; Skilleter, 1996).

This study was undertaken to analyze the effects of plant cover on short-term trends in species richness and abundance of macrobenthic associations in an intertidal flat of Paranaguá Bay. Plant cover was removed to test the hypothesis that habitat complexity plays an important role in structuring infaunal and epifaunal associations.

**Material and Methods**

**Experimental Site.**—Paranaguá Bay (25° 30′ S, 48° 25′ W) is one of the least polluted estuarine systems in southeastern Brazil (Fig. 1). The bay has a well developed high energy euhaline sector (average salinity values close to or higher than 30), with extensive tidal flats, which can reach a width of up to 2 km. Water circulation in Paranaguá Bay is driven mainly by river runoff and tidal forcing, with semidiurnal tide and diurnal inequalities. Strong non-linear interactions allow for the formation of up to six high and low tides per day during neap cycles, when tidal heights are around 80% of the height of spring tides. Wave action, mainly originating from the southeast, is only important at the bay mouth, but winds may produce locally generated surface waves when blowing in the east-west direction (Lana et al., 2000).

Paranaguá Bay is surrounded by a diverse set of natural habitats, which include mangrove swamps, salt marshes, and extensive unvegetated flats. The region as a whole is a transitional zone for tropical mangroves, which begin to be replaced by temperate salt marshes. Pure stands of *S. alterniflora* colonize well-sorted sand sediments in the euhaline sector, as narrow discontinuous belts in front of mangrove woodland (Lana et al., 1991).

The field experiment was conducted at an intertidal flat in Rasa da Cotinga Island (25°31.95′ S, 48°23.99′ W), near the outlet of Paranaguá Bay (Fig. 1). The local flat has a width of about 600 m from the salt marsh belt to the lower spring tide level. The upper region, colonized by *Spartina*, is steeper (0.45 m over 10 m), followed by a gentler slope (0.55 m over 590 m). Local
sediments are mainly well-sorted fine sands, with low organic content in the upper region and well-developed aggregates of shell fragments in the lower region.

**Experimental Procedure and Design.**—Experiments were conducted from January to April 1995. We established two experimental sites, made up of three treatments each, hereafter called unvegetated, vegetated, and cleared plots. Natural differences between sites were slightly related to site elevation, density, and height of shoots. Plots were 14 m² (2 × 7 m) and were separated by ca. 5 m from each other. At each cleared plot, leaves and culms of *S. alterniflora* were clipped at ground level and removed from the experimental site together with attached epibenthic species. One additional plant cutting and removal was carried out 1 wk later; growth or regeneration of leaves and culms were not a problem thereafter. From January to April 1995 each plot was sampled every 2 wks (seven sampling dates, including the setup of the experiment when only vegetated and unvegetated habitats were sampled). At each plot, five random biological core samples were taken with a PVC core tube, 15 cm in height and 15 cm wide (0.02 m² of area), and one sediment sample was taken with a PVC sampler, 5 cm in height and 10 cm wide. We estimated that the removal of biological and sedimentological samples did not affect more than 20% of total plot area throughout the experiment.

The bulk samples were fixed in 10% formalin, dyed with Bengal red (0.0005 g ml⁻¹), and sieved through a 500 µm mesh. Macrofauna were preserved in 70% alcohol. Below-ground material, identified as living plant biomass (whitish rhizomes and roots) and detritus (organic debris and shells), was estimated by drying to constant weight at 75 °C. The water content of the sediment was determined as weight loss after drying. Sediment organic content was calculated after burning subsamples at 550 °C for 1 hr, and carbonate content through acidification (HCl at 10%). Sediments were analyzed, using the pipette and dry sieve method (Carver, 1970). Salinity and temperature of the surface sediment layer were recorded in the field. Daily rain values for the period of the experiment were obtained from a meteorological station situated at the Paranaguá Harbour (Fig. 1).

**Data Analyses.**—Data analyses were applied to a frequency matrix of the 16 top taxa or species in terms of abundance (98% of total). Differences in the structure of assemblages

---

**Figure 1.** Study site (●) in Paranaguá Bay, southeastern coast of Brazil.
among treatments and sampling dates were described by non-metric Multi-Dimensional Scaling ordination (nMDS) on double square-root transformed data, using the Bray-Curtis similarity measure (Clarke and Green, 1988). The multidimensional adjustment of the data to the bi-dimensional scale can be measured by the stress value. Stress values lower than 0.2 represent a good relationship among samples. Similarities among species were calculated from standardized data, with the abundance of species within a given sample divided by the total abundance of this species in all samples. One-way analyses of similarities (ANOSIM) and pairwise comparisons tested for differences among treatments in epifaunal and infaunal nMDS plots (Clarke, 1993).

To test the differences in plots (vegetated, unvegetated, and cleared) and six sampling dates (all dates after clipping vegetation) with regard to the mean abundance of each selected species, weight of detritus, below-ground live biomass of S. alterniflora, sand, silt, clay, carbonate, water, and organic content of sediment we used a repeated measures ANOVA. This repeated measures approach was used because the field experiment was pseudoreplicated sensu Hulbert (1984) and repeated measures ANOVA incorporates the dependence of observations in each treatment (Winer, 1971; Green, 1993; Underwood, 1997). Whenever necessary we used double square-root transformations for homogeneity of variances, as appointed by Cochran’s test.

Whenever significant differences were detected (P < 0.05), a posteriori LSD (least significant difference) test or multiple comparisons test (for significant interaction of the fixed factors) was applied.

The average values of five samples from each plot in each time were used to give the repeated measures, legitimizing replicates and avoiding spatial interdependency of samples. However, taking consecutive samples in the same plot throughout an experiment may introduce a considerable risk of temporal dependence of samples because disturbance from previous samplings can affect the abundance and species richness of benthic assemblages. The dependence of samples can lead to increased or decreased probability of Type I error, depending on whether there are negative or positive serial correlations (Underwood, 1997). To check if samples from a same plot were correlated, we determined the variance among replicates for independently sampled data from previous works on vegetated and unvegetated habitats (Lana and Guiss, 1991; Lana et al., 1997; Netto and Lana, 1999) and compared them with our current data set. The global effect among all treatments was tested using one-way ANOVA in order to detect significant differences of macrofaunal densities among different data sets ($F_{3,82} = 3.81, P < 0.01$). Since the within-sample variance from our data did not differ significantly from previous data sets (LSD test, all $P > 0.05$), we assumed that the dependence of samples was not a fatal problem throughout the experiment.

Results

General Trends of Variation in Non-Manipulated Habitats.—Temperature and salinity ranges were typical for the euhaline sector of Paranaguá Bay during warmer months, varying from 30 to 24 ºC (mean of 27.6 [SD] ± 1.4, n = 20) and 18–32 (mean of 27.2 ± 3.4, n = 19). Heavy rains occurred just before the beginning of the study, with 545 mm of precipitation during the first 2 wks of January and an additional 1045 mm throughout the remaining 3 mo. These represented about 52% of the annual rainfall for 1995 (Mantovanelli, 1999). Close to the end of the experiment, tidal ranges increased progressively towards equinoctial regimes and enhanced the flood time at the experimental site. Sediment was generally symmetric well-sorted fine sand with silt-clay content from 0% to 9.5% (mean of 3.8 ± 2.4, n = 28). Water and organic content of the sediment were higher at vegetated than at unvegetated
habitats, varying from 24% to 36% (mean of 27 ± 2.4, n = 28), and from 0.9% to 3.3% (mean of 1.6 ± 0.7, n = 28).

We identified 60 macrofaunal taxa, with total densities ranging from 1 to 773 ind. 0.02 m$^{-2}$. The surface deposit-feeding polychaetes *Capitella* sp., *Laeonereis acuta* Treadwell, 1923, and *Nereis oligohalina* Rioja, 1946 were numerically dominant and persistent both in vegetated and unvegetated plots. More than two thirds of the total macrofauna occurred in the vegetated plots, where the polychaetes *Isolda pulchella* Müller, 1858, *Capitella* sp., *L. acuta*, and *N. oligohalina* accounted for 82% of the organisms. In the unvegetated plots, *L. acuta* (52%) and *Capitella* sp. (22%) were numerically dominant.

The effects of heavy rainfall just prior to the beginning of the experiment were evident on macrofauna as a whole. At the first sampling date, average benthic densities were 31 ind. 0.02 m$^{-2}$ (SD = 16.3, n = 10) within saltmarsh plots and 6.5 ind. 0.02 m$^{-2}$ (SD = 4.3, n = 10) within unvegetated plots. Faunal densities rapidly recovered and average densities for the remaining sampling dates were 165 ind. 0.02 m$^{-2}$ (SD = 133.5, n = 60) and 104 ind. 0.02 m$^{-2}$ (SD = 56.7, n = 60) for saltmarsh and unvegetated plots, respectively.

Two sample or species groups could be recognized in the nMDS ordinations of vegetated and unvegetated plots (Fig. 2). In the sample analysis the vegetated and unvegetated areas were clearly separated. The only exceptions were the samples of unvegetated plots from the first sampling date, which did not group because of their low faunal densities. In the species analysis the vegetated and unvegetated areas were also clearly evident, with a further distinction between groups of infaunal and epifaunal species. In the unvegetated plots, the infaunal *Capitella* sp., *Glycinde multidens* Müller, 1858, *Sigambra grubei* Müller, 1858, *L. acuta*, *Anomalocardia brasiliana* Gmelin, 1791, *Macoma constricta* (Bruguière, 1792), and unidentified oligochaete species were separated from the epifaunal tanaidacean *Kalliapseudes schubarti*. The effects of heavy rainfall just prior to the beginning of the experiment were evident on macrofauna as a whole. At the first sampling date, average benthic densities were 31 ind. 0.02 m$^{-2}$ (SD = 16.3, n = 10) within saltmarsh plots and 6.5 ind. 0.02 m$^{-2}$ (SD = 4.3, n = 10) within unvegetated plots. Faunal densities rapidly recovered and average densities for the remaining sampling dates were 165 ind. 0.02 m$^{-2}$ (SD = 133.5, n = 60) and 104 ind. 0.02 m$^{-2}$ (SD = 56.7, n = 60) for saltmarsh and unvegetated plots, respectively.

Two sample or species groups could be recognized in the nMDS ordinations of vegetated and unvegetated plots (Fig. 2). In the sample analysis the vegetated and unvegetated areas were clearly separated. The only exceptions were the samples of unvegetated plots from the first sampling date, which did not group because of their low faunal densities. In the species analysis the vegetated and unvegetated areas were also clearly evident, with a further distinction between groups of infaunal and epifaunal species. In the unvegetated plots, the infaunal *Capitella* sp., *Glycinde multidens* Müller, 1858, *Sigambra grubei* Müller, 1858, *L. acuta*, *Anomalocardia brasiliana* Gmelin, 1791, *Macoma constricta* (Bruguière, 1792), and unidentified oligochaete species were separated from the epifaunal tanaidacean *Kalliapseudes schubarti*. The effects of heavy rainfall just prior to the beginning of the experiment were evident on macrofauna as a whole. At the first sampling date, average benthic densities were 31 ind. 0.02 m$^{-2}$ (SD = 16.3, n = 10) within saltmarsh plots and 6.5 ind. 0.02 m$^{-2}$ (SD = 4.3, n = 10) within unvegetated plots. Faunal densities rapidly recovered and average densities for the remaining sampling dates were 165 ind. 0.02 m$^{-2}$ (SD = 133.5, n = 60) and 104 ind. 0.02 m$^{-2}$ (SD = 56.7, n = 60) for saltmarsh and unvegetated plots, respectively.

Two sample or species groups could be recognized in the nMDS ordinations of vegetated and unvegetated plots (Fig. 2). In the sample analysis the vegetated and unvegetated areas were clearly separated. The only exceptions were the samples of unvegetated plots from the first sampling date, which did not group because of their low faunal densities. In the species analysis the vegetated and unvegetated areas were also clearly evident, with a further distinction between groups of infaunal and epifaunal species. In the unvegetated plots, the infaunal *Capitella* sp., *Glycinde multidens* Müller, 1858, *Sigambra grubei* Müller, 1858, *L. acuta*, *Anomalocardia brasiliana* Gmelin, 1791, *Macoma constricta* (Bruguière, 1792), and unidentified oligochaete species were separated from the epifaunal tanaidacean *Kalliapseudes schu-
Species groups of vegetated plots were made up by the infaunal *Heteromastus similis* Southern, 1921, *I. pulchella*, *N. oligohalina*, *Polydora socialis* (Schmarda, 1861), *Lucina pectinata* Gmelin, 1791, and the epifaunal *Neritina virginea* (Linnaeus, 1758), *Sphaeromopsis mourei* (Loyola and Silva, 1960), and an unidentified gammarid species.

**Effects of Plant Cover Removal.**—Live below-ground biomass of *S. alterni-flora* was lower in the unvegetated control, where roots and rhizomes were absent (ANOVA, *P* < 0.005), but did not differ between cleared and vegetated plots throughout the experiment (LSD test, *P* > 0.66; Fig. 3). Detritus, sand, silt, clay, carbonate, organic, and water sediment content did not differ significantly among treatments (ANOVA, all *P* > 0.14), but detritus, sand, and clay contents differed among sampling dates (ANOVA, all *P* < 0.02). With progressively lower rainfall during the experiment, sand content increased in all plots, followed by lower values of clay, and a great variation in silt (Fig. 3). The only significant interaction between treatments and sampling dates was detected for silt content (ANOVA, *P* < 0.03), with a marked decrease of average values at the tenth sampling week in the vegetated plots (multiple comparisons test, *P* < 0.004). Detritus availability tended to increase mainly in the vegetated plots, but decreased significantly in all plots at the tenth sampling week, when the highest values of sand were recorded (Fig. 3).

Epifauna and infauna responded differently to plant cover removal (Figs. 4 and 5). In general, infaunal numbers did not change significantly after the clipping of *Spartina* shoots. nMDS ordination of infaunal species revealed a clear separation between habitats, with higher infaunal numbers in vegetated than in unvegetated plots (ANOSIM, *P* < 0.001; Fig. 6A, Table 1). However, infauna from vegetated plots grouped with infauna from cleared plots, suggesting that plant cover removal did not affect subsurface assemblages.

Infaunal numbers increased for major taxa throughout the experiment (Figs. 4 and 5; Tables 2 and 3). The analysis of variances detected two distinct response patterns for infaunal species, depending on their ability to discriminate between vegetated or unvegetated habitats. The numbers of habitat specialists (vegetated group in Fig. 2b), *N. oligohalina*, *I. pulchella*, *P. socialis*, and *H. similis* were higher in cleared plots than in unvegetated plots (ANOVA, all *P* < 0.02; Table 2) but matched the numbers from vegetated areas (LSD test, all *P* > 0.17). The bivalve *L. pectinata* was the only habitat specialist whose numbers did not differ among plots (ANOVA, *P* > 0.70; Table 3).

The numbers of other infaunal species, such as the polychaetes *Capitella* sp., *L. acuta*, *G. multidens*, *S. grubei*, the bivalves *M. constricta*, *A. brasiliana*, and unidentified oligochaetes (unvegetated group in Fig. 2B) did not differ significantly among cleared, unvegetated, and vegetated plots (ANOVA, all *P* > 0.05; Tables 2 and 3), suggesting that they did not discriminate between habitats. However, significant differences among treatments were detected at the second, fourth, or eighth week of the experiment for the habitat generalists *Capitella* sp., *L. acuta*, and *M. constricta* (ANOVA, all interaction *P* < 0.03, and all multiple comparisons tests *P* < 0.04; Tables 2 and 3). No differences were detected among treatments for the habitat generalist *A. brasiliana*, but the densities differed significantly for each treatment among sampling dates (ANOVA, all *P* < 0.02, and all multiple comparisons tests *P* < 0.02; Table 3). Average densities of the habitat generalist oligochaetes did not differ significantly among plots or sampling dates (ANOVA, *P* > 0.61 and *P* > 0.89, respectively).
Figure 3. Means (± 1 SD) for environmental variables in the plant cover removal experiment. Results of LSD test comparing treatments [unvegetated (U), vegetated (V), and cleared (C) plots] and sampling dates (weeks, W) are indicated above plots. * Significant difference among treatments for specific sampling date in multiple comparisons test.
Figure 4. Means (± 1 SD) for densities of infaunal species (Polychaeta) in the plant cover removal experiment.
Figure 5. Means (± 1 SD) for infaunal (other than Polychaeta) and epifaunal species in the plant cover removal experiment.
Epifaunal numbers were significantly higher in vegetated than in unvegetated plots, and, contrary to infauna, numbers in vegetated plots were also higher than in cleared plots (ANOSIM, P < 0.001; Fig. 6B, Table 1). Differences between unvegetated and cleared plots were less evident (ANOSIM, P = 0.025; Table 1). nMDS ordination showed that samples of the cleared plots were close to vegetated ones on the first sampling date, but progressively matched samples from unvegetated plots until the end of the experiment (Fig. 6B).

Again, the ability to discriminate between unvegetated and vegetated habitats guided epifaunal responses. Whenever plant cover was removed in experimental plots, the response of habitat specialist epifaunal species (vegetated group in Fig. 2B) was opposite to that of the habitat specialist infauna. Densities of *S. mourei* and an unidentified gammarid species did not differ significantly between cleared and unvegetated plots, but were significantly higher in vegetated plots (ANOVA, P < 0.005; Table 3). No differences were detected in the densities of the habitat specialist *N. virginea* among treatments (ANOVA, P > 0.05). The only epifaunal species to show a significant temporal variation, with higher densities at the end of the experiment, was the habitat generalist tanaidacean *K. schubarti* (ANOVA, P < 0.0002; Table 3).

![Figure 6. nMDS ordination for (A) infaunal and (B) epifaunal assemblages from the plant cover removal experiment.](image)

<table>
<thead>
<tr>
<th>Groups used</th>
<th>R-values of infauna</th>
<th>R-values of epifauna</th>
</tr>
</thead>
<tbody>
<tr>
<td>Global</td>
<td>0.49***</td>
<td>0.59***</td>
</tr>
<tr>
<td>Pairwise test</td>
<td>V C U</td>
<td>V C U</td>
</tr>
<tr>
<td>U–V</td>
<td>0.76 ***</td>
<td>0.97 ***</td>
</tr>
<tr>
<td>U–C</td>
<td>0.75 ***</td>
<td>0.13 *</td>
</tr>
<tr>
<td>V–C</td>
<td>-0.01</td>
<td>0.56 ***</td>
</tr>
</tbody>
</table>

Underline ( _ ) denotes no significant differences between means at *** P < 0.001 and * P < 0.03.
Table 2. Results of repeated measures ANOVA of abundance of eight infaunal species (Polychaeta), and a posteriori LSD test for differences in unvegetated (U), vegetated (V), and cleared (C) plots in the plant cover removal experiment. Sampling dates occurred every 2 wks (W).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>MS</th>
<th>F</th>
<th>MS</th>
<th>F</th>
<th>MS</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plot (P)</td>
<td>2</td>
<td>8.66</td>
<td>34.33 **</td>
<td>11.48</td>
<td>77.66 **</td>
<td>2.69</td>
<td>158.29 ***</td>
<td>0.95</td>
<td>25.84 *</td>
</tr>
<tr>
<td>Date (D)</td>
<td>5</td>
<td>1.33</td>
<td>10.37 ***</td>
<td>0.23</td>
<td>2.37</td>
<td>0.88</td>
<td>16.47 ***</td>
<td>0.20</td>
<td>1.99</td>
</tr>
<tr>
<td>P × D</td>
<td>15</td>
<td>0.16</td>
<td>1.23</td>
<td>0.13</td>
<td>1.37</td>
<td>0.07</td>
<td>1.23</td>
<td>0.13</td>
<td>1.33</td>
</tr>
<tr>
<td>Residual 1</td>
<td>3</td>
<td>0.25</td>
<td>0.15</td>
<td>0.02</td>
<td>0.04</td>
<td>0.10</td>
<td>0.10</td>
<td>0.04</td>
<td>0.10</td>
</tr>
<tr>
<td>Residual 2</td>
<td>15</td>
<td>0.13</td>
<td>0.10</td>
<td>0.05</td>
<td>0.10</td>
<td>0.10</td>
<td>0.10</td>
<td>0.04</td>
<td>0.04</td>
</tr>
<tr>
<td>LSD test W2 W12 W10 W6 W4 W2</td>
<td>V C U</td>
<td>V C U</td>
<td>V C U</td>
<td>V C U</td>
<td>V C U</td>
<td>V C U</td>
<td>V C U</td>
<td>V C U</td>
<td>V C U</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>MS</th>
<th>F</th>
<th>MS</th>
<th>F</th>
<th>MS</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plot (P)</td>
<td>2</td>
<td>6.43</td>
<td>1.95</td>
<td>1.10</td>
<td>0.62</td>
<td>0.05</td>
<td>0.37</td>
<td>3.10</td>
<td>17.80 *</td>
</tr>
<tr>
<td>Date (D)</td>
<td>5</td>
<td>3.42</td>
<td>3.10</td>
<td>1.45</td>
<td>7.86 ***</td>
<td>1.22</td>
<td>24.00 ***</td>
<td>2.17</td>
<td>9.98 ***</td>
</tr>
<tr>
<td>P × D</td>
<td>15</td>
<td>0.76</td>
<td>0.69</td>
<td>0.18</td>
<td>0.98</td>
<td>0.21</td>
<td>4.13 **</td>
<td>0.69</td>
<td>3.19 *</td>
</tr>
<tr>
<td>Residual 1</td>
<td>3</td>
<td>3.30</td>
<td>1.79</td>
<td>0.13</td>
<td>0.17</td>
<td>0.17</td>
<td>0.17</td>
<td>0.17</td>
<td>0.17</td>
</tr>
<tr>
<td>Residual 2</td>
<td>15</td>
<td>1.10</td>
<td>0.18</td>
<td>0.05</td>
<td>0.22</td>
<td>0.22</td>
<td>0.22</td>
<td>0.22</td>
<td>0.22</td>
</tr>
</tbody>
</table>

*Where significant interactions were detected, multiple comparisons were used to test for differences in treatments. Underline ( _ ) denotes no significant differences between means at * P < 0.05, ** P < 0.01, and *** P < 0.001.
Table 3. Results of repeated measures ANOVA of abundance of eight infaunal (other than Polychaeta) and epifaunal species, and a posteriori LSD test for differences in unvegetated (U), vegetated (V), and cleared (C) plots in the plant cover removal experiment. Sampling dates occurred every 2 wks.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>M. constricta</th>
<th>A. brasiliana</th>
<th>L. pectinata</th>
<th>Oligochaeta</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plot (P)</td>
<td>2</td>
<td>3.82</td>
<td>0.42</td>
<td>0.30</td>
<td>0.54</td>
</tr>
<tr>
<td>Date (D)</td>
<td>5</td>
<td>7.60</td>
<td>0.63</td>
<td>0.07</td>
<td>0.03</td>
</tr>
<tr>
<td>P x D</td>
<td>10</td>
<td>1.20</td>
<td>0.07</td>
<td>0.08</td>
<td>0.12</td>
</tr>
<tr>
<td>Residual 1</td>
<td>3</td>
<td>1.74</td>
<td>0.81</td>
<td>0.76</td>
<td>0.93</td>
</tr>
<tr>
<td>Residual 2</td>
<td>15</td>
<td>0.25</td>
<td>0.02</td>
<td>0.07</td>
<td>0.11</td>
</tr>
<tr>
<td>LSD test</td>
<td></td>
<td></td>
<td></td>
<td>U C V</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>N. virginea</th>
<th>K. schubarti</th>
<th>Gammaridae</th>
<th>S. mourei</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plot (P)</td>
<td>2</td>
<td>3.23</td>
<td>1.15</td>
<td>1.88</td>
<td>2.65</td>
</tr>
<tr>
<td>Date (D)</td>
<td>5</td>
<td>0.18</td>
<td>0.55</td>
<td>0.08</td>
<td>0.08</td>
</tr>
<tr>
<td>P x D</td>
<td>10</td>
<td>0.09</td>
<td>0.10</td>
<td>0.10</td>
<td>0.05</td>
</tr>
<tr>
<td>Residual 1</td>
<td>3</td>
<td>0.37</td>
<td>0.26</td>
<td>0.06</td>
<td>0.05</td>
</tr>
<tr>
<td>Residual 2</td>
<td>15</td>
<td>0.06</td>
<td>0.05</td>
<td>0.13</td>
<td>0.04</td>
</tr>
<tr>
<td>LSD test</td>
<td></td>
<td>W12 W10 W8 W4 W6 W2</td>
<td>V C U</td>
<td>V C U</td>
<td></td>
</tr>
</tbody>
</table>

\[^5\]Where significant interactions were detected, multiple comparisons were used to test for differences in treatments. Underline (\_) denotes no significant differences between means at ** P < 0.01, and *** P < 0.001.
**Discussion**

Experimental clipping of *S. alterniflora* cover resulted in responses of epi- and infaunal species dependent on their preferred habitat characteristics. Habitat specialists may be more susceptible to plant changes than habitat generalists, while the latter may be more affected by the impact of sediment disturbance than the former. The habitat generalists, such as the numerically dominant deposit feeders polychaetes *Capitella* sp. and *L. acuta*, colonize local flats independently of the presence or absence of plant cover. These subsurface-dwelling species may be protected from any superficial disturbance and, additionally, their sedentary habit may provide a rapid response to sediment disturbance. Other secondary dominants, such as the polychaetes *G. multidens* and *S. grubei*, the bivalves *A. brasiliana* and *M. constricta*, unidentified oligochaetes, and the epifaunal tanaidacean *K. schubarti*, also behaved as generalists and were not affected by the manipulations or plant structures themselves. Most of these species are highly mobile in their search for food and selection of suitable habitat for burrowing (as in the case of the predator polychaetes *G. multidens* and *S. grubei*) or as a result of unpredictability in food availability (as in the case of the suspension-feeder bivalves). In fact, these species have been previously reported from both vegetated and unvegetated areas of the Bay of Paranaguá. (Lana and Guiss, 1991).

On the other hand, we observed that the presence of surface and subsurface plant structures can heavily influence the densities of other epi- or infaunal species, providing food, refuge, or physical support to tubes. The infaunal polychaetes *I. pulchella*, *N. oligohalina*, *P. socialis*, and *H. similes*, and the bivalve *L. pectinata*, live closely associated with roots and rhizomes. As habitat specialists, they did not respond to the removal of surface plant structures, since the viability of roots and rhizomes was not affected by the experiment. This pattern is quite similar to that described by Lana and Guiss (1992) and Netto and Lana (1999) for the slight relationship between local infaunal species and the aerial plant structures. In fact, temporal variations in population density and biomass of *N. oligohalina* were strongly correlated to seasonal variations in below-ground biomass of *S. alterniflora*, suggesting that the reproductive strategies of the polychaete and the seasonal allocation of energy to below-ground tissues of the marsh plant are synchronized (Pagliosa and Lana, 2000).

Surface plant architecture played a major role in structuring epifaunal habitat specialist assemblages. The abundances of epifaunal gastropod *N. virginia*, of isopod *S. mourei*, and of an unidentified gammarid were highest in salt marsh plots, intermediate in cleared plots, and lowest in unvegetated plots. However, the slow epifaunal colonization of artificially created saltmarshes (Levin et al., 1996; Minello and Webb, 1997), the low palatability of *Spartina* to macrobenthic species (Valiela et al., 1984), and the enhancement of macrofaunal densities in fertilized salt marshes (Foreman, et al., 1995; Posey et al., 1995), suggest an indirect trophic influence of the cordgrass. Like submerged aquatic vegetation, the plant blades of *S. alterniflora* may enhance substratum availability and enable epiphytic development, attracting epifaunal grazing organisms and associated epibenthic predators (Bologna and Heck, Jr., 1999; Edgar, 1999). The structural versus trophic importance of salt marshes to estuarine fauna, particularly in the case of subtropical salt marshes, needs to be further analyzed through experimental manipulation of shelter and food.
Clipping cordgrass may alter the competitive interactions of the plant (Mulder and Ruess, 1998) and increase plant susceptibility to environmental change (Baldwin and Mendelssohn, 1998), but a notable outcome of our study was that the biomass of roots and rhizomes was not influenced by the removal of leaves and culms. Levels of light exposure and surface fluid flow intensities were certainly altered in the experimental site, but we were unable to detect any obvious faunal changes. In the same way, temporal changes in sediment characteristics were equivalent in both vegetated and unvegetated sites. The progressive increase of organic detritus and organic content of the sediment indicates an increase of resources for deposit-feeders and grazers. In addition, the concomitant increase in sand content suggests a more dynamically stable environment. The increase in organic detritus and organic content is primarily related to the end of the Spartina flowering season, which is succeeded by an increase of plant mortality rates (Lana et al., 1991). The increase in the sand content may be related to two superimposing effects: i) an abnormally high amount of rainfall in the week prior to the beginning of the experiment, and ii) progressively higher tidal ranges towards the equinoctial tides close to the end of the experiment. The former introduced a large amount of suspended sediments into the estuary, and the latter induced stronger tidal currents that either gradually removed the mud previously deposited or added more sand into the study sites.

Sediment homogeneity between vegetated and unvegetated habitats underscores the hypothesis that plant structure plays a major role in structuring benthic associations in intertidal flats of the euhaline sector of Paranaguá Bay. Short-term trends in the structure of the studied assemblages resemble patterns previously described in the bay, with higher faunal densities in the saltmarsh than in unvegetated habitats (Lana and Guiss, 1991) or similar values of species richness in both habitats (Netto and Lana, 1996, 1997, 1999; Lana et al., 1997).

Seasonal variation in rainfall can strongly disturb the sediment and affect the composition, abundance, and zonation of intertidal macrobenthic species (Turner et al., 1995). Marked variation in macrofaunal densities from summer to autumn are recurrent in local saltmarshes (Lana and Guiss, 1992; Netto and Lana, 1997), mangroves (Blankensteyn, 1994), and unvegetated intertidal flats (Lana and Guiss, 1991). Storms can also affect the superficial sediment dynamics and reduce the availability of food resources for deposit feeders (Bock and Miller, 1995). Pagliosa and Lana (2000) showed that the benthic invertebrates from both vegetated and unvegetated habitats in Paranaguá Bay are highly sensitive to an excess input of freshwater. Therefore, increases in structural complexity of local faunal assemblages can be partially explained by reduced rainfall rates towards the end of the experiment.

In conclusion, the overall response of infaunal or epifaunal species depends on their ability to discriminate between vegetated and unvegetated habitats. Epifaunal habitat specialists were more affected by plant removal than epifaunal habitat generalists. The relative abundance of infaunal habitat specialists and generalists did not change significantly with plant removal, but the abundance of local macrobenthic species was significantly correlated to precipitation levels. Changes in local macrobenthic associations are the result of mixed effects of plant biomass and sediment variation on small spatial scales and physical impacts of summer freshwater runoff on large spatial scales.
ACKNOWLEDGEMENTS

This study was part of the MS thesis of the first author, carried out at the Department of Zoology and Centre for Marine Studies (Universidade Federal do Paraná), and supported by a grant from the Brazilian National Research Council – CNPq. Our sincere thanks to A. Fonseca for the exhaustive discussions and to G. Lessa for the critical reading of the manuscript. The manuscript benefited from the comments of referees and especially from L. Levin.

LITERATURE CITED


ADDRESSES: (P.R.P) Curso de Pós-Graduação em Ciências Biológicas-Zoologia, Departamento de Zoologia, Setor de Ciências Biológicas, Universidade Federal do Paraná, 81531-990, Curitiba, Paraná, Brazil. Present Address: Universidade Federal de Santa Catarina, Centro de Ciências Biológicas, Núcleo de Estudos do Mar, Campus Trindade, 88040-900 Florianópolis-SC, Brazil. E-mail: <ppagliosa@yahoo.com.br>. (P.C.L.) Centro de Estudos do Mar, Universidade Federal do Paraná, 83255-000, Pontal do Sul, Paraná, Brazil.