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Effects of habitat complexity on the structure of macrobenthic association in a *Spartina alterniflora* marsh

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• *Abstract:* The structure and seasonal variability of macrobenthic associations in four different patches on a *Spartina alterniflora* bed at Arrozal Point, Cananéia, São Paulo State are described and compared. In the local intertidal marsh, densities of *S. alterniflora* plants appear in sparsely or densely arranged patches, both in tall and short forms. The infaunal polychaetes *Capitella capitata, Isolda pulchella, Nereis oligohalina* and *Laeonereis acuta* accounted for 44.0% of the total individuals while epifaunal forms such as *Heleobia australis, Littorina angulifera, Tholozodium rhombofrontalis* and *Sphaeromopsis mourei* were the second most abundant components with 39.5%. Classification analyses of sampling time in the same sampling patch indicated that species groups were formed basically by spatial similarity and peak densities of macrofauna and secondarily by temporal patterns. Temporal variations were evident with higher number of species in colder months (winter and spring). Species diversity and evenness did not show clear seasonal patterns, although they were significantly different in sampling patches and time. *Heleobia australis, Littorina angulifera* and *Anomalocardia brasiliensis* were dominant in tall sparse *S. alterniflora* with density peaks occurring in winter/spring periods. *Tholozodium rhombofrontalis* and *Sphaeromopsis mourei* were dominant in short sparse *S. alterniflora* with density peaks in summer. In tall, densely distributed *S. alterniflora* plants the higher densities occurred in winter and the dominant species were *Nereis oligohalina, Isolda pulchella* and *Capitella capitata*. The species *H. australis, L. angulifera* and *A. brasiliensis* predominated in the short *S. alterniflora* plants densely distributed, with faunistic peaks recorded in spring. The results suggest that differences in form and aggregation of *S. alterniflora* impart changes in the structure of macrobenthic fauna associated to this vegetation.

• *Resumo*: A estrutura e variação temporal de associações macrobentônicas de marismas de *Spartina alterniflora*, estruturalmente diferentes com relação à forma (baixa ou alta) e ao grau de agregação (esparsa ou agregada), foram descritas e comparadas, na Ponta do Arrozal, região de Cananéia, costa sul do Estado de São Paulo. Representantes da infauna como os poliquetos *Capitella capitata, Isolda pulchella, Nereis oligohalina* e *Laeonereis acuta* perfizeram 44,0% da fauna coletada, enquanto que formas epifaunais como *Heleobia australis, Littorina angulifera, Tholozodium rhombofrontalis* e *Sphaeromopsis mourei* atingiram 39,5%. Análises classificatórias dos períodos de amostragem indicaram que os agrupamentos de espécies foram formados basicamente pela similaridade espacial e picos de densidade da macrofauna seguidos pelos padrões de variação temporal. Os maiores valores de diversidade ocorreram no inverno e primavera. Os índices de diversidade e equitatividade, embora significativamente diferentes entre locais de amostra e tempo, não mostraram um padrão sazonal muito claro. *Heleobia australis, Littorina angulifera* e *Anomalocardia brasiliensis* foram dominantes entre as plantas altas de *S. alterniflora*, esparsamente distribuídas, com picos de densidade faunística ocorrendo nos períodos de inverno e primavera. Entre as plantas baixas esparsamente distribuídas as espécies dominantes foram *Tholozodium rhombofrontalis* e *Sphaeromopsis mourei*, com maior densidade no verão. Nas plantas altas e agregadas as maiores densidades ocorreram no inverno e as espécies dominantes foram *Nereis oligohalina, Isolda pulchella* e *Capitella capitata*. As espécies *H. australis, L. angulifera* e *A. brasiliensis* dominaram nas marismas baixas e agregadas, apresentando os maiores valores de densidade na primavera. Os resultados sugerem que diferenças na forma e agregação de *S. alterniflora* provocam mudanças na estrutura da fauna macrobentônica associada a esta vegetação.

• *Descriptors:* Habitat complexity, macrobenthic association, *Spartina alterniflora* marsh, Southern coast of São Paulo State, Brazil.

• *Descritores:* Complexidade de habitat, Associações macrobentônicas, marisma de *Spartina alterniflora*, Costa sul do Estado de São Paulo, Brasil.

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Introduction

It has been amply demonstrated that structural elements such as plant cover strongly influence macrobenthic associations and can lead to remarkable faunistic differences between vegetated and bare sites or between habitats with different types of vegetation. Evidence has been provided by studies comparing sites with different species of seagrass (Lewis, 1984; Virnstein & Howard, 1987); vegetated and unvegetated habitats (Lewis & Stoner, 1983; Lana & Guiss, 1991) and sites with seagrass and macroalgae (Schneider & Mann, 1991). The majority of works on grassy bottoms deals with seagrass habitats. Although intertidal marshes and subtidal seagrass meadows are believed to exhibit similarities in their functional and structural roles (Orth *et al.*, 1984), contradictory patterns of macrobenthic organization have been described for those environments, fully justifying more studies of the salt marsh habitat.

Changes in the density or size of artificial plants lead to varied responses from macrobenthic communities (Gunnil, 1983; Edgar, 1990). These alterations are normally attributed to the effect of macrophyta on physical characteristics such as current speed and sediment stability (Peterson *et al.*, 1984) or modifications in biological interactions such as predation (Virnstein, 1977; Nelson, 1979; Heck & Thoman, 1981; Flynn, 1993). Densities of macrobenthic organisms in a salt marsh system often fluctuate greatly with season (Tararam & Wakabara, 1987; Lana & Guiss, 1991; Flynn, 1993), the same is also true to plant biomass, which makes the study of salt marsh structures more difficult.

Over the Cananéia intertidal marsh, densities of *Spartina alterniflora* plants appear in sparsely or densely arranged patches, both in tall and short forms. In this paper, we describe and compare the structure and seasonal variability of macrobenthic associations in such patches of a *S. alterniflora* bed at Arrozal Point.

Material and methods

Cananéia lagoon estuarine region is located in the southern coast of São Paulo state (25°02'S - 47°56'W). At Arrozal Point (Fig. 1), the marsh investigated presents average salinity values higher than 28‰, surface water temperature around 20°C in winter and 32°C in summer. Local tides are characterized by diurnal inequalities. A complete description and characterization of the system is given by Schaeffer-Novelli *et al.* (1990).

At this shore, there is one of the largest marshes in the region with patches of plants loosely aggregated (6 plants/0.03 m^2) comprising groups of scattered individuals, and others with plants densely aggregated (12 plants/0.03 m^2). In both situations *S. alterniflora* can be found in both forms, tall (100 cm) and short (40 cm).

Four intertidal stations were established, comprising patches with tall and short *S. alterniflora* sparsely distributed (Pt1 and Pt2), and densely distributed (Pt3 and Pt4).

Faunal and environmental samples were taken once each season, in July 1988 (winter), October 1988 (spring), January 1989 (summer) and April 1989 (autumn). Surface water temperature was determined by a thermometer. Salinity was determined using a hand refractometer and dissolved oxygen was analyzed according to Strickland & Parsons (1968). Sediment samples were analyzed for silt-clay percentage, mean grain size (Suguio, 1973) and organic matter by the H_2O_2 digestion method.

Faunal samples consisted of 3 replicates for each *S. alterniflora* patch (Pt1, Pt2, Pt3 and Pt4) taken by a corer 20 cm in internal diameter penetrating the sediment to a depth of 10 cm. Twelve samples were taken in each season. *S. alterniflora* leaves were clipped at ground level and searched for epifaunal organisms. Sediment samples were sieved through 1 mm and 0,5 mm meshes, fixed in 10% formalin and then preserved in 70% ethanol. All specimens were identified at the lowest practical taxonomic level and counted. *S. alterniflora* plants of each sample were dried for 24 h in a shady place and weighted in a normal scale. The number and size of plants per corer were counted and measured.

All species with at least 2 individuals per sample (Jackson, 1972) were included in a matrix of $\log(x+1)$ transformed data for subsequent quantitative analyses.

The structure of the macrobenthic associations was evaluated by the total number of individuals (n), species richness (s), diversity (H') and evenness (J'). Species richness was evaluated by the total number of species per sampled patch. Shannon index (H') was used for measuring diversity.

One-way analyses of variance (ANOVA) were used to test for differences in water parameters such as temperature, salinity and dissolved oxygen. Two-way analyses of variance with replication were used to determine differences in sediment (grain size, silt-clay and organic content), community (n, s, H', J') and plant parameters (aggregation level and size), taking into account habitat type and sampling season, as independent factors. A 5 per cent level of confidence was assumed.

Morisita index (Ono, 1961; Grassle & Smith, 1976) and the WPGA (Weighted pair group average) method were used to cluster species (R-mode) and samples (Q-mode). Principal component analyses were employed in order to

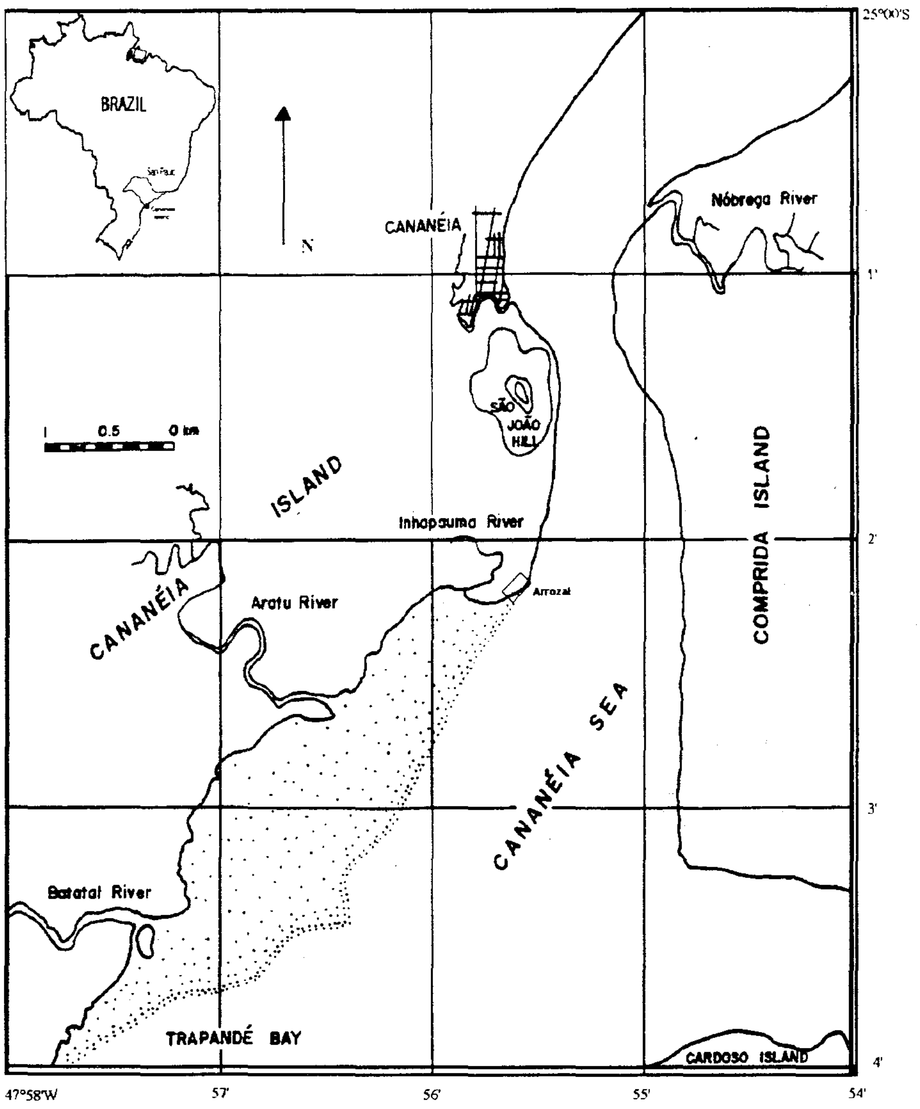

Fig. 1. Location of sampling site (Arrozal) in Cananéia Lagoon estuarine region, São Paulo State, southeastern Brazil.

reduce the multivariate nature of the data to a few interpretable dimensions.

Results

Temporal variations in temperature, salinity and dissolved oxygen of surface water are shown in Figure 2. Table 1 summarizes the variations of these parameters with ANOVA results. These parameters reveal a significant temporal variation.

The temporal variations observed in the total biomass of *S. alterniflora* (leaves, rhizomes and roots) in each patch are shown in Figure 3. Table 2 summarizes the variation of these parameters with the results of two-way ANOVA, as observed, biomass values were statistically different both in patches and in seasons considered. Higher values were associated with dense *S. alterniflora* patches and autumn/winter periods.

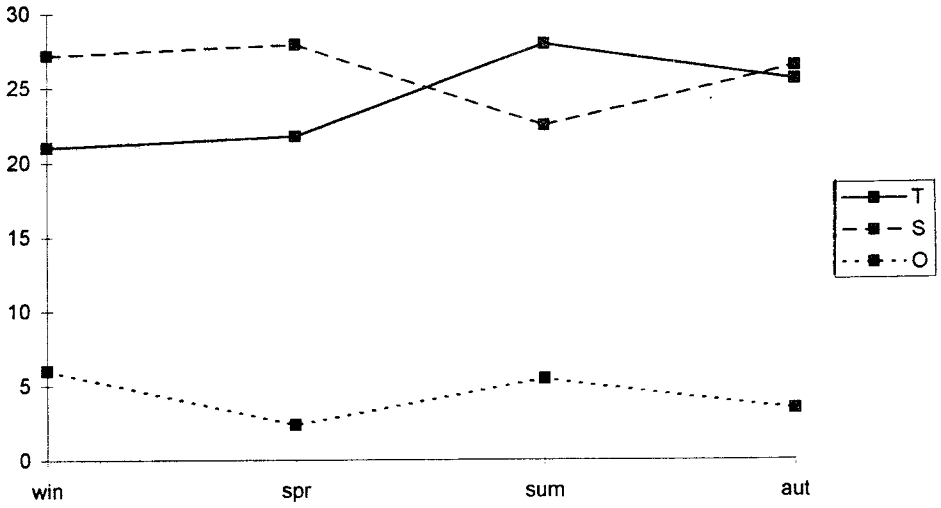

Fig. 2. Temporal variation in temperature (T°C), salinity (S‰) and dissolved oxygen (ml/l) of the superficial water.

Table 1. Variation range of superficial water variables and results of one-way ANOVA (*) = significant difference at 5% level of confidence

Parameters	variation range	p-value
Salinity (‰)	22.4 - 28.1	* 3.19E-7
Temperature (°C)	20 - 28	* 0,00012
Dissolved Oxygen (ml/l)	2.53 - 6.80	*1.15E-07

Sediment parameters were statistically different when different patches were considered, but were similar among sampling times (Table 2). Silt-clay porcentage and sediment organic content were found to have higher values at the dense *S. alterniflora* patches.

A total of 2,023 macrobenthic animals belonging to 31 species were considered, referring to the mean values of species abundance of the three replica of each different patch sample (Table 3). The infaunal polychaetes *Capitella capitata, Isolda pulchella, Nereis oligohalina* and *Laeonereis acuta* accounted for 44.0% of all individuals, while

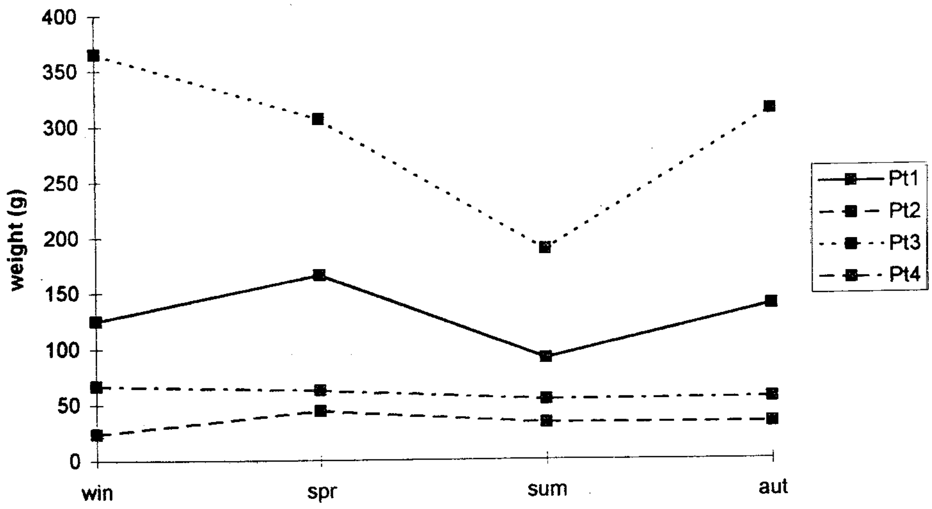

Fig. 3. Seasonal variation in biomass of *Spartina* for each sampling patch (Pt).

Table 2. Variation range of variables and results of two-way ANOVA with replication evaluating effect of sediment parameters, fauna parameters and plant biomass
(*) = significant difference at 5% level of confidence

Parameters	variation range				p-value		
	Pt1	Pt2	Pt3	Pt4	between sites	time	interaction
Mean grain size (Ø)	2.95-3.08	3.0 - 3.08	3.06 - 3.33	3.15 - 4.6	0.295	0.129	0.551
Organic matter (%)	0 - 0.1	0 - 0.1	0.5 - 0.9	0.1 - 0.9	* 2.14E-07	0.06	0.007
Silt-clay (%)	0.1 - 0.27	0.03 - 0.22	5.31 - 12.58	5.4 - 13.58	* 5.96E-07	0.007	0.09
Fauna							
number of species (s)	from 2 to 16	from 0 to 16	from 6 to 14	from 9 to 16	* 1.17E-15	* 7.29E-17	7.29E-15
density (inds./0.03 m^2)	2 - 375	0 - 206	44 - 234	36 - 310	* 1.36E-10	* 2.75E-15	2.25E-13
diversity (H')	0.693 - 1.5	0.25 - 1.96	1.02 - 2.157	1.182 - 2.22	* 6.87E-10	* 4.43E-10	6.90E-06
evenness (J')	0.5110 - 1	0.142 - 0.84	0.57 - 0.841	0.461 - 0.862	* 3.52E-08	* 0.00105	6.94E-11
Biomass of *Spartina* (g)	71.5-182.0	15.0-54.0	188.0-450.0	40.0-73.0	* 4.98E-20	* 0.0025	0.091

epifaunal forms such as *Heleobia australis, Littorina angulifera, Tholozodium rhombofrontalis* and *Sphaeromopsis mourei* accounted for 39.5% of the total. The 13 numerically dominant species accounted for 92.5% of all individuals. The other 18 species were not included in quantitative analyses (Table 3).

Inverse analyses of data from sites in all seasons (Fig. 4) yielded four group species: group a, the infaunal polychaetes *I. pulchella, N. oligohalina* and *C. capitata*; group b, the epifaunal amphipods *Parhyale hawaiensis* and *Platorchestia* sp; group c, the molluscs *H. australis, L. angulifera* and *A. brasiliensis*; and group d, the epifaunal isopods *T. rombofrontalis* and *S. mourei*. Hydrobiidae and *S. grubii* were not grouped probably due to their discontinuous temporal occurrence. *L. acuta* was the only species more abundant in short *S. alterniflora* forms.

Classification analysis of sampling times indicated that groups in the same sample patch were formed primarily by spatial similarity and peak densities of macrofauna and secondarily by temporal patterns. Three groups were identified at 60% similarity level (Fig. 5); the first one comprising samples from the four patches in cold periods, mainly winter; the second, samples collected from dense *S. alterniflora* (Pt3 , Pt4); the third, samples from sparsely distributed *S. alterniflora* (Pt1, Pt2).

Species or group of species showed a strong seasonal component (Fig. 6). In winter, polychaetes from group a (*N. oligohalina, I. pulchella* and *C. capitata*) were the dominant species in tall *S. alterniflora* and *L. acuta* in sparsely distributed *S. alterniflora*. *T. rhombofrontalis* and *S. mourei* (group d), *P. hawaiensis* and *Platorchestia* sp (group b) were also abundant in winter. *H. australis*, *L. angulifera* and *A. brasiliensis* (group c) appeared with higher densities in sparse *S. alterniflora* (Pt1, Pt2). In spring , polychaetes (group a) were restricted to densely distributed *S. alterniflora* (Pt3 and Pt4). Mollusc species (group c) were abundant in all sampling patches. All species exhibited lower densities in summer. Isopod species (group d) dominated in short sparse *S. alterniflora*, while polychaete species (group a) remained restricted practically to dense *S. alterniflora* patches. In autumn , sparse patches of *S. alterniflora* were practically devoid of associated fauna, with molluscs of group c predominating in densely distributed patches, followed by *L. acuta* and polychaete species (group a).

Species richness differed statistically between habitats, with higher values in tall *S. alterniflora* patches (Fig. 7). Temporal differences were evident at the sampled patches, with higher number of species in colder months, winter and spring. Species diversity and evenness, although significantly different between sampling patches and time, did not show any distinct seasonal patterns. Although the rare species which greatly influenced the Shannon index were withdrawn, this information index was still greatly affected by the evenness component, disguising any spatial or seasonal pattern.

In terms of the faunal components associated to the *S. alterniflora* patches observed, it was noticed that in the tall sparse *S. alterniflora* patch (Pt1), group c species, *H. australis*, *L. angulifera* and *A. brasiliensis* were the most abundant; the first two are epifaunal grazers and the third species an infaunal suspension feeder, followed by the infaunal deposit feeders polychaete species (group a). Density peaks in tall sparse *S. alterniflora* patch occurred in winter/spring periods. In the short sparse *S. alterniflora* patch (Pt2), the dominant species were, *T. rhombofrontalis* and *S. mourei*, both grazers, followed by *L. acuta*. Density peak in the tall sparse *S. alterniflora* patch occurred in summer. In the tall dense *S. alterniflora* patch the dominant species were polichaetes of group a , followed by the mud mollusc Hidrobiidae. Density peak in this patch was in winter. In the short dense *S. alterniflora* patch the dominant

Table 3. Density (inds./0.03 m^2) of the species in each sampling location. ( ) = species number used in quantitative analyses.

Species	Pt1	Pt2	Pt3	Pt4
Acteocina canaliculata	3	1	0	4
Bittium varium	3	4	0	4
Costoanachis sp	2	1	0	3
Epitonium sp	0	1	0	1
Heleobia australis (1)	153	40	37	260
Littorina angulifera (2)	25	5	13	14
Nassarius sp	3	3	2	7
Neritina virginia	7	0	3	6
Turbonilla sp	2	1	0	2
Odostomia sp	2	0	8	1
Hydrobiidae (13)	0	0	45	2
Anomalocardia brasiliensis (3)	15	7	7	21
Mytella guyanensis	3	2	9	1
Sphenia antillensis	1	1	4	5
Capitella capitata (4)	253	3	191	68
Isolda pulchella (5)	7	1	39	19
Laeonereis acuta (6)	15	39	12	59
Lumbrineris hebes	0	0	0	7
Neanthes succinea	1	2	2	3
Nereis oligohalina (7)	43	3	53	51
Perinereis ponteni	1	0	5	0
Perinereis vancaurica	3	0	8	0
Sigambra grubii (8)	0	0	14	1
Cassidinidea tuberculata	1	0	5	4
Dies fluminensis	1	1	2	0
Tholozodium rhombofrontalis (10)	24	132	2	15
Sphaeromopsis mourei (11)	3	72	9	14
Parhyale hawaiensis (9)	8	0	19	3
Platorchestia sp (12)	12	7	21	4
Hyale media	1	1	2	2
Zeuxo sp	0	0	11	0
TOTAL	592	327	523	581
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species were molluscs of group c, followed by *L. acuta* and group a species. Density peak in this patch occurred in spring (Fig. 6).

Sample and parameter points of principal components analyses were projected simultaneously in the factorial space (Fig. 8 a and b). There was a broad match with the pattern of responses exhibited by cluster analysis. The first component accounted for 36.6% of the total variance. Species of infaunal polychaetes (group a), epifaunal amphipods (group b), molluscs (group c) and *S. grubii*, with positive coordinates, were opposed to isopod species (group d) and *L. acuta* with negative coordinates. The first species were related to higher *S. alterniflora* biomass. The first axis also distinguished locations with dense *S. alterniflora* from locations with sparsely distributed *S. alterniflora*. Physical-chemical parameters, such as silt-clay percentage and organic matter, besides form growth and biomass plant, showed positive coordinates. Species and site positions on the first axis can be regarded as a response to the aggregation level of *S. alterniflora*. The second component (20.7% of data variance) separated species with higher densities from those with lower densities. Besides, this axis also separated tall *S. alterniflora* patches from short *S. alterniflora* patches. The third component (11.9 % of data variance) separated infaunal species, with negative coordinates related with the rhizome and roots, from epifaunal species. Interpretation of the fourth component was not clear.

Discussion

The results suggest that differences in form and aggregation of *S. alterniflora* plants impart changes in the structure of macrobenthic fauna associated to this vegetation. There was a similar composition of species among marsh locations with marked differences in the relative abundance of the dominant components. Each

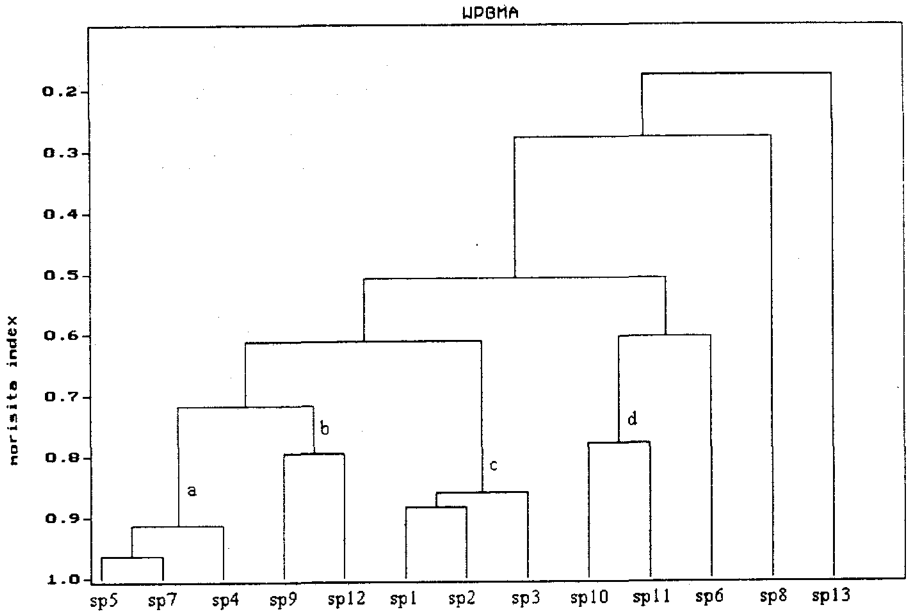

Fig. 4. Dendogram of species. Species groups a (sp4 = *Capitella capitata,* sp5 = *Isolda pulchella,* sp 7 = *Nereis oligohalina*); b (sp9 = *Parhyale hawaiensis,* sp12 = *Platorchestia* sp); c (sp1 = *Heleobia australis,* sp2 = *Littorina angulifera,* sp3 = *Anomalocardia brasiliensis*); d (sp10 = *Tholozodium rhombofrontalis,* sp11 = *Sphaeromopsis mourei*) and others (sp6 = *Laeonereis acuta*, sp8 = *Sigambra grubii* and sp13 = Hydrobiidae) indicated.

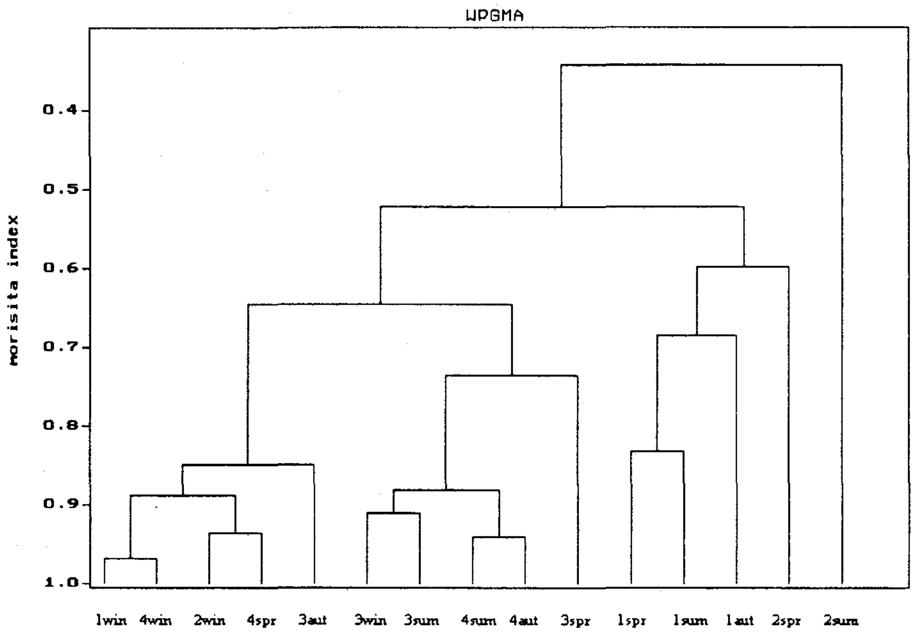

Fig. 5. Dendogram of sampling seasons at four different patches (Pt):1-4. (win = winter, spr = spring, sum = summer, aut = autumn).

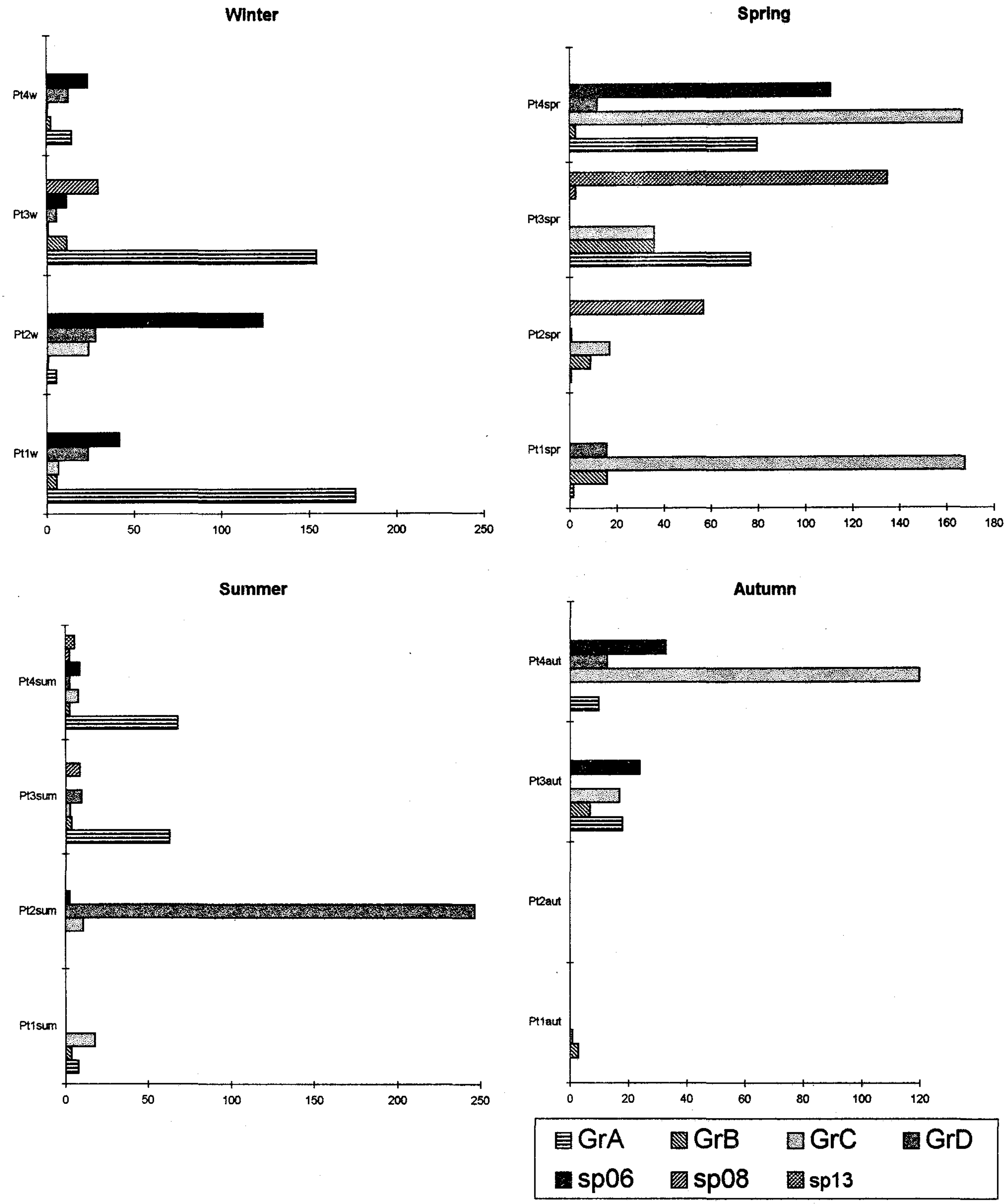

Fig. 6. Distribution and density of species or groups of species per 0.03 m^2 at each patch. (GrA-D = species of groups A-D, sp06 = *Laeonereis acuta*, sp08 = *Sigambra grubii*, sp13 = Hydrobiidae).

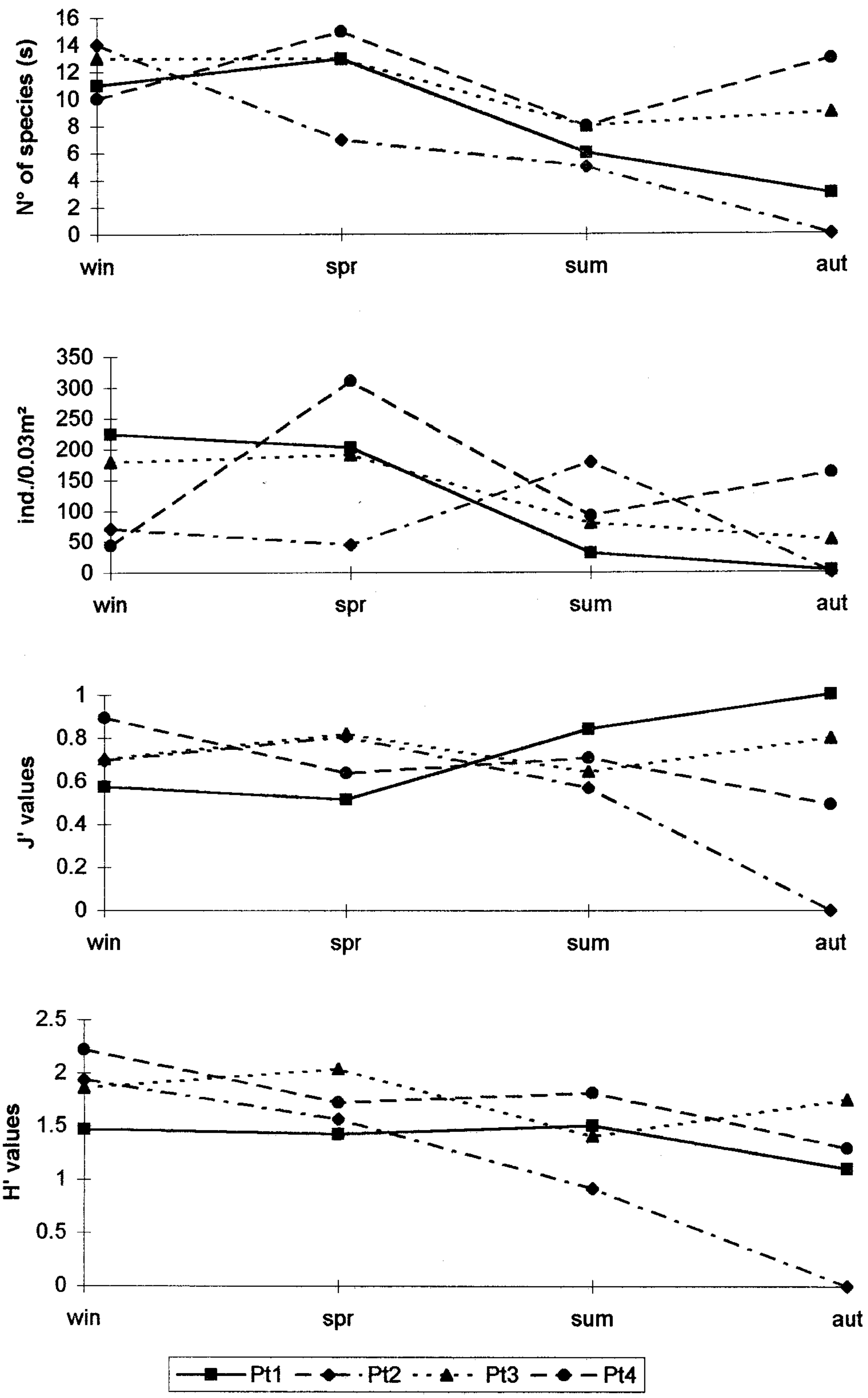

Fig. 7. Temporal variation in number of species (s), diversity (H'), evenness (J') and mean density per 0.03 m^2 of benthic macrofauna at each sampling patch (Pt).

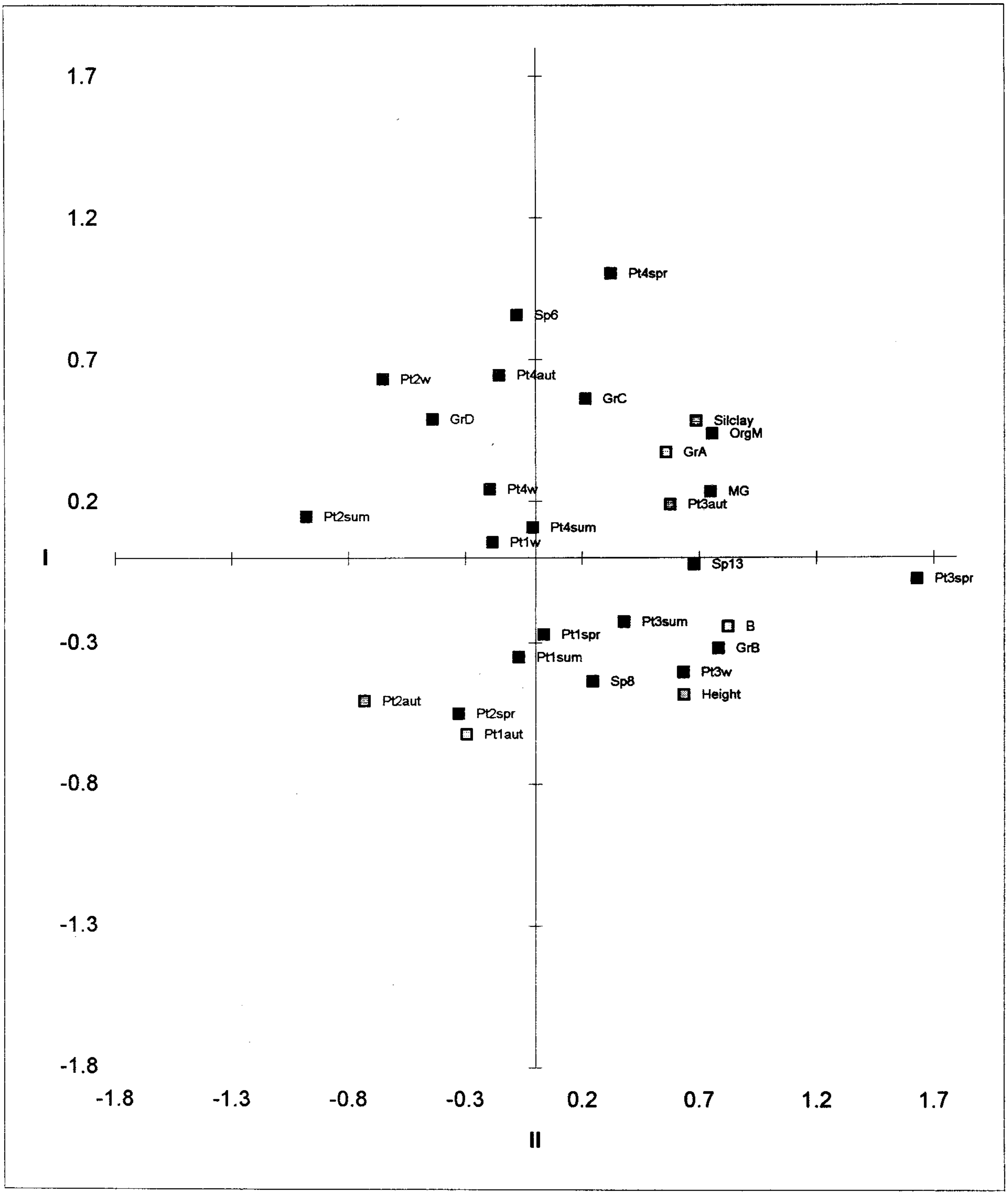

Fig. 8a. Principal components analysis of species, sampling seasons and physico-chemical parameters at each sampling station. Axes I and II. (w = winter, sum = summer; aut = autumn; spr = spring; Pt = patch; Gr = groups; Silclay = % silt-clay; OrgM = organic matter; MG = mean grain size).

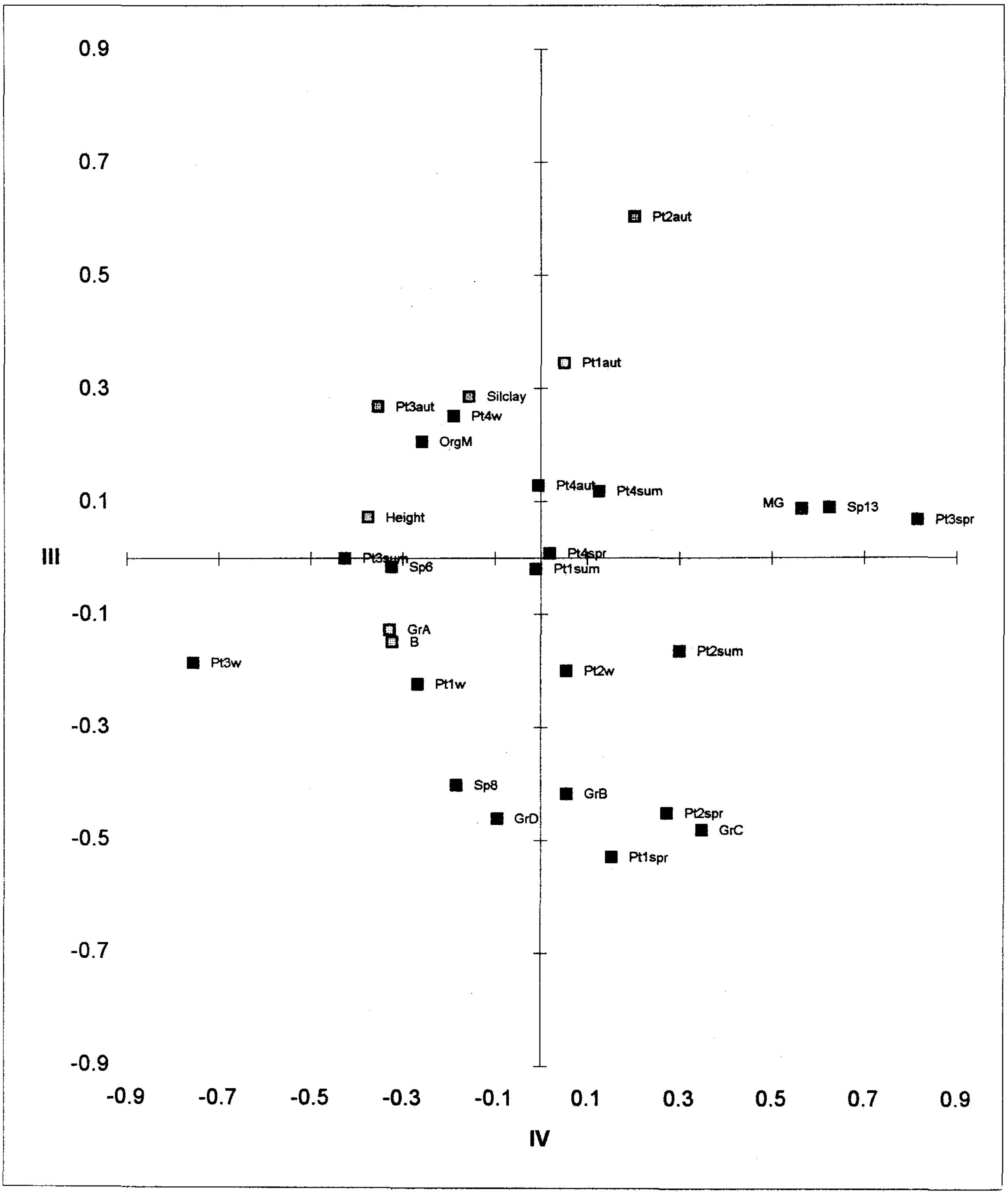

Fig. 8b. Principal components analysis of species, sampling seasons and physico-chemical parameters at each sampling station. Axes III and IV. (w = winter, sum = summer; aut = autumn; spr = spring; Pt = patch; Gr = groups; Silclay = % silt-clay; OrgM = organic matter; MG = mean grain size).

sampled patch displayed an alternation of dominance among the few numerically expressive species. Schneider & Mann (1991) attributed this heterogeneous response to vegetation type to the biology of individual species, with respect to suitability of macrophytes as food resource and living space. Bell & Westoby (1986) pointed out that community measures as well as total abundance of individuals are unreliable variables for testing the effects of height and densities of plants since component species can give opposite responses. These authors showed that preference for a particular plant was highly species-specific, indicating that no vegetation characteristic made it a suitable substratum for all animals.

Small-scaled aggregation of infaunal organisms exists in association with salt marsh vegetation (Rader, 1984; Lana & Guiss, 1991; Flynn, 1993). In the present study the infaunal polychaetes *N. oligohalina, I. pulchella* and *C. capitata preferred patches with higher vegetal biomass deriving mainly from S. alterniflora* level of aggregation. Epifaunal amphipods grazers as *.P. hawaiensis* and *Platorchestia* sp, in the other hand, were related to plant height, numerically more abundant between tall forms of *S. alterniflora*. This finding is in accordance with Stoner's (1980) conclusions that epifaunal amphipods select the vegetation on the basis of blade surface area.

The heterogeneous patterns of temporal variation were strongly influenced by the populational dynamics of the dominant species. The abundance and species richness of tall *S. alterniflora* associations showed a pattern already documented by Flynn (1993) with high densities at cold months, followed by a sharp decline in summer and autumn. Associations related to short *S. alterniflora* forms presented peak densities in summer, when in sparsely distributed *S. alterniflora* patches, or in spring, when in dense *S. alterniflora* patches. These peaks reflect the populational fluctuations of the groups of dominant species, respectively, epifaunal isopods and molluscs.

Mobile organisms densities associated to salt marsh *S. alterniflora* greatly fluctuate with season (Tararam & Wakabara, 1987; Lana & Guiss, 1991; Flynn, 1993). Rapid population increases are explained in terms of the settlement of planktonic larvae and rapid growth rates of brooding invertebrates (Edgar & Moore, 1986). But the factors responsible for the marked populational decline are not well understood. Normally this decline is explained by an increase in predatory activities, but in Cananéia macropredators activity does not justify the population decline (Flynn, 1993), since both, the cage experiment and control experienced this abrupt decline. Heck & Thoman (1981) and Edgar (1990), among others, concluded that their findings were not consistent with the hypothesis of macropredators controlling the fauna. So, it seems that exploitative competition has to be fully investigated. Because the vaste majority of macrobenthic species are generalist feeders which can utilize a variety of detrital, plant and animal material, diffuse exploitative competition can therefore be widespread amongst the macrobenthos, contrasting with the widely held view that the role of competition in structuring macrobenthic communities is minor, especially in comparison with the role of predation.

As Reice & Stiven (1983) suggested, our results also seem to stress that the initial idea of homogeneity created by a monoculture of *S. alterniflora* masks the reality of a truly patchy ecosystem. The presence of *S. alterniflora* in different aggregation levels and growth forms, coupled with seasonal changes of species probably related to detritus availability, play an importante role on the abundance and maintainance of a macrofaunal association. Sediment parameters seem to exert a secondary influence. Further investigations on the feeding strategies of the associated fauna should be carried out to evaluate the effects of food competition in the organization of these communities.

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