Tropical Ecology **42**(2): 231-242, 2001 ISSN 0564-3295

Brachyura (Decapoda, Crustacea) of phytobenthic communities of the sublittoral region of rocky shores of Rio de Janeiro and São Paulo, Brazil

MARIA TERESA MENEZES DE SZÉCHY[1], VALÉRIA GOMES VELOSO[2] & ÉDISON JOSÉ DE PAULA[3]

[1]Universidade Federal do Rio de Janeiro, Centro de Ciências da Saúde, Instituto de Biologia, Departamento de Botânica, Cidade Universitária, Ilha do Fundão, Rio de Janeiro, RJ, Brazil, Cep. 21941.590, Email: szechy@biologia.ufrj.br; [2]Universidade do Rio de Janeiro, Laboratório de Dinâmica de Populações Marinhas, Avenida Pasteur 296, Urca, Rio de Janeiro, RJ, Brazil, Cep. 22290.000. Email: vgveloso@mandic.com.br; [3]Universidade de São Paulo, Instituto de Biociências, Departamento de Botânica, Caixa postal 11.461, São Paulo, SP, Brazil, Cep. 05422.970, Email: ejdpaula@usp.br

Abstract: The density of Brachyura decapods was estimated in fourteen phytobenthic communities of the shallow sublittoral region of the coast of Rio de Janeiro and São Paulo States, Brazil. The variation in abundance of these crabs was analyzed relative to the degree of wave action, size and slope of the rock surfaces and dry weight of the macroalgae. Collections were done in spring, using 50 x 50 cm quadrats, randomly dropped five times on a transect 10 m long, extended parallel to the water line. Of the twelve Brachyura species identified, the most frequent and abundant were *Pachycheles haigae* and *Epialtus brasiliensis*; these showed preference for sites with larger abundance of *Sargassum* spp. or articulated corallines, respectively. In spite of this, the combined abiotic and biotic data, treated through canonical correspondence analysis (CANOCO), showed that the differences in the density of the Brachyura are significant only in relation to the abiotic data, particularly the degree of wave action. This result indicates that, taking into account the environment as a whole, characteristics linked to the vegetation are of secondary importance to the epifaunal community, especially considering motile animals.

Resumen: La densidad de decápodos Brachyura fue estimada en catorce comunidades fitobentónicas de la región de sublitoral somero de la costa de los estados de Rio de Janeiro y São Paolo, Brasil. La variación en la abundancia de estos cangrejos fue analizada en relación al grado de acción del oleaje, el tamaño y la pendiente de las superficies rocosas, y el peso seco de las macroalgas. Las colectas fueron realizadas en la primavera, usando cuadros de 50 × 50 cm, colocados aleatoriamente cinco veces a lo largo de un transecto de 10 m de longitud, paralelo al frente de agua. De las doce especies identificadas de Brachyura, las más frecuentes y abundantes fueron *Pachycheles haigae* y *Epialtus brasiliensis*; éstas mostraron preferencias por sitios con mayor abundancia de *Sargassum* spp. o de coralinas articuladas, respectivamente. A pesar de ello, los datos abióticos y bióticos combinados, examinados por medio de un análisis canónico de correspondencia (CANOCO), mostraron que las diferencias en la densidad de los Brachyura son significativas sólo en relación con los datos abióticos, particularmente con el grado de acción del oleaje. Este resultado indica que, considerado el ambiente como un todo, las características relacionadas con la vegetación tienen una importancia secundaria para la comunidad epifaunística, especialmente considerando animales móviles.

Corresponding Author: Maria Teresa Menezes de Széchy

Resumo: A densidade dos decápodos Brachyura foi estimada em catorze comunidades fitobênticas da região sublitorânea pouco profunda da costa dos Estados de Rio de Janeiro e São Paulo, no Brasil. A variação na abundância destes caranguejos foi analisada em relação ao grau de exposição ás ondas, tamanho e declive da superfície das rochas e peso seco das macroalgas. As coletas processaram-se na primavera, usando quadrados de 50x50 cm, aleatoriamente lançados cinco vezes num transecto com 10 m de comprimento e disposto de forma paralela à linha de água. Das doze espécies de Brachyura identificadas, as mais freqüentes e abundantes foram *Pachycheles haigae* e *a Epialtus brasiliensis*; estes mostraram preferência pelas communidades com maior abundância de *Sargassum* spp. ou de calcárias articuladas, respectivamente. Não obstante esta constatação, os dados abióticos e bióticos combinados, tratados pela análise canónica de correspondências (CANOCO), mostraram que as diferenças na densidade de Brachyura só eram significativas em relação áos dados abióticos, particularmente o grau de exposição ás ondas. Este resultado indica que tendo em consideração o ambiente como um todo, as características ligadas à vegetação feram de importância secundária para a comunidade epifaunal, especialmente considerando os animais com capacidade de locomoção.

Key words: Brachyura, Brazil, corallines, community structure, crabs, density, macroalgae, phytal, *Sargassum*, wave action.

Introduction

The sublittoral region of the rocky shores of the coast of Brazil, like rocky shores of other tropical and subtropical localities, can be defined by the presence of the brown alga *Sargassum* C. Agardh (Phaeophyceae, Fucales) (Lewis 1964; Paula 1989). The abundance of *Sargassum* in these communities can vary with the environment, especially relative to the degree of wave action (Oliveira Filho & Mayal 1976; Paula & Oliveira Filho 1980, 1982), the quantity of herbivores, particularly sea urchins like *Echinometra lucunter* (Linnaeus) (Eston & Bussab 1990; Paula & Oliveira Filho 1982), and other disturbances (Evans *et al.* 1993). The variation in relative abundance of *Sargassum* in benthic communities of the sublittoral region of Rio de Janeiro and São Paulo States is analyzed by Széchy & Paula (2000), who define patterns of community structure based upon dry weight data of macroalgae and macroinvertebrates. Two patterns, that can be characterized by extremes, stand out: (1) in sites not exposed to wave action nor to the air: *Sargassum* dominance; and (2) in sites exposed to wave action and to the air, during low tides: dominance of calcareous algae of the Corallinaceae family, together with the tubeworm *Phragmatopoma lapidosa* Kinberg and with the mussel *Perna perna* (Linnaeus).

It is interesting to note that *Sargassum* and articulated corallines belong to different morpho-functional types (Littler & Littler 1980; Steneck & Dethier 1994), corresponding to different habitats for phytal invertebrates (Dean & Connell 1987; Gee & Warwick 1994; Isaksson & Pihl 1992). The complexity of these habitats can be related, in part, to characteristics of the dominant macroalgae, such as their structure, chemical composition and surface characteristics. It can also be related to the quantity of epibionts and sediments retained by the plants (Edgar 1983a, 1991; Martin-Smith 1993; Masunari 1989; Norton & Benson 1983). Such macroalgae serve as substrate for the fixation of sessile animals, offer refuge for different species of the macro-, meso-, and microfaunas and supply food directly, in the case of herbivores, or indirectly, in the case of detritivores (Abele 1974; Edgar & Aoki 1993; Leber 1985). Members of the sessile fauna may also benefit from consumption of substances exuded by the algae (Williams & Seed 1992). According to Montouchet (1979), in his study of the vagile invertebrates associated with *Sargassum cymosum* C. Agardh from the coast of São Paulo State, some species use the macroalgae as reproductive sites for the development or growth of a determined larval phase.

The epifaunal community of *Sargassum* of the Brazilian coast is basically known for the *S. cymosum* beds along the coast of São Paulo (Barreto 1998; Borojevic 1971; Lima 1969; Lima *et al.* 1995; Mantelatto & Corrêa 1995/96; Masunari 1989; Montouchet 1979; Tararam & Wakabara 1981). The importance of other species of *Sargassum*, for the associated fauna, is also recognized in other localities (Albuquerque & Guéron 1989; Edgar & Aoki 1993; Kito 1977, 1982; Mukai 1971; Norton & Benson 1983; Takeuchi *et al.* 1987). On the other hand, articulated corallines, like *Amphiroa beauvoisii* Lamouroux, are also cited as important habitats for the phytal animals of the Brazilian coast (Masunari 1976, 1982).

Of the components of the phytal macroinvertebrates, the crustaceans are among the most abundant groups (Masunari 1976, 1982; Santos & Correia 1995), previous studies having been concentrated upon the group of amphipods (Barreto 1998; Dubiaski-Silva & Masunari 1995; Tararam & Wakabara 1981; Tararam *et al.* 1986; Wakabara *et al.* 1983). Few studies of the Brachyura of the epifaunal community exist, being restricted mainly to species lists. Melo (1985), Melo *et al.* (1989) and Hiyodo & Fransozo (1994) suggest that communities dominated by *Sargassum* favor the Majidae crabs *Epialtus brasiliensis* Dana and *Acanthonyx petiverii* H. Milne Edwards, most abundant in this habitat. Mantelatto & Corrêa (1995/96) focus upon the seasonal fluctuation of the carcinofauna associated with the *Sargassum* of three beaches on the coast of São Paulo.

The qualitative and quantitative structure of the epifaunal community can be determined by two groups of factors: (1) abiotic factors, principally those related to the degree of exposure to wave action and to the air (Dommasnes 1968; Edgar 1983b, 1983c; Fenwick 1976; Flores *et al.* 1994; L'Hardy 1962; Norton 1971; Takeuchi *et al.* 1987 Veloso & Melo 1993); and (2) biotic factors, related to the characteristics of the plants themselves that serve as animal habitats (Edgar 1983a, 1983c; Dubiaski-Silva & Masunari 1995; Gunnill 1982a, 1982b). In the literature, there is no agreement about each factor is the most important.

This study aimed to analyze the species composition and density of Brachyura occurring in marine phytobenthic communities in the shallow sublittoral region of Rio de Janeiro and São Paulo States, Brazil. For this analysis, the relationship between the Brachyura and the following abiotic and biotic factors were focused upon: degree of wave action, size and slope of the rock surfaces and dry weight of the macroalgae.

Materials and Methods

Eight areas along the coast of Rio de Janeiro and São Paulo States were selected (Fig. 1), based upon Mitchell *et al.* (1979) and Mahiques *et al.* (1990). In these areas, fourteen sampling sites were selected, the criteria being: (1) the presence of *Sargassum* populations that occupied at least 10 m of horizontal extension on the rock surface; and (2) the accessibility and the safety of the field work. The collections were conducted in the spring seasons of 1991 and 1992. Table 1 shows characteristics of the fourteen sampling sites, including the species of *Sargassum* present, the degree of wave action, rock size and slope of the rock surfaces.

The identification of *Sargassum* species was based on Paula (1988). The degree of wave action was determined indirectly, considering the position of the rocky shore relative to the coastline and the presence of physiographic features, as follows: (1) Exposed sampling sites - situated in the mouths or outside of coves or bays, unprotected by physiographic features, and subject to direct wave action. Here *Sargassum* beds were partially exposed to air at low tide; (2) Protected sampling sites - situated inside or facing the inner reaches of coves or bays, and protected by physiographic features, like islands or rocky headlands, subject to neither wave action nor strong currents. Here *Sargassum* beds were sporadically exposed to air, at their upper limit, during low tide; and (3) Those that did not fit into either of the two previous categories were classified as moderately exposed sampling sites. Rock size and slope of the rock surfaces were visually evaluated. Size classification followed that described by Raffaelli & Hawkins (1996). It included: cliffs (tens of metres); large boulders (metres), and small boulders (centimetres). Rock surfaces were classified as gentle/almost horizontal (<20^{o}), intermediate (20^{o}-60^{o}) and steep/almost vertical (>60^{o}).

Five quadrat sampling units (0.25 m^2) were collected at random along a transect 10 m in length, positioned approximately 1 m below the upper limit of *Sargassum* distribution on the rocky

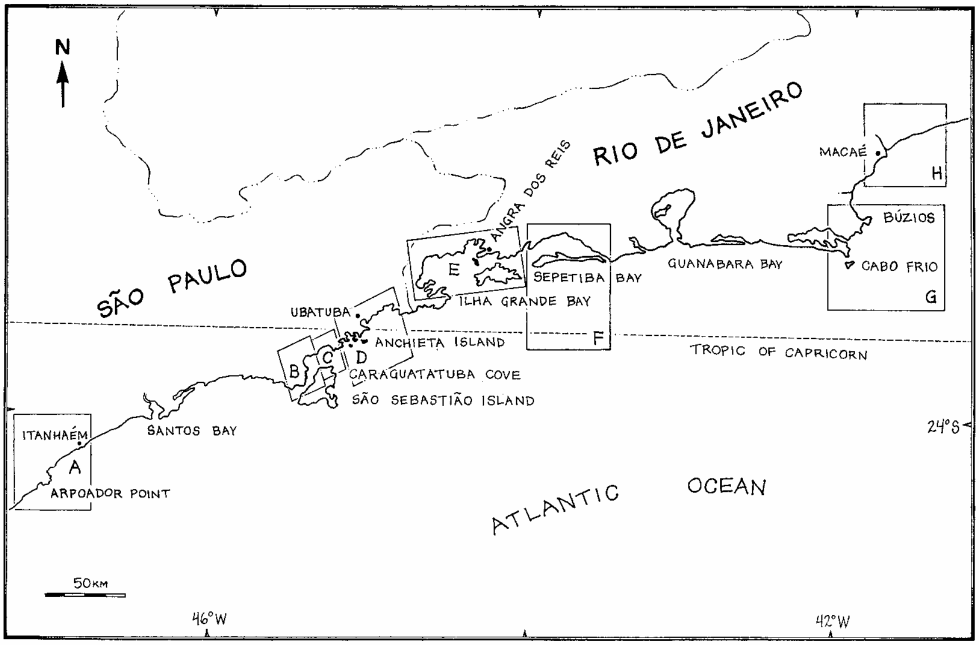

Fig. 1. Studied geographic areas selected along the coasts of Rio de Janeiro and São Paulo States. A-Peruíbe-Itanhaém (sampling sites I and II); B-São Sebastião Channel (sampling site III); C-Caraguatatuba Cove (sampling site IV); D-Ubatuba (sampling sites V to X); E-Ilha Grande Bay (sampling site XI); F-Sepetiba Bay (sampling site XII); G-Cabo Frio-Búzios (sampling site XIII); H- Macaé-northern State line (sampling site XIV).

shore of each sampling site (Fig. 2). The rocky surface scraped with a metal spatula during low tide, and all the material obtained was placed in plastic bags in a 4% formalin solution. In the laboratory, the material was sorted, separating the crabs, the other macroinvertebrates and the macroalgae.

The Brachyura crabs sorted from each sample were identified at the species level, following Melo (1996), and counted. The Xanthidae family was considered as a single group for density comparisons, since some individuals could not be identified at the genus or species levels, due to the loss of their chelas during sample sorting.

The macroalgae sorted from each sample were grouped according to their morpho-functional types, following Steneck & Dethier (1994) and Széchy & Paula (2000) which are: leathery macrophytes (*Sargassum*), articulated calcareous algae (Corallinaceae), corticated macrophytes (*Laurencia* J.V. Lamouroux, *Hypnea* J.V. Lamouroux, *Gracilaria* Greville and others), foliose algae (*Ulva* Linnaeus, *Enteromorpha* Link in Nees, *Dictyopteris* J.V. Lamouroux and others) and filamentous algae (*Cladophora* Kützing, *Sphacelaria* Lyngbye, *Bryocladia* F. Schmitz, *Centroceras* Kützing and others).

Subsequently, the groups of crabs and macroalgae were washed in running water and dried at 70-90oC, until they reached a constant weight. They were weighed with a digital electronic scale, with an error of 0.01 g. The mean dry weight and density values (n = 5) of the sorted organisms were calculated for each sampling site.

Three matrices were created: (1) environmental (env), which differentiates the sampling sites according to degree of wave action, rock size and slope of the rock surface; (2) vegetation (veg), which reveals the phytobenthic community structure, based upon the mean dry weight of the different morpho-functional types of macroalgae; and (3) Brachyura (brac), made up of the mean values, by sampling site, of the density of the different species identified. Data treatment was by canonical correspondence analysis, using the software CANOCO (Ter Braak 1990; Ter Braak & Prentice 1988), which allows for analysis and quantification of the relative contribution of the principal abiotic and biotic factors in the community structure.

Table 1. Characteristics of the sampling sites.

Sampling site	Geographic area	Location	Degree of wave action	Rocky substrate		Species of *Sargassum*	Sampling date
				Rock size*	Slope of the rock surface		
	SÃO PAULO						
I	Peruíbe	Prainha	Exposed	cliff	intermediate	*S. rigidulum*	9.1991
II	Itanhaém (A)	Praia de Peruíbe	Moderately exposed	large boulders	intermediate	*S. stenophyllum*	9.1991
III	São Sebastião Channel (B)	Praia das Cigarras	Moderately exposed	cliff	intermediate	*S. stenophyllum*	9.1992
IV	Caraguatatuba Cove (C)	Praia Martins de Sá	Moderately exposed	cliff	intermediate	*S. stenophyllum*	11.1991
V	Ubatuba (D)	Praia de Itaguá	Moderately exposed	large boulders	intermediate	*S. sulgare* var. *nanum*	10.1991
VI	Ubatuba (D)	Praia de Itaguá	Protected	small boulders	variable	*S. vulgare* var. *vulgare*	11.1991
VII	Ubatuba (D)	Praia de Perequeaçu	Moderately exposed	large boulders	intermediate	*S. cymosum* var. *cymosum*	11.1991
VIII	Ubatuba (D)	Ponta da Fortaleza	Protected	small boulders	variable	*S. filipendula*	10.1991
IX	Ubatuba (D)	Ponta da Fortaleza	Moderately exposed	cliff	intermediate	*S. filipendula*	10.1991
X	Ubatuba (D)	Ponta da Fortaleza	Exposed	cliff	gentle	*S. cymosum* var. *nanum*	10.1991
	RIO DE JANEIRO						
XI	Ilha Grande Bay (E)	Saco de Piraquara de Fora	Protected	cliff	steep	*S. vulgare* var. *vulgare*	11.1992
XII	Sepetiba Bay (F)	Praia de Ibicuí	Moderately exposed	large boulders	steep	*S. cymosum* var. *cymosum*	10.1992
XIII	Cabo Frio/ Búzios (G)	Praia Rasa/Pta do Pai Vitório	Moderately exposed	cliff	gentle	*S. vulgare* var. *vulgare*	10.1992
XIV	Macaé - northen State line (H)	Praia de Itapebuçu	Moderately exposed	cliff	gentle	*S. vulgare* var. *vulgare*	10.1992

* In accordance with the particle size gradient given by Raffaelli & Hawkins (1996): cliff (tens of metres) are bigger than large boulders (metres), and these are bigger than small boulders (centimetres).

Results

All together, twelve species of Brachyura were identified, belonging to the families Porcellanidae, Grapsidae, Majidae and Xanthidae (Table 2). The family Grapsidae was the least prominent, represented by only one species.

Pachycheles haigae and *Epialtus brasiliensis* reached the highest values of mean density per sampling site (Table 3). *Epialtus brasiliensis* occurred in most (13) of the sampling sites. *Megalobrachium roseum* was found in only one sampling site: Praia das Cigarras. The communities that presented the highest values for total density of Brachyura were mainly those of exposed sites, such as Prainha and Ponta da Fortaleza.

Among the different morpho-functional types of macroalgae present in the communities, the leathery macrophytes, represented by *Sargassum*, and the articulated calcareous algae, presented the

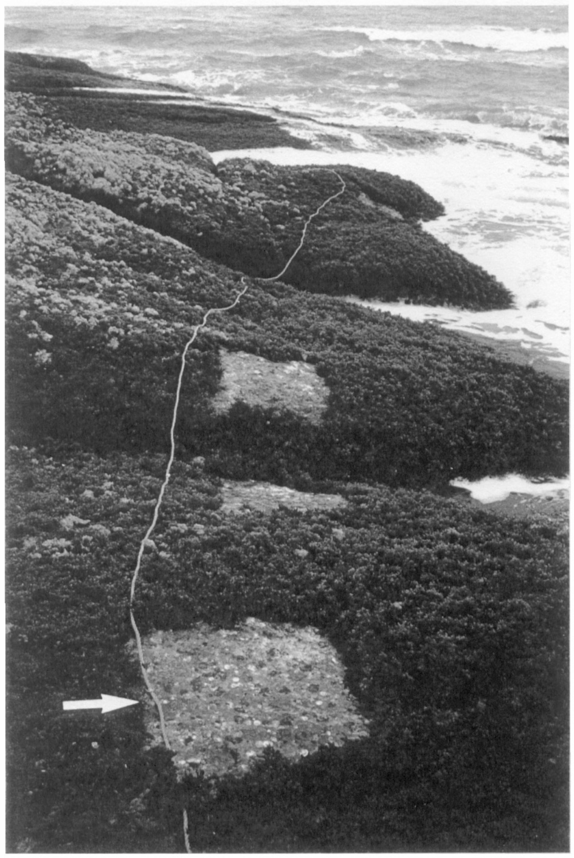

Fig. 2. Photograph showing sampling detail at Praia Rasa (sampling site XIII): the layout of quadrats along the horizontal transect (arrow = one scraped quadrat).

largest dry weight values (Table 4). In general, where *Sargassum* spp. reached their highest dry weight values, the articulated calcareous algae were sparse, with the exception of the site at Praia de Itapebuçu. Macroalgae of other morpho-functional types were not well represented in terms of dry weight, except in some sampling sites. Filamentous algae were abundant in Praia de Peruíbe, in an area where the sand covered the rock surface. The foliose algae were best represented in Praia de Ibicuí. The corticated macrophytes were prominent at Praia de Perequeaçu (Table 4).

The canonical correspondence analysis shows that both environmental and vegetational variables explain the variation in Brachyura species density in the communities. The percentage explained by the environmental matrix was high (40.9%) and significant. The percentage explained by the vegetation matrix was 29.7%, but not significant (Table 5). The amount of variation that remained unexplained by the data was 23.2% being considered a high value in accordance with Borcard *et al.* (1992).

Table 2. Species list of Brachyura decapods for the fourteen sampling sites.

	Porcellanidae
1	*Pachycheles haigae* Rodrigues da Costa, 1960
2	*Pachycheles monilifer* Dana, 1852
3	*Megalobrachium roseum* Rathbun, 1900
	Grapsidae
4	*Pachygrapsus transversus* Gibbes, 1850
	Majidae
5	*Acanthonyx petiverii* H. Milne Edwards, 1834
6	*Epialtus brasiliensis* Dana, 1852
7	*Microphrys bicornutus* Latreille, 1825
8	*Mithrax forceps* A. Milne Edwards, 1875
	Xanthidae
9	*Eurypanopeus abbreviatus* Stimpson, 1860
10	*Hexapanopeus paulensis* Rathbun, 1930
11	*Pilumnus dasypodus* Kingsley, 1879
12	*Pilumnus reticulatus* Stimpson, 1860

However, among the environmental variables analysed by the Monte Carlo permutation test, only the degree of wave action was significant at the level of 1% ($P = 0.01$). Rock size and slope of the rock surface were not significant and cannot explain the differences in the density of the Brachyura among the communities.

Discussion

The greatest frequency of *Epialtus brasiliensis* in the communities corresponds with that observed by Mantelatto & Corrêa (1995/96), for Brachyura inhabitants of *Sargassum cymosum* in the region of Ubatuba, São Paulo. In our study, this crab presented the largest density values where *Sargassum* was abundant, particularly in moderately exposed sites. The preference of *E. brasiliensis* for areas with *Sargassum* was also mentioned by Negreiros-Fransozo *et al.* (1994), in the phytal assemblage of rocky shores of Ubatuba, São Paulo State, Brazil. On the other hand, *Pachycheles haigae*, another common species in the communities studied, attained its largest density values where the articulated corallines were most abundant, and

Table 3. Density of Brachyura species per sampling site (number of individuals. m^{-2}, n = 5). The sampling sites and the species are numbered in accordance with Tables 1 and 2, respectively. x = arithmetic mean; s = standard deviation.

Sampling sites	Species 1	2	3	4	5	6	7	8	Xanthidae
					x (s)				
I	347.2 (77.8)	0 (0)	0 (0)	8.8 (8.8)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
II	10.4 (10.6)	0.8 (1.6)	0 (0)	0 (0)	0.8 (1.6)	12.8 (14.2)	0 (0)	0 (0)	48.8 (19.5)
III	35.2 (21.5)	0.8 (1.6)	0.8 (1.6)	0 (0)	0 (0)	59.2 (44.4)	0 (0)	0 (0)	9.6 (7.4)
IV	0.8 (1.6)	0 (0)	0 (0)	0 (0)	0 (0)	48.8 (50.3)	0.8 (1.6)	0 (0)	4.8 (5.9)
V	0.8 (1.6)	13.6 (27.2)	0 (0)	36.8 (16.8)	0 (0)	83.2 (46.2)	0 (0)	8.8 (8.2)	47.2 (55.1)
VI	0 (0)	0 (0)	0 (0)	0 (0)	1.6 (3.2)	7.2 (8.9)	0 (0)	0 (0)	0.8 (1.6)
VII	0 (0)	0 (0)	0 (0)	0 (0)	0.8 (1.6)	36.8 (26.7)	0 (0)	0 (0)	0.8 (1.6)
VIII	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	14.4 (17.0)	0 (0)	0 (0)	2.4 (1.9)
IX	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	52.0 (36.0)	0 (0)	0.8 (1.6)	7.2 (6.4)
X	144.0 (101.1)	9.6 (12.3)	0 (0)	8.8 (6.4)	0 (0)	21.6 (6.00)	0 (0)	0 (0)	0 (0)
XI	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	3.2 (3.0)	18.4 (12.6)	6.4 (4.1)	6.4 (4.1)
XII	0 (0)	0 (0)	0 (0)	0 (0)	1.0 (1.1)	27.0 (13.7)	0 (0)	0 (0)	13.0 (9.9)
XIII	9.6 (14.0)	0 (0)	0 (0)	0 (0)	20.0 (10.4)	62.4 (22.2)	0.8 (1.6)	0 (0)	10.4 (6.5)
XIV	17.6 (10.6)	4.0 (4.4)	0 (0)	0 (0)	13.6 (13.5)	32.8 (11.7)	0.8 (1.6)	0 (0)	15.2 (8.6)

also where the articulated corallines were not abundant. In both cases, the sampling sites were exposed to wave action. In previous studies, the abundance of *P. haigae* was associated with the presence of mussels, in addition to articulated corallines, and with sites with strong wave action (Veloso & Melo 1993).

This observation supports the interactive character of diverse factors in the determination of the characteristics of marine benthic communities. In this case, the biomass of different morpho-functional types of macroalgae, as well as abiotic factors related to the degree of wave action, stand out.

The role played by the macroalgae in the richness and abundance of the carcinofauna of rocky shore communities is cited by other authors (Edgar 1983c; Mukai 1971). It is easy to understand that the macroalgae of these communities, represented by different species and morpho-functional types, with distinct spatial distribution and abundance, could constitute appropriate habitats for the crabs, depending upon the species and the ontogenetic stage (Beck 1995; Isaksson & Pihl 1992). Two as-

Table 4. Dry weight (g m^{-2}) of the different morpho-functional types of macroalgae at the sampling sites. The samping sites are numbered in accordance with Table 1. x = arithmetic mean; s = standard deviation (n = 5).

Sampling sites	Types of macroalgae									
	Leathery macrophytes (*Sargassum*)		Articulated calcareous		Filamentous		Foliose		Corticated macrophytes	
	x (s)									
I	100.52	(86.04)	410.54	(198.09)	2.67	(2.42)	26.41	(20.04)	1.60	(2.79)
II	115.50	(52.15)	<0.01		113.12	(47.55)	25.28	(21.84)	7.32	(7.37)
III	287.03	(23.64)	<0.01		<0.01		15.50	(9.27)	45.69	(38.40)
IV	159.63	(53.56)	<0.01		2.48	(3.71)	10.35	(10.04)	68.72	(41.90)
V	332.67	(58.75)	12.53	(10.75)	0.02	(0.01)	2.00	(2.39)	34.84	(28.19)
VI	213.94	(82.47)	12.78	(15.44)	0.01	(0.01)	8.56	(7.07)	1.47	(1.77)
VII	277.30	(64.92)	0.08	(0.16)	<0.01		36.32	(18.72)	104.26	(75.51)
VIII	368.39	(42.44)	2.38	(3.32)	1.01	(1.61)	15.18	(9.96)	3.53	(5.92)
IX	318.47	(25.92)	1.00	(2.00)	0.89	(1.34)	2.66	(3.01)	23.12	(22.28)
X	102.86	(41.21)	37.35	(36.04)	0.10	(1.22)	9.88	(8.91)	4.99	(4.39)
XI	414.06	(72.09)	11.52	(8.94)	0.02	(0.02)	9.89	(3.80)	46.50	(30.89)
XII	82.21	(119.52)	3.46	(6.00)	0.50	(0.65)	99.07	(33.56)	7.74	(8.56)
XIII	586.66	(56.77)	0.66	(1.31)	0.05	(0.09)	28.57	(36.53)	8.75	(17.23)
XIV	356.34	(42.88)	478.42	(103.78)	0.01	(0.01)	5.88	(4.65)	4.98	(6.51)

pects of such an association can be considered fundamental for motile animals like the crabs: food supply (Dubiaski-Silva & Masunari 1995; Edgar 1983c; Mantelatto & Corrêa 1995/96) and guarantee of refuge against predators and/or adverse environmental conditions (Abele 1974).

If we analyze the data independently, considering only the macroalgae abundance, we can gain a false impression of its importance for the phytal animals. In our analysis, where the differences in species density of the Brachyura between the communities were not significantly explained by the dry weight data of the macroalgae, we can conclude that the vegetation had a secondary role, agreeing with Dommasnes (1968), Norton (1971), and Takeuchi *et al.* (1987). According to Brook (1978), Highsmith (1985) and Mantelatto & Corrêa (1995/96), the richness and the abundance of the Brachyura species have shown little or no correlation with the *Sargassum* biomass. In fact, we believe that, for many species of crabs, refuge and food availability in any compartment of the habitat are fundamental, whether they are supplied by plant or animal species or by the rocky substrate itself (Stoner & Lewis 1985). Furthermore, as has been demonstrated, artificial substrates also serve as habitats for species of the epifaunal community (Edgar 1991; Hacker & Madin 1991), confirming that, in general, these animals show little preference for a particular group of algae (Dean & Connel 1987; Dubiaski-Silva & Masunari 1995; Edgar 1983a, 1991; Russo 1990).

The importance of the abiotic factor-exposure to wave action - in the explanation of the density variation in the Brachyura species, can be understood in light of the fact that this is a factor that simultaneously comprises various distinct physical

Table 5. Percentage of explanation of the Brachyura matrix (brac) in relation to the environmental (env) and vegetation (veg) matrices. F=F rate; *=significant at the level of 15 (P = 0.01); cov. = covariance.

	% of explanation	F
brac x env	47.13	3.31*
brac x veg	35.85	1.94
brac x env (cov. veg)	40.94	4.91*
brac x veg (cov. env)	29.66	1.94

parameters (Hiscock 1983; Riedl 1971). These parameters interfere directly or indirectly in the recruitment and development of the macroalgae on the rocky shore and, consequently, in the community structure as a whole (Chapman 1986; Underwood & Denley 1984). On the other hand, the cover of macroalgae, including *Sargassum*, favors the sedimentation of organic particulates that may be used as food (Edgar 1983c; Gouvêa & Leite 1980; Hansen 1977; Mantelatto & Corrêa 1995/96).

Therefore, we can raise the hypothesis that the Brachyura crabs that occur in the rocky shore communities search for refuge - mainly from wave action, and for a rich food source among the macroscopic algae, particularly the dominant algae in the environment, irrespective of their species.

Acknowledgements

We thank Alexandre de Castro for help in sorting of the crabs and Ricardo Silva Cardoso for the application of the software CANOCO.

References

Abele, L.G. 1974. Species diversity of decapod crustaceans in marine habitats. *Ecology* **55:** 156-161.

Albuquerque, E.F. & C.O.C. Guéron. 1989. Variação sazonal da fauna vágil de *Sargassum stenophyllum* (Martens) em duas estações com diferentes graus de exposição às ondas, em Ibicuí, Baía de Sepetiba, Estado do Rio de Janeiro, Brasil. *Memórias do Instituto Oswaldo Cruz* **84:** 9-17.

Barreto, C.C. 1998. *Heterogeneidade Estrutural de Três Espécies de Macroalgas Marinhas Bentônicas e Estruturação das Comunidades Fitais Associadas.* Tese (Doutorado). Universidade de São Paulo, São Paulo, Brasil.

Beck, M.W. 1995. Size-specific shelter limitation in stone crabs: a test of demographic bottleneck hypothesis. *Ecology* **76:** 968-987.

Borcard, D., P. Legendre & P. Drapeau. 1992. Partialling out the spatial component of ecological variation. *Ecology* **73:** 1045-1055.

Borojevic, R. 1971. Eponges calcaires de côte sud-est du Brésil, épibiontes sur *Laminaria brasiliensis et Sargassum cymosum. Revista Brasileira de Biologia* **31:** 525-530.

Brook, I.M. 1978. Comparative macrofaunal abundance in turtlegrass (*Thalassia testudinum*) communities in south Florida characterized by high blade density. *Bulletin of Marine Science* **28:** 212-217.

Chapman, A.R.O. 1986. Population and community ecology of seaweed. *Advances in Marine Biology* **23:** 1-161.

Dean, R.L. & J.H. Connell. 1987. Marine invertebrates in an algal succession. III-Mechanisms linking habitat complexity with diversity. *Journal of Experimental Marine Biology and Ecology* **109:** 249-273.

Dommasnes, A. 1968. Variations in the meiofauna of *Corallina officinalis* L. with wave exposure. *Sarsia* **34:** 117-124.

Dubiaski-Silva, J. & S. Masunari. 1995. Ecologia populacional dos Amphipoda (Crustacea) dos fitais de Caiobá, Matinhos, Paraná, Brasil. *Revista Brasileira de Zoologia* **12:** 373-396.

Edgar, G.J. 1983a. The ecology of south-east Tasmanian phytal animal communities. I-Spatial organization on a local scale. *Journal of Experimental Marine Biology and Ecology* **70:** 129-157.

Edgar, G.J. 1983b. The ecology of south-east Tasmanian phytal animal communities. II-Seasonal change in plant and animal populations. *Journal of Experimental Marine Biology and Ecology* **70:** 159-179.

Edgar, G.J. 1983c. The ecology of south-east Tasmanian phytal animal communities. III-Patterns of species diversity. *Journal of Experimental Marine Biology and Ecology* **70:** 181-203.

Edgar, G.J. 1991. Artificial algae as habitats for mobile epifauna: factors affecting colonization in a Japanese *Sargassum* bed. *Hydrobiologia* **226:** 111-118.

Edgar, G.J. & M. Aoki. 1993. Resource limitation and fish predation: their importance to mobile epifauna associated with Japanese *Sargassum*. *Oecologia* **95:** 122-133.

Eston, V.R. & W.O. Bussab. 1990. An experimental analysis of ecological dominance in a rocky subtidal macroalgal community. *Journal of Experimental Marine Biology and Ecology* **136:** 170-195.

Evans, S.M., M.E. Gill, F.G. Hardy & F.O.K. Seku. 1993. Evidence of change in some rocky shore communities on the coast of Ghana. *Journal of Experimental Marine Biology and Ecology* **172:** 129-141.

Fenwick, G.D. 1976. The effect of wave exposure on the amphipod fauna of the alga *Caulerpa brownii. Journal of Experimental Marine Biology and Ecology* **25:** 1-18.

Flores, A.A.V., M.L. Negreiros-Fransozo & A. Fransozo. 1994. Análise preliminar da partilha de habitat por *Pachygrapsus transversus* (Gibbes, 1850) (Crustacea, Grapsidae) numa área intertidal rochosa, Ubatuba, SP. pp. 359. *In*: 2º *Congresso de Ecologia do Brasil*. Universidade Estadual de Londrina, Londrina, Brasil.

Gee, J.M. & R.M. Warwick. 1994. Metazoan community structure in relation to the fractal dimensions of marine macroalgae. *Marine Ecology Progress Series* **103:** 141-150.

Gouvêa, E.P. & Y.M. Leite. 1980. A carcinofauna do fital de *Halimeda opuntia* (Linnaeus) Lamouroux e a variação sazonal de sua densidade. *Ciência e Cultura* **32:** 596-600.

Gunnill, F.C. 1982a. Macroalgae as habitat patch islands for *Scutellidium lamellipes* (Copepoda: Harpacticoida) and *Amphitoe tea* (Amphipoda: Gammaridae). *Marine Biology* **69:** 103-116.

Gunnill, F.C. 1982b. Effects of plant size and distribution on the numbers of invertebrate species and individuals inhabiting the brown alga *Pelvetia fastigiata. Marine Biology* **69:** 263-280.

Hacker, S.D. & L.P. Madin. 1991. Why habitat architecture and color are important to shrimps living in pelagic *Sargassum*: use of camouflage and plant-part mimicry. *Marine Ecology Progress Series* **70:** 143-155.

Hansen, R.B. 1977. Pelagic *Sargassum* community metabolism - carbon and nitrogen. *Journal of Experimental Marine Biology and Ecology* **29:** 107-118.

Highsmith, R.C. 1985. Floating and algal rafting as potential dipersal mechanisms in brooding invertebrates. *Marine Ecology Progress Series* **25:** 169-179.

Hiscock, K. 1983. Water movement. pp. 58-96. *In*: R. Earll & D.G. Erwin (eds.) *Sublittoral Ecology; The Ecology of the Shallow Sublittoral Benthos*. Clarendon Press, Oxford.

Hiyodo, C.M. & A. Fransozo. 1994. Biologia populacional de *Acanthonyx petiverii* H. Milne Edwards, 1834 (Crustacea, Decapoda, Majidae). pp. 373. *In*: *2º Congresso de Ecologia do Brasil*. Universidade Estadual de Londrina, Londrina, Brasil.

Isaksson, I. & L. Pihl. 1992. Structural changes in benthic macrovegetation and associated epibenthic faunal communities. *Netherland Journal of Sea Research* **30:** 131-140.

Kito, K. 1977. Phytal animals in the *Sargassum confusum* region in Oshoro Bay, Hokkaido: phenology of harpacticoid copepods. *Journal of the Faculty of Sciences, Hokkaido University*, Ser. 6, Zoology **20:** 691-696.

Kito, K. 1982. Phytal marine nematode assemblage on *Sargassum confusum* Agardh, with reference to the structure and seasonal fluctuations. *Journal of the Faculty of Sciences, Hokkaido University*, Ser. 6, Zoology **23:** 143-161.

Leber, K.M. 1985. The influence of predatory decapods refuge and microhabitat selection on seagrass communities. *Ecology* **66:** 1951-1964.

Lewis, J.R. 1964. *The Ecology of Rocky Shores*. English Universities Press, London.

L'Hardy, J.-P. 1962. Observations sur le peuplement épiphyte des lames de *Laminaria saccharina* (Linné) Lamouroux, en Baie de Morlaix (Finistère). *Cahiers de Biologie Marine* **3:** 115-127.

Lima, H.S. 1969. *Fauna séssil do Sargassum cymosum da Praia do Lamberto, Ubatuba (Estado de São Paulo): composição qualitativa e considerações sobre a localização das espécies na planta.* Dissertação (Mestrado). Universidade de São Paulo, São Paulo, Brasil.

Lima, L.K., E.H. Morgado & M.O. Tanaka. 1995. Modificações na epifauna vágil associada à alga parda *Sargassum cymosum*- Ubatuba (SP-Brasil). pp. 119. *In: 6º Congreso Latinoamericano de Ciencias del Mar*. Universidad Nacional de Mar del Plata, Mar del Plata, Argentina.

Littler, M.M. & D.S. Littler. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *American Naturalist* **116:** 25-44.

Mahiques, M.M., K. Suguio, M.G. Tessler, V.V. Furtado & B.B. Eichler. 1990. Parâmetros oceanográfico-geológico-geomorfológicos de interesse na caracterização de ecossistemas costeiros do Estado de São Paulo. Vol. 1, pp. 142-150. *In: 2º Simpósio de Ecossistemas da Costa Sul e Sudeste Brasileira: Estrutura, Função e Manejo*. Academia de Ciências do Estado de São Paulo, São Paulo, Brasil.

Mantelatto, F.L.M. & E.K. Corrêa. 1995/1996. Composição e variação sazonal dos caranguejos braquiúros (Crustacea, Decapoda) habitantes de *Sargassum cymosum* na região de Ubatuba, São Paulo, Brasil. *Bioikos* **9-10:** 22-31.

Martin-Smith, K.M. 1993. Abundance of mobile epifauna: the role of habitat complexity and predation by fishes. *Journal of Experimental Marine Biology and Ecology* **174:** 243-260.

Masunari, S. 1976. *O fital de Amphiroa fragilissima (Linnaeus) Lamouroux, 1916 da Praia do Lázaro, Ubatuba, São Paulo*. Dissertação (Mestrado). Universidade de São Paulo, São Paulo, Brasil.

Masunari, S. 1982. Organismos do fital *Amphiroa beauvoisii* Lamouroux, 1816 (Rhodophyta, Corallinaceae). I. Autoecologia. *Boletim de Zoologia da Uni versidade de São Paulo* **7:** 57-148.

Masunari, S. 1989. Ecologia das comunidades fitais. vol. 1, pp. 195-253. *In: 1º Simpósio de Ecossistemas da costa Sul-Sudeste Brasileira: síntese dos conhecimentos*. Academia de Ciências do Estado de São Paulo, São Paulo, Brasil.

Melo, G.A.S. 1985. *Taxonomia e Padrões Distribucionais e Ecológicos dos Brachyura (Crustacea: Decapoda) do Litoral Sudeste do Brasil*. Tese (Doutorado). Univerdidade de São Paulo, São Paulo, Brasil.

Melo, G.A.S. 1996. *Manual de Identificação dos Brachyura (caranguejos e siris) do Litoral Brasileiro*. Plêiade, São Paulo.

Melo, G.A.S., V.G. Veloso & M.C. Oliveira. 1989. A fauna de Brachyura (Crustacea, Decapoda) do litoral do Estado do Paraná - Lista preliminar. *Nerítica* **4:** 1-31.

Mitchell, G.J.P., M.T.M. Széchy & L.A. Mitsuya. 1979. Sinopse das cloroficeas marinhas bentônicas do litoral do Estado do Rio de Janeiro. *Leandra* **8/9:** 91-123.

Montouchet, P.C.G. 1979. Sur la communauté des animaux vagiles associés à *Sargassum cymosum* C. Agardh, à Ubatuba, Etat de São Paulo, Brésil. *Studies on Neotropical Fauna and Environment* **14:** 33-64.

Mukai, H. 1971. The phytal animals on the thalli of *Sargassum serratifolium* in the *Sargassum* region, with reference to their seasonal fluctuations. *Marine Biology* **8:** 170-182.

Negreiros-Fransozo, M.L., A. Fransozo & A.L.D. Reigada. 1994. Biologia populacional de *Epialtus brasiliensis* Dana, 1852 (Curstacea, Majidae). *Revista Brasileira de Biologia* **54:** 173-180.

Norton, T.A. 1971. An ecological study of the fauna inhabiting the sublittoral marine alga *Saccorhiza polyschides* (Lightf.) Batt. *Hydrobiologia* **37:** 215-231.

Norton, T.A. & M.R. Benson. 1983. Ecological interactions between the brown seaweed *Sargassum muticum* and its associated fauna. *Marine Biology* **75:** 169-177.

Oliveira Filho, E.C. & E.M. Mayal. 1976. Seasonal distribution of intertidal organisms at Ubatuba, São Paulo (Brazil). *Revista Brasileira de Biologia* **36:** 305-316.

Paula, E.J. 1988. O gênero *Sargassum* C. Ag. (Phaeophyta-Fucales) no litoral do Estado de São Paulo, Brasil. *Boletim de Botânica da Universidade de São Paulo* **10:** 65-118.

Paula, E.J. 1989. Zonação nos costões rochosos: região entremarés. pp. 266-288. *In: 1º Simpósio de Ecossistemas da Costa Sul-Sudeste Brasileira: Síntese dos Conhecimentos*. Academia de Ciências do Estado de São Paulo, São Paulo, Brasil.

Paula, E.J. & E.C. Oliveira Filho. 1980. Phenology of two populations of *Sargassum cymosum* (Phaeophyta - Fucales) of São Paulo State coast, Brazil. *Boletim de Botânica da Universidade de São Paulo* **8:** 21-39.

Paula, E.J. & E.C. Oliveira Filho. 1982. Wave exposure and ecotypical differentiation in *Sargassum cymosum* (Phaeophyta, Fucales). *Phycologia* **21:** 145-153.

Raffaelli, D. & S. Hawkins. 1996. *Intertidal Ecology*. Chapman & Hall, London.

Riedl, R. 1971. Water movement: general introduction. pp. 1085-1088. *In*: O. Kinne (ed.) *Marine Ecology*. Wiley-Interscience, London.

Russo, A.R. 1990. The role of seaweed complexity in structuring Hawaiian epiphytal amphipod communities. *Hydrobiologia* **194:** 1-12.

Santos, C.G. & M.D. Correia. 1995. Fauna associada ao fital *Halimeda opuntia* (Linnaeus) Lamouroux (Chlorophyta) do recife da Ponta Verde, Maceió, Alagoas, Brasil. *Revista Brasileira de Zoologia da Universidade de São Paulo* **12:** 263-271.

Steneck, R.S. & M.N. Dethier. 1994. A functional group approach to the structure of algal dominated communities. *Oikos* **69:** 476-498.

Stoner, A.W. & F.G. Lewis. 1985. The influence of quantitative and qualitative aspects of habitat complexity in tropical sea-grass meadows. *Journal of Experimental Marine Biology and Ecology* **94:** 19-40.

Széchy, M.T.M. & E.J. Paula. 2000. Padrões estruturais quantitativos de bancos de *Sargassum* (Phaeophyta, Fucales) do litoral dos estados do Rio de Janeiro e São Paulo, Brasil. *Revista Brasileira de Botânica* **23:** 121-132.

Takeuchi, I., R. Kuwabara, R. Hirano & H. Yamakawa. 1987. Species compositions of the Caprellidea (Crustacea: Amphipoda) of the *Sargassum* zone on the Pacific coast of Japan. *Bulletin of Marine Science* **41:** 253-267.

Tararam, A.S. & Y. Wakabara. 1981. The mobile fauna - especially Gammaridea - of *Sargassum cymosum*. *Marine Ecology Progress Series* **5:** 157-163.

Tararam, A.S., Y. Wakabara & F.P.P. Leite. 1986. Vertical distribution of amphipods living on algae of a brazilian intertidal rocky shore. *Crustaceana* **51:** 183-187.

Ter Braak, C.F.J. 1990. Update notes: CANOCO version 3.10. Agricultural Mathematics Group, Wageningen, The Netherlands.

Ter Braak, C.J.F. & I.C. Prentice. 1988. A theory of gradient analysis. *Advanced Ecological Research* **18:** 271-317.

Underwood, A.J. & E.J. Denley. 1984. Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. pp. 151-180. *In*: D.R. Strong, D. Simberloff, L.G. Abele & A.B. Thistle (eds) *Ecological Communities: Conceptual Issues and the Evidence*. Princeton Uninversity Press, Princeton.

Veloso, V.G. & G.A.S. Melo. 1993. Taxonomia e distribuição da família Porcellanidae (Crustacea, Decapoda, Anomura) no litoral brasileiro. *Iheringia*, Sér. Zoologia, **75:** 171-186.

Wakabara, Y., A.S. Tararam & A.M. Takeda. 1983. Comparative study of the amphipod fauna living on *Sargassum* of two Itanhaém shores, Brazil. *Journal of Crustacean Biology* **3:** 602-607.

Williams, G.A. & R. Seed. 1992. Interactions between macrofaunal epiphytes and their host algae. pp. 189-211. *In*: D.M. John, S.J. Hawkins & J.H. Price (eds) *Plant-Animal Interactions in the Marine Benthos*. Clarendon Press, Oxford.