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SECONDARY SUCCESSION ON AN EXPOSED ROCKY INTERTIDAL ALGAL COMMUNITY OF THE STATE OF SÃO PAULO – BRAZIL.

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ABSTRACT – (Secondary succession on an exposed rocky intertidal algae community of the State of São Paulo – Brazil). Succession was studied at the low intertidal level of an exposed rocky shore at Ponta da Fortaleza, Ubatuba, State of São Paulo, where *Sargassum cymosum* var. *nanum* is the dominant alga. Experimental areas were scraped throughout the year and the successional sequences were observed. *S. cymosum* var. *nanum* is a perennial seaweed, an attribute of a biotically competent strategist. Nevertheless, this *Sargassum cymosum* variety is dwarf and exhibits precocious reproductive development, characteristic of opportunistic species. Succession in this community was maintained in its earlier stages both at control and experimental sites, due to desiccation stress, which causes widespread algal mortality at early summer.

RESUMO – (Sucessão secundária em uma comunidade de algas de costão rochoso no litoral de São Paulo, Brasil). Foi estudada a sucessão no nível inferior da região entre-marés em um costão rochoso exposto à ação das ondas, no litoral de São Paulo (Ponta da Fortaleza, Ubatuba). Neste costão, *Sargassum cymosum* var. *nanum* é a alga dominante. Áreas experimentais foram raspadas ao longo do ano onde foi observada a seqüência sucessional. *S. cymosum* var. *nanum* é uma espécie perene, característica de organismos sucessionais tardios. No entanto, esta variedade é anã e apresenta desenvolvimento reprodutivo precoce, característica de espécies oportunistas. Nesta comunidade a sucessão é mantida nos estágios iniciais, tanto nas áreas experimentais como nas áreas controle, devido à dessecação, que causa grande mortalidade de algas no início do verão.

Key words: algal communities, ecology, succession

INTRODUCTION

Succession is defined by Connell e Slatyer (1977) as "the changes observed in an ecological community following a perturbation that opens up a relatively large space". A major factor which determines the colonization of a bare surface is the availability of propagules from parent plants (Hruby & Norton 1979). Both the seasonal nature of reproduction of some species and patchiness in the distribution of the propagules in the water (Hruby & Norton 1979) will limit which will be the first colonizers. Therefore, succession will not only be dependent on biological interactions such as competition for space among colonizing plants and or sessile animals, presence of herbivores, carnivores, and pathogens (Connell & Slatyer 1977), but it will also be related to the season in which free space is available for colonization (Hawkins & Hartnoll 1983).

Seasonality of tropical benthic marine macroalgae has been affirmed by some authors and denied by others (De Wreede 1976). The phenomenon was pointed out for the coast of São Paulo in works on the vertical distribution of intertidal algae (Oliveira Fº & Mayal 1976, Oliveira Fº & Paula 1983) and on the phenology of some perennial species: *Pterocladia capillacea* (Gmelin) Bornet & Thuret, *Sargassum cymosum* C. Agardh and *Gracilaria cervicornis* (Turner) J. Agardh present a greater biomass and/or length during spring and/or summer (Oliveira Fº & Sazima 1973, Paula & Oliveira Fº 1980, Berchez 1985, Plastino 1985). On the other hand *Hypnea musciformis* (Wulfen) Lamouroux, and *Gigartina teedii* (Roth) Lamouroux, show irregular seasonal variations (Schenkman 1980, Braga 1985). These five species are fertile throughout the year. Nevertheless, the best known example of seasonal pattern in this region is provided by *Porphyra,* an ephemeral plant whose leafy stage is abundant only in winter and spring (Oliveira F° & Paula 1983).

In this paper we studied the dynamics of recruitment and the colonization patterns of a *Sargassum cymosum* var. *nanum* Paula & Oliveira F° – dominated community of an exposed rocky shore.

STUDY SITE

Ponta da Fortaleza at Ubatuba São Paulo (23°32'S, 45°10'W) is a sort of narrow and small rocky cape protruding 500 m towards the sea, with its eastern border facing the open sea. Monthly mean air temperatures for the nearby area ranged from 19.3°C in July of 1976 (mean range of the July daily temperatures was 7.4°C) to 27.4°C in February of 1977 (mean range of 1977 February daily temperatures was 9.7°C) – data from Serviço de Meteorologia, Instituto Oceanográfico, Universidade de São Paulo – while water temperatures ranged from 21°C in July to 29°C in March of 1976 – authors' punctual data gathered during the sampling period.

Sargassum cymosum var. *nanum,* a dwarf variety of the species, is the dominant alga, growing on bare rocky surfaces or on areas covered by the calcareous crust *Paragoniolithon solubile* (Foslie & Howe in Howe) Adey, Towsend & Boykins. It is a perennial species, fertile during the whole year, with greater biomass and density values in late spring. Density variations are the result of recruitment of new plants and the removal of established ones (Paula & Oliveira F° 1980, Oliveira F° & Paula 1983). Small *Echinometra lucunter* L. sea urchins (0.45 to 2.65 cm test size) were observed in the area.

METHODS

To determine the effect of temporal variations on the successional sequences, recolonization experiments were initiated every month from February to October of 1976 (except July). Bare areas of 0.25 m^2 were scraped with a putty knife inside the *Sargassum cymosum* var. *nanum* community, and colonization of these patches was followed monthly until February of 1977. The control area consisted of a 2.0 x 0.5 m strip within the low intertidal level close to the experimental quadrats. Scraping with a putty knife does not remove all the encrusting algae, what mimics the main natural disturbance, the removal of the organisms caused by desiccation stress (Oliveira F° & Paula, 1983). The term secondary succession is applied here for the recolonization process observed (see Lubchenco & Menge, 1978).

The Sorensen similarity coefficient (Hruby 1975) was used to measure the similarity among experimental quadrats scraped at different times in each of the observation period, based on presence absence data. These results were afterwards clustered by the weighted pair-group method using arithmetic averages (Davis 1973).

RESULTS

The number of species present in the control area increased from the summer to the spring of 1976, followed by a decline in the next summer (Figure 1, Table 1). *Amphiroa beauvoisii* Lamouroux, *A. brasiliana* Decaisne, *Centroceras clavulatum* (Agardh) Montagne, *Chaetomorpha antennina* (Bory) Kuetzing, *Cladophora vagabunda* (Linnaeus) van den Hoek, *Ectocarpus breviarticulatus* J. Agardh and *Ulva fasciata* Delile occurred predominantly at higher intertidal levels, invading the *S.cymosum* var. *nanum*-dominated areas occasionally and in high densities (except *U.fasciata,* with low density of small plants whenever present in the control area). Ralfsioid crusts and *Chnoospora minima* (Hering) Papenfuss, more abundant at higher intertidal levels, occurred throughout the year in the control area. On the other hand *Dictyopteris delicatula* Lamouroux and *Dictyota ciliolata* Kuetzing presented higher cover levels at the lower limit of the *Sargassum*-dominated area.

Table 2 presents the results of the scraped quadrats. *Paragoniolithon solubile* and ralfsioid crusts remained after the scrape of the surface and lasted through the whole sampling period. Several species were the first to recruit into the quadrats throughout the year. *Chnoospora minima, Cladophora vagabunda, Colpomenia sinuosa* (Roth) Derbès e Solier, *Dictyopteris delicatula, Ulva fasciata, Ectocarpus breviarticulatus, Sphacelaria tribuloides* Meneghini and colonial benthic diatoms were the earliest colonizers. *C. minima* was a persistent species while the last three disappeared soon after recruitment.

The first *Sargassum cymosum* var. *nanum* plants appeared only after a dense cover of the rocky surface had been established by other algal species, 2 to 9 months after the clearance of the several experimental quadrats. Recruitment of *Sargassum* plants was quicker where bare patches were available between late fall and early spring (May to October of 1976).

By February of 1977 the experimental quadrats were indistinct from the control area due to the natural impoverishment of the site during the summer (visual observations). Small *Echinometra lucunter* sea urchins, observed in the area, were never found inside the experimental quadrats.

Two characteristics of the recolonization process can be observed through figure 1:1) a rise in the number of species with increasing colonization time and 2) a quicker occupation of the quadrats scraped during the second half of the year. Several species appeared into the experimental areas only between late winter and early summer (August to December): *Amphiroa beauvoissi, A.brasiliana, Centroceras clavulatum, Champia minuscula* Joly e Ugadim, *Dasya brasiliensis* Oliveira Fº e Braga, *Hypnea musciformis* (Wulfen) Lamouroux, *Jania adhaerens* Lamouroux, *Laurencia* spp, *Sphacelaria tribuloides* and benthic colonial diatoms. Among them, *A.brasiliana, C.minuscula, J.adhaerens* and *Laurencia* spp never recruited on recently cleared patches.

Recolonization data of the eight experimental areas were submitted to an analyses of similarity, and clustered afterwards (Figure 2). Between May and September of 1976, bare areas of roughly similar periods of colonization clustered previously than areas scraped months apart. From October on, well defined successional patterns were difficult to detect, especially due to the occurrence of seasonal species, which recruited only from late winter to early summer, without preference for older or recently scraped areas.

DISCUSSION

Recolonization data showed that succession was maintained in the earlier stages of colonization during most of the year: bare areas were occupied by opportunistic species, rapid colonizers on newly cleared surfaces, for among their attributes they possess high reproductive output, short life spans and high dispersability (Vermeij 1978, Littler & Littler 1980, Seapy & Littler 1982).

The community of *Sargassum cymosum* var. *nanum* is composed essentially of ephemeral or annual seaweeds. The structurally dominant *S. cymosum* var. *nanum* is a perennial seaweed, an attribute of a biotically competent strategist (Vermeij 1978). Nevertheless, this variety is dwarf and exhibits precocious reproductive development, characteristic of opportunistic species, when compared to the *S. cymosum* variety of sheltered sites (Paula 1984). The perènnial encrusting forms present in this community, *Paragoniolithon solubile* and ralfsioid crusts, have a number of attributes of species defined as biotically competent, but at the same time they are well suited for survival in physically or biologically disturbed (heavily grazed) environments (Murray & Littler 1984). The ralfsioid crusts present throughout the year are probably the alternate life-history phase of *Chnoospora minima* (Oliveira Fº & Paula 1983), a perennial species with seasonal decline of the erect thallus during summer and autumn.

Seasonal variation in the number of species was similar in the experimental and control areas, with faster recruitment rates during the spring, and slower rates during the summer. Therefore succession was observed to act in the same way on both areas. Seasonal recruitment patterns cannot be explained either by human induced perturbations such as sewage pollution, which is not the case, or by sea urchin predation: 1) *Echinometra lucunter* urchins were never found inside the experimental quadrats and 2) although they may interfere in the colonization process they are not effective herbivores on this community, for a positive correlation between *E. lucunter* density and *S. cymosum* var. *nanum* biomass was observed at the control area (Paula & Oliveira Fº 1980). Also propagule availability cannot be responsible for the seasonal recruitment pattern of *S. cymosum* because this species is fertile during the whole year (Paula & Oliveira Fº 1980).

Oliveira Fº e Paula (1983) explain the summer decline of this population as a consequence of the exposure to the air for extended periods, due to smoother sea water conditions during this time of the year. This prolonged exposure to the air together with higher air temperatures and insolation levels would cause high desiccation stress. Therefore, summer could be considered a period of severe environmental perturbations for this algal community, while winter and especially spring, with greater water splash and lower air temperature and insolation levels, would be periods favorable to the development of the algae.

The severe reduction in species numbers in early summer due to desiccation provides open spaces available for colonization, which esplains the abundance of the ephemeral algae in this community (Gaines & Lubchenco 1982). A shift from biotically competent seaweeds to stress-tolerant and opportunistic strategists, with succession kept in its earlier stages has been previously reported for other rocky intertidal communities (Littler & Littler 1981, Seapy & Littler 1982).

In conclusion, succession in this *Sargassum cymosum* var. *nanum* community was maitained in its earlier stages both at control and experimental sites due to desiccation stress, which causes widespread algal mortality in early summer.

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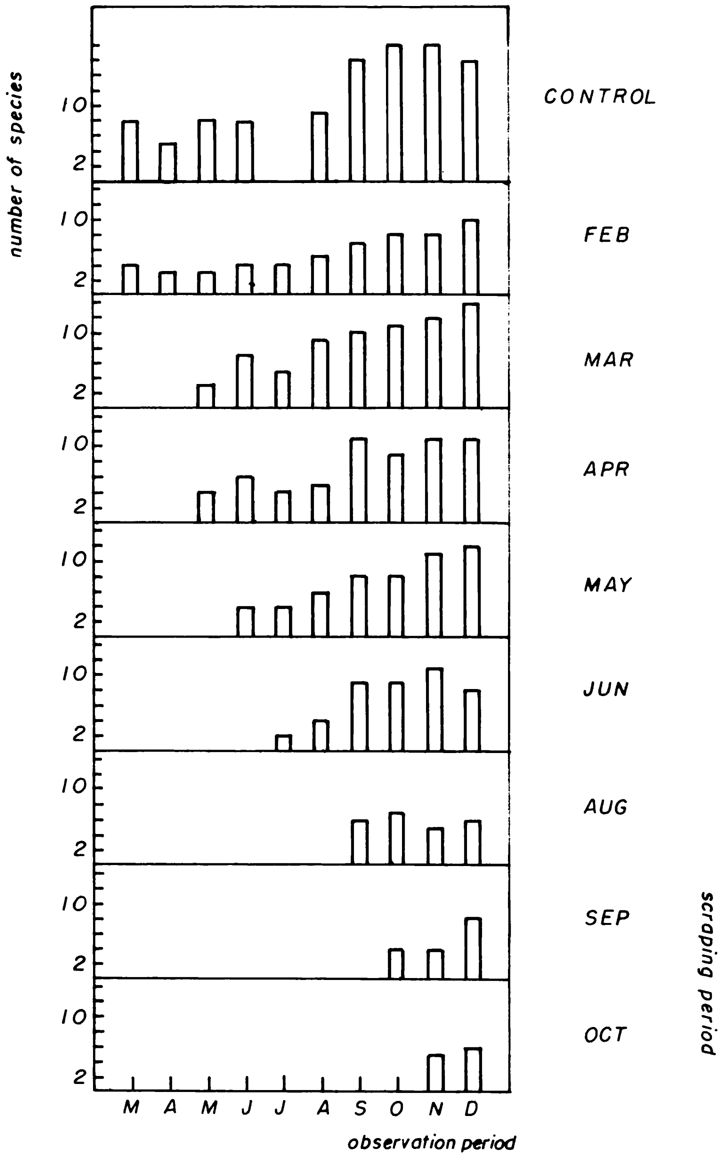

Fig. 1 – Número de espécies presente nas áreas controle e experimentais (quadrados de amostragem raspados em diferentes épocas do ano).

Fig. 1 – Number of species inside control area and experimental quadrats scraped at different times.

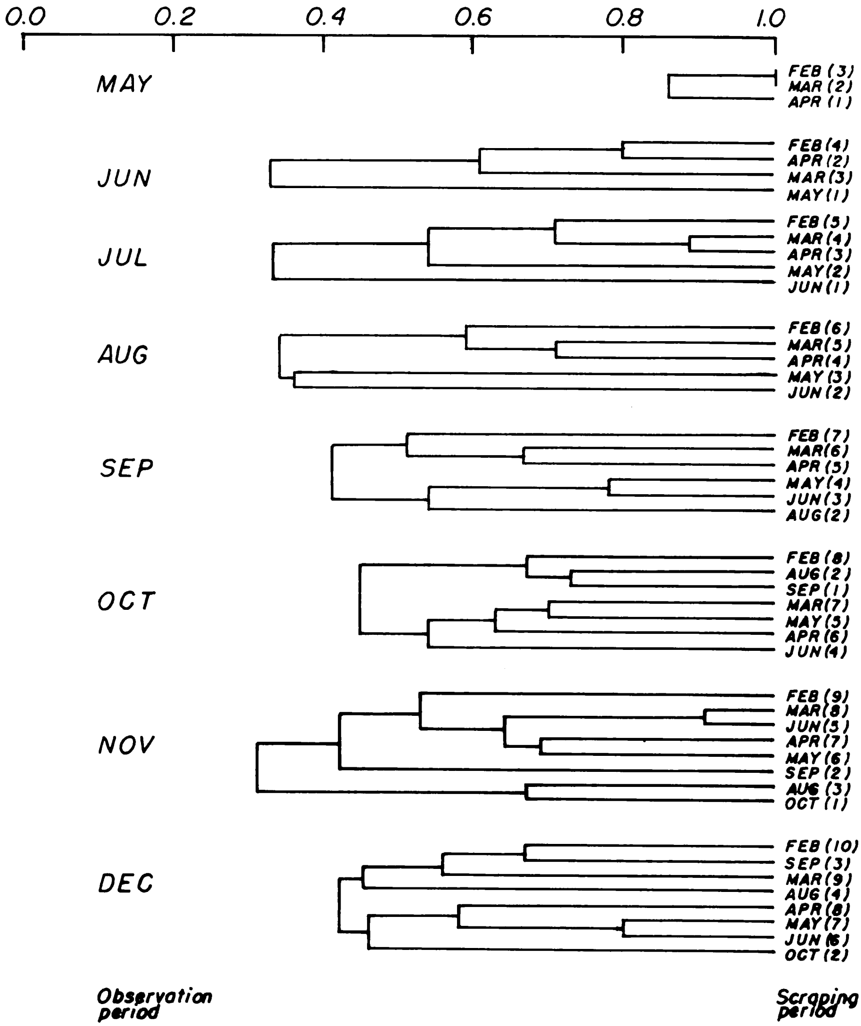

Fig. 2 – Análise de similaridade realizada entre quadrados experimentais raspados em diferentes meses do ano, agrupados por período de observação. Entre parênteses, o número de meses de colonização.

Fig. 2 – Result of the analysis of similarity among experimental quadrats scraped at different times in each of the observation periods. In brackets number of months after scraping.

Table 1 – Species present in the control strip (●) during the sampling periods; species also present above (1) and/or below (L) the control area.

sampling periods taxa	MAR 76	APR	MAY	JUN	AUG	SEP	OCT	NOV	DEC	FEB 77
S. cymosum var. *nanum*	●	●	●	●	●	●	●	●	●	●
Paragoniolithon solubile	●	●	●	●	●	●	●	●	●	●
ralfsioid crust	1●	1●	1●	1●	1●	1●	1●	1●	1●	1●
Chnoospora minima	●	1●	1●	1●	1●	1●	1●	●	●	●
Dictyota ciliolata	●	L	L	●L	●L	●L	●L	●L	●L	L
Colpomenia sinuosa	●		●	●			●	●	●	●
Padina gymnospora	●		●	●		●	●	●	●	
benthic diatoms	●	●	●							
Laurencia spp			●		●	●	●	●	●	
Dictyopteris delicatula	L	L	L	●L	●L	●L	●L	●L	●L	
Cladophora vagabunda	1	1	1	1	1●	1●	1●	1●	1	
Ulva fasciata			1	1	●	●	●	●	●	
Amphiroa spp						●	●	●	●	●
Chaetomorpha antennina	1	1	1	1	1	1●	1●	1●	1●	1
Hypnea musciformis						●	●	●	●	
Dasya brasiliensis						●	●	●	●	
Champia minuscula						●	●	●	●	
Sphacelaria tribuloides						●	●	●	●	
Ectocarpus breviarticulatus	1	1	1	1	1	1	1	1	1	1●
Centroceras clavulatum				1	1	1	●	1	1	1
Jania adhaerens				1	1	1	1	1	1	1
Gymnothamnion sp								●		
Cyanophyceae										1●L

Table 2 – Species present in the experimental quadrats, clustered by period since scraping.

Colonization time	1 month							2 months							
scraping period	feb	apr	may	jun	aug	sep	oct	feb	mar	apr	may	jun	aug	sep	oct
Taxa / Observation period	mar	may	jun	jul	sep	oct	nov	apr	may	jun	jul	aug	oct	nov	dec
S. cymosum var. *nanum*											x				
Paragoniolithon solubile	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
ralfsioid crust	x	x						x	x	x	x		x		
Chnoospora minima	x	x						x	x	x			x	x	
Dictyota ciliolata															x
Colpomenia sinuosa	x	x	x		x	x				x			x	x	x
Padina gymnospora										x		x			
benthic diatoms							x					x			
Laurencia spp															
Dictyopteris delicatula			x		x		x						x		
Cladophora vagabunda					x	x	x				x	x	x		
Ulva fasciata					x	x	x						x		x
Amphiroa beauvoisii												x			x
Amphiroa brasiliana															
Chaetomorpha antennina										x					x
Hypnea musciformis															x
Dasya brasiliensis															
Champia minuscula															
Sphacelaria tribuloides					x										
Ectocarpus breviarticulatus				x	x									x	
Centroceras clavulatum															
Jania adhaerens															
Arthrocardia sp															

Colonization time	3 months							4 months						5 months				
scraping period	feb	mar	apr	may	jun	aug	sep	feb	mar	apr	may	jun	aug	feb	mar	apr	may	jun
Taxa / Observation period	may	jun	jul	aug	sep	nov	dec	jun	jul	aug	sep	oct	dec	jun	aug	sep	oct	nov
S. cymosum var. *nanum*				x			x				x	x	x			x	x	x
Paragoniolithon solubile	x	x	x	x	x		x	x	x	x				x	x	x		x
ralfsioid crust	x	x	x		x		x	x	x	x				x	x	x		x
Chnoospora minima	x	x	x		x		x	x	x	x	x		x	x	x	x	x	x
Dictyota ciliolata		x				x							x			x		
Colpomenia sinuosa		x		x	x	x				x	x	x				x	x	x
Padina gymnospora					x			x			x	x		x				
benthic diatoms							x											
Laurencia spp							x											
Dictyopteris delicatula					x	x					x		x			x		x
Cladophora vagabunda		x		x	x	x	x		x		x	x			x		x	x
Ulva fasciata		x		x	x	x	x				x	x	x		x			
Amphiroa beauvoisii					x						x	x			x	x	x	x
Amphiroa brasiliana												x					x	x
Chaetomorpha antennina			x	x					x			x				x		x
Hypnea musciformis					x							x	x				x	x
Dasya brasiliensis																		
Champia minuscula																		
Sphacelaria tribuloides															x	x		
Ectocarpus breviarticulatus										•					x			
Centroceras clavulatum																x		
Jania adhaerens										x					x		x	
Arthrocardia sp																		

Colonization time	6 months					7 months				8			9		10
scraping period	feb	mar	apr	may	jun	feb	mar	apr	may	feb	mar	apr	feb	mar	feb
Taxa / Observation period	aug	sep	oct	nov	dec	sep	oct	nov	dec	oct	nov	dec	nov	dec	dec
S. cymosum var. *nanum*		x	x	x	x		x	x	x		x	x	x	x	x
Paragoniolithon solubile	x	x	x	x		x	x	x		x	x		x	x	x
ralfsioid crust	x	x	x			x	x	x		x	x		x	x	x
Chnoospora minima	x	x	x	x	x		x	x	x	x	x		x	x	x
Dictyota ciliolata							x					x			
Colpomenia sinuosa		x	x	x	x		x	x	x		x	x	x	x	x
Padina gymnospora	x					x				x			x		x
benthic diatoms						x			x					x	
Laurencia spp				x	x				x			x			
Dictyopteris delicatula			x					x				x		x	
Cladophora vagabunda		x		x		x	x		x	x	x		x		x
Ulva fasciata	x	x		x		x	x		x	x	x		x	x	x
Amphiroa beauvoisii		x	x	x	x		x	x	x		x	x			
Amphiroa brasiliana			x	x	x			x	x		x	x		x	
Chaetomorpha antennina		x						x		x	x			x	
Hypnea musciformis				x	x		x	x	x		x	x		x	
Dasya brasiliensis												x			
Champia minuscula											x	x		x	
Sphacelaria tribuloides		x				x				x				x	
Ectocarpus breviarticulatus															x
Centroceras clavulatum			x		x				x						
Jania adhaerens				x			x	x	x					x	x
Arthrocardia sp												x			

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