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Replacement of the compound ascidian species in a southeastern Brazilian fouling community

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● *Abstract:* The replacement of compound ascidians on two series of ceramic plates (225 cm^2) has been studied for nine months in the São Sebastião Channel. One of the series was initiated in the summer and the other in the winter. Five species were the most abundant and frequent on the plates. *Diplosoma listerianum* (Milne-Edwards, 1841) and *Symplegma brakenhielmi* (Michaelsen, 1904) showed the higher percent values of cover in the beggining of succession. Although *Didemnum speciosum* (Herdman, 1886) recruited in high numbers, its cover was only important after some months because of its slow growth rate. *Clavelina oblonga* Herdman, 1880 was a typical late successional species with low recruitment intensity and slow growth rate, and *Botryllus niger* (Herdman, 1886) was characterized by its constant appearing and disappearing. The overgrowth between ascidian species was not seen and it seems probable that the replacement of species was related to the death of early colonizers that presented a shorter life span.

● *Descriptors:* Ecological succession, Colonies, Fouling organisms, Recruitment, Artificial substrata, *Diplosoma listerianum, Symplegma brakenhielmi, Didemnum speciosum, Clavelina oblonga, Botryllus niger,* Canal de São Sebastião, São Paulo, Brazil.

● *Descritores:* Sucessão ecológica, Colonias, Organismos incrustantes, Recrutamento, Substrato artificial, *Diplosoma listerianum, Symplegma brakenhielmi, Didemnum speciosum, Clavelina oblonga, Botryllus niger,* Canal de São Sebastião, São Paulo, Brasil

Introduction

The sequence of species within a marine hard surface community depends on the time of the year the process starts, especially in habitats where reproduction is markedly seasonal (Osman, 1977; Sutherland & Karlson, 1977). The results that come up of the contact between each par of interacting species are various and increase further the unpredictability of the course of succession at each stage (Breitburg, 1985).

Jackson (1977; 1979), Buss (1979) and Woodin & Jackson (1979) introduced the concept of functional groups (all organisms which utilize and affect their environment in a similar way) in an attempt to recognize more general rules in community structure that otherwise could be masked by a taxonomic view. The primary division into functional groups of animals living on hard substrata can be based on body plan and functional organization, i.e., the animals can be either solitary or colonial (Jackson, 1977; Woodin & Jackson, *op. cit.*).

Even seeing succession on hard substrata through a functional group view, it is not possible to make the process more predictable. In a Jamaican coral reef environment, Jackson (1977) determined that solitary animals, employing a more opportunistic strategy, usually appeared early in succession, whereas colonial animals formed a late successional group due to their capacity to dominate the assemblage by outcompeting the solitary ones. On a further example however, Greene *et al.* (1983), studying the fouling community on the northwestern American coast, observed a remarkably different result. In their study, free space was rapidly occupied by colonial

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animals, whereas solitary animals gradually increased in abundance through time until they eventually dominated the primary space. This was achieved because colonial animals suffered mass mortality and recession that gave the longer-living solitary ones the opportunity to escape in size from overgrowth.

Many species of colonial ascidians colonize hard substrata in the São Sebastião Channel and because they constitute an uniform taxonomic and functional group it seemed interesting to study the development of their communities. Thus the purpose of the present study is to describe the initial succession of these colonial ascidians.

Study site

The study site was located approximately 5 km south of São Sebastião (Latitude 23°49'42"S, Longitude 45°25'16"W), in the São Sebastião Channel, in the northern coast of São Paulo State, Brazil (Fig. 1). This channel isolates São Sebastião Island, popularly known as Ilhabela, from the continent. It is 20 km long, 5-6 km wide on both extremes, and 2 km wide in the central region, with a maximum depth of 47 m.

On both insular and continental edges of the channel, there are sandy shores lying between more or less proeminent and extensive rocky shores. Boulder fields are common in shallow waters next to the rocky shores. A general description of the flora and fauna of one of this rocky shores can be found in Giordano (1986). It is possible to extend this description to other nearby rocky shores in the region.

In the São Sebastião Channel compound ascidians are found both in the intertidal and sublitoral zones. In the intertidal they are attached to the underside surfaces of boulders, crevices or depressions, sites generally little exposed to the sun during low tides. In the sublitoral they can be also found on the top surfaces of rock. Compound ascidians can also attach themselves on algae, living or dead shells, mangrove roots and artificial substrata.

Materials and methods

The experimental site was located at Cabelo Gordo de Dentro Shore (Fig. 1) within the area of the Centro de Biologia Marinha (CEBIMar) of Universidade de São Paulo. As this site, 100 m offshore, some galvanized iron tubes were buried into the soft sediment and bore horizontal tubes from which artificial substrata could be hung.

In order to determine the reproductive period of the species, 12 unglazed ceramic plates ("lajotão colonial") (15 x 15 cm^2) were immersed monthly during 1985. They were fixed to a PVC plataform in groups of four. The three groups were immersed close to each other at approximately 1 m depth in a horizontal position, with the ceramic plates facing the bottom. These plates were brought to the laboratory each month and after recording the recruits, all organisms were scraped off and the plates were washed in freshwater, dried in the sun and aftewards the clean plates were immersed again. All the plates used in this work were old ones and that did not seem to alter the recruitment of larvae.

Ceramic plates were also used to study the development of the compound ascidian community which covered most available space on the plates. In this case, 14 plates were monitored monthly in a nondestructive manner for nine months. As will be discussed later, the recruitment plates showed a remarkable difference in the numbers of recruits between summer and winter. For this reason, seven plates were immersed at the beginning of the summer (01-02-86), and the remnant seven at the beginning of the winter (06-30-86).

Records of the long term plates were also made on a monthly basis. The plates were kept in a running sea water tank for two days during which data were recorded. Each plate was put into a bowl completely filled with sea water. A sheet of glass was laid on the top of the bowl touching the water to permit better vision from above. A sheet of transparent plastic was placed on the glass on which the outlines of the colonies were traced. The plates were observed with a dissecting microscope through the glass. Each plate had an identifying tag on one corner to permit sequential observations in the same position, and each colony received a code number. The area covered by each colony was measured with a planimeter.

By overlaying subsequent sketches of the plates it was possible to observe new recruits, the rate of space occupation, and the mortality of the colonies.

Results

Ten species of compound ascidians could be recorded on the plates but from these only five were very frequent and abundant, so that this paper will be primarily concerned only with these, *Didemnum speciosum* (Herdman, 1886), *Diplosoma listerianum* Milne-Edwards, 1841, *Botryllus niger* (Herdman, 1886), *Symplegma brakenhielmi* (Michaelsen, 1904) and *Clavelina oblonga* Herdman, 1880.

The recruitment plates showed that the larvae of these species were available in the plankton during the whole year except for *B. niger* and *C. oblonga* (Fig. 2). Throughout the year, colonies were collected on the rocky shores next to the experimental site. Careful searches revealed the presence of larvae almost all year round. However the intensity of recruitment was not uniform between months (Fig. 3). Greater numbers of larvae recruited during the summer and fall months than during the winter and spring. The average number of colonies encountered on the plates showed a significant correlation with the water temperature (Spearman coefficient $r = 0.82$, $p < 0.01$). Water salinity varied little during the study (from 32.0 to 35.5‰) and could not be correlated with variation in recruitment.

The species showed different abilities to recruit on the clean surface of the ceramic plates. *Didemnum speciosum* was the best recruiter followed by *D. listerianum*, and *B. niger* was the poorest one (Fig. 2).

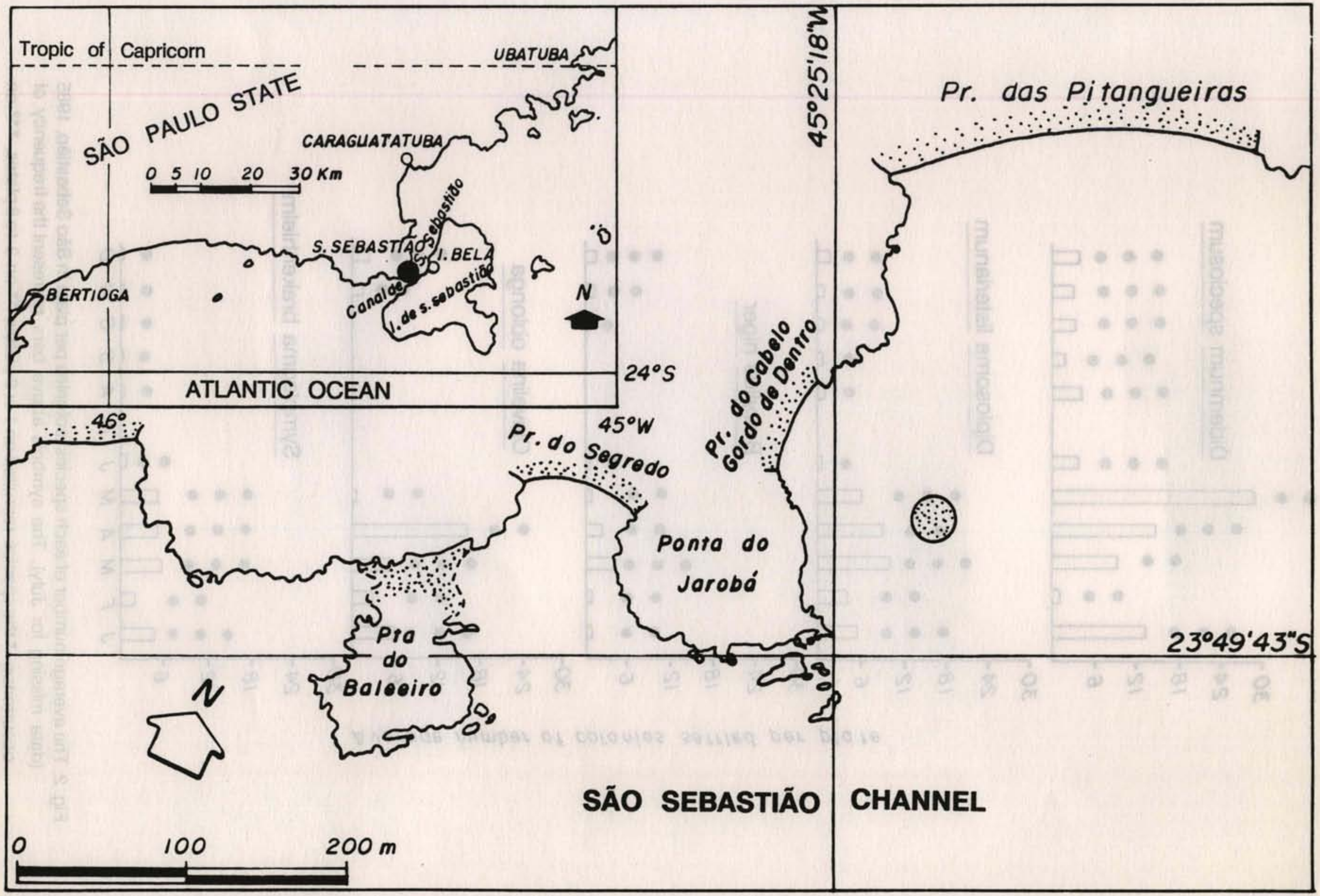

Fig. 1. The localization of the São Sebastião Channel and the study site where the plates were immersed ( ).

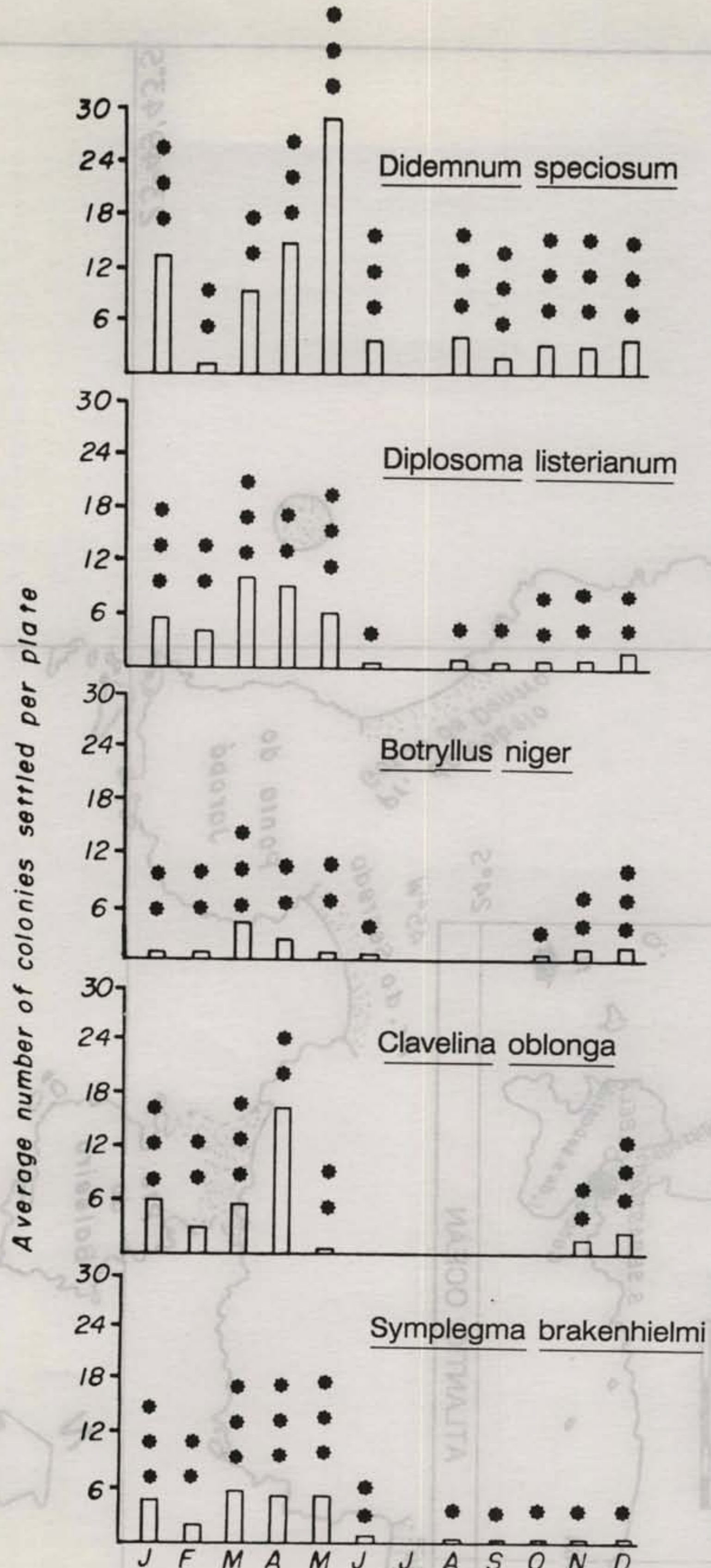

Fig. 2. The average number of each species' colonies per plate in São Sebastião, 1985 (data missing for July). The symbols above bars represent the frequency of occurrence: * the species recruited on 1 or 2 plates, ** on 3 to 8 plates, *** on 9 to 12 plates.

The initial colonization was much faster on summer plates than on the winter ones due to the greater recruitment in this season. Summer plates had an average of 97 colonies in the first month but this number decreased subsequently. The winter plates reached 50 colonies in the second month and this number decreased after the fifth month. These plates were not observed after one month but it is improbable that the number of colonies had exceeded the average of 50.

The growth rate was also greater during summer months than in winter, so that the 135-day-old summer plates were more than 100% covered by ascidians (barnacles settled on the sides of the plates increasing their area; there was also epizoic growth). The winter plates had a maximum ascidian cover of only 61%. This was achieved in the second month due to the fast growth of *D. listerianum* which dominated these plates at this time.

Both summer and winter plates showed a similar pattern in terms of ascidian species number (Fig. 4a). The decrease in number of species in the summer plates occurred as a consequence of the greater dominance of *D. speciosum* and *C. oblonga*. In the winter series, there was a high growth of the bryozoan *Zoobotryon pellucidum* in November and the ascidian cover was very reduced.

The winter plates were more diverse than the summer plates (Fig. 4b,c). In the summer plates, diversity increased during the two first months due to the high recruitment of different species, after when the diversity suffered a steady decrease associated with the greater dominance. In the winter plates diversity initially decreased as a consequence of the fast growth and dominance of *D. listerianum*. Then this species almost disappeared from the plates and diversity increased again without reaching a constant value.

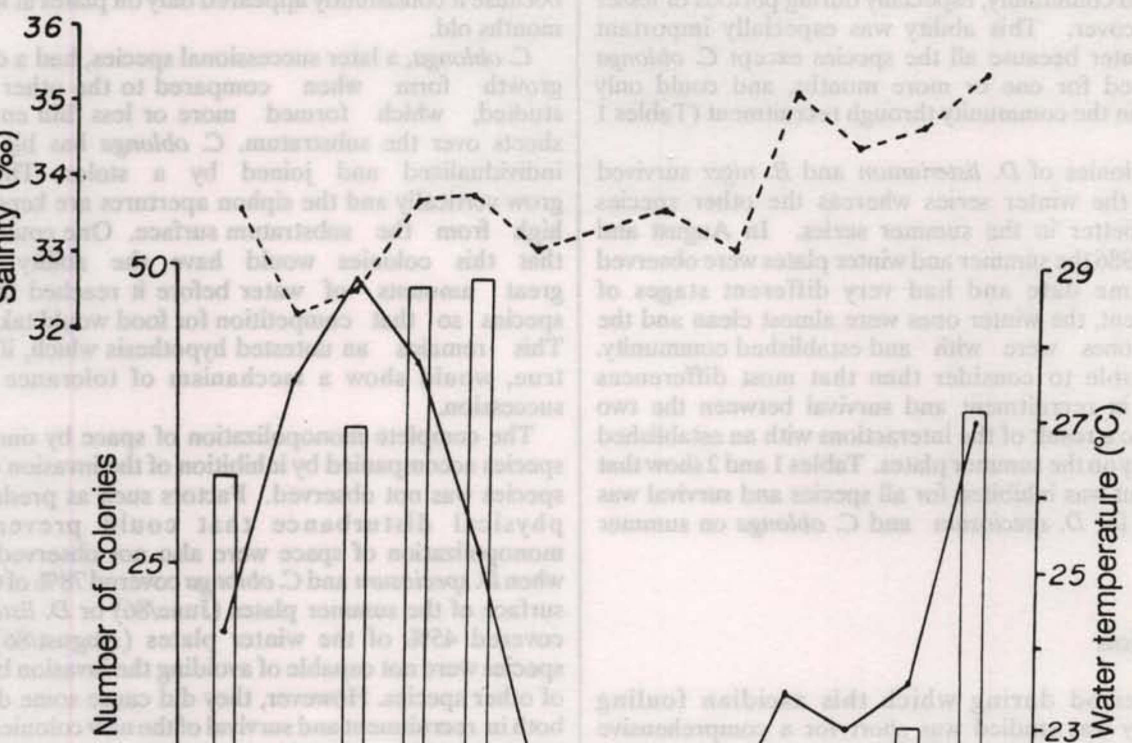

Fig. 3. The average number of settled colonies per plate between January/85 and January/86 (data missing for July); the water temperature (———) and salinity (- - - - - -).

A pattern of ascidian species sequence could be observed for the summer plates (Fig. 5). *D. listerianum* covered most space during the first months because of its fast growth. *S. brakenhielmi* was also an important space occupier during the beginning of community development. In spite of the great recruitment of *D. speciosum*, its colonies showed a low growth rate so that it only turned into a dominant species after two months of observation. *C. oblonga* had also low growth rate and became a dominant with *D. speciosum* only after four and half months (Fig. 5). *B. niger* was generally a rare species.

This pattern was not so clear for the winter plates (Fig. 6). *D. listerianum* also dominated the plates during the second month of immersion. After that the plates became more diverse with a greater cover of *C. oblonga* each month. *D. speciosum* became an important space occupier only after eight months. Isolated peaks of cover were observed for *B. niger* in October (95 days) and *S. brakenhielmi* in December (170 days) (Fig. 6). In these plates other species also appeared as important space occupiers: *Distaplia bermudensis* and *Trididemnum orbiculatum*.

The overlays of colony outlines of each plate showed that recruitment occurred during the whole period of this study. Thus all the species could invade the established community, especially during periods of lesser ascidian cover. This ability was especially important during winter because all the species except *C. oblonga* disappeared for one or more months, and could only reappear in the community through recruitment (Tables 1 and 2).

The colonies of *D. listerianum* and *B. niger* survived better in the winter series whereas the other species survived better in the summer series. In August and October 1986 the summer and winter plates were observed at the same date and had very different stages of development, the winter ones were almost clean and the summer ones were with and established community. It is possible to consider then that most differences observed in recruitment and survival between the two series were a result of the interactions with an established community on the summer plates. Tables 1 and 2 show that recruitment was inhibited for all species and survival was enhanced for *D. speciosum* and *C. oblonga* on summer plates.

Discussion

The period during which this ascidian fouling community was studied was short for a comprehensive discussion about the successional process, or even to determine if there were definite patterns of species changes. Nevertheless it was possible to verify the existence of earlier colonizers such as *D. listerianum* and *S. brakenhielmi* on the summer plates, or *D. listerianum* and *B. niger* on the winter plates. There were also later successional species such as *D. speciosum* and *C. oblonga*. The "earlier" and "later" terms are here used as relative terms to distinguish species by their times of peak abundance.

The successional models discussed by Connell & Slatyer (1977), agree that some species will always be the first to colonize because they evolved features that enhance their colonizing abilities (see Hutchinson, 1951; Connell & Slatyer, 1977, and Sousa, 1979 for example).

In this study, *D. listerianum* appeared as a consistent early successional species. It had continuous breeding all the year long, recently recruited colonies grew very fast, and sexual maturity was reached in one month. It was also a poor invader of the established community, indicating a need of clear space for settling and growing. This species was elsewhere recorded as an early colonist that dominates the space during the first months of fouling community development, but also quickly disappears from it (Silva *et al.*, 1980; Greene & Schoener, 1982).

All the five species studied were able to settle on clean ceramic surfaces even within the short period of a week (a less frequent event for *B. niger*, though). Therefore, these species can be considered good colonizers and they do not need facilitation from an earlier species to settle. However, only *D. listerianum*, *S. brakenhielmi* and *D. speciosum* in the summer series and *D. listerianum* and *B. niger* in the winter series had high survival rates during the first two months. The established community seemed to enhance (or facilitate) the survival of *D. speciosum* and *C. oblonga* at least on the summer plates. Another species, *Distaplia bermudensis*, seemed to need some type of modification to the plates condition to settle, because it consistently appeared only on plates at least two months old.

C. oblonga, a later successional species, had a different growth form when compared to the other species studied, which formed more or less thin encrusting sheets over the substratum. *C. oblonga* has big zooids, individualized and joined by a stolon. The zooids grow vertically and the siphon apertures are kept 2-3 cm high from the substratum surface. One could expect that this colonies would have the ability to filter great amounts of water before it reached the other species so that competition for food would take place. This remains an untested hypothesis which, if proved true, would show a mechanism of tolerance in this succession.

The complete monopolization of space by one or few species accompanied by inhibition of the invasion of other species was not observed. Factors such as predation or physical disturbance that could prevent this monopolization of space were also not observed. Even when *D. speciosum* and *C. oblonga* covered 78% of the total surface of the summer plates (June/86) or *D. listerianum* covered 45% of the winter plates (August/86), these species were not capable of avoiding the invasion by larvae of other species. However, they did cause some decrease both in recruitment and survival of the new colonies, as can be observed by comparing the summer and winter plates in August and October/86.

The inhibition of larval recruitment by an established assemblage is relatively common in communities of sessile marine organisms (Sutherland, 1974; Sutherland & Karlson, 1977; Sousa, 1979; Dean & Hurd, 1980; Breitburg, 1985). The phenomenon in the present study was probably a consequence of the decreasing space available for settlement as has been observed in other studies (Russ, 1980; Dean & Hurd, 1980; Dean, 1981). No species seemed to have allelochemical substances since all of them permitted recruitment on their own tunic (not a common event).

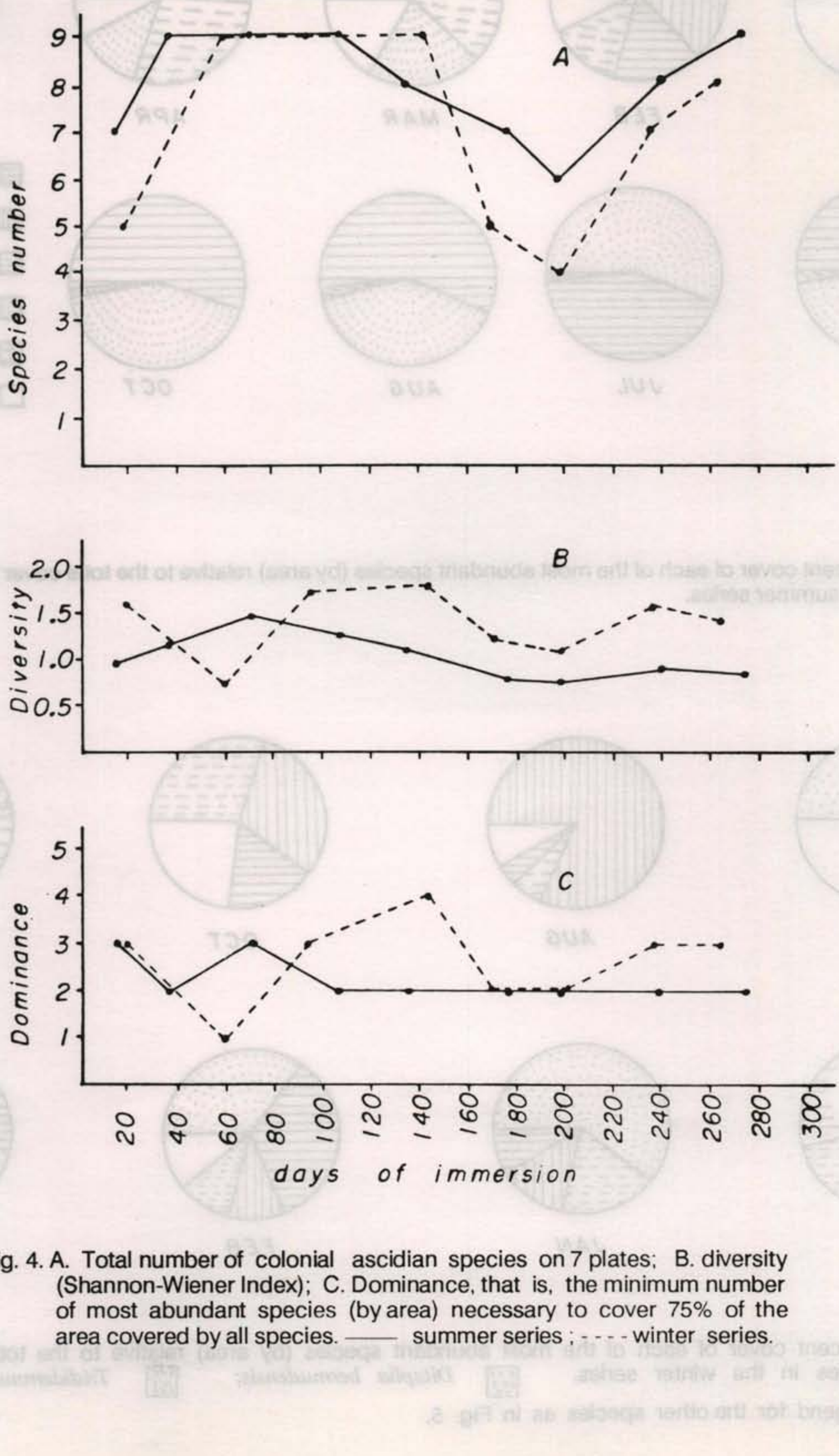

Fig. 4. A. Total number of colonial ascidian species on 7 plates; B. diversity (Shannon-Wiener Index); C. Dominance, that is, the minimum number of most abundant species (by area) necessary to cover 75% of the area covered by all species. —— summer series ; - - - - winter series.

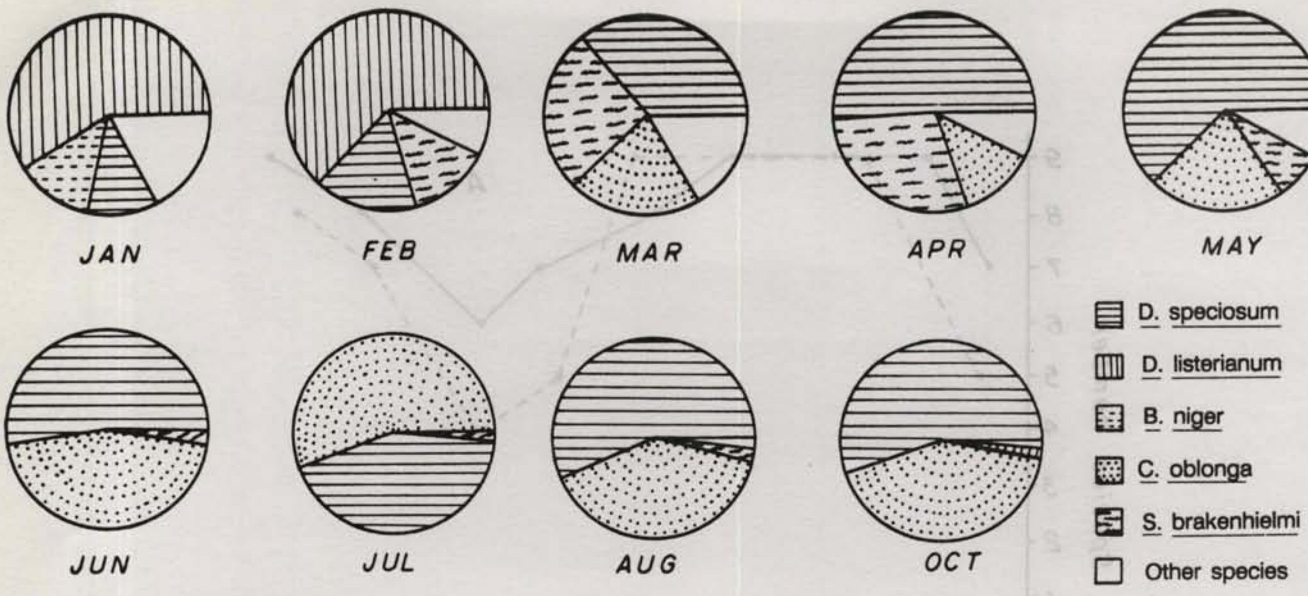

Fig. 5. Percent cover of each of the most abundant species (by area) relative to the total cover of the plates in the summer series.

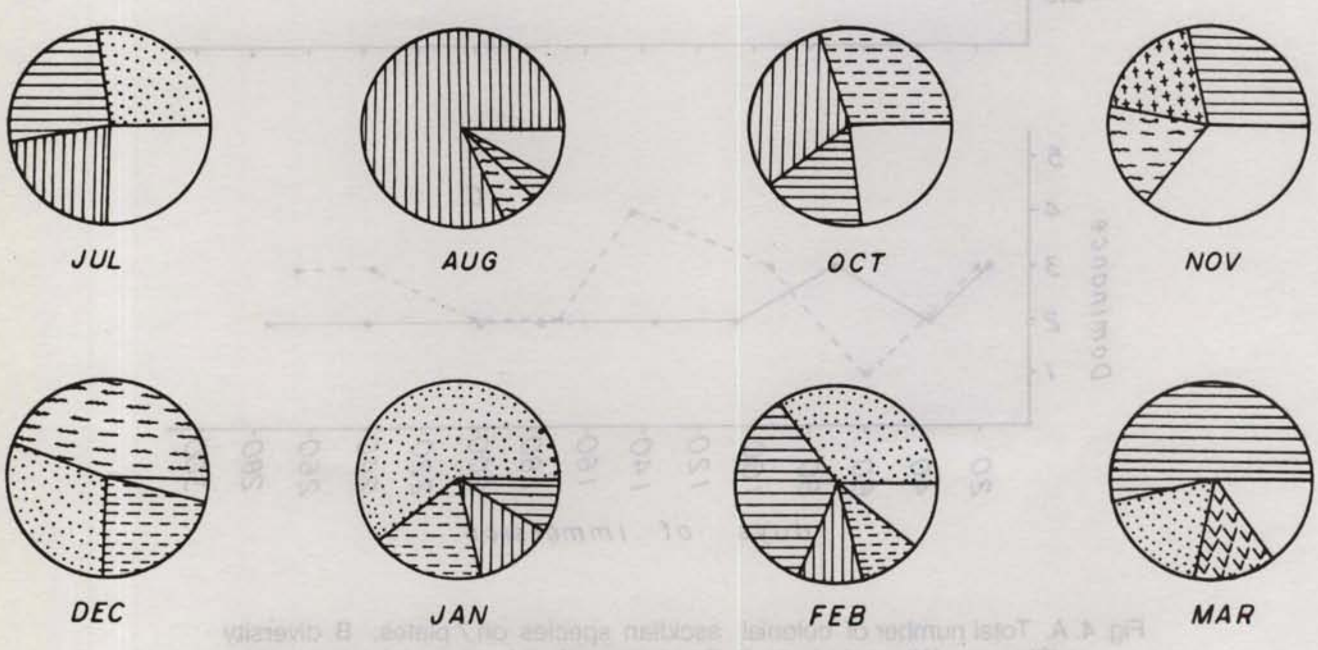

Fig. 6. Percent cover of each of the most abundant species (by area) relative to the total cover of the plates in the winter series. ***Ditaplia bermudensis;*** ***Trididemnum orbiculatum.*** **Legend for the other species as in Fig. 5.**

Table 1. Dynamics of the ascidian colonies in the summer series (7 plates pooled). Tot. Area = somatory of the area of all ascidian species (cm^2); Col Number = number of colonies of each species; Recruit. = percent of recently recruit colonies from the "Col Number"; Surviv. = percent of colonies from this month that could be found in the next month; Area = total cover of the species (cm^2). Dsp = *Didemnum speciosum*, Dl = *Diplosoma listerianum*, Bn = *Botryllus niger*, Co = *Clavelina oblonga*, Sb = *Symplegma brakenhielmi*

Sp.		JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	OCT
	Tot. Area	22.72	836.4	907.5	1187.3	1592.9	1423.8	1292.9	1389.2	1169.1
	Col Number	144	227	159	72	47	81	78	89	73
Dsp	Recruit.	100.0	69.2	24.5	26.4	12.8	19.8	19.2	36.0	13.7
	Surviv.	68.0	63.4	56.0	77.8	85.1	66.7	87.2	61.8	-
	Area	2.4	133.9	327.9	580.2	999.3	743.3	555.3	785.0	643.6
	Col Number	69	76	134	33	4	1	0	2	1
Dl	Recruit.	100.0	75.0	21.6	45.5	50.0	100.0	-	100.0	0.0
	Surviv.	81.1	43.4	17.9	9.1	0.0	0.0	-	50.0	-
	Area	13.0	528.8	131.7	61.2	107.2	.2	0.0	4.5	22.8
	Col Number	62	108	37	26	22	12	8	14	4
Bn	Recruit.	100.0	75.9	43.2	38.5	45.5	75.0	62.5	85.7	0.0
	Surviv.	45.1	19.4	43.2	42.3	13.6	33.3	37.5	28.6	-
	Area	2.7	25.8	14.4	12.2	15.3	1.7	1.0	4.1	.9
	Col Number	50	96	54	65	63	37	47	62	45
Co	Recruit.	100.0	79.2	16.7	55.4	42.9	5.4	14.9	12.9	4.4
	Surviv.	44.0	50.0	55.6	72.3	79.4	89.2	78.7	79.0	-
	Area	1.3	33.2	183.5	137.6	338.9	643.8	719.8	544.0	486.2
	Col Number	9	51	104	117	46	16	7	10	3
Sb	Recruit.	100.0	90.2	63.5	47.0	28.3	37.5	57.1	.8	66.7
	Surviv.	55.5	70.6	57.7	29.1	17.4	25.0	28.6	10.0	-
	Area	1.4	111.0	241.8	335.6	126.2	22.4	16.1	27.2	1.4

Table 2. Dynamics of the ascidian colonies in the winter series (7 plates pooled, 5 for March). Tot. Area = somatory of the area of all ascidian species (cm^2); Col Number = number of colonies of each species; Recruit. = percent of recently recruited colonies from the "Col Number"; Surviv. = percent of colonies from this month that could be found in the next month; Area = total cover of the species (cm^2). Legend as in Table 1

Sp.		JUL	AUG	OCT	NOV	DEC	JAN	FEB	MAR
	Tot. Area	6.6	959.8	471.8	355.2	10.2	2.6	67.1	213.2
	Col Number	78	140	77	44	0	1	14	19
Dsp	Recruit.	100.0	87.1	29.9	29.5	-	100.0	100.0	36.8
	Surviv.	23.1	41.4	49.3	0.0	-	0.0	50.0	-
	Area	1.6	38.6	79.9	97.2	0.0	.2	22.7	114.2
	Col Number	8	27	65	6	1	1	23	12
Dl	Recruit.	100.0	88.9	23.1	16.7	100.0	100.0	100.0	66.7
	Surviv.	100.0	66.7	4.6	0.0	0.0	0.0	17.4	-
	Area	1.3	795.5	135.4	2.6	.7	.4	7.0	6.7
	Col Number	5	33	65	70	17	2	10	12
Bn	Recruit.	100.0	87.9	47.7	38.6	23.5	100.0	100.0	75.0
	Surviv.	80.0	78.8	61.5	15.7	0.0	0.0	50.0	-
	Area	.6	45.4	136.8	58.1	2.2	.5	6.8	12.4
	Col Number	26	94	24	17	18	8	18	32
Co	Recruit.	100.0	86.2	54.2	58.8	66.7	87.5	77.8	81.2
	Surviv.	57.7	16.0	29.2	35.3	22.2	75.0	33.3	-
	Area	1.5	14.4	1.9	10.4	3.0	1.6	23.7	40.4
	Col Number	2	10	18	14	3	0	0	2
Sb	Recruit.	100.0	100.0	55.6	71.4	66.7	-	-	100.0
	Surviv.	0.0	60.0	22.2	7.1	0.0	-	-	-
	Area	.8	58.2	70.8	59.1	4.4	0.0	0.0	2.0

The inhibition model predicts that the late successional species are those resistant to predation and damage caused by physical disturbances (Connell & Slatyer, 1977; Sousa, 1979). In this study, the late successional species, *D. speciosum* and *C. oblonga*, were exactly the ones with the longer-living colonies. Colonies of *D. listerianum* began to degenerate after two or three months. The life cycle of *C. oblonga* is known in the Bermudas, where it lasts 18 months (Berrill, 1932). The life cycle of *B. niger* lasts three to four months in Puerto Rico (Morgan, 1977). For the other species data are not available.

Competitive interactions among adults were weak. Space is an important limiting resource and competition for space between sessile invertebrates usually involves overgrowth and smothering of an inferior species. However, cases of complete overgrowth between ascidian species were not observed during this study (unpubl. data). More common were encounters in which the margins of contacting colonies stopped growing or in which one species just started overgrowth by elevating the edge of the colony. But it was not effective and did not lead to the overgrown colony's death.

Spatial rearrangement was always seen between subsequent observations in spite of little overgrowth. This suggests that predation, physical disturbance, or death of established colonies occurred during the census interval (Sousa, 1979). The long time between successive observations made it difficult to distinguish among them. There was always a chance that space was cleared just before the observation, but I never encountered signs of predation or disturbance such as tracks or well defined clearings. On the other hand, degenerating colonies were very common and I believe they supplied space for the healthier ones.

If this is the case, succession occurs in this fouling community as a consequence of the death of earlier colonizers which are shorter-living species (eg. *D. listerianum*). The capacity of late successional species to recruit onto clean surfaces guarantees them space in the community. They grow according to the opportunities for occupying space left by dying colonies of the earlier colonizers. The longer the life span of the species, the longer it will persist in the community waiting for the death of their neighbours. Thus described, this succession fits well the inhibition of Connell & Slatyer (1977).

The time when the space is made available is believed to be very important to the subsequent succession because it determines which species will colonize first and will take advantage of this priority. This is specially true in habitats where species reproduction is remarkably seasonal (Osman, 1977; Sutherland & Karlson, 1977; Bros, 1987). The continuous breeding of the compound ascidians in São Sebastião decreases the importance of the time of year when space is made free for colonization. Nevertheless, the decrease in recruitment and growth rate during winter did have an effect on succession. Space was available for longer time, giving more species the opportunity to colonize the plates. The winter plates were generally more diverse than the summer ones and other groups became important space occupiers like the arborescent bryozoan *Zoobotryon pellucidum* that dominated the plates during November and December/86.

Within colonial ascidians the growth form is variable and a functional analysis based on morphological features could show some patterns. Jackson (1979) divided colonial sessile marine animals into six basic growth forms, each of them associated with different adaptive characteristics.

The present results corroborate Jackson's predictions. The earlier species, *D. listerianum*, has a growth form that is linear or branching initially, after what it grows in all directions forming sheet-like encrustations. Its thin and delicate tunic indicates that this species allocates little energy to produce protective structures, but instead, it favors rapid growth and early maturity (gonads are present in one-month-old colonies). The later species *C. oblonga*, on the other hand, grows as mounds or trees since the individualized zooids grow vertically from a common base. Its tunic is much more resistent than that of *Diplosoma*, in order to protect and sustain the colony. As predicted by Jackson, this species has a low growth rate and is more commited with a strategy of maintenance of the space of attachment and of the integrity of the colony until it reaches maturity.

Greene & Schoener (1982) also observed a replacement of morphological types within their system. During the first 20 weeks there was an abundance peak of vine-like species. These were replaced by sheet-like forms, and three-like forms dominated space only after the plates were submerged for a year.

When cleaning the nine-month-old plates I observed that almost the whole primary space was occupied by living barnacles and that ascidians were actually occupying secondary space on the barnacle tests. Due to the plasticity and flexibility of colonial ascidian's tunics, they can easily grow around obstacles. This allows other species to live between or within the colonies, making the community very complex. At the end of this study, however nothing can be said about the stability or climax characteristics of this fouling community because of the short period of observations.

Conclusions

Compound ascidians are important early colonizers of cleared artificial substrate at the São Sebastião Channel. Recruitment was continuous the year round for most species, but it was enhaced in summer months. Growth was also faster during summer; summer plates were easily dominated and had low diversity. On the other hand, winter plates had more cleared space for longer and ended up more diverse. A pattern of species replacement could be observed and it seems that the death of early colonizers was the cause of replacement, since most species were present on the plates at any time and competitive interactions such as overgrowth were not observed.

Resumo

Ascidians coloniais são muito comuns nas comunidades incrustantes crípticas no Canal de São Sebastião, São Paulo, Brasil. Elas colonizam, com sucesso, substratos artificiais tão logo estes são imersos. Neste trabalho, placas de cerâmica de 225 cm^2 foram utilizadas como substrato para o estudo do

recrutamento e do processo inicial de sucessão de ascidias coloniais. Os resultados apresentados referem-se às cinco espécies mais abundantes e freqüentes. *Diplosoma listerianum* caracterizou-se como uma espécie inicial de sucessão, dominando as placas durante os primeiros dois meses. Trata-se de uma espécie oportunista, com reprodução contínua ao longo do ano, alta taxa de crescimento e ciclo de vida curto. *Symplegma brakenhielmi* também apresentou maiores procentagens de cobertura durante o início da sucessão. *Didemnum speciosum* foi a espécie mais abundante logo após a imersão das placas, mas devido a uma taxa de crescimento mais lenta, somente após alguns meses é que esta espécie passou a dominar o espaço sobre as placas. *Clavelina oblonga* caracterizou-se como uma espécie tardia típica, com recrutamento pouco intenso, crescimento vertical e a presença de estruturas de proteção como, por exemplo, uma túnica grossa e resistente. *Botryllus niger* foi uma espécie menos abundante que desaparecia freqüentemente de todas as placas, reaparecendo geralmente através de recrutamento sobre outras espécies.

Recobrimento de uma espécie pela outra não foi um tipo de interação freqüente entre ascidias durante a sucessão e parece mais provável que a substituição de espécies tenha ocorrido em função da morte dos indivíduos que colonizaram primeiro e que pertenciam a espécies de ciclo de vida curto. O espaço, que desta forma se tornava disponível, era ocupado pelo crescimento de espécies mais persistentes que haviam garantido sua presença sobre as placas através de recrutamento e da alta sobrevivência das jovens colonias.

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