Vol. 129: 215–228, 1995 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published December 14

A bank of microscopic forms on disturbed boulders and stones in tide pools

B. Santelices*, A. J. Hoffmann, D. Aedo, M. Bobadilla, R. Otaíza

Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

ABSTRACT: Disturbed marine habitats contain banks of microscopic forms that develop into macroscopic vegetation under adequate conditions. This study examined seasonal species turnover, time-space community development and species-area relationships of an assemblage of microscopic forms, on boulders and stones in 2 tidal pools in central Chile (32° 46' S; 71° 33' W). A total of 25 taxa were found in the assemblage, with low species turnover throughout the year. The assemblage contained about twice the number of species present in the water column and about half the number present in the macroscopic vegetation. Species present in the macroalgal vegetation and in the water column accounted for 70% of the taxa in the assemblage; the remaining 30% suggested propagule sources outside the study area. Colonization and succession experiments indicated that the banks were formed by ephemeral and perennial species. Most perennials are slow-growing and crustose, of low-colonizing capacity; the bank seemed more important for the survival of these perennial species than for fugitive forms. Species richness in the bank correlated with the surface area of boulders. For areas larger than 40 cm^2, species richness was significantly higher on individually sampled stones than on equivalent surfaces subsampled from larger boulders, suggesting that species richness follows predictions of the intermediate disturbance hypothesis. The number of species was high, suggesting that disturbance affects the macroscopic expression of diversity rather than the total number of species.

KEY WORDS: Banks of microscopic forms · Disturbance · Diversity · Seaweed · Species-area relationship

INTRODUCTION

Algal spores lack a dormancy period and germinate as they become attached to suitable substratum. Some species survive as microscopic stages with suspended growth, others exhibit direct development. In many marine habitats the population of microscopic algal forms may include different ecological components. One component consists of the microscopic stages that may perennate in habitats occupied by macroscopic vegetation. These stages are of diverse green (Tanner 1981), brown (Pedersen 1981) and red algae (West & Hommersand 1981). The second component corresponds to developmental stages (germlings, prostrate discs or filaments) that through suspended growth survive stressful conditions for macroscopic thalli. First described for kelps (Burrows 1958, Clendenning 1961, Kain 1966, Smith 1967, Anderson & North 1969), stages with suspended growth have been documented for several species (Chapman & Burrows 1970, Sheader & Moss 1975, Schonbeck & Norton 1980, Richardson 1981, 1982, Hay & Norris 1984, Novaczeck 1984a, b, Lewis et al. 1987). The third component consists of recently germinated seaweed propagules with direct development. The fourth component is represented by unicellular algae, like diatoms (not considered in the present study).

The capacity of these microscopic forms to develop into macroscopic vegetation was demonstrated by Burrows (1958) and Neushul & Dahl (1967) by incubating boulders and chips devoid of macroscopic vegetation. Through an analogy with the 'seed bank' of land plants, Chapman (1986) coined the term 'bank of microscopic forms' for populations of microscopic phases that develop into macroalgal vegetation under adequate environmental conditions. These banks

*E-mail: bsanteli@genes.bio.puc.cl

should be common in habitats where disturbances — mainly boulders being overturned by wave action (Lieberman et al. 1979, Sousa 1979a) or grazing (reviewed by Santelices 1990) — prevent the development of macroscopic vegetation. Although the factors regulating some functions of the banks of microscopic forms have been identified (Santelices 1990, Hoffmann & Santelices 1991), no bank has been studied in terms of species composition, seasonal turnover or successional changes. We first examined seasonal variations in species composition of an assemblage of microscopic forms on disturbed boulders in tide pools.

The propagules of the bank examined might have originated from the algal vegetation around the pools, from outside the study site, or both. To assess these alternatives, we compared the assemblage of microscopic forms, the propagules present in the water column (the 'spore cloud'; Santelices 1990) and the macroscopic vegetation around the pools through simultaneous sampling.

In contrast to land plants where early successional phases contribute to seed banks more than late successional species (Harper 1977, Leck et al. 1989), it has been hypothesized that, in banks of microscopic forms, persistence of stages with suspended growth is more likely to occur in late successionists than in pioneering species (Santelices 1990). To test this hypothesis, we studied colonization patterns and temporal development of the assemblage of microscopic forms on field-incubated, previously sterilized, natural substrate, and determined the life style of the seaweeds thus obtained.

Although no bank has yet been characterized ecologically, Lieberman et al. (1979) described colonization and temporal replacement of macro- and microforms on seasonally devastated cobble substratum off Ghana during a 2 to 4 mo growing season. These authors found 77 taxa, with no correlation between species richness and cobble area, which suggested that banks of microscopic forms might not follow the pattern of species-area curve (see McGuiness 1984a for a review). Hence, we evaluated the hypothesis of the species-area relationship in our assemblage of microscopic forms.

MATERIALS AND METHODS

Study site. The sampling areas were 2 tide pools of around 50 m diameter and 1.5 m depth at Los Molles (32° 46' S; 71° 33' W) in central Chile; the bottom was covered with round granite boulders and stones 3 to 50 cm diameter and was devoid of macroscopic vegetation, due to the combined effects of boulder overturning and grazing (see Santelices 1990 for a review). Black sea urchins *Tetrapygus niger* and snails *Tegula atra* and *T. tridentata* were frequent grazers. Pools remained covered with water (20 to 50 cm) even during the lowest low tides.

Assemblage of microscopic forms as related to spore clouds and macroalgal vegetation. Species occurrence was compared on boulders in pools, in the water column, and on rocks around pools. Many boulders and large stones were rather flat, and their upper surfaces were easy to observe, so they were used to study the assemblage of microscopic forms. Using the 'running mean' technique (Kershaw 1964) in species richness and algal cover, it was found that 9 replicate boulders represented the minimum sampling number for adequate diversity and coverage. It was also found that a surface of 50 cm^2 contained about 80% of all the species found on larger surfaces (up to 350 cm^2).

Nine randomly chosen boulders of about 50 cm^2 upper surface were sampled at each pool in November 1990 and in April, June, September and November 1991. They were placed separately in plastic containers with seawater and carried to the laboratory. The upper surfaces were examined under a stereomicroscope in a search for algae. Microscopic slides were prepared whenever necessary for identification. Boulders were incubated in SWM-3 culture medium (McLachlan 1973) in 1000 ml glass beakers under constant conditions of photon flux density (50 to 70 µmol m^{-2} s^{-1}), temperature (14°C) and photoperiod (12:12 h LD cycle). After 15 d boulders were again examined. This incubation period did not usually increase the number of species but improved confidence in correct identification.

Water samples were collected as described by Hoffmann & Ugarte (1985). Eight samples of 1000 ml seawater were collected from pools in low tide and during incoming tides. From each sample, a subsample of 500 ml was transferred to a 100 × 80 mm sterilized glass petri dish. Dishes were taken to the laboratory in insulated containers and left for 18 h at 13°C in darkness to allow for sedimentation and spore attachment. Hoffmann & Camus (1989) showed that a high proportion of spores settled within 2 to 3 h in similar water volumes and that, mainly among red algae, most spores that did not attach within 15 to 18 h were non-viable. The water was replaced by 200 ml of enriched seawater medium (SWM-3) [McLachlan (1973); without TRIS, pH 7.5 to 8, GeO_2 added when necessary]. Cultures were incubated as described above. Sporelings growing in the culture dishes were then identified.

Specimens of all algae found around the pools and up to 200 m away were sampled. In the laboratory they were identified and examined for reproductive structures.

Species composition of the bank of microscopic forms, the propagule cloud and the macroscopic vege-

tation were compared using the chi-squared test (Sokal & Rohlf 1981). Similarity in species composition between seasons and between assemblages was calculated using Jaccard's index [$J = S_{ij}/(S_{ij} + S_i + S_j)$] and Dice's index [$D = 2S_{ij}/(2S_{ij} + S_i + S_j)$] where S_{ij} is the number of species common to samples i and j, S_i is the number of species present on sample i but absent on sample j and S_j is the number of species present on sample j but absent on sample i. Using these 2 alternative indices, we attempted to reduce the possibility that results would depend on the properties of the index. The 2 indices include joint presences in the numerator; but while the matches are double-weighted in the numerator of the Dice index, they are not so in the Jaccard index.

Colonization and succession. Two series of boulders were incubated in the field to study the temporal development of the assemblage of microscopic forms. Flat boulders (50 to 80 cm^2 of upper surface) were collected in the pools, brought to the laboratory, washed and brushed under running freshwater, autoclaved for 18 min at 120°C, allowed to dry and checked under a stereomicroscope for live algal remains. One end of the boulder was painted with water-resistent, non-toxic paint for further recognition. Boulders were brought back to the pools and left there for different periods.

In the first experimental series we studied early colonization of the substrate. Sterilized boulders were placed in the pools in October 1990, and March, May and August 1991, and removed 30 d later. This allowed us to compare seasonal species richness with the assemblages of microscopic forms on resident boulders collected on the same dates. Ten boulders were recovered at each sampling. Species richness and species cover were quantified. The point-intercept method was applied using 1 cm^2 quadrats with 100 intercept points. Quadrats were randomly placed 15 times on 3 parallel 5 cm transects along the largest dimension of the upper boulder surface and examined with a stereomicroscope. Although 10 boulders in each sampling were the minimum acceptable number to provide for adequate species richness and cover representation, the cover value for each species on each boulder was highly variable. Therefore, seasonal data were used only to calculate average cover value for each species at each sampling but could not be used for statistical comparisons of cover values among species. The 4 independently sampled seasonal averages were used as replicate values to test for significant differences in the cover values of selected species on newly incubated versus resident substratum (Student's t-test; Sokal & Rohlf 1981).

The second boulder series was designed to evaluate patterns of species replacement during succession. About 100 sterilized and marked boulders were placed in the pools in March 1991; the excessive number was used to allow for accidental losses. Nine replicate boulders were collected after 30, 60, 120 and 180 d of incubation (i.e. June, July, September and November 1991). Species richness and cover were measured and compared with the naturally occurring assemblage as well as with the colonization series, using Jaccard's index. For comparisons of cover values between selected species the Student t-test was used.

Species-area relationship. To measure the development of the assemblage of microforms as a function of area, the species-area relationship of the community was calculated. We found that 5 or 6 replicates were sufficient to detect significant differences between observed and expected values of species richness (*sensu* McGuiness 1984a). Hence, 6 randomly chosen stones and boulders of 8 predetermined sizes were sampled in the pools. Boulder size was estimated by measuring the surface area of the upper side. The species-area relationship was evaluated by the number of species of microscopic forms found on each area. According to McGuiness (1984a, b) and McGuiness & Underwood (1986) this is called the observed species-area curve. The expected curve under the hypothesis of random placement was generated using Simberloff's (1976) method as applied by McGuiness (1984a, b). The 6 largest replicate boulders (316.0 cm^2) were subsampled by dropping quadrats the size of the smaller surfaces (9.0 to 142.0 cm^2) onto their surfaces. The number of algal species found within the quadrats was counted. The subsampling quadrat was placed randomly each time, with no bias toward the centre or the edge of the rock. Covariance analysis was used to evaluate differences between expected and observed values.

RESULTS

Assemblage of microscopic forms and its relation to spore clouds and macroalgal vegetation

Assemblage of microforms

A total of 25 taxa were found on the stones from the pools (Table 1). However, the number of species present in the assemblage may be slightly higher because some taxa (e.g. *Gelidium* spp., *Polysiphonia* spp., *Colpomenia* spp.) could not be identified to species level solely based on juvenile, non-reproductive thalli. Thus, each genus may include more than 1 species. Taxon richness varied from 14 to 18 taxa in late spring-early summer to 24 taxa in winter (Table 1). Sixty percent of the taxa were found in all seasons and 12% in 3 sea-

Table 1 Seasonal variation in taxa composition in the assemblage of microscopic forms, the water samples and macroscopic vegetation at the study site. x: presence; –: absence; x̲: fertile thalli found; a: *Gelidium rex*; b: *G. lingulatum*; c: *G. chilense*; d: *Polysiphonia paniculata*; e: *P. scopulorum*; f: *P. pacifica*; g: *Colpomenia tuberculata*; h: *C. sinuosa*; i: *C. phaeodactyla*. Percentages of common taxa at each sampling date (A) with next sampling (seasonal change); (B) between microforms and propagules in water column; (C) between microforms and macrovegetation; (D) between propagules in water column and microforms; (E) between macrovegetation and microforms. Similarity values with microforms (upper line: Jaccard Index, lower line: Dice Index); (F) between assemblage and water samples; (G) between assemblage and macroscopic vegetation

Taxa	Assemblage of microscopic forms					Propagules in the water					Macroscopic vegetation				
	Nov 90	Apr 91	Jun 91	Sep 91	Nov 91	Nov 90	Apr 91	Jun 91	Sep 91	Nov 91	Nov 90	Apr 91	Jun 91	Sep 91	Nov 91
1 *Porphyra columbina*	x	x	x	x	x	x	x	–	x	x	x̲	x̲	x̲	x̲	x̲
2 *Ralfsia confusa*	x	x	x	x	x	–	–	x	–	x	x	x	x	x	x
3 *Gelidium* spp.	x	x	x	x	x	–	–	–	–	–	x̲a,b	x̲a,b,c	x̲a,c	x̲a,b,c	x̲b
4 *Nothogenia fastigiata*	x	x	x	x	x	–	–	–	–	–	x̲	x̲	x̲	x̲	x
5 *Hildenbrandia lecanellieri*	x	x	x	x	x	–	–	–	–	–	x̲	x̲	x̲	x̲	x̲
6 *Ectocarpus* sp.	x	x	x	x	x	x	x	x	x	x	x̲	–	x̲	–	x̲
7 *Hincksia mitchelliae*	x	x	x	x	x	x	x	x	x	x	–	–	x̲	–	–
8 *Cladophora* sp.	x	x	x	x	x	–	–	–	–	–	x̲	x	x̲	x̲	x
9 *Ulva* sp.	x	x	x	x	x	x	–	–	–	–	x̲	x̲	x̲	x̲	x̲
10 *Enteromorpha clathrata*	x	x	x	x	x	x	x	x	x	x	–	–	–	–	–
11 *Blidingia minima*	x	x	x	–	x	x	x	x	x	x	–	–	–	–	–
12 *Bryopsis* sp.	x	–	x	x	x	–	–	–	–	–	–	–	x	x	x
13 *Enteromorpha intestinalis*	–	x	x	x	x	–	–	–	x	x	x̲	x̲	x̲	x̲	x̲
14 *Mazzaella laminarioides*	–	x	x	x	x	–	–	–	–	–	x̲	x̲	x̲	x̲	x̲
15 *Acrochaete* sp.	–	x	x	x	x	–	–	x	–	–	x̲	x̲	x̲	x̲	x̲
16 *Polysiphonia* spp.	x	x	x	–	x	–	–	–	–	–	x̲d,e,f	x̲d	x̲	x̲	x̲d,f
17 *Petrocelis franciscanus*	x	x	–	–	–	–	–	–	–	–	–	–	–	–	–
18 *Enteromorpha compressa*	–	x	x	–	–	–	–	–	–	–	–	–	–	–	x̲
19 *Ulothrix* sp.	–	x	x	–	–	–	–	–	–	–	–	–	–	x	x
20 *Colpomenia* spp.	–	x	x	–	–	–	–	–	–	–	x̲g,h	x̲h	x̲h,i	x̲h,i	x̲h
21 *Petalonia fascia*	–	x	x	x	–	–	–	–	–	–	–	–	–	–	–
22 *Rhizoclonium ambiguum*	–	–	x	x	x	–	x	–	–	x	x	x	x	x	x
23 *Enteromorpha prolifera*	–	–	x	–	x	x	x	–	–	x	x̲	–	x̲	x̲	x̲
24 *Compsonema* sp.	–	–	x	x	–	–	–	–	–	–	–	–	–	–	–
25 *Gymnothamnion elegans*	–	–	x	–	–	–	–	–	–	–	–	–	x	x̲	–
26 *Corallina officinalis*	–	–	–	–	–	–	–	–	–	–	x̲	x̲	x̲	x̲	x̲
27 *Ceramium rubrum*	–	–	–	–	–	–	–	–	–	–	x̲	x̲	x̲	x̲	x̲
28 *Centroceras clavulatum*	–	–	–	–	–	–	–	–	–	–	x̲	x̲	x̲	x̲	x̲
29 *Chaetomorpha firma*	–	–	–	–	–	–	–	–	–	–	x̲	x̲	x̲	x̲	x̲
30 *Codium dimorphum*	–	–	–	–	–	–	–	–	–	–	x	x	x	x	x
31 *Lessonia nigrescens*	–	–	–	–	–	–	–	–	–	–	x̲	x̲	x̲	x̲	x̲
32 *Scytosiphon lomentaria*	–	–	–	–	–	–	x	–	–	–	x	x	x	x̲	x
33 *Adenocystis utricularis*	–	–	–	–	–	–	–	–	–	–	x	x	x	x	x
34 *Bosiella* sp.	–	–	–	–	–	–	–	–	–	–	x̲	x̲	x̲	x̲	x̲
35 *Grateloupia doryophora*	–	–	–	–	–	–	–	–	–	–	x̲	x̲	x̲	x	x
36 *Montemania horridula*	–	–	–	–	–	–	–	–	–	–	x̲	–	x̲	x	x̲
37 *Schottera nicaensis*	–	–	–	–	–	–	–	–	–	–	x	–	x	x	x
38 *Gigartina chamissoi*	–	–	–	–	–	–	–	–	–	–	–	x	x	x	x̲
39 *Herposiphonia* sp.	–	–	–	–	–	–	–	–	–	–	x	x	x	x	x
40 *Endarachne binghamiae*	–	–	–	–	–	–	–	–	–	–	x	x	x	x	x
41 *Glossophora kunthii*	–	–	–	–	–	–	–	–	–	–	x̲	x	x	x	x
42 *Dendrymenia skottsbergii*	–	–	–	–	–	–	–	–	–	–	–	x	x	x	x
43 *Chaetomorpha linum*	–	–	–	–	–	–	–	–	–	–	x̲	x̲	–	x̲	–
44 *Gastroclonium cylindricum*	–	–	–	–	–	–	–	–	–	–	–	x̲	x̲	–	–
45 *Ahnfeltia concinna*	–	–	–	–	–	–	–	–	–	–	–	x̲	x̲	–	–
46 *Gigartina* sp.	–	–	–	–	–	–	–	–	–	–	–	–	x̲	–	x̲
47 *Ahnfeltia durvillaei*	–	–	–	–	–	–	–	–	–	–	–	–	x̲	x̲	–
48 *Mastocarpus papillatus*	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–
49 *Laurencia chilensis*	–	–	–	–	–	–	–	–	–	–	x	–	x	–	–
50 *Gymnogongrus disciplinalis*	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–
51 *Herposiphonia subdisticha*	–	–	–	–	–	–	–	–	–	–	–	x	–	–	–
52 *Plocamium cartilagineum*	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–
53 *Heterosiphonia subsecundata*	–	–	–	–	–	–	–	–	–	–	–	x	–	–	–
Total no. of taxa	14	20	24	17	18	7	8	6	6	9	32	33	43	36	36
Common taxa (%): (A)	62	71	74	75											
(B)	43	25	25	29	50	(D) 86	63	100	83	100					
(C)	64	60	75	71	83						(E) 28	36	42	33	42
Similarity values with microforms:															
– Jaccard Index						(F) 0.40	0.22	0.25	0.28	0.50	(G) 0.24	0.29	0.37	0.29	0.38
– Dice Index						0.57	0.36	0.40	0.43	0.67	0.39	0.45	0.54	0.45	0.56

sons. Only 7 taxa (28%) were restricted to 1 or 2 seasons. Taxa common to any 2 successive samples ranged from 62 to 75%, reflecting a high level of temporal similarity.

Assemblage of microscopic forms and spore clouds

Twelve taxa developed in the water samples (Table 1); 4 taxa were found in all water samples and 2 taxa in 3 or 4 samples. The other 6 exhibited a more patchy temporal presence. In addition, 11 taxa (92%) were found in the assemblage of microscopic forms. Throughout the year the assemblage contained 62 to 100% of the taxa present in the water samples.

In contrast, the presence of species from the assemblage was lower in the spore cloud; 14 of the 25 taxa (56%) did not appear in water samples. Throughout the year the propagules in the water accounted for 25 to 50% of the taxa present in the assemblage (Table 1). The missing taxa had either extended or patchy occurrence in the assemblage. Floristic similarity between the assemblage and the spore cloud (Table 1) was mostly low. Values were lowest in fall and winter, when the number of taxa in the assemblage increased, with no parallel increase in the spore cloud. When comparing the 11 taxa common to the spore cloud and the assemblage of microscopic forms it was found that only 3 had similar temporal occurrence (Fig. 1). Only 6 taxa were found more frequently in the assemblage than in spore clouds, while the opposite was true for 2 species. Comparisons of temporal occurrence of all species in both groups showed significant differences ($\chi^2 = 9.97$; df = 1; $p = 0.002$). However, considering only the 11 common species, differences were not significant ($\chi^2 = 1.14$; df = 1; $p = 0.28$).

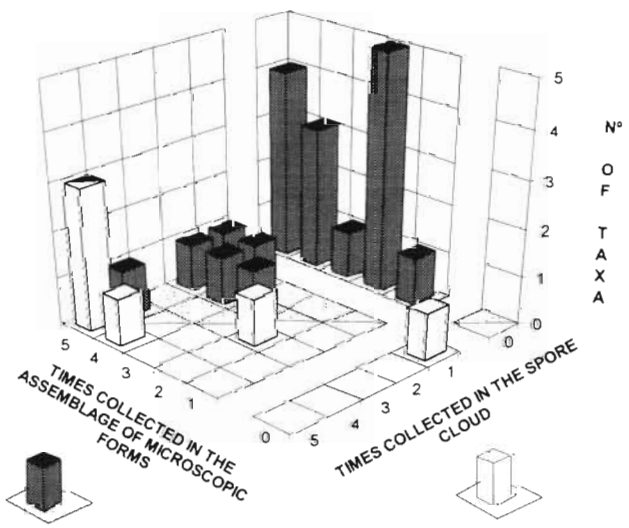

Fig. 1. Comparison of temporal occurence of macroalgal species in the assemblage of microscopic forms and in the spore cloud. Fourteen species were exclusive to the assemblage (none present in the spore cloud); and 1 was exclusive to the spore cloud (none present in the assemblage). The remaining 11 taxa were common to both groups

Assemblage of microscopic forms and macroscopic vegetation

The macroscopic vegetation collected simultaneously with the assemblage included 48 taxa (Table 1). About 60% were found in all seasons while about 30% occurred in 1 or 2 seasons. Roughly 40% of the taxa were fertile during all seasons, while 36% were sterile throughout the study period. The remaining taxa were intermittently fertile.

The macroalgal vegetation contained 20 of the 25 species (80%) occurring in the assemblage of microscopic forms (Table 1), a value that varied between 60 and 83% during the year. In contrast, the assemblage contained only 41% of the taxa in the macroscopic vegetation. The rest were never found in the assemblage. Throughout the year, the occurrence of macroalgal vegetation in the assemblage ranged from 28 to 42%, although the missing species (Table 1) included several with extended presence and fertility. Floristic similarity was low most of the year (Table 1), showing

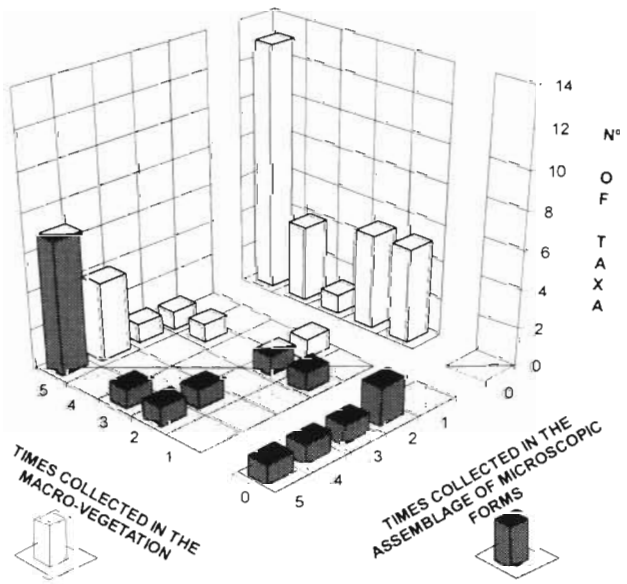

Fig. 2. Comparison of temporal occurrence of macroalgal species in the assemblage of microscopic forms and in the macroscopic vegetation around the pools. Twenty-eight taxa were found exclusively among macroscopic vegetation (none present in the assemblage); 5 species were exclusive to the assemblage (none present in the macroscopic vegetation). The other 20 taxa were common to both groups

temporal but non-seasonal fluctuations. Only 8 of the 48 taxa had equivalent temporal occurrence (Fig. 2) in both groups. Eight other species were found more often in the macroscopic vegetation than in the assemblage, while the opposite was true for 4 species. A chi-squared test comparing the temporal occurrence of all species in both groups showed significant differences ($\chi^2 = 11.95$; df = 1; p = 0.0005). However, if the comparison was restricted to common species, differences were non-significant ($\chi^2 = 0.57$; df = 1; p = 0.45).

Assemblage of microscopic forms as a function of spore cloud and macroscopic vegetation

When taken separately, propagules in the water and species in the macroscopic vegetation accounted for only part of the assemblage of microscopic forms. However, when put together, they accounted for 88% of the taxa in the assemblage (Fig. 3). No significant differences in temporal occurrence were found (χ^2 = 0.44; df = 1; p = 0.50) when comparing the bank versus propagules plus macrovegetation.

The combined data on the presence and fertility of macroscopic vegetation together with the presence of propagules in the water suggested that the assemblage of microforms was of heterogeneous origin. Over half of the taxa in the assemblage, including most of its more permanent members (80%), can be explained by constant presence and frequent fertility in the macrovegetation (Taxa 1, 3, 4, 5, 6, 8, 9, 13, 14, 15 and 16; Table 1). In some cases, their propagules were also found in water samples (Taxa 1, 6, 9, 13 and 15; Table 1). Two frequent members (*Ralfsia confusa* and *Bryopsis* sp.) and 2 less frequent members (*Rhizoclonium ambiguum* and *Ulothrix* sp.) of the assemblage also occurred among the macrovegetation, but their propagules were infrequent in the water. Propagule output of these species may be patchy over time. Once established, these taxa may persist for some time in the assemblage. Other taxa were never found in the macroscopic vegetation and their presence in the assemblage of microscopic forms suggested propagule sources away from the study site. While propagules of *Enteromorpha clathrata* or *Blidingia minima* were often present in the water, propagules of *Petrocelis franciscanus*, *Petalonia fascia* or *Compsonema* sp. were never found.

During the study period, 16 taxa of the macroalgal vegetation were fertile at least once, but never appeared in the assemblage or in the water. This was evident in 8 taxa that were found fertile in at least 3 seasonal samples. No commosn trait seems to characterize these species: they are filamentous opportunistic Chlorophyta (e.g. *Chaetomorpha firma*) or filamentous (*Ceramium rubrum*, *Centroceras clavulatum*), articulated calcareous (*Corallina officinalis*, *Bosiella* sp.) frondose (*Grateloupia doryophora*) or cylindrical (*Montemaria horridula*) Rhodophyta.

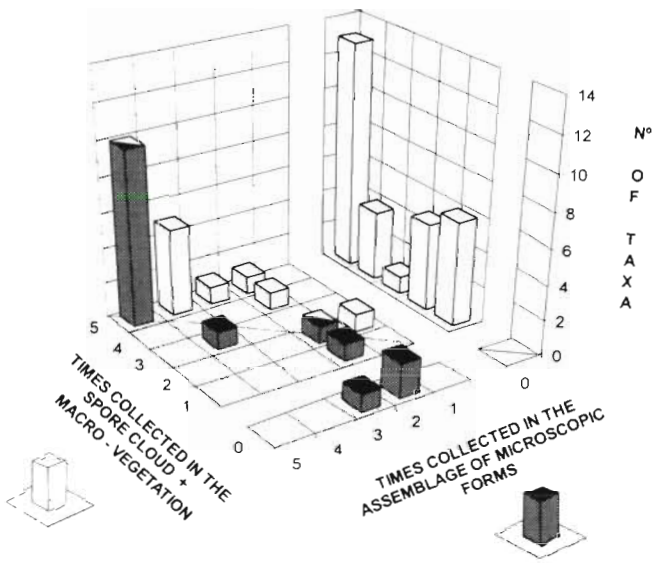

Fig. 3. Comparison of temporal occurrence of macroalgal species in the assemblage of microscopic forms and in the combined presence of taxa in the spore cloud and in the macroscopic vegetation. Three species were exclusive to the assemblage while 29 taxa were exclusive to the macroalgal vegetation plus the spore cloud (none present in the assemblage). Twenty-two other species were common to all groups

Colonization and succession

The assemblage of microforms developing within 30 d on sterilized boulders showed marked similarity with the assemblage occurring on the resident boulders (Table 2). This was true for number of taxa, percentage of common taxa, and similarity values. Depending on the season, 12 to 20 taxa of microforms recruited on the sterilized stones, i.e. slightly less than on resident stones during each corresponding season (14 to 24 taxa). No significant differences were found in the number of taxa between both types of stones (t = 1.028; p = 0.343) when the frequency values of 4 seasons were used as replicates. The algal cover was also roughly similar (t = 0.2951; p = 0.7778) and 77 to 95% of the species were present on old stones.

Despite the similarities mentioned, the assemblage of microforms on new boulders did not account for all the species found on old boulders. Results suggest (Table 2) that, irrespective of the number of taxa found in each season on both substrates, 3 or 4 species never developed on the new stones, implying that not all species had the same colonizing ability. According to cover values during the different seasons and sub-

Table 2. Taxa present on stones and boulders naturally occurring in the experimental pools (control), on previously sterilized boulders and stones incubated for a month in the experimental pools (colonization), and on previously sterilized boulders and stones incubated for up to 180 d in the same experimental pools (succession). Percentages of common taxa at each sampling date: (A) between control and colonization; (B) between colonization and control; (C) between control and succession; (D) between succession and control. x: presence; –: absence. Similarity values (upper line is values after Jaccard Index, lower line is values after Dice Index); (E) between successive samplings of control boulders; (F) between control and colonization, at each sampling; (G) between control and succession

Taxa	Control						Colonization				Succession (30 d) (60 d) (120 d) (180 d)			
	Nov 90	Apr 91	Jun 91	July 91	Sept 91	Nov 91	Nov 90	Apr 91	Jun 91	Sept 91	Jun 91	Jul 91	Sept 91	Nov 91
Porphyra columbina	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Ralfsia confusa	x	x	x	x	x	x	–	x	–	–	–	–	–	–
Gelidium spp.	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Nothogenia fastigiata	x	x	x	x	x	x	–	x	x	–	x	x	x	x
Hildenbrandia lecanellieri	x	x	x	x	x	x	x	x	x	–	x	x	x	x
Ectocarpus sp.	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Hincksia mitchelliae	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Cladophora sp.	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Ulva sp.	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Enteromorpha clathrata	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Blidingia minima	x	x	x	x	–	x	x	x	–	x	–	x	x	x
Bryopsis sp.	x	–	x	x	x	x	–	–	x	–	x	x	x	x
Enteromorpha intestinalis	–	x	x	x	x	x	–	x	x	–	x	x	x	x
Mazzaella laminarioides	–	x	x	x	x	x	–	–	–	–	–	–	x	x
Acrochaete sp.	–	x	x	x	x	x	x	x	x	x	x	x	x	x
Polysiphonia spp.	x	x	x	x	–	x	x	x	–	x	x	x	x	x
Petrocelis franciscanus	x	x	–	–	–	–	–	–	x	–	–	–	–	–
Enteromorpha compressa	–	x	x	–	–	–	–	x	x	–	x	x	x	–
Ulothrix sp.	–	x	x	–	–	–	x	–	–	x	x	x	–	x
Colpomenia spp.	–	x	x	x	–	–	–	x	x	–	x	x	x	–
Petalonia fascia	–	x	x	x	x	–	–	x	x	x	x	x	x	x
Rhizoclonium ambiguum	–	–	x	x	x	x	–	–	x	–	x	x	x	–
Enteromorpha prolifera	–	–	x	x	–	x	–	–	x	–	x	x	x	x
Compsonema sp.	–	–	x	x	x	–	–	x	x	x	x	x	x	x
Gymnothamnion elegans	–	–	x	x	–	–	–	x	x	–	–	x	–	–
Total no. of taxa	14	20	24	22	17	18	12	19	20	13	20	22	21	19
Common taxa (%): (A)		71	85	79		59	(B) 83	89	95	77				
(C)			83	91	94	89					(D) 100	91	77	84
Similarity values of control:														
– Jaccard Index (E)		0.62	0.76	0.92	0.77	0.75	(F) 0.63	0.77	0.76	0.52	(G) 0.83	0.83	0.74	0.76
– Dice Index		0.76	0.86	0.96	0.87	0.86	0.77	0.87	0.86	0.69	0.91	0.91	0.85	0.86

strata, 2 groups could be distinguished. The first group was formed by 8 species (Fig. 4) with higher cover values on new than on old stones. Although differences were significant in only 1 case (*Acrochaete* sp.), the trend was shown by all species, most of which were part of the fertile vegetation around the pools and with propagules usually present in the water.

The second group had less cover on new than on old stones (Fig. 5). Differences were significant in 3 of the 6 species. This group seemed to be heterogeneous. While *Mazzaella laminarioides* and *Ralfsia confusa* did not recruit on the new stones in any season within 30 d of field incubation, *Cladophora* sp., *Petrocelis franciscanus*, *Nothogenia fastigiata* and *Hildenbrandia lecanellieri* recruited during some seasons but with lower cover values on new than on old stones. In these species, scarce propagule output and limited dispersal capacity probably limit colonization of new substrate; most are crustose taxa, probably with slow growth rates. They never appeared in the water cultures (Table 1), although *Nothogenia fastigiata*, *Hildenbrandia lecanellieri* and *Mazzaella laminarioides* were often fertile in the macroscopic vegetation. In addition, *Ralfsia confusa* was never fertile during the study period and *Petrocelis franciscanus* was not found at the study site. Their recruitment on new stones during June 1991 was probably due to propagules from outside the area.

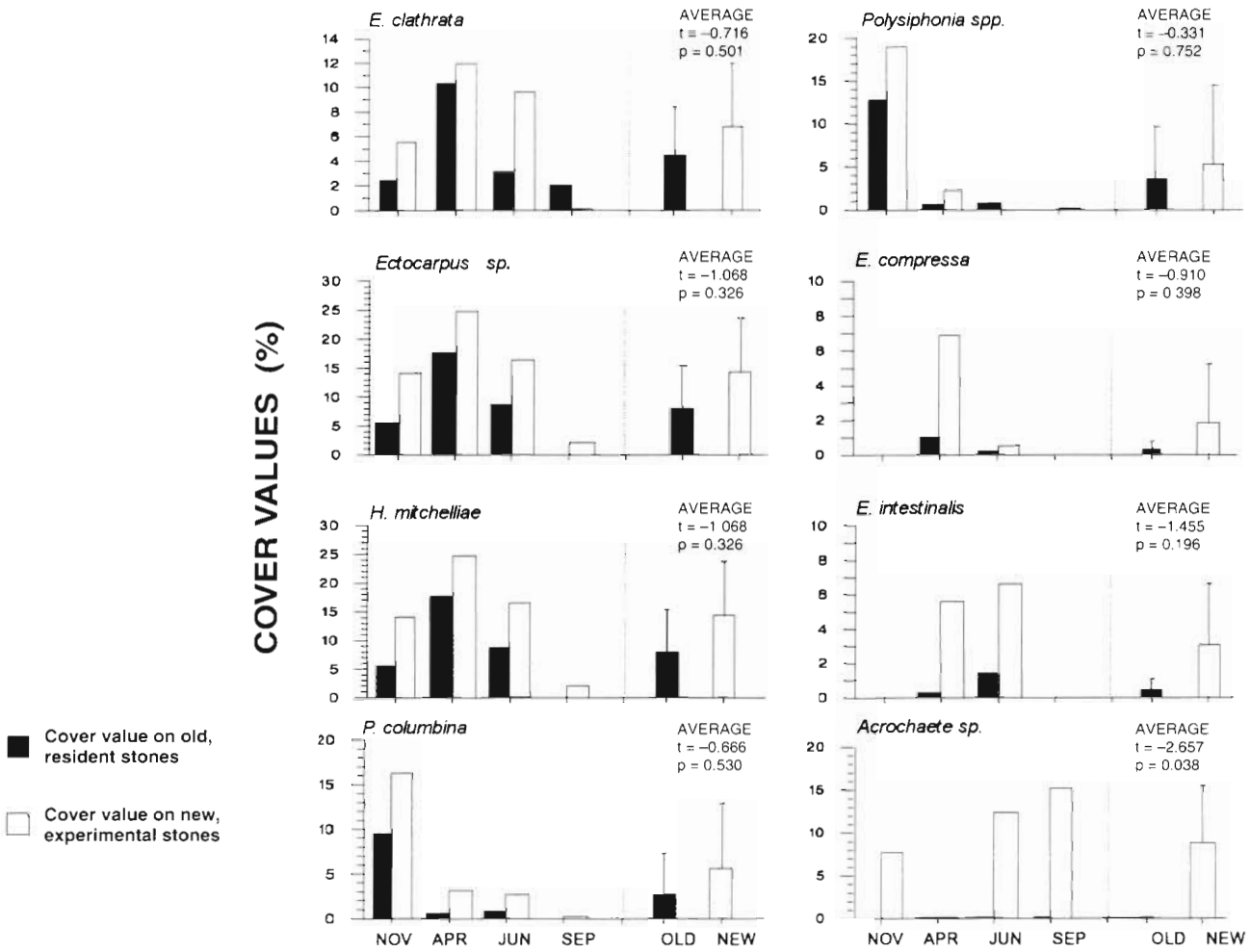

Fig. 4. Species of the assemblage of microscopic forms with higher cover values on new than on old substrate. Respective average, standard deviations, *t*-test and p-values were calculated using the 4 seasonal estimations as replicates. Error bars are 1 SD

Field exposure of new boulders for 60, 120 and 180 d resulted in slight increases in number of taxa and percentage of common species (Table 2). Irrespective of some seasonal differences, these assemblages resembled the corresponding assemblages on old boulders.

The 2 groups of species characterized above by their different colonizing ability maintained contrasting patterns during 60 to 180 d of field exposure. In the first group, early colonizers like *Ectocarpus* sp., *Hincksia mitchelliae* and *Enteromorpha intestinalis* showed gradual cover reduction as succession progressed (Fig. 6). *Porphyra columbina* and *Enteromorpha clathrata* maintained higher cover on new than on old stones over time, while some species (*Acrochaete* sp., *Bryopsis* sp.) appeared on new stones in several seasons but never on old ones.

Species in the second group like *Cladophora* sp. and *Hildenbrandia lecanellieri* usually had larger cover values on old boulders than on new ones (Fig. 7). *Nothogenia fastigiata* showed similar fluctuations on new and old boulders. *Ralfsia confusa* did not recruit on new boulders during 180 d of field incubation. For *Mazzaella laminarioides*, no recruitment was observed after 30 or 60 d of field incubation, but it occurred after 120 d reaching higher cover values on new than on old substrate.

Once a species had appeared on experimental stones, it tended to persist (Table 2). Such was the pattern shown by 16 of the 22 taxa (70%). Five taxa (22%) disappeared after variable periods: *Gymnothamnion elegans* after 30 d, *Ulothrix* sp. after 60 d, and *Enteromorpha compressa*, *Colpomenia* sp. and *Rhizoclonium ambiguum* after 180 d. *Ulothrix* sp., absent from the 120 d sample, reappeared in the last one. Thus, although most species were almost permanently present, a few had restricted presence in the assemblage. They also showed patchy temporal presence on old stones, suggesting lack of recruitment or slow growth rates.

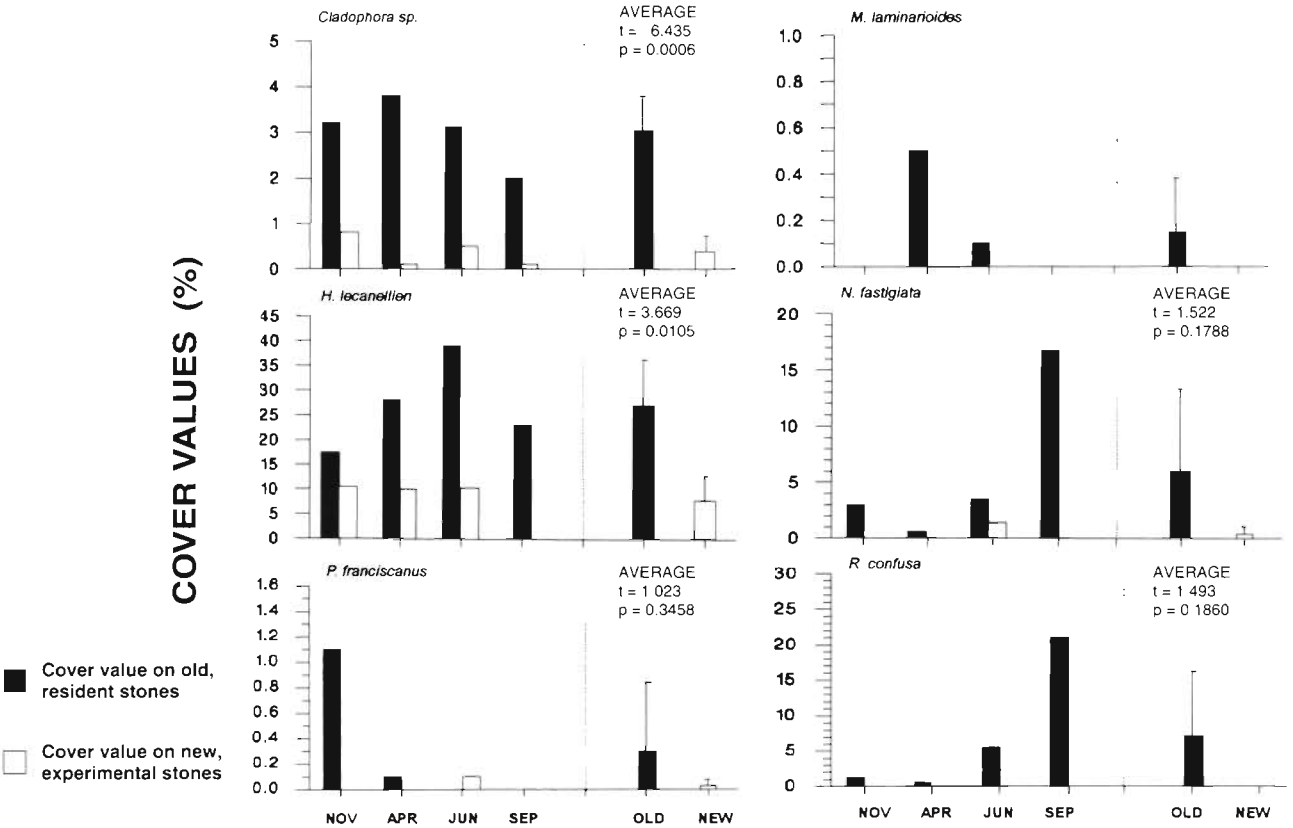

Fig. 5. Species of the assemblage of microscopic forms with higher cover values on old than on new substrate. Respective average, standard deviations, *t*-test and p-values were calculated using the 4 seasonal estimations as replicates. Error bars are 1 SD. Lack of recruitment of *Mazzaella laminarioides* in the experimental series did not allow statistical comparisons

Species-area relationship

The assemblage of microscopic forms showed a positive relationship between boulder surface area and number of species (Fig. 8). The smallest boulders (6 to 10 cm^2) had 3 to 6 species; the number of taxa increased with increasing areas, up to 50–70 cm^2, tending to slow down thereafter. The larger surfaces examined (142.0 ± 37.5 and 316.0 ± 50 cm^2) had an average of 15 to 20 species.

Although the curves of the species-area relationship were similar for the expected and observed series (Fig. 8), species richness was significantly higher (covariance analysis for slopes, $F = 10.93$; df = 1; p = 0.0015) on individually sampled stones and boulders (observed) than on equivalent surfaces subsampled from larger boulders (expected). Differences became significant for boulders with surfaces larger than 40 cm^2, mainly due to the absence of delicate frondose and filamentous forms like *Blidingia*, *Acrochaete*, *Hincksia*, *Compsonema*, *Enteromorpha prolifera*, *Rhizoclonium* or *Ceramium* in the subsampled series (Table 3).

DISCUSSION

Although the existence of a bank of microscopic forms has been suggested before (Chapman 1986, Santelices 1990, Hoffmann & Santelices 1991) this is the first characterization of an assemblage in terms of species composition, seasonal species turnover and time-space community development. Lieberman et al. (1979) attempted to characterize a somewhat similar assemblage, but only in terms of species turnover.

The bank of microscopic forms studied here consisted of 14 to 24 taxa, with little species turnover throughout the year: less than 30% of the taxa were restricted to 1 or 2 seasons, and most were found in all seasons. The bank contained about twice the number of taxa found as propagules in the water and about half the number of taxa found in the macroscopic vegetation. Most taxa developed within a month of field-incubated new boulders, demonstrating fast development of the community. Successional changes mainly affected the surface covered by the diverse species.

The bank appears to be a rather permanent assemblage with most species present in all seasons. How-

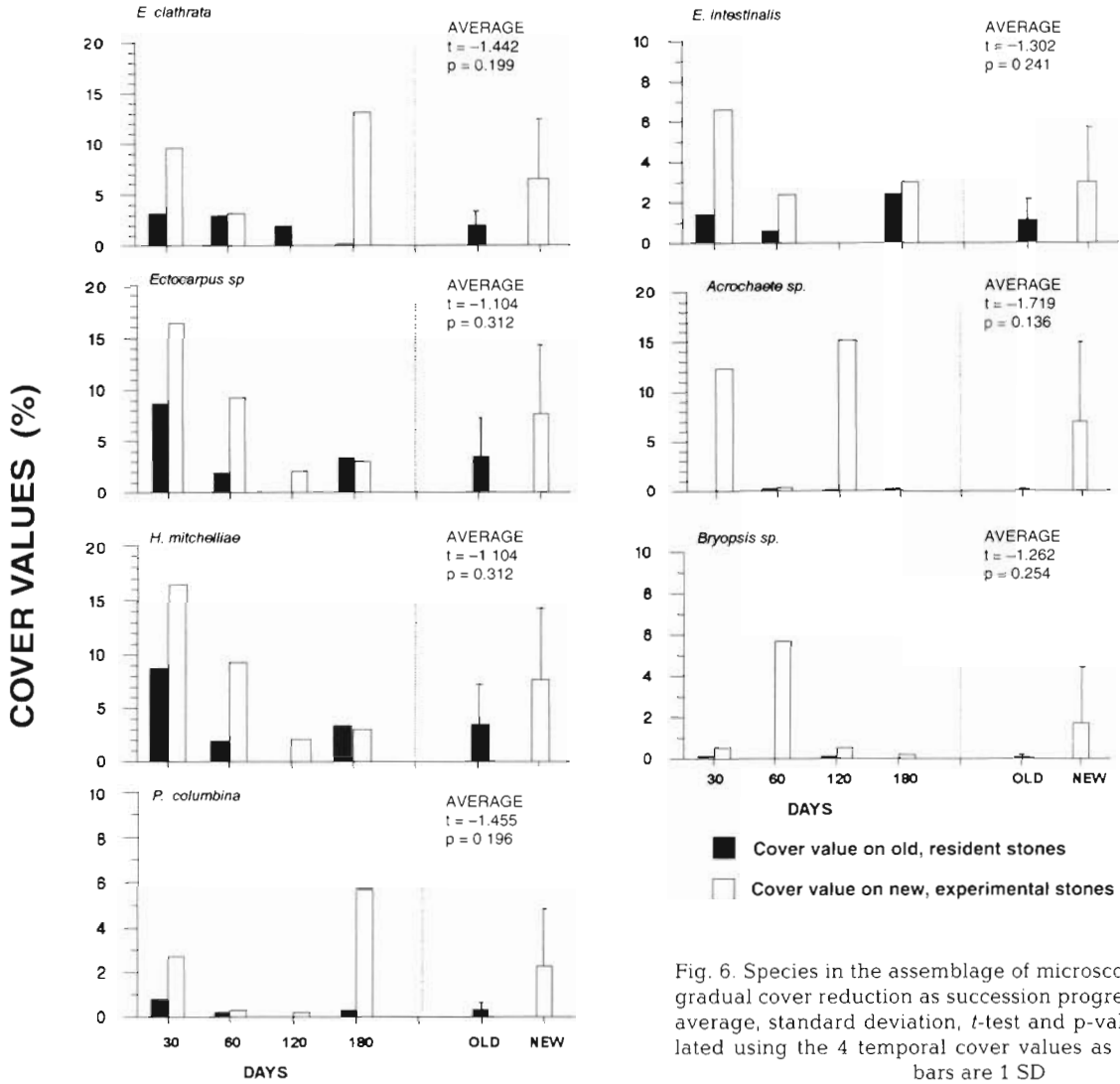

Fig. 6. Species in the assemblage of microscopic forms with a gradual cover reduction as succession progresses. Respective average, standard deviation, *t*-test and p-values were calculated using the 4 temporal cover values as replicates. Error bars are 1 SD

ever, comparisons with the fertile macroscopic vegetation, propagule availability, and colonization and succession patterns suggest a heterogeneous origin of the bank. The presence of about 70% of the species can be explained because they occur in the macroscopic vegetation; some are fertile most of the year and their propagules are often found in the water. For these species, the assemblage of microscopic forms mainly represents a nursery ground for them. They maintain a persistent pool of propagules that quickly recruit on new substrate and would replenish the bank whenever they are destroyed by boulder overturning or grazing. Most of these species are ephemerals, with large dispersal shadows (Amsler & Searles 1980, Sousa 1984, Hoffmann & Ugarte 1985, Reed et al. 1988). *Enteromorpha clathrata* and *Blidingia minima* — not found in the macroscopic vegetation, but whose propagules often appeared in the water — can also be ascribed to this group. The frequent occurrence of the latter species in the bank indicates spatial displacement of propagules originating outside the area. They resemble the classical ephemerals and pioneer species described for land plants (see Leck et al. 1989 for a review), with persistent seed pools, uniform spatial distribution and large dispersal capacity (Kemp 1989, Alvarez-Buylla & Martínez-Ramos 1990).

The bank of microscopic forms also contains species whose propagules are rarely present in the water. Some, like the filamentous *Rhizoclonium* and *Ulothrix* have patchy temporal distributions. However, the most important in terms of number of taxa and seasonal presence is a group of algae with crustose morphology: *Ralfsia confusa*, *Hildenbrandia lecanellieri*, the crustose phase of *Nothogenia fastigiata* and the crustose base of *Petalonia fascia* and *Mazzaella laminarioides*. Once settled, these crusts may persist in the bank, not as dormant stages but as slow-growing forms. Crusts on the boulders are generally small (less than 2 cm^2

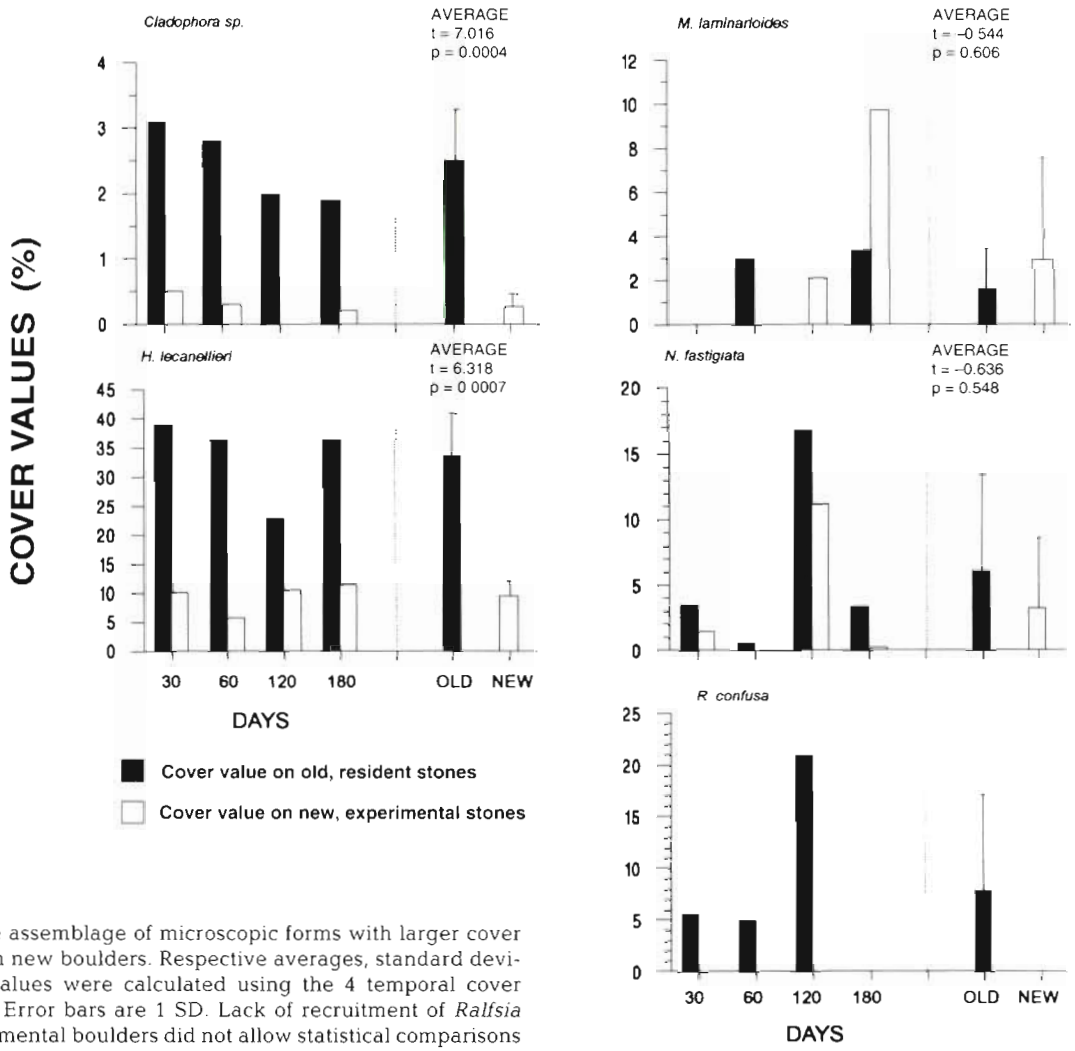

Fig. 7 Species in the assemblage of microscopic forms with larger cover values on old than on new boulders. Respective averages, standard deviation, *t*-test and p-values were calculated using the 4 temporal cover values as replicates. Error bars are 1 SD. Lack of recruitment of *Ralfsia confusa* in the experimental boulders did not allow statistical comparisons

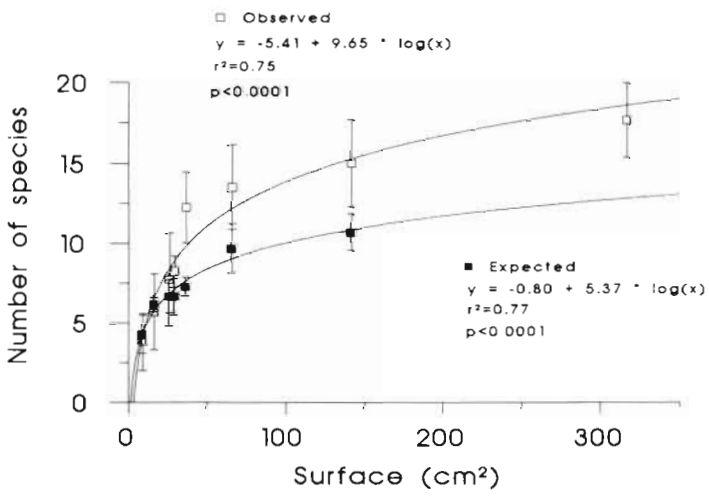

Fig. 8. Comparison between expected and observed species-area relationships in the assemblage of microscopic forms. Error bars are ± 1 SD of the mean

diameter) and tend to persist in small irregularities or crevices. These findings are consistent with the capacity of crustose algal morphologies to survive disturbances such as boulder overturning, grazing or sand abrasion (Slocum 1980, Dethier 1981, Littler & Littler 1983). The frequency of crusts in banks and their persistence in refuges resembles the situation described for mussel beds (Santelices & Martínez 1988), and stresses the importance of the banks of microscopic forms for survival of crusts in disturbed habitats.

Life history characteristics, cellular plasticity and morphological convergences complicate the application of the r- and k-selection concepts to seaweeds (Littler & Littler 1980, 1983, Vermaat & Sand-Jensen 1987, Santelices 1990). However, some crustose species and crustose stages of others exhibit slow growth rates, low recruitment and therefore a tendency to k lifestyles, resembling 'perennials' of seed banks, whose relative

Table 3. Presence of macroalgal taxa in the assemblage of microscopic forms as a function of increasing boulder surface. x: presence; E: expected; O: observed

Taxa	Average boulder surface ± range (cm^2)														
	9.0±1.7		16.5±1.5		26.5±2.0		30.0±1.0		37.0±5.7		66.0±21.5		142.0±37.5		316.0±50.0
	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O
Enteromorpha clathrata	x	x	x	–	x	x	x	x	x	x	x	x	x	x	x
Enteromorpha intestinalis	x	x	x	x	x	x	x	–	x	x	x	x	x	x	x
Hildenbrandia lecanellieri	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Blidingia minima	x	–	x	–	x	x	x	–	x	–	x	–	x	–	x
Acrochaete sp.	x	–	x	–	x	–	x	x	–	–	x	–	x	x	x
Ralfsia confusa	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Ectocarpus sp.	–	x	x	x	x	x	x	x	x	–	x	x	x	x	x
Ulva sp.	–	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Enteromorpha compressa	–	–	x	–	x	–	–	–	–	–	–	–	x	–	x
Mazzaella laminarioides	–	–	x	–	x	–	–	–	x	–	x	–	x	–	x
Hincksia mitchelliae	–	–	x	–	x	x	x	–	x	–	x	x	x	x	x
Cladophora sp.	–	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Porphyra columbina	–	–	x	x	x	x	x	x	x	x	x	x	x	x	x
Compsonema sp.	–	–	x	–	x	–	–	–	x	–	x	–	x	–	–
Polysiphonia spp.	–	x	–	x	x	–	–	x	x	x	x	x	x	x	x
Petalonia fascia	–	–	–	–	x	–	–	–	x	–	x	–	x	–	–
Enteromorpha prolifera	–	–	–	–	x	–	x	–	–	–	x	–	–	x	x
Corallina officinalis	–	x	–	–	–	x	x	x	x	–	x	x	x	x	x
Gelidium spp.			–	x	–	–	–	–	–	–	x	x	x	–	x
Nothogenia fastigiata									x	–	–	–	–	–	–
Rhizoclonium ambiguum									x	–	x	–	x	–	–
Ulotrix sp.											x	–	x	–	–
Colpomenia spp.											x	–	–	–	–
Ceramium rubrum											x	–	x	–	x
Antithamnion sp.											x	x	–	–	x
Bryopsis sp.											x	–	–	–	–
Chaetomorpha firma													x	–	–
Gymnothamnion elegans													x	–	x
Total no. of taxa	6	9	14	9	17	11	13	10	17	8	24	13	23	13	20

importance varies from one system to the other (see reviews by Cavers & Benoit 1989, Kemp 1989, Leck 1989).

The data on colonization and succession on experimental boulders support the distinction between ephemerals and perennating crusts, with markedly different patterns of persistence and growth. After ephemerals have recruited on boulders, the relative importance of some of these species decreases as succession progresses. The bank appears to function as a developmental stage for the pioneer or fugitive species. Even in the absence of a bank, pioneer species can easily colonize and use any new substrate. In contrast, the perennating forms exhibit less colonization capacity but, once established, they tend to persist in the community. Thus, the bank of microscopic forms is most important for the survival of perennating crusts with slow growth. As anticipated (Santelices 1990), this is in sharp contrast with the patterns described for the seed banks of land plants.

In land plants and invertebrate assemblages with long-term dormancy, dormant stages accumulate as new seeds or eggs are added over time (Harper 1977, De Stasio 1989). A key result of such long-term dormancy is survival of catastrophic events and rapid repopulation of habitats. Another is the possibility of storing genetic variation. Only some of these effects are likely to occur in the assemblages of microscopic forms examined. If disturbance of boulders were reduced, repopulation would proceed both from the assemblage and from propagules produced by pioneer species dominating the community. Under such circumstances, fast turnover of the pioneer species would reduce the probability of co-occurrence of individuals from very different generations. In contrast, the bank might be a reservoir for genetic variation for the crustose component. Once disturbance decreases it is not clear whether the macroalgal vegetation originates anew from recruitment, or from microscopic stages present in the bank. Although several authors have examined seaweed recruitment on artificial substrate (see Reed et al. 1988 and Santelices 1990 for reviews) the role of the bank of microscopic forms has not been evaluated. The closest approach (Flavier & Zingmark 1993) correlated macroalgal distribution with temporal and spatial distribution of recruited propagules.

The species-area relationship found in our bank of microscopic forms only partially agreed with previous findings in similar communities: species richness correlated significantly with boulder surface area, in contrast to the lack of relationships described for seasonally devastated cobble substrate of tropical areas (Lieberman et al. 1979). Furthermore, species richness was significantly higher on individually sampled stones larger than 40 cm^2 than on equivalent surfaces subsampled from larger boulders. Since there was practically no empty surface on either type of boulder, our results are consistent with predictions of the Intermediate Disturbance Hypothesis (Sousa 1979a, b, 1980, McGuiness 1984a, b). Disturbance, represented here by overturning of boulders, interrupts the course of competition that in equivalent areas of larger boulders (therefore with less overturning), results in a smaller number of species. In large boulders filamentous forms were the forms most favoured by reductions in disturbance. On the other hand, the high species richness in the 2 microscopic assemblages on the disturbed habitats studied (approximately 25 taxa in our study and over 70 in Lieberman et al. 1979) are in contrast with the low numbers (6 taxa) reported by Sousa (1979a, b, 1980). The smaller boulders in Sousa's studies (corresponding to medium size boulders in ours) were frequently disturbed, hence available for colonization shortly before being disturbed again. Thus, few species could colonize these boulders and grow to observable size in the short time between disturbances. As a result, species richness was consistently low. However, boulders and stones have small refuges where microscopic forms of macroalgae persist. Therefore, the low species richness due to high disturbances that affects the macroscopic vegetation does not affect the microscopic forms in the same way. Future studies should evaluate the numerical relationships between species richness and disturbance, and should include both macroscopic and microscopic assemblages, to find out whether high disturbances effectively reduce species richness or only affect their macroscopic expression.

Acknowledgements. This study was made possible by the financial support of grants FONDECYT No. 801-90, FONDECYT 1930581 and SAREC-CONICYT 90-7 Suggestions by 3 anonymous reviewers are gratefully acknowledged.

LITERATURE CITED

Alvarez-Buylla ER, Martínez-Ramos M (1990) Seed bank versus seed rain in the regeneration of a tropical pioneer tree. Oecologia 84:314–325

Amsler CD, Searles RB (1980) Vertical distribution of seaweed spores in a water column offshore of North Carolina. J Phycol 16:617–619

Anderson EK, North WJ (1969) Light requirements of juvenile and microscopic stages of the giant kelps, *Macrocystis*. Proc Int Seaweed Symp 6:3–15

Burrows EM (1958) Subtidal algal population in Port Erin Bay, Isle of Man. J mar biol Ass UK 37:687–703

Cavers PB, Benoit DL (1989) Seed banks in arable land. In: Leck MA, Parker VT, Simpson RL (eds) Ecology of soil seed banks. Academic Press, San Diego, p 309–328

Chapman ARO (1986) Population and community ecology of seaweeds. In: Blaxter JHS, Southwood AJ (eds) Adv mar Biol 23:1–161

Chapman ARO, Burrows EM (1970) Experimental investigations into the controlling effects of light conditions on the development and growth of *Desmarestia aculeata* (L.) Lamour. Phycologia 9:103–108

Clendenning KA (1961) Photosynthesis and growth in *Macrocystis pyrifera*. Proc Int Seaweed Symp 4:56–65

De Stasio BT Jr (1989) The seed bank of a freshwater crustacean: copepodology for the plant ecologist. Ecology 70:1377–1389

Dethier M (1981) Heteromorphic algal life histories: the seasonal pattern and response to herbivory of the brown crust, *Ralfsia californica*. Oecologia 49:333–339

Flavier AB, Zingmark RG (1993) Macroalgal recruitment in a high marsh creek of North Inlet Estuary, South California. J Phycol 29:2–8

Harper JL (1977) Population biology of plants. Academic Press, London

Hay ME, Norris JN (1984) Seasonal reproduction and abundance of six sympatric species of *Gracilaria* Grev. (Gracilariaceae; Rhodophyta) on a Caribbean subtidal sand plain. Hydrobiologia 116/117:63–94

Hoffmann AJ, Camus P (1989) Sinking rates and variability of spores from benthic algae in Central Chile. J exp mar Biol Ecol 126:281–291

Hoffmann AJ, Santelices B (1991) Banks of algal microscopic forms: hypotheses on their functioning and comparisons with seed banks. Mar Ecol Prog Ser 78:71–85

Hoffmann AJ, Ugarte R (1985) The arrival of propagules of marine macroalgae in the intertidal zone. J exp mar Biol Ecol 92:83–95

Kain JM (1966) The role of light in the ecology of *Laminaria hyperborea*. Br Ecol Soc Symp 6:319–334

Kemp PR (1989) Seed bank and vegetation processes in deserts. In: Leck MA, Parker VT, Simpson RL (eds) Ecology of soil seed banks. Academic Press, San Diego, p 257–281

Kershaw KA (1964) Quantitative and dynamic ecology. Edward Arnold Publ Co Ltd, London

Leck MA (1989) Wetland seed bank. In: Leck MA, Parker VT, Simpson RL (eds) Ecology of soil seed banks. Academic Press, San Diego, p 283–305

Leck MA, Parker VT, Simpson RL (1989) Ecology of soil seed banks. Academic Press, San Diego

Lewis SM, Norris JN, Searles RB (1987) The regulation of morphological plasticity in tropical reef algae by herbivory. Ecology 68:636–641

Lieberman M, John DM, Lieberman D (1979) Ecology of subtidal algae on seasonally devastated cobble substrates off Ghana. Ecology 60:1151–1161

Littler MM, Littler DS (1980) The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. Am Nat 116:25–44

Littler MM, Littler DS (1983) Heteromorphic life-history strategies in the brown algae *Scytosiphon lomentaria* (Lyngb.) Link. J Phycol 19:425–431

McGuinness KA (1984a) Equations and explanations in the study of species-area curves. Biol Rev 59:423–440

McGuinness KA (1984b) The species-area relations of the communities on intertidal boulders: testing the null hypothesis. J Biogeogr 11:439–456

McGuinness KA, Underwood AJ (1986) Habitat structure and the nature of communities on intertidal boulders. J exp mar Biol Ecol 104:97–123

McLachlan J (1973) Growth media-marine. In: Stein JR (ed) Handbook of phycological methods. Cambridge University Press, Cambridge, p 25–52

Neushul M, Dahl AL (1967) Composition and growth of subtidal parvosilvosa from Californian kelp forest. Helgoländer wiss Meeresunters 15:480–488

Novaczeck I (1984a) Development and phenology of *Ecklonia radiata* at two depths in Goat Island Bay, New Zealand. Mar Biol 81:189–197

Novaczeck I (1984b) Response of *Ecklonia radiata* (Laminariales) to light at 15°C with reference to the field light budget at Goat Island Bay, New Zealand. Mar Biol 80:263–272

Pedersen PM (1981) Phaeophyta: life histories. In: Lobban CS, Wynne MJ (eds) The biology of seaweeds. University of California Press, Berkeley p 194–217

Reed DC, Laur DR, Ebeling AW (1988) Variation in algal dispersal and recruitment: the importance of episodic events. Ecol Monogr 58:321–335

Richardson JP (1981) Persistence and development of *Dasya baillouviana* (Gmelin) Montagne (Rhodophyceae, Dasyaceae) in North Carolina. Phycologia 20:385–391

Richardson JP (1982) Life history of *Bryopsis plumosa* (Hudson) Agardh (Chlorophyceae) in North Carolina, USA. Botanica mar 25:177–183

Santelices B (1990) Patterns of reproduction, dispersal and recruitment in seaweeds. Oceanogr mar Biol A Rev 28:177–276

Santelices B, Martínez E (1988) Effects of filter-feeders and grazers on algal settlement and growth in mussel beds. J exp mar Biol Ecol 118:281–306

Schonbeck MW, Norton TA (1980) Factor controlling the lower limits of fucoid algae on the shore. J exp mar Biol Ecol 43: 131–150

Sheader A, Moss B (1975) Effect of light and temperature on germination and growth of *Ascophyllum nodosum* (L.) Le Jol. Estuar coast mar Sci 3:125–132

Simberloff DS (1976) Experimental zoogeography of island: effects of island size. Ecology 57:629–648

Slocum CJ (1980) Differential susceptibility to grazers in two phases of an intertidal alga: advantages of heteromorphic generations. J exp mar Biol Ecol 46:99–110

Smith R (1967) Sublittoral ecology of marine algae on the North Wales coast. Helgoländer wiss Meeresunters 15: 467–469

Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. Freeman, San Francisco

Sousa WP (1979a) Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol Monogr 49:227–254

Sousa WP (1979b) Disturbance in marine intertidal boulder fields: the non-equilibrium maintenance of species diversity. Ecology 60:1225–1239

Sousa WP (1980) The responses of a community to disturbance: the importance of successional age and species life histories. Oecologia 45:72–81

Sousa WP (1984) Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. Ecology 65:1918–1935

Tanner CE (1981) Chlorophyta: life histories. In: Lobban CS, Wynne MJ (eds) The biology of seaweeds. University of California Press, Berkeley, p 218–247

Vermaat JE, Sand-Jensen K (1987) Survival, metabolism and growth of *Ulva lactuca* under winter conditions: a laboratory study of bottlenecks in the life cycle. Mar Biol 95:55–61

West JA, Hommersand MH (1981) Rhodophyta. In: Lobban CS, Wynne MJ (eds) The biology of seaweeds. University of California Press, Berkeley, p 133–193

This article was submitted to the editor

Manuscript first received: December 30, 1994
Revised version accepted: July 11, 1995