toral zone represents the principal centre of formation and diffusion of the endemic species of the Mediterranean is confirmed. From the ecological stand point, the flora, living under the constant influence of the bottom currents is arranged in two different strata both in the infralittoral and in the circalittoral zone. The canopy layer, composed of rheophilic species acts as a sort of barrier to depress the water movement, reducing the impact of hydrodynamic factors and thus permitting the development of a considerable number of sciaphilic species.

References

1. Giaccone, G., Sortino, M., Solazzi, A., Tolomio, C. Lavori dell'Ist.Bot. e del Giard. Col. di Palermo 25,103-119 (1973).
2. Giaccone, G., Scammacca, B., Cinelli, F., Sartoni, G., Furnari, G., Giorn. Bot. Ital. 106, 211-229 (1972).
3. Giaccone, G., Sortino, M., Lavori dell'Ist. e del Giard. Col. di Palermo 25, 166-183 (1974).
4. Cinelli, F., Fresi, E., Mazzella, L., Ponticelli, M.P.,Giorn Bot. Ital. 113, 173-188 (1979).
5. Colantoni, P., Giornale di Geologia 40 (1), 181-207 (1975).
6. Giaccone, G., Rizzi Longo, L., Mem. Biol. Mar.Ocean. 6 (3), 69-123 (1976).
7. Giaccone, G., Annuario W.W.F. Italia 6 (19), 1-118 (1978).
8. Boudouresque, C.F., Bull.Mus.Hist.nat.Marseille 33,147-225 (1973)
9. Feldmann, J., Thèse Sci.nat. Rouen (1937).
10. Giaccone, G., Mem. Biol.Mar.Ocean. 2 (2), 37-59 (1972).
11. Giaccone, G., Bruni, A., Atti, Ist.veneto Sci.Lett.Arti. 131, 59-103 (1973).
12. Por, F.D.,Lessepsian migration,Springer-Verlag, Berlin-Heidelberg-New York 1978
13. Boudouresque, C.F., Belsher, T., Marcot-Coquegniot, J.:Trav. sci. Parc nation. Port-Cros 3, 89-120 (1977).

THE ECOLOGICAL IMPORTANCE OF KELP-LIKE HOLDFASTS AS A HABITAT OF INVERTEBRATES IN CENTRAL CHILE.

II. Factors affecting community organization.

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Introduction

A critical evaluation of the non-productive, ecological roles played by brown algal holdfasts as habitats of invertebrates is not found in the literature. Most pertinent studies are either taxonomic treatments (1,2,3,4) with only occasional mention to aspects of population dynamics and faunal community organization, or compare the structure of these communities over a wide range of environmental conditions (5,6,7,8,9,10). Holdfasts normally provide refuge from wave impact and predation (2,3,4,5,6,7,11) and function as settlement areas and nursery grounds as in the case for some filamentous algae (12,13). However no attention has been paid to the patterns of holdfast colonization by invertebrates and to the effects of holdfast morphology in structuring such communities. This report is the second part of a study aimed at understanding the ecological roles played by brown algal holdfasts in the intertidal rocky habitat of Central Chile. It will analyse holdfast attributes important in structuring the faunal community and will characterize holdfast colonization patterns. A detailed analysis of the structure of this community has been given elsewhere (14).

Materials and methods

A total of 31 holdfasts of *Lessonia nigrescens* Bory and 22 of *Durvillea antarctica* (Chamisso) Hariot were collected between Jan-

Fig. 1. Schematic representation of chambers and channels in holdfasts of L. nigrescens (A) and D. antarctica (B).

uary 1976 and March 1978 in three localities of Central Chile (Horcón, Valparaíso and Las Cruces). Both algae are typically from the infralittoral fringe (15) on exposed rocky shores. The holdfasts of these 2 species differ in morphology (Fig.1). Usually only one chamber exists in D. antarctica and numerous in L. nigrescens.

In the laboratory, the larger macro-invertebrates (≥1mm) were removed from the holdfasts. Then the area of water interchange (defined as the sum of the area of all holes≥5mm on the holdfast surface) and the internal volume of the holdfast (free of algal tissue) were measured. Each holdfast was then dissected under a microscope to remove the smaller invertebrates. Holdfasts heavier than 0.5k were subsampled; four randomly selected, radial sections examined from each holdfast. The animals so gathered were sorted by species, counted and wet weighted. Biomass data of the 43 invertebrate taxa found were used to calculate diversity indexes (16,17) and association values among holdfasts (18). Samples were grouped following the linkage method (19).

Results and discussion

Volume of internal cavity is positively correlated with holdfast weight (Figs.2A,2D) and invertebrate biomass (Figs.2B,2E), which is expected, since chambers and channels in the holdfasts are excavated by the animals. However, the largest amounts of biomass were found

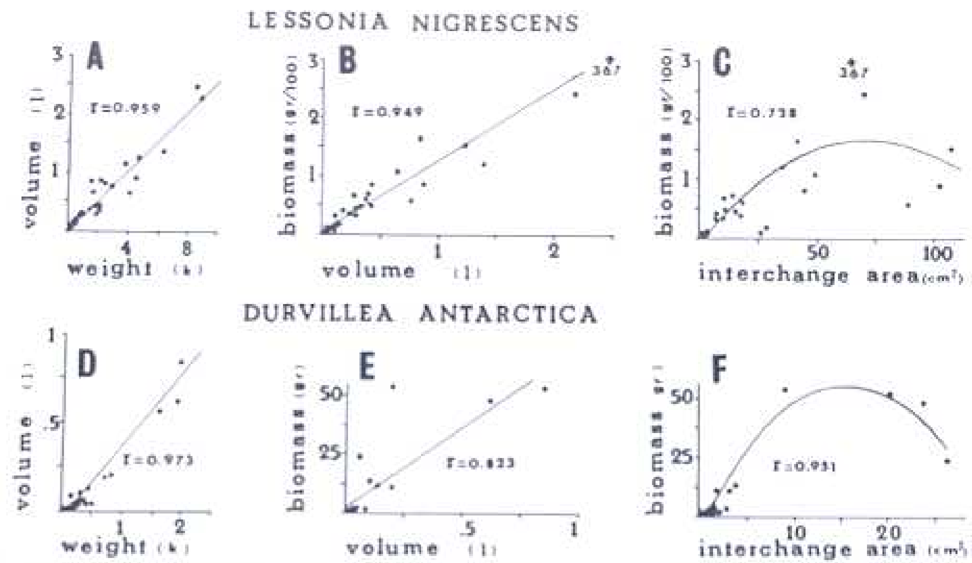
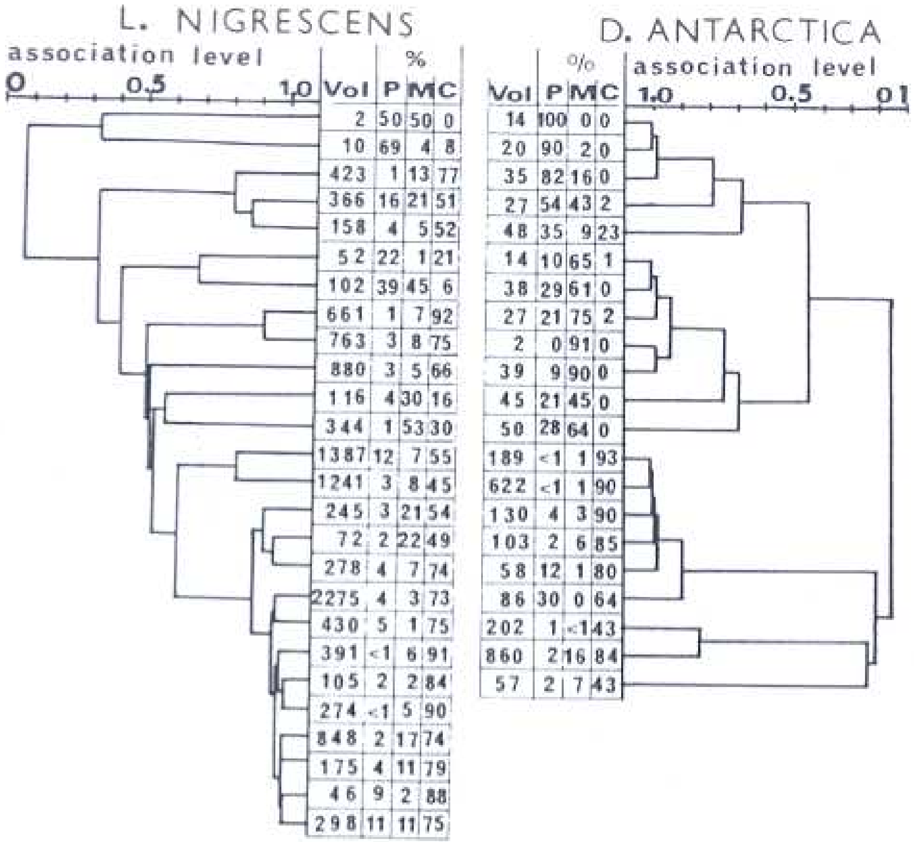


Fig.2. Relationship between parameters of the holdfast and animal biomass. Regression equations: A:y=251.212x + 27.92; B:y=0.12x + 7.019; C:y=4.849x - 0.033x² - 10.274; D:y=392.486x - 53.376; E:y=0.069x + 2.523; F:y=7.622x - 0.235x² - 5.843. With n=31 for A, n=26 for B,C and n=22 in D,E,F. Volume in cc. All correlation coefficients p<0.01.

in holdfasts with areas of water interchange of intermediate values (Figs.2C,2F). Filter feeders, depending on the volume of water flow through the holdfast, are a high percentage of the total invertebrate biomass found in these algae (58-70%). Their reduction with increasingly larger interchange area seems related to reductions in the shelter offered by the holdfast and to increments in predator densities inside the holdfast.

Cluster analysis shows the existence of three groups of holdfasts in D. antarctica (Fig.3). Two groups of holdfasts, with volume ≤50cc, are dominated each by polychaetes or mussels. A third group of holdfasts, of larger size, is dominated by crabs which apparently replace the two other invertebrate groups as the holdfasts increase in size. This predictable pattern of succession is absent from L. nigrescens.



L. nigrescens

Vol	P (%)	M (%)	C (%)
2	50	50	0
10	69	4	8
423	1	13	77
366	16	21	51
158	4	5	52
52	22	1	21
102	39	45	6
661	1	7	92
763	3	8	75
880	3	5	66
116	4	30	16
344	1	53	30
1387	12	7	55
1241	3	8	45
245	3	21	54
72	2	22	49
278	4	7	74
2275	4	3	73
430	5	1	75
391	<1	6	91
105	2	2	84
274	<1	5	90
848	2	17	74
175	4	11	79
46	9	2	88
298	11	11	75

D. antarctica

Vol	P (%)	M (%)	C (%)
14	100	0	0
20	90	2	0
35	82	16	0
27	54	43	2
48	35	9	23
14	10	65	1
38	29	61	0
27	21	75	2
2	0	91	0
39	9	90	0
45	21	45	0
50	28	64	0
189	<1	1	93
622	<1	1	90
130	4	3	90
103	2	6	85
58	12	1	80
86	30	0	64
202	1	<1	43
860	2	16	84
57	2	7	43

Fig.3. Cluster diagram of holdfasts based on biomass of animals. (Vol = volume in cc., P,M,C are the percentages of the biomass corresponding to polychaetes, mussels and crabs).

The existence of more than one chamber in the holdfast of L. nigrescens probably allows more species to fully utilize the holdfast internal volume without replacement among them. It is not surprising then that the cumulative diversity is higher in L. nigrescens than in D. antarctica (Fig.4). This is so even though both algal species show an essentially similar species assemblage in their holdfast faunal community.

These results also indicate that the general models of colonization

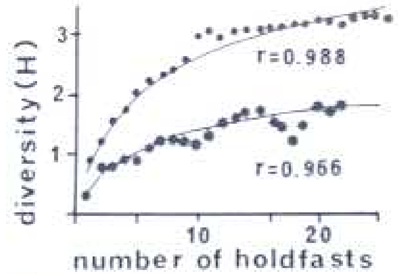


Fig.4. Cumulative diversity in holdfasts of L. nigrescens (•, H=0.857 + 0.812 lnx) and D. antarctica (•, H= 0.277 + 0.468 lnx).

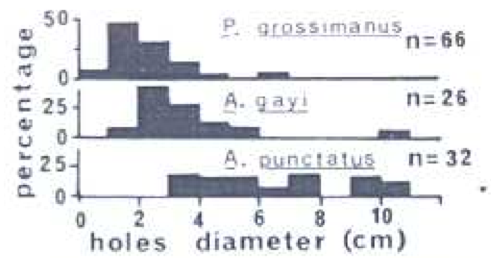


Fig.5. Distribution of 3 species of crabs in holes of different sizes. (Observed in L. nigrescens May and June 1979).

and species succession proposed in the literature (20) do not apply for multichambered algal holdfasts. The existence of several chambers allows the permanence of the first invaders in the community without species replacement at late successional stages. Species replacement, however, might occur in any given holdfast chamber, (providing that the connection with the exterior increases in size with time), as Fig.5 suggests for three species of crabs (Kruskal-Wallis Test (21), $p<0.01$).

In conclusion, this research characterizes invertebrate community development inside brown algal holdfasts to be an atypical process. Invertebrate biomass inside holdfasts increases as the volume increases and as long as this structure provides refuge from wave impact and predation to filter feeders. Colonization processes vary according to the uni or multichambered structure of holdfasts. In uni-chambered holdfasts colonization is a predictable process with species replacement; colonization of multichambered holdfasts is atypical with permanence of first invaders in the community.

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References

1. Colman, J.: J. mar. biol. Ass. U.K. 24, 129-183 (1940).
2. Moore, P.G. : J. mar. biol. Ass. U.K. 51, 589-604 (1971).
3. Moore, P.G. : Cah. Biol. mar. 14, 493-518 (1973).
4. Moore, P.G. : J. exp. mar. Biol. Ecol. 32, 53-96 (1978).
5. Jones, D.J. : Helgolander wiss Meeresunters 22, 417-441 (1971).
6. Jones, D.J. : Helgolander wiss Meeresunters 23, 248-260 (1972).
7. Jones, D.J. : Mar. Biol. (berl). 20, 351-365 (1973).
8. Moore, P.G. : J. exp. mar. Biol. Ecol. 13, 97-125 (1973).
9. Moore, P.G. : J. exp. mar. Biol. Ecol. 13, 127-163 (1973).
10. Moore, P.G. : J. exp. mar. Biol. Ecol. 16, 257-300 (1974).
11. Moore, P.G. : J. exp. mar. Biol. Ecol. 10, 59-80 (1972).
12. Bayne, B.L. : Anim. Ecol. 33, 513-523 (1964).
13. Wigham, G.D. : J. mar. biol. Ass. U.K. 55, 45-67 (1975).
14. Cancino, J., Santelices, B. : Biología Pesquera, Chile (in press)
15. Stephenson, T.A., Stephenson, A. : Life between tidemarks on rocky shores, W.H. Freeman & Co., San Francisco (1972).
16. Brillouin, L. : Science and information theory, Second edition, Academic Press, New York (1962).
17. Pielou, E.C. : Ecological diversity, John Wiley & Sons, New York (1975).
18. Morisita, M. : Mem. Fac. Sci. Kyushu Univ. Ser. E (Biol). 3, 65-80 (1959).
19. Sokal, R.R., Sneath, P.H.A.: Principles of numerical taxonomy. W.H. Freeman & Co., San Francisco (1963).
20. Connell, J.H., Slatyer, R.: Amer. nat. 111, 1119-1144 (1977).
21. Siegel, S. : Nonparametric statistics. McGraw-Hill. Kogakusha Ltd., Tokyo (1956).