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ZOARIAL FORMS IN THE DEVELOPMENT OF A BRYOZOAN COMMUNITY*

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RESUMEN

Formas zooariales en el desarrollo de una comunidad de Briozoos.

Se ha estudiado la dinámica de las relaciones entre diversas formas zoariales de Briozoos Cheilostomata durante la evolución de una comunidad sobre sustrato artificial a lo largo de un acantilado infralitoral del Mediterráneo nord-occidental. Los briozoos membraniporiformes caracterizan las primeras fases de colonización. En seguida en las zonas más superficiales, las formas erectas y flexibles aumentan notablemente y tienden a prevalecer sobre las formas incrustantes. En las áreas más profundas en cambio, las colonias membraniporiformes siguen siendo predominantes. Los diversos tipos zoariales que se han considerado, presentan grandes diferencias por lo que respecta, ya sea a la capacidad de fijarse y crecer sobre superficies desnudas y lisas o sobre substratos ocupados por otros organismos, ya sea la posibilidad de adaptarse a las variaciones que sufre el substrato en el transcurso del tiempo. Las variaciones en la abundancia relativa de los diversos tipos morfológicos está correlacionada con la disminución del espacio primario y, por lo tanto, con las nuevas condiciones ecológicas a nivel de las superficies del sustrato.

Palabras clave: ecología del benthos, dinámica de comunidad, briozoos, formas zoariales.

SUMMARY

The dynamics of the relations between different zoarial forms of cheilostome bryozoans, during the development of a community on artificial substrates, have been studied along an infralittoral cliff of the northwestem Mediterranean Sea.

Membraniporiform bryozoans (thick membraniporiform and thin membraniporiform zoarial types) prevail during the first stages of colonization. Later, at shallow depth, erect flexible forms (tuft-like zoarial type) tend to increase prevailing over the encrusting ones and, at greater depth, membraniporiform colonies continue to play a major role. The studied zoarial types show differences both in their ability to settle and to grow on bare and smooth surfaces and on substrate occupied by other organisms, and also to adjust to modifications of the substrate through time. The variations in the relative abundance of different zoarial forms correspond to changes in the availability of primary space and to new ecological conditions close to the substrate surface.

Key words: benthos ecology, community dynamics, bryozoans, growth forms.

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INTRODUCTION

In bryozoans, as in other modular benthic organism, the ability to attain ecological resources is closely connected to the colony form. Colony form affects both physiologic functions (mainly feeding and reproduction) and the responses to varying environmental conditions.The relation between the physical properties of the environment (in particular water movement, substrate, sedimentation) and the colony architecture in bryozoans has been repeatedly invoked (STACH, 1936; GAUTIER, 1962; LAGAAJI & GAUTIER, 1965; COOK, 1968; SCHOPF, 1969; CHEETHAM, 1971; HARMELIN, 1976; RIDER & COWEN, 1977; HARMELIN *et* al., 1985; GORDON, 1987) and has proven a valuable tool for paleoecological interpretation (SCHOPF, 1969; BIGEY, 1986). Colony form influences the relations between organisms, and the possibility of gaining and holding space and competing for available resources (CHEETHAM, 1971; BUSS, 1979a; 1979b; JACKSON, 1977; JACKSON & WINSTON, 1981; LIDGARD & JACKSON, 1982; LIDGARD, 1984; HARMELIN, 1985; MCKINNEY, 1985; 1986) interacting with many other factors (RUBIN, 1987). JACKSON (1979) brought back all the forms of colonial animals and sponges to six basic forms (runners, sheets, mounds, plates, vines, trees) and considered variations in shape parameters as a function of growth-form which he interpreted as adaptations to various selective forces. He also proposed a series of hypotheses regarding the importance of sessile animals shape to variations in their life history attributes, growth processes and distribution in space and time. The growth forms of modular organisms have also been ordered along a continuum between two opposite extreme called "phalanx" and "guerilla" (LOVETT DOUST, 1981; SCHMID & HARPER, 1985) according to how far modules originating by clonal growth are placed from their parent modules. SACKVILLE HAMILTON *et al.* (1987) predicted difference between guerrilla and phalangeal architectures in their response to selection. MCKINNEY & JACKSON (1989) recently reviewed the main trends in the study of growth forms and their implications as adaptive strategies, in bryozoan life history and evolution.

Notwithstanding the large number of theoretical predictions and hypotheses, experimental evidences are still scarce. We give experimental data supporting the ecological significance of different morphological strategies during the development of a bryozoan cheilostome community. We focus on the following points: a) how the community changes through time from the point of view of the equilibrium between the bryozoan growth and b) how each colony form faces ecological modifications occurring at the substrate level through time.

STUDY AREA AND METHODS

The study area was a submerged puddingstone cliff of the Promontory of Portofino (Western Mediterranean Sea). We studied two series of experimental plates (300×200×3 mm. asbestos-cement panels) submerged along the vertical rocky surface at 3, 5, 10, 15 and 20 m. depth, for periods of 2, 3, 4, 6, 12, 25 and 36 months. The panels were placed on metal frames and set vertically at a distance of about 10 cm. from the cliff wall. Panels were examined under a dissecting microscope in order to identify and arrange the species into different groups according to their zoarial form.

Quantitative data were expressed in terms of frequency of each zoarial type, namely the sum of the occurrence of all species belonging to each type in a grid of 100 unit surfaces (2x3 cm.) overlapped to the panel (PISANO & BALDUZZI, 1985). The diversity and evenness indices were calculated as in PIELOU (1969), on the basis of zoarial type frequencies. The relationship between the percent cover of the substratum (independent variable) and both the frequency of each zoarial type and the erect forms/encrusting forms frequency ratio (dependent variables) was analyzed by the Pearson's correlation coefficient.

As previously piiblished (BIANCHI, 1979; RELINI *et al.*, 1983), the two sides of the panels are very different; the front side is dominated by algae and the sheltered side is colonized mainly by bryozoans and serpulids. Even the biomass of the community is quite different on the two sides (PISANO *et al.*, 1981). For this study only the sheltered side facing the cliff of each panel was considered.

Informations about the general trends of colonization and about the vertical distribution of the bryozoan species and the zoarial forms are reported by PISANO & BALDUZZI (1985) and by BOYER *et* al. (1988). Here we discuss the successional aspects at two levels (3 m. and 15 m.) taken as representative examples of a "shallow" and a "deep" ecological situation along the vertical gradient.

RESULTS AND DISCUSSION

GROWTH FORMS

A total of 71 species of cheilostome bryozoans were recorded from the panels at the various depths and arranged into seven zoarial types (fig. 1). As species lists and detailed definitions of zoarial types are reported in other papers (Pisano & Boyer, 1985, in part; Boyer *et al.*, 1986) we only summarize some information here.

The **thin membraniporiform** type includes species with membraniporiform zoaria **(Stach,** 1936) which are unilaminate, thin and adhere strongly to the substrate. This group comprises the highest percentage of species found on all the panels studied (30%).

The **thick membraniporiform** type comprises mebraniporiform species with strong calcification and the ability to form superimposed layers or to grow with the basal lamina perpendicular to the substrate. Therefore they are efficient in maintaining their position against spatial competitors, in overgrowing other organisms, and in growing over irregular surfaces. This type comprises 26% of all species.

The **creeping** type includes **scrupariform** (Cook, 1968) and **catenicelliform** (Stach, 1936) species. The colonies form uniseriate chains of loosely aggregated modules which are capable of settlement and rapid growth on different substrate types.

The **tuft-like** type includes **cellulariform** (Cook, 1968) and **buguliform** (Moyano, 1979) species, with erect, branched and flexible zoaria.

The **celleporiform** type corresponds to Stach (1936) description (see also Gautier, 1962 and Lagaaij & Gautier, 1965).

The **reteporiform** (Stach, 1936) type comprises species of genus ***Sertella:*** zoaria are erect, rigid, with strong calcification and typically fenestrate.

The **petraliform** type corresponds to the zoarial form described by Stach (1936): the colonies are encrusting, thin, unilaminate. Zooids are frequently disjunct, maintaining contact only by tubular processes, and have typical rootlets giving the zoarium flexibility and capability to grow on irregular surfaces.

TREND THROUGH TIME

The trend in the graphs (Fig. 2, 3, 4, 5) shows the pattern in the establishment of the

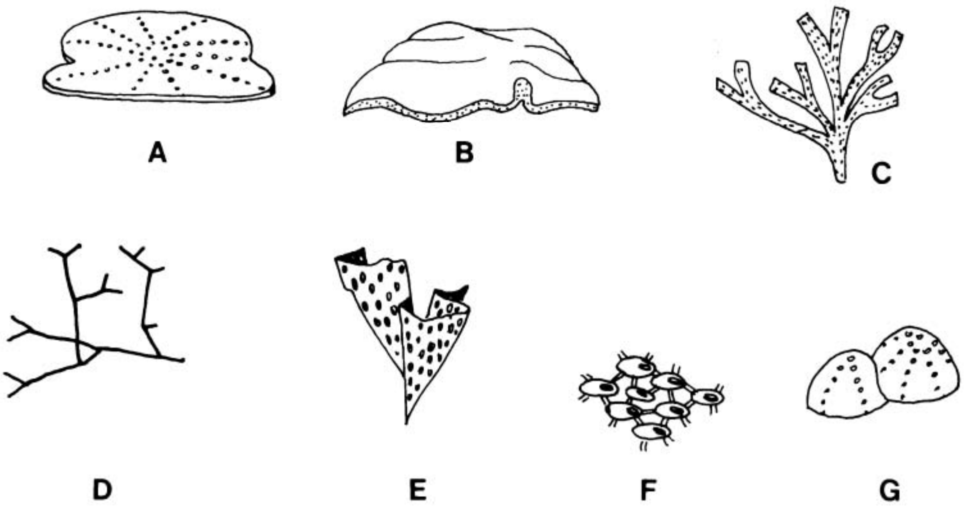

Figure 1. Zoarial **types including species found on panels studied (A:** ***thin memhraniporiform; B: thick memhraniporiform; C: tuft-like; D: creeping; E: reteporiform;*** F: ***petraliform; G: celleporiform).***

Tipos zoariales **que comprenden las especies encontradas en los paneles que se han estudiado** (A: ***thin memhraniporiform;*** B: ***thick membraniporiform; C:*** *tuft-like*; ***D: creeping; E: reteporiform; F: petraliform;*** G: ***celleporiform).***

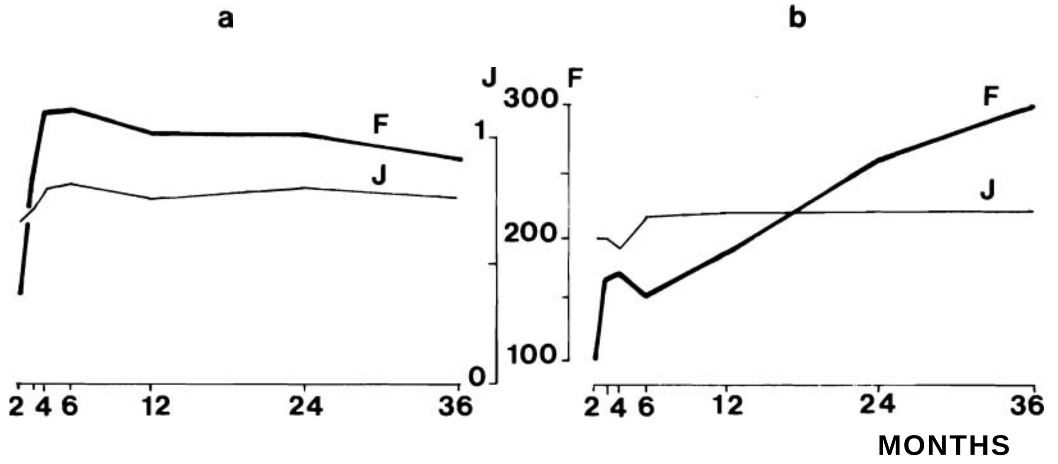

FIGURE 2. Trend though time of abundance (F = sum of frequency of zoarial types) and evenness (J) at 3 m. depth (a) and at 15 m. depth (b).

Evolución temporal de la abundancia (F = suma de la frecuencia de los tipos zoariales) y del evenness (J) a 3 metros de profundidad (a) y a 15 metros (b).

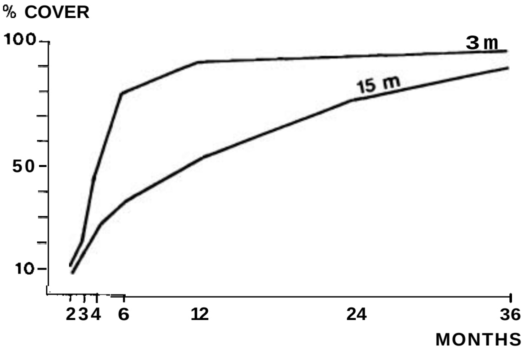

FIGURE 3. Temporal variation of coverage of substrate at two different depths, namely 3 and 15 m.

Variación temporal de la cobertura del substrato a 3 y 15 metros de profundidad

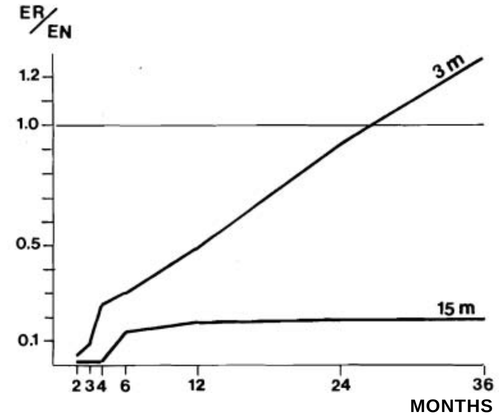

FIGURE 4. Variation in time of quantitative ratio erect forms (tuft-like, reteporiform, celleporiform) to encrusting forms (thin and thick mempraniporiform) at 3 and 15 m. depths.

Variación en el tiempo de la relación cuantitativa entre formas erectas y formas incrustantes a 3 y 15 metros de profundidad.

bryozoan community for two depths, 3 and 15 m., chosen as example of a shallow water and a deeper water situation.

At 3 m. depth, abundance (Fig. 2 a) reached its maximun value after 6 months, then slowly decreased. The evenness curve indicates some variations in quantitative ratio between zoarial types. Within the 6 and 12 month period (fig. 3) more than 90% of the panel surface was covered by bryozoans and other organisms. This corresponds to the end of a "recruitment period" and the beginning of a "maturation period" in the development of the community (PISANO & BOYER, 1985). The ratio of erect to encrusting forms increased during the considered period (Fig. 4). This ratio changes from 1:3 to 1:1 between 6 and 24 months, resulting from a progressive increase in the tuft-like type and a decrease in the membraniporiform type which, between 24 and 36 months, almost disappeared

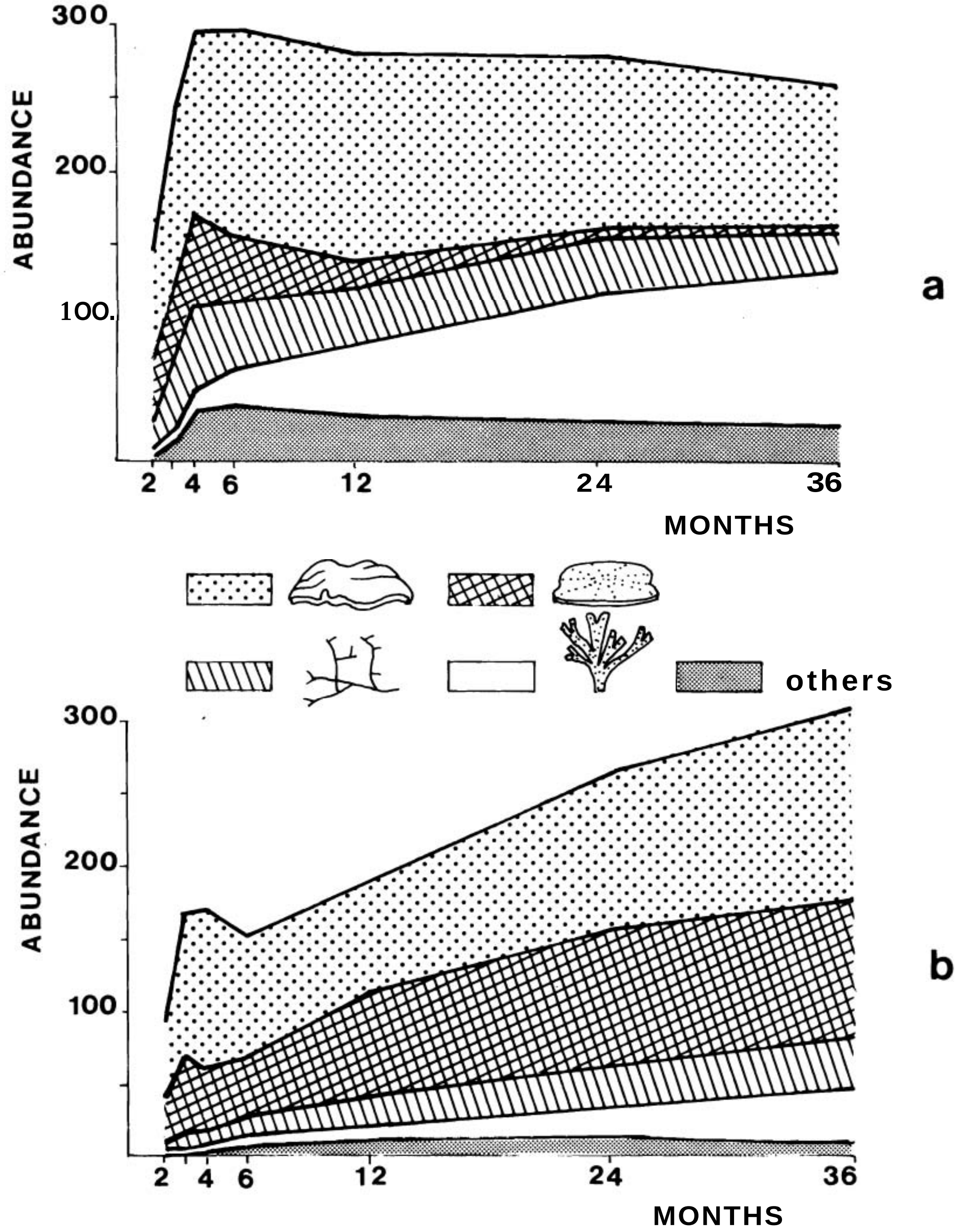

FIGURE 5. Variation in time in abundance of zoarial types (a = 3 m. depth and b = 15 m. depth).

Variación en el tiempo de la abundancia de los tipos zoariales (a= 3 metros; b= 15 metros de profundidad).

(Fig. 5a). The Pearson's r=0.834, computed from the log transformed percent cover and erect forms/encrusting forms ratio, confirm the high degree of non linear relationship between these variables.

At 15 m. depth, abundance (Fig. 2b) clearly continued to increase with time; the zoarial types kept settling and growing for the whole period studied and a consistent quantitative relation between the different types was maintained (see trend of evenness curve in Fig. 2b). Percent cover (fig. 3) was only 80% between the 24th and 36th month period, indicating than primary recruitment had not yet been completed. The ratio erect/encrusting was consistently about 1:10, after 6 months (Fig. 4); the encrusting forms were always dominant, and all groups maintained their levels of abundance (Fig. 5b) (Pearson's r=0.446 between log transformed percent cover and erect/encrusting ratio).

No evident phenomena of predation or anomalous physical disturbance have been observed in the time period considered, and we can consider that the changes in the relative abundance of zoarial types were determined by the development process itself. In addition, important changes have been observed only in the shallow community, where different stages in the development of the community are clearly recognizable (PISANO & BOYER, 1985).

Membraniporiform tipes (thick and thin) are dominant during the first stages of colonization. Both forms can be considered typical "sheets" (BUSS, 1979a; JACKSON, 1979) during the recruitment period and are favoured by the availability of extensive free and smooth surface on which they are fast-growing as "two-dimensional" encrusters (KAUFMANN, 1970). The thin membraniporiform type can quickly occupy the available space in the early colonization phases, but tends to disappear when biotic interactions increase; from this point of view they can be considered as a pioneer group.

The thick membraniporiform species were equally good colonizers at the beginning, but they held their position through time by raising their growing edge above the substrate, developing into "plates" or "mounds" (JACKSON, 1979).

Where space was always available, at 15 m. depth, both thin and thick membraniporiforms showed a similar sheet-like form: the thin encrusting colonies were not inhibited in their growth, and the thick colonies did not fully express their competitive ability.

Tuft-like colonies were stable at 15 m. depth, however they increased and tended to become dominant at the shallower station. This zoarial form shows the highest correlation with the increasing surface cover (r=0.90). This flexible "tree" growth form, that cannot find a stable attachment on the bare surface, were favoured during the later stages of community development for severa1 reason.

Species of this form are able to avoid competition when primary substrate becomes scarce because of the limited surface required for attachment. Their form assures sufficient access to the resources in the water column and, at the same time, a physical distance from the substrate associated processes. Erect unilaminate colonies referable to this type offer the least resistence to the outflow of filtered water and are hydrodynamically efficient in eliminating filtered water (MCKINNEY, 1986); this possibly gives them a certain advantage in the competition for food.

Tuft-like species, furthermore, as strictly branched tree forms, are able through shading to alter the bottom conditions adjacent to their area of attachment, contributing to the modification of the microclimatic conditions at the level of substrate and to community maturation. Species belonging to this zoarial type, especially arborescent buguloideans, are common in environments quite different such as the deep-sea soft bottoms of New Zealand recently studied by GORDON (1987), where they can adhere to substrate particles with their rootlets.

Creeping colonies were always present throug time, in small but constant quantities. They are quick invaders of primary space at the beginning and colonize secondary surfaces as epibionts.

CONCLUSIONS

In conclusion we wish to underline some points of general interest.

— During the establishment of the community, morphological changes start when the primary surface becomes limited. Modifications consist of replacements or, more often, variations in relative abundance of zoarial forms and correspond to modifications of the substrate, both in availability of primary space for settlement and in new conditions close to the substrate surface. Morphological groups react in a well defined way to the temporal environmental variations.

— The zoarial type resulted a more useful describer of community development processes than single species. In fact, pioneer species were not clearly recognized from our many year experience on colonization in the same environment (RELINI *et al.*, 1983; PISANO & BALDUZZI, 1985; PISANO & BOYER, 1985); whereas one of the zoarial types (the thin membraniporiform), showing a tendency to be replaced, plays a pioneer role.

Furthermore an ecological classification based on growth forms in modular organisms as bryozoans can add information to more conventional ecological classifications, based on r-selected and K-selected features, as stressed by JACKSON & COATES (1986), HUGHES (1987), SACKVILLE HAMILTON *et al.* (1987).

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