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STRUCTURE OF CNIDARIAN POPULATIONS IN MEDITERRANEAN SUBLITTORAL BENTHIC COMMUNITIES AS A RESULT OF ADAPTATION TO DIFFERENT ENVIRONMENTAL CONDITIONS

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SUMMARY

The presence and abundance of Cnidarians, extremely common in Mediterranean sublittoral benthic communities, exerts a profound effect on the entire structure of such communities, although the roles of Anthozoans and Hydrozoans differ in accordance with their different biological characteristics. Structural differences in benthic cnidarian populations were observed in three sublittoral communities located within 100 m of each other yet differing considerably in light intensity and water movement. Species-area and Shannon's diversity-area curves were computed for each community from reticulate samples constituted by 18 subsamples of 289 cm^2. Species-area curves were fitted to semilogarithmic functions, while diversity-area curves were fitted to Michaelis-Menten functions by the method of least squares. Species richness, species distribution, alpha-diversity, and pattern diversity were estimated from the fitted curves. Patch size for Anthozoans was smaller than that for Hydrozoans in all three communities. Diversity was greatest in the communities with the lowest and with the highest light intensity and water flow levels, but species richness was highest in the intermediate community. The most structured community (with the most heterogeneous species distribution pattern) had the largest organisms with the longest life spans. It is suggested that the difference of water flow conditions in these three communities leads to the development of different spatial patterns of individuals and colonies. The size, shape and small-scale distribution of these organisms are probably correlated to their ability of enhancing prey capture under different water flow conditions.

KEY WORDS: Cnidarians, benthos, population structure, diversity-area curves, Western Mediterranean.

INTRODUCTION

Cnidarians are extremely abundant in nearly all Mediterranean marine benthic communities. However, the highest number of species is found on rocky sublittoral bottoms, where cnidarians make up a substantial proportion of the biomass of such communities (TRUE, 1970; GILI & ROS, 1985a). Cnidarians constitute one of the dominant group of benthic organisms in sciaphilic communities where algal growth is limited by low light irradiance. In such places, different communities develop in relation to light intensity. Strong changes in irradiance can occur in short spaces where holes and caves open on rocky walls. Light attenuation from outside to inside the caves involves a gradient in species composition along an horizontal axis, a gradient which is enhanced by the decrease in water hydrodynamism along the same axis

(RIEDL, 1966). This gradual change in species composition has led Mediterranean benthic biologists to define three different communities (PÉRÈS & PICARD, 1964; ROS *et al*., 1985; GILI & ROS, 1985b) named (from outside to inside) coralligenous community, semidark cave community and dark cave community.

According to previous observations made in sublittoral communities (RIEDL, 1966; GILI *et al*., 1986; ZABALA *et al*., 1989), the water flow is intense and bidirectional in the coralligenous, moderate and unidirectional at the entrance of the caves and reduced even though constant inside the cave. This decrease in water flow intensity involves a parallel zooplankton depletion (RIEDL, 1966; M. Zabala, personal communication).

Passive organisms, such as hydroids and anthozoans, are particularly dependent on adequate degrees of water movement (RIEDL, 1971). Many benthic cnidarians are passive suspension feeders and depend upon water current to carry suspended food across their food-capturing surfaces. The ability and distribution of benthic cnidarians is enhanced to maximize the volume of food-laden water they encounter per unit time (WAINWRIGHT & KOEHL, 1976).

The shape, size and spatial distribution of benthic cnidarians affects the water flow around them. Individuals or colonies can survive in rapid or moderate flow if they are small, aggregate or if they adjust their body shape and size to surrounding objects or organisms, (KOEHL, 1984). These organisms, whose structures affect the water flow, operate like obstacles that decrease fluid velocity and increase the turbulence in their surface layer (VÖGEL, 1981; LaBARBERA, 1984) and, therefore, enhance the possibilities of prey retention and catch. Under fast flow conditions, feeding ability could be enhanced by the presence of neighbours with high body size (SEBENS, 1984). However, under moderate flow velocities, populations of small colonies or less aggregated individuals alter the flow over the substratum, turbulence and pattern of particle transport (ECKMAN, 1983; OKAMURA, 1984). Our hypothesis is that the different hydrodinamical regimes in these three benthic communities, partly because of resulting differences in food supply, do condition the spatial distribution of the species, and therefore the population structure and patch size.

The structure of a community is determined by the spatial distribution of the species within it. Studies designed to find a representative sampling area, based on species-area curves, diversity-area curves, and spatial variations in biomass, provide a considerable amount of information on community structure for calculating patch size. Thus, structure and minimal area are closely related and, even though minimal sampling area may vary according to the criteria applied by different researchers (e.g., BOUDOURESQUE & BELSHER, 1979; HAWKINS & HARTNOLL, 1980; BALLESTEROS, 1986), a series of numerical parameters can be obtained for comparing the structural complexity of communities. The interest in obtaining such parameters is obvious since topics such as patch-size can be quantified and different communities can easily be compared (BALLESTEROS, 1986).

The object of the present study is to examine differences in the structure of three benthic cnidarian populations occupying a short but sharp light-intensity and water-flow gradient. The consequence of such environmental gradients would be that colonies and individuals would have a different spatial pattern in each community which lead to different patch-sizes. Cnidarians make up a taxocoenosis that can be quite representative of the community as a whole (WEINBERG, 1978; GILI *et al*., 1989a) and for this reason they may be a good indicator of the structural pattern within each benthic community.

MATERIALS AND METHODS

Samples were collected off the northeastern coast of the Medes Islands (Costa Brava, Northwestern Mediterranean, UTM 31TEG15), where transition between the coralligenous community and the dark cave community occurs in a reduced space (Fig. 1).

Three samples were obtained by denudation (BOUDOURESQUE, 1971), scraping a surface consisting of 3 x 6 squares measuring 17 x 17 cm each. So, each sample consisted of 18 squares of 289 cm^2, making a total surface area of 5,202 cm^2 (Fig. 1). The squares (subsamples) were separated in the laboratory, and the hydrozoans and anthozoans were quantified in terms of:

- total biomass, measured as dry weight

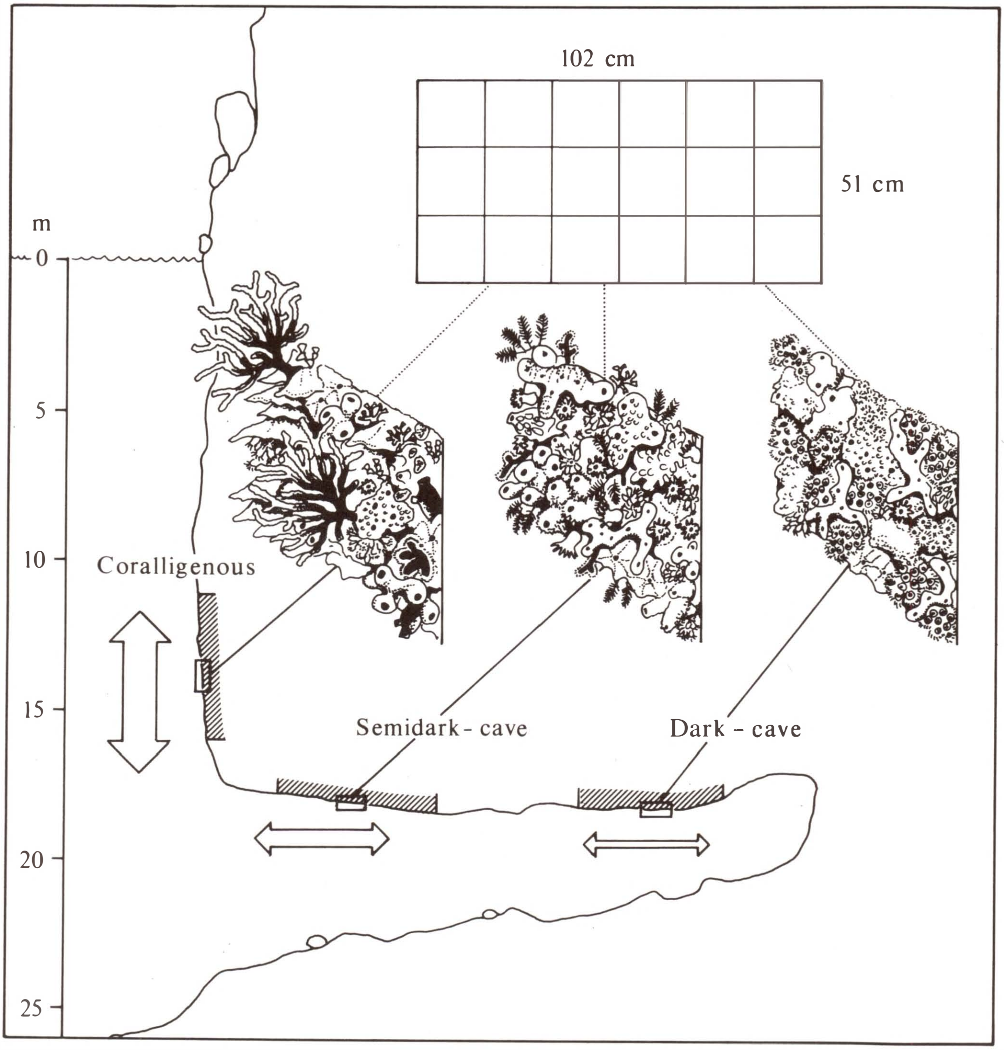


FIGURE 1. Diagrammatic localization and configuration of the three communities studied. The reticulate rectangle above the community diagrams shows the spatial distribution of samples in each community. The width and direction of arrows roughly indicates the intensity and direction of water movement in each community.

in grams, after drying each species at 110 °C for 24 h;

- organic matter, i.e., ash-free dry weight; ashes were prepared by burning samples for 6 h at 500 °C, in order to minimize the importance of accreted skeletons.

Two data matrices were thereby obtained for the samples, in each of which x_{ij} was the biomass (or organic matter) for species i in subsample j. Species-area and diversity-area curves were derived from these data matrices for total cnidarians, anthozoans, and hydrozoans. The species-area curves were fitted to a semilogarithmic function of the form

$$y = a \ln x + b,$$

where **y** was the number of species and **x** was the surface area in cm^2. The diversity-area curves were fitted to a Michaelis-Menten function:

$$y = Ax / (B + x)$$

were **y** was the diversity in bits and **x** the surface area in cm^2.

The following structural parameters (BALLESTEROS, 1986) were then calculated:

1) Number of species per sample.

2) Species distribution (**k**): the value of **k** in the fitted species-area curve; the semilogarithmic equation thus obtained can be expressed as a power equation:

$$x = k.e^{\lambda y}$$

The parameter **k** is a good index for defining the shape of the curve, indicating changes in slope for different patch sizes. The higher the value of **k**, the larger the surface area required to obtain a representative number of species for the community.

3) The parameter **a**, related to species richness, equal to the slope of the line fitting the species-area curve on the semilogarithmic coordinates.

4) The Molinier 20/5 point (NÉDÉLEC, 1979), corresponding to the point on the species-area curve at which a 20 % increase in surface area yields a 5 % increase in the number of species; this point can be regarded as the minimum species patch size value (BALLESTEROS, 1986).

5) Species diversity (**A**), the asymptotic value of diversity when the diversity-area curve is fitted to a Michaelis-Menten function.

6) Pattern diversity (**S**), the value of surface area corresponding to the Calleja $1 \cdot 10^{-3}$ point on the diversity-area curve when fitted to a Michaelis-Menten function; this parameter also furnishes the area at which diversity practically stabilizes (minimal structural area; NIELL, 1974).

All these parameters were used as indicators in evaluating the structure of the benthic cnidarian populations found.

RESULTS

A total of 39 cnidarian species were recorded in the three communities (Table I). *Paramuricea clavata* was the dominant species in the coralligenous community, although other species of solitary madreporarians, zoantharians, and alcyonarians formed small but dense colonies that contributed a substantial portion to the total biomass of the community. Unlike the other communities, some species of hydrozoans were present, forming dense colonies that made up a significant share of the total biomass. The semidark-cave community presented the largest number of species. Small colonies of *Hoplangia durotrix* predominated in this community, although other solitary madreporarians also had high biomass values. An important number of species shared in the hydrozoan biomass, and colonies were not large. In the dark-cave community four madreporarian species account for a great part of the total

TABLE I. Biomass (n) in grams (dry weight) per m^2, and frequency (f) in 18 samples for all species in the three (coralligenous, semidark-cave, and dark-cave) communities considered.

Species	Community					
	Coralligenous		Semi-dark cave		Dark-cave	
	n	f	n	f	n	f
HYDROZOA						
Bougainvillia ramosa	0.0124	1	0.9838	5	-	-
Perigonymus repens	0.0986	1	-	-	-	-
Clava multicornis	0.0880	1	-	-	-	-
Eudendrium motzkossowskae	0.0098	1	0.4912	4	-	-
Eudendrium capillare	0.1406	2	0.4402	3	-	-
Halecium tenellum	3.5226	5	0.0408	1	-	-
Halecium labrosum	1.3380	4	0.8912	5	-	-
Clytia haemisphaerica	0.8790	4	0.4246	10	0.0064	1
Obelia dichotoma	1.3814	8	0.3316	12	-	-
Hebella scandens	0.0078	1	0.0394	5	-	-
Sertularella gaudichaudi	16.7862	4	0.1028	1	-	-
Antennella secundaria	0.1624	2	-	-	0.0846	1
Aglaophenia octodonta	0.0158	1	-	-	-	-
Coryne pusilla	-	-	0.0060	1	-	-
Eudendrium racemosum	-	-	2.3782	11	1.1588	2
Halecium mediterraneum	-	-	0.0100	1	-	-
Phialella quadrata	-	-	0.0676	2	-	-
Laomedea pelagica	-	-	0.0368	2	-	-
Synthecium evansi	-	-	0.2806	3	-	-
Plumularia setacea	-	-	0.0400	2	-	-
Nemertesia antennina	-	-	0.0582	4	0.0080	1
Aglaophenia pluma	-	-	0.0002	1	0.0040	1
Eudendrium rameum	-	-	-	-	1.7194	3
Laomedea angulata	-	-	-	-	0.0032	1
SCYPHOZOA						
Stephanoscyphus eumedusoides	-	-	-	-	0.0580	6
ANTHOZOA						
Alcyonium acaule	8.6820	5	-	-	-	-
Parerythropodium coralloides	8.1902	12	0.1192	3	0.0098	1
Paramuricea clavata	266.9146	9	-	-	-	-
Epizoanthus arenaceus	0.1934	1	-	-	-	-
Parazoanthus axinellae	14.8068	8	-	-	-	-
Hoplangia durotrix	1.3972	1	162.5834	13	183.7603	17
Caryophyllia smithi	11.4878	9	6.0980	5	1.9984	4
Caryophyllia inornata	14.8224	6	41.9614	8	279.0548	7
Leptopsammia pruvoti	83.3340	12	33.9306	7	327.0448	17
Corallium rubrum	-	-	1.8490	1	58.5484	6
Cornularia cornucopiae	-	-	0.0354	3	-	-
Rolandia rosea	-	-	11.0832	13	0.7326	9
Corynactis viridis	-	-	6.0132	12	0.1672	4
Polycyathus muellerae	-	-	-	-	289.4380	3

biomass. Two of these species formed dense colonies, moderate (*H. durotrix*) or large (*P. muellerae*) in size. Unlike the other two communities, the solitary madreporarians formed facies, while just two species accounted for nearly the total hydrozoan biomass (Table I).

Figure 2 sets out in more general and summarized form the percentage of species in each of the three communities according to three categories, namely, average life span, biomass (dry weight), and polyp size (taken as mouth size). Each of these three categories has been divided into five subdivisions. In the coralligenous community the highest percentages corresponded to the lower and upper subdivisions in all three categories; in the

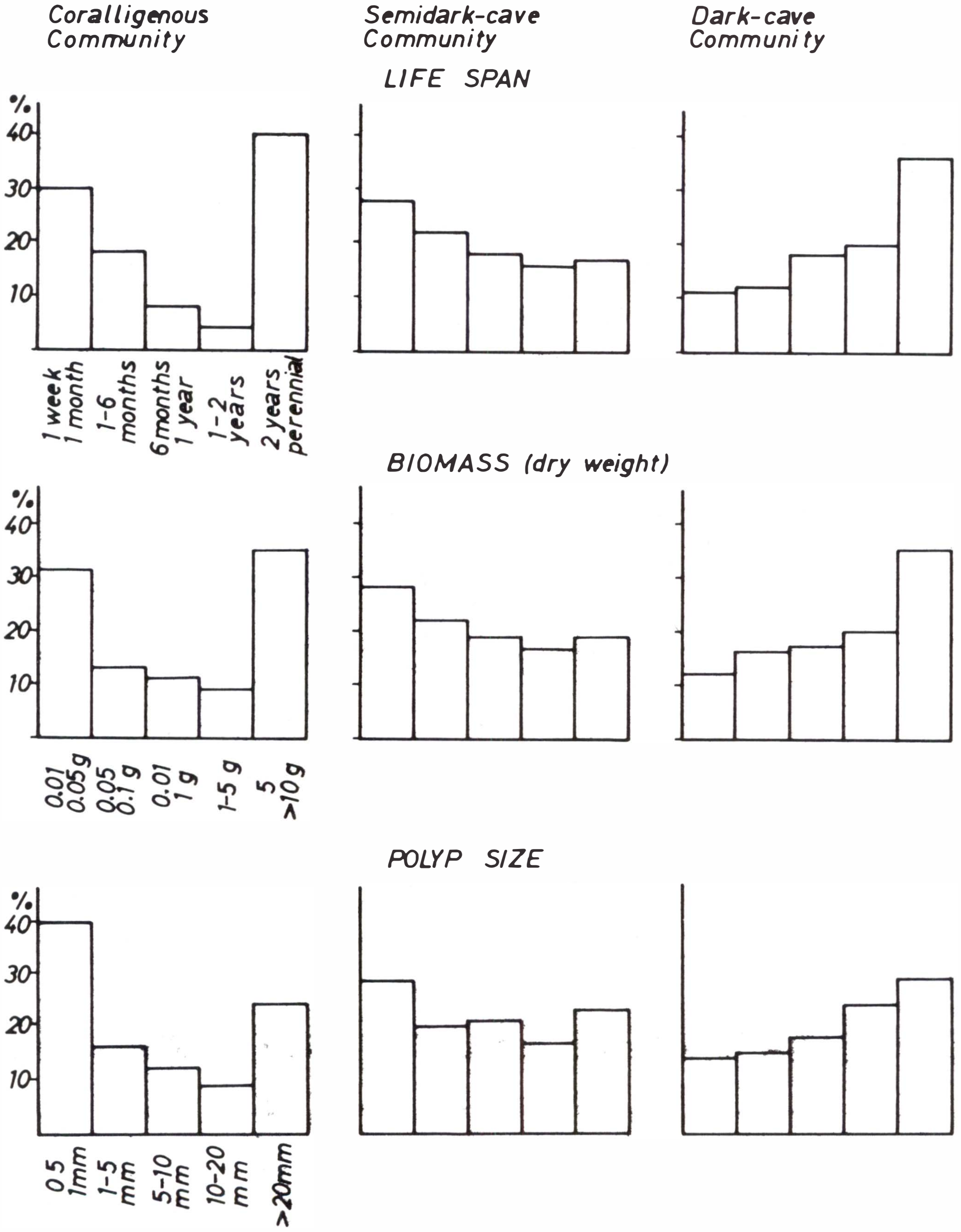


FIGURE 2. Percentage number of species in each of the three (coralligenous, semidark-cave, dark-cave) communities studied in terms of life-span, biomass (dry weight), and polyp size (based on mouth size). Each category has been divided into five subdivisions.

TABLE II. Parameters calculated from the species-area curves (the number of species, N, refers to the total number collected in each community; the Molinier 20/5 point is a measure of patch size in cm^2).

	k	a	r	N	$M_{20/5}$
TOTAL CNIDARIANS					
Coralligenous	129.9	6.245	0.999	23	4976
Semidark-cave	100.4	6.793	0.999	27	3846
Dark-cave	113.9	4.577	0.999	17	4636
ANTHOZOANS					
Coralligenous	38.4	1.857	0.993	9	1472
Semidark-cave	32.4	1.812	0.983	9	1240
Dark-cave	42.8	2.180	0.993	10	1640
HYDROZOANS					
Coralligenous	176.0	4.075	0.988	14	6742
Semidark-cave	150.9	4.980	0.995	18	5779
Dark-cave	275.7	2.398	0.985	7	10559

TABLE III. Parameters calculated from the diversity-area curves (S is a measure of patch size in cm^2). -, not significant data.

	A	S	r
TOTAL CNIDARIANS			
Coralligenous			
dry weight	2.08	508	0.997
ash-free dry weight	1.49	320	0.963
Semidark-cave			
dry weight	2.02	317	0.787
ash-free dry weight	3.05	575	0.997
Dark-cave			
dry weight	2.25	565	0.959
ash-free dry weight	2.47	617	0.971
ANTHOZOANS			
Coralligenous			
dry weight	1.77	441	0.999
ash-free dry weight	1.10	228	0.911
Semidark-cave			
dry weight	1.89	424	0.936
ash-free dry weight	2.49	565	0.997
Dark-cave			
dry weight	2.24	559	0.961
ash-free dry weight	2.28	571	0.969
HYDROZOANS			
Coralligenous			
dry weight	2.34	555	0.974
ash-free dry weight	2.46	585	0.977
Semidark-cave			
dry weight	3.26	790	0.998
ash-free dry weight	3.08	742	0.998
Dark-cave			
dry weight	-	-	-
ash-free dry weight	-	-	-

semidark-cave community the percentage of species in each subdivision within each category was approximately equal; and in the dark-cave community the percentage of species became progressively larger in the upper part of the range for each category.

The fits of the species-area curves presented higher values of **k**, associated with species distribution over surface area, in the coralligenous and dark-cave communities (Table II). On the other hand, the highest value of **a**, associated with species richness, was attained in the semidark-cave community. The trends for these two parameters were very similar for the anthozoans in the first two communities, whereas there were substantial differences for the hydrozoans: the value of **a** was highest in the semidark-cave community, while the dark-cave community yielded the highest value of **k** (Table II).

The fits of the diversity-area curves gave similar values for species diversity in all three communities. However, there were appreciable differences between the value of **A** for biomass as dry weight and for biomass as ash-free dry weight, particularly in the semidark cave community. The value of **A** for anthozoans followed the same trend as for the total cnidarians, whereas for hydrozoans the highest value was for the semidark-cave community. The low biomass of hydrozoans in the dark-cave community gave rise to non-significant fits of the diversity-area curves to the Michaelis-Menten function for this community. For biomass including ashes, the pattern-diversity (**S**) value for total cnidarians was highest for the dark-cave community and lowest for the semidark-cave community. In contrast, for ash-free biomass, the value of **S** increased from the coralligenous community to the dark-cave community (Table III). The values of **S** for anthozoans alone followed a similar trend to those for total cnidarians, but for the hydrozoans the value was lower in the coralligenous community both for ash-free biomass and biomass including ashes.

The behaviour of the two types of curve considered (see the shapes of the curves in figure 3) suggests that the values of **k** and **S** furnish very similar indications of patch size in the three communities. In any case, patch size for total cnidarians was slightly higher qualitatively in the coralligenous community and slightly higher quantitatively in the dark-cave community. Patch size was smallest for the semidark-cave community. For anthozoans patch size was highest in the dark-cave community, lowest in the semidark-cave community. In contrast, for hydrozoans patch size was qualitatively highest in the dark-cave and coralligenous communities but quantitatively highest in the semidark-cave community. For ash-free biomass, however, patch size was smallest in the coralligenous community for both anthozoans and total cnidarians.

DISCUSSION

Patch size for total cnidarians based on the species-area curves was somewhat larger in the coralligenous community than in the cave communities because of the distribution of the dominant species (*P. clavata*), in the former community, whose larger and long lived colonies affect the settlement and development of the other species, which grew scattered in the basal stratum. On the other hand, the lower level of spatial competition in the cave communities probably enables certain madreporarians to form large colonies by budding as well as dense aggregations of small colonies or individuals through larval recruitment, resulting in a smaller

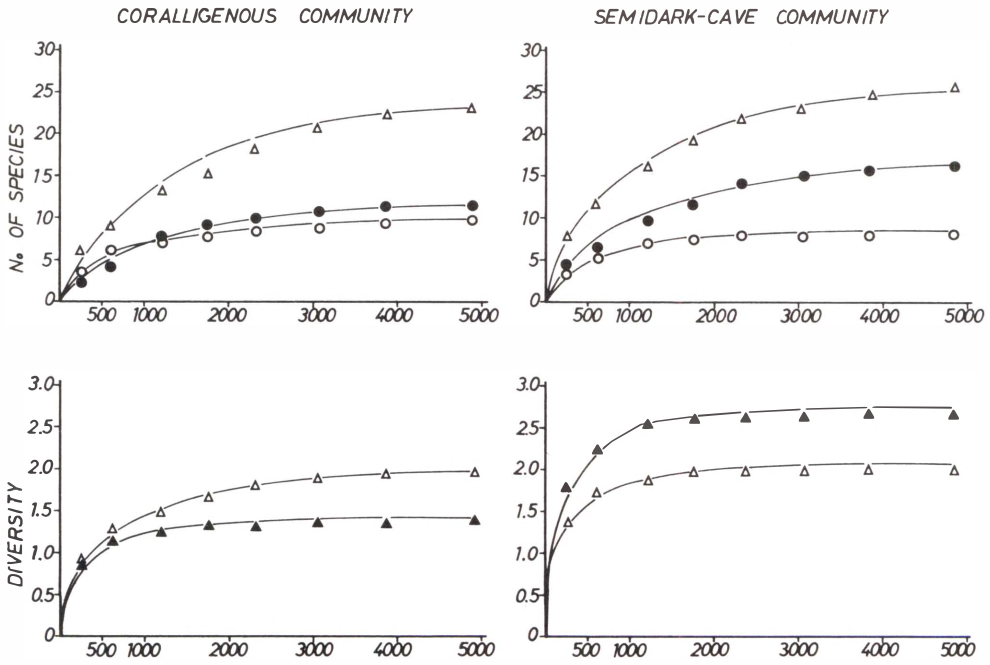
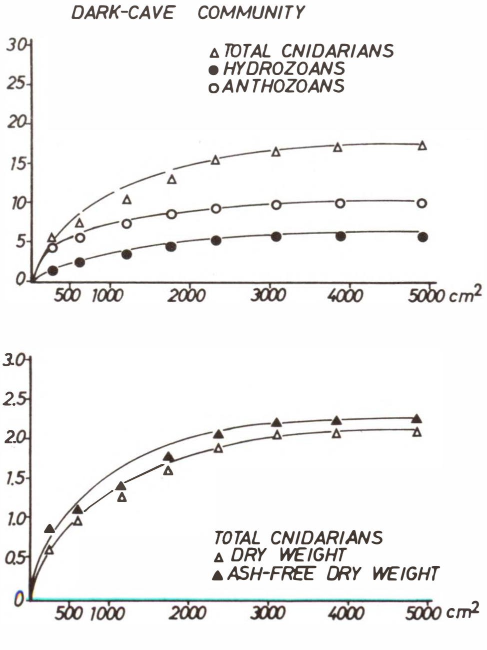


FIGURE 3. Species-area and diversity-area curves for the three (coralligenous, semidark-cave, and dark-cave) communities for each of the three groups (total cnidarians, hydrozoans, and anthozoans) considered, with

patch-size.

From a quantitative point of view, the larger patch size for cnidarians in the dark-cave and coralligenous communities, compared with that in the semidark-cave community, is caused by the presence of larger species, which attain high biomass levels, in the first two. These species left little room for other species, which were therefore confined to smaller patches. As a consequence, in the coralligenous community a high percentage of larger species with high biomasses coexisted with many other much smaller species (Fig. 3). This was still more evident in the dark-cave community, in which patch size was largest thanks to the patchy distribution of madreporarian colonies.

The lowest patch size occurred in the semidark-cave community, reflecting the occupation of the available space by smaller species. Individuals or colonies of these, in turn, occupied smaller areas, thereby allowing a larger number of species to coexist. Both solitary anthozoan species and small colonies of anthozoans and hydrozoans contributed to this. Unlike the hydrozoans in the other two communities, the hydrozoans in the semidark-cave community enjoyed a greater number of potential sites to colonize among the anthozoan individuals and colonies.



quantitative curves for both biomass measures (dry weight and ash-free dry weight) used.

Quantitatively, the difference in patch size as measured in terms of total dry weight and ash-free dry weight is indicative of the importance of the skeletal carbonates of certain anthozoans in determining the structural patterns in the communities. This was quite clear in the case of the coralligenous community, in which the difference between *P. clavata* and all the other species increased, and, as a result, patch size and diversity decreased, when the skeletal weight contribution was disregarded. In contrast, in the semidark-cave community the converse held true, while in the dark-cave community there was hardly any change. Due to the predominance of madreporarians in these last two communities, which, compared to gorgonians have high organic matter contents despite their calcium skeletons (GILI & ROS, 1985b), differences between species biomass measured as dry weight and as ash-free dry weight were minimal in the dark-cave community and decreased (i.e., diversity increased) in the semidark-cave community. Dominance of a community by a single species, termed a facies, also exerts an important effect on patch size (ROS *et al.*, 1985). This was true in the case of *P. clavata* in the coralligenous community and, in part, of *P. muellerae* in the dark-cave community. Such dominance caused total cnidarian biomass to be higher in these two communities (GILI & ROS, 1985b). In contrast, in a study of similar communities off Marseilles by TRUE (1970), the highest biomass was recorded for a semidark-cave community, occupied by a facies of *Corallium rubrum*; for this reason, patch size was quite similar to that in a coralligenous community, also occupied by a facies of *P. clavata.*

Benthic cnidarians are suspension feeders and as such are dependent upon the external availability of food transported by the water flow. In the context of a flow gradient like that existing in the three communities studied, it would seem reasonable to expect potential food sources to be most abundant in the coralligenous community and least abundant in the dark-cave community. Greater food availability and greater colonizing ability would be associated with a larger number of species and, therefore, with a larger patch-size (WRIGHT, 1983; KEOUGH, 1984). However, the community situated in between the two extremes had the smallest patch size and the highest number of species. The largest patch size found in the coralligenous community is consistent with the observations by WRIGHT (1983) and would be caused by the large area covered by *P. clavata*, which has a colonial habit well adapted to capturing prey in high water flows (LEVERSEE, 1976), and a certain gregarious nature that apparently facilitates the capture of prey in certain anthozoan species (McFADDEN, 1986).

Sessile cnidarians found in slowly-moving water, in the dark-cave community, tend to have morphological and physiological adaptations which compensate for the lack of external transport (WAINWRIGHT & KOEHL, 1976), among them: tolerance of low oxygen levels; feeding on motile prey in lower concentrations; aperiodical appearance of potential prey. At the same time, scleractinians in dark-caves may have a lower energy demand than other benthic cnidarians in temperate waters (SEBENS, 1987). In the less accessible parts of caves the amount of water movement is not adequate to cover the demands for the development of dense populations like those found in the entrance of the cave or in the coralligenous community (RIEDL, 1971). The minimum range of water movement allows the zooplankton and oxygen concentrations near the organisms to fall and, thus, become intolerable to most sessile cnidarians, like hydroids or some octocorals, with high food requirements. In the coralligenous community again, under conditions of high water movement, the zooplankton availability increases and allows the development of a diversified population of benthic cnidarians; large colonies (gorgonians) close to others of moderate (e.g. alcyonarians) or small size (e.g. hydroids). However, the lower availability of food in the dark-cave community would act, probably, to reduce competition so that the species were able to grow and occupy a large space (SEBENS, 1982).

The moderate water movement in semidark-cave community enables the establishment of an intermediate spatial distribution pattern as a consequence of the development of colonies or individuals of moderate and small size. Under these moderate flow conditions, feeding ability could be enhanced by the presence of neighbours, or by forming aggregations of small and clonal colonies (ECKMAN, 1983; McFADDEN, 1986).

In consequence, as shown in figure 2, the coralligenous and dark-cave communities contained higher percentages of longer-lived species that capture larger prey items than did the semidark-cave community. In this type of species, which have adopted more of a K strategy (*sensu* MacARTHUR & WILSON, 1967; see GILI & ROS, 1985a), the level of competition with other species similar in habits and biology is higher (CONNELL, 1975), which tends to favour coexistence by more dissimilar species, like the r-strategists or opportunistic ones (CONNELL & SLATYER, 1977; GILI & ROS, 1985a), which are smaller, shorter-lived, and more specialized in the capture of smaller prey. In the semidark-cave community the lower, yet nonetheless sufficient, level of food availability enabled colonies and individuals to develop but not to attain large sizes. This, in turn, enabled a larger number of species to coexist, but the patch-size would decrease because of the lack of compartmentation caused by spatial-structuring species such as *P. clavata* in the coralligenous community and the total quantitative dominance of *Hoplangia durotrix*. The qualitative dominance by hydroids and by a few octocorals in the semidark-cave community is indicative of the ecotone character of this community, dominated as it is by r-strategists.

The seasonality observed in the major part of the Mediterranean hydroids (e.g. BOERO & FRESI, 1986; LLOBET *et al.*, 1991) could change the spatial pattern observed in communities such as semidark-caves, where these organisms play an important structural role. But their great capacity for continuous growth and recruitment enhance their presence and similar distribution in this community (GILI *et al.*, 1989b).

In conclusion, in communities in which the growth of certain biomass-storing, structure-creating species is enhanced, there is a tendency towards the contagious distribution of individuals of a single species, resulting in larger patch-sizes. This occurs in a situation of large food availability as is the case in the coralligenous community with *P. clavata* or in highly food-limited environments such as in the dark-cave communities, where species with low food requirements can survive. Nevertheless, if there are few biomass-storers, or if there are none, specially adapted to a given environment, species richness could be increased by the appearance of opportunistic forms (e.g. hydroids) due to lower competitive levels. Also, patch-size decreases because of the lack of a rigid structural pattern and low spatial heterogeneity.

Spatial arrangements of particular populations can probably be correlated with the ways in which certain colonies and individuals modify water currents (e.g., HISCOCK, 1983) and affect the flow forces and feeding currents. This suggestion reveals the importance of size, shape and patch distribution of these animals to their ability to utilize moving water, catch suspension preys and successfully colonize sublittoral benthic communities.

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