

Structure of a deep-water community of *Halimeda tuna* (*Chlorophyceae, Caulerpales*) from the North-Western Mediterranean

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Abstract

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A deep-water community dominated by *Halimeda tuna* and *Mesophyllum lichenoides* is described from the rocky bottoms of the North-Western Mediterranean. Other sciophilic algae such as *Udotea petiolata*, some *Peyssonnelia* species and *Lithophyllum expansum* are also abundant. Algal biomass ranges between 1200 and 2100 g dw m⁻² while percentage coverage ranges from 180 to 400 %. The variations observed in algal coverage adequately describe the seasonal pattern of the community, which is characterized by a high development of erect algae in summer months and a low development in winter. The species richness, as well as both species and pattern diversity reach a maximum in summer. Summer's maximum irradiances and the low irradiances received between november and february seem to account for the seasonal pattern described above. Community structure and environmental factors affecting the deep-water *Halimeda* populations from the North-Western Mediterranean are compared with those found in other deep-water seaweed communities from the Mediterranean and other seas. Finally, the phytosociological affinities between these *Halimeda* populations and the deep-water Mediterranean associations previously described is assessed.

Keywords: Marine phylobenthos, structure, deep-water, *Halimeda*, Mediterranean.

Resumen

BALLESTEROS, E. (1991). Estructura de una comunidad de *Halimeda tuna* (*Chlorophyceae, Caulerpales*) en aguas profundas del Mediterráneo noroccidental. Collect. Bot. (Barcelona) 20: 5-21.

Se describe una comunidad dominada por *Halimeda tuna* y *Mesophyllum lichenoides* en los fondos rocosos profundos del Mediterráneo Noroccidental. Dichas especies coexisten con *Udotea petiolata*, diversas especies de *Peyssonnelia* y *Lithophyllum expansum*, como especies más aparentes. La biomasa algal oscila entre 1200 y 2100 g ps m⁻² mientras que el porcentaje de recubrimiento varía entre el 180 y el 400 %. Las variaciones encontradas en el recubrimiento algal describen adecuadamente el comportamiento estacional de la comunidad, el cual se caracteriza por un elevado desarrollo del estrato erecto durante el

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verano. La riqueza específica y la diversidad son también elevadas en verano. La mayor disponibilidad de luz veraniega parece explicar este comportamiento. La estructura de la comunidad y los factores ambientales a los que está sometida se comparan con los descritos en otras comunidades profundas del Mediterráneo y otros mares. Finalmente, se discute la afinidad de estas poblaciones de *Halimeda* con las distintas asociaciones descritas en la zona circalitoral del Mediterráneo Occidental.

Palabras clave: Fitobentos marino, estructura, aguas profundas, *Halimeda*, Mediterráneo.

Introduction

Mediterranean deep-water phytobenthic communities have been scarcely studied in comparison with photophilic and sciaphilic communities from the infralittoral zone. The main reason to explain it is the difficulty to sample with autonomous diving equipment at depths where circalittoral communities are usually found (BALLESTEROS, 1990a). Nevertheless, these communities are very interesting because of their particular floristic composition, rich in Mediterranean endemisms (BOUDOURESQUE, 1973). Also they are a paradigmatic example of oligotrophic environments with so low irradiances that light usually is the environmental factor that limits seaweed growth.

Our goal is to characterize by means of quantified species lists and some structural parameters the average composition and seasonal changes of a deep-water community widespread in the North-Western Mediterranean, dominated by the erect and articulated chlorophyte *Halimeda tuna* and the encrusting coralline *Mesophyllum lichenoides*. Environmental factors have been also monitored along the year 1983 to account for monthly and yearly values of irradiance, nutrient concentration and temperature.

Materials and methods

The study area is located in a little island off Tossa de Mar (NW Mediterranean, 41° 48'N 2° 26'E). Biological and environmental characteristics are extensively described in BALLESTEROS (1984). The community of *Halimeda tuna* appears from 12-15 meters to 30-35 meters depth. The community is restricted to very inclined walls, where it occurs sometimes overhanging, and oriented towards north, in shallow waters. It does not appear in subhorizontal rocky bottoms until a depth of 20-22 meters, where it becomes the dominant community (BALLESTEROS, 1984). It is limited upwards by the *Codium vermilara* community (BALLESTEROS, 1989a) and, occasionally, by the community of *Cystoseira costeroides* (BALLESTEROS, 1990a). Downwards its limit is usually determined either by the biocoenosis of coarse sands and fine gravels under bottom currents (SGFC) (PERES, 1967), either by rocky bottoms with a community dominated by encrusting calcareous algae and soft species of *Peyssonnelia* (BALLESTEROS, 1984).

The community structure has been established from samples taken seasonally (january, april, june, september) by scraping off all organisms (BOUDOURESQUE, 1971). Although the community is optimally developed between 22 and 32 meters, samples were collected in an almost vertical wall at 18 meters depth. Because of the time necessary to collect each sample was approximately 90 minutes, a relatively shallow area was selected to dive safely. Samples were composed of 16 subsamples of 7×7 or 8×8 cm² arranged in a reticulate manner (BALLESTEROS, 1986). Each subsample was carefully sorted in the laboratory. Abundance was quantified as coverage in cm² and biomass (g dw), using procedures described in BALLESTEROS (1986). Species/abundance matrices were obtained for each sample, with each x_{ij} representing the biomass (or coverage) of the species i in the subsample j . Species/area curves, diversity (Shannon)/area curves, homogeneity (Kulczinsky)/area curves and the variation of

the variance: mean ratio for the biomass distribution in function to sampling area were computed from those matrices. Afterwards, the following structural parameters, extensively described in BALLESTEROS (1986), were estimated:

- Biomass
- Coverage
- Species richness (R): the number of species corresponding to the Calleja point $5 \cdot 10^{-2}$ in the species/area curve.
- Specific distribution (k): value of k defined as

$$k = e^{-b/a}$$

where a and b correspond to the slope and the ordinate axis intersection in the species/area curve fitted to a semilogarithmic function

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

where y is the number of species and x the sampled area in cm^2 .

- Molinier 20/5 point (NEDELEC, 1979): the sampling area at which a 20 % increment in sampling area resulted in a 5 % increment in species number. It can be considered as a qualitative minimal area.
- Species diversity (A): asymptotic value of diversity when the diversity/area curve is fitted to a Michaelis-Menten function.
- Pattern-diversity (S): surface corresponding to the Calleja point $1 \cdot 10^{-3}$ in the diversity/area curve fitted to a Michaelis-Menten function. This surface obviously corresponds to the area at which diversity is practically stabilized, so it is related to the structural minimal area.

Species were also qualified attending to their ecological preferences and the relative abundances of the main ecological supergroups (BOUDOURESQUE, 1985) were considered to typify the community.

Species terminology follows criteria established by BALLESTEROS (1990b).

Irradiance at 23 meters depth was computed from weekly Secchi disk measurements according to the method proposed by WEINBERG & CORTEL-BREEMAN (1978). Temperature was monitored weekly and water samples for determination of dissolved nutrients (nitrates, nitrites, phosphates) were collected monthly. The methodology followed in dissolved nutrient analysis was the one recommended in GRASSHOFF *et al.* (1983).

Results

Relevés are presented in table 1. The erect stratum is totally dominated by *Halimeda tuna* and the encrusting layer is mainly constituted by *Mesophyllum lichenoides*. An unidentified Melobesiae, *Lithophyllum expansum* and *Peyssonnelia rosa-marina f. saxicola* are also abundant in the basal layer. An intermediate stratum made by scattered thalli of *Udotea petiolata* and *Peyssonnelia* species (mainly *P. squamaria* and *P. harveyana*) is scarcely developed. Small Florideae such as *Plocamium cartilagineum*, *Gloiocladia furcata*, *Polysiphonia banyulensis*, *Rodriguezella pinnata*, *Dasyopsis plana*, *Contarinia peyssonneliaeformis*, *Myriogramme carnea* and *Erythroglossum sandrianum* grow between the margins of the encrusting algae and the *Halimeda* bases. Thalli of *Halimeda* are covered by numerous epiphytes e. g. minute Melobesiae, *Falkenbergia rufolanosa*, *Callithamnion decompositum*, *Hypoglossum hypoglossoides*, *Callithamnion byssoides*, *Apoglossum ruscifolium*) which are commonest in spring and summer. Also, different species of Mesogloiacae start to develop in spring and cover a great part of the *Halimeda* segments during summer.

Variations in the biomass of the different samples is mainly caused by the amount of encrusting algae, so coverage better represents the annual cycle of species abundance in the community. Maximum coverage is attained at early summer, reaching nearly 400 %. Minimum coverage only attains 180 % (table 2).

The species/area curves are represented in figure 1. Species richness is minimal at early spring, increases quickly in summer and declines in autumn and winter. Values of specific distribution are very high and reach a maximum in autumn while the rest of the year the values are medium and quite similar (table 2). The sampling area needed to obtain a good representation of the species composition has been estimated to range from 600 to 1000 cm².

Species diversity is not very high because of the dominance of two to three species in the community. Species diversity ranges from 0.8 to 2.9 bits (based on biomass values) or 2.2 to 2.7 bits (based on coverage values) (table 3). Species diversity is highest at early summer, in coincidence with a high number of species in the community. Pattern-diversity is very low in autumn; the bad adjustement of the experimental curve to a Michaelis-Menten function (table 3, figs. 2, 3) is caused by the asymptotization of the curve at sampling areas equal or perhaps lower than a subsample size. Diversity stabilization always occurs at sampling areas below 300 cm² (table 3; figs. 2, 3). Kulczinsky's similarity index stabilizes at different sampling areas depending on the season. A similarity index of, at least, 0.7, is always attained at areas of 400 cm² (figs. 4, 5). The homogenous biomass distribution inside the community is detected in the low values of the variance: mean ratio (fig. 6). Areas of 400 cm² always have a ratio lower than 1.

According to these results, areas of 400 cm² are large enough to quantitatively represent the community, but areas of 100 cm² should be preferred in order to obtain a good representation of the species composition.

Sciaphilic species largely dominate the community (table 4). The coralligenous concretion species group (CC) (BOUDOURESQUE, 1985) is represented by *Myriogramme carnea*, *Polysiphonia elongata*, *Spermothamnion johannis*, *Rodriguezella pinnata*, *Ceramium diaphanum* v. *lophophorum*, *Sphondylothamnium multifidum* f. *disticha* and *Didymosporangium repens*. As it usually occurs in coralligenous communities, where species belonging to other sciaphilic groups dominate, representatives of the CC group have a low coverage.

Annual irradiance reaching the community of *Halimeda tuna* situated at 23 meters depth amounts 1330 cal g cm⁻² y⁻¹ that corresponds to 1.77 W m⁻² or the 2.1 % of the surface irradiance (BALLESTEROS, 1989b). Yearly distribution of irradiance is represented in figure 7, and ranges from 0.34 cal g cm⁻² d⁻¹ (november) to 7.59 cal g cm⁻² d⁻¹ (august). Temperature ranges from 12.4 to 21.1 °C (fig. 7) and nitrate concentration in seawater is lower than 0.1 micromols l⁻¹ from late may to early october. Seawater is phosphate-depleted for most of the year, with the exception of the autumnal months (fig. 7).

Discussion

The genus *Halimeda* is widespread in tropical and subtropical areas (HILLIS, 1959) and there are a large number of species adapted to different environmental conditions (HILLIS-COLINVAUX, 1977). *Halimeda tuna* is the only species inhabiting the Mediterranean basin and its wide geographical distribution extends to the Atlantic, Pacific and Indian Oceans. The abundance of *Halimeda tuna* in Mediterranean deep-waters has previously been reported by other authors (FELDMANN, 1937; MEINESZ, 1980), and it has been found growing to 75 meters in Maltese waters (DREW, 1969). Some species of *Halimeda* grow to a depth of 140 meters in clear tropical waters (LITTLER *et al.*, 1985; HILLIS-COLINVAUX, 1986a), where irradiances as low as 0.05 % of surface irradiance have been estimated (HILLIS-COLINVAUX, 1986b, LITTLER *et al.*, 1986). In our case, the annual irradiance average is about 2.1 % of the surface irradiance,

with seasonal variations ranging from 0.4 % (november) to 9.2 % (august). The lower limit of stands of *Halimeda tuna* approximately occurs at 35 meters depth in Tossa de Mar, with a mean biomass of 13 g dw m⁻² and mean coverage of 4 % (BALLESTEROS, 1984). At these depths, yearly irradiance only amounts 0.4 % of surface irradiance (BALLESTEROS, 1989b), which is one order of magnitude higher than relative irradiances found at the lower limit of *Halimeda* in tropical waters. These differences may be partially attributed to the seasonal variations present in Mediterranean waters (ZABALA & BALLESTEROS, 1989). We suggest that the reduced irradiances from november to february –which only amount 0.15 % of surface irradiance at 35 meters depth– would account for the bathymetric displacement of *Halimeda* lower limit to shallower waters in the Mediterranean. Also, a greater environmental stability in tropical seas would allow a closer adaptation of *Halimeda* to dim light.

Nevertheless, growth of *Halimeda* at irradiances lower than 2-3 % of surface irradiance is noteworthy. In fact, water transmittance along the year mainly corresponds to that of oceanic water types II and III and to coastal water type 1 (BALLESTEROS, 1984) in the Jerlov's classification of optical water types (JERLOV, 1976). Thus, a great percentage of available light reaching deep-water rocky bottoms belong to the blue spectral band (table 5), which can be efficiently absorbed by chlorophylls (KIRK, 1983). Also, physiological research on *Halimeda* and other Caulerpales has demonstrated the existence of different mechanisms to improve *Halimeda* adaptation to dim light. Caulerpales have two accessory photosynthetic pigments, siphonein and siphonoxanthin (YOKOHAMA, 1981), specifically absorbing green light (YOKOHAMA, *et al.*, 1977). Siphonoxanthin + siphonein / chlorophyll a and chlorophyll b / chlorophyll a ratios increase with depth, which has been demonstrated to be favourable for growing in deep-waters (RAMUS *et al.*, 1976a; YOKOHAMA & MISONOU, 1980). *Halimeda tuna* increases its pigment concentration at low irradiances (SOLAZZI & TOLOMIO, 1976); this increase in chlorophyll may be enough to absorb all the available light (RAMUS *et al.*, 1976b). In addition, the morphology of *Halimeda* thalli maximizes the efficiency in light absorption, in the same way that does the morphology of *Codium* species (RAMUS, 1978). Finally, deep-water species of *Halimeda* utilize available light energy very efficiently (JENSEN *et al.*, 1985), thus suggesting that photosynthetic processes may be saturated at low irradiances.

Nutrient concentration detected in Mediterranean deep-waters are similar to that reported from tropical reefs (WOLANSKI *et al.*, 1988, *but the temperature is much lower* (HILLIS-COLINVAUX, 1986b). The influence of low temperature in the no occurrence of *Halimeda* in shallow waters from the Gulf of Lions has been already noted by other authors (COPPEJANS, 1977; MEINESZ, 1980) but any mechanism has been proposed to explain this fact. At this concern we point out that temperature influence on photosynthesis and respiration rates, as well as changes in spatial competence abilities, should be involved.

Halimeda biomass ranges from 136.9 to 472.8 g dw m⁻² (table 2), with a great seasonal variation. These values are higher to those usually reported from shallow water *Halimeda* populations in tropical reefs (2-10 g dw m⁻²) (BACH, 1979; HAY, 1981), but lower than those obtained by WOLANSKI *et al.* (1988) in deep-water *Halimeda* banks from the Great Barrier reef. *Halimeda* coverage is also higher to coverages reported from seaward reefs at Enewetak Atoll (50 %) (HILLIS-COLINVAUX, 1986b) and San Salvador Islands (8.6 %) (LITTLER *et al.*, 1986). Nevertheless, differences are not as great as they would seem, as measures made by these authors may be underestimated because of the methodology used to determinate coverage.

The spatial structure of *Halimeda tuna* community is quite different from other Mediterranean phytobenthic communities dominated by erect algae. Tusf algae and epiphytic algae are scarcerly developed. The overall biomass is similar to biomass values from lower infralitoral and circalittoral communities (table 6). The maintenance of high biomass values in deep-waters may be caused by a greater contribution of encrusting corallines to the overall biomass. Differences in coverage values are not significative because coverage is measured in

different ways according to each author. Average species diversity and pattern diversity are lower to values found in other sciophilic Mediterranean communities (table 6). The number of species is rather high (76 species per sample), though lower than species richness from shallower communities (table 6). The high species richness in summer may be attributed to high irradiances reaching the community, which allows the growth of some species. This feature also has been observed in deep-water algal communities from East Florida (HANISAK & BLAIR, 1988). The reduced diversity and species richness of the *Halimeda tuna* community may be related to stress caused by low irradiances, which prevents the development of photophilic species, and reduces heterogeneity because *Halimeda* has no spatial competitors at such dim light.

Attending to structural changes in the community, two stages can be discerned along an annual cycle: the stage of diversified community, with a reduced coverage of *Halimeda* and other soft algae, and the stage of developed community, characterized by a high coverage of *Halimeda* (BALLESTEROS, 1990c). The conversion of the diversified community stage to the developed community stage takes place through a production phase, when *Halimeda* growth is highest. A diversification phase can also be distinguished in late autumn, when a sudden fall in *Halimeda* production is detected (BALLESTEROS, in press). Nevertheless, although seasonality is far from negligible, it is not as obvious as seasonal changes usually found in shallow water communities, as predicted by BALLESTEROS (1990c).

Studies about rocky bottoms with sciophilic assemblages from the Western Mediterranean (AUGIER *et al.*, 1971; BOUDOURESQUE, 1973; CINELLI *et al.*, 1976; CINELLI *et al.*, 1979) always present a few *relevés* sometimes non quantified, and coming from geographically distant places. Under these premises, the application of multivariate analysis techniques (BOUDOURESQUE, 1973; CINELLI *et al.*, 1979) only segregates the main groups of similar *relevés*. The attribution of those groups to the sigmatist concept of plant association (BRAUN-BLANQUET, 1979) results very critique because of its heterogeneity. In the basis of a sigmatist analysis, two associations have been recognized in the circalittoral rocky bottoms of the North-Western Mediterranean: the *Cystoseiretum zosteroidis* (GIACCONE, 1973) and the *Rodriguezelletum strafforellii* (AUGIER & BOUDOURESQUE, 1974). These associations are related to those already described by FELDMANN (1937) from the Alberes Coast (association of *Cystoseira spinosa* and *Cystoseira zosteroides*, association of *Lithophyllum expansum* and *Spongites (?) hauckii*). The *Cystoseiretum zosteroidis* is characterized by some sciophilic and rheophilic species (GIACCONE, 1973) while the *Rodriguezelletum strafforellii* is characterized by some species belonging to the coralligenous concretions ecological group (BOUDOURESQUE, 1985). Some of the CC species occur in the community of *Halimeda tuna* from Tossa de Mar, so our community must be closely related to the *Rodriguezelletum strafforellii*.

The scarce validity of the concept of characteristic species in benthic bionomy has been already emphasized (BALLESTEROS & ROMERO, 1988). The author's opinion is that, at least, two different plant communities can be included into the *Rodriguezelletum strafforellii* in the North-Western Mediterranean. Both are characterized by a certain degree of presence of CC species but they are clearly differentiated by their species abundances and by their structure.

The community dominated by *Halimeda tuna* and *Mesophyllum lichenoides*, which has been exhaustively described in this study is largely extended in the Gulf of Lions and the Costa Brava (GILI & ROS, 1985). The same or a very similar community has been found in other places of the Spanish Mediterranean, in particular the Columbretes Islands, the seamount Placer de la Barra Alta, Eivissa Island and Cabrera Island (author's unpublished data). The bathymetric distribution of this community of *Halimeda tuna* and *Mesophyllum lichenoides* ranges from 12-15 meters to 30-35 meters in the Gulf of Lions, but it descends to 50 or more meters in the clear waters of insular territories. The community develops at irradiances ranging approximately from 2.3 to 0.3 W m⁻², which respectively corresponds to 3 and 0.4 % of the surface irradiance. Temperature ranges between 12.5 and 21.1° C and

nutrients maintain average concentrations higher than values reported from surface waters.

Halimeda and *Mesophyllum* are progressively displaced by other algae at irradiances lower than 0.4 % of surface irradiance. *Lithophyllum expansum*, *Spongites (?) hauckii* and *Peyssonnelia rosa-marina* are the main bioconstructors of the so-called platform coralligenous (LABOREL, 1961). This community is devoid of an erect vegetal stratum and only small sciaphilic algae such as *Kallymenia* and *Rodriguezella* species, soft *Peyssonnelia* species, and some Rhodymeniales and Ceramiales, are scattered among the dominant encrusting algae (BALLESTEROS, 1984). This community is widespread at depths ranging from 30-35 to 60-70 meters in the Gulf of Lions and it closely agrees with the association of *Lithophyllum expansum* and *Spongites (?) hauckii* described by FELDMANN (1937).

More data are necessary to assess at which rank should be assigned these two communities (associations, subassociations, facies). Future research is needed to elucidate composition and distribution of deep-water Mediterranean communities from rocky bottoms to properly classify them.

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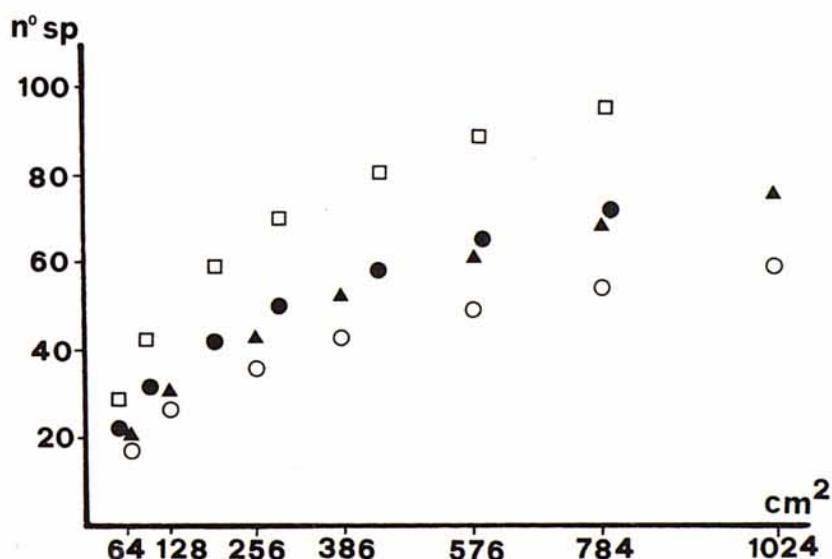


Figure 1 - Species/area curves in the *Halimeda tuna* community. Different samples are figured with different symbols: winter (030182) (black circles), spring (040482) (white circles), summer (290682) (squares) and autumn (270982) (triangles).

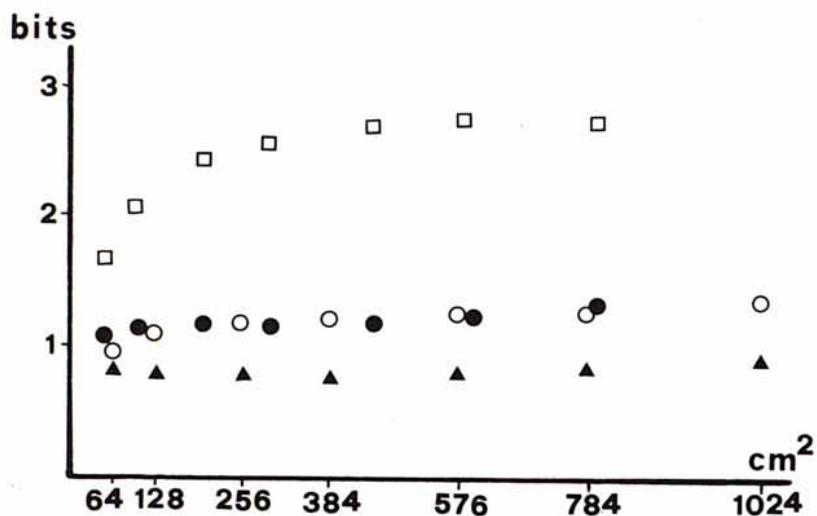


Figure 2 - Diversity (computed from biomass values)/area curves. Symbols as in figure 1.

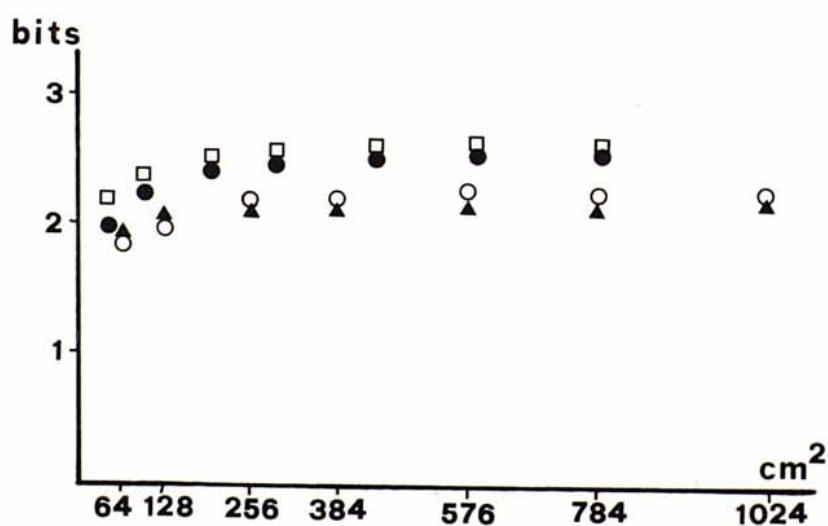


Figure 3 - Diversity (computed from coverage values)/area curves. Symbols as in figure 1.

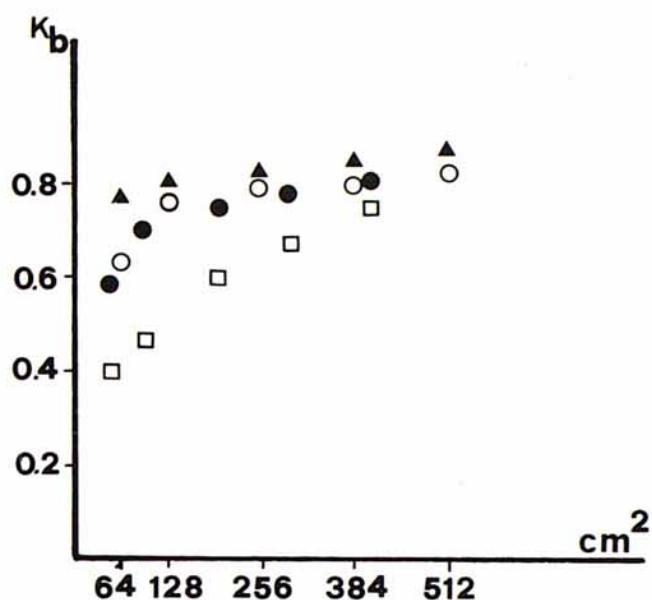


Figure 4 - Quantitative similarity (computed from biomass values)/area curves. Symbols as in figure 1.

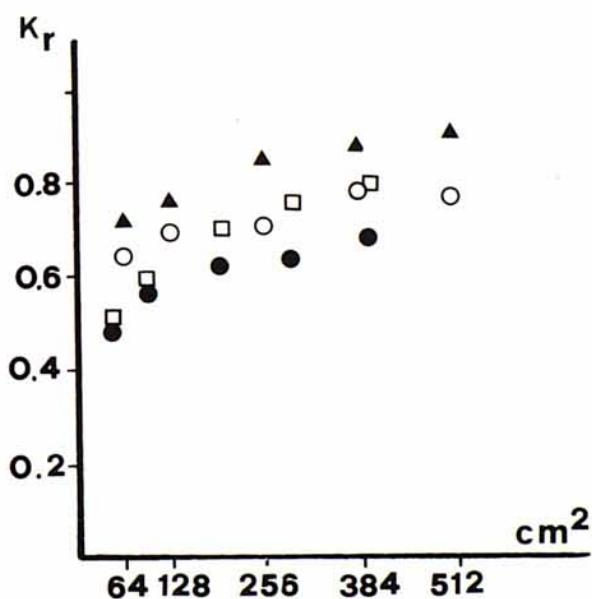


Figure 5 - Quantitative similarity (computed from coverage values)/area curves. Symbols as in figure 1.

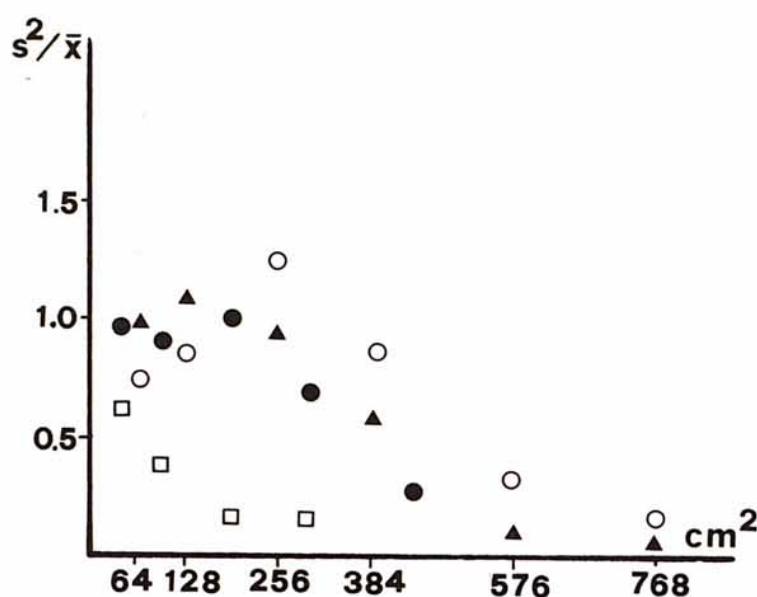


Figure 6 - Variation of the variance: mean ratio of the biomass distribution in relation with sampling area.

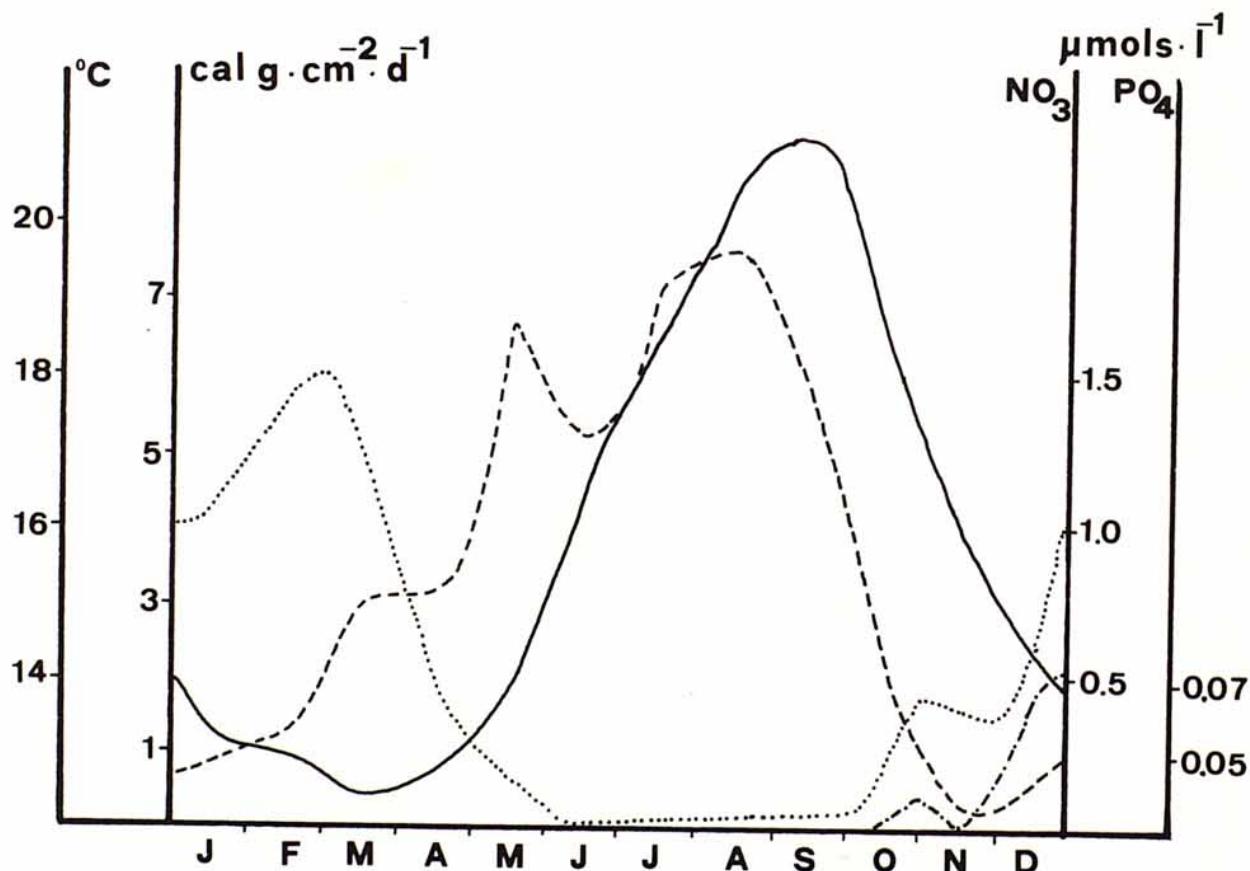


Figure 7 - Variation of temperature ($^{\circ}\text{C}$) (solid line), irradiance ($\text{cal g cm}^{-2} \text{d}^{-1}$) (broken line), nitrate (dotted line) and phosphate (point and line line) concentration in seawater (all in micromol l^{-1}) at the community of *Halimeda tuna* off Tossa de Mar along the year 1983.

Table 1

	1	2	3	4
<i>Halimeda tuna</i> (Ellis & Solander) Lamouroux	57,5 136,9	83,8 203,3	205,9 472,8	91,6 161,6
<i>Mesophyllum lichenoides</i> (Ellis) Lemoine	73,4 927,1	78,5 1189,9	32,0 415,2	112,5 1794,6
<i>Melobesiae</i> (unidentified)	4,2 4,2	28,3 28,3	71,3 71,3	21,4 21,4
<i>Lithophyllum expansum</i> Philippi sensu Lemoine	1,0 28,9	13,4 109,5	13,1 244,2	1,5 35,8
<i>Udotea petiolata</i> (Turra) Boergesen	8,7	0,8	2,8	1,1
sa	29,8	0,8	3,9	1,3
<i>Hypoglossum hypoglossoides</i> (Stackhouse) Collins & Harvey	0,1 0,1	0,3 0,2	2,0 0,7	7,1 2,5
<i>Callithamnion decompositum</i> J. Agardh	1,0 1,0	0,9 0,9	3,8 3,9	2,8 2,5
<i>Fosliella farinosa</i> (Lamouroux) Howe	0,5 0,2	3,7 1,2	0,4 0,1	0,1 0,1
<i>Contarinia peryssonneliaeformis</i> Zanardini	0,8 1,2	0,6 0,9	1,7 2,5	1,1 1,6
<i>Callithamnion byssoides</i> Arnott ex Harvey	0,4 0,4	0,1 0,1	1,0 1,0	1,7 1,7
<i>Myriogramme carnea</i> (Rodríguez) Kylin	0,1 0,1	1,1 0,3	0,1 0,1	1,7 0,7
<i>Apoglossum ruscifolium</i> (Turner) J. Agardh	0,4 0,4	0,2 0,1	0,5 0,1	0,4 0,8
<i>Polysiphonia banyulensis</i> Coppejans	0,2 0,2	0,1 0,1	0,1 0,1	1,3 1,2
<i>Erythroglossum sandrianum</i> (Zanardini) Kylin	0,1 0,1	0,3 0,1	0,9 0,3	0,3 0,1
<i>Plocamium cartilagineum</i> (L.) Dixon	1,1 1,0	0,2 0,2	0,4 0,4	0,1 0,1
<i>Compsothamnion thuyoides</i> (Smith) Schmitz	0,5 0,5	0,3 0,3	0,3 0,3	0,1 0,1
<i>Falkenbergia rufolanosa</i> (Harvey) Schmitz-stadio	0,8 0,8	0,1 0,1	0,2 0,2	0,1 0,1
<i>Ptilothamnion pluma</i> (Dillwyn) Thuret	0,2 0,2	0,1 0,1	0,1 0,1	0,3 0,3
<i>Lyngbya sordida</i> (Zanardini) Gomont	0,2 0,2	0,2 0,1	0,2 0,2	0,2 0,1
<i>Gloiocladia furcata</i> (C. Agardh) J. Agardh	0,2 0,2	0,1 0,1	0,3 0,3	0,2 0,2
<i>Ceramium codii</i> (Richards) Mazoyer	0,4 0,4	0,1 0,1	0,1 0,1	0,1 0,1
<i>Sphacelaria cirrosa</i> (Roth) C. Agardh	0,4 0,4	0,1 0,1	0,1 0,1	0,1 0,1
<i>Halopteris filicina</i> (Grateloup) Kützing	0,4 0,9	0,1 0,1	0,1 0,1	0,1 0,1
<i>Polysiphonia elongata</i> (Hudson) Sprengel	0,1 0,1	0,0 0,0	0,3 0,3	0,1 0,1
<i>Cladophora hutchinsiae</i> (Dillwyn) Kützing	0,1 0,1	0,1 0,1	0,3 0,3	0,1 0,1
<i>Cladophora pellucida</i> (Hudson) Kützing	0,1 0,1	0,1 0,1	0,1 0,1	0,1 0,1

	1	2	3	4
<i>Spermothamnion johannis</i> G. Feldmann	0,1	0,1	0,1	0,1
<i>Cladophora</i> sp.	0,1	0,1	0,1	0,1
<i>Peyssonnelia squamaria</i> (Gmelin) Decaisne	10,5	18,0	0,9	0,0
<i>Peyssonnelia harveyana</i> J. Agardh	21,3	2,6	1,5	0,0
<i>Peyssonnelia rubra</i> (Greville) J. Agardh	0,4	1,2	10,6	0,0
<i>Rodiguezella pinnata</i> (Kützing) Schmitz	1,1	5,5	29,8	0,0
<i>Palmophyllum crassum</i> (Naccari) Rabenhorst	0,6	0,5	0,0	0,1
<i>Nithophyllum micropunctatum</i> Funk	5,1	1,0	0,0	0,1
<i>Seirospora sphaerospora</i> J. Feldmann	0,2	0,0	0,3	0,6
<i>Ceramium diaphanum</i> Roth var. <i>lophophorum</i> G. Feldmann	0,2	0,2	0,6	0,0
<i>Antithamnionella spirographidis</i> Schiffner	0,2	0,3	0,8	0,0
<i>Champia parvula</i> (C. Agardh) Harvey	0,8	0,0	0,1	0,1
<i>Aglaozonia chilosa</i> Falkenberg-stadio	0,3	0,0	0,1	0,1
<i>Botryocladia boergesenii</i> J. Feldmann	0,0	0,2	0,3	0,0
<i>Polysiphonia furcellata</i> (C. Agardh) Harvey	0,1	0,0	0,1	0,1
<i>Cladophoraceae</i> (unidentified)	0,1	0,0	0,1	0,1
<i>Wrangelia penicillata</i> C. Agardh	0,0	0,1	0,1	0,1
<i>Antithamnion heterocladium</i> Funk	0,1	0,0	0,1	0,1
<i>Monosporus pedicellatus</i> (Smith) Solier	0,1	0,0	0,0	0,1
<i>Polysiphonia macrocarpa</i> Harvey	0,1	0,0	0,1	0,1
<i>Aphanocladia stichidiosa</i> (Funk) Ardré	0,0	0,1	0,1	0,1
<i>Ceramium giacconei</i> Cornaci & Furnari	0,1	0,1	0,1	0,0
<i>Sphaelaria plumula</i> Zanardini	0,1	0,0	0,1	0,1
<i>Erythrotrichia carnea</i> (Dillwyn) J. Agardh	0,1	0,0	0,1	0,1
<i>Peyssonnelia rosa-marina</i> Boudouresque & Denizot	0,1	0,1	0,0	0,1
<i>Lithothamnion</i> sp. s. l.	0,0	0,0	16,0	4,4
<i>Peyssonnelia bornetii</i> Boudouresque & Denizot	0,0	0,0	213,6	39,6
	8,5	0,0	91,2	27,3
	23,1	0,0	0,0	1,4
				3,4

	1	2	3	4
<i>Castagnea irregularis</i> Sauvageau	0,0	0,0	8,9	0,0
<i>Lithophyllum incrustans</i> Philippi	0,0	0,0	8,2	0,0
<i>Castagnea</i> sp.	0,0	0,0	4,7	0,0
<i>Seirospora interrupta</i> (Smith) Schmitz	0,0	0,0	81,5	0,0
<i>Myrionema magnusii</i> (Sauvageau) Loiseleur	0,0	0,0	0,7	0,0
<i>Chrysymenia ventricosa</i> (Lamouroux) J. Agardh	0,0	0,0	0,6	0,0
<i>Rhodymenia ardissonae</i> J. Feldmann	0,0	0,0	0,4	0,0
<i>Rhodophyllis strafforellii</i> Ardisson	0,0	0,0	0,4	0,0
<i>Lophosiphonia scopulorum</i> (Harvey) Womersley	0,0	0,0	0,3	0,0
<i>Graudia sphacelarioides</i> Debès & Solier	0,0	0,0	0,2	0,0
<i>Lomentaria chylocladiella</i> Funk	0,0	0,0	0,2	0,0
<i>Stylonema alsidii</i> (Zanardini) Drew	0,0	0,0	0,1	0,0
<i>Dasya corymbifera</i> J. Agardh	0,0	0,0	0,1	0,0
<i>Ceramium echionotum</i> J. Agardh	0,0	0,0	0,1	0,0
<i>Cryptonemia lomatia</i> (Bertoloni) J. Agardh	0,0	0,0	0,1	0,0
<i>Ceramium rubrum</i> (Hudson) C. Agardh	0,0	0,0	0,1	0,0
<i>Nereia filiformis</i> (J. Agardh) Zanardini	0,0	0,0	0,1	0,0
<i>Acrosorium venulosum</i> (Zanardini) Kylin	0,0	0,0	0,1	0,0
<i>Griffithsia schousboei</i> Montagne	0,0	0,0	0,1	0,0
<i>Lyngbya meneghiniana</i> Gomont	0,0	0,0	0,1	0,0
<i>Castagnea cylindrica</i> Sauvageau	0,0	0,0	0,1	0,0
<i>Cladophora cf. lehmanniana</i> (Lindenberg) Kützing	0,0	0,0	0,1	0,0
<i>Pringsheimiella scutata</i> (Reinke) Marchewianka	0,0	0,0	0,1	0,0
<i>Jania corniculata</i> (L.) Lamouroux	0,0	0,0	0,1	0,0
<i>Gigartinal</i> unidentified	0,0	0,0	0,1	0,0
<i>Pterothamnion plumula</i> (Ellis) Nägeli var. <i>bebbi</i> (Reinsch) J. Feldmann	0,0	0,0	0,1	0,0
<i>Enteromorpha</i> sp.	0,0	0,0	0,1	0,0

	1	2	3	4
<i>Cladophora coelothrix</i> Kützing	0,0 0,0 0,0	0,0 0,0 0,0	0,0 0,0 0,0	0,1 0,1 0,1
<i>Didymosporangium repens</i> Lambert	0,0 0,0 0,0	0,0 0,0 0,0	0,0 0,0 0,0	0,1 0,1 0,1
<i>Gelidiella</i> sp.	0,0 0,0 0,0	0,0 0,0 0,0	0,0 0,0 0,0	0,1 0,1 0,1
<i>Contarinia squamariae</i> (Meneghini) Denizot	0,0 0,0 0,0	0,0 0,0 0,0	0,0 0,0 0,0	0,1 0,1 0,1
<i>Codium vermilara</i> (Olivi) Delle Chiaje	0,0 0,0 0,0	0,0 0,0 0,0	0,0 0,0 0,0	0,1 0,1 0,1
<i>Ulvella lens</i> Crouan & Crouan	0,0 0,0 0,0	0,0 0,0 0,0	0,0 0,0 0,0	0,1 0,1 0,1
<i>Giffordia</i> sp.	0,0 0,0 0,0	0,0 0,0 0,0	0,0 0,0 0,0	0,1 0,1 0,1
<i>Phaeophila viridis</i> (Reinke) Parke & Burrows	0,0 0,0 0,0	0,0 0,0 0,0	0,0 0,0 0,0	0,1 0,1 0,1
<i>Stylocladia cornu-cervi</i> Reinsch	0,0 0,0 0,0	0,0 0,0 0,0	0,0 0,0 0,0	0,1 0,1 0,1
<i>Derbesia tenuissima</i> (De Notaris) Crouan & Crouan	0,0	0,0	0,0	0,1

Table I - Seasonal variation in the species composition of the *Halimeda tuna* community. Species abundance is expressed in percentage of coverage (first quantity) and g dw m⁻² (second quantity). *Relevé* 1 corresponds to 030182, 2 to 040482, 3 to 290682 and 4 to 270982.

Table 2

n. ^o	Date	Biomass	% cov	K	R	M20/5
1	030182	1194,1	178,9	15,8	55,8	606
2	040482	1646,3	218,6	19,7	39,9	755
3	290682	1652,4	398,0	16,3	83,7	635
4	270982	2099,4	256,7	25,4	54,7	974

Table II - Seasonal variation in biomass (g dw m⁻²), percentage coverage, species distribution (*k*), species richness (*R*) and qualitative minimal area (*M20/5*) for the different samples.

Table 3

n. ^o	Date	Ab	Sb	r _b ²	Ar	Sr	r _r ²
1	030182	1,24	97	0,637	2,66	197	0,994
2	040482	1,31	149	0,998	2,28	167	0,982
3	290682	2,88	285	0,992	2,67	166	0,996
4	270982	0,82	50	0,065	2,19	130	0,958

Table III - Seasonal variation in species diversity (*A*) and pattern-diversity (*B*) calculated from biomass values (b) or coverage values (r). Correlation coefficients between experimental and adjusted curves fitted to a Michaelis-Menten function are also indicated.

Table 4

Ecological group	quantitative dominance	qualitative dominance
Sciaphilic	84,4	61,1
<i>Posidonia</i> leaves	0,9	2,8
Rocky infralittoral	0,6	5,5
Photophilic	0,3	6,3
Thionitrophilous	—	2,1
Mediolittoral	—	0,7
Others	13,8	21,5

Table IV - Qualitative and quantitative dominance of the main ecological groups.

Table 5

spectral band (nm) depth (m)	350-450	450-510	510-570	570-650	650-700
23	14,1	44,4	36,5	5,0	$5 \cdot 10^{-3}$
40	8,9	49,9	39,0	2,2	$1 \cdot 10^{-5}$

Table V - Percentages of yearly irradiance distributed in five intervals of wave-length reaching 23 and 40 meters depth in coastal waters off Tossa de Mar.

Table 6

	D	S	N	Ar	Sr	B	% cov.	Reference
<i>Halimeda tuna</i> community	17,5	784-1024	76	2,5	156	1648	263	this study
<i>Rhodymenio-Codietum vermilarae</i>	11,0	1024	123	3,9	246	1810	305	BALLESTEROS (1989a)
<i>Cystoseiretum zosteroidis</i>	17,5	1600	132	3,5	281	1425	201	BALLESTEROS (1990a)
<i>Cystoseiretum spinosae</i>	20,0	400	68	4,0	—	1381	333	BALLESTEROS (unpublished data)
<i>Udoteo-Peyssonnelietum</i>	variable	400	37	3,3	—	—	149	BOISSET (1987)
<i>Peyssonnelietum rubrae</i>	variable	600	38	3,2	—	—	158	BOUDOURESQUE (1973)
<i>Lithophyllum expansum</i> community	35,0	1600	38	2,8	343	1596	122	BALLESTEROS (1984)

Table VI - Structural parameters of some sciaphilic infralittoral and circalittoral communities from the North Western Mediterranean. Depth (D, in meters), sampling area (S, in cm²), N (number of species per sample), species diversity (Ar, in bits), pattern-diversity (Sr, in cm²), biomass (B, in g dw m⁻²) and percentage coverage (% cov) are indicated.