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ECOLOGY OF TUNISIAN COMMERCIAL SPONGES

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Summary : In Tunisia the sponge family Spongiidae (order Dictyoceratida) is represented by 15 species, 3 of which are commercially used : *Spongia agaricina, S. zimocca* and *Hippospongia communis.*

An undisturbed sponge bed is described on the basis of a detailed quantitative sampling program. Rock outcrops amidst *Posidonia* sand flats below a depth of 10 m are most favorable habitats for massive sponge growth. The alga *Caulerpa prolifera* is characteristic for this particular biotope. There are 6 common massive sponges in the study area. They belong to 3 closely related genera (*Spongia, Hippospongia* and *Ircinia*) but only *Spongia zimocca* and *Hippospongia communis* are commercially usable. Epizoic organisms are mainly attached to the surface of *Hippospongia* and can effect the shape and thus the commercial quality of this sponge. Endozoans are common in all 6 species. Their number and biomass are correlated with the development of the internal canal system in the host. The snapping shrimp *Synalpheus gambarelloides* belongs to the abundant endobionts which can be considered parasitic because it feeds on the host sponge. It does not, however, cause major structural damage.

The present findings agree with data from the literature that the relation between sponges and their endofauna is mainly inquilinistic and that sponges constitute a highly efficient ecological niche for interstitial organisms.

Résumé : En Tunisie la famille des Spongiidae (Ordre des Dictyoceratida) est représentée par 15 espèces dont 3 sont commercialisées : *Spongia agaricina, S. zimocca* et *Hippospongia communis.*

La description, donnée ici, d'un fond à spongiaires non perturbé, a eu pour base un programme détaillé d'échantillonnages effectués en vue d'une étude quantitative. Les affleurements de roche au milieu de fonds sablo-vaseux à *Posidonia* à une profondeur inférieure à 10 m représentent des habitats favorables à un développement massif des éponges. L'algue *Caulerpa prolifera* est caractéristique de ce biotope particulier. Il existe 6 éponges massives communes dans la zone étudiée ; elles appartiennent à 3 genres très proches les uns des autres (*Spongia, Hippospongia* et *Ircinia*), mais seules *Spongia zimocca* et *Hippospongia communis* sont commercialisées. Les organismes épizoïques sont surtout fixés à la surface de *Hippospongia* et peuvent en affecter la forme, et, de ce fait même, sa qualité sur le plan commercial. Les endobiontes sont communs aux 6 espèces ; leur nombre et leur biomasse sont en corrélation avec le développement du système de canaux internes chez l'hôte. La crevette *Synalpheus gambarelloides* fait partie des nombreux endobiontes, qui peuvent être considérés comme parasites, puisqu'elle se nourrit de l'éponge hôte, sans, toutefois, en altérer la structure.

Les présentes observations sont en accord avec celles déjà mentionnées dans la littérature, à savoir que la relation qui existe entre les éponges et la faune qu'elles hébergent est à rattacher à des phénomènes de commensalisme et que ces éponges constituent une niche écologique particulièrement apte à héberger une faune interstitielle.

INTRODUCTION

During the past century Tunisia has been the leading single producer country (over 40 %) of Mediterranean commercial sponges. The economic importance of this product had generated substantial research on the systematics (Topsent, 1924), physiology (Allemand-Martin, 1906), embryology (Allemand-Martin, 1921 ; Tuzet and Pavans de Ceccatty, 1958) and, above all on culture methods (Cotte, 1910 ; Allemand-Martin, 1914 ; Heldt, 1951) of usable sponges. Similar trends of research and cultivation technology developed also in central America (Florida, Cuba, Bahamas : Moore, 1910) particularly, after a sponge disease had drastically reduced the majority of the natural population (Storr, 1964).

The purpose of this study was to learn more about the natural environment favoring growth of these sponges, about their distribution and density and about their interactions with the associated flora and fauna. The results will help to locate and evaluate potential new fishing grounds and cultivation localities and to make recommendations for efficient and rational exploitation.

The following report is based on fieldwork conducted in Tunisia during October 1969, May-July 1970 and August-September 1971. Survey collecting and laboratory methods used are explained in the introductions to the appropriate chapters. Specimens collected are deposited at the Institut National Scientifique et Technique d'Océanographie et de Pêches (I.N.S.T.O.P.), Salammbô.

SYSTEMATIC POSITION OF COMMERCIAL SPONGES

Only species and varieties of two sponge genera, *Spongia* and *Hippospongia*, have a network of branching organic fibers that is well developed and elastic enough to provide softness and water absorbing qualities necessary for commercial use. The fibers, "spongin B" fibers, have been demonstrated to belong to the collagen class and to be composed of bundles of unbranched 10 nm filaments (Gross et al. 1956). Frequently embedded, usually in large numbers, are reddish-brown granules of lepidocrocite (Towe and Rützler, 1968). Both genera of commercial sponges belong to the family Spongiidae (order Dictyoceratida), characterized by a reticulated spongin skeleton without distinct stratification of the fibers and by small spherical choanocyte chambers. All six known Mediterranean genera of this family are represented in Tunisian waters with a total of fifteen species which are listed below. The genus *Verongia* is excluded because it has been shown to belong in a different family (Verongiidae) on account of its biochemical affinities (Bergquist and Hartman, 1969).

Spongia agaricina Pallas

Synonyms : *Euspongia officinalis* L. var. *agaricina* (Pallas)
Spongia officinalis L. var. *lamella* Schulze

References : Arndt (1937), Vacelet (1959). Common names : Elephant ear ; oreille d'éléphant. Remarks : This sponge has good commercial qualities but is little used because of its shape.

Spongia nitens (Schmidt)

Synonyms : *Ditela nitens* Schmidt
Euspongia officinalis L. var. *nitens* (Schmidt)

References : Topsent (1934), Vacelet (1959). Remarks : Not abundant, not commercially used.

Spongia officinalis Linnaeus

Reference : Arndt (1937). Remarks : Only variety *exigua* Schulze is reported from Tunisia. Its size is under 5 cm, the skeleton is dark brown and shows little elasticity. Not abundant, no commercial value.

Spongia zimocca (Schmidt)

Synonym : *Euspongia zimocca* (Schmidt)

Figure : 1 b

Reference : Arndt (1937). Common name : Zimocca. Remarks : Topsent (1924) described a variety *adjimensis* (common name : Adjimi) of this species. It has the shape of an inverted cone, is smaller and has longer conules. Its skeleton is rather hard. The typical form (only encountered during this study) is not abundant and has fair commercial qualities.

Hippospongia communis (Lamarck)

Synonyms : *Hippospongia equina* (Schmidt)
Hippospongia communis (Lamarck) var. *equina* (Schmidt)

Figure : 1 c

References : Arndt (1937), Vacelet (1959). Common names : Honeycomb, horse sponge ; Djerba, Sfax (ienne), éponge commune, éponge équine (and many more). Remarks : Most common commercial sponge in the Mediterranean.

Cacospongia mollior Schmidt

References : Topsent (1934), Vacelet (1959). Remarks : Species not abundant, not found during the present study.

Cacospongia scalaris Schmidt

Reference : Vacelet (1959). Remarks : This species is abundant in shallow water (2 m) in the Golfe de Gabès. In the field it can be confused with commercial species (*Spongia*) except that it is easily torn.

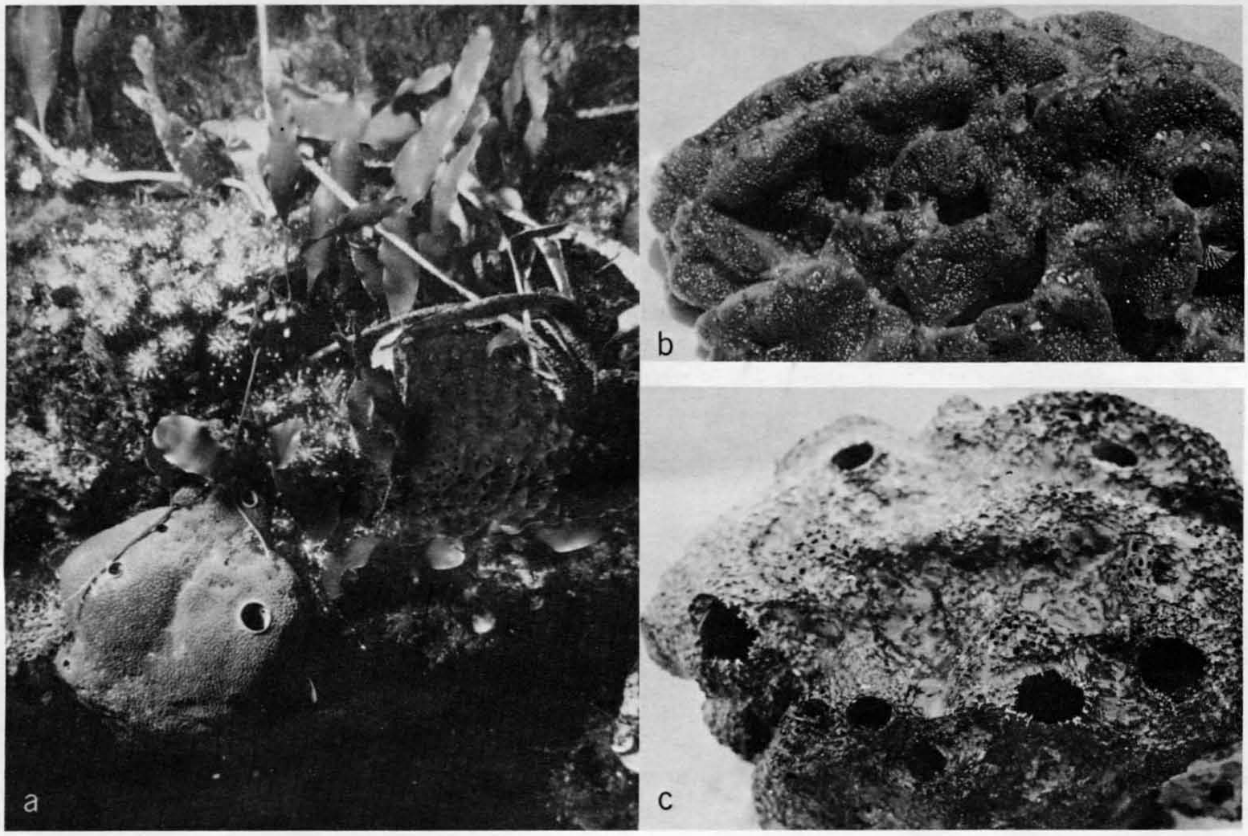

Figure 1 – Characteristic sponges and their habitat. a : Underwater view of *Ircinia fasciculata* (left), *I. muscarum* (right), *Paralcyonium elegans* and *Caulerpa prolifera* (x 0.3). b : *Spongia zimocca* (x 0.5). c : *Hippospongia communis* (x 0.6).

Oligoceras collectrix Schulze

References : Topsent (1934), Vacelet (1959). Remarks : Not abundant, not found during this study.

Ircinia fasciculata (Pallas)

Figure : 1 a

References : Vacelet (1959), Sarà (1962). Remarks : This species is usually fully exposed to light. Many large specimens exhibit groups of openings which are smaller than oscula and lack a raised membranous collar. They penetrate ectosomal membranes which cover subectosomal spaces. Their formation is possibily induced by endobionts.

Ircinia oros (Schmidt)

Reference : Vacelet (1959). Remarks : This species always occurs subdued light conditions.

Ircinia variabilis (Schmidt)

References : Topsent (1934), Sarà (1962, 1974 a). Remarks : The variability of color and shape in this species is a result of the great range in gradients of light and watermovement. Only one of Topsent's varieties, *truncata*, was frequently encountered during this study. It has a small base and flat top, like an inverted cone, with oscula restricted to the top. This species is easily confused with small specimens of *Ircinia fasciculata*.

Ircinia (Sarcotragus) muscarum (Schmidt)

Synonym : *Filifera muscarum* Schmidt

Figure : 1 a

References : Topsent (1934), Vacelet (1959). Remarks : As pointed out by Vacelet (1959) this species is difficult to be distinguished from *Ircinia (Sarcotragus) foetida* (Schmidt). The latter species has been reported from Tunisia by Topsent (1934) but was not encountered during the present study.

Ircinia (Sarcotragus) spinosula (Schmidt)

Synonym : *Filifera spinosula* Schmidt

Reference : Vacelet (1959). Remarks : This species superficially resembles a *Spongia* or *Cacospongia* in the field. It can, however, not be confused because of its extremely tough consistency.

Fasciospongia cavernosa (Schmidt)

Synonym : *Cacospongia cavernosa* Schmidt

Reference : Vacelet (1959). Remarks : This species is frequently overgrown by other organisms.

Fasciospongia caerulea Vacelet

Reference : Vacelet (1959). Remarks : This species was not found during the present study.

COMMUNITY STRUCTURE OF A SPONGE BED

After having surveyed the coast of Tunisia from Cap Serrat to the Island of Djerba (Rützler, unpublished report), we chose an area off Rass Salakta (between Mahdia and Rass Kaboudia) for closer study. Main criteria for selection were abundance of commercial sponges undisturbed by fishing activities and proximity of sponge beds to a shore based facility (field laboratory). A semi-circle of 2 km radius around the fishing village of Salakta was surveyed by radiating transects using small boat and SCUBA apparatus. Beyond a zone of sand and rock close to shore, extensive fields of *Posidonia oceanica* start in an average depth of 6 m. This very uniform feature continues far beyond the 20 m isobath, the seaward boundary of our surveys. Areas of sand and mud occur between the stands of *Posidonia* which are elevated by 1 m and more above the seafloor because successive colonization takes place on sediments trapped by the plants. Large growing sedentary animals are very rare because of the limited availability of solid substrates and the strong exposure of the shore line to wave action.

Towards east-southeast of Salakta village (due 108°) there is a series of rock outcrops which starts at the intertidal and could be followed to the 20 m isobath, about 2 km off-shore. They constitute the submarine extension of the Salakta cape. In shallow water (1-6 m) the rock ridges give support to low growing algae and sponges of the genus *Ircinia* which are tough enough to withstand the waves. Below 6 m, however, stands of *Posidonia* and accumulations of sand in depressions obscure the rock structures. Between 10 and 20 m depth where wave forces become significantly reduced, commercial and other sponges become abundant and also other sedentary animals gain quantitative importance.

For methodological convenience, we chose to establish one representative large quadrat of 200 m^2 bottom area (14 x 14 m) for detailed study rather than taking numerous small random samples. The quadrat was selected after considerable surveying in order to avoid unusually rich (in sponges) or poorly populated areas and to ascertain balanced occurrence of substratum types. The quadrat is situated at 35°23′10″ E, 1.4 km east-southeast from Salakta, at a bottom depth of 14 m. It was marked semi-permanently with a surface buoy. All other labeling was done with small underwater buoys and with plastic tags fixed by pitons or concrete nails. For mapping of the bottom types and for orientation purposes, the quadrat was subdivided into 2 x 2 m squares. All measurements were taken with a calibrated iron bar.

The quantitative part of this work was conducted during the period 19 August to 16 September 1971. Predominant wind directions during that time were from the northwest (92 %) and from the east (8 %), generating currents above the bottom with peaks of 5 to 35 cm sec^{-1} (estimated from movement of suspended particles). Judging from the abundance of *Posidonia* leaves, piled up on the supralittoral of close-by beaches, much stronger forces must act upon this environment during autumn and winter storms. Horizontal visibility 2 m above the bottom (12 m) varied from 8-16 m during northwest winds but was at times reduced to 3 m during east winds. In deeper water (20 m bottom depth) east of the quadrat we observed during a period of high turbidity that the water became clear below a thermocline in 16 m of depth. During that day (12 September 1971, noon) temperatures were 27.1°C at the surface, 26.8°C in 14 m and 24.7°C in 20 m.

1 – Bottom types and indicator organisms :

A map of the quadrat is shown in figure 1. The black numbered squares designate location of samples which have been used for closer analysis of substrate and organisms and for estimates of the biomass. Black

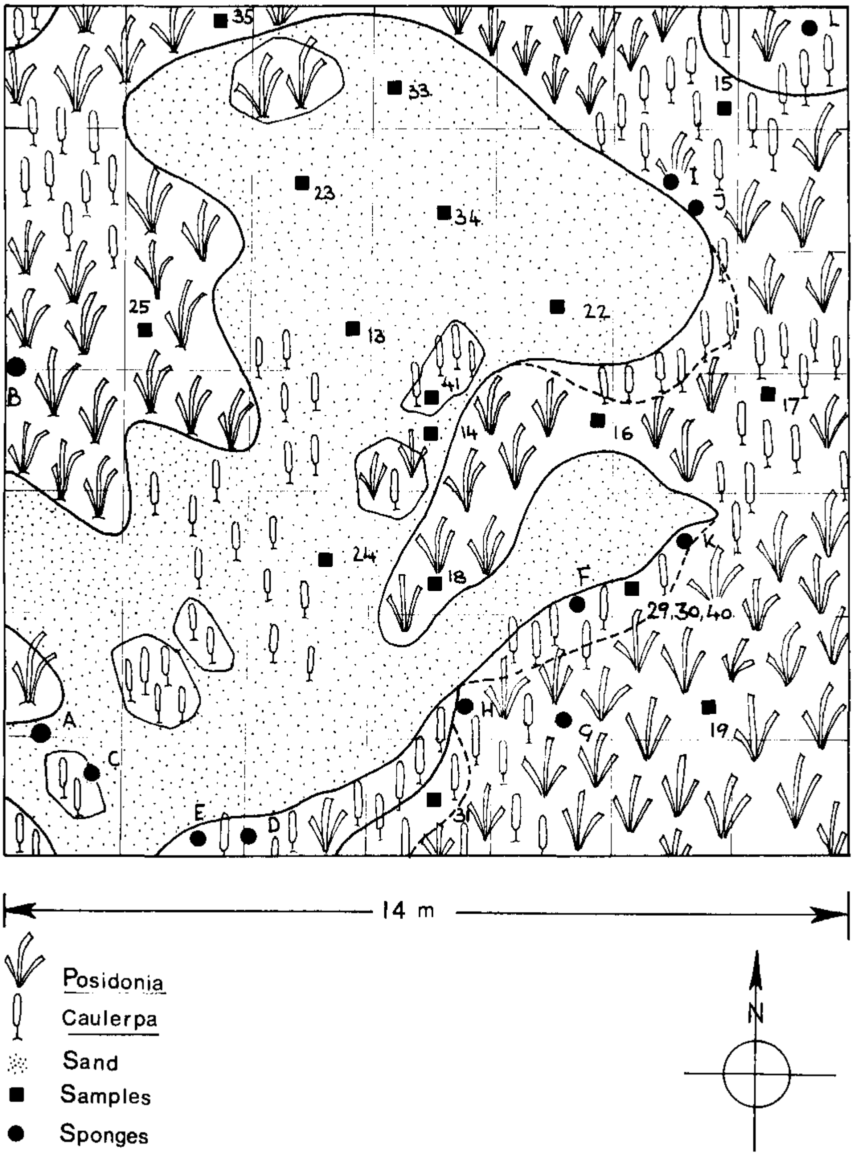

Figure 2 Distribution of bottom types on Salakta quadrat. Interrupted lines indicate position of caves. Numbers designate samples taken, letters designate position of sponges labeled for long-term observation.

circles with letters mark the location of large sponges which were photographed and measured *in situ* but were left undisturbed for future reference.

The total projected surface area of the quadrat was roughly characterized by *Posidonia* (40 %), Sand (38 %) and *Caulerpa* (22 %). Some small caves undercutting *Posidonia* and rook formations are characterized by coralline algae and sponges and add about 3 % to the surface area.

1.1. Posidonia : Posidonia oceanica (Linnaeus) was calculated to have a mean density of 218 plants per m^2 with a mean wet weight of 8.9 kg m^{-2}. It is not only one of the most abundant organisms in the study area but the plants function as an efficient sediment trap, they provide shelter for fragile invertebrates and fishes and substrate for numerous sessile organisms. The leaves of *Posidonia* supported a specialized flora and fauna of minute algae, hydroids and incrusting bryozoans. Loose tufts of the brown alga *Dictyota linearis* (Agardh) were hanging on many of the plants. Most rhizomes were thickly overgrown by a spectrum of organisms usually characteristic of shaded rocky substrates (Siribelli, 1963). *Pseudolithophyllum* sp. (Corallinacea) ; *Dysidea fragilis* (Montagu), *Crambe crambe* (Schmidt) (Porifera) ; *Schizobrachiella* sp., *Sertella (= Retepora)* sp. (Bryozoa) ; and *Didemnum* sp. (Tunicata) are the most common forms incrusting *Posidonia* rhizomes. Occasionally, but not in the quadrat area, *Hippospongia communis* (Lamarck) has been found attached to or growing around the rootstocks.

1.2. Sand : Sand covers all the depressions amidst the *Posidonia* meadows. Its surface is always several centimeters to about one meter below the level of the *Posidonia* rhizomes, whether there are rock outcrops or not. In the quadrat area rock ridges and boulders support *Posidonia*, but rock was also encountered 10-20 cm below the sand surface. Long-term observations of mapped areas will show whether these sand areas are stable formations or whether depressions are filled in and grown over and other areas cleared from existing plant cover perhaps during winter storms.

Sampling the quadrat sand area showed that substantial amounts of barely degraded plant materials (*Posidonia* leaves, *Caulerpa*) were buried. Also, similar materials were suspended close to the bottom in current-protected niches. Three cores of 200 cm^3 (10 cm deep) were taken and tested in a simple manner to get approximate values on the sediment composition. They were wet-sieved through 2 mm and 0.06 mm mesh sieves to remove larger plant particles and to separate the mud from the sand. The two fractions were dried (80° C) and weighed. Subsamples (10 g for sand, 4 g for mud) were then exposed to 10 % hydrochloric acid (approximate calcium carbonate content) and to 10 % sodium hypochlorite (approximate organic content). The residue was rinsed and dried on 0.8 μm membrane filters (80° C) and weighed. The values in Table 1 are given in percent dry weight (mean of 3 samples).

Table 1 : Composition of sand samples from the quadrat.

Samples	Fraction	HCL soluble	Na OCl soluble	Insoluble
$\frac{13+33+34}{3}$	Sand 62.4 %	71.0 %	11.2 %	17.8 %
	Mud 37.6 %	39.2 %	45.5 %	15.3 %

The data show that the sand has a high content of mud which is rich in organic materials. There is no distinction made, of course, between living and dead organic matter.

To assess the dominant groups of the meiofauna 3 similar samples as mentioned above were taken with a 5 cm diameter corer. Two cores hit rock 10 cm, one 15 cm below the substratum surface. The short cores were split in 2, the large one in 3 parts to give 100 cm^3 subsamples representing 3 depth layers. The results of specimen counts are given in Table 2.

Table 2 : Quantitative distribution (specimen numbers) of dominant meiofauna taxa in quadrat sediments.

Samples	Taxa	Sediment depth (mm)		
		0 - 50	51 - 100	101 - 150
$\frac{22+23}{2}$	Turbellaria	15	44	-
	Nematoda	269	617	-
	Polychaeta	64	115	-
	Copepoda	196	688	-
	Total	146	1464	
24	Turbellaria	16	6	33
	Nematoda	98	96	115
	Polychaeta	29	20	25
	Copepoda	148	59	480
	Total	291	181	653

These data, which do not consider dynamic processes (migration) indicate a preference of the meiofauna for the deepest sediment layer overlaying the solid rock substratum.

1.3. Caulerpa : *Caulerpa prolifera* Lamouroux is conspicuous and characterizes most substrates suitable for growth of large sponge species in the study area but, by itself has little importance in biomass or area of attachment. The typical *Caulerpa* habitat is confined to exposed edges of rock outcrops and other areas not too favorable to *Posidonia* settlement, including inclined and semi-shaded habitats. This alga, due to the development of stolons even succeeds in settling on mobile (sand) substrata and on living sponges, as do some coelenterates and bryozoans (Rützler, 1970).

The character of the *Caulerpa* habitat can be described by estimating average area coverage of principle organisms from six 0.25 m^2 squares counted *in situ* within the *Caulerpa* zone. Coverage by *Caulerpa prolifera* was calculated by multiplying the length of stolons occurring in the sample by the average width of the leaves (12 mm). The results are listed in Table 3.

Table 3 : Average area coverage of dominant organisms in the *Caulerpa* habitat.

Chlorophyta	
Caulerpa prolifera Lamouroux	5.6 %
Phaeophyta	
Dictyota linearis (Agardh)	10.3 %
Dictyopteris membranacea (Stackhouse)	10.6 %
Angiospermae	
Posidonia oceanica (Linnaeus)	9.3 %
Porifera	10.1 %
Coelenterata	
Paralcyonium elegans Milne Edwards	9.7 %
Miscellaneous algae and invertebrates	25.2 %
Rock	14.7 %
Sand	4.5 %

All massive large (> 50 cm^2 projected area coverage) sponges growing in the quadrat area belonged to the order Dictyoceratida and occurred within the *Caulerpa* habitat. They were counted and their area coverage was measured (Table 4).

Table 4 : Specimen numbers and projected area coverage of large massive sponges in the quadrat area.

Species	Specimens	Area coverage (cm^2)
Hippospongia communis	9	1584
Cacospongia scalaris	2	172
Ircinia fasciculata	8	888
Ircinia oros	2	330
Ircinia variabilis	16	1296
Ircinia (*S.*) *muscarum*	6	1784
Ircinia (*S.*) *spinosula*	8	632

Similar habitats as described above were searched for *Hippospongia* specimen density during several dives. As a result 3-25 specimens with a minimum diameter of 15 cm were counted per 100 m^2 survey area. These values can not be compared with those given above because the survey area excluded sand or *Posidonia* bottoms.

1.4. Caves : Although caves are small and rare in the study area they form a distinct habitat. Because of the bottom depth (14 m) very shallow caves and even rock overhangs cause a decrease of light intensity that excludes most algae except corallines. The caves border upon and include the sand bottom. It is likely that they were created by a combination of abrasion by moving coarse sediments and by bioerosion. Burrowing organisms are very abundant in the cave rock and include sponges (*Cliona celata, Cliothosa hancocki* ; see Rützler, 1974), polychaetes (*Polydora* sp.), sipunculids and mollusks (*Lithophaga* sp., *Gastrochaena* sp.).

The cave habitat is characterized by crustose coralline algae and incrusting sponges [*Crambe crambe* (Schmidt), *Spirastrella cunctatrix* Schmidt, *Dysidea fragilis* (Montagu)]. Two of the large keratose species can also be found in this habitat but were absent in the quadrat area : *Spongia zimocca* and *Ircinia oros.*

2. Sponges as biotopes :

Many organisms, from blue-green algae to fishes are known to be in epi– or endobiotic relation with sponges although the records are usually hidden in specialized literature. Genus or species names often point to this relationship ("*Spongicola*") or to the genus or species of the host. Summary presentations are available for some groups (e.g. symbiotic algae : Sarà, 1964b ; Entoprocta : Rützler, 1968 ; Crustacea : Arndt, 1933 ; Pisces : Tyler and Böhlke, 1972) and have been recently reviewed by Sarà and Vacelet (1973).

General faunistic studies of sponge dwellers are available for several host species in different geographic locations. Santucci (1922) studied epi– and endobionts of *Geodia* (Choristida) from different bottom types in the Adriatic. Relating specimen numbers to sponge weight he found larger numbers of endozoans in *Geodia* from detritus bottoms than in those collected on rocky bottoms.

Pearse (1932) reports on *Spheciospongia* (Hadromerida), *Spongia* and *Ircinia* ("*Stematumenia*") (Dictyoceratida) from the Caribbean. He found more guests per cm^3 *Spheciospongia* in small specimens and in deep water. He also noted that there was little host specificity, although some sponge species are favored by some endobionts. In a later paper on *Ircinia* (Dictyoceratida), *Haliclona* (Haplosclerida), *Iotrochota* and *Thalysias* ("*Aulospongus*") (Poecilosclerida). Pearse (1950) noted that the number of animals in sponges was dependent on locality and habitat and on the presence of good sized internal canals. Storr (1964) listed a number of inhabitants and epizoics of Florida commercial sponges. He found no detrimental effects except some damage to the commercial value caused by a large crab (*Pilumnus*). He did, however, review the literature describing a disease caused by the fungus *Spongiophaga.* Fishelson (1966) studied *Spirastrella* (Hadromerida) from the Red Sea. He found that the inhabitants were not specific for Porifera but that they concentrate because of the shelter provided by the branched water passages of the sponge. Long (1968) described the associates of *Suberites* (Hadromerida), *Microciona* (Poecilosclerida), *Halichondria* (Halichondrida) and *Homaxinella* (Axinellida) in the east Pacific. He found that sponges had properties that either attracted or inhibited colonization. Density variations in the endofauna were found to be greater in shallow than in deeper water.

Sube (1970) studied some selected associates of *Verongia, Ircinia, Cacospongia* (Dictyoceratida), *Suberites, Cliona* (Hadromerida) and *Mycale* (Poecilosclerida) in the Mediterranean. He found no connection between sponge size and density of the inhabitants but great variations in different host species and under different ecological conditions. He found species specificity to be very rare but that the preferred location of certain endobionts inside the host was rather constant. This author and Connes et al. (1971) studied also the histology of tissue reaction of sponges to the presence of foreign organisms.

Pansini (1970) made a quantitative survey of inquilinism in Mediterranean *Spongia, Ircinia* and *Petrosia.* Among his interesting results is the fact that the total number of endobionts was strongly reduced during the winter months (January – April).

2.1 Epibionts of Salakta Sponges : Of seven massive keratose sponge species examined in the study area three species (*Ircinia fasciculata, I. muscarum* and *I. spinosula*) were almost free of epibionts, except for some spots with small filamentous algae. These evidently settled where the exopinacoderm was interrupted by mechanical injury. In *Spongia zimocca* and *Ircinia variabilis* this growth of small epizoic algae occurred more frequently and stolons of *Caulerpa prolifera* were also observed attached to the sponge surface. Of *Ircinia oros* only two specimens were found but both had almost 30 % of their surface covered by a brown algal felt and by foliaceous red algae (*Peyssonnelia* sp.). In contrast to these species *Hippospongia communis* was always overgrown by several organisms so that between 3 % and 55 % of the surface area was covered. Some specimens were attached to *Posidonia* along their side and even grew entirely around the lower portion of this plant. Table 5 lists the common epibionts observed in the study area. Also Storr (1964) found large numbers of algae epizoic on Florida commercial sponges which would, at times distort the shape of the sponges thus reducing their commercial value.

Table 5 : Average area coverage of epibionts on *Hippospongia.*

Chlorophyta	
Caulerpa prolifera, Halimeda sp., Udotea sp.	19.0 %
Phaeophyta	
Dictyota sp., Padina sp.	14.7 %
Rhodophyta	
Peyssonnelia sp., Pseudolithophyllum sp., Jania sp.	31.3 %
Porifera	
Spirastrella cunctatrix, Hemimycale columella, Ircinia oros	13.5 %
Coelenterata	
Paralcyonium elegans	12.3 %
Bryozoa	
Sertella sp.	6.1 %
Tunicata	
Didemnum sp.	3.1 %

2.2 – Endobionts in Salakta Sponges : For comparative study of the endofauna six related species of keratose sponges (Spongiidae, Dictyoceratida) were chosen. They were all collected in the same environment and depth in close proximity of the quadrat. The species vary considerably in the development and size of their internal canal and cavity system.

2.2.1 – Interstitial space system : A simple cut through any of the sponges studied reveals the size classes of its internal canals which are independent of the size of the specimen or of any environmental influences. *Hippospongia communis, Ircinia muscarum* and *I. fasciculata* have many large exhalant canals and lacunae with porous tissue in between, *Spongia zimocca, Ircinia oros* and *I. variabilis* have few, moderately sized,exhalant canals and consist predominantly of porous tissue.

To obtain quantitative values for the interstitial space system alcohol preserved material was tested as follows. Three samples of each species (approximately 200 cm^3 each) were tightly wrapped under water in very thin plastic foil, lifted from the water, quickly blotted dry and weighed. After removing the plastic wrap

Table 6 : Average interstitial space volumes (in cm^3) for six sponge species. Related to 1 cm^3 sponge volume.

Species	Pore volume	Canal volume	Total interstitial volume
Spongia zimocca	0.61	0.18	0.79
Hippospongia communis	0.35	0.43	0.78
Ircinia fasciculata	0.37	0.35	0.72
Ircinia muscarum	0.32	0.37	0.69
Ircinia oros	0.43	0.10	0.33
Ircinia variabilis	0.41	0.09	0.50

the samples were turned around without squeezing until the water stopped dripping from the large pores and weighed again. The weight difference was called canal volume. Then the sample was queezed well, blotted and weighed again. The new weight difference is the pore volume. This method had more repeatable results than catching and measuring the water running from the interstice. The total volume of the sample was determined by measuring its displacement after tight wrapping in thin plastic foil to prevent the water from entering the interstitial spaces. Weight or volume of the foil can be neglected because of the relative size of the sample and because the error is the same for all species tested. The results of the tests are given in Table 6.

It can be assumed that the canal volume is a measure of the space available to those endobionts that are important in terms of biomass.

2.2.2 – Quantitative assessment of the endofauna : The specimens used for endofauna studies were cleaned from epibionts, cut from the substrate and taken to the field laboratory in individual plastic bags. There they were measured and representative portions were kept for weight and volume determinations. Large sponges were cut into 2-3 cm thick slices, smaller ones in halves or quarters. The larger endobionts could be separated at once, the others were extracted by the oxygen depletion method (Kirsteuer, 1967), or by shaking sponge fragments in magnesium chloride solution isotonic to seawater, or in 4 % formalin – seawater. The endofauna was partly sorted and preserved in the field, partly preserved unsorted and sorted later on in the Mediterranean Marine Sorting Center (Khereddine). Neutralized 4 % formalin-seawater was used as fixative but most of the material (except nematodes and some polychaetes) was subsequently transferred into 80 % ethyl alcohol. All weight determinations (wet weight) of the endofauna were made from alcohol preserved material to the nearest mg. The sponges were weighed to the nearest 0.1 g (wet weight), their volume was determined as described earlier.

Table 7 summarizes the quantity of sponge material used for extraction, Table 8 lists the taxa extracted and the quantitative raw data of the endofauna from each host species. Table 9 relates the total values for the endofauna to units of weight and volume of the host sponges.

Table 7 : Total sponge material extracted.

Species	Number of specimens	Area coverage (cm^2)	Wet weight (g)	Volume (cm^3)
Spongia zimocca	2	166	112	415
Hippospongia communis	40	7400	9732	51222
Ircinia fasciculata	2	230	406	1400
Ircinia muscarum	4	1312	3469	10840
Ircinia oros	1	400	391	1186
Ircinia variabilis	6	516	1655	3598

Santucci (1922) reports 5-51 specimens of endobionts per kg *Geodia cydonium.* This range is much lower than the average figures for the present material (except *Ircinia oros*). The specific weight of sponges, however, varies greatly with the amount and nature of the skeleton. *Geodia* is a comparative heavy sponge with a large amount of siliceous spicules. Numbers related to volume of the host as given by other authors are better comparable.They are summarized in Table 10.

To see whether there is a relation between the average canal volume of the investigated sponge species and the number or weight of the endobionts,the data were plotted as shown in figure 3. Except for the aberrant specimen value for *Ircinia oros* there appears to be a positive correlation between canal volume and specimen numbers, a negative correlation between canal volume and specimen weight. Excluding *Ircinia oros* the correlations were calculated to be significant at the 5 % level. This situation can be explained by the assumption that a system of large canals offers fewer niches which are occupied by a few large growing organisms, whereas the system of small canals supports a large number of small-sized occupants. In the case of *Ircinia oros,* unknown micro-environmental conditions could cause selection of a few specialized forms but more material is needed to exclude a sampling error.

Table 8 : Total endofauna extracted from six sponge species. S : number of specimens ; W : wet weight in g ; + : to small to be weighed.

Host Sponges / Endofauna Taxa	*Spongia zimocca*		*Hippospongia communis*		*Ircinia fasciculata*		*Ircinia muscarum*		*Ircinia oros*		*Ircinia variabilis*	
	S	W	S	W	S	W	S	W	S	W	S	W
Turbellaria			2	+								
Rhynchocoela	1	+	3	+	1	+					1	+
Kinorhyncha											2	+
Nematoda	16	+	93	+	41	+	6	+			87	+
Entoprocta			70	+	31	+	128	+				
Sipunculida	1	0.048	14	0.477					1	0.082		
Polychaeta	59	0.169	581	19.641	98	0.646	121	6.055	11	1.430	277	3.913
Acarina	3	+	7	+							3	+
Caprellidea			3	+			6	+	1	+	1	+
Gammaridea	11	+	329	0.300+	74	+	262	0.204+	1	+	384	0.240+
Copepoda	48	+	488	+	62	+	21	+			612	+
Cumacea			1	+								
Caridea	6	0.192	694	77.157	10	1.887	183	15.089	1	0.157	5	0.365
Brachyura			18	7.827+			1	0.142	1	+		
Isopoda	12	0.018+	10	0.061+	5	+	6	0.028+			19	0.100+
Mysidacea					1	+						
Ostracoda	4	+	85	+			1	+			6	+
Tanaidacea	3	+	10	+	5	+	1	+			30	0.059+
Pycnogonida			10	+			1	+			1	+
Decapoda, misc.					1	+					1	+
Crustacea, larvae			248	0.022+			9	+				
Opisthobranchia			5	+								
Prosobranchia			13	+								
Pelecypoda	3	+	11	0.348+	5	+					5	+
Polyplacophora			2	+								
Ophiuroidea	1	+	10	+	1	+	16	1.422+			4	+
Crinoidea			1	+								
Pisces			3	0.279								
Total	168	0.427+	2711	106.112+	335	2.533+	762	22.940+	16	1.669+	1471	4.677+

2.2.3 – Ecological consequences of endobiosis : Although numerous invertebrates and fishes are known to feed on sponges (e.g. Arndt, 1933 ; Long, 1968 ; Randall and Hartman, 1968) the relation between sponges and their endofauna is generally considered inquilinistic. A number of parasites have been identified among the endobionts on the basis of structural damage inflicted upon the host (Sube, 1970 ; Connes et al., 1971). Similar effects became apparent during the present study although detailed histological work was not undertaken.

Table 9 : Average specimen number and weight (in g) of endofauna per unit host sponge.

Sponge species	Endofauna number kg^{-1}	weight kg^{-1}	number dm^{-3}	weight dm^{-3}
Spongia zimocca	1500	3.8	405	1.0
Hippospongia communis	279	10.9	53	2.1
Ircinia fasciculata	825	6.3	239	1.8
Ircinia muscarum	220	6.6	70	2.1
Ircinia oros	41	4.3	13	1.4
Ircinia variabilis	883	2.8	409	1.3

Table 10 : Published average numbers of endobionts per unit volume of the host sponge.

Species	Number endobionts cm^{-3}	Source
Spongia officinalis	0.4 (April) - 3.6 (June)	Pansini (1970)
Spongia zimocca	0.4	Present paper
Hippospongia communis	0.05	Present paper
Ircinia fasciculata	0.2	Present paper
	1.2 (April) - 16.2 (July)	Pansini (1970)
Ircinia muscarum	0.07	Present paper
Ircinia oros	0.01	Present paper
Ircinia strobilina	0.005	Pearse (1950)
Ircinia variabilis	0.4	Present paper
Petrosia ficiformis	0.9 (April) - 4.7 (November)	Pansini (1970)
Microciona prolifera	0.8	Long (1968)
Halichondria panicea	1.15	Long (1968)
Spheciospongia vesparia	0.16	Pearse (1932)
	0.04	Pearse (1950)
Suberites lata	0.1	Long (1968)
Suberites massa	0.8	Sube (1970)

All specimens under study, even with high densities of endo– and epibionts had a healthy appearance. Growth form of *Hippospongia communis* was greatly altered by incorporated *Posidonia* rhizomes and by other attached organisms but the effects were rather on the commercial quality than on the well-being of the sponge. On the basis of live observations and stomach contents, we were able to identity five species of parasites. All of these were crustaceans and had been observed feeding on their host or had fragments of sponge skeleton fibers in their intestinal tract. Under the microscope the latter can easily be distinguished from other fibrous materials by the presence of embedded lepidocrocite granules (Towe and Rützler, 1968). In the absence of other characteristics (like spicules) in spongiids, this is a convenient feature which enables the identification of even minute quantities of spongin fibers (Figure 4c).

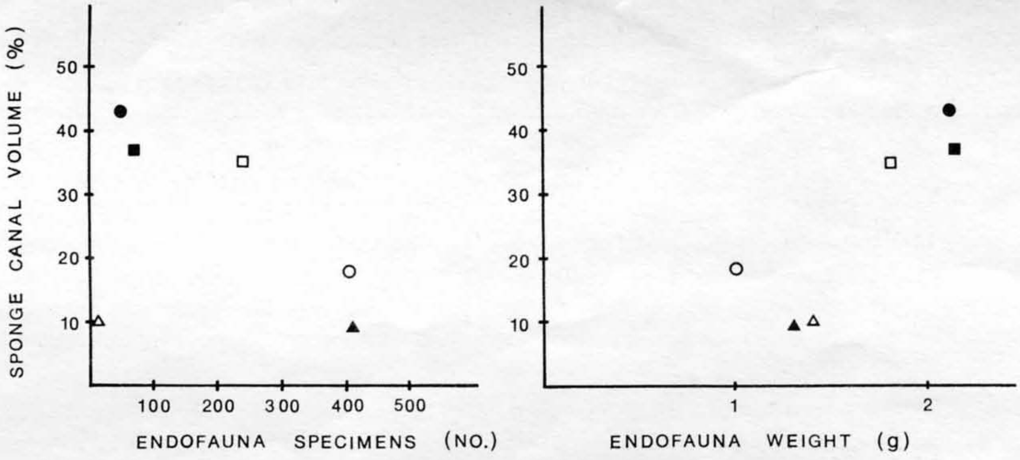

Figure 3 – Relationship between canal volume of sponges and average number (left) and weight (right) of their endofauna, per dm^3 sponge. White circles : *Spongia zimocca* ; black circles : *Hippospongia communis* ; white squares : *Ircinia fasciculata* ; black squares : *I. muscarum* ; white triangles : *I. oros* ; black triangles : *I. variabilis.*

Synalpheus gambarelloides (Nardo) [= *S. laevimanus* (Heller)] (Caridea, Decapoda) was found regularly inside the canal system of all species studied. Eggs and larvae were also present during the time of observation (May, June, August, September). Larvae were observed to leave the sponge and re-enter by eating their way through the surface (Forstner, personal communication). The adults occupy the canals, sometimes in pairs facing an opening in the sponge surface which can be a functional osculum. Some of the openings are possibly produced by the shrimp or they are non-functional oscula. Close observation of the claw showed that it can function like scissors (Figure 4a) rather than pincers as it would appear from many illustrations of the species. The stomach contents of this shrimp regularly included sponge fibers. No remains of other food organisms could be identified although it can be expected that other food sources are used because the species is abundant also in habitats other than sponges.

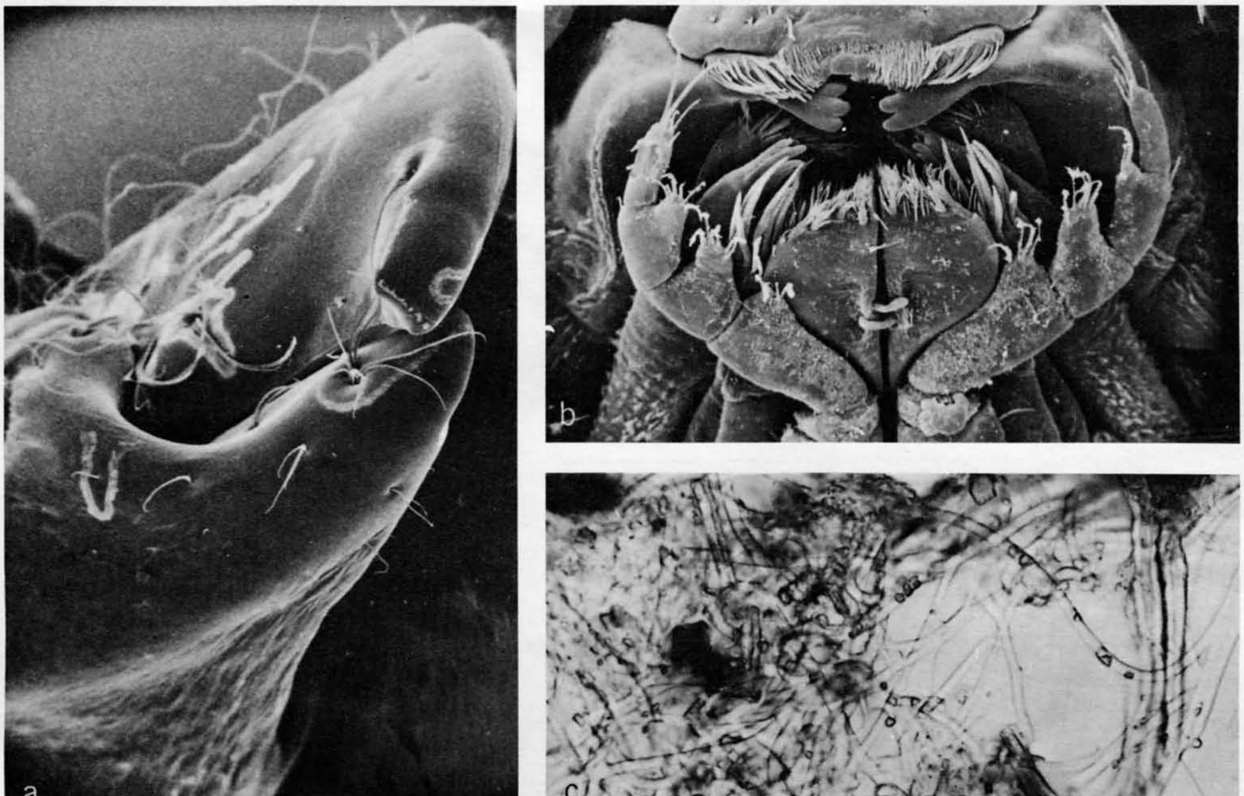

Figure 4 – Sponge feeding endobionts. a : Scissor-like claw of *Synalpheus gambarelloides* (x 55). b : Mouth parts of *Dynamene bidentata* (x 200). c : Spongin fibers of *Hippospongia*, with lepidocrocite granules from stomach contents of *Synalpheus* (x 550).

Cymodoce longistylis (Miers) (Isopoda) and a small unidentified asellote isopod were found regularly in *Hippospongia communis, Ircinia fasciculata, I. muscarum* and *I. variabilis.* Both isopods fed on their hosts.

Dynamene bidentata (Adams) (Isopoda) (figure 4b) eats small circular tunnels into the surface of *Ircinia fasciculata* and *I. variabilis* The isopod fits snug into the burrow where it was found upside-down closing the entrance with its pleotelson and uropods. Some burrows were occupied by pairs.

Polycheria sp. (Gammaridea, Amphipoda) bites shallow oval burrows into the surface of *Ircinia fasciculata* and *I. variabilis.* Population density can reach 10-12 per cm^2 sponge surface. Burrows of *Dynamene bidentata* can be interspersed with those of *Polycheria* sp. in the same sponge specimen. The amphipod lies on its back in the cavity and may not feed on the sponge beyond the excavation of the burrow. A similar behavior was described for *P. osborni* which lives in the compound tunicate *Amaroucium* (Skogsberg and Vansell, 1928). *P. antarctica* is known as parasite of sponges as *Suberites, Halichondria* and *Tedania* (Arndt, 1933).

No sponge remains were found in the intestinal tract of any of the larger polychaetes. The most abundant sponge dwelling species in the present material was *Nereis (Ceratonereis) costae* Grube which accounted for up to 40 % of the total polychaete biomass. This species is usually found in algal populations, *Posidonia* and rock although some records from sponges are available. A closely related species, *Nereis (Ceratonereis) hircinicola* (Eisig) is well known as a sponge dweller (Bellan, 1964).

From our observations and from literature data it appears that the majority of sponge endobionts are mere lodgers. Any damage done to the host is easily repaired. Although most of the endofauna could not be identified to species there is no evidence for an obligate association between spongiids and any of their endobionts.

The question arises as to how efficient these sponges are as a biotope. For this purpose their endofauna was compared with that of three other habitats which are abundant in the quadrat area : rock (well burrowed by former and present activity of sponges, polychaetes, sipunculids, mollusks), *Posidonia* and sand. Obviously the comparison has to be approximate because neither weight nor volume can serve as a unit of reference. Projected surface area was therefore chosen as a compromise and because it is a common sample unit in quantitative ecology. Its magnitude is well defined in sponges. For *Posidonia* all the plants per collecting square (0.25 m^2) were extracted less some fugitive animals (squids, fishes) which could escape before the plants were cut off and placed in a plastic bag. For rock it includes a depth of about 5 cm below the collecting square. This was the average depth of penetration for major burrowers which could also be reached by chisel during collecting. For sand collecting depth (below the sand surface) was the underlying rock (10-15 cm). Averages in Table 11 were taken form all the sponge samples, from 3 samples (0.25 m^2) each for *Posidonia* and rock, and from 3 cores (5 cm diameter) for sand.

Table 11 : Average specimen numbers and weight (g) of endofauna from biotopes relative to unit projected surface area.

Biotope	Number dm^{-2}	Weight dm^{-2}
Sponges	105.1	0.97+
Rock	16.1	0.32+
Posidonia	43.0	0.53+
Sand	7997.5	+

It is not surprising that the meiofauna is well ahead in specimen numbers but relatively insignificant in biomass. Evaluating specimen numbers as well as biomass we can agree with Pearse (1932) that certain sponges are "veritable living hotels".

CONCLUSIONS

1/ **Hippospongia communis** (Lamarck) is still the most common and desirable commercial sponge in Tunisian waters. *Spongia agaricina* Pallas and *S. zimocca* (Schmidt) are also taken by local fishermen but both species are less abundant and less valuable because of their shape. All three belong to the sponge family Spongiidae (order Dictyoceratida) which, in Tunisia, is represented by a total of 15 species.

2/ Surveys using small boats and SCUBA apparatus show that usable sponges are common far beyond the established fishing grounds. The preferred environment is characterized by a *Posidonia-Caulerpa* community, with sand and some rock outcrops in between. Since the coastline is generally quite exposed, a minimum depth of 10 m is required to assure sufficient protection from wave action.

3/ Among the common massive spongiids *Hippospongia* is particularly susceptible to being overgrown by epibionts. Various algae, sponges, cœlenterates, bryozoans and tunicates can cover up to 55 % of its surface area.

4/ A rich endofauna is usually dwelling in the canal system of massive sponges, the centre of numerous studies in the past. Six massive spongiid species occur in the study area. Their internal canal system is potentially available to colonization. *Hippospongia communis, Ircinia muscarum* and *I. fasciculata* have predominately large canals and lacunae, *Spongia zimocca, Ircinia oros* and *I. variabilis* are provided with a system of narrow canals. Specimen numbers and weights of 28 endofauna taxa, if related to units of sponge volume show that fewer but larger organisms dominate in hosts with large canals, whereas more but smaller endobionts find niches in sponges with small canals.

5/ On the basis of their stomach contents five species of endobiotic crustaceans can be considered parasitic because at least part of their diet consists of sponge tissue. The most abundant of these is the snapping shrimp *Synalpheus gambarelloides.* Most of the structural damages inflicted, however, are readily repaired by the host.

6/ The majority of sponge dwellers are mere inquilines. A quantitative comparison of sponge inhabitants with those of 3 other abundant substrata (porous rock, *Posidonia,* sand) shows that certain sponges are very efficient ecological niches.

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