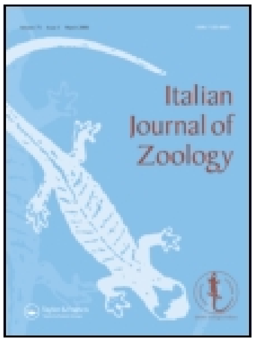

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Morphotypes of *Spongia officinalis* (Demospongiae, Dictyoceratida) in two Mediterranean populations

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ABSTRACT

Morphological differences of *Spongia officinalis* were evaluated at the intra- and inter-population level both in time and space. Body shape analysis in a population from Portofino (W. Mediterranean) revealed that no significant morphological differences occurred at the two depth levels, whereas body size fluctuations, remodelling of the aquiferous system and fragmentation processes were common phenomena during a long-term study. The morphological comparison in two populations from Crete (E. Mediterranean) and Portofino revealed a divergence in macro-morphological traits, whereas notable homogeneity of their diagnostic skeletal micro-traits was observed. These data suggest that gross morphology can play a key role as a diagnostic trait in the taxonomy of Mediterranean populations.

KEY WORDS: Bath sponges - External morphology - Skeletal architecture - Geographical varieties - Taxonomy - Mediterranean Sea.

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INTRODUCTION

The absence both of true tissues and a coordination centre, the reversibility of cell differentiation and the modular/clonal organisation lead to a high degree of body plan plasticity in many sponge species (Storr, 1976; Wilkinson & Vacelet, 1979; Palumbi, 1984; Bond & Harris, 1988; Barthel, 1991; Bavestrello & Sarà, 1992; Pronzato & Pansini, 1994; Gaino *et al.*, 1995). Notable body shape changes at the individual level occur in sponges as a natural feature in the life cycle or, to a lesser extent, during physiological performances such as expansion-contraction activities, locomotion and reproduction (Fell, 1974; Reiswig, 1975; Fell *et al.*, 1979; Pansini & Pronzato, 1990; Gaino *et al.*, 1991; Manconi & Pronzato, 1991; Pronzato & Pansini, 1994; Usher *et al.*, 2001).

Among dictyoceratids, *Spongia officinalis* L., 1759 displays a high degree of plasticity due to its regenerative and re-organisational capability by body shape remodelling (Gaino & Pronzato, 1989; Pronzato *et al.*, 1998). Our ultimate and main aims were to improve the knowledge of the population traits of *S. officinalis* within the framework of a research focusing on the Mediterranean bath sponge diversity, conservation, and management, and to set up a protocol to discriminate commercial varieties used by fishermen and traders (Arndt, 1935; Vacelet, 1987; Vacelet *et al.*, 1988; Gaino & Pronzato, 1989; Pronzato *et al.*, 1996, 1999, 2000; Rizzello *et al.*, 1997; Manconi *et al.*, 1999; Pronzato, 1999; Perez & Capo, 2001). In the present paper, data are reported on macro- and micro-morphological traits recorded in two distant populations of *S. officinalis* from the western and eastern Mediterranean Sea. Inter-population comparison of morpho-traits such as size, body shape, and skeletal network was performed; intra-population body shape variations were also investigated at two depth levels, over one-year period.

MATERIALS AND METHODS

Data from the Ligurian Sea (Fig. 1) were collected during our long-term studies on benthic assemblages at the Portofino Promontory before the occurrence, in 1999, of a catastrophic mass mortality of sessile invertebrates, that deeply involved sponges, as well (Cerrano *et al.*, 2000). Comparative analysis was performed on a population from Crete (Fig. 1), given its position in the centre of the eastern Mediterranean Basin and the rare availability on the international market of a stock of bath sponges homogeneous with respect to both habitat and geographic origin.

Inter-population comparison of body shape

Several specimens (n = 119) of *S. officinalis* were collected by SCUBA method on hard sea-bottoms in Crete (63 specimens) and at the Portofino Promontory (56 specimens) on submerged rocky cliffs, both at 10-20 m depth in similar environmental conditions (Pronzato *et al.*, 1998; Georgopoulos *et al.*, 2000). Sponges were processed according to the traditional method for bath sponges by soaking and squeezing in sea water, freshwater rinsing, and air and sun drying in order to obtain cleaned spongin skeletons. Sev-

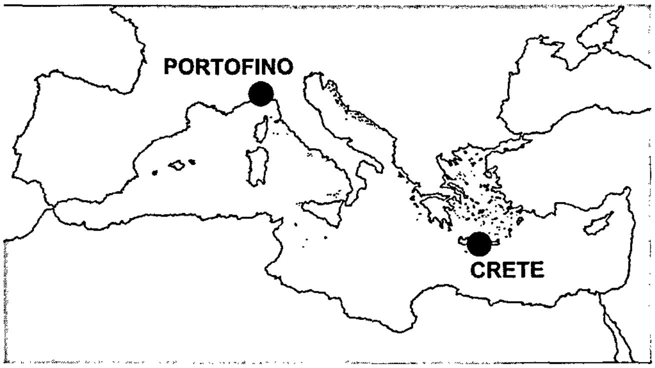

Fig. 1 - Map of sampling localities of *S. officinalis* in the Mediterranean Sea.

eral measurements were taken of these specimens (volume, weight, maximum height, maximum diameter, perimeter, area covered). Size, number, and density of oscules were also evaluated for each specimen; our samples contained two size classes (0.2-0.3 cm and 0.7-1.5 cm) according to oscule diameter which was discriminated as large (>0.5 cm) and small (<0.5 cm). Photographic images of each entire skeleton were digitalised, and perimeters and areas were measured by means of a Graphtec Digitizer KD 4300 connected to a PC (Pronzato & Pansini, 1994).

Volume, calculated with the method of Bavestrello *et al.* (1986), was compared with skeletal weight, a linear correlation being obtained for both populations (R^2 = 0.9747 at Portofino, and R^2 = 0.9585 Crete). Consequently, values of skeletal weight, easily measured by a Mettler P120, were used as biometric parameter. The ratios of areas covered to heights, areas covered to weights, and maximum diameters to heights were also calculated and expressed as mean values ± SD; Student's t-test was carried out on data sets.

Inter-population comparison of skeletal micro-traits

Fragments and slides of cleaned skeletons of 119 specimens from Portofino and Crete were analysed by Light Microscopy (LM) to focus on traits such as distribution and size of conules and oscules at the sponge surface, texture of the skeletal network, mesh size, shape and thickness of spongin fibres, and presence of foreign material in primary and secondary fibres. To investigate the pattern of spongin deposition in skeletal fibres, 10 samples (5 from Portofino and 5 from Crete) of skeletal network were critically point dried in CO_2 (Pabish CPD 750), then sputtered with gold-palladium (Balzers SCD 004) and observed under a Philips EM 515 scanning electron microscope (SEM).

Intra-population comparison at two depth levels

Two groups of 24 specimens each were studied *in situ* on the rocky cliff of the Portofino Promontory, at two depth levels (5-10 and 20-25 m) where environmental conditions were well known (Pronzato *et al.*, 1998). All specimens, marked with a numbered plastic plate (Fig. 2), were photographed *in situ* using a Hasselblad camera in a waterproof box during a single photographic session. Photographic images were digitalised for biometric evaluation (see above). Mean values, SD, and Student's t-test were calculated for the data sets.

Intra-population comparison throughout one year

Another group of 21 sponges from Portofino, belonging to the population considered above and regularly distributed in a depth range of 5-25 m, was monitored over a period of one year (September 1994-October 1995) in order to record shape variations in time. Each specimen was photographed six times from the same distance and viewpoint in order to collect a comparable series of shots. These temporal series of images were analysed as previously indicated.

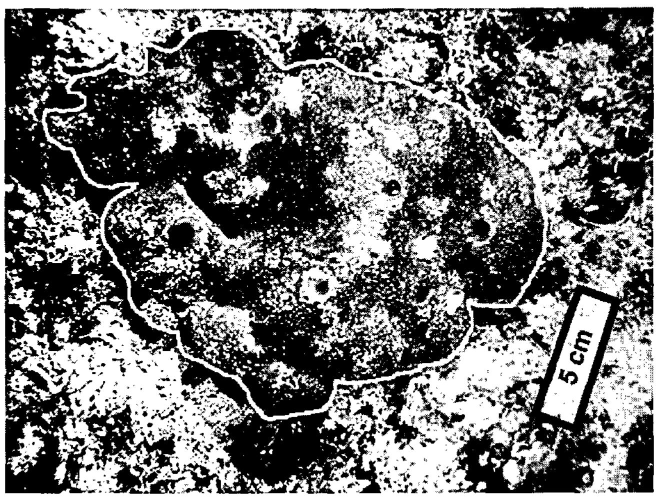

Fig. 2 - A specimen of *S. officinalis* belonging to the Portofino population monitored with the photographic non destructive method (see text).

RESULTS

Inter-population comparison of body shape

In the Portofino population, perimeter of naked skeletons ranged from 17.05 to 136.32 cm, area covered from 14.54 to 626.46 cm^2, total number of oscules from 1 in the smallest specimen to 91 in the largest one, dried skeletal weight from 2.02 to 111 g, maximum diameter from 5.9 to 39.6 cm, and body height from 2.7 to 13.5 cm. With regard to the Cretan specimens, perimeter ranged from 21.78 to 102.81 cm, area covered from 26.57 to 578.67 cm^2, total number of oscules from 5 to 513, dried skeletal weight from 1.22 to 80.13 g, maximum diameter from 6.8 to 30.2 cm and body height from 2.2 to 11.9 cm. Mean values and standard deviations are reported in Table I. The Student's t-test proved non-significant for perimeter, weight, and maximum diameter values, but significant ($P < 0.05$) for area measurements, and highly significant ($P < 0.001$) for height and total number of small and large oscules (Table I). A high level of significance ($P < 0.001$) was recorded also for the following ratios: maximum diameter/height, area/height, area/weight, large oscules/cm^2 of sponge surface, small oscules/cm^2 of sponge surface, and total oscules/cm^2 of sponge surface (Table I).

Inter-population comparison of skeletal micro-traits

The two populations of *S. officinalis* from Portofino and Crete shared all the diagnostic skeletal micro-traits

TABLE I - *Mean values of morpho-traits in* Spongia officinalis *from Portofino and Crete Island. Probabilities according to the Student's* t*-test.*

	Portofino	Crete	P
Perimeter (cm)	45.844 ± 19.67	51.78 ± 22.26	NS
Weight (g)	17.39 ± 20.01	18.06 ± 18.26	NS
Max. diameter (cm)	14.22 ± 5.75	15.82 ± 6.34	NS
Area (cm²)	112.12 ± 103.09	160.25 ± 129.81	<0.05*
Height (cm)	6.63 ± 2.25	5.02 ± 1.94	<0.001
Large oscules (n°)	6.26 ± 6.65	2.26 ± 4.21	<0.001
Small oscules (n°)	8.64 ± 11.69	80.84 ± 94.58	<0.001
Total oscules (n°)	14.91	83.11	<0.001
Large oscules/cm²	0.057 ± 0.053	0.011 ± 0.316	<0.001
Small oscules/cm²	0.097 ± 0.108	0.493 ± 0.312	<0.001
Total oscules/cm²	0.149 ± 0.11	0.502 ± 0.312	<0.001
Max. diameter/height	2.23 ± 0.75	3.309 ± 1.276	<0.001
Area/height	16.20 ± 10.62	31.27 ± 23.26	<0.001
Area/weight	7.49 ± 2.09	11.83 ± 4.43	<0.001

in the same size range as follows: secondary fibres (20--25 µm in diameter), free of inorganic inclusions, were characterised by a typical helicoidal twisting (Fig. 3A, E); a notably extended linear course with few anastomoses frequently characterised secondary fibres (Fig. 3A, E, G-H). Primary fibres, filled with foreign material predominantly sand grains, were arranged more or less radially from the sponge base up to the surface, to support the choanosomal skeleton. Primary fibres (50-100 µm in diameter) were usually connected by an almost regular three-dimensional network (mesh 50-80 µm in diameter) of secondary fibres (Fig. 3B, F) frequently webbed at the junctions with primary ones. The ectosomal skeleton was a network of secondary fibres supported by apices of primary ones to form the axis of conules (Fig. 3C, G); the conule distribution was more or less regular (Fig. 3D, H) with an inter-conular space of 2-3 mm, while conular height was usually 1-3 mm but ranged up to 4-5 mm along the oscular margins.

Intra-population comparison at two depth levels

Perimeters of live specimens photographed *in situ* at Portofino ranged from 19.55 to 69.66 cm at 5-10 m depth, and from 25.28 to 84.58 cm at 20-25 m depth. The areas covered ranged from 15.91 to 241.68 cm² at 5-10 m depth and from 30.83 to 211.11 cm² at 20-25 m. Mean values and standard deviations are reported in Table II. The total number of oscules ranged from 5 to 71 at 5-10 m depth and from 4 to 28 at 20-25 m. The density of large oscules ranged from 0.025/cm² at 5-10 m depth to 0.014/ cm² at 20-25 m depth, while that of small oscules ranged from 0.18/cm² at 5-10 m to 0.072/cm² at 20-25 m depth (Table II). The comparison between specimens investigated by Student's t-test (Table II) at the lower (Fig. 4A) and higher depths (Fig. 4B) at the Portofino cliff revealed no significant differences.

Intra-population comparison in time

The one-year-long monitoring of living target sponges at Portofino from September 1994 to October 1995 showed that mean values of perimeter, area covered, and active oscules did not change significantly in relation to time (Fig. 5A-C), and that specimens could fragment into clonal strains (Fig. 6A). Contraction of oscules (Fig. 6B-C) and their appearance/disappearance on the sponge surface (Fig. 6C) were frequently observed also in specimens that recorded inconspicuous body size variations without other body shape changes (Fig. 6B-C).

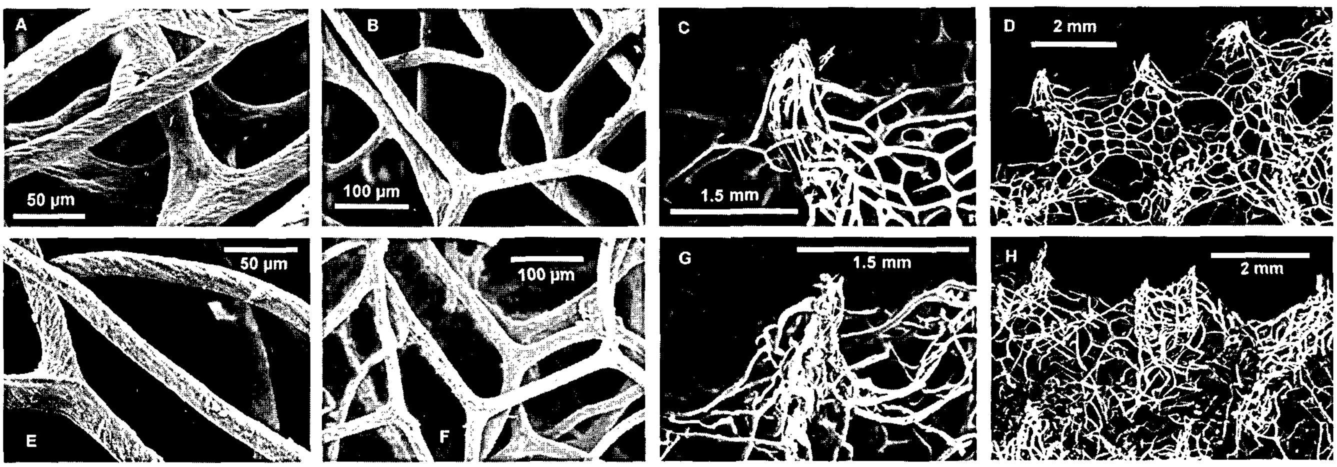

Fig. 3 - Scanning electron micrographs of skeletal micro-morphological traits in *S. officinalis* from Crete (**A-D**) and Portofino (**E-H**). **A**, **E**, secondary fibres with the peculiar twisted pattern of spongin at the surface. **B**, **F**, network of secondary fibres. **C**, **G**, conules with axial primary fibres supporting the ectosomal network of secondary fibres. **D**, **H**, conulose surface in the ectosomal skeleton.

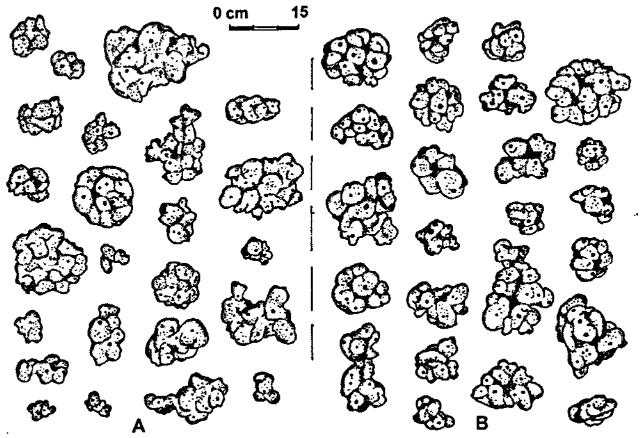

Fig. 4 - Morphotypes of *S. officinalis* photographed at the Portofino cliff at 8-10 m (A) and at 20-25 m depth (B).

TABLE II - *Mean values of* Spongia officinalis *morpho-traits at two depth levels in Portofino cliff. Probabilities according to the Student's* t*-test.*

	Portofino 5-10 m	Portofino 20-25 m	P
Perimeter (cm)	37.73 ± 17.23	41.68 ± 1.34	NS
Covered area (cm^2)	78.66 ± 62.04	146.19 ± 53.83	NS
Small oscules (no.)	14.25 ± 14.78	10.48 ± 1.41	NS
Large oscules (no.)	1.58 ± 2.15	2.12 ± 2.83	NS
Total oscules (no.)	15.83 ± 15	17.00 ± 4.24	NS
Small oscules/cm^2	0.18	0.072	NS
Large oscules/cm^2	0.025	0.014	NS
Total oscules/cm^2	0.201	0.116	NS

DISCUSSION

No significant differences in body shape characters were revealed in living specimens of *S. officinalis* between the two depth levels at Portofino, although the whole population displayed a wide range of size classes at both investigated depth levels (Fig. 4).

Also, the constancy of values for mean area covered, perimeter, and number of oscules during the one-year survey suggested that few variations of biomass generally occurred in the Portofino population (Fig. 5). Instead, the long-term observations highlighted the spatial shift of oscules, and their increase/decrease in diameter also suggested modifications of the aquiferous system architecture (Fig. 6), even though these variations might be due simply to short-term contractile phenomena depending on the filtering activity status. In the long term, the most evident phenomena were mainly fragmentation and re-organisation of the sponge body (Fig. 6A) in accordance with the clonal strategies of sponges and their phenotypic plasticity (Wulff, 1985, 1991; Pronzato & Pansini, 1994; Pronzato & Manconi, 1995). A wide temporal variability in body shape and size due to fragmentation into clonal strains and subsequent regenera-

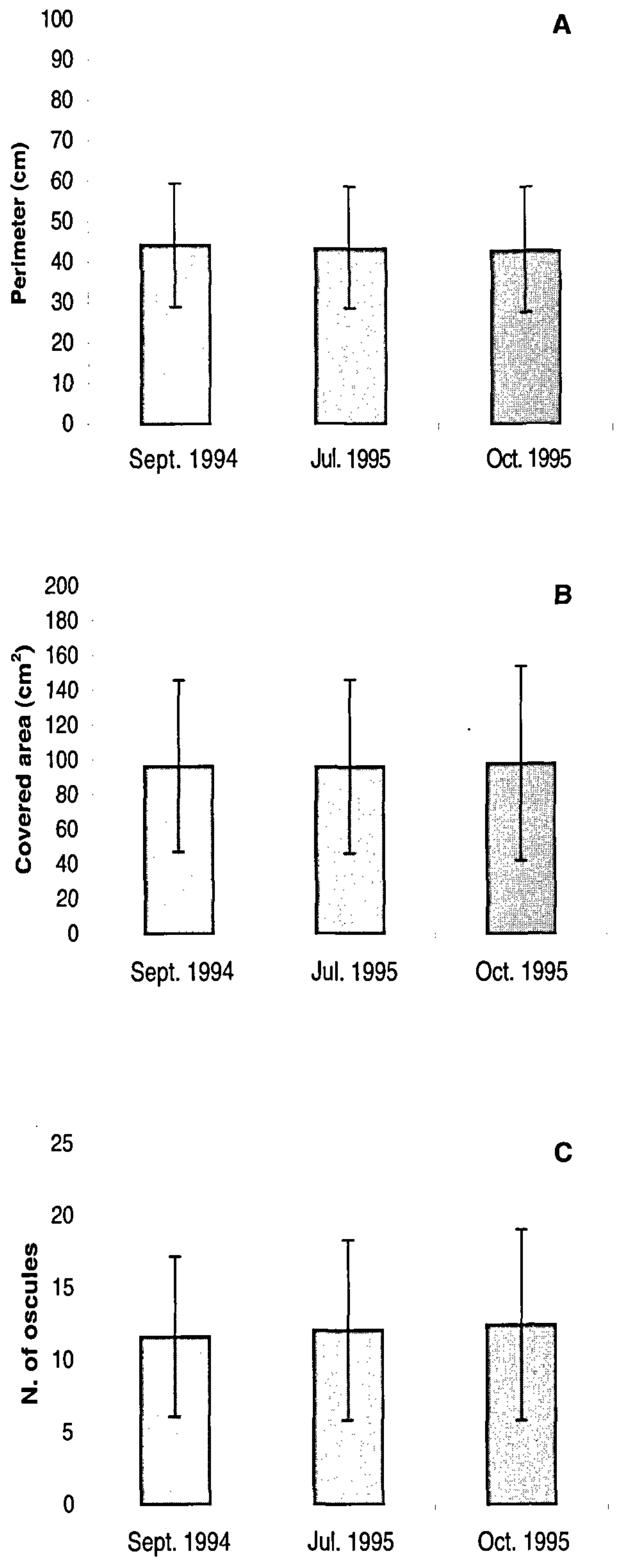

Fig. 5 - One-year analysis of the main body shape traits in living specimens of *S. officinalis* from Portofino. Mean values (± SD) of perimeter (A), area covered (B), and number of oscules (C).

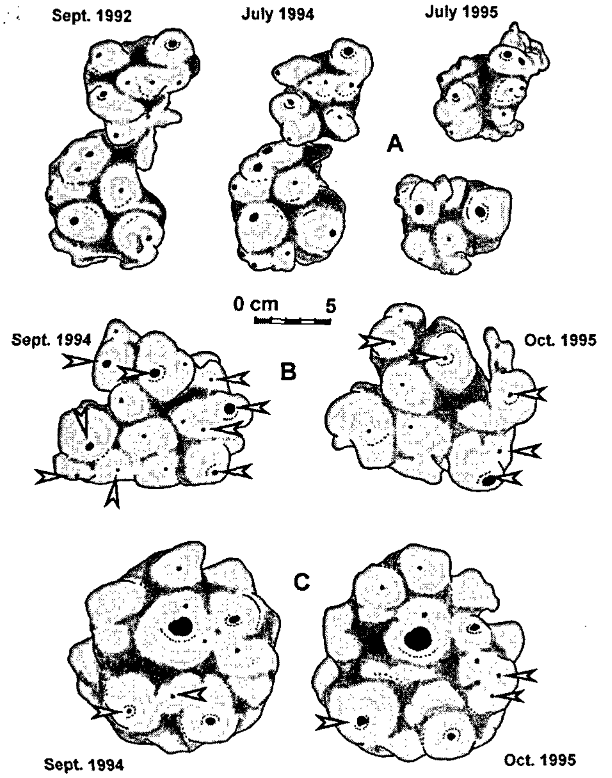

Fig. 6 - Some remodelling phenomena observed in *S. officinalis* during the temporal analysis. **A**, fragmentation into clonal strains. **B-C**, size variations and contraction of oscules; arrows indicate the appearance/disappearance of oscules and their size changes.

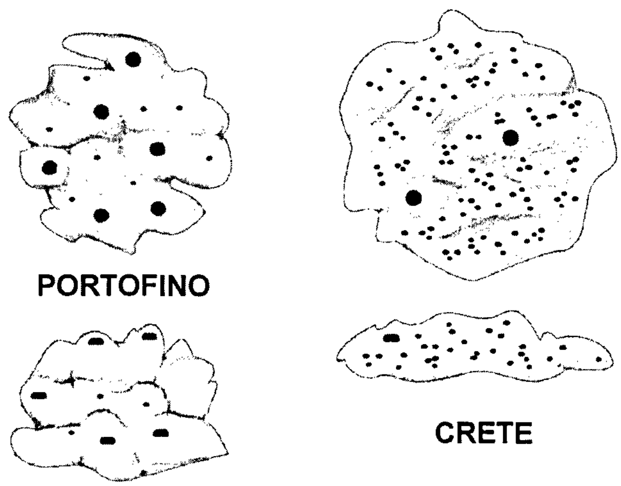

Fig. 7 - Schematisation of the two morphotypes of *S. officinalis* from the eastern and western Mediterranean. Portofino specimens appear massive with several large oscules and a few small ones, whereas the Cretan specimens have a flattened shape with a high number of small oscules and a very low number of large oscules.

tive processes and re-aggregation phenomena characterise Mediterranean populations of other species such as *Oscarella lobularis*, *Cacospongia mollior*, *Anchinoe tenacior*, *Clathrina clathrus*, *Chondrosia reniformis* and *Chondrilla nucula* (Pansini & Pronzato, 1990; Pronzato & Pansini, 1994; Gaino *et al.*, 1995).

Plastic vs conservative body shape strategies were displayed by different specimens (Fig. 6), but no differences were encountered between the two groups of sponges at the two different depths (Fig. 4), which led us to consider the Portofino population as homogeneous.

LM and SEM analyses of the skeletal micro-traits evidenced a notable uniformity in the two tested populations from the eastern and western Mediterranean (Fig. 3). Micromorphology of skeletal traits seemed highly conservative in distant populations of *S. officinalis*, whereas the general body architecture was significantly divergent in the two geographical regions. In synthesis, sponges from Portofino appeared massive with several large oscules and a few small ones, while specimens from Crete tended to have a flat body with a large number of small oscules, and a few large ones (Fig. 7; Table I).

These data allow the different bath sponge banks and their geographical origin to be distinguished according to the traditional experience of sponge traders and fishermen. It is, however, not easy to define from a zoological and taxonomic point of view this empirical knowledge. Although a generalisation cannot be made when only two sites are compared, the present morphometric data appear to discriminate between populations and support the diagnostic validity of macromorphological characters for distinguishing geographical morphs of *S. officinalis*. Skeletal micro-characters, on the other hand, are highly conservative and shared by the two populations, confirming the taxonomic validity of *S. officinalis* in both the eastern and western Mediterranean.

A general improvement in knowledge of Mediterranean populations and morphotypes of *S. officinalis* could lead to the promotion of an international quality trade mark to characterise the geographic provenience and protect the high quality and value of Mediterranean commercial sponges from extra-Mediterranean stocks. New investigations are however needed for better defining the gross morphology of populations from other Mediterranean localities. Also, mechanical properties of the spongin skeleton such as flexibility, softness and resiliency, together with the colour of the skeleton according to the abundance of iron granules in the spongin fibres (Vacelet *et al.*, 1988) are useful traits for identifying and characterising the provenience and quality of bath sponges.

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