

M. Mercurio · G. Corriero · E. Gaino

## Sessile and non-sessile morphs of *Geodia cydonium* (Jameson) (Porifera, Demospongiae) in two semi-enclosed Mediterranean bays

Received: 12 February 2005 / Accepted: 7 April 2005 / Published online: 28 September 2005  
© Springer-Verlag 2005

**Abstract** Morphological plasticity and ecological aspects of the demosponge *Geodia cydonium* (Jameson) were studied from seasonal samples collected over 1 year in two semi-enclosed Mediterranean bays of the Southern Italian coast (Marsala lagoon and Porto Cesareo basin). Sponge specimens present two morphs: sessile and non-sessile, both of which showed constant size distribution and density over the studied year. Sessile specimens were larger in size than non-sessile ones. This feature is particularly evident at Porto Cesareo, where these sponges have a more compact skeletal network than at Marsala (evident both in the cortical spicule size and sponge silica content). Sessile specimens adhere to hard rocky substrates (Porto Cesareo) or phanerogam rhizomes (Marsala); non-sessile ones occur on soft bottom areas. Several morphological and structural features of the non-sessile forms differ in the two environments, but the difference in body shape seems to play the most relevant role in enhancing the colonization of incoherent substrates. Indeed, at Marsala, where the large amount of silt and clay determines the occurrence of a markedly reduced anoxic layer just below the surface of the sediment, non-sessile specimens of *G. cydonium* are fairly spherical and thus able to roll, dragged by slow circular currents. In addition, the usual association with the red alga *Rytiphloëa tinctoria*, which almost constantly forms a thick and continuous layer around the sponge, allows them to avoid contact with the substrate. The non-sessile specimens from Porto Cesareo inhabit sandy soft bottoms and are flattened. In such an environment,

affected by moderate wave turbulence, the flattened shape widens the contact surface between the body and the substrate, thereby reducing the risk of stranding. The evident signs of abrasion, provided by scanning electron microscopy investigations, on both cortical spicules and outermost sponge surface suggest that sponges rub on the bottom. Sediment, epibiotic organisms, and the phanerogam leaves protect this sciaphilous sponge from high solar radiation, allowing the specimens to live in these shallow environments.

### Introduction

Sponges are organisms whose gross morphology is not static. Indeed, remodelling processes take place throughout their life cycle, allowing sponges to adapt to their environment (Palumbi 1984; Bond and Harris 1988; Gaino et al. 1995; Bell et al. 2002). This plastic morphology is essential for survival, since it gives better opportunity for feeding (Vogel 1981), reproduction and dispersal (Wulff 1985, 1991, 1995; Corriero et al. 1996a), water current adaptation (Vogel 1981; Palumbi 1984; Kaandorp 1991, 1999; Kaandorp and Kluijver 1992; Bell and Barnes 2000; Bell et al. 2002; McDonald et al. 2002), and protection against predators (Guide 1976; Hill and Hill 2002) as well as preventing sediment settlement (Bell 2004).

In order to meet the environmental needs, sponges are capable of modifying their body shape (Palumbi 1986; Kaandorp 1999) but phenotypic variations are not unlimited because a sponge can arrange its body pattern into a limited range of forms (Kaandorp and Kluijver 1992). The skeletal components are also not static, since seasonal changes in the number of spicules have been observed, resulting in an increased inorganic content (Stone 1970; Schonberg and Barthel 1997; Mercurio et al. 2000). Moreover, differences in skeletal components may also be related to differences in wave exposure (Palumbi 1986; Bell et al. 2002; McDonald et al. 2002).

Communicated by R. Cattaneo-Vietti, Genova

M. Mercurio · G. Corriero (✉)  
Dipartimento di Zoologia, Via Orabona, 4-70125 Bari, Italy  
E-mail: g.corriero@biologia.uniba.it  
Tel.: +39-80-544-3358  
Fax: +39-80-544-3358

E. Gaino  
Dipartimento di Biologia Cellulare e Ambientale, Via Elce di Sotto,  
06123 Perugia, Italy

The finding, in Mediterranean lagoons, of peculiar non-sessile specimens of *Geodia cydonium* coexisting with the typical sessile forms (Mercurio et al. 1997a,b), stresses the fact that acclimatization can lead to a free-existing morphotype in a phylum typically represented by sessile forms. The occurrence of these non-sessile specimens corroborates Burton's (1932) assumption, derived from observations of a sponge collection consisting of specimens belonging to different taxa, that even adult sponges may spend their life floating just above the sea-floor and may be lifted by currents of moderate force. Unattached sponges have been found in other shallow sub-littoral environments (Sarà and Vaculet 1973; Corriero 1990; Bell and Barnes 2002) and in the deep sea, where conditions are relatively stable over time (Barthel and Tendal 1993).

The purpose of this study is to analyse populations of *G. cydonium* (Jameson) (Porifera, Demospongiae) in two semi-enclosed bays located along the Southern Italian coast, namely Marsala lagoon (Sicily) and Porto Cesareo basin (Apulia), in order to investigate the morphology and skeletal architecture of sessile and non-sessile specimens along with the strategy employed by this sciaphilous sponge to protect itself from high solar radiation.

## Materials and methods

### Study sites

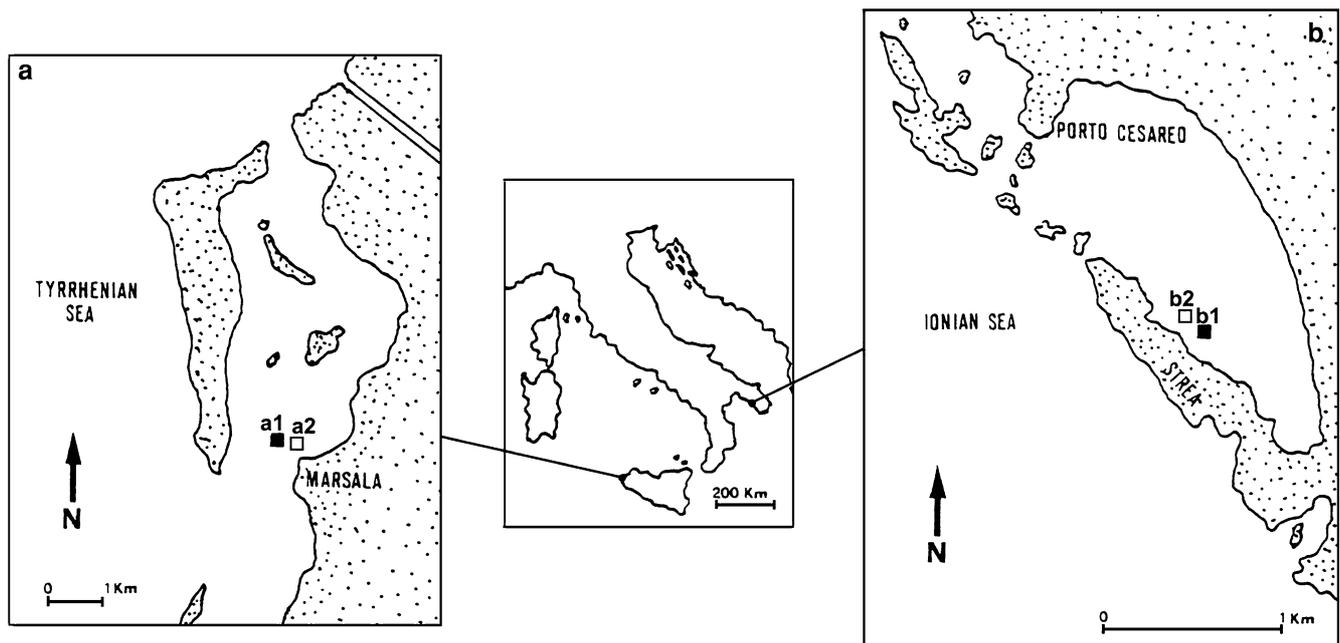
Both the studied sites are characterized by low water movement and moderate input of organic matter (Magazzù 1977; Genchi et al. 1983; Congedo 1988).

Marsala lagoon (Fig. 1a) (NW Sicily, 37°14'N; 12°40'E) covers an area of 20 km<sup>2</sup> with a maximum depth of 2.5 m (Magazzù 1977). It is characterized by a high water exchange with the sea, mainly through the southern opening, which reduces thermohaline oscillations. However, the presence of 'reefs' of *Posidonia oceanica* (L.) Delile (Molinier and Picard 1953; Calvo and Fradà Orestano 1984) greatly decreases the wave action even in the outermost part of the lagoon (Corriero et al. 1989). Hard substrates are scarce, mainly represented by algal or animal calcareous concretions and by the rhizomes of the phanerogam *P. oceanica*. Demosponges are a very important component of the macrozoobenthos, being represented by 36 species and high biomass values (Corriero 1989, 1990).

Porto Cesareo basin (SW Apulia, 40°15'N; 17°54'E) (Fig. 1b) measures 2,500 m in length and 700–800 m in width, with a maximum depth of 2.5 m (Passeri 1974). The basin communicates with the sea through a channel system that allows a considerable inflow of sea water (Corriero 1990). The bottom of the basin consists primarily of mixed sands but rocky shores, rocks and pebbles are also present. Thirty-nine species of demosponges occur in the basin showing high coverage values (Corriero 1990; Corriero et al. 1996b; Mercurio et al. 2001).

### Species studied

*Geodia cydonium* (Jameson 1811) is a well-known Atlantic–Mediterranean demosponge that is very common in sciaphilous environments (Uriz 1981). At the study sites, in addition to rich populations of sessile



**Fig. 1** The study sites with the sampling areas of sessile (black squares: a1, b1) and non-sessile (white squares: a2, b2) specimens. **a** Marsala lagoon (NW Sicily, 37°14'; 12°40'). **b** Porto Cesareo basin (SW Apulia, 40°15'; 17°54')

specimens, many non-sessile specimens also occur (Corriero 1990; Mercurio et al. 1997a,b, 2001).

In Marsala lagoon, the sessile specimens settle primarily on the rhizomes of *P. oceanica*, at depths ranging between 0.5 and 2 m (Corriero 1989) (Fig. 1a, a1). The non-sessile specimens occur on the soft bottom of the lagoon in wide storage areas, about 2 m deep (Mercurio et al. 1997a) (Fig. 1a, a2).

In Porto Cesareo basin, the sessile specimens of *G. cydonium* mainly colonize the middle part of the basin on rocky calcareous substrates, at a depth of 1–2 m (Fig. 1b, b1). The non-sessile specimens are located in an adjacent area but on soft bottoms (Mercurio et al. 1997b) (Fig. 1b, b2).

### Sampling protocol

In each site, sampling of *G. cydonium* was carried out using SCUBA equipment; the collection of data was limited to the two areas where sessile and non-sessile specimens were observed during previous research (Corriero et al. 1984; Corriero 1989, 1990; Mercurio et al. 1997a,b; Gherardi et al. 2001) (Fig. 1a, b).

Due to the remarkable population dispersal at Porto Cesareo, with respect to Marsala (Corriero et al. 1984; Corriero 1989, 1990; Mercurio et al. 1997a,b), sponges were collected inside sampling squares differing in dimensions: a square of 25 m<sup>2</sup> at Porto Cesareo and a square of 5 m<sup>2</sup> at Marsala. Sampling was carried out with seasonal frequency (January, April, June, and October 2002) in the areas a1, a2, b1, and b2 (Fig. 1a, b).

Sessile specimens were collected by removing the rhizomes of *P. oceanica* (Marsala) or by scraping the calcareous substrate (Porto Cesareo). Non-sessile specimens were collected using a dredge with a 5 mm mesh size (knot-to-knot). Immediately after collection specimens were fixed in 4% formaldehyde in sea water. The density values of both the sessile and non-sessile specimens were evaluated. For each specimen, measurements of volume and shape were taken. Volumes (ml) were measured by enveloping each specimen with a plastic film and dipping it into a graduated beaker containing water; the size distribution is expressed as the logarithm of volume + 1. The shape of sessile and non-sessile specimens is expressed as the ratio between the maximum base diameter and the maximum height (shape coefficient).

### Epibiotic and sediment covering on the sponge surface

Before collection, a semi-quantitative analysis of epibiotic organisms was carried out covering the external surface of each specimen (expressed as a percentage) using a 15×15 cm<sup>2</sup>, divided by a nylon thread into 25 smaller squares of side 3 cm. A semi-quantitative abundance index (according to Relini 2003) was assigned to the epibiotic organisms in each smaller squares to indicate their coverage (+ = < 1%; 1 = < 5%;

2 = 5–25%; 3 = 25–50%; 4 = 50–75%; 5 = 75–100%). The coverage reported for each sponge specimen is the mean value of the 25 smaller squares. The most common epibiotic organisms were identified. Moreover, a quantitative estimation of the sediment layer covering the sponge surface was made using a small corer (2 cm in diameter). Two samples were collected for each specimen by introducing the corer vertically into the sponge to a depth of 2 cm. The sediment layer was removed from the sponge fragment and then the dry weight sediment was measured.

In order to investigate the cortical skeletal ultra-structure of sessile and non-sessile sponges, fragments of sponge tissue, dissected from some specimens before their fixation in toto, were fixed for scanning electron microscopy (SEM) in 2.5% glutaraldehyde in a buffer of cacodylate and filtered sea water to a final pH 7.4. After 2 h, the fixed material was then dehydrated in a graded ethanol series and critical point dried using a CO<sub>2</sub> Bal-Tec CPD 030 apparatus, mounted on stubs with silver-conducting paint, and coated with gold palladium (20 nm) in an Emitech K 550X Union Evaporator. Specimens were observed under an SEM Philips XL30 at an accelerating voltage of 10 kV.

### Spicule size and silica content

For morphometric analysis of the spicule size, sponge samples (0.5 cm<sup>3</sup>) were cleaned by boiling in nitric acid 65%, washed repeatedly in distilled water and alcohol, and gently agitated to suspend the spicules. Thereafter, the spicule suspension was spread over a microscope slide and evaporated to dryness. The average seasonal diameters of the cortical sterraster and choanosomal oxyaster were calculated by measuring 50 randomly selected spicules for each slide.

The silica concentration of the cortex and choanosome was determined for each specimen by the following procedure: a piece of sponge, measuring about 1 cm<sup>3</sup>, was weighed after dehydration at 100°C for 24 h, and the silica was subsequently eliminated by digestion with 5% hydrofluoric acid for 12 h. After drying, the sample was again weighed and the silica content estimated by calculating the difference between the two dry weights.

### Environmental parameters

Samples of soft bottoms were collected from areas inhabited by non-sessile sponges (a2 and b2) in order to obtain the particle-size analysis. Sampling was performed using a corer (3.2 cm in diameter) introduced vertically into the sediment for 20 cm. The sediment was divided into two fractions by wet sieving (63 μm). The larger fraction (gravel and sand) was then analysed dry using a mechanical sieve shaker, and the fraction less than 63 μm (silt and clay) by determination of sedimentation rate. Moreover, redox measurements were made in situ according to Bagander (1976).

## Results

### Population structure

#### Marsala

A total of 50 sessile specimens of *G. cydonium* and 19 non-sessile ones were collected over the sampling period. The mean density of sessile specimens was  $2.5 \pm 0.48/\text{m}^2$ , ranging from  $2.2/\text{m}^2$  recorded in October to  $3.0/\text{m}^2$  recorded in January; the mean density of non-sessile specimens was  $0.95 \pm 0.1/\text{m}^2$  ranging from  $0.8/\text{m}^2$  recorded in July to  $1.0/\text{m}^2$  recorded in January, April, and October.

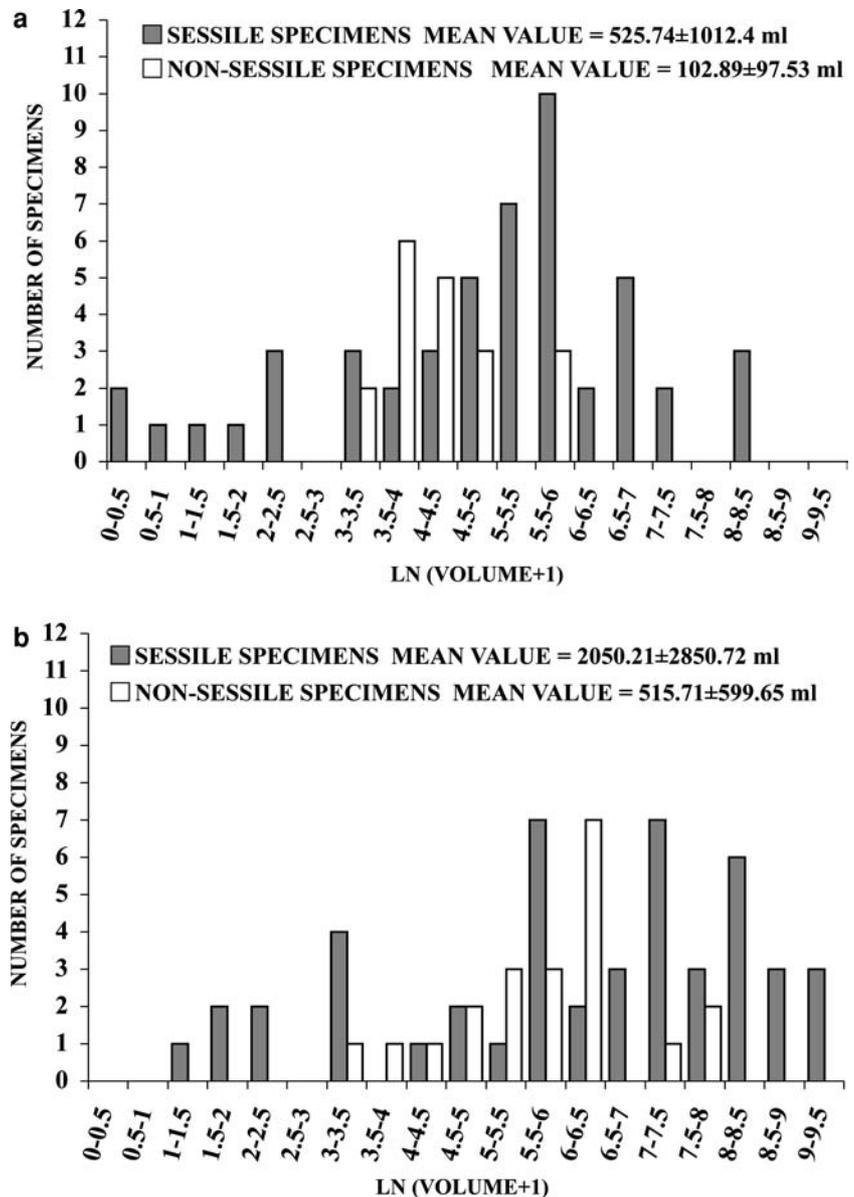
Seasonal monitoring did not show significant differences in the volume distribution of the sessile and non-sessile specimens ( $P > 0.05$ ; Kruskal–Wallis test). The sessile specimens had larger dimensions than the

non-sessile ones, their mean volume being  $525.74 \pm 1012.4$  vs  $102.89 \pm 97.53$  ml ( $P < 0.05$  Mann–Whitney *U*-test). The analysis of the volume frequency histograms (Fig. 2a) indicated a concentration of the non-sessile specimens in the middle classes, with two peaks in the distribution between 3.5 and 4.5 (corresponding to values ranging between 33 and 90 ml). The sessile specimens showed a wider distribution up to 8.5 (4,913 ml). The non-sessile specimens lacked small size classes ( $< 3 = 19$  ml).

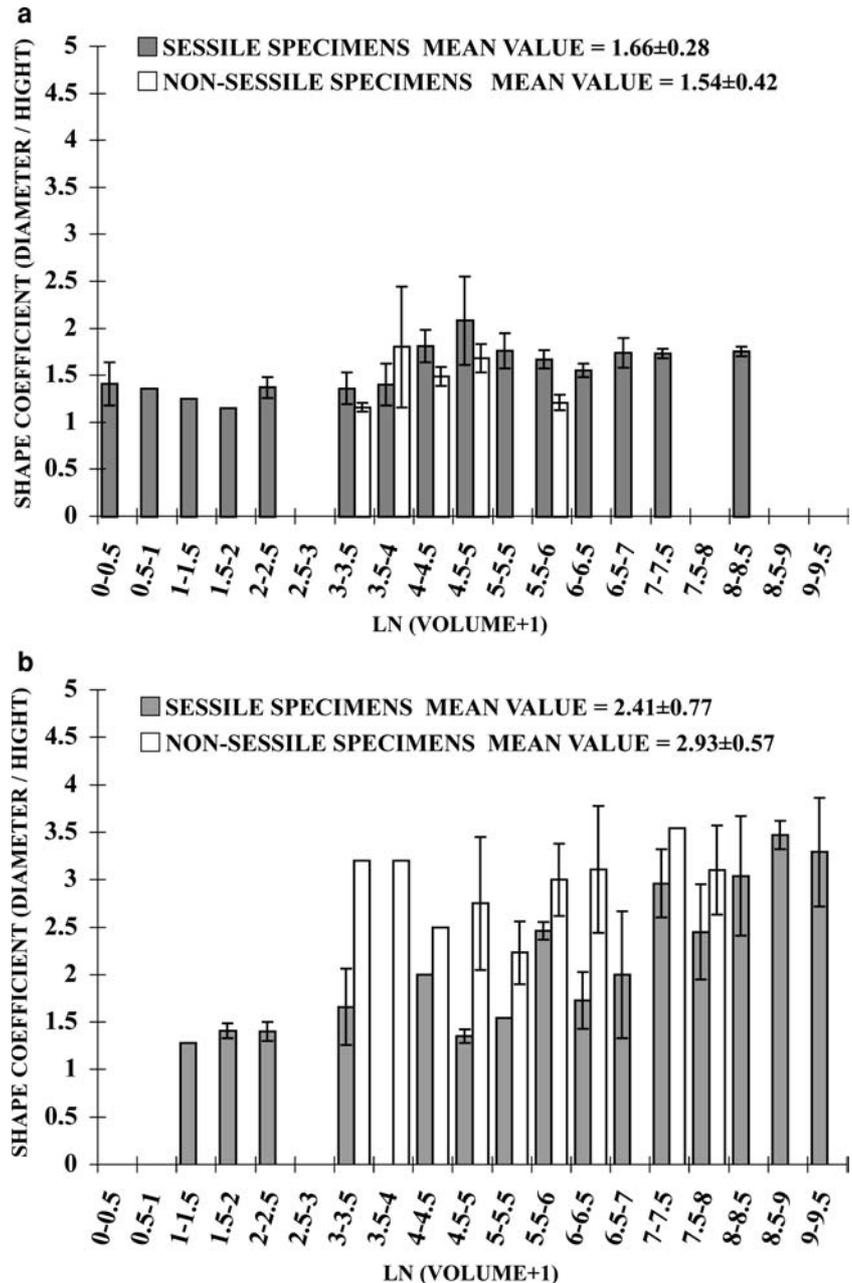
#### Porto Cesareo

A total of 47 sessile specimens of *G. cydonium* and 21 non-sessile ones were collected. The mean density of sessile specimens was  $0.47 \pm 0.075/\text{m}^2$ , ranging from  $0.36/\text{m}^2$  recorded in January to  $0.52/\text{m}^2$  recorded in April and July; the mean density of the non-sessile

**Fig. 2** *Geodia cydonium*: volume–class distribution (expressed as  $\ln(\text{volume} + 1)$ ) of sessile and non-sessile specimens collected throughout the sampling period in Marsala lagoon (a) and in Porto Cesareo basin (b)



**Fig. 3** *Geodia cydonium*: shape coefficient distribution in the volume classes (mean value  $\pm$  SD) of sessile and non-sessile specimens in Marsala lagoon (a) and in Porto Cesareo basin (b)



specimens was  $0.21 \pm 0.02/\text{m}^2$ , ranging from  $0.2/\text{m}^2$  recorded in January, April, and July to  $0.24/\text{m}^2$  recorded in October.

The mean volume of the sessile specimens was about four times higher than that of the non-sessile ones ( $2,050.21 \pm 2,850.72$  vs  $515.71 \pm 599.65$  ml), even if the statistical analysis with the *U*-test ( $P=0.47$ ) did not reveal significant differences. The analysis of the volume frequency histogram (Fig. 2b) indicated a fairly wide distribution. The sessile specimens showed a wider distribution up to 9.5 (10,000 ml). The non-sessile specimens lacked small size classes ( $< 3 = 19$  ml) and showed one peak between 6 and 6.5 (corresponding to values ranging between 33 and 90 ml). Seasonal monitoring did not show significant differences between the volume

distribution of the sessile and non-sessile specimens ( $P > 0.05$ ; Kruskal–Wallis test).

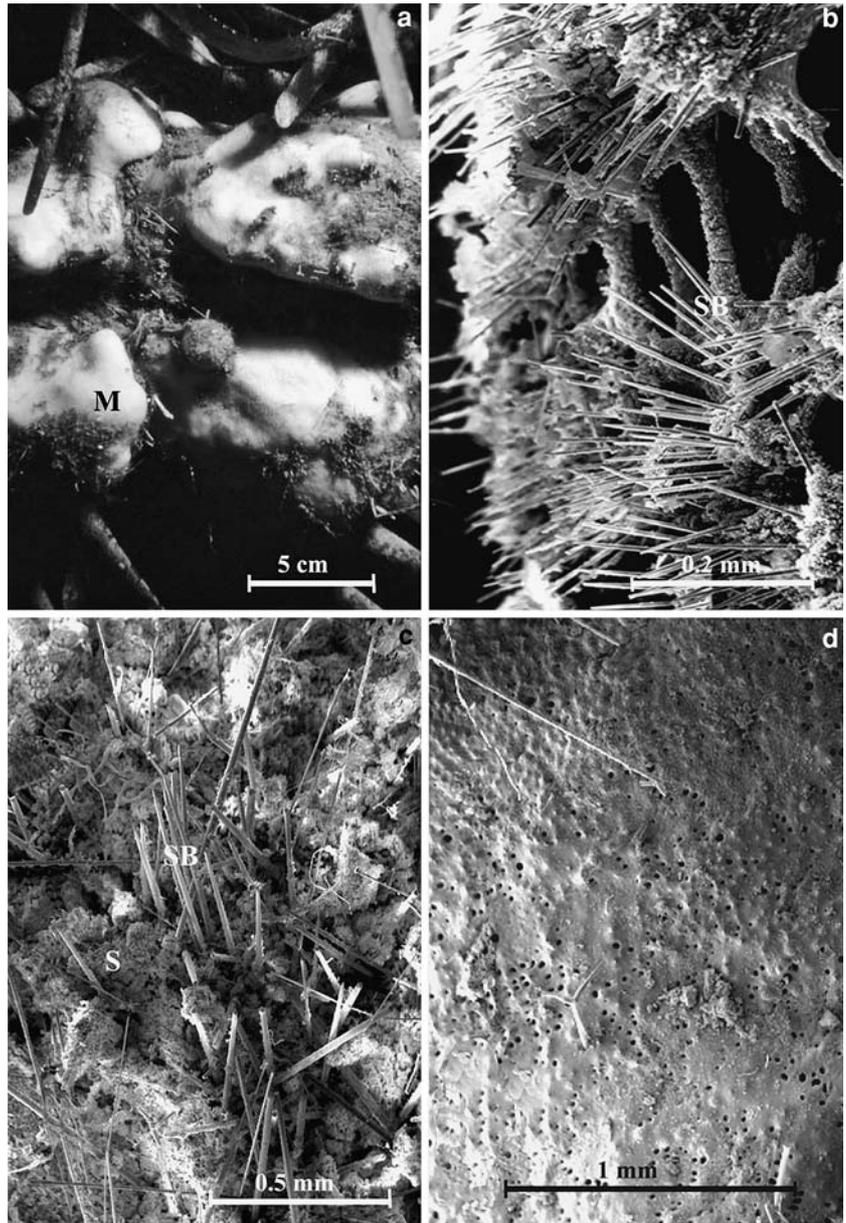
#### Sponge shape and external covering

##### *Marsala*

The mean values of the shape coefficient of sessile and non-sessile specimens ( $1.66 \pm 0.28$  and  $1.54 \pm 0.42$ , respectively) revealed a more spherical shape in the latter specimens ( $P < 0.05$  Mann–Whitney *U*-test) (Fig. 3a).

Figure 4a shows that the sessile specimens are globous and have mamelons protruding from the sponge surface, where epibionts and sediment form irregular

**Fig. 4** Sessile specimens of *Geodia cydonium* in Marsala lagoon. **a** Detail of the external surface of the sponge showing protruding mamelons (M). **b** SEM view of spicule bundles (SB) emerging from the sponge surface. **c** SEM view of sediment (S) entrapped by sponge spicule bundles (SB). **d** SEM view of cribrous regions without spicule bundles



patches. Ultrastructural investigation allowed us to observe that, while in the regions covered with sediment the spicule bundles are very frequent (Fig. 4b) and retain the sediment (Fig. 4c), and in the cribrous regions the surface is very clean and spicules are almost absent (Fig. 4d). In these specimens the sediment layer, expressed as  $\text{g}/\text{cm}^2$  (dry weight), varied from 0.02 to  $0.11 \text{ g}/\text{cm}^2$  (mean value  $0.06 \pm 0.03 \text{ g}/\text{cm}^2$ ); the covering of the sponge surface by epibionts varied from 5 to 35% (mean value  $19.3 \pm 9.3\%$ ). The frondose bryozoans *Margaretta cereoides* (Ellis and Solander) together with the macroalga *Caulerpa prolifera* (Forsk.) Lamouroux were the most common epibionts.

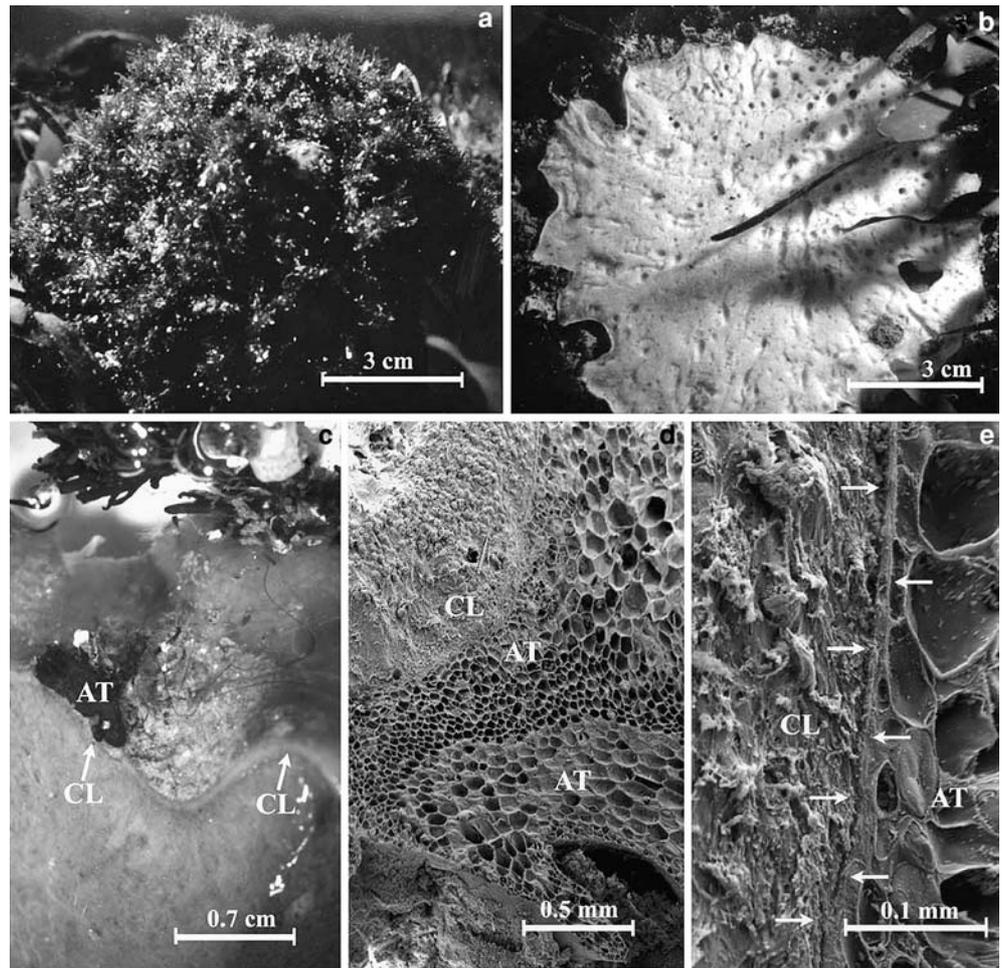
Figure 5a shows that the non-sessile specimens are sub-spherical, which is more evident in cross-sectioned specimens (Fig. 5b). The slow circular water currents make sponges roll on the soft substrate. Most of them

(about 90%) are covered with a thick layer of the red alga *Rytiphloëa tinctoria* (Fig. 5a), which is firmly attached to the sponge cortical region (Fig. 5c). SEM images show that even though the thallus deepens into the cortex, algal tissues do not penetrate into the choanosomal region (Fig. 5d). The alga tightly adheres to the sponge surface (Fig. 5e). Only on occasion, does the thallus penetrate inwards throughout the opening outside of the aquiferous canal system. The covering of the sponge surface with *R. tinctoria* varied from 70 to 85% (mean value  $78.3 \pm 7.64\%$ ); the sediment coat ranged from 0.08 to  $0.16 \text{ g}/\text{cm}^2$  (mean value  $0.12 \pm 0.04 \text{ g}/\text{cm}^2$ ).

#### *Porto Cesareo*

The comparison between the mean value of the shape coefficient calculated for sessile and non-sessile sponges

**Fig. 5** Non-sessile specimens of *Geodia cydonium* in Marsala lagoon. **a** A subspherical specimen covered with a thick layer of the red alga *Rytiphloëa tinctoria*. **b** Cross section of the specimen in (a). **c** Algal thallus (T) tightly adherent to the thin cortical layer (CL). **d** SEM view of the algal thallus (AT) deepening into the cortical layer (CL). **e** SEM view detail of the relationship between the algal thallus (AT) and the cortical layer (CL). Note the tight adhesion between sponge and algal tissues (arrows)



( $2.41 \pm 0.77$  and  $2.99 \pm 0.57$ , respectively) indicates that the latter individuals show a more evident flattened shape ( $P < 0.05$ , Mann–Whitney  $U$ -test) (Fig. 3b).

Sessile (Fig. 6a) and non-sessile specimens (Fig. 7a) show a massive shape, even though the sessile sponges are more massive and have a brain-shaped pattern.

The sessile individuals are covered with a continuous layer of macrobenthic organisms and sediment (Fig. 6a). Cross sections of sessile individuals examined under a stereomicroscope reveal the particular thickness of the cortical layer (Fig. 6b), a feature confirmed by SEM images that show numerous and densely packed sterrasters filling this layer in its extension (Fig. 6c). Spicule bundles emerge from the cortex and form a dense palisade that entraps sediment and algal filaments (Fig. 6d). Sediment on the sponge cortical surface varied from 0.13 to 0.48 g/cm<sup>2</sup> (mean value  $0.30 \pm 0.11$  g/cm<sup>2</sup>), while the covering by epibionts varied from 10 to 70% (mean value  $32.3 \pm 18.01\%$ ); epibiotic organisms consisted of algae (mainly *Padina pavonia* (Linneus) and various species belonging to *Cystoseira*), but many species of demosponges (mainly *Tedania anhelans* Lieberkühn), hydroids, bryozoans, and worms were also present.

The non-sessile sponges are characterized by an upper surface similar to that of the sessile individuals (Fig. 7a), whereas the lower part, in contact with the

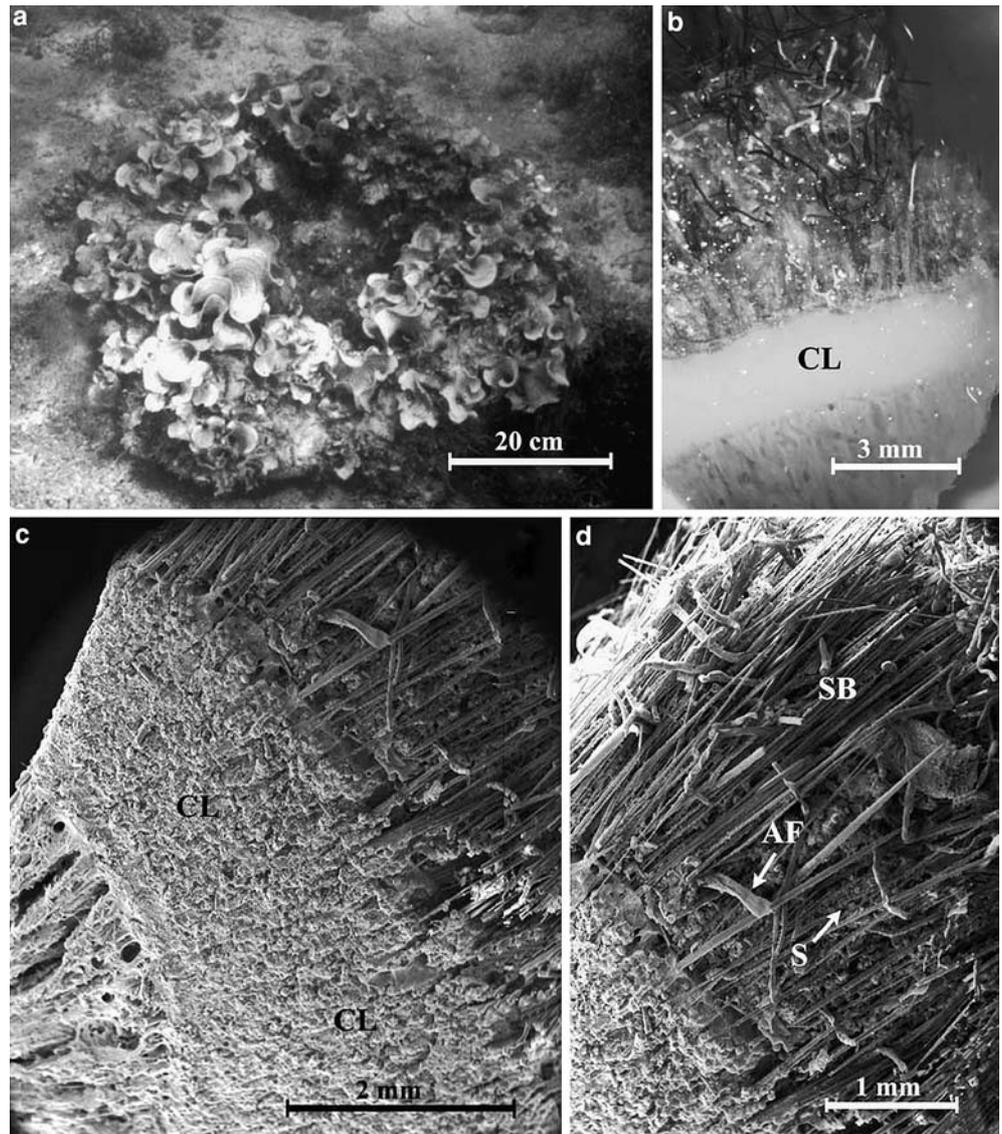
substrate, lacks both epibionts and sediment (Fig. 7b). The smooth appearance of this lower part is due to the scraping of the sponge on the soft bottom. Owing to the gradual loss of the integrity of the cortical region, spicule bundles break and their main axes adhere to the sponge surface where they are amidst the sterrasters (Fig. 7c). The scraping of the sponge on the substrate causes a gradual smoothing of the cortical sterrasters that lose their typical pattern (Fig. 7d). Sediment on the sponge cortical surface varied from 0.11 to 0.20 g/cm<sup>2</sup> (mean value  $0.16 \pm 0.03$  g/cm<sup>2</sup>), while the covering by epibionts varied from 5 to 20% (mean value  $10.71 \pm 4.46\%$ ). Epibiotic organisms were the same as the sessile specimens.

#### Skeletal features

##### Marsala

The mean values of choanosomal oxyaster diameter, calculated for sessile and non-sessile specimens, were  $19.83 \pm 3.41$  and  $21.65 \pm 2.66$  μm, respectively (Fig. 8a, b). The mean value of cortical sterraster diameter was  $40.05 \pm 3.13$  μm in the sessile specimens and  $37.43 \pm 4.35$  μm in the non-sessile ones. A seasonal

**Fig. 6** Sessile specimens of *Geodia cydonium* in Porto Cesareo basin. **a** A specimen covered with a layer of macrobenthic organisms. **b** Cross section showing the thick cortical layer (CL). **c** Detail under SEM showing the thick cortical layer (CL) filled up by densely packed sterrasters. **d** Detail under SEM of spicule bundles (SB) that formed a palisade emerging from the sponge cortex. Note that sediment (S) and algal filaments (AF) are intermingled with the spicules



comparison of spicule diameter both in sessile and non-sessile specimens, showed no significant differences ( $P > 0.05$ ; Kruskal–Wallis test). In contrast, cortical sterraster diameters were significantly higher in the sessile specimens than in the non-sessile ones ( $P < 0.05$ , Mann–Whitney  $U$ -test) while no significant differences were noted for the choanosomal oxyaster diameters between the sessile and non-sessile specimens ( $P > 0.05$ , Mann–Whitney  $U$ -test).

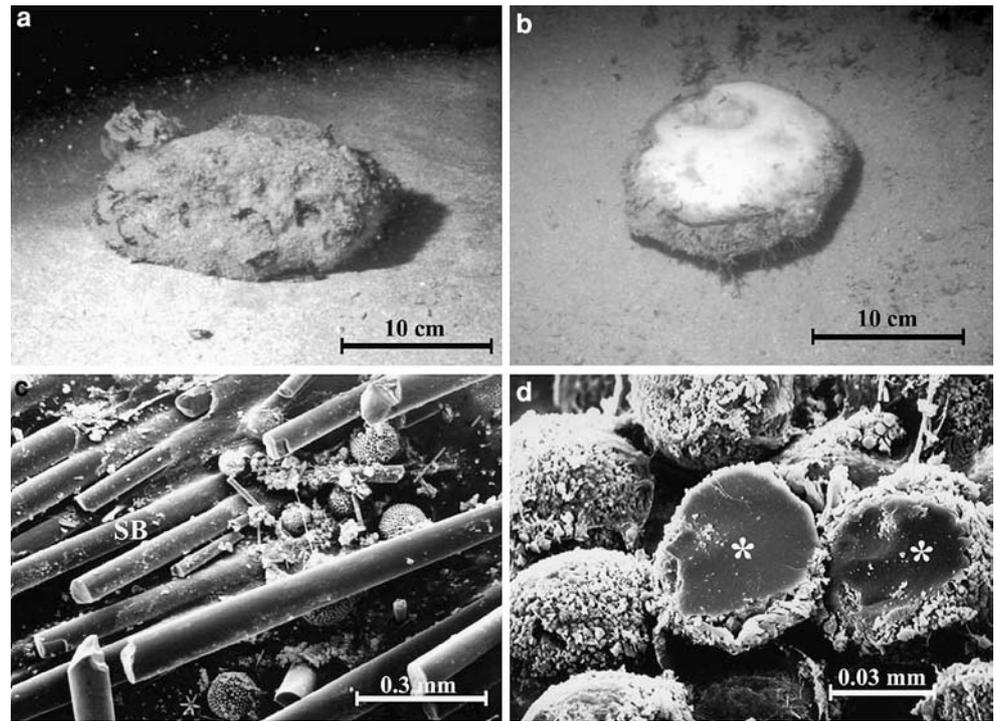
As for the choanosomal silica content, the mean values observed in the sessile and non-sessile specimens were  $58.78 \pm 7.26\%$  and  $53.99 \pm 10.57\%$ , respectively. The cortical silica content was  $68.03 \pm 10.51\%$  in the sessile specimens and  $56.19 \pm 11.84\%$  in the non-sessile ones (Fig. 8c, d). A seasonal comparison of choanosomal and cortical silica content both in sessile and non-sessile specimens showed no significant differences ( $P > 0.05$ ; Kruskal–Wallis test). The choanosomal silica content was not significantly different between the sessile and non-sessile specimens ( $P > 0.05$ , Mann–Whitney  $U$ -test). In

contrast, the cortical silica content was significantly higher in the sessile specimens than in the non-sessile ones ( $P < 0.05$ , Mann–Whitney  $U$ -test).

#### *Porto Cesareo*

The mean value of choanosomal oxyaster diameters observed in the sessile and non-sessile specimens were  $23.96 \pm 1.85$  and  $20.53 \pm 3.82$   $\mu\text{m}$ , respectively (Fig. 9a, b). The mean value of cortical sterraster diameter was  $70.05 \pm 2.35$   $\mu\text{m}$  in the sessile specimens and  $71.18 \pm 3.34$   $\mu\text{m}$  in the non-sessile ones (Fig. 9a, b). A seasonal comparison of spicule diameter in sessile and non-sessile specimens, showed no significant differences ( $P > 0.05$ ; Kruskal–Wallis test). In addition, the choanosomal oxyaster and cortical sterraster diameters were not significantly different between the sessile and non-sessile specimens ( $P > 0.05$ , Mann–Whitney  $U$ -test).

**Fig. 7** Non-sessile specimens of *Geodia cydonium* in Porto Cesareo basin. **a** The upper surface of a non-sessile specimen covered with sediment and macrobenthic organisms. **b** The lower part of the same specimen of (a), lacking epibionts and sediment. **c** SEM view of broken spicule bundles (SB) adherent to the outermost sponge surface. **d** SEM view of some cortical sterrasters (asterisks) made smooth by scraping on the substrate



As for the choanosomal silica content, the mean values observed in the sessile and non-sessile specimens were  $69.06 \pm 4.17\%$  and  $72.56 \pm 5.27\%$ , respectively. The cortical silica content was  $82.92 \pm 2.9\%$  in the sessile specimens and  $83.91 \pm 3.93\%$  in the non-sessile ones (Fig. 9c, d). The seasonal comparison of the silica content of sessile and non-sessile specimens showed no significant differences ( $P > 0.05$ , Kruskal–Wallis test). Both the cortical and choanosomal silica contents were not significantly different between the sessile and non-sessile specimens ( $P > 0.05$ , Mann–Whitney  $U$ -test).

#### Environmental parameters Marsala

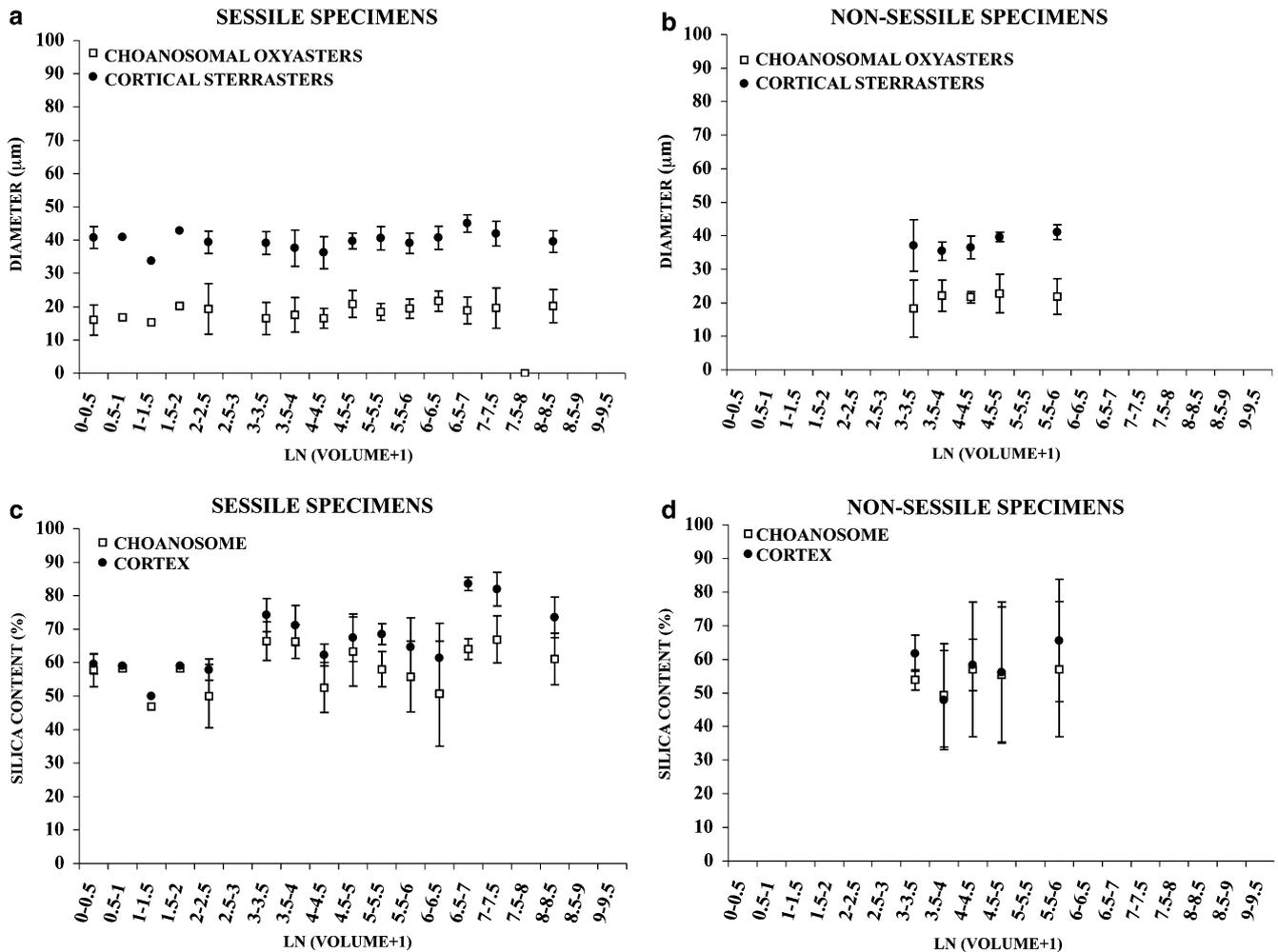
Particle size analysis of the sediment collected in the area a2, showed high contents of the smallest fractions (silt = 22.44% and clay = 24.25%) (Table 1). Moreover, redox measurement showed the presence of a negative electric potential (–110 mV) starting from 1 cm deep; this negative electric potential gradually increased with depth (Table 1).

#### Porto Cesareo

Particle size analysis of the sediment collected in the area b2, showed a low content of the smallest fractions (silt = 0.28% and clay = 0.76%), while the sand fraction prevailed (92.55%) (Table 1). In the same area, redox measurement showed the presence of a weak negative electric potential (–26 mV) starting from 3 cm under the bottom surface (Table 1).

#### Discussion and conclusions

Present data and literature records (Labate 1968; Parenzan 1976; Pulitzer-Finali 1983; Corriero et al. 1984, 1996b; Corriero 1990; Mercurio et al. 2001) show that, in the studied sites of Marsala and Porto Cesareo, *G. cydonium* is a very persistent species. It occurs with sessile and non-sessile specimens, the former constituting the largest portion of the populations in both environments, and characterized by high abundance values and large size. Rich populations and cases of gigantism have also been previously reported for other demosponges (*Cliona copiosa*; *Phorbas paupertas*) from these Mediterranean environments (Corriero 1989; Mercurio et al. 2001). As regards *G. cydonium*, several massive specimens, up to 1 m in diameter, have been described by Parenzan (1976) for the basin of Porto Cesareo. Santucci (1922) mentioned the finding of a specimen of 29 kg (drilled weight), from a bay on the east Adriatic coast. Such large sizes, probably the largest among Mediterranean shallow demosponges, exclusively occur in specimens inhabiting sheltered, shallow environments and, according to Corriero (1990), may be related to favourable trophic and hydrodynamic conditions. However, the large size could also be dependent on other ecological factors, such as the availability of silica in the water. It is well known that the increase of silica in the water may enhance the silica content and the spicule size in many species of demosponges (Jørgensen 1944, 1947; Hartman 1958; Stone 1970; Pé 1973; Fröhlich and Barthel 1997; Schönberg and Barthel 1997). Our data show that at Porto Cesareo, where significantly higher



**Fig. 8** *Geodia cydonium* in Marsala lagoon. Volume–class distribution of the spicule size (mean value  $\pm$  SD) in sessile (a) and non-sessile (b) specimens. Volume–class distribution of the silica content (mean value  $\pm$  SD) in sessile (c) and non-sessile (d) specimens

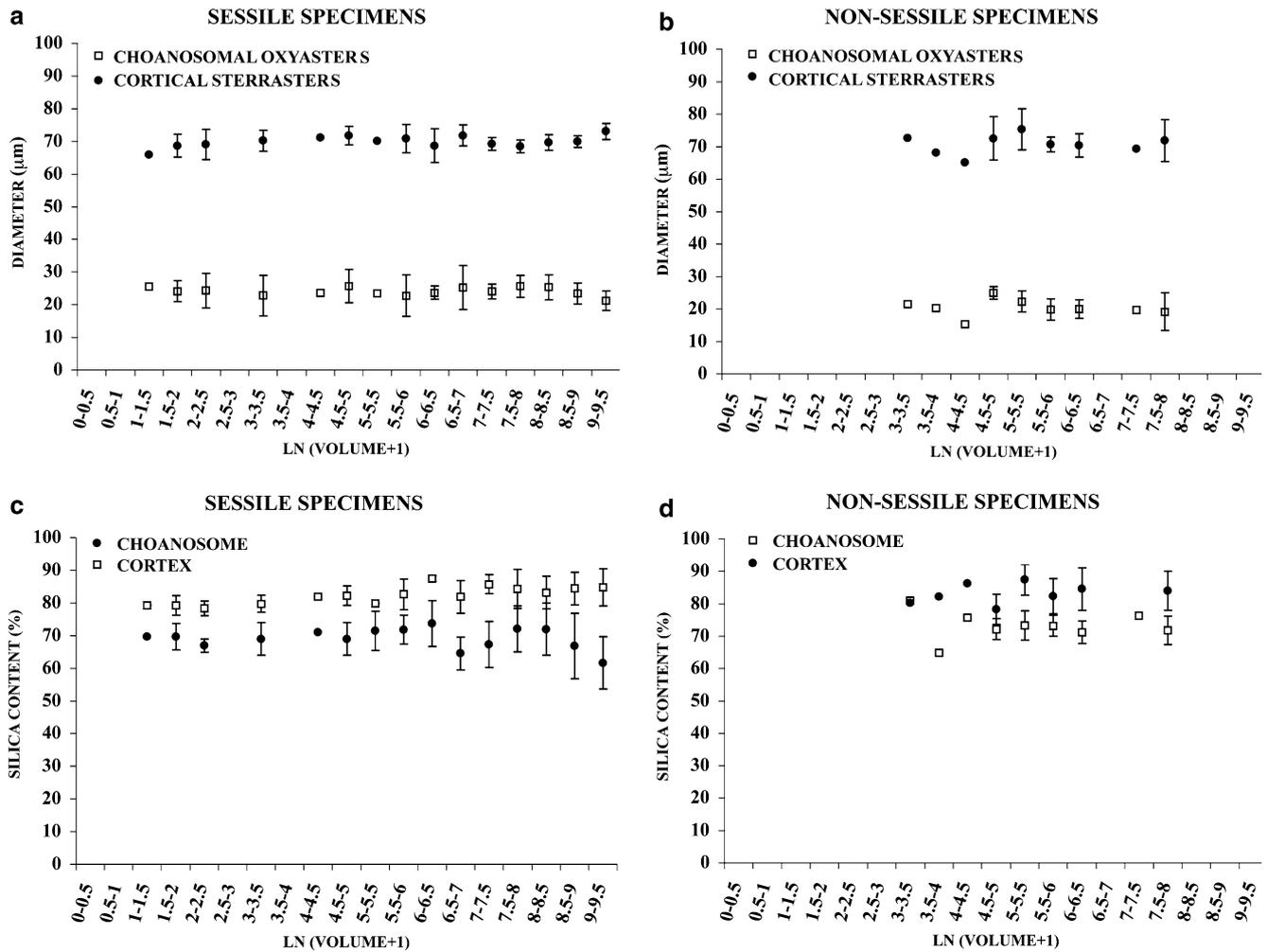
silica water concentrations occur (Mercurio et al. 2000), the specimens of *G. cydonium* are characterized by a larger amount of silica, larger cortical spicules, and larger body size than those of Marsala. Therefore, a strong skeletal support, related to a high availability of water silica content, could play a role in the increase in the sponge size.

From the bulk of data reported in the current literature, *G. cydonium* is a sciaphilous species with a wide bathymetric range. In shallow waters, it is common in caves, crevices or under large stones (Uriz 1981; Pulitzer-Finali 1983).

In the high light exposed bottoms of Marsala and Porto Cesareo, *G. cydonium* protects itself against high solar radiation with a sediment layer and an epibiotic covering, both set on the external surface of the sponge. The deposition of sediment and the settlement of epibiotic organisms may be favoured by the occurrence of a palisade structure consisting of monoaxon spicules protruding from the cortical surface of the sponge. The occurrence of such a protective screen is also observed in other sponges living in these two studied sites, for

example, *Tethya aurantium* and *T. anhelans* (both sites), *Stelletta stellata* (Porto Cesareo) (Corriero et al. unpublished data). In particular, in the non-sessile specimens from Marsala lagoon, the protection from solar radiation is largely due to the thick coat formed by the red alga *R. tinctoria*, which is almost constantly associated with the non-sessile sponges. The algal thallus seems to contribute to strengthening the cortical layer of the sponge body, thereby partially substituting the skeletal components, as indicated by the lower values of cortical silica content and cortical spicule size than those of the sessile ones. The sessile specimens, which grow on the rhizome of *P. oceanica*, show a lower level of sediment covering the sponge surface. In this habitat, however, phanerogam leaves screen the sponge surface against the solar radiation.

The most relevant feature of *G. cydonium* in the studied environments consists of the development of the free-living habitus. In such sink lagoons, the partially sediment-buried habitus is quite common (Corriero 1989; Ilan and Abelson 1995; Rutzler 1997; Calcinaï et al. 2001), whereas unattached, free-living forms are



**Fig. 9** *Geodia cydonium* in Porto Cesareo basin. Volume-class distribution of the spicule size (mean value  $\pm$  SD) in sessile (a) and non-sessile (b) specimens. Volume-class distribution of the silica content (mean value  $\pm$  SD) in sessile (c) and non-sessile (d) specimens

**Table 1** Particle-size analysis and redox measurement in Marsala lagoon and Porto Cesareo basin

Marsala—a2 area			
Particle-size analysis		Redox	
Gravel	0.92%	Under water surface	155 mV
Sand	52.39%	Sediment surface	110 mV
Silt	22.44%	1 cm (Under bottom surface)	–110 mV
Clay	24.25%	2 cm (Under bottom surface)	–185 mV
		3 cm (Under bottom surface)	–223 mV
Porto Cesareo—b2 area			
Particle-size analysis		Redox	
Gravel	6.41%	Under water surface	144 mV
Sand	92.55%	Sediment surface	123 mV
Silt	0.28%	1 cm (Under bottom surface)	97 mV
Clay	0.76%	2 cm (Under bottom surface)	50 mV
		3 cm (Under bottom surface)	–26 mV

rarer. Temporary non-sessile stages have been described for sponges from soft bottoms of shallow tropical environments (Ayling 1980; Battershill and Bergquist 1990; Wulff 1985, 1991). More recently, Bell and Barnes

(2002), monitoring the shallow demosponges *Hymeniacidon perlevis* and *Suberites ficus* over a 1-year period, noticed the presence of unattached forms showing fluctuations in their density in relation to local current flow.

In the studied lagoons, the non-sessile forms of *G. cydonium* are persistent, being repeatedly reported over the last 15 years (Mercurio et al. 1997a,b, 2001; Corriero 1989, 1990). Constant density and size distribution values have been observed throughout the year of study, even though they were lower than those recorded for the coexisting sessile specimens.

The non-sessile forms differ in the two environments in several morphological and structural features, but the differences in body shape seem to play the most relevant role for enhancing the colonization of such incoherent substrates.

At Marsala, the non-sessile specimens of *G. cydonium* are fairly spherical. As observed by Riggio and Sparla (1985), owing to its spherical shape, the sponge is able to roll on the soft bottom dragged by slow circular currents. This feature protects sponges from sinking into the sediment. Here, indeed, the large amount of silt and clay on the bottom, determines the occurrence of a markedly reduced anoxic layer just below the surface of the sediment. In this environment, the possibility of exposure to a non-oxygenated condition is the major problem for the unattached sponges. In addition, the usual association with the red alga *R. tinctoria*, which forms a thick and continuous layer around the sponge, allows non-sessile specimens of *G. cydonium* to avoid contact with the substrate.

At Porto Cesareo, the non-sessile sponges inhabit sandy bottoms affected by moderate wave turbulence (Corriero 1990) and are flattened. Their flattened shape widens the contact surface between the body and the substrate, thereby reducing the risk of stranding. The signs of abrasion, evident on both cortical spicules and outermost sponge surface, suggest that these sponges rub on the bottom.

The free-living habitus of *G. cydonium* may have a particular relevance in affecting the local and temporal distribution of this species and may play a pivotal role in enhancing the colonization process of environments, often lacking hard substrates.

In conclusion, the documented persistence of unattached specimens of *G. cydonium* in semi-enclosed bays suggests that these free-moving sponges can be regarded as the expression of a peculiar strategy for survival. Further investigations on the reproductive features and relationships between sessile and non-sessile forms may prove if this phenomenon is actually adaptive and how it can contribute to population maintenance.

**Acknowledgements** This work was financially supported by the Italian Ministero dell'Università e della Ricerca Scientifica e Tecnologica funds (ex MURST 40 and 60%). All the experiments complied with the current Italian laws.

## References

- Ayling AL (1980) Patterns of sexuality, asexual reproduction and recruitment in some subtidal marine Demospongiae. *Biol Bull* 158:271–281
- Bagander LE (1976) Redox measurements in natural waters and sediments. In: Dybern B, Ackefors H, Elmegren R (eds) Recommendations on methods for marine biological studies in the Baltic Sea. Department of Zoology, University of Stockholm
- Barthel D, Tendal OS (1993) The sponge association of the abyssal Norwegian–Greenland Sea: species composition, substrate relationships and distribution. *Sarsia* 78:83–96
- Battershill CN, Bergquist PR (1990) The influence of storms on asexual reproduction, recruitment and survivorship of sponges. In: Rutzlet K (ed) New perspectives in sponge biology. Smithsonian Institution Press, Washington, DC, pp 397–403
- Bell JJ (2004) Evidence for morphology-induced sediment settlement prevention on the tubular sponge *Haliclona urceolus*. *Mar Biol* 146:29–38
- Bell JJ, Barnes DKA (2000) The influence of bathymetry and flow regime on the morphology of sublittoral sponge populations at Lough Hyne MNR. *J Mar Biol Assoc UK* 80:707–718
- Bell JJ, Barnes DKA (2002) The relationship between sedimentation, flow rates, depth and time at Lough Hyne Marine Nature Reserve. *Ir Nat J* 27:106–116
- Bell JJ, Barnes DKA, Turner JR (2002) The importance of micro and macro morphological variation in adaptation of a sublittoral demosponge to current extremes. *Mar Biol* 140:75–81
- Bond C, Harris AK (1988) Locomotion of sponges and its physical mechanism. *J Exp Zool* 246:271–284
- Burton M (1932) Sponges. *Discov Rep* 6:237–392
- Calcinai B, Bavestrello G, Boyer M, Cerrano C, Pansini M (2001) Poriferi biodemolitori e biocostruttori nella zona di marea della Bunaken Marine Reserve (North Sulawesi, Indonesia). *Biol Mar Medit* 8:201–208
- Calvo S, Fradà Orestano C (1984) L'herbier à *Posidonia oceanica* des côtes siciliennes: les formations récifales du Stagnone, vol 1. In: Boudouresque CF, Jeudy de Grissac A, Olivier J (eds) *Int Work Posidonia oceanica Beds*. Gis Posidonie, France, pp 29–37
- Congedo (1988) Studio ecologico dell'area marina di Porto Cesareo. Tiemme Industrie Grafiche. Galatina, Lecce
- Corriero G (1989) The sponge fauna from the Stagnone di Marsala (Sicily): taxonomic and ecological observations. *Boll Musei Ist Biol Univ Genova* 53:101–113
- Corriero G (1990) Distribuzione ed ecologia dei Poriferi in ambienti "confinati mediterranei". Ph.D. thesis, University of Genova, Italy
- Corriero G, Pansini M, Sarà M (1984) Sui poriferi dell'insenatura della Strea a Porto Cesareo (Lecce). *Thal Sal* 14:3–10
- Corriero G, Balduzzi A, Sarà M (1989) Ecological differences in the distribution of two *Tethya* (Porifera, Demospongiae) species coexisting in a Mediterranean coastal lagoon. *Pubbl Staz Zool Napoli (I. Mar Ecol)* 10(4):303–315
- Corriero G, Sarà M, Vaccaro P (1996a) Sexual and asexual reproduction in two species of *Tethya* (Porifera, Demospongiae) from a Mediterranean coastal lagoon. *Mar Biol* 126:175–181
- Corriero G, Scalera Liaci L, Mercurio M (1996b) Il popolamento a Poriferi della Riserva Marina di Porto Cesareo. In: Riass 57th Cong Naz UZI. San Benetto del Tronto, Italy, pp 28
- Fröhlich H, Barthel D (1997) Silica uptake of the marine sponge *Halichondria panicea* in Kiel Bight. *Mar Biol* 128(1):115–125
- Gaino E, Manconi R, Pronzato R (1995) Organizational plasticity as a successful conservative tactic in sponges. *Anim Biol* 4:31–43
- Genchi C, Calvo S, Lugaro A, Ragonese S (1983) Idrologia di una laguna costiera e caratterizzazione chimico-fisica dei sedimenti recenti in relazione alla distribuzione dei popolamenti vegetali sommersi (lo Stagnone di Marsala). *Quad IRPEM* 4:23–34
- Gherardi M, Giangrande A, Corriero G (2001) Epibiotic and endobiotic polychaetes of *Geodia cydonium* (Porifera, Demospongiae) from the Mediterranean Sea. *Hydrobiologia* 443:87–101
- Guide VG (1976) Sponge predation in the oyster reef community as demonstrated with *Cliona celata*. *J Exp Mar Biol Ecol* 25:109–122

- Hartman WD (1958) Natural history of the marine sponges of southern New England. Yale University Bulletin 12, Peabody Museum of Natural History, Yale University, New Haven, CT
- Hill MS, Hill AL (2002) Morphological plasticity in the tropical sponge *Anthosigmella varians*: responses to predators and wave energy. *Biol Bull* 202:86–95
- Ilan M, Abelson A (1995) The life of a sponge in sandy lagoon. *Biol Bull* 189:363–369
- Jørgensen CB (1944) On the spicule-formation of *Spongilla lacustris* (L) 1 The dependence of the spicule-formation on the content of dissolved and solid silicic acid in the milieu. *K danske Vidensk Selsk Biol Skr* (19)7:1–45
- Jørgensen CB (1947) On the spicule-formation of *Spongilla lacustris* (L.) and *Ephydatia fluviatilis* (L) 2 The rate of growth of the spicules. *K danske Vidensk Selsk Biol Skr* (20)10:1–22
- Kaandorp JA (1991) Modelling growth forms of the sponge *Haliclona oculata* (Porifera, Demospongiae) using fractal techniques. *Mar Biol* 110:203–215
- Kaandorp JA (1999) Morphological analysis of growth forms of branching marine sessile organisms along environmental gradients. *Mar Biol* 134:295–306
- Kaandorp JA, de Kluijver MJ (1992) Verification of fractal growth models of the sponge *Haliclona oculata* (Porifera) with transplantation experiments. *Mar Biol* 113:133–143
- Labate M (1968) Ecologia dei Poriferi di acque superficiali di “Porto Cesareo” (Mar Ionio). *Boll Zool* 35(4):348
- Magazzù G (1977) Usefulness of the Marsala lagoon for aquaculture. Nutrients and primary production. *Rapp P-v Réunion Comm int Explor scient Mer Méditerr* 24(6):81–82
- McDonald JI, Hooper JNA, McGuinness KA (2002) Environmentally influenced variability in the morphology of *Cinachyrella australiensis* (Carter 1886) (Porifera: Spirophorida: Tetillidae). *Mar Freshw Res* 52:79–84
- Mercurio M, Scalera Liaci L (1997a) Sulla forma non sessile di *Geodia cydonium* (Jameson) in un ambiente superficiale. *Biol Mar Medit* 4(1):407–409
- Mercurio M, Scalera Liaci L, Corriero G (1997b) Modificazioni morfologiche in esemplari non sessili di *Geodia cydonium* (Jameson) (Porifera, Demospongiae). In: *Riass 58th Congr Naz UZI*. Cattolica, Italy, 39 pp
- Mercurio M, Corriero G, Scalera Liaci L, Gaino E (2000) Silica content and spicule size variations in *Pellina semitubulosa* (Porifera, Demospongiae). *Mar Biol* 137:87–92
- Mercurio M, Scalera Liaci L, Corriero G (2001) La fauna a poriferi del bacino della Strea di Porto Cesareo (LE). *Biol Mar Medit* 8(1):403–412
- Molinier R, Picard J (1953) Notes biologiques à propos d'un voyage d'étude sur les côtes de Sicile. *Ann Inst Océanogr* 28:163–188
- Palumbi SR (1984) Tactics of acclimation: morphological changes of sponges in an unpredictable environment. *Science* 225:1478–1480
- Palumbi SR (1986) How body plans limit acclimation: responses of a demosponge to wave force. *Ecology* 67:208–214
- Parenzan P (1976) Un habitat marino di tipo subtropicale a Porto Cesareo. *Atti VI Simp Naz Cons Nat, Bari*, pp 151–157
- Passeri L (1974) Sedimentazione carbonatica attuale e diagenesi precoce nella laguna di Porto Cesareo (Penisola Salentina). *Extra Suppl Boll Geol It* 92:3–40
- Pè J (1973) Etude quantitative de la régulation du squelette chez une éponge d'eau douce, vol 84. *Archs Biol, Bruxelles*, pp 147–173
- Pulitzer-Finali (1983) A collection of Mediterranean Demospongiae (Porifera) with, in appendix, a list of the Demospongiae hitherto recorded from the Mediterranean Sea. *Ann Mus Civ St Nat Genova* 84:445–621
- Relini G (2003) Il biofouling Parte Prima: il macrofouling. *Biol Mar Medit* 10(Suppl):285–326
- Riggio S, Sparla MP (1985) Notes on fauna inhabiting *Rytiphloea tinctoria* (Clem) C Ag *aegagropyla* in the stagnone Sound (Western Sicily). *Rapp Comm Int Mer Medit* 29(4):143–144
- Rutzler K (1997) The role of psammobiontic sponges in the reef community. *Proceedings of the Eighth International Coral Reef Symposium*, vol 2, pp1393–1398
- Santucci R (1922) La *Geodia cydonium* come centro di associazione biologica. In: *Mem CIII Com Talas It. Premiate officine Carlo Ferrari* (ed) Venezia, pp 5–20
- Sarà M, Vacelet J (1973) Ecologie des Démosponges. In: *PP Grassé, Masson et Cie* (eds) *Traité de Zoologie*, vol 3. Spongiaires. Paris, France, pp 462–576
- Schönberg CHL, Barthel D (1997) Inorganic skeleton of the demosponge *Halichondria panicea*. Seasonality in spicule production in the Baltic Sea. *Mar Biol* 130:133–140
- Stone AS (1970) Seasonal variation in the gross biochemical composition of *Hymeniacidon perleve* (Montagu). *J Exp Mar Biol Ecol* 5:265–271
- Uriz MJ (1981) Estudio sistemático de las esponjas *Astrophorida* (Demospongia) de los fondos de pesca de arrastre, entre Tossa y Calella (Cataluña). *Bol Inst Espa Oceano* 6(320):8–58
- Vogel S (1981) Life in moving fluids—the physical biology of flow. Willard Grant Press, Boston
- Wulff JL (1985) Dispersal and survival of fragments of coral reef sponges. *Proc Int Coral Reef Symp* 5:119–124
- Wulff JL (1991) Asexual fragmentation, genotype success, and population dynamics of erect branching sponges. *J Exp Mar Biol Ecol* 149:227–247
- Wulff JL (1995) Effects of a hurricane on survival and orientation of large erect coral reef sponges. *Coral Reefs* 14:55–61