

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/225417434>

# Silica content and spicule size variations in *Pellina semitubulosa* (Porifera: Demospongiae)

ARTICLE *in* MARINE BIOLOGY · JANUARY 2000

Impact Factor: 2.39 · DOI: 10.1007/s002270000336

CITATIONS

20

READS

27

## 4 AUTHORS, INCLUDING:



**Mercurio Maria**

Università degli Studi di Bari Aldo Moro

21 PUBLICATIONS 246 CITATIONS

SEE PROFILE



**Giuseppe Corriero**

Università degli Studi di Bari Aldo Moro

60 PUBLICATIONS 823 CITATIONS

SEE PROFILE



**Elda Gaino**

Università degli Studi di Perugia

158 PUBLICATIONS 1,667 CITATIONS

SEE PROFILE

M. Mercurio · G. Corriero · L. Scalera Liaci · E. Gaino

## Silica content and spicule size variations in *Pellina semitubulosa* (Porifera: Demospongiae)

Received: 10 October 1999 / Accepted: 13 April 2000

**Abstract** The variations in both silica content and spicular size were studied in two populations of the demosponge *Pellina semitubulosa* (Lieberkühn). Samples were collected over a period of 1 year (June 1994 to May 1995) in two Mediterranean coastal basins: Porto Cesareo (southwestern Apulia) and Marsala (north-western Sicily). The values of spicule size (length and width) and sponge silica content were significantly higher in the population of Porto Cesareo, where the highest water silica concentration was recorded. In both Porto Cesareo and Marsala the sponge silica content showed a seasonal trend, positively correlated with water temperature values. In both populations, the smallest spicules were found in specimens collected from summer to late autumn, after sexual reproduction. Secretion of new spicules may be connected with the process of remodelling occurring in sponges after gamete and larval release.

### Introduction

Skeletal architecture, including spicule shape and size, represents the basic trait utilized in sponge taxonomy. In particular, in the groups in which siliceous spicules have a homogeneous morphology, their size represents the main useful character for species identification (de Weerdt 1985). Nevertheless, it has been demonstrated that, even in the same species, spicule dimensions are not constant, since seasonal variations, due to both water

temperature and silica concentration, have been recorded (Jørgensen 1944, 1947; Hartman 1958; Stone 1970; Elvin 1971; Pé 1973; Simpson 1978; Jones 1987a, b; Bavestrello et al. 1993a, b; Fröhlich and Barthel 1997; Schönberg and Barthel 1997). Similarly, there is compelling evidence that sponge silica content also varies according to the season (Bavestrello et al. 1993b).

It has been hypothesized that spicule growth is the result of a two-part system in which length depends upon the increase in the organic axial filament, and width upon silica deposition (Simpson 1984). On this account, it has been proved that variations in both chemical and physical factors affect spiculogenesis. In *Hymeniacidon perleve* from English Channel coasts, cyclic trends on the average size of sponge spicules have been positively correlated with the values of the environmental orthosilicic acid (Stone 1970). Lower water temperature values seem to enhance silica uptake, as suggested by variations in spicule size observed along latitudinal (Topsent 1917; Hentschel 1929; Hartman 1958; Hooper 1991) and bathymetric gradients (Bavestrello et al. 1993a). The wave activity occurring in superficial habitats represents another ecological parameter affecting spiculogenesis as demonstrated in *Halichondria panicea*, the skeletal strength of which reflects the intensity of the wave action (Palumbi 1986).

In addition to abiotic parameters, the synthesis of skeletal components may reflect sponge growth and reproduction. Elvin (1976) found a different spicule/sponge volume relationship in male and female specimens of *Haliclona permollis*. Indeed, a positive correlation between spicule growth and sponge volume occurs only in females. A possible relationship between spicule size and sponge reproduction has been proposed by Jones (1991) for *Haliclona rosea* and hypothesized by Bavestrello et al. (1993b) for *Chondrilla nucula*. More recently, Fröhlich and Barthel (1997) showed in *Halichondria panicea* a significant drop in the silica uptake during female reproduction.

The present work constitutes an attempt to estimate the influence of dissolved silica and water temperature

---

Communicated by R. Cattaneo-Vietti, Genova

---

M. Mercurio · G. Corriero (✉) · L. Scalera Liaci  
Dipartimento di Zoologia, Via Orabona 4, 70125 Bari, Italye-mail: g.corriero@biologia.uniba.it  
Fax: +39-80-5443358E. Gaino  
Dipartimento di Biologia Animale ed Ecologia,  
Via Elce di Sotto, 06123 Perugia, Italy

on both spicule growth and sponge silica content under natural conditions. Indeed, many data on this subject have been derived from laboratory experiments in which sponges were only tested for short periods (Elvin 1971; Simpson 1978; Fröhlich and Barthel 1997). Thus, for a period of 1 year we studied two populations of *Pellina semitubulosa* living under different environmental conditions, with focus on the effect of sexual reproduction on spiculogenetic activity.

## Materials and methods

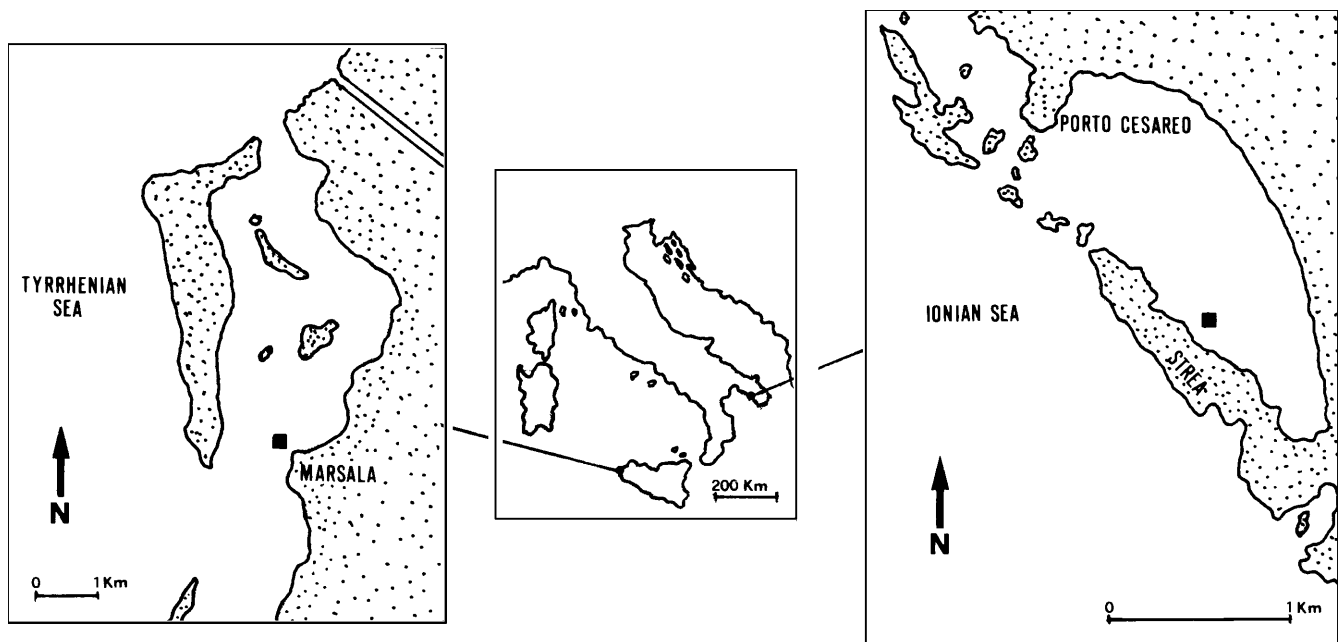
### *Pellina semitubulosa* (Lieberkühn)

Specimens of *P. semitubulosa* were studied from two sites on Italian coasts, namely the Porto Cesareo Basin and the Marsala Lagoon. In Porto Cesareo, *P. semitubulosa* is cushion-shaped, and often grows as an epibiont on both algal thalli and various sponge species (e.g. *Stelletta stellata* and *Geodia cydonium*). Thin funnels protrude perpendicularly to the sponge surface. In contrast, in Marsala, *P. semitubulosa* tends to be a free-living sponge. In this condition the sponge has a cylindrical shape and shows slightly raised oscular openings, uniformly distributed over its surface. Sessile specimens, mainly adherent to *Posidonia oceanica* rhizomes, show an irregularly shaped massive body, with scattered oscular funnels.

### Study sites

Porto Cesareo is a shallow, sheltered basin on the southwestern coast of Apulia (40°15'N; 17°54'E) (Fig. 1, right panel). This basin is elongated (NW to SE oriented) and measures 2500 m in length and 700 to 800 m in width, with a maximum depth of 2.5 m (Passeri 1974). It communicates with the open sea through a channel system that allows considerable water exchange between the basin and the sea. The bottom of the basin is mostly composed of mixed sands together with calcareous boardings, rocks and pebbles.

**Fig. 1** Study sites and sampling areas (■). Left panel: Marsala Lagoon (northwestern Sicily); right panel: Porto Cesareo Basin (southwestern Apulia)



The Marsala Lagoon covers an area of 20 km<sup>2</sup> along the northwestern coast of Sicily (37°14'N; 12°40'E) (Fig. 1, left panel). It is separated from the open sea by a group of islets and by a large barrier of *Posidonia oceanica* (L.) Delile (Calvo and Fradà Orestano 1984). The average depth of the environment is about 1 m. The bottom is composed of fine sediments with notable portions of coarse sand. Hard substrata are essentially represented by rhizomes of *P. oceanica* and by algal or animal calcareous concretions (Corriero et al. 1989). The water movement is low and mainly linear, owing to the combined action of the wind and the tidal currents. However, the large openings of the lagoon allow considerable water exchange with the sea, which damps the thermo-haline oscillations.

### Sampling protocol

Fifteen specimens of *Pellina semitubulosa* were collected monthly from June 1994 to May 1995, both in Porto Cesareo and in Marsala.

Concomitantly, water temperature was measured by using a portable DELTA OHM, HD 8706 probe. Water silica concentration was measured in 250-ml samples of seawater filtered through a membrane filter (Millipore, 1 µm). The method for determination of soluble forms of silicon was based on the reaction of orthosilicic acid with molybdate in forming silicomolybdic acid (Grasshoff 1964). The absorbance of the reduction product of the silicomolybdic acid (molybdenum blue) was measured with a spectrophotometer at 650 nm.

For morphometric analysis of the spicule size, sponge samples were cleaned of tissue by boiling them in 65% nitric acid, washed repeatedly in distilled water and alcohol, and gently agitated to suspend spicules. Thereafter, the spicule suspension was spread over a microscope slide and evaporated to dryness. The average monthly length and width of oxeas were calculated by measuring 50 randomly selected spicules from each slide.

The silica concentration for each specimen was determined 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.

In order to ascertain the presence of reproductive elements (gametes, embryos and larvae), sponge fragments were fixed for 3 h

in a buffer of 2.5% glutaraldehyde in artificial seawater. Thereafter, selected material was rinsed in seawater, dehydrated and embedded in paraffin. Sections (5  $\mu\text{m}$  thick) were stained with toluidin blue. Ten 1.5  $\text{mm}^2$  microscopic sections from each specimen were observed, and the total number of spermatid cysts, embryos and larvae was counted; the rare occurrence of mature eggs induced us to disregard their count. In order to quantitatively evaluate reproductive entities, Abercrombie's formula, as suggested by Elvin (1976), was used. The formula is: the number of reproductive entities per cubic millimeter =  $N[(t/D) + t](cf)$ , where  $N$  is the average number of spermatid cysts, embryos and larvae observed in each microscopic field;  $t$  is the thickness of the section (5  $\mu\text{m}$ );  $D$  is the diameter of the reproductive entities;  $cf$  (= 500) is the constant factor converting the volume of each observation (0.0020  $\text{mm}^3$ ) to 1  $\text{mm}^3$ . The number of reproductive entities was calculated for each specimen and for each month.

### Statistics

In both populations, monthly differences in reproductive elements (number of spermatid cysts, embryos and larvae) and skeletal components (spicular length and width as well as silica content) were evaluated by comparing means and confidence intervals. A two-way ANOVA was utilized to test the significance of the differences in size of skeletal elements and sponge silica content between the two populations. Moreover, auto- and cross-correlation analyses were utilized to explore the relationships between sponge skeleton (silica content and spicule size) and environmental parameters (silica concentration and water temperature).

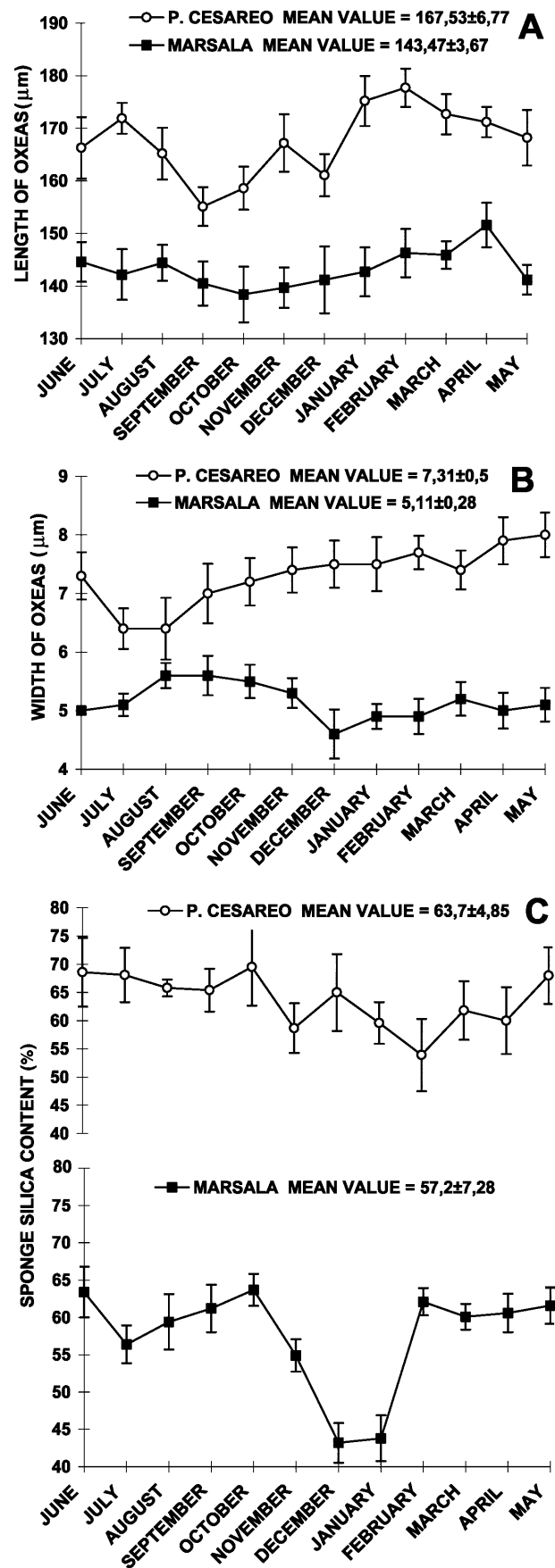
Finally, a non-parametric test (Mann-Whitney's  $U$ -test) was utilized to test the differences in the environmental parameters between the two sites.

## Results

### Spicule size and sponge silica content

The mean value for oxea lengths of specimens of *Pellina semitubulosa* from Porto Cesareo was  $167.5 \pm 6.8 \mu\text{m}$ . The lowest value occurred in September ( $155.1 \pm 5.8 \mu\text{m}$ ) and the highest in February ( $177.7 \pm 5.1 \mu\text{m}$ ). Oxea length showed cyclic variations, with highest values in winter and lowest values in the late summer and early autumn (Fig. 2A). The mean value of oxea length for specimens from Marsala was  $143.5 \pm 3.7 \mu\text{m}$ ; the lowest value occurs in October ( $138.4 \pm 7.4 \mu\text{m}$ ) and the highest one in April ( $151.6 \pm 8.2 \mu\text{m}$ ). Oxea length at this site showed only slight fluctuations between the lowest values observed from September to December and in May and the highest ones observed from February to April (Fig. 2A). Oxea length was significantly different both between sites and among months ( $p < 0.001$ ).

The mean value for oxea widths observed in specimens from Porto Cesareo was  $7.3 \pm 0.5 \mu\text{m}$ ; minimum values were observed in July ( $6.4 \pm 0.6 \mu\text{m}$ ) and August ( $6.4 \pm 0.5 \mu\text{m}$ ); the maximum value occurred in May



**Fig. 2** *Pellina semitubulosa*. Trends in spicule size, **A** oxea length and **B** oxea width, and **C** silica content (percent values) in the populations from Porto Cesareo and Marsala (June 1994 to May 1995). Monthly values refer to a mean of 15 specimens (95% confidential limits)

( $8 \pm 0.6 \mu\text{m}$ ). Oxea width at this site was fairly constant, showing a significant decrease in July only (Fig. 2B). The mean value of oxea width for specimens from Marsala was  $5.1 \pm 0.3 \mu\text{m}$ ; this parameter showed slight fluctuations between the minimum value observed in December ( $4.6 \pm 0.5 \mu\text{m}$ ) and the maximum values observed in August ( $5.6 \pm 0.3 \mu\text{m}$ ) and September ( $5.6 \pm 0.4 \mu\text{m}$ ) (Fig. 2B). Oxea width was significantly different both between sites and among months ( $p < 0.001$ ).

As for the silica content, the mean value observed in the specimens from Porto Cesareo was  $63.7 \pm 4.8\%$ ; the lowest value was  $53.9 \pm 6.4\%$  (February) and the highest was  $69.5 \pm 6.8\%$  (October). Silica content significantly decreased from October to February, then it increased to May and until September remained fairly constant (Fig. 2C, upper part). In this study area, the increase in sponge silica content was coincident with a decrease in spicule length ( $r = 0.6$ ,  $n = 12$ ,  $p = 0.04$ ). The mean value of the silica content in specimens from Marsala was  $57.2 \pm 7.3\%$ ; the minimum values were in December ( $43.2 \pm 3.2\%$ ) and January ( $43.8 \pm 4.3\%$ ) and the maximum in October ( $63.7 \pm 3\%$ ). The silica content showed a significant decrease from October to January; in February it sharply increased; afterwards, the trend was fairly constant until June (Fig. 2C, lower part). Silica content was significantly different both between sites and among months ( $p < 0.001$ ).

#### Relationship between sponge skeleton and environmental parameters

The values for water temperature and silica concentration recorded in Porto Cesareo and Marsala from June 1994 to May 1995 are reported in Fig. 3A and B, respectively.

In Porto Cesareo the annual mean water temperature was  $19.9 \pm 5.9^\circ\text{C}$ ; the highest value occurred in August ( $27.2^\circ\text{C}$ ), the lowest in February ( $11.9^\circ\text{C}$ ). In Marsala the mean value was  $20.6 \pm 6.2^\circ\text{C}$ ; the highest value occurred in August ( $28.5^\circ\text{C}$ ), the lowest in January ( $12.2^\circ\text{C}$ ). The water temperatures recorded in Porto Cesareo and Marsala did not show significant differences.

In Porto Cesareo the annual mean water silica concentration was  $1.9 \pm 0.8 \text{ mg l}^{-1} \text{ SiO}_2$ ; the highest value occurred in October ( $4.1 \text{ mg l}^{-1} \text{ SiO}_2$ ), the lowest in November ( $0.9 \text{ mg l}^{-1} \text{ SiO}_2$ ). In Marsala the mean value was  $0.3 \pm 0.3 \text{ mg l}^{-1} \text{ SiO}_2$ ; the highest value occurred in December ( $0.8 \text{ mg l}^{-1} \text{ SiO}_2$ ), the lowest in March ( $0.04 \text{ mg l}^{-1} \text{ SiO}_2$ ). The water silica concentrations were significantly higher in Porto Cesareo than in Marsala ( $p < 0.01$ ; Mann-Whitney's  $U$ -test).

In both studied areas, there was a positive correlation between water temperature and sponge silica content for zero time lag ( $r = 0.81$  and  $p = 0.001$  at Porto Cesareo;  $r = 0.60$  and  $p = 0.045$  at Marsala). In addition, spicule width and length in Porto Cesareo were correlated to

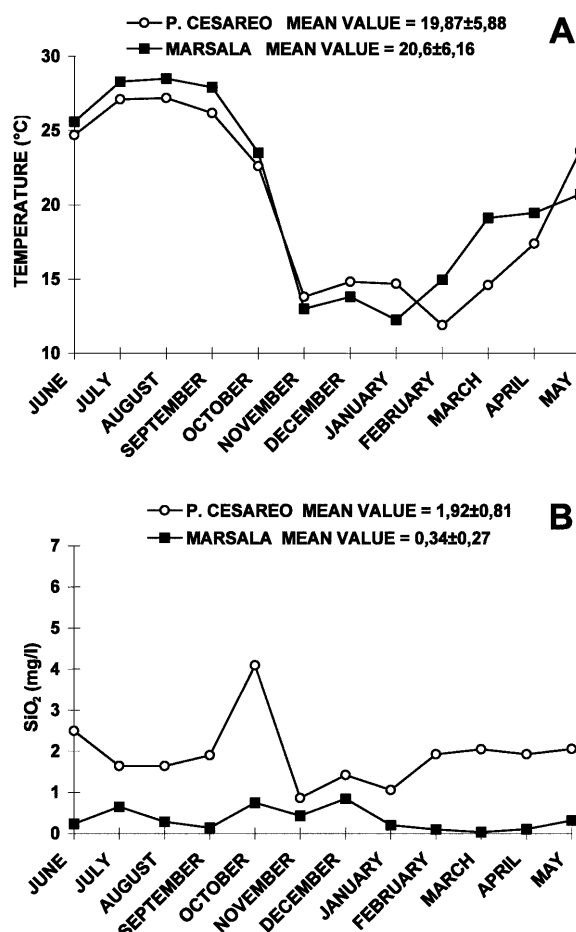


Fig. 3 Trends in A temperature and B silica concentration, in the waters of Porto Cesareo and Marsala, during the observation period (June 1994 to May 1995)

water temperature ( $r = -0.72$ ,  $p = 0.011$  and  $r = -0.60$ ,  $p = 0.048$ , respectively) when the latter series was shifted by a 1 month time lag.

Even though in both studied areas no correlation was observed between water silica content and sponge skeleton, it was interesting to note that at least in Porto Cesareo, the highest water silica concentrations corresponded to the highest sponge silica contents and to the shortest spicule lengths.

#### Relationship between sponge skeleton and reproduction

Fig. 4A, B reports the monthly variation in numbers of spermatid cysts, embryos and larvae.

Spermatid cysts occurred in *Pellina semitubulosa* specimens from Porto Cesareo from March to June. The highest densities were found in March ( $442.2 \pm 320$  elements  $\text{mm}^{-3}$  tissue) and progressively decreased to  $89 \pm 50 \text{ mm}^{-3}$  by June. Embryos and larvae appeared in the sponge tissue in April, with low density values ( $4.5 \pm 8.8 \text{ mm}^{-3}$ ). Their presence was observed in the

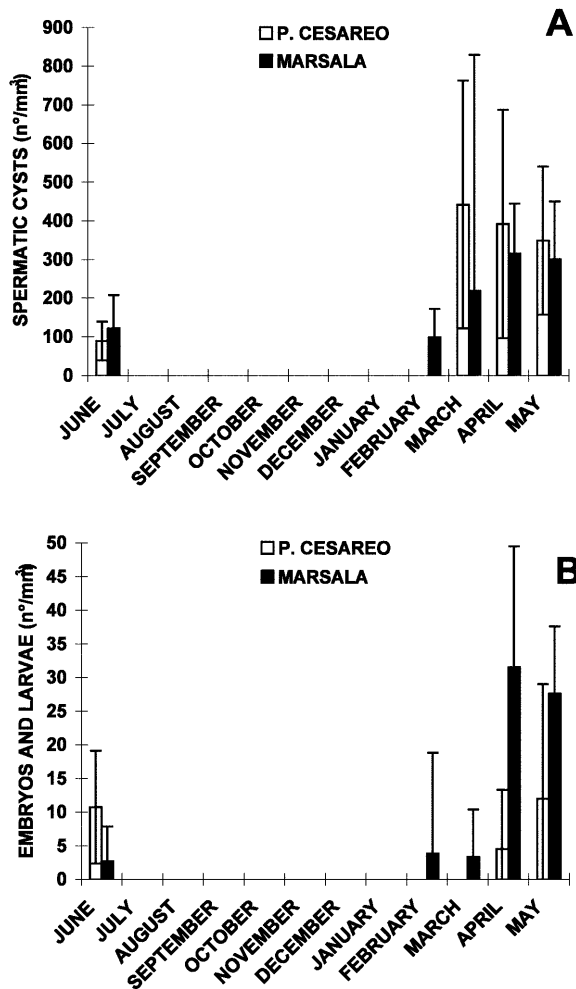


Fig. 4 *Pellina semitubulosa*. Trends in number of reproductive elements per cubic millimeter of sponge tissue for **A** spermatogenic cysts and **B** embryos and larvae, in the populations from Porto Cesareo and Marsala (June 1994 to May 1995). Monthly values refer to a mean of 15 specimens  $\pm$  SD

following 2 months, during which time embryos and larvae reached their highest densities.

In the population of Marsala, spermatogenic cysts appeared in February and persisted until June. Highest densities were observed in April ( $314.7 \pm 129.5 \text{ mm}^{-3}$ ) and May ( $300.7 \pm 148.9 \text{ mm}^{-3}$ ), and lowest values in February ( $98.2 \pm 73.6 \text{ mm}^{-3}$ ) and in June ( $122.2 \pm 85.4 \text{ mm}^{-3}$ ). In the course of spermatogenesis, embryos and larvae coexisted with spermatogenic cysts. The number of developing embryos and larvae within the parental tissue drastically increased from March to April (from  $3.4 \pm 7$  to  $31.5 \pm 18 \text{ mm}^{-3}$ ). This peak was followed by a sudden decrease from May to June (from  $27.6 \pm 10$  to  $2.7 \pm 5.2 \text{ mm}^{-3}$ ).

According to statistical analysis, the two populations did not differ significantly in the number of cysts, embryos and larvae.

A comparative investigation on the impact of reproductive activity on spiculogenesis proved that spicule length and width, together with silica content, were not

related to sperm differentiation. The presence of embryos and larvae did not affect spicule length and width. Silica content only increases concomitantly with larval release (see Figs. 2C, 4B).

## Discussion and conclusions

Investigation on the effects of environmental parameters on sponge spicule growth and silica uptake gave conflicting results (Elvin 1971; Simpson 1978; Fröhlich and Barthel 1997), mainly because of the poorly understood physiological mechanisms of silica deposition.

As far as *Pellina semitubulosa* is concerned, by comparing the trends of spicule size and water silica concentration, it becomes evident that the spiculogenetic activity in the population from Porto Cesareo is enhanced by the higher water silica concentration. In particular, the spicule size of the sponges living in Marsala is remarkably smaller than that of Porto Cesareo. This feature is consistent with previous results showing a positive correlation between the size of demosponge spicules and the silica concentration of the surrounding water (Jørgensen 1944, 1947; Hartman 1958; Stone 1970; Pé 1973; Fröhlich and Barthel 1997; Schönberg and Barthel 1997). Nevertheless, in Porto Cesareo the minimum size of spicules is concomitant with the maximum concentration of silica in the water. This apparently contrasting result could be related to the secretion of new spicules, a process that parallels the notable rearrangement of the sponge body after gamete and larval release.

With regards to the dependence of spiculogenetic activity on water temperature, it is worth stressing that, in spite of the similar trends in water temperature in the studied areas, a relationship between temperature and both spicule dimensions and sponge silica content was more evident in the population of Porto Cesareo. Here, the winter temperature decrease corresponded to a decrease in sponge silica content and to an increase in the length and width of spicules. These data suggest that, in winter, the sponge does not synthesize (or, at least, reduces the synthesis of) new spicules. Conversely, spiculogenesis takes place from summer and late autumn, as observed in numerous other sponge species (Simpson 1978; Fröhlich and Barthel 1997; Schönberg and Barthel 1997). The drop in silica content, observed from November to January in the population of Marsala, might be related to an important growth period in the sponge preceding sexual reproduction, which takes place in the months that follow. Nevertheless, the drop in silica content could be due to the extrusion of spicules, a process demonstrated in other sponge species (Connes 1968; Mawet and Rasmont 1971).

An active spiculogenesis seems to occur in both populations after sexual reproduction. This assumption is supported by the relevant number of spicules which are reduced in size. Spiculogenetic activity is consistent with the need for increased skeletal construction during

the sponge body remodelling after the release of gametes and larvae.

In summary, the studied populations of *Pellina semitubulosa* showed that: (1) sponge silica content and spicule size vary at the two study sites according to differences in water silica concentration; (2) sponge silica content is correlated with water temperature; (3) gamete differentiation and post-fertilization processes do not interfere with spicule growth; and (4) gamete and larval release triggers the secretion of new spicules.

**Acknowledgements** We would like to thank M. Scardi for his help in the statistical analyses, C. Nonnis Marzano for her help in collecting specimens and G. Giovine for her technical assistance. This work has been 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 current Italian laws.

## References

- Bavestrello G, Bonito M, Sarà M (1993a) Influence of depth on the size of sponge spicules. *Scientia mar* 57(4): 415–420
- Bavestrello G, Bonito M, Sarà M (1993b) Silica content and spicular size variation during an annual cycle in *Chondrilla nucula* Schmidt (Porifera, Demospongiae) in the Ligurian Sea. *Scientia mar* 57(4): 421–425
- Calvo S, Fradà Orestano C (1984) L'herbier à *Posidonia oceanica* des côtes siciliennes: les formations récifales du Stagnone. In: Boudouresque CF, Jeudy de Grissac A, Oliver J (eds) International Workshop *Posidonia oceanica* Beds. Vol. 1. GIS Posidonie, Marseille, France, pp 29–37
- Connors R (1968) Etude histologique, cytologique et expérimentale de la régénération et de la reproduction asexuée chez *Tethya lyncurium* Lamarck (= *T. aurantium* Pallas) (Demosponges). PhD thesis, University of Montpellier, Montpellier, France
- 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
- de Weerdt WH (1985) A systematic revision of the northeastern Atlantic shallow-water Haplosclerida (Porifera, Demospongiae), Part I: introduction, Oceanapiidae and Petrosiidae. *Beaufortia* 35(5): 61–91
- Elvin DW (1971) Growth rates of the siliceous spicules of the freshwater sponge *Ephydatia muelleri* (Lieberkühn). *Trans Am microsc Soc* 90(2): 219–224
- Elvin DW (1976) Seasonal growth and reproduction of an intertidal sponge *Haliclona permollis* (Bowerbank). *Biol Bull mar biol Lab, Woods Hole* 151: 108–125
- Fröhlich H, Barthel D (1997) Silica uptake of the marine sponge *Halichondria panicea* in Kiel Bight. *Mar Biol* 128(1): 115–125
- Grasshoff K (1964) On the determination of silica in sea water. *Deep-Sea Res* 11: 597–604
- 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, Connecticut
- Hentschel E (1929) Die Kiesel und Hornschwämme des nördlichen Meeres. *Fauna arct* 5: 858–1042
- Hooper JA (1991) Revision of the family Raspailiidae (Porifera, Demospongiae), with description of Australian species. *Invert Taxon* 5: 1179–1418
- Jones WC (1987a) Seasonal variations in the skeleton and spicule dimensions of *Haliclona elegans* (Bowerbank) sensu Topsent (1887) from two sites in North Wales. In: Jones WC (ed) European contributions to the taxonomy of sponges. *Publ Sherkin Is Mar Stat* 1: 109–129
- Jones WC (1987b) Skeletal variation in embryo-containing specimens of *Haliclona rosea* (Bowerbank) from Anglesey, North Wales. In: Vacelet J, Boury-Esnault N (eds) Taxonomy of Porifera of the NE Atlantic and the Mediterranean Sea. Springer-Verlag, Berlin, pp 101–124
- Jones WC (1991) Monthly variations in the size of spicules of the haplosclerid sponge, *Haliclona rosea* (Bowerbank). In: Reitner J, Keupp H (eds) Fossil and recent sponges. Springer-Verlag, Berlin, pp 404–420
- 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
- Mawet A, Rasmont R (1971) L'éjection de spicules par des éponges au cours de leur morphogénèse. *Archs Biol, Liège* 82: 543–565
- Palumbi SR (1986) How body plans limit acclimation: response of a demosponge to wave force. *Ecology* 67(1): 208–214
- Passeri L (1974) Sedimentazione carbonatica attuale e diagenesi precoce nella laguna di Porto Cesareo (Penisola Salentina). *Boll Soc Geol Ital* 92(Suppl): 3–40
- Pé J (1973) Étude quantitative de la régulation du squelette chez une éponge d'eau douce. *Archs Biol, Liège* 84: 147–173
- Schönberg CHL, Barthel D (1997) Inorganic skeleton of the demosponge *Halichondria panicea*. Seasonality in spicule production in the Baltic Sea. *Mar Biol* 130(2): 133–140
- Simpson TL (1978) The biology of the marine sponge *Microciona prolifera* (Ellis and Solander). III. Spicule secretion and the effect of temperature on spicule size. *J exp mar Biol Ecol* 35: 31–42
- Simpson TL (1984) The cell biology of sponges. Springer-Verlag, Berlin
- Stone AR (1970) Seasonal variations of spicule size in *Hymeniacidon perleve*. *J mar biol Ass UK* 50: 343–348
- Topsent E (1917) Spongiaires. In: Joubin L (ed) Deuxième expédition antarctique française (1908–1910) commandée par le Dr. Jean Charlot. Masson, Paris, pp 1–88