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RESEARCH ARTICLE

A 3-year investigation of sexual reproduction in *Geodia cydonium* (Jameson 1811) (Porifera, Demospongiae) from a semi-enclosed Mediterranean bay

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Abstract The reproductive cycle of *Geodia cydonium* in a semi-enclosed Mediterranean bay (Porto Cesareo, SW Apulia) was studied with monthly frequency over a 3-year period. The investigation was carried out by utilizing a technique consisting of tagging ten individuals with a PVC stick and cutting off, by means of a metal cork borer, small samples (cylinders about 5 cm^3 in volume) from each of them for histological analysis. Sexual reproductive elements were detected in all individuals, but in the third year some specimens showed reduced reproductive activity or complete infertility. Spermatogenesis occurred in a short period (from June to August) whereas oogenesis lasted longer (from spring to late summer). Spermatic cysts occurred when the frequency of specimens with oocytes reached its maximum values. A relationship between water temperature and the onset of gamete differentiation was observed. *G. cydonium* is here confirmed oviparous and gonochoric with a sex ratio in favour of the females. However, in contrast with current literature on Porifera—which suggests that only a limited number of sponges, all belonging to the same species are sexually active—the sexual reproduction of this species involves all the examined individuals. This finding can be explained by the methodological approach used in this research, which differs from the traditional way of assessing the sponge reproductive cycle by analysing randomly collected specimens within a population. The study of a series of individuals over time represents a better "model technique" for investigating sponge sexual reproduction and the effect of environmental parameters on gamete differentiation.

Introduction

Numerous aspects of reproduction have been investigated over the years in several species of marine sponges, with particular attention to the cytodifferentiation of gametes (see review in Fell 1983; Simpson 1984; Gaino et al. 1986; Sarà 1992; Gaino and Sarà 1994), but little is known about the reproductive efforts and patterns of anatomical–histological changes in sponges.

The traditional way to assess the sponge reproductive cycle is based on histological and ultrastructural sections of specimens randomly collected within a population throughout the year (Lévi 1951; Vacelet 1964; Chen 1976; Fell and Jacob 1979; Tanaka and Watanabe 1990; Kaye and Reiswig 1991; Meroz-Fine and Ilan 1995; Corriero et al. 1998; Boury-Esnault 1999; Ereskovsky 2000; Sidri et al. 2005). The percentage of samples undergoing reproduction found in most of these studies is often so low that it leaves open the possibility that individuals have cyclic breeding periods, e.g. functioning first as males, then switching to egg production (Simpson 1980). Nevertheless, as different individuals are usually examined at each sampling period, there is no means of knowing whether reproduction is an annual, biannual, or multi-annual event, or whether

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there is a lag in the reproductive timing within the population. This procedure by itself inadequately outlines the gametogenic cycle and often the type of sexuality cannot be rigorously established (Ayling 1980). In contrast, Ayling (1980), Wapstra and van Soest (1987) and Usher et al. (2004) reported valuable information on the sexual cycle of some demosponges obtained from investigating tagged individuals over time.

Notwithstanding literature data, which report hundreds of recordings of the demosponge *Geodia cydonium* worldwide, the only investigation on the reproductive cycle of this sponge is limited to one Southern Italian population (Scalera Liaci and Sciscioli 1969). This study proved that this species is oviparous, thereby widening the knowledge on the oviparous sponges, which are notoriously very scarce (Scalera Liaci et al. 1971; Fromont 1988; Watanabe and Masuda 1990; Rosell 1996; Mariani et al. 2000; Sidri et al. 2005).

We present here the reproductive cycle of ten appropriately tagged specimens of *G. cydonium*, which were investigated over a 3-year period in a semi-enclosed bay located along the Italian coast at Porto Cesareo (SW Apulia, Ionian Sea). In addition, since sea water temperature appears to play a pivotal role on the sponge reproductive process (Diaz 1973; Reiswig 1983; Simpson 1984; Fell 1993; Witte et al. 1994; Fromont 1999; Ereskovsky 2000), this parameter was also recorded in order to assess its relationship with the reproductive cycle of this species.

Materials and methods

Description of the study site

Porto Cesareo bay (South-western Apulia, South Italy—40°15′N; 17°54′E) (Fig. 1) measures 2,500 m in length and 700–800 m in width, with a maximum depth of 2.5 m (Passeri 1974). The bay communicates with the sea through a channel system that allows a considerable inflow of sea water. The water movement within the bay, however, is significantly lower than in the open sea (Corriero 1990). The bottom consists primarily of mixed sands; though calcareous substrates, rocks and pebbles are also present. Thirty-nine species of demosponges occur in Porto Cesareo bay showing high coverage values (Corriero 1990; Corriero et al. 1996b; Mercurio et al. 2001).

Species studied

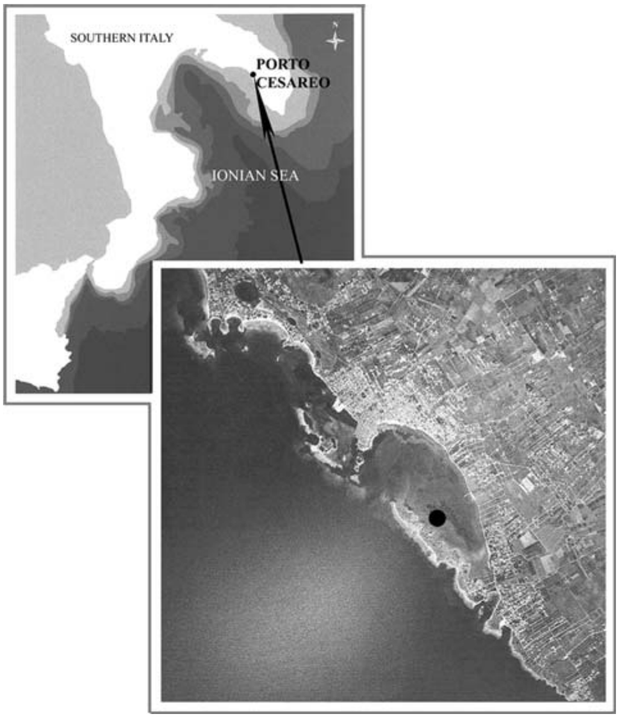

Fig 1 Porto Cesareo bay (SW Apulia, 40°15′; 17°54′) and sampling area (*black circle*)

Geodia cydonium (Jameson 1811) is a well known demosponge, which is very common in the Atlantic–Mediterranean area (Uriz 1981). This species has been described as very variable in shape: irregularly massive (Uriz 1981), cushion-encrusting (Pulitzer-Finali 1983), spherical or sub-spherical (Corriero 1987), columnar/cylindrical (Morri et al. 1994); its surface can be smooth or grooved and is frequently covered by epibiotic flora and fauna or by sediment (Mercurio et al. 2006); the consistency is usually hard and compact.

The external colour is whitish or grey and yellowish inside. Specimens are very variable in dimensions; generally the mean diameter is about 10–20 cm, but larger specimens are also reported. The largest specimen collected in the North Adriatic Sea was 29 kg in weight and 180 cm in diameter (Santucci 1922). This species is characterized by a peculiar stratification of its tissue: a thick external coriaceous cortex which protects a soft internal choanosome. The cortical layer is about 2 mm thick, but is thinner in the area of external openings (cribrous area).

At Porto Cesareo *G. cydonium* is a very common species. The specimens are irregularly massive, with brain-like surface, and mainly settle on calcareous rocky substrates, at a depth of 1–2 m, in the middle part of the basin (Mercurio et al. 2006). The results of a survey performed in the same study area during 2002 indicated a mean density for this species of 0.47 ± 0.075 specimen/m^2 with a fairly wide volume–class distribution ranging between about 800 and 8,000 ml (Mercurio et al. 2006). The mean volume of the 47 specimens collected during this study was 2,050.21 ± 2,850.72 ml, ranging from 3.0 to 12,500 ml (Mercurio et al. 2006). According to Parenzan (1976), in this environment, *G. cydonium* can grow up to 1 m in diameter.

Sampling

Within an area of approximately 100 m^2, ten large specimens (ranging in volume from about 1 to 8 litres) of *G. cydonium* (Fig. 2a) were selected and tagged with PVC coloured sticks. For histological investigations, from October 1995 to September 1998, a metal cork borer was used monthly by SCUBA divers to cut off from each specimen a small fragment of the sponge body (a cylinder about 5 cm^3 in volume). The sponge tissue soon regenerated and 1 month later the surface of the cut sponge appeared as a light depression completely covered by new cortex. Concomitantly, water temperature was measured monthly by using a portable probe DELTA OHM, HD 8706.

The study of the reproductive cycle was carried out on histological sections (5 μm thick) obtained from samples embedded in paraffin. For these observations, sponge fragments were fixed in 4% formaldehyde in sea water, immediately after collection. Then they were desilicified with 15% hydrofluoridic acid in artificial sea water for 1.5 h, dehydrated in ethanol and embedded in paraffin. Sections, obtained by using a Reichert-Jung 2030 microtome, were stained with toluidine blue. For each specimen, examined under a light microscope, several parameters were recorded, as follows: presence/absence of gametes, mean diameter and mean volume of oocytes (not including pseudopodia) and sperm cysts (assuming both to be spherical), the density (number/mm^3) of reproductive elements and the corresponding percentage of sponge tissue involved in reproduction. The calculation of the investment in reproduction was carried out by using a camera lucida coupled with an optical microscope and projecting histological sections on graph paper. This technique allowed us to trace the surface of each section. The dimension of each area, whether including gametes or not, was then recorded with a KURTA IS/ADB digitizer connected to a PC. The corresponding volume was calculated by multiplying the surface of each histological section by the thickness of the section (5 μm). The quantitative evaluation of the density of the reproductive elements was carried out using the Abercrombie formula (1941) as suggested by Elvin (1976). The formula is: $d = N \times (t/D + t)\ (k)$, where d is the density, N is the number of gametes observed in each histological section, t is the thickness of the section (5 μm), D is the diameter of the reproductive entities (mean value for each specimen obtained by measuring the diameter of ten reproductive elements) and (k) is a constant factor converting the volume of each section to 1 mm^3.

Results

Description of sexual elements

The sponge fragments, each about 5 cm^3 in volume, consist of a thick superficial cortical layer (2 mm) and of an inner choanosomal region, which represents the most extended portion of the fragment. Only the choanosomal region is involved in gamete differentiation.

In the early phase of differentiation, the oocytes of *G. cydonium* measure about 10–15 μm; they show a large nucleolated nucleus and a very translucent cytoplasm owing to the lack of yolk (Fig. 2b). As gamete maturation proceeds, oocytes reach their maximum diameter of 40–45 μm, and have pseudopodia emerging from their peripheral border (Fig. 2c, arrows). Oocytes can often be observed fairly close to one another and separated by mesohyl elements and collagen (Fig. 2c). Their cytoplasm is gradually enriched by stored material that also fills the pseudopodia (Fig. 2c).

Spermatic cysts measure from about 25 to 40 μm (Fig. 2d). Sperm differentiation takes place asynchronously since gametes can be observed in different phases of maturation in the same specimen.

Sexual cycle

Over the 3-year period of observations, oocytes were found in eight individuals of *G. cydonium* (specimens 1–7, 9), and sperm cysts were found in the remaining ones (specimens 8, 10). None of the individuals showed the coexistence of oocytes and sperm cysts. These data confirm the gonochoric condition of this species and indicate a sex ratio favouring female sponges.

Trends in the sexual cycle of the specimens over the monitoring period are summarised in Fig. 3 a, b, c. For female lineage, the onset of gamete differentiation differs from year to year. Indeed, in the first year of observation (October 1995–September 1996), female reproductive elements were found in April in three of the monitored specimens, where they occupied 0.03% of the sponge choanosomal region and the last elements were observed in August in eight individuals, occupying 0.15% of this sponge region. The highest reproductive effort was observed in July where all the female individuals showed oocytes in 0.20% of their choanosomal region. In this month, oocytes reached

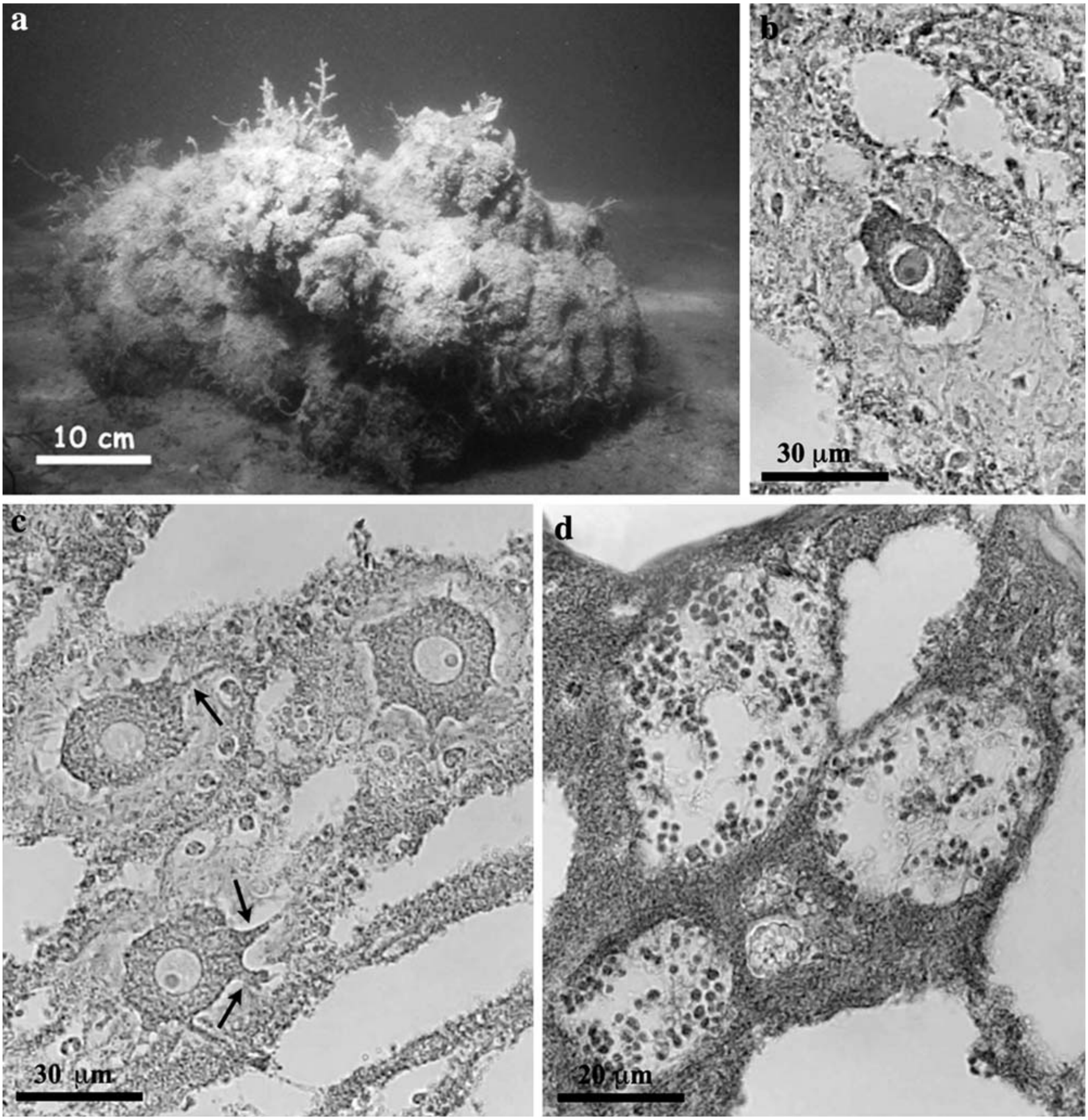

Fig 2 **a** Tagged specimens of *G. cydonium* ($n = 10$) in the study area. **b** Oocyte of *G. cydonium* in the early phase of differentiation. **c** Mature oocytes with globous pseudopodia (*arrows*) emerging from their peripheral border. **d** Spermatic cysts in the choanosomal region

the mean maximum size of 38 µm (maximum size = 55 µm recorded in the individual 6).

In the second year (October 1996–September 1997) female gametes were observed in June in three individuals, occupying 0.09% of the choanosome, and the last ones in September in four specimens, occupying 0.004% of this region. Although August was the month in which the frequency of reproductive female specimens reached the highest values, the widest areas of occupied tissue was recorded in July (0.20%), when oocytes measured 31 µm (mean). In the third year (October 1997–September 1998) oogenetic activity was limited to three months, from June to August. The highest frequency of specimens with oocytes occurred in July whereas the highest extent of the sponge choanosome occupied by female elements (0.10%) was in August, when they show a mean diameter of 26 µm.

The gamete dimensional trend and the percentage of sponge choanosomal region they occupied over the

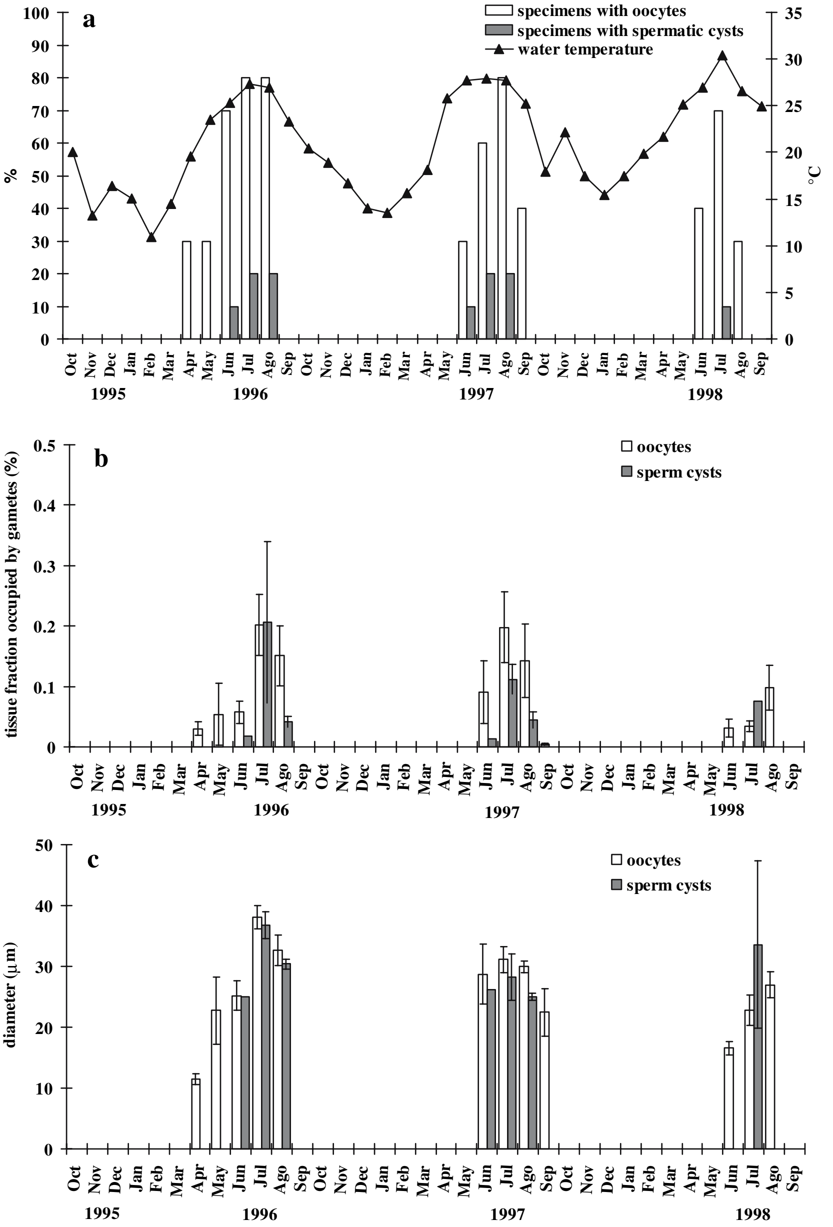

Fig 3 Sexual cycle trend of *G. cydonium* over the study period. **a** Monthly frequency of specimens with oocytes and sperm cysts and seasonal variations of water temperature in the study area. **b** Mean monthly tissue fraction (percentage ± standard error) of sponge occupied by gametes (% volume). **c** Mean monthly diameter (± standard error) of gametes

3-year period of monitoring are reported for each individual in Fig. 4.

Analysis of the data shows that there is a marked decrease not only in the frequency of reproductive specimens but also in the duration of the reproductive period. This is particularly evident in four individuals (1, 2, 5, 6) where a gradual reduction was evident from the first to the third year; in the individual 4, this reduction is evident by comparing the second with the third year; in the individual 7, by comparing the first and the second year. In the remaining individuals (3, 9), reproductive activity increased in the second year, followed by a decrease in the third year.

As far as the sperm cysts are concerned, they were only found in two individuals (8, 10). The period of their presence overlaps in the first 2 years, occurring from June to August, but in the individual 8, gametogenesis was slightly de-phased and started in July. In the third year, this individual was the only one having sperm cysts in July. In this month, cyst size showed the highest values: a mean of 37 μm in the first year (maximum size = 62.5 μm recorded in sample 8), 29 μm in the second, and 33.6 μm in the single individual in the third year. The percentage of choanosome occupied by sperm cysts varied from a mean of 0.21 in the first year to 0.11 in the second, and 0.07 in the single individual

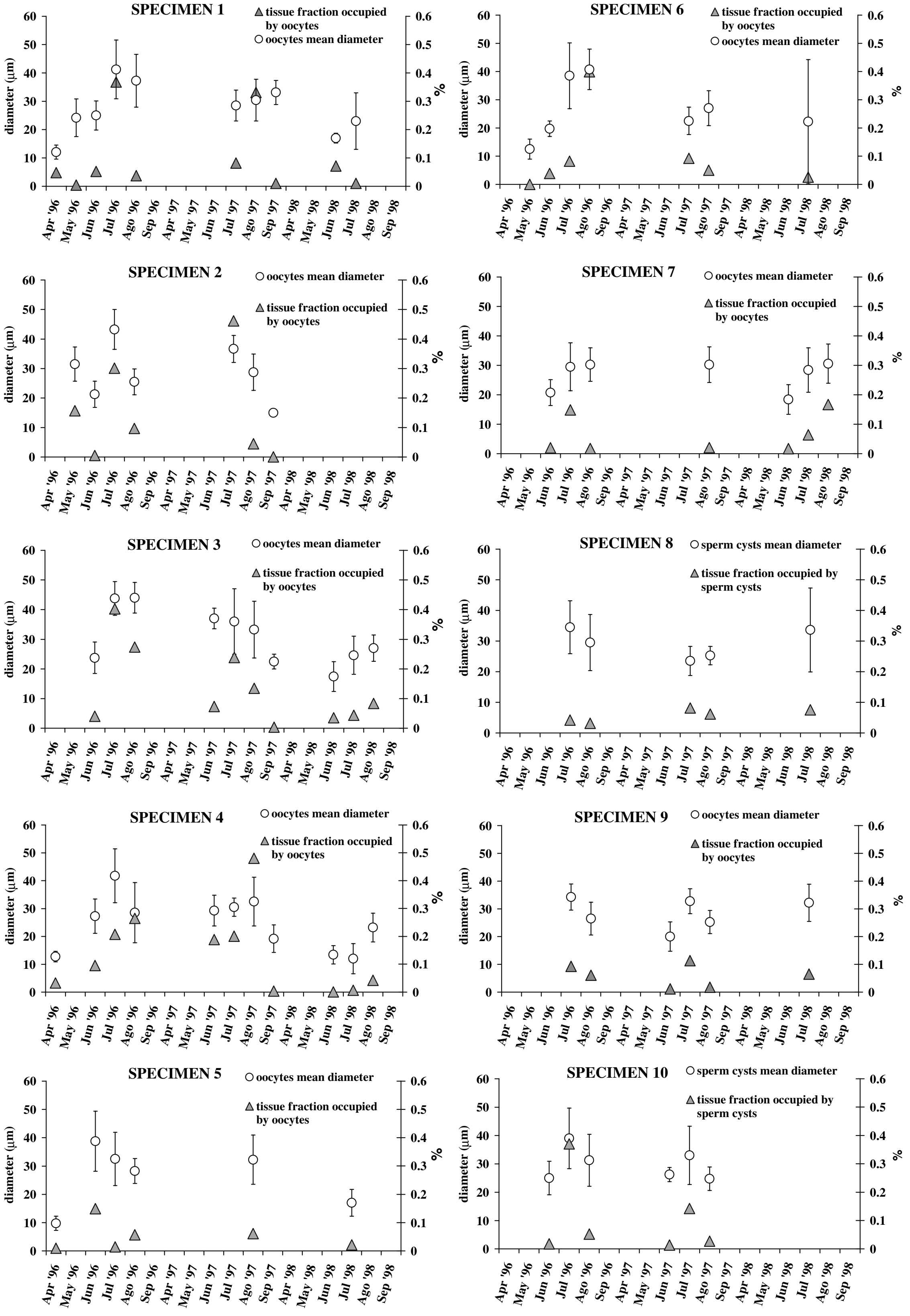

Fig 4 Gamete dimensional trend (mean values ± standard deviation) and monthly tissue fraction (%) occupied for each individual of *Geodia cydonium* monitored

in the third year. As observed for oogenesis, spermatogenesis gradually reduced during this last period.

Relationship between water temperature and sexual reproduction

The mean water temperatures recorded in the study area over the 3-year period of investigation were 19.6°C during the first year, 20.9°C during the second year and 22.1°C during the last year. The lowest temperatures were registered in February during the first 2 years (10.9 and 13.5°C, respectively) and in January in the third year (15.4°C). July always showed the maximum temperature: 27.3; 27.9; 30.3°C, respectively (Fig. 3a).

The comparison between the water temperature values and the reproductive cycle of *G. cydonium* shows that during the first 2 years, the onset of oogenesis (presence of small oocytes) took place concomitantly with a sharp increase in the water temperature (about 5°C in the first year and 7°C in the second), which occurs during late spring (from April to June) (Fig. 3a). The maximum reproductive effort (highest frequency of reproductive specimens and maximum diameter of oocytes) occurred in summer (from June to August) when water temperature values were beyond 25°C. Males occurred from June to August, concomitantly with the maximum effort of the sponge in oocytes production (Fig. 3a). In contrast, during the third year, female and male sexual activity showed a short overlapping period at the highest water temperature recorded.

Discussion

The technique used in the present investigation, based on the employment of a marker for sampling the same individual over time, allowed us to confirm the gonochoric condition of *G. cydonium*. This is in agreement with previous observations on sampling carried out randomly within a sponge population (Scalera Liaci and Sciscioli 1969). Neither embryos nor larvae were observed in the sponge tissue, thereby confirming that the species is oviparous, a condition already ascertained by Scalera Liaci and Sciscioli (1969).

Our methodological approach shows that sexual reproduction occurs with seasonality: the oogenetic cycle starts in late spring and stops at the end of summer. As the oogenesis proceeds, the number of individuals with oocytes increases along with the increase of oocyte dimensions. Female gametes should be released when they measure 40–45 μm, the maximum value recorded in the studied specimens.

Spermatic cysts, deriving from choanocyte chambers (Scalera Liaci and Sciscioli 1969), occur for a short period concomitantly with the highest intensity of the oogenesis. This sexual pattern, also reported for other demosponges (Scalera Liaci et al. 1971, 1973; Tanaka and Watanabe 1990; Fell 1993), probably represents the most common means of sexual reproduction among oviparous sponges in temperate seas.

The occurrence of sperm cysts in only two of the ten sponges suggests a sex ratio in favour of females, a condition that seems to be fairly common among Porifera (Scalera Liaci et al. 1971; Wapstra and Van Soest 1987; Corriero et al. 1996a, 1998; Mercurio et al. 2000; Meroz-Fine et al. 2005).

The literature reports that the annual reproductive index in sponges is usually low, with only a limited number of specimens, generally not exceeding 50%, able to differentiate gametes (Scalera Liaci et al. 1973; Corriero et al. 1996a, 1998). Scalera and Sciscioli (1969) reported for *G. cydonium* an annual reproductive index of 38.1% with a peak of reproductive specimens in August (58%). Therefore, it is quite surprising that all the individuals of *G. cydonium* monitored in the present study reproduce for two consecutive years out of the three investigated. It is well known that gamete production in sponges varies from individual to individual, probably according to age and size (see Simpson 1980 for a review). Indeed, it has been frequently observed that the relative amount of resources put into reproduction increases with age (Graham 1985). Here we intentionally selected the ten specimens of *G. cydonium* among the larger individuals to minimize the effects of sampling, indirectly biasing this study towards specimens with increased probability of sexual activity. Nevertheless, we believe that the methodology used in the present paper, if extended to a wider number of specimens of various sizes, could represent a better approach for studying reproductive processes in sponges and should be considered in future investigations on this subject. However, better knowledge of the sponge reproduction from studying tagged specimens has also been demonstrated by Usher et al. (2004) who investigated *Chondrilla australiensis*, previously studied by Fromont (1999). The study of tagged individuals has established a better definition of the details of reproduction in this species, including the reproductive nature of this sponge, the timing and frequency of gametogenesis and spawning and details of the biology of the developmental process.

In *G. cydonium,* the percentage of choanosomal tissue occupied by gametes is low and fairly similar in females and males (maximum values observed, 0.48 and 0.37%, respectively), whereas in other oviparous species such as *C. australiensis* (Usher et al. 2004) and *Chondrilla nucula* (Sidri et al. 2005), a higher energy investment in reproduction has been observed with a consistent reduction in the aquiferous system which appears to seriously deplete the nutritional status of the sponge. By contrast, in viviparous species, such as *Tedania anhelans* (Nonnis Marzano et al. 2000) and *Pellina semitubulosa* (Mercurio et al. 2000), the density of sperm cysts is far higher than that of the oocytes.

The data here recorded show that in *G. cydonium* the onset of reproduction does not occur simultaneously in all individuals. In particular, oocytes are often present in spring whereas spermatogenesis occur later on. However, we cannot exclude that these oocytes can grow slowly and remain longer in the sponge tissue.

The time of onset of sexual activity in the many individuals varied over the 3 years of study. A slight asynchrony in the reproduction within the same population has been previously described for other sponge species (Bergquist 1978; Corriero et al. 1998). The mechanisms controlling the onset and lasting of reproduction and gamete growth are still scarcely known. However, many authors emphasize the relationship between variations in sexual activity and different environmental conditions (Storr 1964; Rader and Winget 1985; Wapstra and van Soest 1987; Pronzato and Manconi 1991; Pronzato et al. 1993). Indeed, among the exogenous factors affecting sponge reproduction, water temperature appears to exert an important role by affecting the reproductive cycle of various species of Porifera (Storr 1964; Simpson 1968, 1984; Diaz 1973; Fell 1976, 1993; Ereskovsky 2000; Meroz-Fine et al. 2005). A relationship between the increase in water temperature and the timing of sexual reproduction has been described for *Cliona vastifica* (Hartman 1958), *Haliclona loosanoffi* (Hartman 1958; Wells et al. 1964; Fell 1976), *Hippospongia lachne* (Storr 1964), *Petrosia ficiformis* (Lepore et al. 1995), *Mycale contarenii* (Corriero et al. 1998) and *C. australiensis* (Usher et al. 2004).

In the studied individuals of *G. cydonium*, young oocytes are evident in April and June, when water temperature suddenly increases by several degrees. Egg growth proceeds during the warmer season when sperm differentiation also takes place. This trend, markedly overlapping during the first 2 years, changes in the summer of the final year, possibly because of an unusual event of water warming, which affects sponge metabolism (Zocchi et al. 2003). It is thus very likely that water temperature plays a pivotal role in also controlling the reproductive cycle of *G. cydonium*. A further hypothesis on the decrease in reproductive activity could be linked to the costs of the regenerative processes in sponges subjected to such a long period of disruptive sampling. Tissue regeneration in sponges is a well known phenomenon, which starts immediately after cutting (Pronzato et al. 1999; Corriero et al. 2004), and generally leads to a rapid reparative processes (Simpson 1984). Several studies demonstrate that the rapid regeneration observed after experimental wounding is important to prevent fouling of exposed skeletal elements (Leys and Lauzon 1998; Duckworth 2003), to maintain competitive superiority in space-limited systems (Jackson and Palumbi 1979), to reattach if fragmented (Wilkinson and Thompson 1997) and to regain optimal size and shape for feeding (Bell 2002). In *Geodia barretti* explants derived from choanosomal tissue regenerated into healthy sponges, equalling the original weight approximately after 6 weeks. In addition the development of eggs cells in cultivated fragments demonstrate that *G. barretti* is able to continue its reproductive cycle despite manipulation and reduction in size (Hoffmann et al. 2003). In *G. cydonium*, tissue samples of approximately 10 g cultivated for the extraction of bioactive metabolites formed a robust contact with the cultivation trays after just 2–3 days. Moreover, two pieces of tissue from the same sponge placed in close contact fused together after 2–3 days, demonstrating the high regenerative capacity of this species (Muller et al. 1999). As a consequence, the monthly sampling of small fragments (5 cm^3 in volume) collected from large specimens of *G. cydonium* should not be responsible for the decrease in sexual activity observed in the third year.

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