Marine Biology (2005) 147: 243–250
DOI 10.1007/s00227-004-1532-2

RESEARCH ARTICLE

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# Changes in morphology and physiology of an East Mediterranean sponge in different habitats

Received: 27 January 2004 / Accepted: 19 November 2004 / Published online: 21 January 2005


**Abstract** The sponge *Tetilla* sp. (Tetractinomorpha: Tetillidae) is a common species in the eastern Mediterranean. This sponge inhabits four different habitat types differing in wave impact and irradiance levels. Two of these habitats (a shallow cave and deep water) are characterized by relatively calm water, whereas the other two (shallow exposed site and tide pools) are in turbulent water with high energy flow. The present study examined the influence of physical (depth, illumination and water motion) and biotic factors on morphology, skeletal plasticity and reproductive traits among the four spatially separated populations. Sponges from tidal pools had significantly larger body volume than sponges from deep water and from shallow caves (ANOVA: tidal-deep $P < 0.0001$; tidal-shallow caves $P < 0.05$). Sponges from exposed habitats were significantly larger than deep-water sponges (ANOVA: $P = 0.01$). In addition, individuals from tide pools and from the exposed habitat had a significantly higher proportion of structural silica than sponges from the calmer deep water and from the cave sites. Oxea spicules in sponges from the calm habitats were significantly shorter than in those from the tidal pools and the exposed habitats. The percentage of spicules out of a sponge's dry weight in individuals transplanted from deep (calm) to shallow (turbulent) water significantly increased by $21.9 \pm 12.9\%$. The new spicule percentage did not differ significantly from that of sponges originally from shallow water. Oocyte diameter differed significantly between habitats. The maximal size of mature eggs was found in deep-water sponges in June ($97 \pm 5$ μm). In the shallow habitats, a smaller maximal oocyte diameter was found in the cave, in May ($56.5 \pm 3$ μm). Furthermore, oocyte density in shallow-water sponges was highest in May and decreased in June (with $88.2 \pm 9$ and $19.3 \pm 9$ oocytes $mm^{-2}$, respectively). At the same time (June), oocyte density of deep-water sponges had just reached its maximum ($155 \pm 33.7$ oocytes $mm^{-2}$). The difference in oocyte size and density between deep- and shallow-water individuals indicates an earlier gamete release in the shallow sponge population. The results suggest that plasticity in skeletal design of this sponge indicates a trade off between spicule production and investment in reproduction.

Communicated by O. Kinne, Oldendorf/Luhe

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## Introduction

The phylum Porifera exhibits considerable morphological variations, which have been suggested to be related to environmental impact, such as exposure to wave action (Palumbi 1986), depth (Bavestrello et al. 1993; Pronzato et al. 2003), illumination intensity (Becerro et al. 1994; Uriz et al. 1995) and level of sedimentation (Manconi and Pronzato 1991; McDonald et al. 2002). An individual's form (i.e. skeleton and three-dimensional form) may vary through time, particularly in populations from intertidal and shallow marine habitats (Palumbi 1986; Hill and Hill 2002). In different environments, the external (three-dimensional shape) and internal shape (size and number of spicules, proportion of spongin) of individuals from the same species may vary widely, with different morphologies reflecting adaptation to the surrounding conditions (Bell and Barnes 2000). Local irradiance and water movement are the two most influential environmental factors in shaping sponge morphology (Kaandorp 1999). Palumbi (1986) suggested that variation in spicule morphology derives from a sponge's adaptive response to different

environmental conditions. He found that colonies of *Halichondria panicea* from high-wave-force habitats were stronger and stiffer than those from low-wave-force habitats. These biomechanical changes are due to increased spicule number and size in sponges from areas of high wave action. It was also found that sponges that recruit to environments with high water velocity and large sediment particles may devote additional energy to constructing a more robust inorganic frame at the expense of softer organic tissue (McDonald et al. 2002). Sponge stiffness increases with higher proportion of spicules in dry mass (Palumbi 1986). Sponge spicules function mainly as reinforcing fibers, and stress experienced by the sponge is thus transferred from pliable organic matter to the spicules (Koehl 1982).

Variations in environmental conditions may also influence sponge reproductive traits such as timing (Sarà 1992). Most studies suggest that seasonal changes in sea temperature may be the major proximate environmental factor controlling the annual reproduction cycle (Sarà 1992; Fan and Dai 1999; Fromont 1994; Meroz-Fine and Ilan 1995). Variations in reproductive traits have been documented between geographically distinct populations of the same sponge species (Witte et al. 1994). However, the relative contribution of genetic and environmental sources to reproductive variation has rarely been studied (Fan and Dai 1999).

In the eastern Mediterranean, the sponge *Tetilla* sp. (Tetractinomorpha: Spirophorida: Tetillidae) is distributed along a wide gradient of wave force and illumination intensities in four different habitats. Two of the habitats are characterized by calm water and less illumination (relatively deep water and caves), while the other two are in turbulent water (exposed area and intertidal pools). We compared sponge morphology, specimen size, skeletal plasticity and reproductive traits among the four spatially separated populations. The results suggest that plasticity in skeletal design of this sponge indicates a trade-off between spicule production and investment in reproduction. Although several studies have examined the morphological diversity of sponge species in different water-flow regimes (Wilkinson and Evans 1989; Alvarez et al. 1990; Diaz et al. 1990; Bell and Barnes 2000), only a few have focused on a single species under various wave or water-flow conditions (Palumbi 1984; McDonald et al. 2002; Pronzato et al. 2003).

The present study examined populations of *Tetilla* sp. across a range of habitats in order to assess the potential influence of environmental factors on this sponge's growth and physiology, as expressed in its morphology and reproduction.

## Materials and methods

### Study site

The study followed and examined sponges over 2 years, along the Mediterranean coast of Israel (Sdot Yam, 32°29.77′N; 34°53.23′E). Three shallow habitats were selected: "cave"—a subtidal cave characterized by relatively calm water and low illumination; "pool"—tidal pools (30–80 cm deep) characterized by high turbulence at high tide or stormy weather and still water at low tide and with high irradiance; and the third habitat, "exposed", is fully exposed to currents and wave action (at a depth of 3–5 m) and receives high illumination. The fourth habitat, "deep", is located in deeper water (30 m; 1.5 nautical miles west of the exposed site) with no wave action and lower illumination compared to the shallow-water habitats.

### Measurement of water movement—comparison between habitats

To compare the differences between habitats with regard to water movement, the latter was evaluated using the dissolution rate of clod cards (Doty 1971; Jokiel and Morrissey 1993). The technique allows for assessing relative water movements between sites without the need to use instruments for directly measuring water velocity, current velocity, flow intensity, turbulence intensity, or water motion over an extended period of time. This method quantifies weight loss of a soluble substance such as gypsum. The weight loss is directly related to water flow (Jokiel and Morrissey 1993), although it is not always reliable (Porter et al. 2000). We prepared 24 clod cards according to the general instructions of Doty (1971) by mixing and stirring gypsum with deionized water in a ratio of 1:1 (v:v). We poured the slurry into 500-ml cylindrical plastic molds, tapped it vigorously several times to dislodge air bubbles and allowed it to harden before removing the clod cards. After removal, the cards were dried for 3 days or longer in an oven at 37–40°C to a constant weight, and the bottoms were sanded until the cards had reached a uniform weight of $340 \pm 1.2$ g. Next, the clods were glued to 15×15 cm plastic plates with waterproof epoxy cement (propoxy20, Hercules Chemicals, Passaic, NJ 07055, USA). Holes were punched in the plastic plates to allow fastening of the cards to four stainless steel trays. The initial weight of the dry cards attached to the plastic plates was recorded. Groups of six clod cards were attached to a stainless steel tray, and each tray was located in one of the three shallow habitats and the deeper habitat. Because of technical impediments, the tidal pool chosen for the deployment of the stainless steel tray was not the one from which the experimental sponges were taken. Instead of a seaward tidal pool the tray was attached in a leeward pool. After 42 h of exposure to water flow in the four habitats, the clod cards were returned to the laboratory for final drying and weighting. It was expected a priori that water motion would differ between the habitats. The currents at shallow-open and exposed habitats, as well as at the shallow tidal pool, were expected to be the strongest, whereas the shallow-water cave and the deep-open habitats were expected to

experience much calmer water flow. The statistical analysis of the rate of gypsum dissolution initially used was a one-way ANOVA (analysis of variance), followed by a priori (planed) comparisons (Statistica 6.1).

### Sponge volume and spicule content

To calculate total sponge volume, three perpendicular axes (width, length, height) were measured before removing the sponge from the substrate (from the deep and exposed habitats, each $n=20$; tidal habitat $n=21$; cave $n=5$). One-way ANOVA was applied to test the difference in sponge volume between habitats. Spicule content was measured by drying sponge samples of known volume for 24 h at 80°C, weighing the dry sample and combusting it for 6 h at 500–550°C (Paine 1964). Following sponge combustion, the weight of each sample, containing just the remaining siliceous spicules, was measured. For each sample, the fraction of dry mass devoted to spicules was calculated as combusted mass (spicules) divided by total (pre-combusted) dry mass. One-way ANOVA and post hoc Scheffé were conducted to examine the differences in spicules' content between the different habitats.

### Measurements of intact sponge spicule

Spicules were measured (deep habitat $n=77$; exposed habitat $n=64$; cave $n=66$; intertidal pools $n=90$) after separating the ectosome from the choanosome (each zone measured separately). The sponge organic tissue was removed using concentrated hydrochloric acid (HCl). The spicules were washed three times in distilled water and resuspended in 100% ethanol by gently agitating the tube. Immediately thereafter, a subsample of 30 µl was spread on a glass slide (Fry 1970). The length of the most abundant type of spicule was measured separately from the choanosome and the ectosome. One-way ANOVA and post hoc Scheffé were conducted to determine if spicule length is different between habitats.

### Sponge transplantation

To examine the existence of morphological plasticity of *Tetilla* sp. (i.e. in spicule amount and size) we conducted reciprocal transplantation experiments. Thirty specimens were removed from deep water to the shallow exposed site, and vice versa. Groups of five to seven sponges were tied to individual plastic nets and attached to the rocky substrate using steel nails. After 6 months the nets were removed from the substrate, and spicule quantity was measured for each sponge. *T*-test analysis was conducted to compare the spicule content of deep-water sponges transplanted to shallow water, with the original spicule content of shallow-water sponges, and vice versa. As a control for transplantation effects, five deep-water sponges were removed and attached to the substrate in deep water, while five sponges from an exposed shallow habitat were attached at the shallow site.

### Sponge reproduction

Samples were taken monthly from five sponges at each habitat in order to study their gamete development, using classic histological (haematoxylin eosin) techniques (Ilan and Loya 1990). For each sponge, fecundity and gamete size were measured ($n=10$, for each sample).

Seawater temperature (ST) data from 6 and 30 m were obtained using Onset Stow Away data-loggers (hourly sampling) to correlate gamete development with ST trends. Two-way ANOVA was conducted to examine if oocyte diameter differed significantly between habitats and months.

## Results

### Measurement of water movement—comparison between habitats

The dissolution rate of clod cards varied significantly between the four habitats (Fig. 1, one-way ANOVA: $F=36.863$, $df=3$, $P<<0.001$). We used planed comparisons to examine the differences in water flow that were assumed a priori to exist between the various habitats. The results indicated that in addition to the obvious difference found between the shallow open habitat and the rest of the habitats, the shallow tidal pool was significantly different from the cave and the deep-water habitats ($P<0.01$, $F=9.602$), and the deep-water habitat experienced significantly less water motion ($P<0.05$, $F=5.824$) than the shallow-water cave.

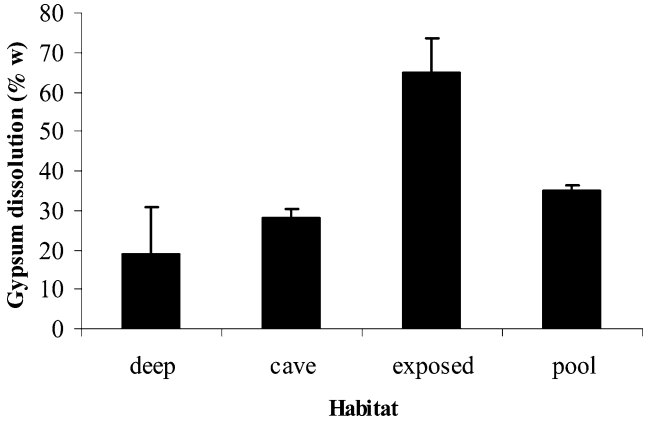


**Fig. 1** Comparative gypsum dissolution in the various habitats studied (mean percent, +SD, $n=6$ at each habitat) [*deep* exposed, deep-water habitat (30 m); *cave* a subtidal cave (3 m depth); *exposed* shallow-water, fully exposed habitat (at a depth of 3–5 m); *pool* tidal pools (0.3–0.8 cm deep)]

## Sponge volume and spicule content

The volume of sponges from the tidal pools was significantly higher ($17 \pm 5.1$ cm$^3$) than that of sponges from the deep water ($5.9 \pm 3.7$ cm$^3$) and shallow cave ($7.5 \pm 4.4$ cm$^3$) (one-way ANOVA: $F = 10.442$, $df = 62$; tidal–deep $P < 0.0001$; tidal–cave $P < 0.05$). The volume of sponges from the exposed habitat was significantly higher than that of deep-water sponges (one-way ANOVA: $F = 10.442$, $df = 62$, $P = 0.01$). The volume of sponges from tidal pools and from the shallow exposed area did not differ significantly (Fig. 2A).

Sponge inorganic content (i.e. spicules), expressed as percentage of dry weight, differed significantly between habitats (one-way ANOVA: $F = 20.274$, $df = 19$, $P < 0.0001$). Individuals from tidal pools ($n = 5$) and the exposed habitat ($n = 4$) had the highest spicule content $34.2 \pm 6.1$ and $29.8 \pm 3.4\%$, respectively, and did not differ significantly. Individuals from the cave ($n = 5$) and from deep water ($n = 9$) had a spicule content of $20.7 \pm 2.5$ and $16.8 \pm 4.4\%$, respectively, and did not differ significantly (Fig. 2; Table 1). A post hoc Scheffé analysis was used to compare the habitat means after an overall significant difference was found ($P < 0.0001$). Spicule content of individuals from the deep and the cave habitats, however, differed significantly from that of individuals from the exposed or tidal-pool habitats (Table 1).

**Table 1** *Tetilla* sp. Comparison of spicule content in sponges from different habitats (Scheffé analysis)

| Habitats | *P*-value |
|---|---|
| Deep–Exposed | 0.0011 |
| Deep–Cave | 0.4952 |
| Deep–Tidal pools | < 0.0001 |
| Exposed–Cave | 0.0469 |
| Exposed–Tidal pools | 0.5372 |
| Cave–Tidal pools | 0.0013 |

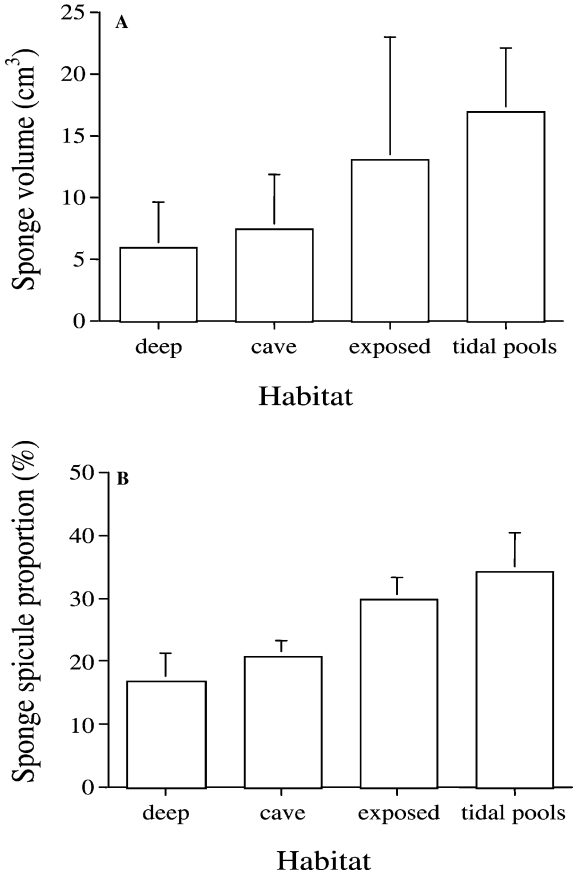


**Fig. 2** *Tetilla* sp. from different habitats: deep (30 m), shallow caves (3–5 m), shallow exposed (3–5 m) and tidal pools (0.3–0.8 m): **A** mean (+SD) sponge volume ($n = 20$ each for deep and exposed habitats; $n = 5$ in the cave; $n = 21$ in tidal pools) and **B** mean (+SD) spicule weight fraction [dry specimens (24 h, 80°C)/combusted specimens (6 h, 500–550°C)]

## Measurements of intact sponge spicule

The most abundant spicule type in *Tetilla* sp. was the oxea, although the sponges also contained protriaene and microoxea. Within each habitat, oxea spicules from the sponge choanosome did not differ significantly in length from those obtained from the ectosome. We therefore calculated the mean spicule length of a sponge in each habitat for the whole sponge (choanosome + ectosome). There was, however, a significant difference in the length of spicules between habitats (one-way ANOVA: $F = 7.8$, $df = 293$, $P = 0.0001$). Spicules of sponges from the calm habitats (cave and deep) were shorter than those from the tidal pools and exposed habitats (Fig. 3). Spicules from deep-water sponges were significantly shorter than those from the shallow tidal pools and exposed habitats (Scheffé analysis: both

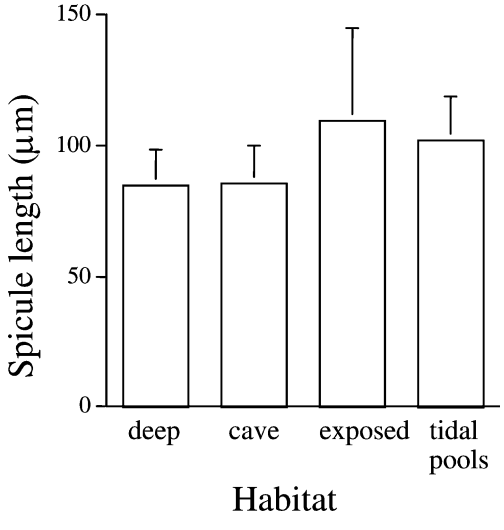


**Fig. 3** *Tetilla* sp. Mean (+SD) length of oxea (the most abundant spicule type) of sponges, from four habitats (deep $n = 77$, exposed $n = 64$, cave $n = 66$, tidal pools $n = 90$)

$P < 0.05$). Spicules of sponges from the cave were also significantly shorter than those from the exposed habitat (Scheffé analysis: $P < 0.05$).

### Sponge transplantation

The percentage of spicules out of a sponge's dry weight in individuals transplanted from deep to shallow water was examined 6 months after transplantation and shown to have increased significantly by $21.9 \pm 12.9\%$ ($t$-test: $df = 18$, $P < 0.0001$). The new spicule percentage did not differ significantly from that of sponges originally from shallow water (Fig. 2B) ($t$-test: $t = -1.165$, $df = 12$, $P = 0.27$). The sponges of the controls maintained their original percentage of spicules out of a sponge's dry weight at each depth ($29.8 \pm 3.4$ and $16 \pm 3.4\%$ in shallow and deep water, respectively).

Transplantation of sponges from shallow to deep water resulted in reduction in sponge size. After 6 months, these sponges seemed to deteriorate, and we therefore excluded them from the analysis.

### Sponge reproduction

Examination of histological preparations from *Tetilla* sp. individuals revealed some reproductively active specimens throughout the year. *Tetilla* sp. was found to be a gonochoric species, as no specimen was found simultaneously containing both oocytes and spermatic cysts. Oocytes were detected in most histological preparations, from all studied habitats, and almost all year round. The oocytes possessed a prominent nucleus and a nucleolus (Fig. 4A). Spermatic cysts were found just in one of the histological preparations (Fig. 4B). Maximal oocyte diameter differed significantly between habitats and months (two-way ANOVA: $F = 68.9$, $df = 5$, $P < 0.001$). Scheffé analysis revealed a significant difference in diameter between each two habitats (deep–exposed, deep–cave, deep–tidal; two-way ANOVA: $P < 0.001$), except for the cave–tidal, where no significant difference was found. The maximal size of a mature oocyte in the deep-water sponges was in June, with a mean size of $97 \pm 5$ μm when temperature was 25.5°C. In the shallow-water cave habitat, maximal oocyte diameter was in May, with a mean size of $56.5 \pm 3$ μm (Fig. 5A) when temperature was 23°C. During that month (May), the oocytes of deep-water sponges were 30% larger than those from the shallow water, with an average size of $73.5 \pm 5$ μm. Oocyte maturation in shallow-water sponges occurred earlier in the year than in deep-water sponges (Fig. 5A). In June, when the shallow-water temperature was 27°C, mean oocyte diameter in shallow-water sponges had already decreased, probably following gamate release during May. Meanwhile, oocytes of the deep-water sponges continued to increase in size by an additional 30%, reaching their maximal diameter ($97 \pm 5$ μm) in June, before being released (Fig. 5A).

Further indication of the timing of gamete release can be seen from the pattern of fecundity. Oocyte abundance in shallow-water sponges was highest in May, with $88.2 \pm 9$ oocytes $mm^{-2}$ and decreased to $19.3 \pm 9$ oocytes $mm^{-2}$ in June. At the same time (June), oocyte abundance in deep-water sponges reached its maximum of $155 \pm 33.7$ oocytes $mm^{-2}$ (Fig. 5B).

## Discussion

Sessile marine organisms frequently exhibit morphological and physiological acclimation to different environmental conditions (Palumbi 1986; Fan and Dai 1999). This study shows that *Tetilla* sp. exhibits plasticity in its morphology and reproductive timing as a consequence of environmental factors. *Tetilla* sp. from different habitats were found to be plastic in total volume, spicule content and size, mature egg size, fecundity and reproductive timing. *Tetilla* sp. were observed to acclimate their morphology to highly illuminated current-swept water as well as to very calm water with much lower illumination (such as in a cave). Sponges from high-energy sites (tide pools and exposed shallow sites) had the highest proportion of spicules, while those from calm-water habitats (the deep site and the cave) had significantly lower spicule content (Fig. 2B). These findings are in agreement with previous reports of flow effect on sponge morphology (Palumbi 1986; Bell and Barnes 2000; Bell et al. 2002; McDonald et al. 2002). It

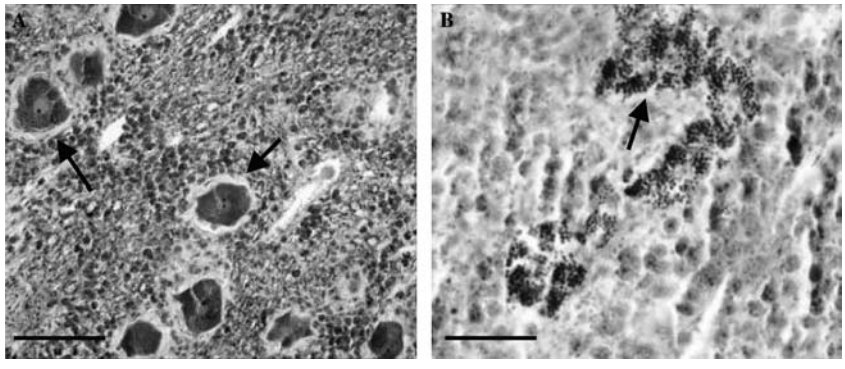


**Fig. 4** Reproduction of *Tetilla* sp. **A** Sponge oocytes (*arrows*) from deep water, in June. **B** Spermatic cysts (*arrows*). *Scale bar*: 100 μm

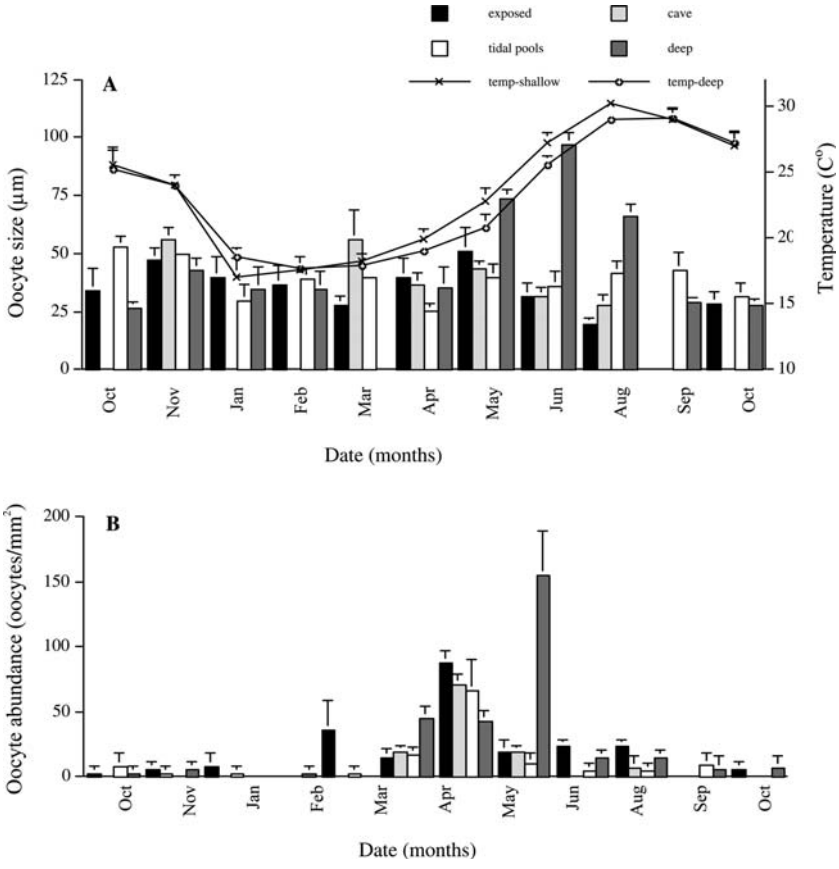


**Fig. 5** Reproduction of *Tetilla* sp. **A** The relationship between oocyte size (*bars*of mean + SD) in sponges from different habitats and annual monthly means of sea water temperatures (*curves*). **B** Annual oocyte abundance (mean + SD) in sponges from different habitats

was found that in *Halichondria panicea*, sponges inhabiting habitats with high wave forces had a greater spicule density than those from habitats with low wave force. Sponge stiffness increased when a higher proportion of sponge dry mass was devoted to spicules. A greater proportion of spicules provides a more rigid and robust form, which consequently suffers little deformation even under high water velocity. The influence of water flow on sponge form may be linked to the necessity for greater structural support through spicule reinforcement in areas of high water flow (Palumbi 1986).

It should be noted that our estimates of the relative water motion at each habitat somewhat underestimated the water movement at the tide pool habitat because of the location of the clod card deployment (on the leeward side, whereas the sponges were from the seaward side of the same small island). This may explain the absence of difference in sponge size and spicule content between the habitats, while our assessment of the water movement as reflected by the gypsum dissolution showed significant difference between the examined habitats.

The thickness and the length of the spicules contribute to the rigidity and the flexibility of the sponge too. Palumbi (1986) found that spicules of *H. panicea* from high-wave-force sponges were the same length as those from low-wave-force sponges, but were thicker and had greater surface area and volume. We found no differences in spicule thickness, but those at the high-energy sites were significantly longer in comparison with those found in sponges from calm-water habitats. Similarly, spicules in *Cliona celata* were significantly longer at high-energy sites, compared to low-energy sites (Bell et al. 2002). Long spicules may not make more rigid tissues (Koehl 1982), but they can provide a degree of flexibility (Bell et al. 2002). This, together with higher spicule abundance, may also be important in helping sponges adapt to high-energy environments (Bell et al. 2002).

Sponges were transplanted reciprocally between exposed and deep habitats. The transplanted sponges from deep to exposed shallow water significantly increased their spicule contents. After 6 months, sponges transplanted into exposed habitat had spicule content similar to that of local non-manipulated sponges. Palumbi (1984) also found that sponges quickly begin production of stiffer and stronger tissues after transplanted to high-wave-energy environments, but delay formation of new, weak tissues in calm habitats.

The present research also revealed plasticity of reproductive traits, such as timing of gamete release and mature oocyte size of *Tetilla* sp. Oocytes of shallow-water sponges grew faster, and spawning occurred 1 month earlier, in comparison with deep-water sponges. We conclude that the earlier spawning in shallow-water sponges is due to an earlier rise in sea temperature compared with the deeper habitats (Fig. 5A). Shallow-

water sponges produced oocytes of maximal size when the water temperature was 23°C, about 80% of its maximum in that habitat (28.5°C in August), while the deep-water sponges reached their maximal oocyte size in June, at 25.5°C, about 80% of the maximum temperature in this habitat. Earlier spawning of inshore corals was found also during mass spawning on the Great Barrier Reef (Babcock et al. 1986), where the earlier spawning of inshore corals has been attributed to an earlier rise in sea temperature.

There was a difference in fecundity of sponges from different habitats. Such interhabitat variation might indicate environmental differences leading to phenotypic variation in reproductive output. The oocyte abundance in shallow-water sponges was 57% less than in deep-water sponges. In contrast, the shallow-water sponges were found to be bigger and to have a higher spicule proportion. A similar phenomenon was observed by Frøhlich and Barthel (1997), who showed that during the most intense phase of reproduction specimens of *Halichondria panicea* exhibited a significant drop in their silica uptake. Obviously these sponges did not produce spicules during this time. Such an explanation might also be valid for the *Tetilla* specimens from highly exposed habitats, which need more energy to invest in spicule production, rather than investing it in reproduction. Variability in oocyte size between populations has also been found in corals: *Pocillopora verrucosa* (Sier and Olive 1994) and *Echinopora lamellose* (Fan and Dai 1995). This phenomenon may reflect an increasing investment in larval survivorship and perhaps represent a response to the unfavorable environment at high latitudes (Sier and Olive 1994).

We suggest that the effects shown in this study of environmental factors on sponge volume, spicule size, spicule abundance and reproductive traits may indicate a trade-off between spiculogenesis and sexual reproduction. The sponges from deep-water had a lower proportion of spicules, but exhibited higher fecundity. Spiculogenic activity is consistent with the need for increased skeletal construction at high-energy sites, and thus could be related to decreased reproductive activity (Frøhlich and Barthel 1997). Since archaeocytes are the major cell type correlated with growth and reproduction and there is an extensive use of these cells, a reduction in their numbers may occur, which could significantly affect one or both of these biological functions, thus allocating energy between reproductive activities and growth. Similarly Becerro et al. (1997) found a trade-off between reproduction and production of chemical defense. In two compared habitats (shaded and well illuminated habitats), allocation to defense was found to be negatively correlated with reproduction and growth.

**Acknowledgements** The authors are indebted to R. Tsadok for his invaluable help in the field work. This study benefited much from the reviews of referees who provided constructive criticism on an earlier version of the manuscript.

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