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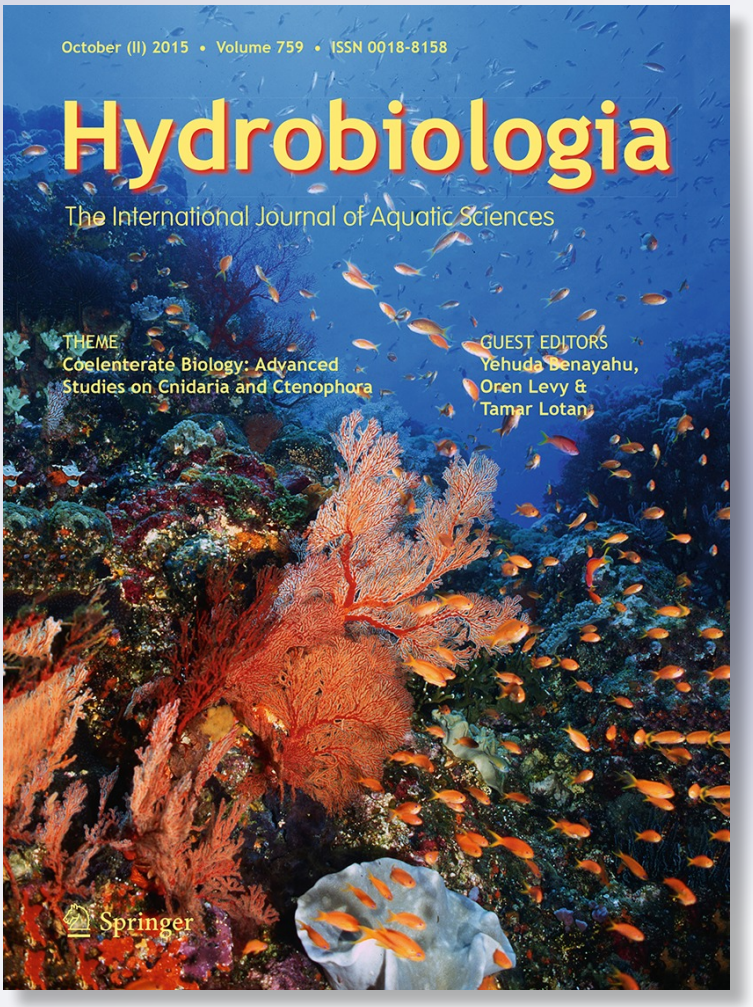

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COELENTERATE BIOLOGY

Reproductive features of the Red Sea octocoral *Sarcophyton auritum* Verseveldt & Benayahu, 1978 are uniform within generic boundaries across wide biogeographical regions

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Abstract The octocoral *Sarcophyton auritum* Verseveldt & Benayahu, 1983, is considered endemic to the Red Sea. We investigate here for the first time its distribution on the Eilat reefs and its sexual reproductive features. Quantitative surveys revealed *S. auritum* is relative rarity with the Morisita index indicating that the colonies exhibit a clumped distribution, frequently growing in groups. This spatial distribution may result from the species' reproductive features. *S. auritum* was found to be gonochoric. Female colonies demonstrated a prolonged oogenic cycle (18–21 months), featuring two size groups of oocytes, each presenting a separate developmental cycle. The male spermatogenetic cycle was shorter (8–10 months), with one developmental cycle at a time. Colonies spawned annually on a single night, demonstrating an intraspecific synchronized spawning. The spawning occurred on a full-moon night in July. Cleavage of the embryos can be equal or unequal, resulting in the respective formation of regular blastulae along with bizarre-shaped embryos that subsequently develop into the planulae. The findings indicate that the reproductive features of *Sarcophyton* soft corals are consistent within the genus, thus supporting the tested hypothesis of the study that among reef soft corals these features are consistent within generic boundaries across all Indo-Pacific regions studied so far.

Keywords Octocorallia · Life history · Gonad development · Spawning · Embryogenesis · Red Sea

Introduction

The mode and timing of reproduction are key life-history characteristics in determining the population dynamics, ecology, and evolution of all organisms (Stearns, 1992). Most octocorals are gonochoric, featuring either male or female reproductive structures in separate colonies, while a few are hermaphroditic, in which each mature colony contains both male and female reproductive structures (e.g., Benayahu & Loya, 1986; Schleyer et al., 2004; Kahng et al., 2011). Among octocorals asexual reproduction is quite common and, as a modular organism, colony growth is conducted by polyp budding (Kahng et al., 2011). Asexual reproduction plays a major role in the life history and population growth of some octocorals (Simpson, 2009). As demonstrated by Kahng et al. (2011), so far all the studied octocorals also feature sexual reproduction, of

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which there are three types: broadcasting of eggs and sperm, internal brooding of panula larvae, and external surface brooding (Benayahu, 1991; Lasker, 2006). Broadcasters release large numbers of eggs and sperm into the water column, where fertilization occurs. Gamete release into the water is often synchronized with the lunar phase and/or water temperature (Benayahu et al., 1990; Hellström et al., 2010). The larvae develop from the externally fertilized eggs, remain planktonic for a period of days to weeks, and then settle and metamorphose into founder polyps (Fabricius & Alderslade, 2001).

Among octocorals male and female gonads develop along the polyp mesenteries, originating from the gastrodermis (e.g., Tyler et al., 1995; Kruger et al., 1998; Hwang & Song, 2007). As the gonads increase in size they extend into the polyp cavity, occupying most of its space (e.g., Benayahu & Loya, 1986; Schleyer et al., 2004; Simpson, 2009). A good indicator of gonad development is that of their diameter during the course of their gametogenic cycle (e.g., Excoffon et al., 2004, 2011). Spermatogenesis commonly takes place more rapidly than oogenesis (e.g., Benayahu, 1997; Kahng et al., 2011). In tropical broadcast-spawning octocorals, studies have shown a display of synchronous maturation and spawning of gametes among colonies (e.g., Benayahu et al., 1990; Fitzsimmons-Sosa et al., 2004; Linares et al., 2007). Several studies have revealed that spawning behavior of octocorals coincides with the lunar cycle (Kahng et al., 2011). Among most octocorals, post-fertilization transition of zygotes to the planula-larvae takes place within less than 7 days (e.g., Babcock, 1990; Dahan & Benayahu, 1997; Gutierrez-Rodriguez & Lasker, 2004).

The Eilat reefs constitute the northernmost edge of coral-reef distribution. Endemic species have developed throughout time in the Red Sea, resulting from its geographical separation from the Indian Ocean (Loya & Klein, 1994; Wehe & Fiege, 2002). Octocorals represent a diverse group on the reefs and are considered to be the second most important benthic component after the stony corals (e.g., Benayahu & Loya, 1981; Dinesen, 1983; Huston, 1985; Chanmethakul et al., 2010).

The current study deals with the ocotocoral *Sarcophyton auritum* Verseveldt & Benayahu, 1978, originally described from the Gulf of Aqaba (Red Sea) and recently also recorded from the Saudi Arabian reefs (Haverkort-Yeh et al., 2013). This species is considered to date as endemic to the Red Sea. The present study is the first to examine aspects of its biology beyond its original taxonomic description. The study engages with its distribution on the Eilat reefs (northern Gulf of Aqaba) and with the species' reproductive features, including gametogenic cycle, spawning events, and embryonic development to the planula stage. The findings from the study enabled us to confirm the hypothesis that the reproductive features of reef soft corals are consistent within generic boundaries and across wide biogeographical regions.

Materials and methods

Abundance of *S. auritum*

In order to examine the distribution of *S. auritum* on the Eilat reefs a quantitative survey was conducted. A preliminary field survey had indicated that *S. auritum* is rather uncommon there and, therefore, two sites were chosen where the species had previously been commonly observed. The first site extended from the northern border of the Eilat Coral Beach Nature Reserve to the southern fence of the Interuniversity Institute for Marine Sciences (IUI); and the second was a diving site known as "The Caves", located south of the IUI (Fig. 1). The survey was conducted from January 2011–August 2012 by SCUBA diving. On the surface water, a snorkeler with a GPS recorded the coordinates of each observed colony, after receiving an agreed signal from the divers. The first site was 1,440 m long and the second one was 120 m long. The underwater search for colonies was performed in sectors parallel to the coast, at depths of 0.5–12 m. During the survey the number of colonies and their depth were recorded. Later, the coordinates of the GPS were synchronized to Google Earth and the surveyed areas were divided into 10 × 10 m plots. To study the spatial distribution of *S. auritum* colonies the Morisita index (I_δ) (Morisita, 1959; Sokal & Rohlf, 1981) was applied as follows:

$$I_\delta = \frac{q\sum n_i(n_i-1)}{N(N-1)}$$

with F was calculated as:

$$F_0 = \frac{I_\delta(N-1)+q-N}{q-1}$$

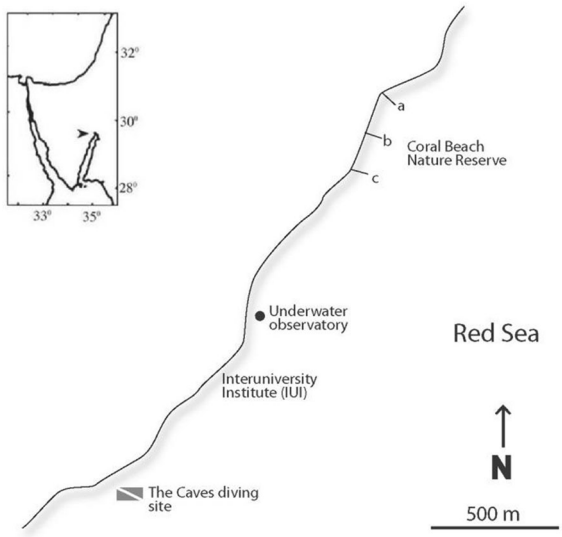


Fig. 1 Map of the study sites at the northern Gulf of Eilat. **a** Northern border of Eilat Nature Reserve, **b** North Bridge, **c** South Bridge

Here q represents the number of quadrates, n_i the number of colonies in the i quadrate, N the total number of colonies, and I_δ the Morisita index. Comparing F_0 to the critical value in the F-distribution ($F_{\infty,q-1}$) determined significance. Using Google Earth, the sites were divided into 10 × 10 m quadrates. According to this index, values >1 indicate a clumped (aggregated) distribution, if equal to 1—even, and if >1—random.

Reproduction studies

To study the reproductive features of *S. auritum*, monthly samples (January 2011–August 2012, except April 2012) were collected from eight random colonies at the reef (4–15 m) across from the Eilat underwater observatory (Fig. 1). Cuttings of ~1 cm^3 were removed from the polypary of colonies featuring >20 cm disk diameter, in order to ensure that only sexually mature colonies were sampled (see Schleyer et al., 2004). The polyp cavities of the samples were examined under a compound microscope for the presence of gonads and sex determination features. Gonads were removed from ~10 polyp cavities, wet preparations were made, their diameter was measured under a light microscope (Nikon OPTIPHOT), and the data were analyzed by Image J measuring program. The results are presented as monthly mean gonad diameter ± SD. Subsamples were removed monthly from polyp cavities of six out of the eight sampled colonies (3 female and 3 male) for histological sections. Three sections from three different areas (high, middle, and low) from each sample were mounted on microscopic slides, stained with Ehrlich's hematoxylin and eosin (Carson, 1997), and examined for sex determination and gonads. All statistical analyses were performed using SPSS v.15.1 at a significance level of $\alpha = 0.05$.

Spawning and embryogenesis

The predicted spawning event of 2012 was based on the monthly gonad measurements of *S. auritum* samples (see "Results" section). Therefore, in order to capture released gametes, starting from 1 July 2012 (two nights preceding the full moon and until spawning took place), plankton nets were placed at dusk (~17:00 pm) over four pre-sampled female and three male colonies (disk diameter > 20 cm) at the reef across from the Eilat underwater observatory. At midnight the plankton nets were removed from the colonies and transferred to the IUI in PVC containers filled with seawater. The contents of the 1 L PVC trap containers were then transferred to a ~10 L container filled with 0.45 µm filtered seawater (FSW), and the water samples were examined under a microscope, revealing naturally fertilized eggs (see "Results" section). Twelve hours post-spawning the early embryonic stages were placed in 50 mL tubes (40 per tube) filled with FSW and reared in an incubator (LE-509 MRC) at 25°C under a 12–12 h light–dark regime (60 W lamp). When the embryos had achieved the planula stage they were shipped by air to TAU and maintained there under similar conditions, with the FSW changed daily in the tubes. For scanning electron microscopy (SEM) examination of the developmental stages, samples were fixed in 4% seawater glutaraldehyde every 6 h during the first 52 h post-spawning, and then daily for 4 days (10–20 animals each time). The embryos were dehydrated in a series of graded ethyl alcohol, followed by critical point drying, gold coating, and then examined with a Jeol-840a SEM at 25 kV.

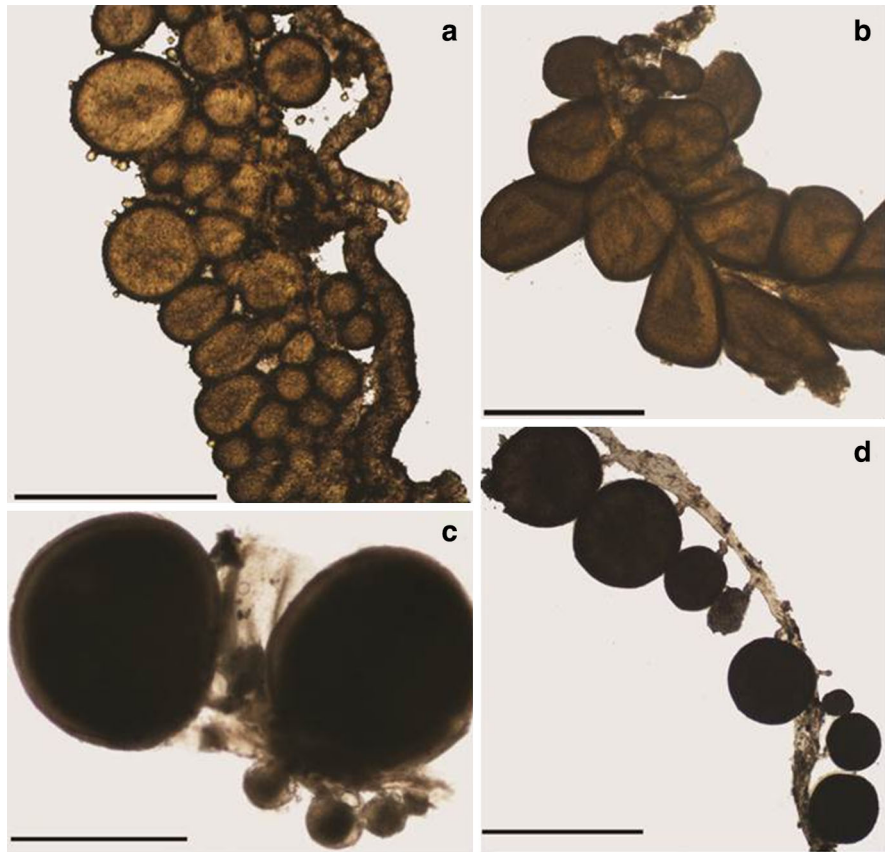


Fig. 2 *Sarcophyton auritum*. Sperm sacs and oocytes removed from polyp cavities viewed under a compound microscope. **a** Sperm sacs on mesentery (February 2011). **b** Advanced development stages of sperm sacs (April 2011). **c** Oocytes of two size groups prior to spawning (June 2012). **d** Oocytes of the small and large size groups attached by a pedicel to the mesentery (May 2012). *Scale bars* 500 μm

Results

Abundance of *S. auritum*

At both study sites (Fig. 1) colonies of *S. auritum* were recorded at depths of 0.5–12 m. At the northern site, the Coral Nature Reserve, 133 colonies were counted, and at the southern one, the Cave Diving site, 11 colonies. Of the total 144 colonies counted at both sites, only 10 (6.9%) grew as solitary, and the rest as groups of at least two. Small colonies, <20 cm in polypary-diameter, were mostly found growing adjacent to larger ones. The Morisita index (I_δ) calculated for the northern site, for plots of 10 × 10 m along the 1,440 m long surveyed area ($n = 147$ plots), was 10.9 ($F_0 = 9.8$, greater than the critical value of $\alpha = 0.01$) and for the southern one ("The Cave" diving site—120 m, $n = 12$ plots) $I_\delta = 11$ ($F_0 = 11$, greater than the critical value of $\alpha = 0.01$), thus indicating a clumped distribution of colonies at both sites ($1 << I_\delta$).

Reproduction studies

Spermary and oocyte development

S. auritium was found to be a gonochoric octocoral (Fig. 2). The gonads of both sexes developed along the mesenteries of the autozooids. Under light microscope, the sperm sacs of live wet mounts were revealed to be spherical, transparent, and white-cream in color. At maturation some became oval (Fig. 2a, b). At onset of development the oocytes were spherical (Fig. 2c, d), partially transparent cream in color and, later, when attaining a diameter of >300 (see ahead), they became opaque.

Measurements of the preserved *S. auritum* male samples revealed the annual developmental cycle of the sperm sacs (Figs. 2a, b, 3a–c) and their monthly mean maximal diameter (Fig. 4). Histological sections in May (2011 and 2012) showed spermaries with a hollow center, indicating spermatozoa with flagella projecting toward the sperm sac center (Fig. 3a, b),

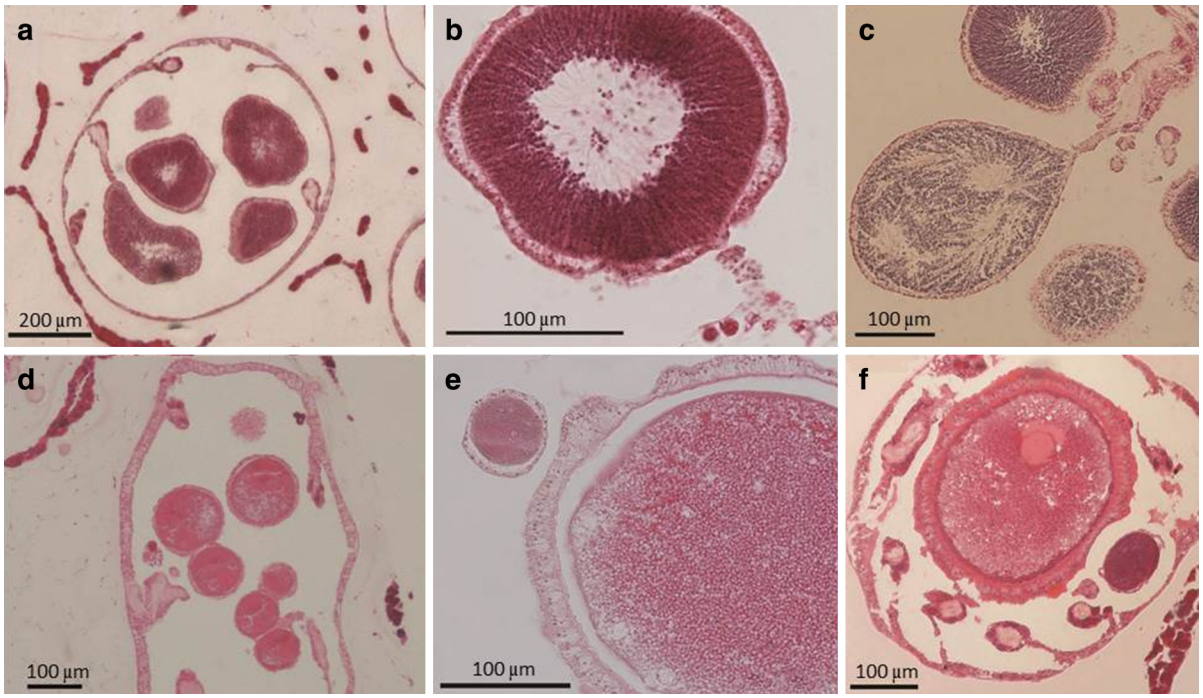


Fig. 3 *Sarcophyton auritum.* Hematoxylin and Eosin-stained sections. **a** Polyps with sperm sacs (June 2012). **b** Sperm sac in polyp cavity, spermatid flagella oriented toward center of sac (May 2012). **c** Mature sperm sacs prior to spawning (June 2011). **d** Longitudinal section of polyp cavity with early developmental stages of oocytes (August 2012). **e** Oocytes of two size groups in polyp cavity (June 2011). **f** Oocytes of two size groups, nucleus in periphery of large oocyte (May 2012)

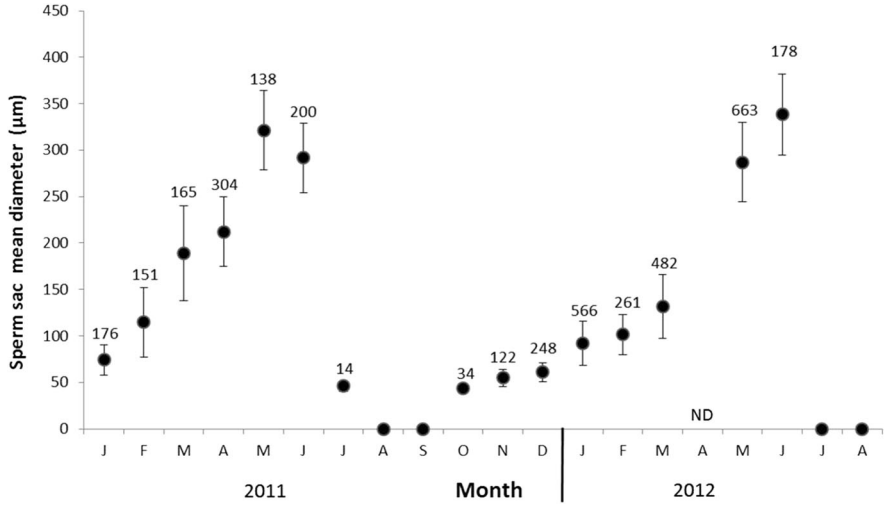


Fig. 4 *Sarcophyton auritum.* Monthly mean diameter of sperm sacs (±SD). Number of measured sperm sacs is indicated above bars, *ND* no data

and in June of both years the sperm sacs were loaded with mature sperm (Fig. 3c) (see also Schleyer et al., 2004; Hellström et al., 2010). One-way ANOVA revealed that the mean diameter of the sperm sacs significantly differed between months (Fig. 4, $P < 0.001$). Post-hoc Tukey test ($\alpha = 0.05$) was conducted to compare the mean diameter values of the different months. The analysis showed a significant increase in mean diameter of the spermaries from January 2011 to June 2011 indicated that

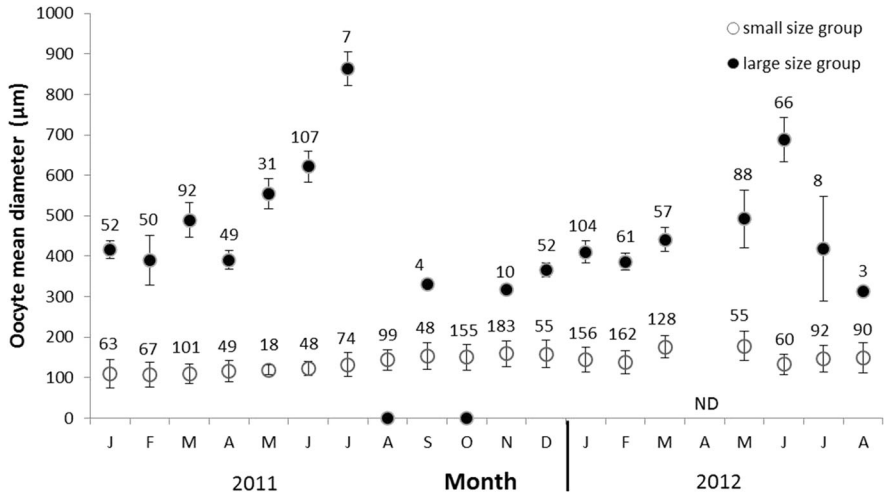


Fig. 5 *Sarcophyton auritum.* Monthly mean diameter (±SD) of large size group oocytes (*bold*) and small size group (*blank*). Number of measured oocytes is indicated above bars, *ND* no data

spermatogenesis had been completed prior to the inferred spawning event of 2011. The absence of spermaries in July 2011 indicated that the inferred spawning had taken place shortly before. Later, in October 2011, small sperm sacs appeared featuring a mean diameter of 43 ± 5 µm ($n = 34$), and these significantly grew in size until June 2012, reaching 338 ± 44 µm ($n = 178$). Spawning was observed in July 2012, and thereafter, in August, no sperm sacs were found. The smallest sperm sacs found in the wet mounts and the histological sections were 15 µm (November 2012) and the largest—585 µm (March 2012).

Examination of the female colonies revealed the presence of oocytes in all months. The autozooids featured oocytes of two size groups, juxtaposed within the polyp cavity, with small oocytes found among larger ones (Figs. 2c, d, 3d–f). The monthly mean maximal oocyte diameter presented two size groups: the largest ones prior to spawning (June 2011 and 2012) but which were absent in the following month (August 2011 and 2012). The remaining oocytes were immature, of the small size group, with a maximal diameter of 300 µm, as also found all year round (Fig. 5, small size group). Histological sections in May and June of both years revealed oocytes of the larger size group, featuring a granular cytoplasm and a nucleus located at their periphery, indicating a ripe stage (Fig. 3f). A significant difference was found between the interaction of months and mean diameter of the two size groups (two-way ANOVA, $P < 0.001$). The following statistical analyses were conducted separately for each size group. One-way ANOVA revealed that the average diameter of oocytes of the large size group (>300 µm) significantly differed among months (Fig. 5, large size group, $P < 0.001$). Post-hoc Tukey test ($\alpha = 0.05$) was conducted to compare the mean diameter values of the different months, which significantly increased from January 2011 (416 ± 23 µm, $n = 52$) to June 2011 (621 ± 39 µm, $n = 109$). In July 2011 the large size group disappeared, thus implying spawning, although one out of the three examined colonies still featured a few large oocytes with a mean diameter of 864 ± 41 µm ($n = 7$). In August, September, and October 2011 no oocytes of the large size group were present, except for a few in September in one of the colonies (323 ± 8 µm, $n = 4$). The oocytes of the large size group reappeared in November 2011 (317 ± 5 µm, $n = 10$) and significantly increased in size until June 2012 (689 ± 55, $n = 66$). In July 2012 the large size group disappeared, indicating spawning. In one out of the four examined colonies a few large size oocytes (=n) were found following spawning, in July (419 ± 65 µm, $n = 8$), and also in August 2012 (313 ± 2 µm, $n = 3$).

Oocytes of the small size group (<300 µm) were present throughout the entire study period. One-way ANOVA revealed that their mean diameter significantly differed among months ($P < 0.001$). Post-hoc Tukey test ($\alpha = 0.05$) was conducted to compare the mean diameter between the months (Fig. 5, small size group) which revealed no distinct change in size with time (Fig. 5). Oocyte development began as the

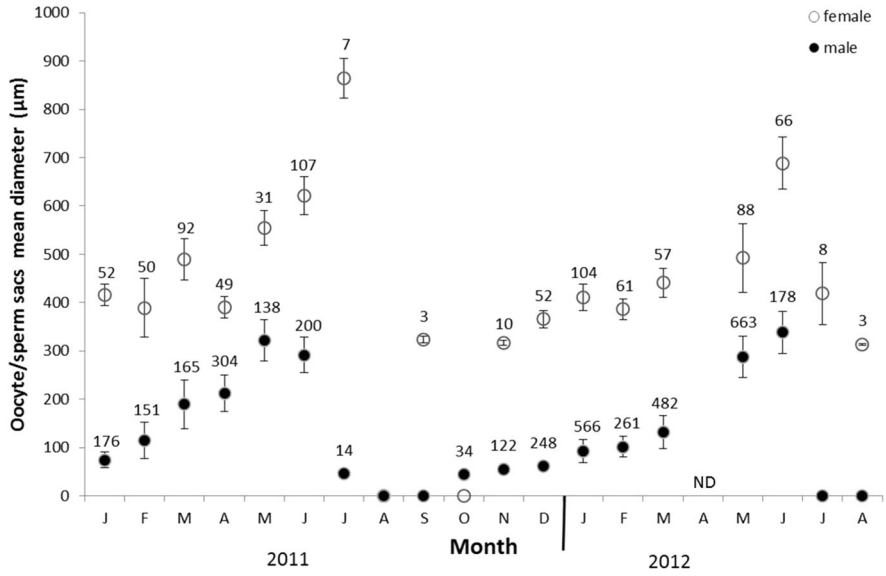


Fig. 6 *Sarcophyton auritum*. Monthly mean diameter (±SD) of oocytes (*blank*) and sperm sacs (*bold*). Number of oocytes or sperm sacs is indicated above bars, *ND* no data

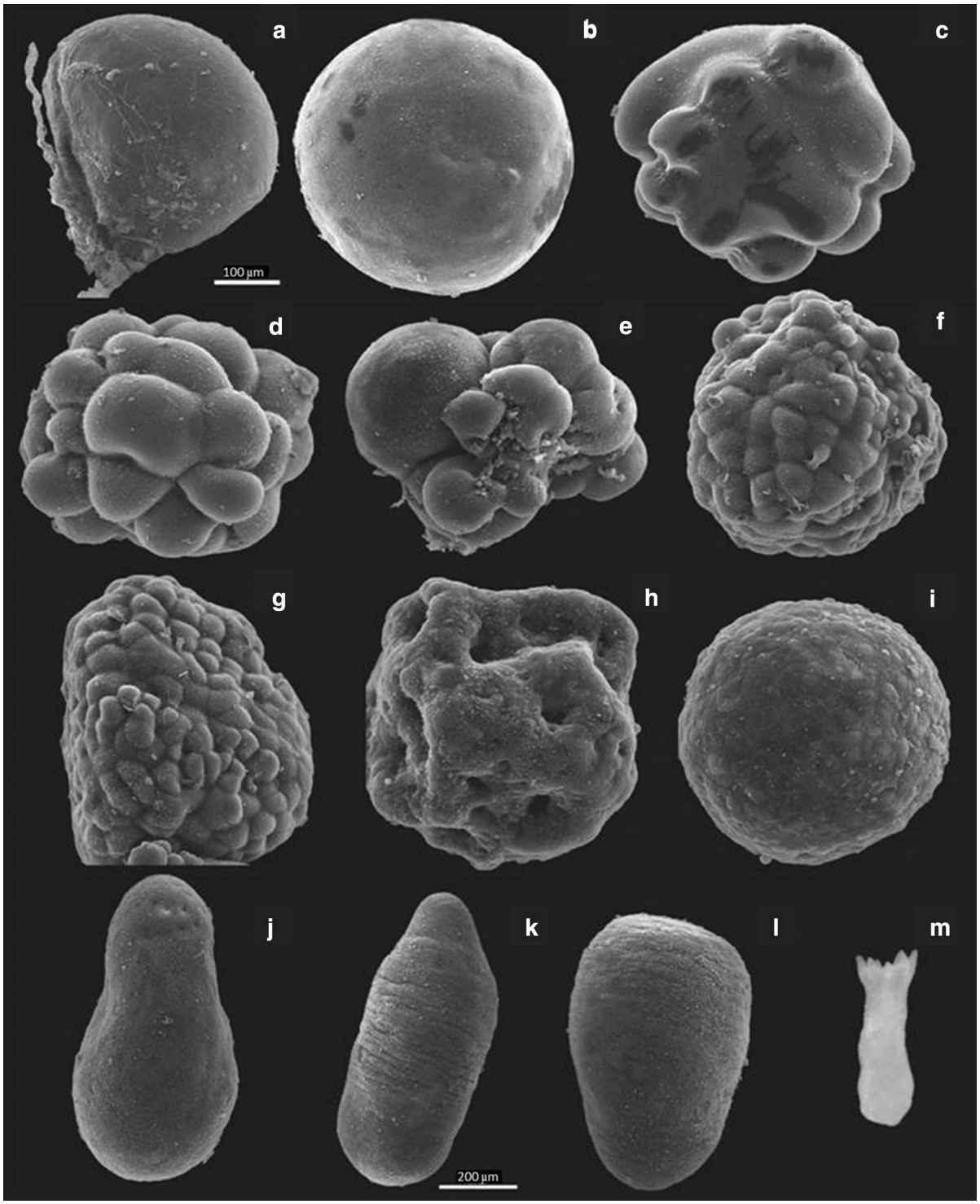
small size group during May–July, then in November (probably of the following year) reached a size > 300 µm, reflecting the large size group, and development continued until spawning on the full-moon night of July (2011 and 2012). The presence of the small size group during all months indicates a continuous formation and development of oocytes, reflected also in their maintaining a mean diameter < 300 µm. In contrast, the large size group of oocytes demonstrated a steady increase in their mean diameter over a period of 6–9 months. Oogenesis of *S. auritum* thus requires 18–21 months. The largest oocyte measured was 1,006 µm (May 2012), and the smallest—17 µm (July 2012).

The number of male and female gonads per 10 mm long section of the gastrovascular cavity of the autozooids was determined prior to the inferred spawning event of both years, and considered as fecundity. At that time they filled most of the cavities and featured up to 130–160 sperm sacs ($n = 21$ polyps) and 45–60 oocytes ($n = 26$ polyps) per 10 mm section. Comparison of the interaction between months and the mean oocyte diameter of the large size group versus the interaction between months and mean sperm sacs diameter (Fig. 6) revealed a significant difference (two-way ANOVA, $P < 0.001$), thus further supporting the different lengths of time required until maturation for males (8–10 months) and females (18–21 months).

Spawning and embryogenesis

Mature oocytes (Fig. 7a) and sperm sacs were found in polyp cavities of *S. auritum* on 22 June 2011 but were absent on 19 July, following the full moon, thus implying the occurrence of spawning. The monthly examination of colonies of both sexes during 2011 (see above) enabled us to predict the actual spawning of 2012. Indeed, on 3 July 2012, coinciding with the full moon, spawning was observed on the IUI reef from 18:00 to 24:00. Three out of the four netted colonies released thousands of positively buoyant white-cream eggs (Fig. 7b). Although sperm release was not noted underwater, the nets were removed from the male colonies and the water content of the attached PVC containers was mixed with that of the female ones.

In the laboratory the spawned eggs underwent initial cleavage 1–6 h post-spawning. Unequal cleavage led to blastula development, featuring larger cells at the vegetal pole compared to the animal one (Fig. 7c). In the following hours some of the eggs underwent holoblastic, equal and synchronous divisions, resulting in embryo formation with a regular blastomere arrangement (Fig. 7d). Other blastulae exhibited bizarre shapes, derived from an unequal and asynchronous cleavage (Fig. 7e). Some embryos remained floating in the water column and others sank to the bottom of the experimental containers. Subsequent divisions, 12–18 h post-spawning, led to the



development of blastulae with blastomeres of equal size. Some blastulae were perfectly round while others revealed irregular shapes (Fig. 7f, g). At 18–32 h post-spawning some embryos demonstrated a plicate surface (Fig. 7h) also featuring cilia and microvilli (Fig. 8a–c). At 32–38 h the plication disappeared

◀**Fig. 7** *Sarcophytun auritum.* SEM images of embryonic stages and a primary polyp. **a** Mature oocyte on pedicle. **b** Spawned egg. **c** Blastula (1–8 post-spawning). **d** Regular embryo (6–8 post-spawning). **e** Irregular embryo (8–12 post-spawning). **f–g** Blastulae (12 post-spawning). **h** Embryo with dented surface (18–32 post-spawning). **i**. Blastula with uniform surface (32–38 post-spawning). **j**. Pear-shaped planula (38–48 post-spawning). **k** Partially extended planula (3–5 days post-spawning). **l** Contacted planula. **m** Primary polyp (day 20). **a** *Scale bar* refers to (**a**–**j**, **l**); **k** scale bar refer only itself

(Fig. 7i). At 38–48 h majority of the embryos had become round to pear-shaped early planulae (Fig. 7j). At hour 48–76 the planulae became elongated, with a pointed end and a round end. Most of the planulae were attached by mucus threads to the bottom of the PVC container, occasionally in clumps. The surface of the young planulae (42–52 h post-spawning) featured microvilli and scattered long cilia, some emerging from a collar comprised of microvilli (Fig. 8d, e). On days 3–5 post-spawning most of the planulae tended to alternately contract and extend (Fig. 7k, l). Out of the initial thousands of embryos only eight planulae had survived by day 16, and only a single one metamorphosed into a primary polyp, which settled upside down to the water surface. On day 20 it featured eight tentacles (Fig. 7 m).

Discussion

Abundance of *S. auritum*

The Morisita index indicated that the *S. auritum* colonies exhibited a clumped distribution ($1 \ll I_\delta$), reflecting the frequent occurrence of colonies growing in groups. Octocorals exhibit different mechanisms of vegetative propagation, such as fragmentation, polyp detachment, budding, and more (e.g., Lasker, 1988; Fabricius & Alderslade, 2001; Kahng et al., 2011). During the present survey a few colonies revealed evidence of asexual reproduction, as small buds emerged from the base of the mother colony (Mandelberg-Aharon, 2014). Clumped dispersion, as found in some octocorals, can result from such vegetative propagation (e.g., Lasker, 1983; Karlson et al., 1996). Therefore, the local abundance of a given species is related both to the probability of larval settlement and survival, and to the probability of the subsequent vegetative reproduction of the resultant colonies. The current study revealed that *S. auritum* reproduces sexually, along with asexual abilities (see Mandelberg-Aharon, 2014). Thus, it is suggested that the clumped dispersion of *S. auritum* results from the activity of both these modes of reproduction.

Reproductive studies

The current study examined for the first time the annual gonad development and reproductive mode of *S. auritum*. The species was found to be gonochoric (Fig. 2), similar to most other octocorals (Kahng et al., 2011). Its gonads developed in the autozooids as commonly found in dimorphic octocoral species (e.g., Kahng et al., 2011). No hermaphroditic colonies were found in the current study, unlike in a number of gonochoric octocorals that may feature a low occurrence of hermaphroditism (e.g., the South-African *S. glaucum*: Schleyer et al., 2004, Mediterranean *Eunicella singularis*: Ribes et al., 2007, and Hawaiian *Carijoa riisei*: Kahng et al., 2008).

Female colonies of *S. auritum* demonstrated a prolonged oogenic cycle lasting 18–21 months, featuring two size groups of oocytes, each presenting a different developmental cycle (Figs. 3d–f, 5). Notably, the spermatogenetic cycle was shorter and lasted 8–10 months (Fig. 6). These features have been considered common among octocorals (Simpson, 2009; Kahng et al., 2011), as was found for example in *Lobophytum crassum* (see Yamazato et al., 1981), *S. glaucum* (see Benayahu & Loya, 1986), *Sinularia polydactyla* (see Slattery et al., 1999), and *Eunicella singularis* (see Ribes et al., 2007). Among most reef-dwelling fleshy octocorals spermatogenesis is mostly completed within less than a year and is shorter than oogenesis, which usually lasts 12–24 months (e.g., Benayahu et al., 1990; Schleyer et al., 2004; Fan et al., 2005). Such a prolonged oogenic cycle corresponds to the concept that it requires higher energetic investment than spermatogenesis (Kahng et al., 2011). Similar to other octocorals, the mature oocytes of *S. auritum* featured a relatively large diameter of 621 ± 39 µm ($n = 107$) and 689 ± 55 µm ($n = 66$) (2011 and 2012, respectively). These large oocytes may enhance survivorship of the sexual recruits through the provision of maternal nutrients during the early stages of development until initiation of feeding (Kahng et al., 2011).

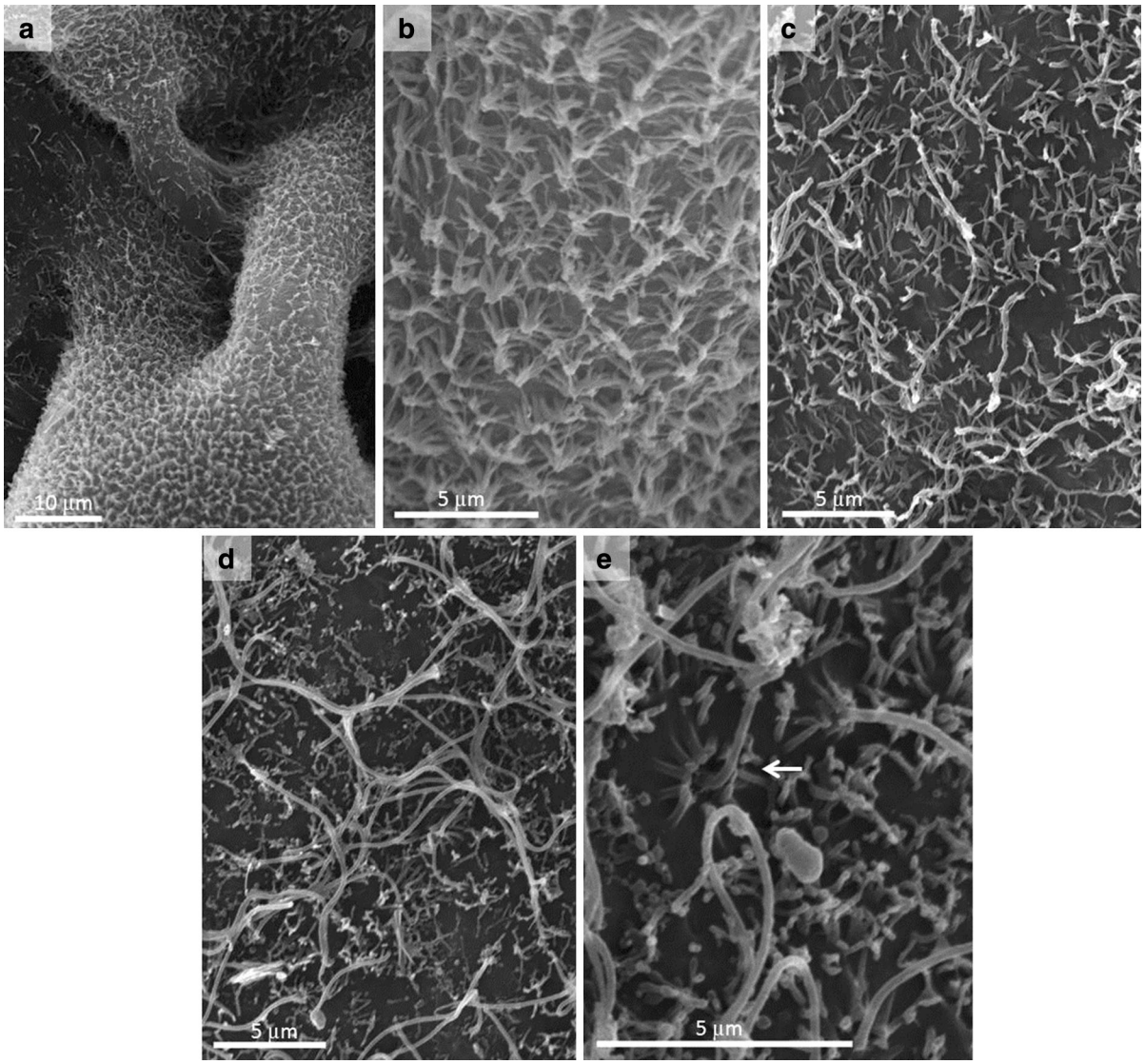


Fig. 8 *Sarcophyton auritum.* SEM images of surface microstructure of embryos. Blastula surface cilation 18–32 post-spawning: **a** Cilia on blastula surface. **b** Dense cilia. **c** Blastula surface microvilli. Planula microvillar surface 42–52 h post-spawning: **d** Microvilli with long cilia. **e** Cilia emerging from a collar of microvilli (*arrow*)

Spawning events of shallow-water octocorals commonly coincide with the lunar phases (e.g., Alino & Coll, 1989; Babcock, 1990; Brazeau & Lasker, 1990; Ben-Yosef & Benayahu, 1999; Linares et al., 2007). Studies of northern Red Sea octocorals have revealed a temporal reproductive isolation among species, with each exhibiting a synchronous population spawning, coinciding with the different lunar phases (Benayahu et al., 1990). Shlesinger & Loya (1985) suggested three advantages of intraspecific synchronization spawning to a given stony coral species: first, reducing gamete wastage, hybridization, and disruptive gene flow; second, increasing the probability of successful fertilization; and third, reducing interspecific competition both among corals and between corals and algae. Studies have suggested that among stony corals synchronized gonad development and subsequent spawning reduce predation risk by overwhelming the predators' capacity to feed (e.g., Richmond & Hunter, 1990; Lasker & Kim, 1996; Guest, 2008). Mass

spawning was observed on the Great Barrier Reef, Australia (Harrison, 2011), in which numerous scleractinian and octocoral species released gametes within a highly synchronized short period of time, lasting 2–8 nights after full moon (Harrison, 2011; Kahng et al., 2011). *S. auritum* colonies at Eilat spawned during a single night, demonstrating an intraspecific synchronized spawning. The spawning occurred on a full-moon night (July 2012). This thus corresponds to the common pattern found in broadcasting octocorals in Eilat (Benayahu et al., 1990).

Eilat is located at the northernmost limit of coral-reef distribution (30°N latitude) and studies have shown that broadcasting scleractinians and octocorals reproduce during the warm summer season, when the seawater temperature is rising or warmest (e.g., Benayahu et al., 1990; Richmond & Hunter, 1990; Hwang & Song, 2007). During the current study, seawater temperature in both 2011 and 2012 started to increase from April onward, reaching a maximum in July–August (IUI data base http://www.iui-eilat.ac.il). It thus seems that *S. auritum* behaves similarly to other octocorals, such as *Cladiella* sp., *Lobophytum* sp., *Sarcophyton* sp., and *Sinularia* sp. on the GBR (Alino & Coll, 1989) and *S. glaucum* in South Africa (Schleyer et al., 2004), whose spawning is determined not only by the phase of the moon but also by water temperature. Moreover, the elevated seawater temperature may also affect the rate of larval metamorphosis and reproduction during the warm months and increase spat abundance (Ben-David-Zaslow & Benayahu, 1996; Nozawa & Harrison, 2000).

The histological sections and wet preparation of *S. auritum* did not reveal any embryos or larvae within the polyp cavities. Thus, its fertilization is external, similar to that of *S. glaucum* (Benayahu & Loya, 1986; Schleyer et al., 2004). In the current study an exception was observed when a few oocytes of the large size group were found in one colony following spawning on the full moon night (July 2011 and 2012). It is probable that these colonies had failed to spawn and some oocytes had remained in their gastrovascular cavities and were later probably reabsorbed (Lueg et al., 2012). The possibility of multiple spawning events in *S. auritum*, as reported for *S. elegans* from the GBR (Hellström et al., 2010), is unlikely, since no spermaries were found following spawning. Our current findings, therefore, suggest the occurrence of a single annual spawning event for *S. auritum*.

Embryogenesis

Among broadcast spawners the period of embryogenic development from spawning to the planula stage appears to be shorter (36–72 h) compared to that in brooders (6–7 days) (e.g., Benayahu, 1989; Simpson, 2009). Spawners release gametes into the water column and in order to decrease the risk of propagule mortality the gametes have developed a relatively short embryonic phase, as found in the current study for *S. auritum* (38–48 h, Fig. 7). Such a trait has been suggested to reduce predation, damage from wave action, and smothering by sediment (Benayahu & Loya, 1983, 1986; Harrison, 2011).

Embryogenesis of *S. auritum* resembles that of other octocorals. Cleavage of its embryos is either equal or unequal, resulting in the respective formation of regular blastulae along with bizarre-shaped embryos (Fig. 7d, e) (e.g., *Rhytisma* (=*Parerythropodium*) *fulvum fulvum*: Benayahu & Loya, 1983 and *Briareum hamrum* (=*Clavularia hamra*): Benayahu, 1989). Subsequent development leads to the gastrula stage (Fig. 7f, g) and, subsequently, planulae (Fig. 7j) (*Ptilosarcus gurneyi*: Chia & Crawford, 1973; *S. glaucum*: Benayahu & Loya, 1986 *B. hamrum*: Benayahu, 1989). The embryos feature a ciliated surface (Fig. 8) (~18–32 h post-spawning) and the planula stage reveals microvilli in a collar structure (Fig. 8), as known in other octocorals (e.g., *R. fulvum fulvum*: Benayahu & Loya, 1983; *B. hamrum:* Benayahu, 1989; *Dendronephthya gigantea*: Hwang & Song, 2007). These surface structural features have a sensory or feeding role (Farrant, 1986). The embryogenesis of *S. auritum* thus appears to resemble that commonly found among other octocorals.

The current findings do not allow us to draw quantitative conclusions regarding polyp metamorphosis and their subsequent development. It should be noted nonetheless that in the present study planulae metamorphosis into primary polyps was relatively slow (~16–20 days post-spawning) compared to that found in other studies (e.g., *Ovabunda* (=*Xenia*) *macrospiculata:* Benayahu & Loya 1984a, b; *Lobophytum compactum:* Michalek-Wagner & Willis, 2001). It is possible that the low rate of planula metamorphosis into primary polyps was due to an absence of metamorphic cues (e.g., Vermeij et al., 2009).

In conclusion, *S. auritum*, an endemic species to the Red Sea, is rather rare and features a clumped distribution. It displays the common life-history traits found among coral-reef octocorals of the Indo-Pacific genus *Sarcophyton*, which features a wide zoogeographical distribution (Verseveldt & Benayahu, 1983 and references therein; Kahng et al., 2011). Thus, the current findings support the hypothesis that reproductive features of reef soft corals are consistent within generic boundaries, across all Indo-Pacific regions studied so far.

Its reproductive traits lead to sustained populations of *S. auritum* at the northernmost edge of its zoogeographical distribution, despite its rather low abundance there. Undoubtedly, such traits further facilitate the octocoral diversity in the region and support their dispersal even at the high latitude northern Red Sea reef-system.

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