Sexual Reproduction of a Soft Coral: Synchronous and Brief Annual Spawning of Sarcophyton glaucum (Quoy & Gaimard, 1833)

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SEXUAL REPRODUCTION OF A SOFT CORAL: SYNCHRONOUS AND BRIEF ANNUAL SPAWNING OF *SARCOPHYTON GLAUCUM* (QUOY & GAIMARD, 1833)

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ABSTRACT

The sexual reproduction of the alcyonacean octocoral *Sarcophyton glaucum* (Quoy & Gaimard, 1833) was studied for a period of about four years on the coral reefs of the northern Red Sea. *S. glaucum* is a dioecious species with gonads borne in the autozooids. The smallest colonies bearing testes measure 11 cm^3 (6–7 years old) while females attain maturity at a much larger colony size of at least 61 cm^3 (> ten years old). Sex ratio of the population is 1:1. The annual development of the sperm sacs takes 10–12 months. Oogenesis occurs every year, however egg maturation requires 22–23 months, resulting in the presence of two cohorts of oocytes in each female. The mature eggs are large with a maximal diameter of 500–750 μm. *S. glaucum* has a brief annual spawning period which occurs in the majority of the population during a single night (in 1980, spawning was on 9 July). The large size of the eggs is not the ultimate cause for their prolonged period of oogenesis. Nevertheless, the synchronous maturation of numerous eggs produced by a colony during a brief spawning period demands high energy expenditure which is allocated during two years. Fertilization is external and fully developed planulae are obtained 36 h after spawning. The larvae swim actively for 14 days, hence, promoting wide dispersal of the species. Life history features of *S. glaucum* include large body size, late age at the onset of reproduction, prolonged oogenic cycle, slow growth of the colony, and long life span.

INTRODUCTION

Anthozoans are capable of reproducing sexually in a variety of ways (Campbell, 1974; Chia, 1976; Fadlallah, 1983). Little attention has been paid to the sexual biology of soft corals (Octocorallia: Alcyonacea). Some studies have focused on planulating species of the family Xeniidae (Gohar, 1940; Benayahu and Loya, 1984a, b). Among members of the family Alcyoniidae several modes of sexual reproduction have been recorded. The temperate species *Alcyonium digitatum releases gametes, and A. hibernicum* has internal parthenogenesis of planular development (Hartnoll, 1977). Although alcyoniids are very common on coral reefs, little is known about their sexual reproduction and gonadal development. Yamazato *et al.* (1981) present circumstantial evidence for gamete spawning in *Lobophytum crassum,* and an external mode of planular brooding was described in the alcyoniid *Parerythropodium fulvum fulvum* (Benayahu and Loya, 1983). Moreover, recently spawned eggs were collected from several alcyoniids in the Great Barrier Reef, Australia (Bowden *et al.* 1985).

Among the Red Sea soft corals, the alcyoniids are very abundant and constitute 52% of the total number of soft coral species (Benayahu, in prep.). *Sarcophyton glaucum* (Fig. 1) is one of the most conspicuous alcyoniids on the Red Sea reefs and at numerous

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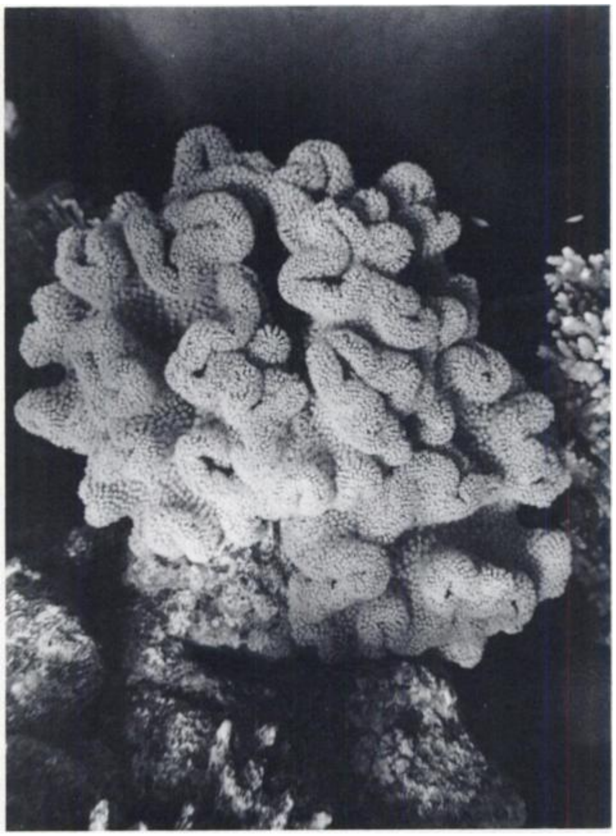

FIGURE 1. A colony of *Sarcophyton glaucum*.

sites across the Indo-West Pacific Ocean (Verseveldt, 1982). Early studies on soft corals deal with the morphology and anatomy of *S. glaucum* (Moseley and Oxon, 1876; Pratt, 1903); however, virtually nothing is known about its life history. This paper examines various aspects of sexual reproduction in *S. glaucum*. We present the annual cycle of gonadal development, population sex-ratio, size at the onset of reproduction, mode of reproduction, and its annual duration. In addition, we report for the first time direct evidence for a synchronous and brief annual gamete release of a soft coral.

MATERIALS AND METHODS

The study was conducted at two reef locations in the northern Gulf of Eilat. One site was Muqebla', 12 km south of Eilat, where the shallow *Sarcophyton* population (3–5 m) was studied. The deep water population (27–30 m) was examined near the Marine Laboratory of Eilat (M.B.L.). The two populations were studied from October 1977 to July 1981. Almost every month fragments of 10–12 cm^2 each were cut out from the disk of 10–20 large colonies, sampled in both locations. Additionally, 10 large colonies were numbered by plastic tags in each depth, and were sampled monthly to follow gonadal development within the same colony. All samples were preserved in 4% formalin in seawater.

The polyp cavities of the samples were examined with a binocular stereoscope for genital development and sex determination. Wet mounts of septa from each fragment were examined microscopically; the diameter of oocytes and sperm sacs was measured with a micrometer. Oocytes were scanned by electron microscopy following the method of Benayahu and Loya (1983).

To determine the relationship between colony size and the onset of sexual maturity, colonies of various sizes were collected prior to each breeding season (1978–1980). Formalin fixation of these colonies caused their complete contraction. Water displacement from a graduated cylinder was used to determine the volume of each colony (for further details see Benayahu and Loya, 1984a). These colonies were sectioned with a scalpel, and their sexual condition was recorded.

Spawning of *S. glaucum* was followed during June–August 1980. Colonies were maintained in 0.4 m^3 tanks filled with filtered running seawater. Plankton nets filtered the run-off from the outlets. After spawning the fertilized eggs were collected and reared into planulae in aerated seawater aquaria (25°C). In addition, during the summer of 1980, sequential underwater examination of gonads was performed in hundreds of colonies. Spawning in the field along a depth gradient (0–35 m) was inferred by the disapperance of mature oocytes or sperm sacs.

RESULTS

Gonads

S. glaucum is a dioecious soft coral. The gonads of both sexes develop in the autozooids on the four lateral and the two ventral mesenteries. Gonads are borne along the entire length of the polyp cavities. The number of oocytes or sperm sacs produced by each polyp is determined by its cavity length. In large colonies such a cavity can exceed 10–15 cm. One cm of a cavity contains as many as 25–35 oocytes or 50–70 sperm sacs. Prior to the breeding season (see below) the gonads fill most of the available space of the autozooids (Fig. 2a, b). Young and sexually immature polyps are located along the margins of the colony.

The spherical oocytes are an opaque cream color, and a few weeks before ripening they become pink. The sperm sacs are rounded, transparent, and white. Therefore, even in the field, sex is easily determined by these colors. After preservation in alcohol or formalin the gonads become yellow. Size measurements of the oocytes and the sperm sacs indicate a marked synchronization in the reproductive state of different polyps within a colony. No sex changes were detected during the study within the 20 tagged colonies.

Size at sexual maturity and sex ratio

Examintion of 186 colonies of various size groups indicates that all specimens smaller than 10 cm^3 are sexually immature. The smallest testes-producing males are at least 11 cm^3. Females attain maturity at a much larger colony size of 61 cm^3. Most of the large colonies (>61 cm^3) are fertile and only a small percentage of the population lacks gonads.

Sex ratio within the population was obtained from the regular monthly samples throughout the study. In the shallow reef (3–5 m) 267 colonies were examined, of which 141 were females and 126 males. A total of 243 colonies sampled at the deep reef (27–30 m) resulted in 136 females and 107 males. No significant deviation from a 1:1 sex ratio in both reef zones was found (χ^2 test, $P > 0.05$).

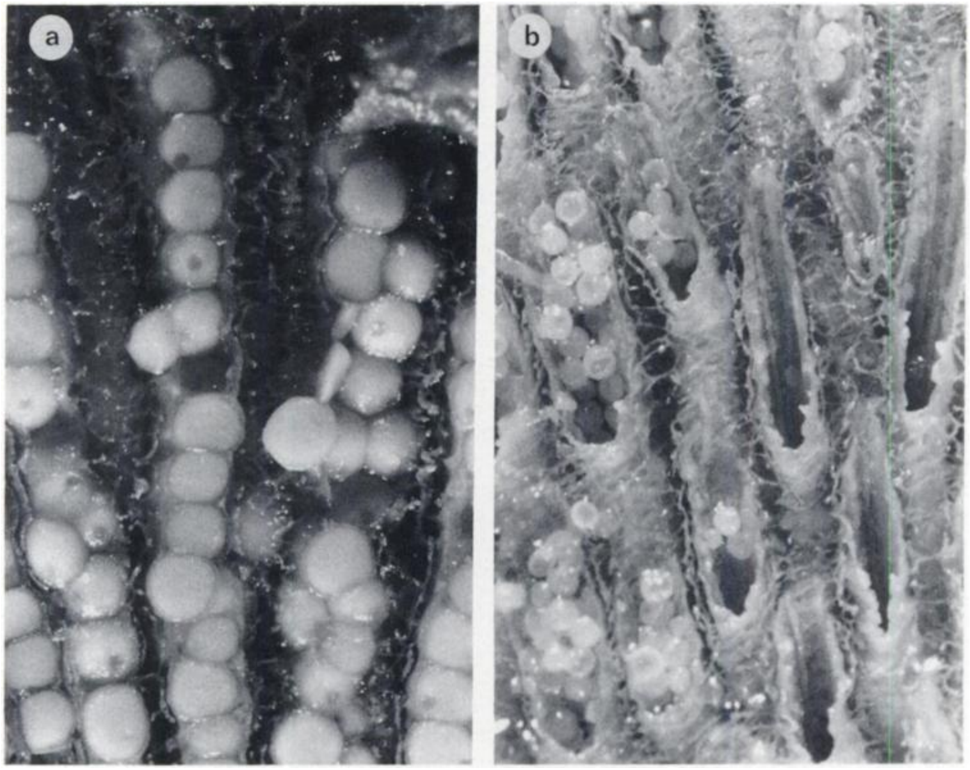

FIGURE 2. *Sarcophyton glaucum* a. Oocytes in polyp cavities of a sectioned colony (×25). b. Sperm sacs in polyp cavities of a sectioned colony (×100).

Annual cycle of gonadal development

Figure 3 demonstrates the monthly changes in the mean maximal diameters of sperm sacs in shallow water (Fig. 3a) and in deep water (Fig. 3b). Young testes (80 μm) are found in 3–5 m depth during August–September (Fig. 3a) and in 27–30 m during September–October (Fig. 3b). Their build-up generally takes 10–12 months. The testes' common diameter is approximately 400 μm prior to spawning.

Examination of female colonies reveals oocytes throughout the whole year. Distinctly, each autozooid contains genital products of two size classes, *i.e.*, small oocytes arranged among larger ones (Fig. 4). Figure 5 presents size ranges of these two cohorts throughout the study. In the shallow reef small oocytes (<80 μm) appeared in September–October (Fig. 5a). In the deep reef the oogenic cycle started a bit earlier in August–September (Fig. 5b). Oocyte growth proceeded through the following 22–23 months. Mature oocytes with a diameter of 500–650 μm were recorded in July. In the deep reef ripe oocytes were also present later in August (Fig. 5b).

Spawning and development

The sequential monthly sampling of *S. glaucum* for about 4 years (Figs. 3, 5) indicated the approximate time of spawning, based on presence of oocytes or sperm sacs in a given month and their absence in the next. In 1980 we directly observed

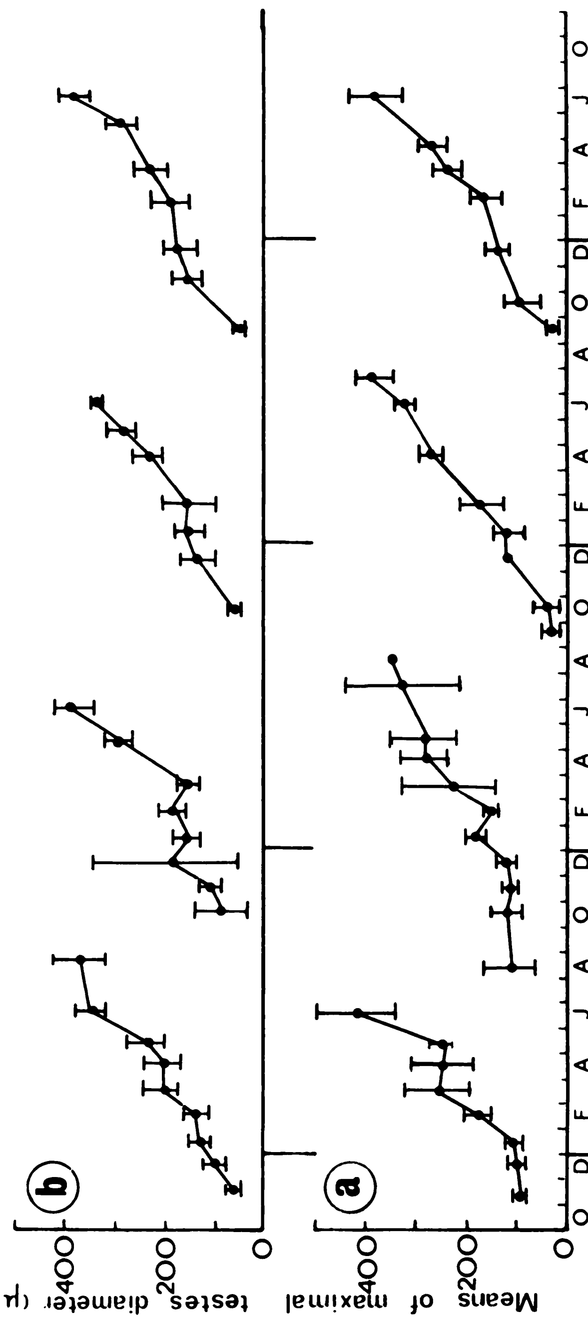

FIGURE 3. Monthly changes of the means of maximal sperm sacs diameter of *Sarcophyton glaucum* in 3–5 m (a) and in 27–30 m (b).

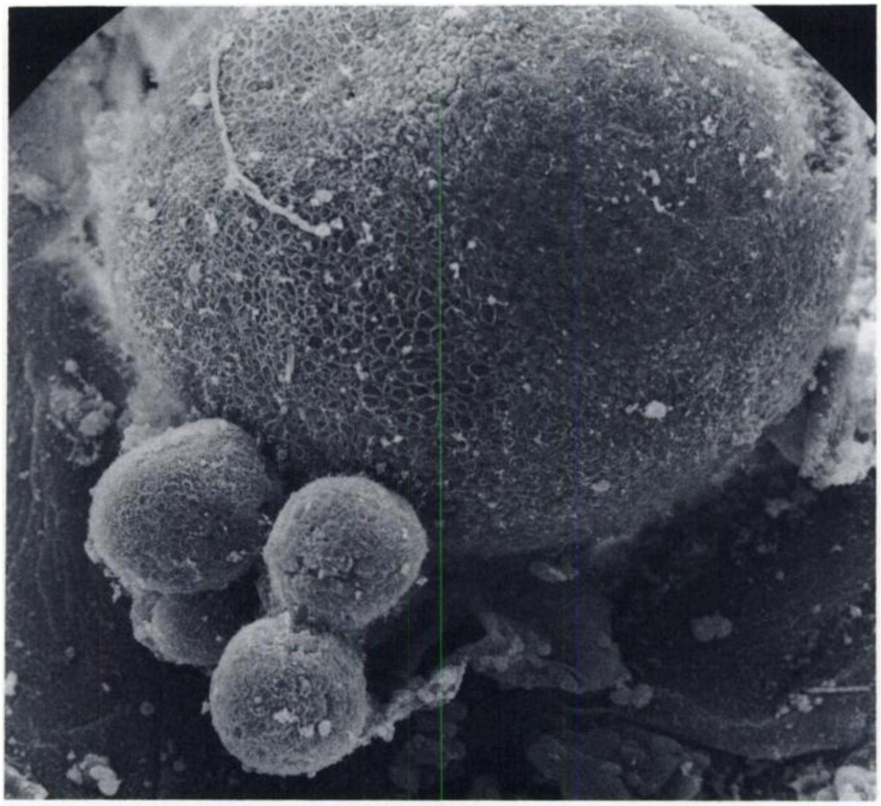

FIGURE 4. Two size classes of oocytes inside a polyp cavity of *Sarcophyton glaucum* (×220).

spawning of colonies maintained in aquaria. *S. glaucum* spawned during a single night (9 July), between 2000 and 2200 h. The eggs (Fig. 6a) are positively buoyant. A day later no genital products were observed in the polyp cavities of these colonies. Daily underwater surveys along a wide depth gradient (0–35 m) conducted prior to and on 9 July, indicated oocytes or testes in the entire population. Eighteen hours later (10 July) no oocytes or testes were found in colonies at a depth of 0–18 m. At greater depths, where only sparse populations of *S. glaucum* exist, few colonies still contained genital products, indicating a possibility of delayed spawning in this zone (see also Benayahu and Loya, 1983).

Colonies of *S. glaucum* were never found with embryos. Fertilization is probably external and 12 h after spawning blastulae were observed in the lab. A day later the majority of the embryos developed into pear-shaped young planulae. Further development, 36 h after fertilization, leads to the formation of a fully developed pink ciliated planula (Fig. 6b) measuring 900 μm in length and 250 μm in width. The larvae actively swam through the water, exhibiting various patterns of rotation or spiral swimming. They remained active for up to 14 days after spawning. Then they settled down on calcareous substrates and started to metamorphose into polyps.

DISCUSSION

The soft coral *S. glaucum* is a broadcasting species with externally developing larva. Gonadal structures of *S. glaucum* is similar to that of other soft corals (Benayahu

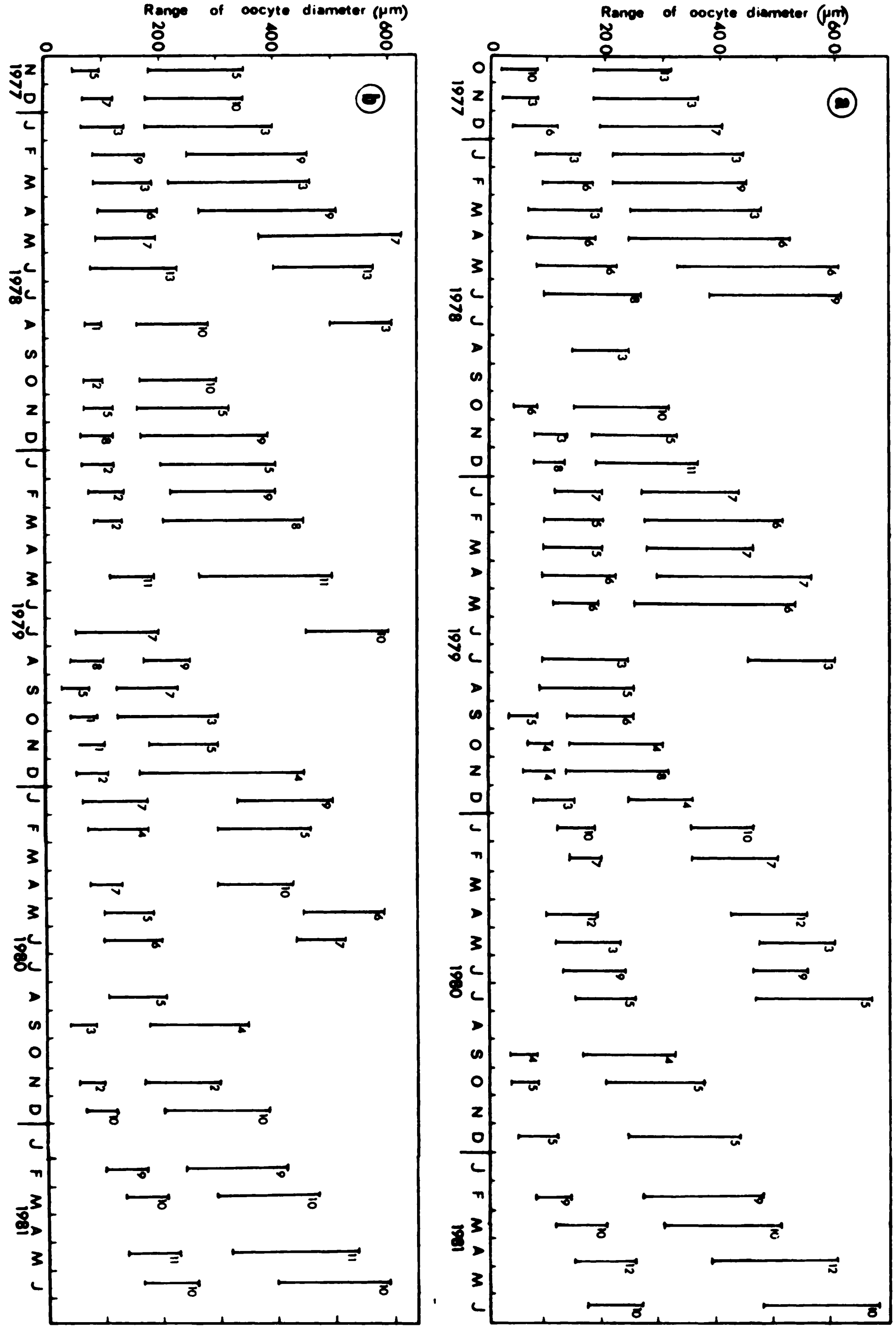

FIGURE 5. Monthly changes of the size range of oocyte cohorts of *Sarcophyton glaucum* in 3–5 m (a) and in 27–30 m (b). Sample size is indicated beside the bars (*i.e.*, number of female colonies examined in each date).

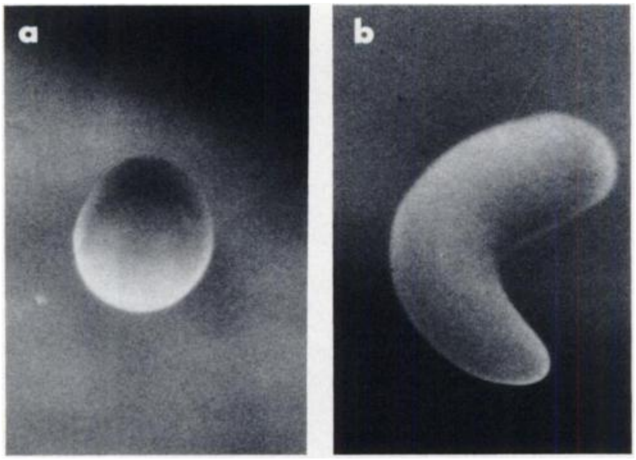

FIGURE 6. *Sarcophyton glaucum* a. Egg (×35). b. Mature planula (×50).

and Loya, 1984a). The gonads are borne only in the autozooids as in the majority of dimorphic alcyonaceans (Gohar, 1940; Yamazato *et al.* 1981). Previous evidence on age of onset of reproduction among soft corals is concerned with *Xenia macrospiculata* (2 years) and *P. f. fulvum* (3–4 years) (Benayahu and Loya, 1983, 1984a). The present study indicates that *S. glaucum* starts to reproduce only after gaining a substantially large colony size corresponding to 6–7 years of age for males, and 10 years for females (Benayahu, 1982). That is, young colonies of *S. glaucum* allocate energy for growth rather than for reproduction (see also van Moorsel, 1983). This feature enables the coral to initially capture space on the reef, and only at a later age to reproduce (Kojis and Quinn, 1981). Growth rate of *S. glaucum* is very slow (increase of disk diameter of only a few mm per year, Benayahu, 1982). Hence the large size of numerous *Sarcophyton* colonies, which have a disk diameter of 70–80 cm, suggests the existence of a long life span in this species.

Several studies on reproduction of stony corals present the maximal egg diameter of many species and discuss the biological significance of this parameter (Rinkevich and Loya, 1979; Fadlallah and Pearse, 1982; Harriot, 1983a, b). Only few comparative data are available on maximal oocyte diameter of soft corals. Table I shows the maximal egg diameter in several alcyonaceans and their mode of reproduction. Only some of these values are derived from long-term and sequential sampling of the species. Although the information at hand is incomplete, it appears that soft corals have large eggs (450–750 μm), regardless of their mode of reproduction. These findings do not coincide with the hypothesis made for stony corals suggesting that broadcasting corals might be expected to produce large eggs, whereas planulating species produce small eggs (Rinkevich and Loya, 1979; Fadlallah, 1983). Additional measurements of alcyonacean eggs (Benayahu, in prep.) together with the results presented in Table I suggest that large eggs are widespread among soft corals. Further studies are required in order to ascertain the significance of this conclusion.

A prolonged period of egg maturation as exhibited by *S. glaucum* (Fig. 5) was also recorded in *L. crassum* (Yamazato *et al.* 1981) and in two scleractinian corals (Fadlallah and Pearse, 1982). Completion of an oogenic cycle within 2 years leads to a simultaneous presence of two oocyte group sizes within a colony. Fadlallah and Pearse (1982) suggest that development of large oocytes requires such a long period of oo-

TABLE I

Maximal egg diameter in several soft corals and their mode of reproduction.

Coral species	Egg diameter (μm)	Mode of reproduction	Reference
Alcyonium digitatum (Linnaeus)	600	Broadcast	Hartnoll, 1977
A. hibernicum (Renouf)	500–640	Brood	Hartnoll, 1977
A. siderium Verrill	700	Brood	Feldman, 1970 (In: Sebens, 1983)
Lobophytum crassum von Marenzeller	600	Broadcast	Yamazato *et al.* 1983
Parerythropodium fulvum fulvum (Forskål)	600–700	Surface brooding	Benayahu and Loya, 1983
Sarcophyton glaucum (Quoy & Gaimard)	600	Broadcast	This study
Heteroxenia fuscescens (Ehrenberg)	700	Brood	Personal observation
Xenia macrospiculata Gohar	500	Brood	Benayahu and Loya, 1984a
X. umbellata (Savigny)	500–600	Brood	Ashworth, 1899
**Cladiella pachyclados* (Klunzinger)	450	—	Pratt, 1903
**Sinularia dura* (Pratt)	500	—	Pratt, 1903
**Anthelia formosa* Utinomi	450–700	—	Utinomi, 1950
**Heteroxenia elizabethae* (Kölliker)	750	—	Hickson, 1931

A (—) indicates that information was not supplied by the authors. An (*) indicates that egg size was derived from occasional measurements.

genesis. However, large oocytes (500–750 μm) in other soft corals achieve maturity within an annual cycle of less than a year (Benayahu an Loya, 1983, 1984a). We therefore conclude that large egg size *per se* is not the ultimate cause for a two year period of development. Species with a prolonged period of oocyte growth have a costly reproductive investment (Bell, 1980). We further suggest that a massive egg production coupled with synchronous maturation and very brief spawning period are characteristic of such species, thus demanding a long time for egg maturation. The slow growth rate of *S. glaucum* (Benayahu, 1982) provides an additional indication that its egg production leads to high energy expenditure over a long period of time (Fig. 5).

Recent studies on reproduction of scleractinian corals have demonstrated a large proportion of broadcasting species (Kojis and Quinn, 1982; Harriot, 1983a; Babcock, 1984; Harrison *et al.* 1984; Shlesinger and Loya, 1985). Currently, among reef soft-corals, only two species are known to spawn pelagic gametes (Table I: *L. crassum* and *S. glaucum,* see also Bowden *et al.* 1985). A brief period of spawning each year occurs in many scleractinian corals (Harrison *et al.* 1984, Shlesinger and Loya, 1985). In contrast, *S. glaucum* is the only soft coral thus far documented with such a mode of gamete release. Undoubtedly the extent of broadcasting in this group has to be adequately determined.

S. glaucum has a markedly short period of planular development (36 h). Previous studies indicate that oviparous octocorals have a rather short embryogenesis: *A. digitatum,* 3–4 days (Matthews, 1917); *Renilla köllikeri,* 2 days (Satterlie and Case, 1979); *Clavularia obesa,* 2 days (Mori and Tanase, 1973); *Pistilosarcus gauernyi,* 3–4 days (Chia and Crawford, 1973). Information on duration of planular embryogenesis in brooding octocorals includes the alcyonaceans *Xenia macrospiculata,* 14 days (Benayahu, 1982) and *Parerythropodium fulvum fulvum,* 6 days (Benayahu and Loya, 1983). These findings may imply a rapid planular development among broadcasting octocorals, whereas brooding in this group involves a prolonged embryogenesis. Spawned gametes are exposed to dangers such as predation or mechanical damage. We therefore suggest that in broadcasting octocoral species, faster embryogenesis increases spat survival and the chances for successful colony development. Octocoral larvae are sluggish and spend only a few hours in the water column prior to their final attachment (Benayahu and Loya, 1983, 1984b). Conversely, planulae of the broadcasting octocoral *S. glaucum* are capable of swimming far away from their parents hence promoting wide dispersal and extensive geographical distribution (Verseveldt, 1982).

Life history traits of *S. glaucum* are comprised of large body size, late age at the onset of reproduction, slow growth rate, and a long life span. Its reproductive strategy demonstrates a prolonged oogenic cycle coupled with a brief annual spawning. The pelagic eggs and planulae are exposed to a high mortality rate, hence offspring survival is decreased. In addition, *S. glaucum* has stable population size and poor colonization capabilities of newly exposed reef surfaces (Benayahu, 1982). In view of these life history traits, *S. glaucum* may be regarded as a K-selected species (*sensu* Pianka, 1970). This soft coral has never been observed to be excluded by other benthic reef organisms nor suffer from predation (see Ne'eman *et al.*, 1974). Therefore, even if a broader aspect of K-selection is considered including interspecific competitive ability and predator avoidance (Green, 1980), *S. glaucum* may be further viewed as a K-selected species. We have elsewhere demonstrated that life history characteristics of the soft coral *X. macrospiculata* include small body size, early onset of reproduction, high fecundity, prolonged planulation period and capacity to rapidly exploit space all year round (Benayahu and Loya, 1984a, b, 1985). Therefore, the two soft corals *X. macrospiculata* and *S. glaucum* demonstrate markedly different life history tactics and may be situated on opposing ends of an "r-K continuum" (*sensu* Pianka, 1970).

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