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LIFE HISTORY STUDIES ON THE RED SEA SOFT CORAL *XENIA*
MACROSPICULATA GOHAR, 1940. I. ANNUAL DYNAMICS
OF GONADAL DEVELOPMENT

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ABSTRACT

Xenia macrospiculata Gohar, 1940 is a dominant xeniid species on the coral reefs of the Gulf of Eilat. The colonies are dioecious and the gonads develop along the four lateral and two sulcal mesenteries, except for the anthocodial part of the polyps. The population starts to reproduce at a markedly early age of two years and the percentage of sexually mature colonies increases with coral size. The sex ratio of the population is significantly skewed toward a higher abundance of males.

A synchronization of gonadal development occurs among the polyps within a colony. In every annual cycle the development of initial gonadal primordia starts in September or October and it lasts until April–May. In addition to these gonads, more oocytes and sperm sacs continue to appear along the mesenteries of male and female colonies during the succeeding 7–8 months. Due to the prolonged period of gonadal initiation, the population contains colonies in various stages of development. The successive maturation of gametes starts every annual cycle in May and lasts for 4–5 months. During this time polyp cavities become filled with an unusual compact arrangement of various sizes of oocytes or sperm sacs. The early age of first reproduction combined with the prolonged gametogenic season increase the reproductive potential of *X. macrospiculata* and contribute to its high abundance at the studied reefs.

INTRODUCTION

The dominance of soft corals of the family Xenidiidae at the coral reefs of the northern Red Sea has been noted by Fishelson (1970), Schuhmacher (1974), and Benayahu and Loya (1977, 1981). In this area there are 20 species of *Xenia* (Benayahu and Loya, in prep.) included in a diverse assemblage of soft corals. *Xenia macrospiculata*, one of the most abundant xeniids in the Red Sea, has been described by Gohar (1940a) from the reefs of El-Ghardaqa (Egypt); its present zoogeographical distribution extends to various localities along the Red Sea and Madagascar (Verseveldt, 1971). The aggregations of *X. macrospiculata* create large beds that monopolize the reef substrate (Fig. 1a). In many shallow reef zones their coverage is very high, exceeding 70% of the surface area. In addition, colonies of *X. macrospiculata* exhibit a special mode of active movement, which enables them to utilize vacant space rapidly (Benayahu and Loya, 1981).

Studies on Red Sea xeniids with an emphasis on the reproduction of *Heteroxenia fuscescens* were carried out by Gohar (1940a, b) and Gohar and Roushdy (1961). Yet, no quantitative study was conducted on the annual dynamics of gonadal development of any *Xenia* species, except for the scant information given by Ashworth

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(1899) and Hickson (1931). Similarly, long term and quantitative aspects of the life history of xeniid populations are lacking.

This paper deals with the life history of *X. macrospiculata* in shallow water (3–5 m) and in a deeper reef zone (27–30 m). It is the first quantitative account on the sexual reproduction of a xeniid coral concerned with sex ratio, colony size at reproduction, and annual dynamics of male and female gonadal development.

MATERIALS AND METHODS

Two reef areas were selected at the Gulf of Eilat for the study. A very dense population of *X. macrospiculata* is found at Muqebla', 12 km south of Eilat (Fig. 1a). At this coral reef, the shallow population (3–5 m) was studied. The deep water population (27–30 m) was sampled at the reef in front of the Marine Biological Laboratory of Eilat (M.B.L.). The two reefs were studied from March 1977 until July 1981. Every month 20 large colonies were collected randomly from each locality by SCUBA diving. The colonies were carefully detached from the substrate and preserved in 4% buffered formalin. In the laboratory the colonies were sectioned longitudinally (Fig. 2a) and examined under a binocular microscope for the presence of gonads, sex determination, and the percent of space along the edges of the mesenteries occupied by oocytes or sperm sacs. We also examined possible synchronization in the reproductive state of mesenteries derived from one polyp, in polyps from the same branch, and in branches of the same colony. Fine-pointed forceps were used to prepare wet mounts of mesenteries from each colony so that the size range of oocytes and sperm sacs could be measured. In order to distinguish between colonies with male or female initial gonadal primordia (IGP), histological sections were examined. Formalin-fixed colonies were rinsed with fresh water and then transferred into 70% methyl alcohol. Decalcification was carried out for 10 min by formic acid and sodium citrate (Rinkevich and Loya, 1979a). Paraffin sections (10 μ m) were stained with Delafield hematoxylin and eosin.

Xenia macrospiculata exhibits a diurnal pattern of polyp and colony contraction (Fig. 1b), and hence it is difficult to measure the size of living colonies. In order to determine the relationship between size and the presence of gonads, colonies of various sizes were sampled prior to the breeding season of 1978 and 1979, on both shallow and deep reefs. The colonies were preserved in formalin, which caused their complete contraction. Water displacement from a graduated cylinder was used to determine the volume of each colony: every colony was introduced into a cylinder and the amount of the displaced water was measured by pipette with an accuracy of ± 0.1 ml. In addition, these colonies were sectioned and their sexual maturity was recorded.

RESULTS

General features of the colonies and the gonads

X. macrospiculata colonies are small sized soft corals, attaining a height of only a few cm (Fig. 1c). Living corals are creamy brown, although numerous sclerites often cause a chalky appearance, especially within the shallow water population. Each colony is attached to the substrate by a basal part of its stalk (Fig. 1c). Many colonies are composed of a few branches, each terminating with a polyp-bearing capitulum. The polyp cavity runs from its free part above the capitulum (anthocodium) and passes into the syndete, the coenenchymal part of the stalk (Figs. 1c, 2a).

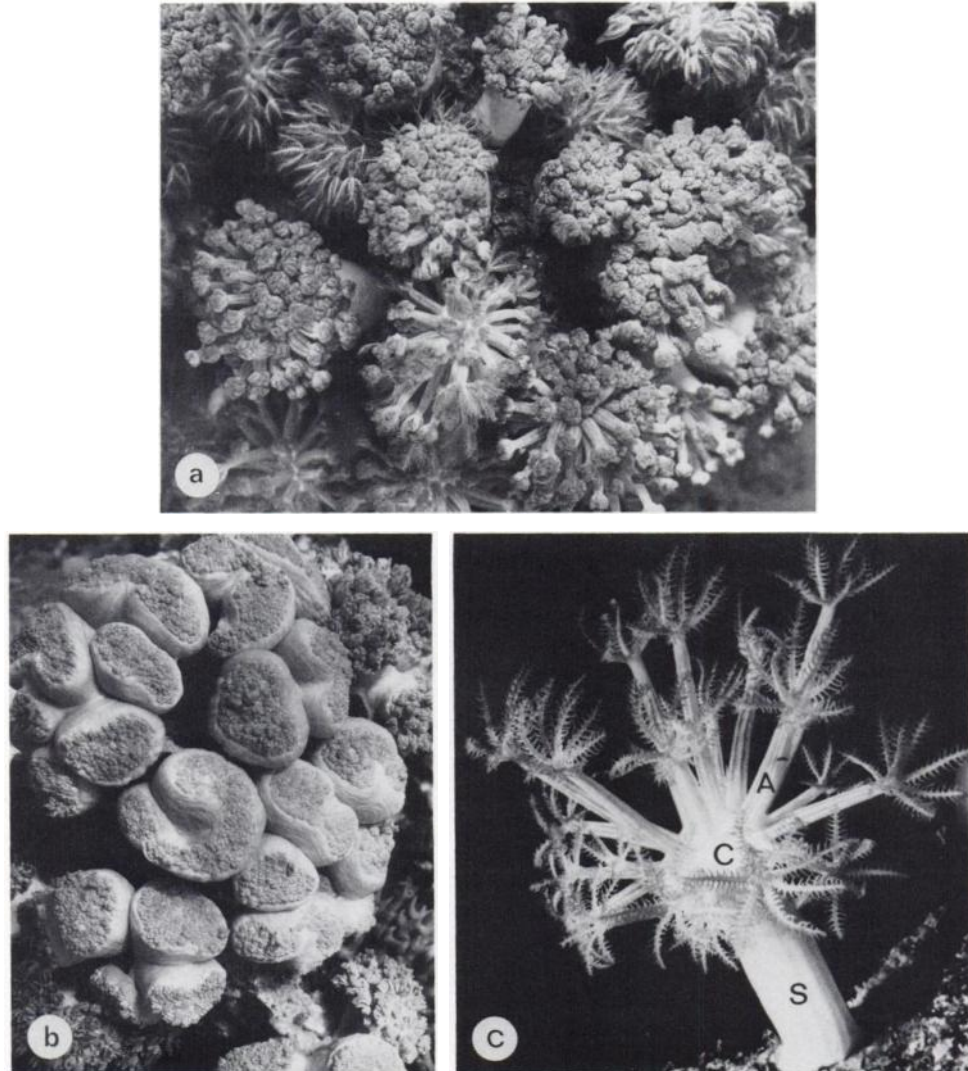


FIGURE 1. Colonies of *Xenia macrospiculata*. a: Aggregation of colonies at the coral reef of Muqebba'. b: Colonies with retracted polyps. c: Colony with extended polyps ($\times 4$). Abbreviations: A—anthocodium, C—capitulum, S—stalk.

X. macrospiculata colonies are dioecious. Hermaphroditic colonies are very rare; among more than 2000 colonies examined, only three bore both sperm sacs and oocytes. The gonads are arranged along the four lateral and two sulcal mesenteries (Fig. 2b), except for the anthocodial part of the polyps. Every year the initial gonadal primordia (IGP) start to develop at the upper part of the polyp cavity, below the anthocodium, on a small triangular projection of the septum. As maturation proceeds, more gonads develop along the edges of the mesenteries, gradually covering the surface of the mesenteries. Toward the end of gonadal development, they frequently fill most of the polyp cavities (Fig. 2c, d). The development of the IGP starts simultaneously

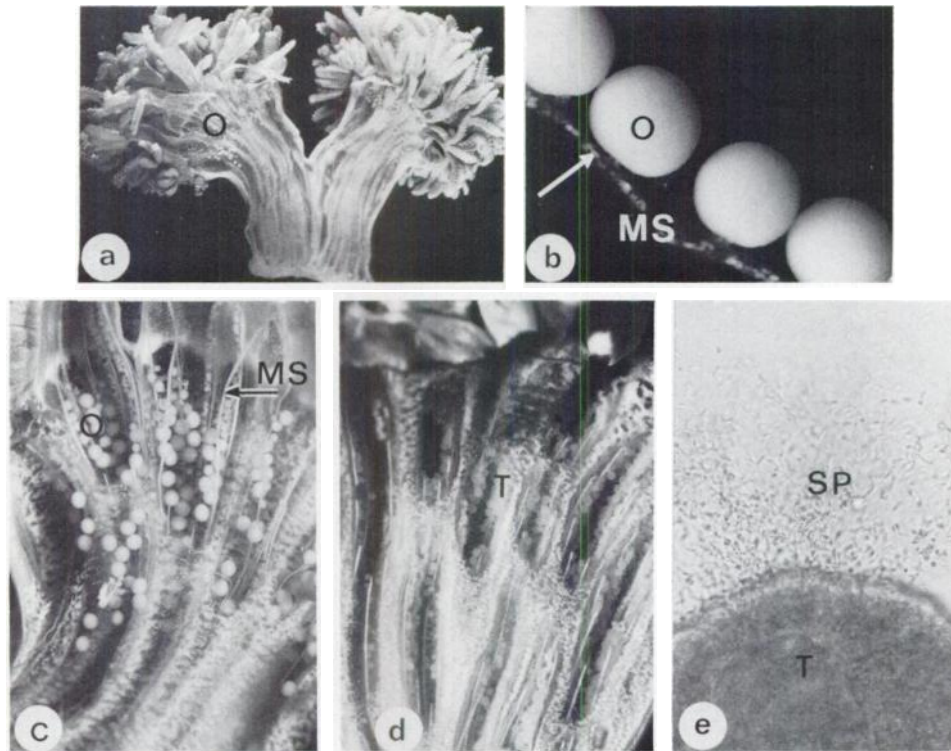


FIGURE 2. Gonads of *Xenia macrospiculata*. a: Longitudinal section through a colony showing oocytes in the syndetial part of the polyp cavities ($\times 1$). b: Oocytes arranged along a mesentery, arrow indicates the sclerites ($\times 40$). c: Oocytes in the polyp cavities of a sectioned colony ($\times 7$). d: Testes in the polyp cavities of a sectioned colony ($\times 3$). e: Mature spermatozoa burst a sperm sac. Abbreviations: MS—mesentery, O—oocyte, SP—spermatozoa, T—testes.

in all polyps of a colony. Further appearance and growth of the oocytes or the sperm sacs is completely synchronized within an individual coral.

When the diameter of the oocytes or testes is less than 30–40 μm , they can be distinguished only by histological sections. After they attain this size, sex determination is easily done by observing their color. The oocytes are spherical, opaque, and cream-white. The sperm sacs are rounded, transparent, and cream-colored. After preservation in alcohol or formalin they become yellow. Microscopic examination of the gonadal smears indicates that each oocyte contains a nucleus and a nucleolus. The sperm sacs are granulated and mature spermatozoa tend to rupture their wall (Fig. 2e). The gonads are attached to the mesenteries by short pedicels and they are surrounded by an endodermal layer rich with zooxanthellae.

Figure 3 presents the monthly reproductive state of the population during the study period in both shallow (Fig. 3a) and deep reefs (Fig. 3b). Throughout the year the majority of the colonies in each monthly sample of 20 colonies contain male or female gonads and a certain proportion of the population harbors IGP. The first IGP in the population usually start to appear in September or October and their initiation lasts a few months.

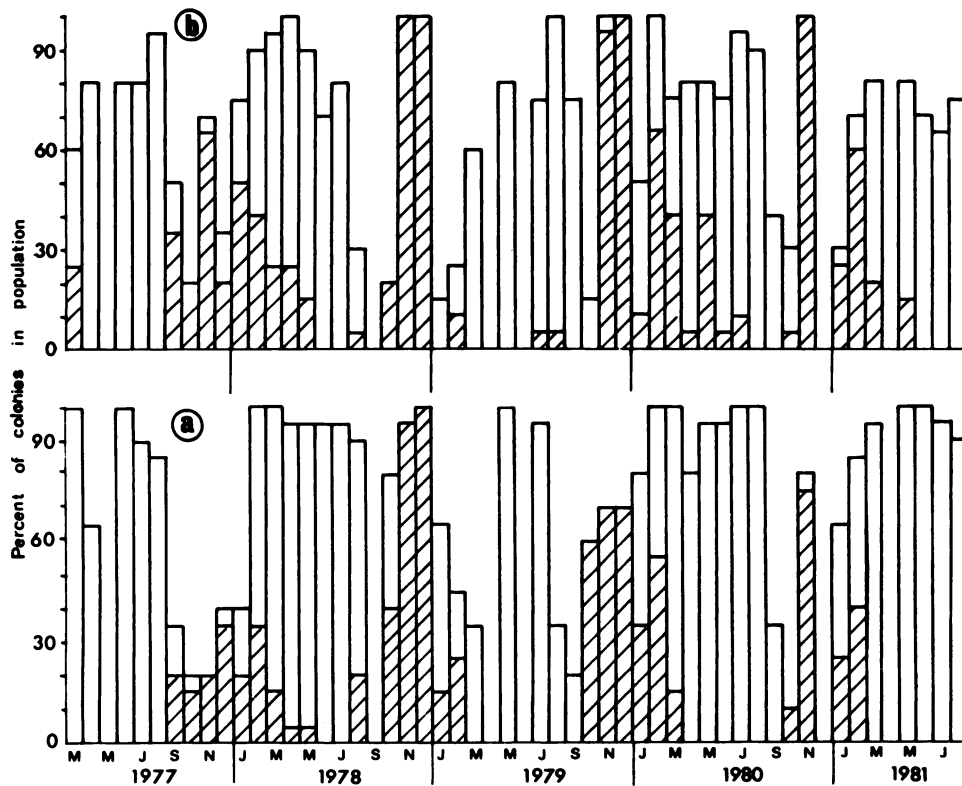


FIGURE 3. The monthly percentage of *Xenia macrospiculata* colonies with male or female gonads (blank bars) and with initial gonadal primordia—IGP (dashed bars) in 3–5 m (a) and in 27–30 m (b).

Colony size, gonadal development, and sex ratio

Figure 4 shows the size frequency distribution of *X. macrospiculata* colonies and their reproductive state in shallow water (Fig. 4a) and on the deep reef (Fig. 4b) prior to the breeding season. The colonies are divided into size groups according to their volume (cm^3). It is evident that even in the smallest size groups, gonads from both sexes are found. There is a consistent increase in the percentage of mature colonies with increasing volume in the shallow reef area, but there is a deviation from this pattern among the deep water colonies (size groups: 2.1–2.5 and 2.6–3.0 in Fig. 4b). In addition, a higher percentage of males than females is recorded in all shallow size groups (Fig. 4a) and in the majority of the deep corals (Fig. 4b). The differences between the patterns exhibited in these figures are due to local aggregations of *X. macrospiculata* composed of colonies of one sex, formed by asexual reproduction (Benayahu, 1982).

Among 624 sexually mature colonies sampled at 3–5 m, 39% were females and 61% males. At a depth of 27–30 m, out of 251 colonies, 32% were females and 68% males. These results indicate that in the population, male colonies are significantly more abundant than females (χ^2 , $P < 0.05$).

Annual cycle of oocyte development

The monthly changes in size-range of the oocytes are presented in Figure 5a for the shallow population and in Figure 5b for the deep one. These figures illustrate a

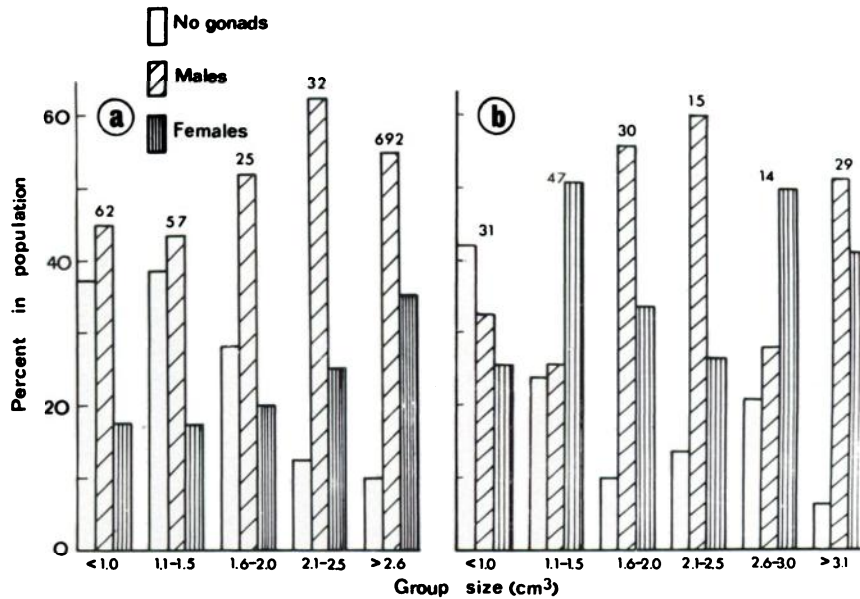


FIGURE 4. Size frequency distribution and sexual state of *Xenia macrospiculata* in 3-5 m (a) and in 27-30 m (b). Sample size of each group size is indicated above the bars.

similar annual pattern for both populations. The results indicate that rarely in September, but usually in October, colonies of *X. macrospiculata* bear IGP, which measure approximately 40 μ m. The same narrow and low size range of oocytes is also recorded during the following months. By February, the oocytes reach a size of about 100 μ m and IGP continue to develop until April-May (Fig. 5). In addition to the IGP more oocytes appear along the mesenteries for a period of 7-8 months (October-May). The prolonged oogenesis generates a wide range of oocyte sizes for several months

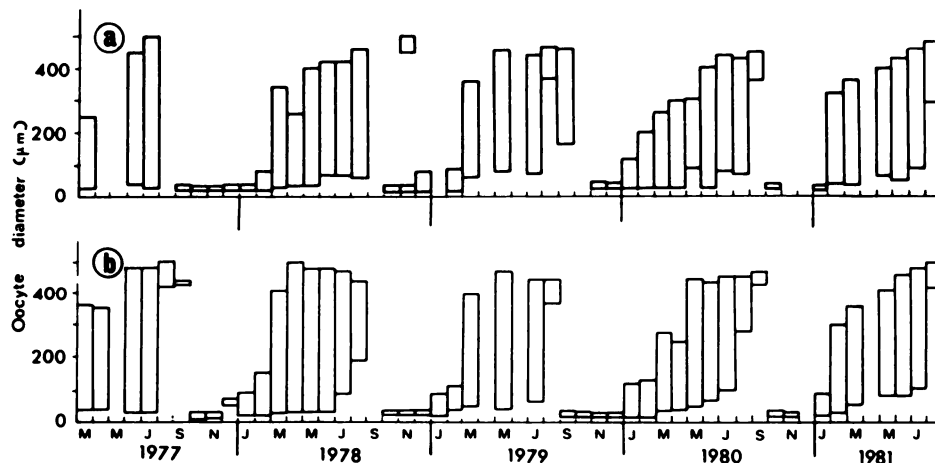


FIGURE 5. Monthly changes in the size-range of oocytes of *Xenia macrospiculata* in 3-5 m (a) and in 27-30 m (b).

during the annual cycle. In June, some of the oocytes attain their maximal diameter of approximately $450 \mu\text{m}$. During July, August, and September the size range is still high but becomes narrower ($200\text{--}500 \mu\text{m}$). Note the result obtained in November 1978 (Fig. 5a), where the population consists of colonies with IGP and mature eggs. This is the only time when oocytes of $500 \mu\text{m}$ were found late in November.

The monthly changes in mean maximal oocyte diameter on the shallow reef is presented in Figure 6a and on the deep reef in Figure 6b. These figures indicate that a successive increase of the oocyte diameter starts yearly in October. Low standard deviations around the means were recorded at the beginning and at the end of each developmental cycle. The wide range of oocyte-diameter, usually found at the middle of each cycle (February–May), causes increased deviations around the mean values. June is the first month when oocytes of at least $400 \mu\text{m}$ are recorded and such large oocytes are found throughout the following months until September (Fig. 6). The

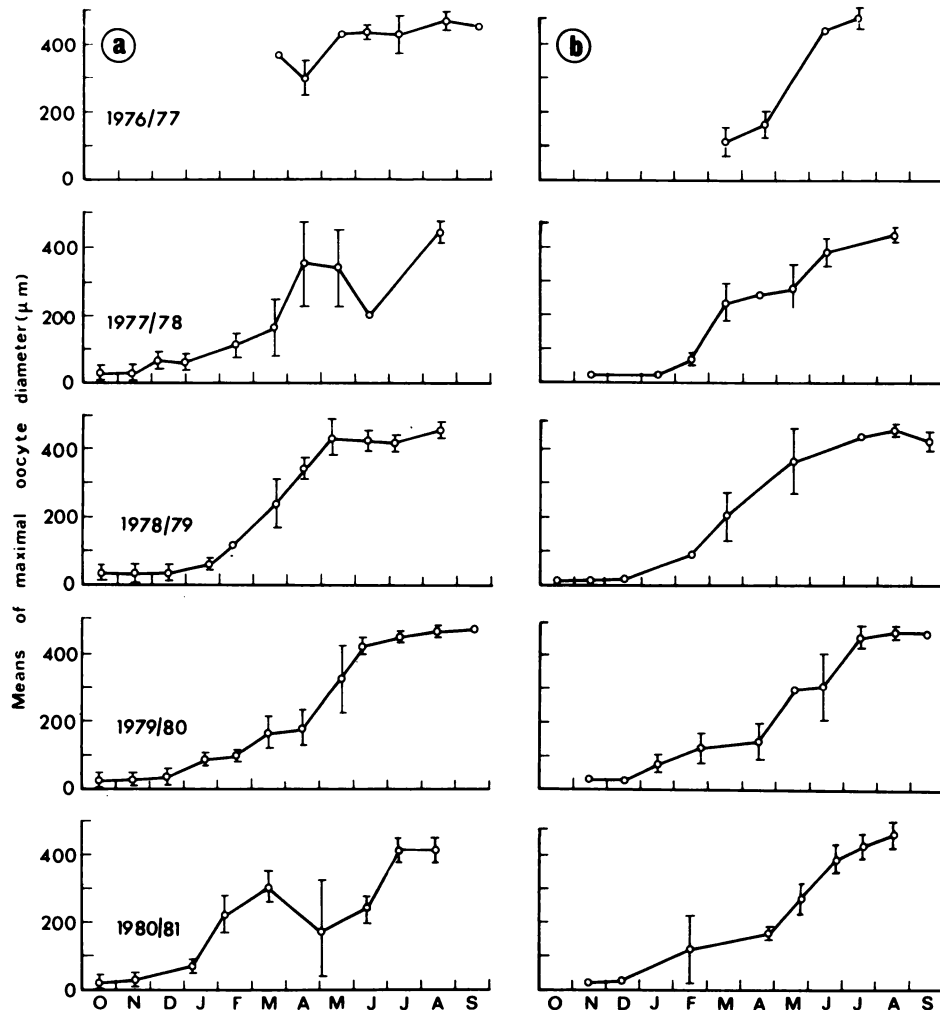


FIGURE 6. Monthly changes of the means of maximal oocytes diameter of *Xenia macrospiculata* in 3–5 m (a) and in 27–30 m (b).

largest oocytes recorded attained a diameter of 500 μm , which indicates a similar pattern of oocyte-development in the two depth zones.

The means of mesenterial areas covered by oocytes fluctuate during the annual gonadal development throughout the year (Fig. 7). A successive increase in space occupied by the oocytes along the septae is evident during October–May due to initiation of newly developed oocytes and their continued growth. Since gonadal development is not synchronized within the population, high standard deviations in mean cover of oocytes along the mesenteries were recorded during April–September. A decrease in this cover usually takes place from July, caused by transfer of ripe eggs into the brooding pouches of the colonies (see Discussion).

Annual cycle of sperm sac development

The monthly changes in the spermaries size-range are illustrated in Figures 8a and 8b for the two reefs. Sperm sac primordia start to appear in October. During the following months their diameter gradually increases. Simultaneously, as described

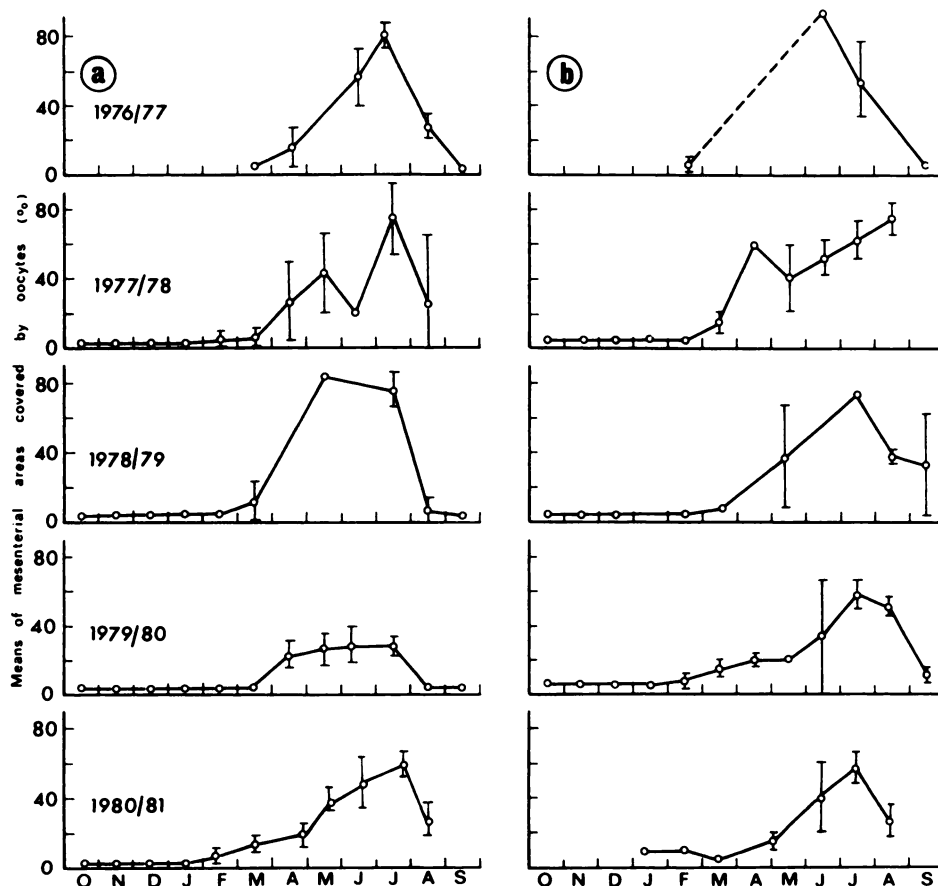


FIGURE 7. Monthly means of mesenterial areas covered by oocytes of *Xenia macrospiculata* in 3–5 m (a) and in 27–30 m (b).

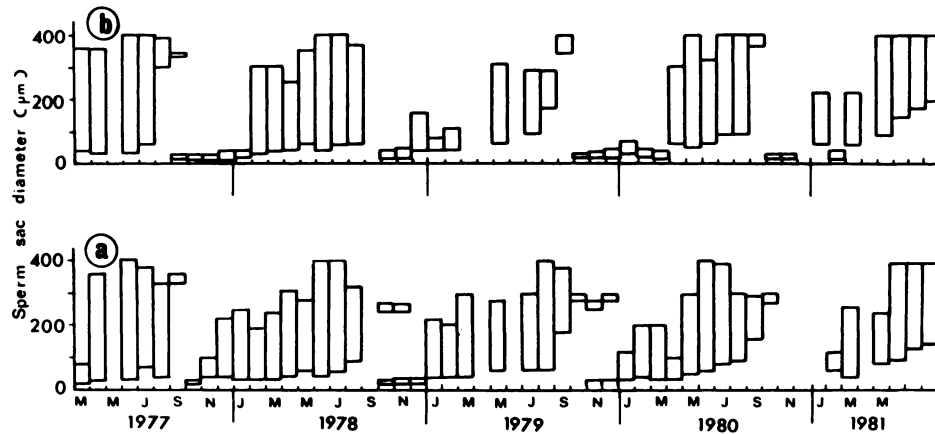


FIGURE 8. Monthly changes in the size ranges of sperm sacs of *Xenia macrospiculata* in 3–5 m (a) and in 27–30 m (b).

for the females (Fig. 5), further initiation of sperm sacs takes place in the population. In May, a wide range of sperm sac-diameter is recorded, and their size reaches a maximum value of 400 μm (Fig. 8). The size range of spermaries decreased during June–September due to the maturational process. Notice the presence of large sperm sacs in the deep-water population during October–November 1978 and November–December 1979 (Fig. 8b).

Figure 9 illustrates the monthly changes of the mean of maximal testes diameter in the shallow and deep reefs' populations. In almost every annual cycle during the first 2–5 months of development of the sperm sacs, diameters of less than 100 μm are attained. Thereafter, a faster rate of increase in size occurs until the spermaries reach their maximal size during June–July.

The means of mesenterial areas covered by sperm sacs throughout the study period are shown in Figure 10. During the first 5–6 months of each annual cycle, the space occupied by the testes usually does not exceed 10% of the septal length. The results indicate that every year during April, the surface occupation of the mesenteries by the sperm sacs accelerates rapidly, attaining a maximum of 80–90% at June–July. Towards August–September the massive spawning causes a decrease of the mesenterial areas covered by sperm sacs. The high standard deviations around the mean values (Figs. 10a, b) are due to the lack of synchronization in the development of male gonads within the population.

DISCUSSION

The present knowledge of the sexual reproduction of alcyonacean corals is mainly based on the boreal species *Alcyonium digitatum* (Hickson, 1901; Hartnoll, 1975). Among the coral reef soft-corals, *Heteroxenia fuscescens* have been studied by Gohar (1940a, b) and Gohar and Roushdy (1961). The recent studies of Yamazato and Sato (1981) on *Lobophytum crassum* and of Benayahu and Loya (1983) on *Parerythrodium fulvum fulvum*, add to the information on the life history of alcyonacean corals.

The gonadal structure of *X. macrospiculata* fits well with that of other soft corals (Ashworth, 1900; Hickson, 1901, 1931; Gohar and Roushdy, 1961). The male or

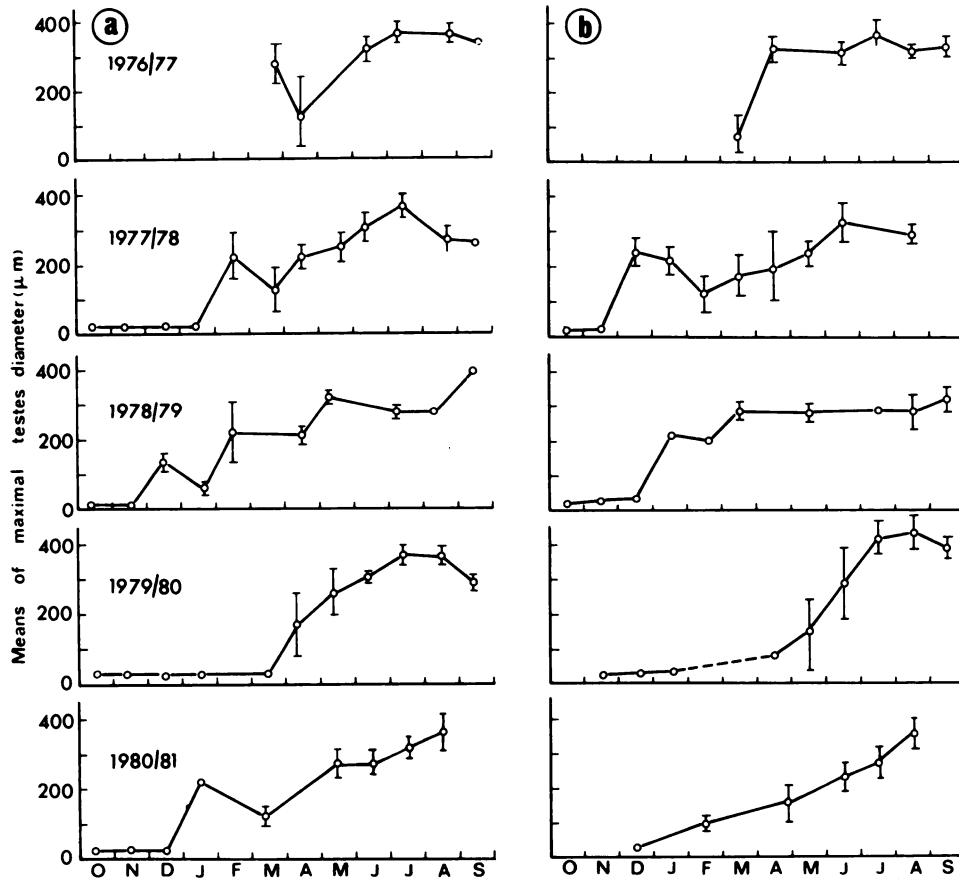


FIGURE 9. Monthly changes in the maximal means of testes diameter of *Xenia macrospiculata* in 3-5 m (a) and in 27-30 m (b).

female gonads develop along the mesenteries, originating from the endodermal tissue. While growing in size, they bulge into the syndetal part of the polyp cavity. The oocytes or the sperm sacs are attached to the mesenteries by short pedicels and surrounded by a ciliated endodermal layer. *X. macrospiculata* is a dioecious species like the majority of soft corals, although it should be noted that among the xeniids, four species are hermaphroditic: *H. elizabethae*, *H. fuscescens*, *H. ghardaqensis*, and *X. viridis* (Ashworth, 1899; Gohar 1940a).

The current study indicates the presence of male and female gonads in part of even the smallest colonies within the population (Fig. 4). Present knowledge lacks detailed information on the growth rate of *X. macrospiculata*. However, field experiments dealing with substrate colonization indicate that a linear relationship exists between colony size and age (Benayahu, 1982). The results of this study point out that colonies of about 1 cm³ are approximately 1-2 years old. The annual maturation of the gonads in the studied species lasts at least five months (Fig. 3). Therefore, it is unlikely that a one year old colony is sexually mature. Thus, we suggest that the smallest *Xenia* colonies capable of producing gonads are approximately 2 years old. *Parerythropodium fulvum fulvum* starts to reproduce at the age of 3-4 years (Benayahu

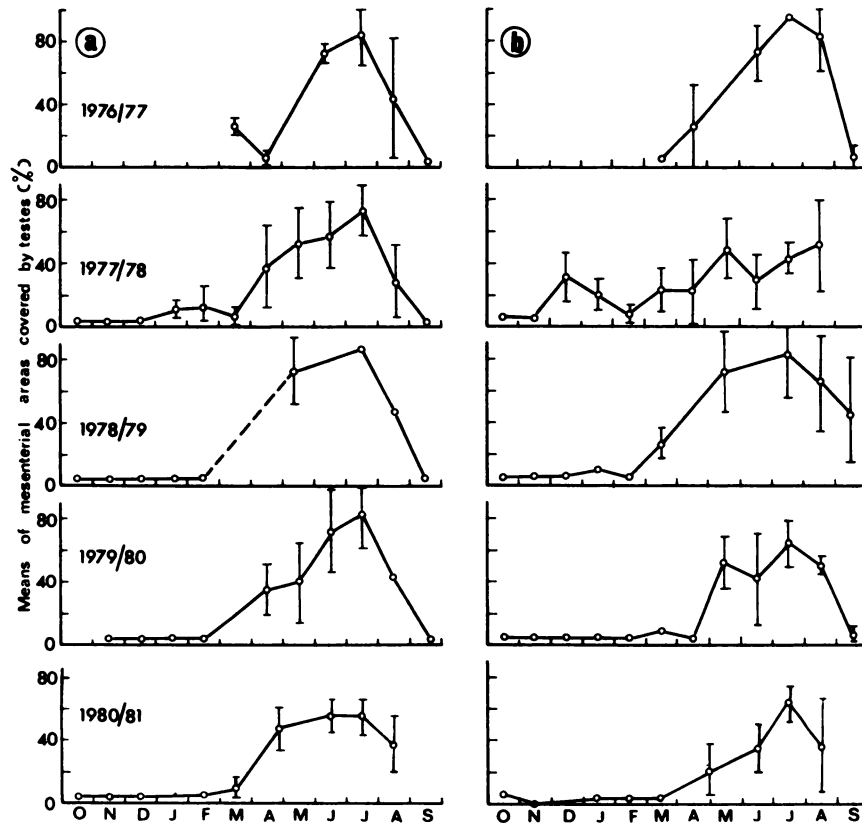


FIGURE 10. Monthly means of mesenterial areas covered by testes of *Xenia macrospiculata* in 3-5 m (a) and in 27-30 m (b).

and Loya, 1983) and *Sarcophyton glaucum* at 7-10 years (Benayahu, 1982). Reduction of age for first reproduction as exhibited by *X. macrospiculata*, suggests a shift towards high reproductive effort of the population ('r'-selection of Pianka, 1970).

The sex ratio of *X. macrospiculata* indicates a significantly higher abundance of males. We suggest that such a sex ratio is advantageous for a sessile dioecious coral such as *X. macrospiculata*, which possesses internal fertilization (Benayahu and Loya, 1984). The aggregates of *X. macrospiculata* tend to be unisexual (Benayahu, 1982), causing large distances of several meters between male and female colonies. In order to secure sperm-egg interaction, large amounts of spermatozoa are furnished by the numerous males.

Xenia macrospiculata exhibits a marked synchronization in gonadal development within the same colony. However, due to the prolonged period of gonadal initiation, the population contains colonies of various sexual stages (Figs. 3, 5, 8). Consequently, a wide range of sizes in oocytes and sperm sacs is evident almost year-round. Throughout the breeding season (May-September), the gametes gradually mature. The ripe eggs successively detach from the mesenteries, are fertilized, and pass into special brooding chambers where they develop into planulae (Benayahu and Loya, 1984). In each annual cycle, the last gonadal primordia appear around April (Fig. 5). It is likely that these eggs ripen late and are fertilized at the end of the breeding season.

The reproductive potential of *X. macrospiculata* in terms of egg production per polyp depends on the colony size. Large colonies with long polyp cavities contain several hundred eggs in each polyp. Space for the development of oocytes and testes is used very efficiently and they tend to develop along nearly the entire length of the mesenteries (Figs. 7, 10). In each polyp young gonads develop beside older ones, thus achieving a maximal space occupation. We suggest that this feature coupled with the early age of first reproduction and the prolonged period of gonadal initiation benefit reproductive success of *X. macrospiculata*.

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