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SURFACE BROODING IN THE RED SEA SOFT CORAL *PARERYTHROPODIUM FULVUM FULVUM* (FORSKÅL, 1775)

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ABSTRACT

Parerythropodium fulvum fulvum (Forskål, 1775) is an encrusting soft coral commonly found between 3 and 40 m, at the coral reefs of the Gulf of Eilat. The annual gonadal development and sexual reproduction of this species were studied both in shallow water (3–5 m) and in the deep reef zone (27–30 m). *P. f. fulvum* is a dioecious species. Sex ratio of the shallow population favors higher abundance of females, while on the deep reef a 1:1 sex ratio was recorded. These differences are probably due to local aggregations of colonies of the same sex caused by asexual reproduction. Oocytes and sperm sacs are found even in very young colonies (1–3 years). The frequency of sexually mature males is higher than mature females among small corals.

Young oocytes appear annually in August and within 10–11 months reach their maximal diameter. Sperm sacs start to develop later and mature after 7–9 months. A marked synchronization in the development of the oocytes and the testes exists among different polyps within each colony. Spawning occurs at dusk, and is fully synchronized by lunar periodicity (a few days after the new moon and a few days preceeding its last quarter). Fertilization takes place inside the polyp cavities. The shallow water population breeds prior to the deeper one with the whole reproductive period lasting approximately two months (end of June, beginning of August).

Among anthozoans, *P. f. fulvum* represents a unique mode of sexual reproduction and planulae development. This species is oviparous, yet eggs cleave on the surface of the female colonies while entangled in a mucoid suspension. We term this mode of planula development "surface brooding". Within 6 days after fertilization the planulae complete their development, detach from the surface of the colony, and sink to the bottom.

The encrusting growth form of *P. f. fulvum* is characterized by a thin coenenchyme and short polyp cavities, yet the eggs exhibit a large diameter (500–700 μm). Egg production of *P. f. fulvum* is rather low (18–24 eggs per polyp), but it is compensated for by surface brooding, which protects the offspring during embryogenesis. It is suggested that surface brooding is an adaptation to the encrusting shape of the colony and it maximizes fecundity.

INTRODUCTION

The soft corals (order Alcyonacea) are a large and diverse group of species among the Octocorallia. Several studies deal with alcyonacean distribution emphasizing their importance as space utilizers (Cary, 1931; Maragos, 1974; Veron *et al.*, 1974; Schuhmacher, 1975; Pearson, 1981). Other investigations discuss their ecological

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importance in the Red Sea coral reefs (Fishelson, 1970, 1973; Benayahu and Loya, 1977, 1981). Despite their abundance on many Indo-Pacific coral reefs (Bayer, 1973), little information exists on their life history and reproductive tactics.

Most of our knowledge on the reproduction of alcyonacean corals is based on early literature dealing with the widespread boreal species *Alcyonium digitatum* (Linnaeus, 1758) (Lacaze-Duthiers, 1865; Hickson, 1895; Hill and Oxon, 1905; Matthews, 1917). More recently, this species has been investigated by Hartnoll (1975, 1977). Extensive studies have been carried out on the Red Sea soft corals of the family Xeniidae (Gohar, 1940a, b; Gohar and Roushdy, 1961). These studies are mainly concerned with the biology and reproduction of *Heteroxenia fuscescens* (Ehrenberg, 1834). Recently, Yamazato and Sato (1981) have studied the reproductive biology of *Lobophytum crassum* Von Marenzeller, 1886.

Approximately 200 alcyonacean species have been recorded from the Red Sea (Benayahu and Loya, in prep.), but little is known about their life histories. The present work summarizes the results of a four-year quantitative study on the ecology and the reproductive pattern of *Parerythropodium fulvum fulvum* (Forskål, 1775) (family Alcyoniidae). This species was originally described from the Red Sea, but its present zoogeographical distribution extends to the reefs of Madagascar and east to Indonesia (Verseveldt, 1969).

Colonies of *P. f. fulvum* have an encrusting membranaceous growth form (Fig. 1), and is among the most abundant soft corals on the coral reefs of the Gulf of Eilat (Benayahu and Loya, 1977). This paper is concerned with the distribution and reproductive strategy of *P. f. fulvum* in shallow water (3–5 m) and in deeper reef zones (27–30 m). We have studied the annual development of gonads, sex ratio, colony size at first reproduction, and the mode and duration of sexual reproduction. In addition, we examined the chronology of planulae embryogenesis, as well as the post-larval development and morphogenesis. This study describes surface brooding, a unique mode of external planulae development among the alcyonacean corals.

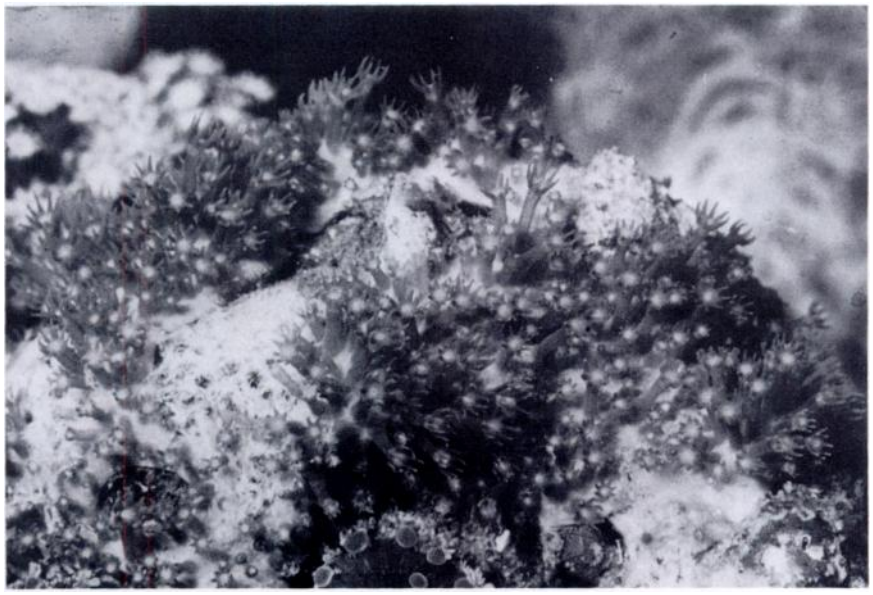

FIGURE 1. A living colony of *Parerythropodium fulvum fulvum*.

MATERIALS AND METHODS

The present study was carried out at two reef localities. One site was Muqebla', 12 km south of Eilat, where the shallow water population at 3–5 m depth was studied, the deep water population (27–30 m) was studied near the Marine Biological Laboratory of Eilat. Distributional studies and the correlation between spawning periodicity and depth were also carried out at this location. Sampling, underwater measurements, and observations were carried out by SCUBA diving. The living coverage and abundance of *P. f. fulvum* were studied by a series of line transects (10 m each) following the method described by Loya and Slobodkin (1971).

In order to determine the relationship between colony size and the onset of sexual maturity, small colonies were collected prior to the breeding season. These colonies were carefully removed from the substrate by forceps and were preserved in 4% buffered formalin. In the laboratory, each colony was numbered, its boundaries outlined on paper and then the drawings cut out by scissors. Each piece of paper was separately weighed using an analytical balance with a precision of 10^{-4} g. The weight of the paper pieces increased linearly with the colonies surface, and they represented the size of the corals.

The populations at the two reef sites were studied during approximately 4 years, from November 1977 to July 1981. Almost every month, fragments of 10–20 large colonies were randomly sampled in Muqebla' (3–5 m) and in the Marine Biological Laboratory (M.B.L.) reef (27–30 m). Ten large colonies were numbered with plastic tags in shallow water and on the deep reef. Fragments of these colonies were sampled every month during 3 years, to study the annual sequence of gonadal development within the same colony.

The polyp cavities of the formalin-fixed material were examined with a binocular stereoscope for genital development and sex determination. Additionally, wet mounts of septa with gonads from 25 polyps of each colony were examined microscopically; the diameter of the oocytes and sperm sacs was measured. Paraffin sections (10 μm) were employed to study gonadal structure. Sections were stained in hematoxylin (Delafield) and eosin after decalcification in formic acid-citrate (Rinkevich and Loya, 1979a).

Preliminary observations during the summers of 1978 and 1979 revealed that spawned eggs of *P. f. fulvum* remained on the surface of the colonies. During the summers of 1980 and 1981, prior to the breeding season, female colonies were collected and maintained in aquaria with running sea water. Determination of the exact timing of egg expulsion was done by continuous observations in the laboratory, and in the field along a depth gradient to 30 m. Fertilized eggs were reared in aerated sea water containers. Cleavage stages were compared to field material collected successively every 12 h. Synchronization of egg cleavage was studied by examining hundreds of embryos.

Material for scanning electron microscopy was fixed in 2% glutaraldehyde. After dehydration in a series of graded ethyl alcohols, the samples were dried from liquid CO_2 by the critical point method. The dried preparations were coated with gold and examined with a Jeol-S35 scanning electron microscope at 25 kV.

RESULTS

Abundance and depth distribution

The abundance of *P. f. fulvum* in shallow water is extremely variable. Previous results indicated that its coverage varies from 1.1% to 44.0% on different reef flats

and from 7.0% to 45.6% on different fore-reef zones (Benayahu, 1975). The present study across the M.B.L. reef indicates a lower living coverage (5.1 ± 2.3%) per 10 m transect at 18–40 m depth. The colonies tend to aggregate: young colonies are almost always found growing near larger ones. The smaller individuals are often found in poorly illuminated environments such as crevices or the undersides of dead stony corals.

Colonies of *P. f. fulvum* exists in two color morphs: yellow-brown and gray, but there is no taxonomic difference between them (Verseveldt, 1969). Figure 2 exhibits the depth distribution of the two morphs from shallow water to a depth of 30 m. Coral abundance is expressed as number of colonies per 10 m transect. The yellow brown colonies are the most common, while the gray corals are less abundant. Whereas the yellow-brown morph is found along the whole depth range studied, the gray morph is common only below 20 m. This pattern of distribution was qualitatively observed in many other reef localities along the coral reefs of the Gulf of Eilat.

Gonadal development

P. f. fulvum is a dioecious species. In both sexes the gonads develop on the four lateral and two ventral mesenteries of the polyp. Each polyp produces 18–24 genital products. The oocytes and the testes are located on the middle part of the mesentery and directed towards the center of the polyp cavity. Occasionally, few colonies of *P. f. fulvum* contain parts with thick coenenchyme. In such polyps the mesenteries may exceed a length of 6–12 mm, whereas in the most common ones they are only a few mm long. In the thick coenenchyme polyp-type, where much more space is

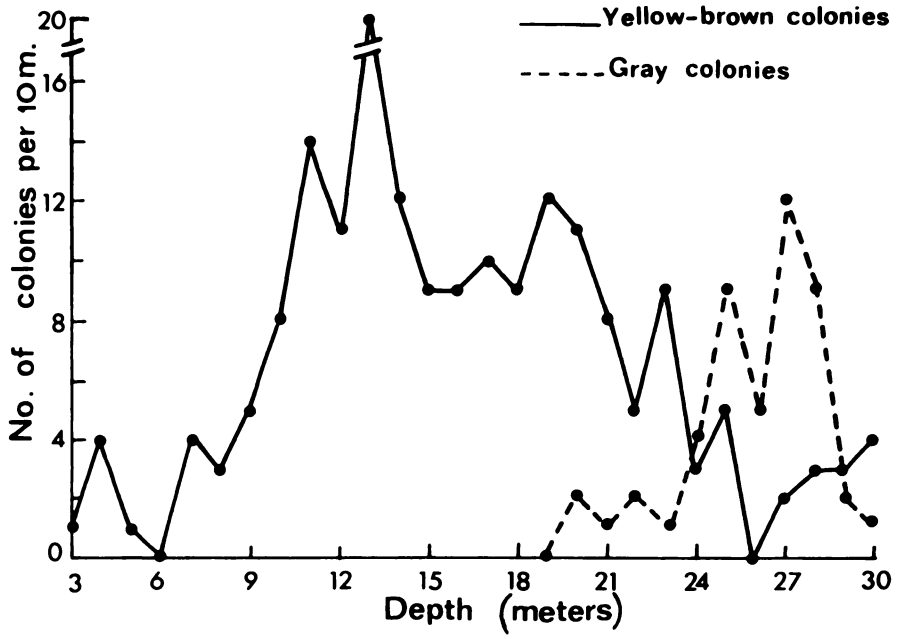

FIGURE 2. Depth distribution of the two color morphs of *Parerythropodium fulvum fulvum*. The abundance in terms of number of colonies per 10 m transect.

available, up to 100 eggs or sperm sacs may develop. Measurements of the diameter of the oocytes and sperm sacs indicate a marked synchronization in the reproductive state among different polyps within each colony (see below). No sex changes were detected during the study within the 20 tagged colonies.

Oocytes of living colonies of the abundant morph are characterized by a lemon-yellow color, while sperm sacs are transparent yellow. After preservation in formalin or alcohol their color becomes paler. The oocytes of the gray colonies are opaque-gray, while the testes are very transparent.

Size at sexual maturity and sex ratio

A few weeks before the spawning period (early June), 216 small (young) colonies were randomly collected in order to determine the minimum size at sexual maturity. We define a sexually mature specimen as one having either ripe spermatozoa or ripe oocytes (see below). The surface area of the sampled colonies ranged from less than 1 cm^2 to a maximum size of 5–7 cm^2. Table I represents the breeding state of these colonies in all size groups. Oocytes and sperm sacs are found even in the smallest colonies, but the frequency of mature males is higher than that of mature females. In addition, the percent of colonies with gonads increases with colony size.

Information on the population sex ratio was derived from samples collected during May–June, throughout the entire study. In shallow water 281 large colonies were examined, of which 60% were females. A X^2 test, at 0.05 level, indicates a significant deviation from a 1:1 sex ratio. A total of 220 colonies collected at 30 m depth resulted 54% males, indicating a 1:1 sex ratio ($P > 0.050$).

Annual cycle of gonadal development

Figure 3 demonstrates the relative percentage of colonies with oocytes or testes in each monthly sample. Figure 3a represents the results obtained from shallow water and Figure 3b represents the results obtained from the deep-reef. The percentage of colonies in the population without gonads fluctuates during an annual cycle, due to the timing of their development. Yet, Figure 3 shows that only a low percentage of colonies does not contain gonads prior to the spawning season.

TABLE I

Relationship between the size of young colonies and onset of reproduction of Parerythropodium fulvum fulvum

Group size (weight)*	No. of colonies	No. of males	No. of females	No. of immature colonies	Percent colonies with gonads
1–10	60	4	1	55	8.3
11–20	77	14	0	63	18.2
21–30	26	11	2	13	50.0
31–40	21	10	2	9	57.1
41–50	16	6	5	5	68.8
51–60	6	4	2	0	100.0
>60	10	3	7	0	100.0
Total	216	52 (24.1%)	19 (8.8%)	145 (67.1%)	

* Weight of paper images (in g 10^{-4}) determined the size group (see Materials and Methods for further explanation).

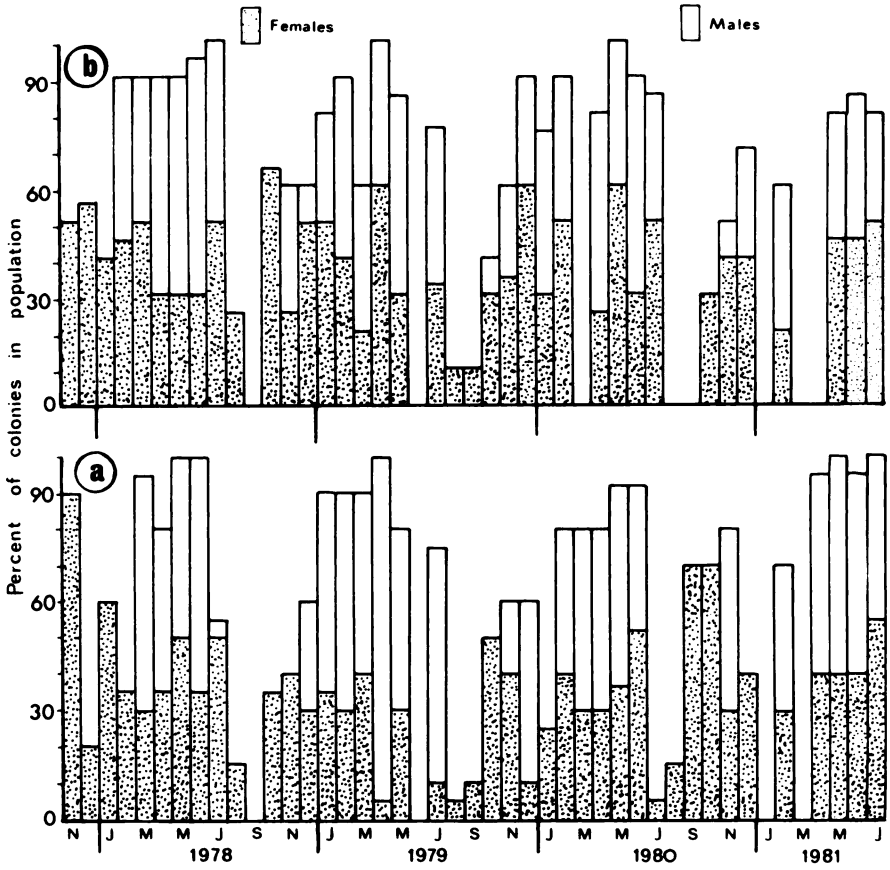

FIGURE 3. Abundance of female and male colonies of *Parerythropodium fulvum fulvum* with gonads in each monthly sample. Figure 3a represents results obtained from 3 m depth and Figure 3b represents the results from 30 m depth. The blank spaces in some of the months indicate that no sampling was done that period.

Figure 4 represents the annual changes in the mean maximal diameters of oocytes and sperm sacs in shallow water (Fig. 4a) and in deep water (Fig. 4b). The first young oocytes appear in August. They grow rapidly and within 10–11 months reach their maximal size. The diameter of the largest oocytes was 700 μm, however, the majority of the ripe oocytes ranged in size from 400 to 600 μm. Figure 4 also demonstrates that the annual development of the sperm sacs starts a few months after oocyte initiation. The first young spermaries are found every year during October, although their appearance can be delayed in part of the population until December. The development of the sperm sacs generally takes 7–9 months. The largest reach 480 μm, although the common diameter at maturity is about 400 μm. Spawning occurs mainly during June–July. The annual development of female and male gonads exhibited the same pattern throughout the research period (Fig. 4). This pattern is markedly synchronized within the population as indicated by the low standard deviations around the mean maximal diameters of the oocytes and sperm sacs.

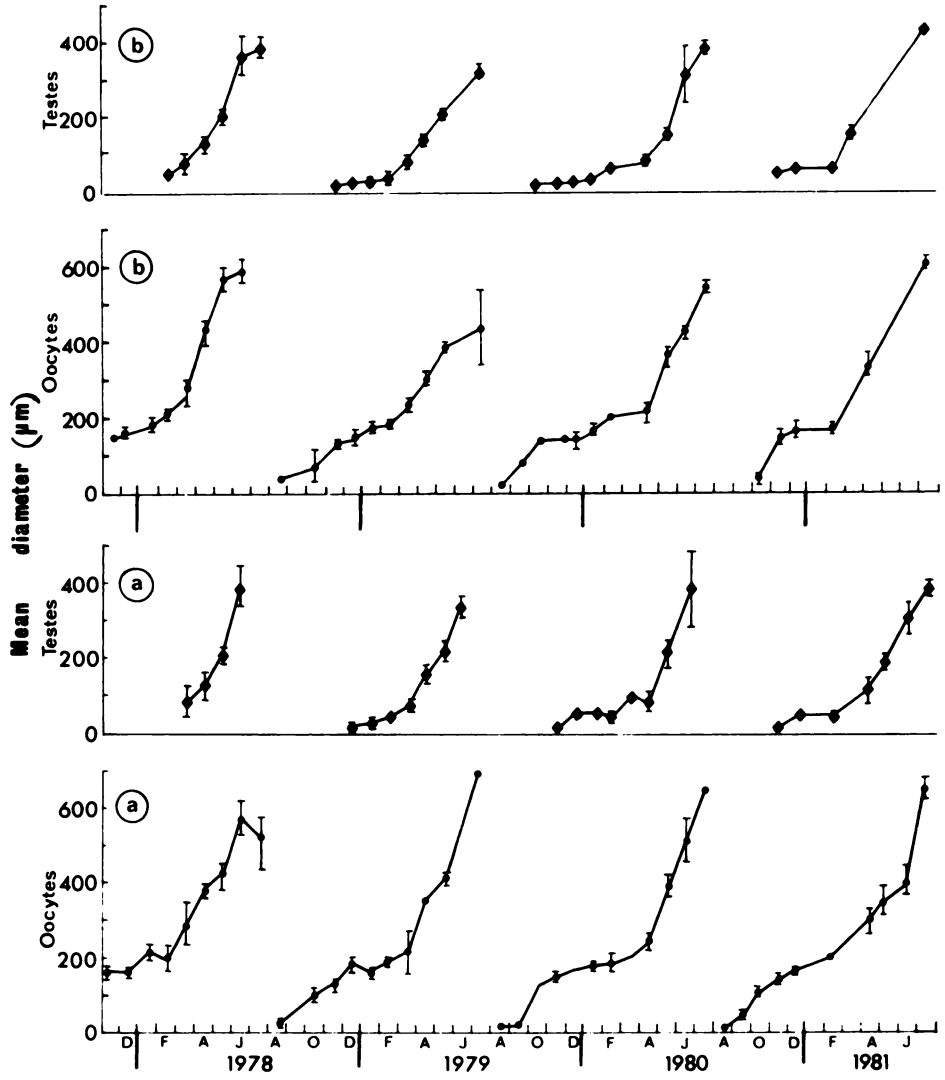

FIGURE 4. Mean maximal diameters of oocytes and sperm sacs of *Parerythropodium fulvum fulvum* at 3 m depth (Fig. 4a) and 30 m depth (Fig. 4b).

Ultrastructure of the gonadal surface

The oocytes and the sperm sacs of *P. f. fulvum* are surrounded by a ciliated follicular layer (Fig. 5a, b). These cells are derived from the endodermal epithelium of the septa. Each oocyte or testis is attached to the mesentery by a pedicle of approximately 100 μm (Fig. 5a). The cells of the polyp cavity are covered by cilia of about 20 μm in length. The flagella of the gonadal surface and that of some other endodermal cells are located in small pits. Each flagellum is surrounded at its base by 8 elevated folds of cell surface, in a palisade formation (Fig. 5c), similar to the arrangement described by Mariscal and Bigger (1976) in other octocorals. SEM

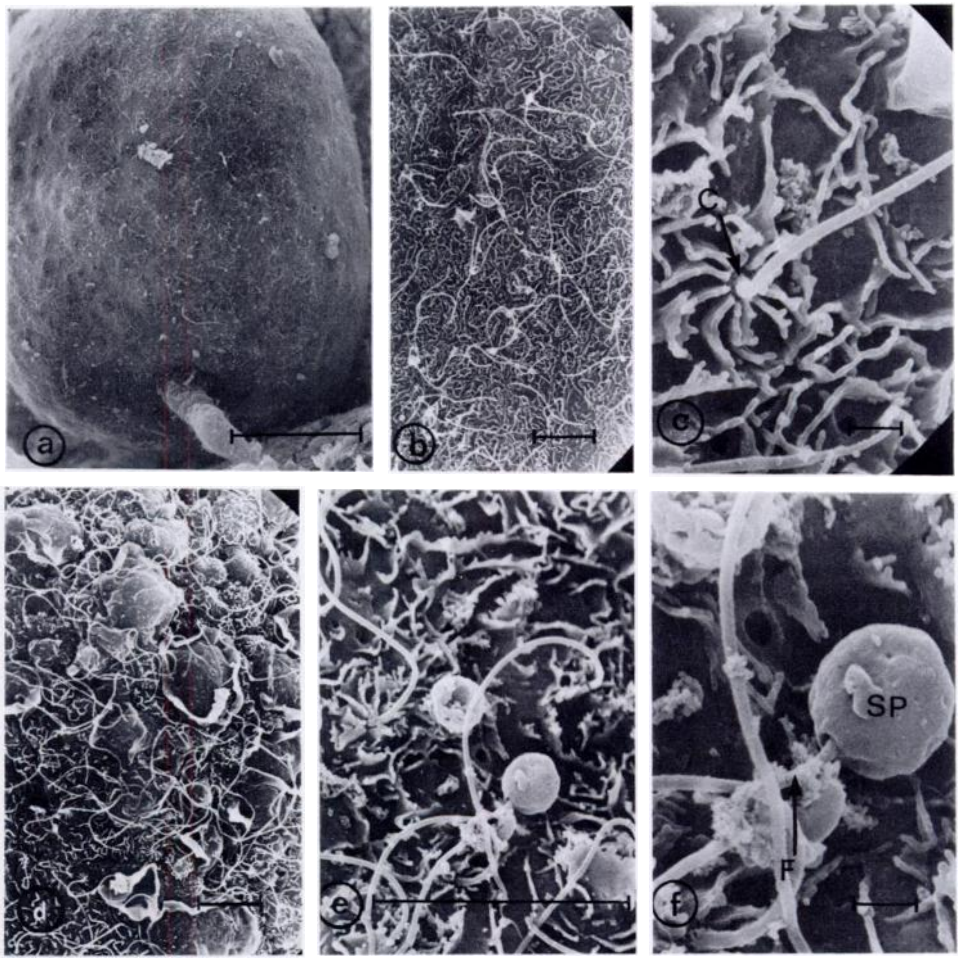

FIGURE 5. Ultrastructure of the gonadal surface of *Parerythropodium fulvum fulvum*. a: an oocyte attached with a pedicle to the mesentery. Bar = 100 μm. b: ciliary follicular endoderm of an oocyte. Bar = 10 μm. c: endodermal cilium surrounded by 8 elevated folds, cilium base (C). Bar = 10 μm. d: outer surface of a sperm sac. Bar = 10 μm. e: sperm cells on the testis. Bar = 1 μm. f: magnified sperm cell flagellum (F), sperm cell (SP). Bar = 1 μm.

examination reveals that the outer surface of the sperm sacs is elevated into hillocks and fold-like crests (Fig. 5d). In addition, microvilli and cilia are located among them (Fig. 5d, e). Immature sperm cells are found attached to the surface of the testes. They probably burst the spermary wall during fixation (Fig. 6e, f). The diameter of their rounded head is 2 μm, while their tail exceeds a length of 12 μm.

Spawning, fertilization, and embryogenesis

After spawning, all the eggs of *P. f. fulvum* remain on the surface of the female colonies, where they develop into planula larvae (Fig. 6a). The lemon-yellow color of the eggs make them very apparent even from a distance of several meters. The eggs are suspended in transparent, gelatinous material secreted by the corals. This

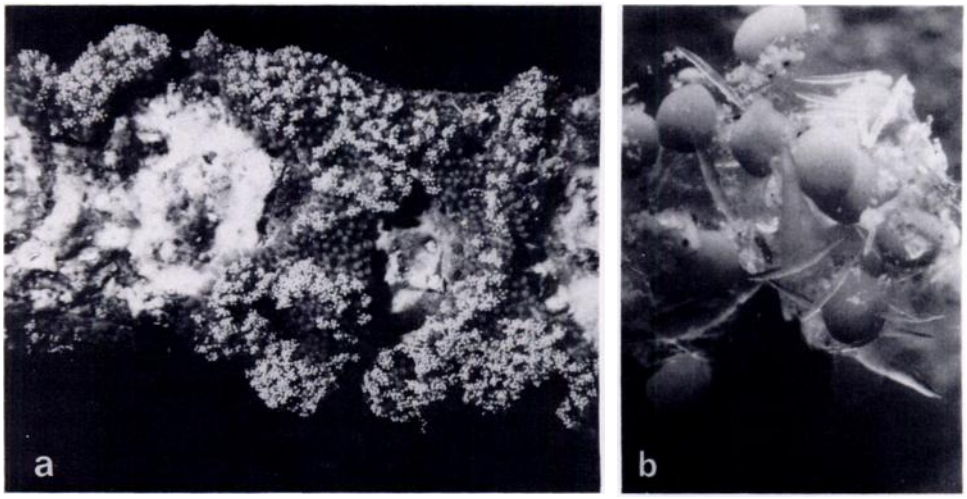

FIGURE 6. Spawning of *Parerythropodium fulvum fulvum* a: colony covered by spawned eggs embedded in mucus. b: eggs and sclerites entangled in mucus (×10).

mucus cover also contains many sclerites which are torn from the polyps during egg expulsion (Fig. 6b). Various organic and inorganic particles adhere to the mucus. The mucus flocks remain on the surface of the colonies for a week, and during this period cleavage takes place within the mucus.

Successive observations suggest that shortly before spawning the eggs of *P. f. fulvum* are fertilized within the polyp cavities. Thus, some female colonies that were kept in aquaria during the breeding season failed to spawn. Nevertheless, cleavage occurred inside their polyps. Additional evidence supporting internal fertilization was detected by SEM observations. Fixation of female colonies a few hours after egg expulsion revealed clusters of mature spermatozoa along the mesenterial filaments.

The eggs of *P. f. fulvum* are of the telolecithal type. Normally, cleavage occurs on the surface of the female colonies. The fertilized eggs lack a follicular layer, which is most probably detached before fertilization (Fig. 7a). Cleavage of the eggs begins within 3–5 h after fertilization. The first two divisions are meridional and equatorial (Fig. 7b). Throughout cleavage highly irregular, lobed structures are formed (Fig. 7c). The holoblastic, unequal cleavage produces a morula with large cells at the vegetal pole and smaller cells at the animal pole (Fig. 7d). Further divisions 24 h after fertilization lead to the formation of a round blastula (Fig. 7e). Histological sections indicate that this is a steroblastula, lacking a blastocoel. The thin external cell layer forms a cortex, while the inner cells are filled with yolk platelets.

The surface of the blastula (Fig. 8a) is characterized by folds and microvilli 1–2 μm long. Numerous microvilli are located between the neighboring cells (Fig. 8b). Ciliated ectodermal cells are recognized at a later stage on the young developing planula (Fig. 8c). During the third day after fertilization the diameter of the embryo is 350 μm (Fig. 7f). After four days a gastrula develops with a length of 600 μm (Fig. 7g). A young planula bearing an oral opening is found one day later (Fig. 7h). The young planula is rounded and gradually changes to an egg-like and then a pear-like shape (Fig. 7i). At this stage the young larvae are motionless, still embedded in the mucus. By the 6th day the planulae elongate; their aboral end is tapered while the oral side is rounded.

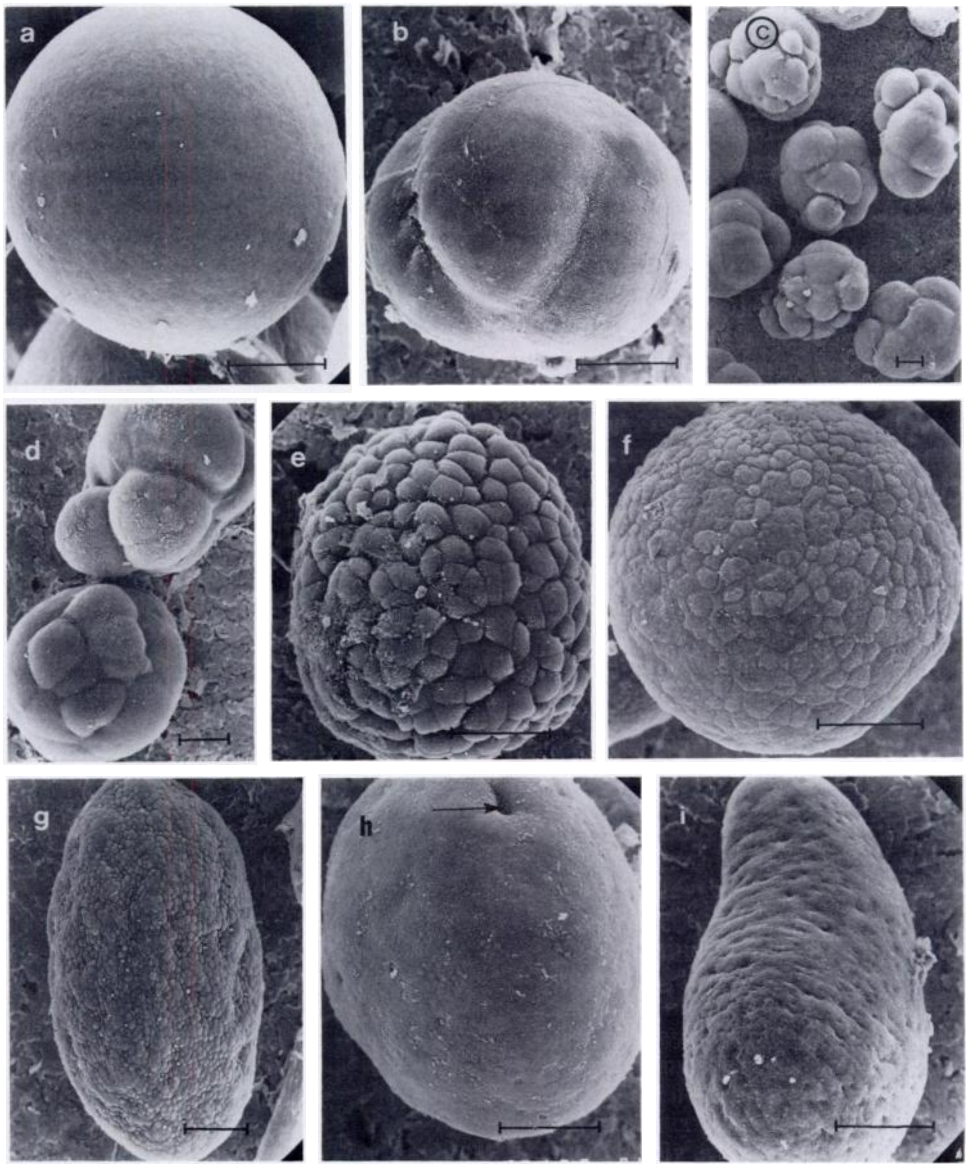

FIGURE 7. Embryogenesis of the planula larva of *Parerythropodium fulvum fulvum*. Bar = 100 μm. a: an egg without follicular layer. b: first two divisions of the egg. c: young embryos. d: irregular embryos. e: 24 h blastula. f: 48–72 h blastula. g: gastrula, 4 days after fertilization. h: young planula, arrow points to mouth opening. i: mature planula.

Planulae structure and behavior

Seven days after fertilization the mucus with the mature planulae in it starts to detach from the surface of the colonies and sink near the "mother colony" (Fig. 8d). The mucoid substance starts to degrade, and the larvae begin to move with their cilia. Figure 8e presents a fractured mature planula, where dense ciliary ec-

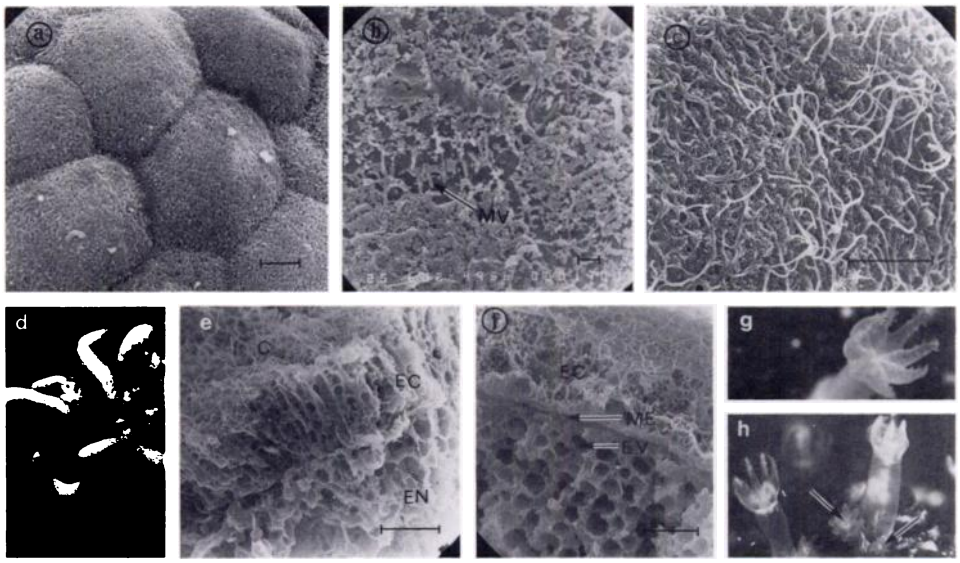

FIGURE 8. Planula structure and post larval development of *Parerythropodium fulvum fulvum*. a: blastula cells. Bar = 10 μm. b: microvilli (MV) on the surface of 24 h blastula cells. bar = 1 μm. c: ciliated blastula cells. Bar = 10 μm. d: mature planula (×18). e: fracture of mature planula, cilia (C), ectoderm (EC), endoderm (EN) Bar = 10 μm. f: fractured mature planula, ectoderm (EC), mesoglea (ME), endodermic vacuole (EV). Bar = 10 μm. g: 12–16 day old polyp (×8). h: young colony, arrows indicate buds of young polyps.

toderm and endodermal cells can be seen. The mesoglea of the planula is very thin, bounded by vacuolated endodermal cells (Fig. 8f), which probably serve for yolk storage. The cilia are uniformly scattered on the ectodermis, however due to the larval contractions, they might be hidden among the body folds. The planula larvae are elongated, barrel-shaped and recognized by their typical lemon-yellow color. When fully extended their maximal length reaches 2.4–3.2 mm. During the first days after maturation the planulae tend to change their shape by body contractions, from elongated to rounded and *vice versa*. Most of the time the larvae are attached to the substrate on their oral side by mucus secretion. Occasionally swimming is observed, typified by a corkscrew rotation along the oral-aboral axis. The larvae also tend to crawl over the substrate for short distances of a few cm.

Post-larval development and formation of a young colony

Laboratory and underwater experiments dealing with substrate selection by the planulae (Benayahu and Loya, in prep.) have enabled us to follow the morphological changes occurring during planulae metamorphosis. Development within the planulae population is not synchronized; differences in the developmental stages in the same age group may vary by as much as 3 to 5 days. During the first 3–7 days after planulae maturation they attach to the substrate and develop into young cone-shaped polyps, surrounded by 8 tentacular buds. During days 7–10 the tentacles elongate, and 8 septa are observed inside the polyp cavity. The development of the first pair of tentacular pinnules occurs during days 11–12. In days 12–16 an additional 4–7 pairs of pinnules develop on each tentacle (Fig. 8g). Within the next

month 2–3 secondary polyps develop in the young colony, and sclerites are seen within the polyp body (Fig. 8h).

Rhythmicity of spawning

Table II presents the timing of egg expulsion in the population of *P. f. fulvum*. The dates in the table represent the first day of each spawning (which may last 2–3 days). Successive underwater observations indicate that spawning starts around the middle of June and lasts for approximately two months. The process begins at dusk, and corresponds to a lunar periodicity, lasting from a few days after the new moon to a few days preceeding its last quarter.

Although egg expulsion is synchronized, it does not occur simultaneously within the population. A sample of 130 colonies was examined underwater at the beginning of the breeding season in June 1978, a few days after first spawning was observed. The majority of the colonies from both sexes had not yet spawned, and only a minor number had shed part of their gametes.

Figure 9 represents the reproductive state of the shallow water population of *P. f. fulvum* sampled during summer 1980 at Muqebla'. The colonies are divided into 4 groups: males with sperm sacs, females with oocytes in the polyp cavities, females with eggs on their surface (brooding females), and colonies without any genital products. The first two dates represent the population reproductive structure before the breeding season. The majority of the colonies still contain gametes in their polyp cavities. The histograms from 21 and 22 June (Fig. 9) indicated the reproductive state a few days after gamete expulsion, which took place on 18 June (Tabel II). These results show a decrease in the percentage of male colonies with testes, hence, an increase in the number of colonies without any genital products. During these days, only a minor proportion of the population brood their larvae. Seven to ten days after spawning, in 26 and 28 June, no brooding females could be found. Similar reproductive structure was found at the two following dates. After the 15 July spawning (Table II), the population consisted of brooding females and colonies without gonads (17 July, Fig. 9). Underwater observations over large areas at various reef localities indicated that only a negligible percentage of corals spawned on 2 July 1980.

Figure 10 presents the reproductive structure of the population along a depth gradient at the M.B.L. reef during the breeding season of 1980. The upper part of the figure illustrates the results obtained on 18–20 July, and the lower part that of 2–4 August. The massive spawning of July (Table II) occurred along all the depth range studied. A few days after spawning, brooding females were observed, especially at a depth of 5–20 m. Consequently, a marked decrease of females with oocytes was noted. At reef zones deeper that 5 m, the percent of male corals with sperm

TABLE II

Timing of egg expulsion in the population of Parerythropodium fulvum fulvum

Date	Moon phase	Depth m
25 June 1978	Full moon—Last quarter	1–4
27 June 1979	New moon—First quarter	1–6
18 June 1980	New moon—First quarter	1–3
2 July 1980	Full moon—Last quarter	1–18
15 July 1980	New moon—First quarter	15–25
30 July 1980	Full moon—Last quarter	30–35
4 July 1981	Full moon—Last quarter	1–5

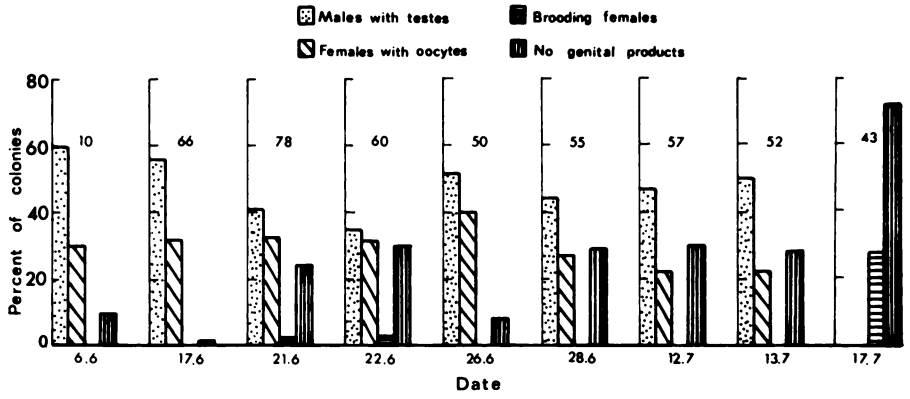

FIGURE 9. The reproductive state of shallow water population of *Parerythropodium fulvum fulvum* at Muqebla' during the breeding season of 1980. The numbers within each sampling date represent the sample size.

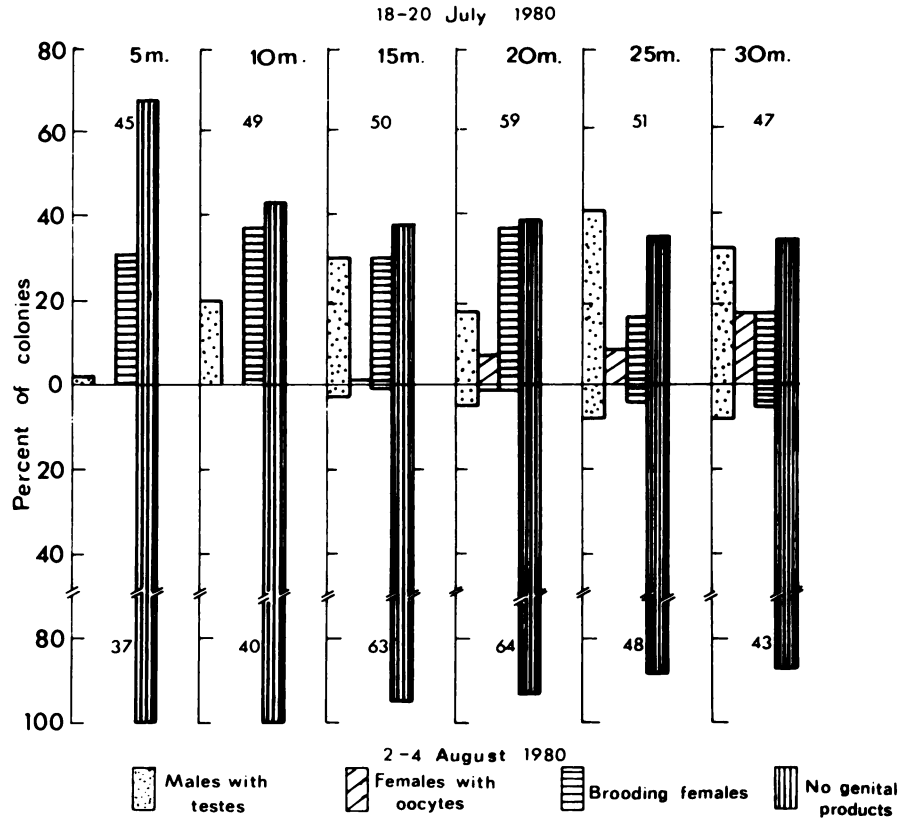

FIGURE 10. The reproductive structure of *Parerythropodium fulvum fulvum* along a depth gradient during the breeding season of 1980.

sacs still remained high. The spawning of 30 July (Table II) was recorded below 5 m depth. However, brooding colonies were observed only at 20–30 m depth. The lower part of Figure 10 indicates that after this spawning almost the whole population remained without genital products, except for a small number of males at a depth below 15 m. Figures 9 and 10 point out that the shallow water population breeds before the deeper one, and the whole reproductive period takes place during approximately two months.

Discussion

During the last several years much interest has been focused on the life history of scleractinian corals (Harrigan 1972; Stimson, 1978; Rinkevich and Loya, 1979a, b; Szmant-Froelich *et al.*, 1980; Kojis and Quinn, 1981, Fadlallah and Pearse, 1982a, b). Although the significance of alcyonacean corals within the coral reef environment is well recognized, only scant surveys were conducted on their life history. The present study elucidates for the first time various aspects of the reproductive dynamics of the common Red Sea soft coral *P. f. fulvum.*

The general morphological features of the gonads of *P. f. fulvum* resemble those of *Alcyonium digitatum* (Hickson, 1895; Hill and Oxon, 1905) and *Heteroxenia fuscescens* (Gohar and Roushdy, 1961). Field experiments dealing with the colonization capacity of *P. f. fulvum* (Benayahu, 1982) indicate that all colonies above the age of 3–4 years old develop gonads. Small sized colonies mostly contain male gonads, while females become sexually mature at an older age. These results fit well with the common pattern found in other corals (Harrigan, 1972; Hartnoll, 1977; Grigg, 1977; Rinkevich and Loya, 1979b).

Sex ratios of *P. f. fulvum* differed between the shallow water and the deep reef populations. This may be due to local aggregations of the species (Benayahu, 1975). Such uneven distribution of individuals can cause local clumps of one sex. Additionally, asexual reproduction of *P. f. fulvum* formed by fragmentation (Benayahu, 1982), may cause deviation from a 1:1 sex ratio.

Fecundity of gorgonian octocorals has been determined as the number of planulae produced per polyp (Grigg, 1977). Thus, the alcyonaceans *Heteroxenia fuscescens* (Gohar, 1940a) and *Alcyonium digitatum* (Hartnoll, 1975) with long polyp cavities are characterized by high egg production. However, in *P. f. fulvum,* which has an encrusting growth form and short polyp cavities, fecundity is low (18–24 eggs per polyp).

Several studies reported lunar periodicity in the reproduction of stony corals (Harrigan, 1972; Stimson, 1978; Rinkevich and Loya, 1979b). This study documents a distinct lunar rhythmicity in the breeding of an alcyonacean coral. Lobel (1978) suggests that such spawning may act as a cue synchronizing simultaneous reproductive readiness within a species. We further speculate that this mechanism is critically important within colonies like *P. f. fulvum,* which breed only a few days per year. It should be noted that the time lag in spawning at greater depths (Fig. 10) is probably due to differences in time of the peak water temperature along depth gradient, as suggested by Grigg (1977) in his study on gorgonians.

Among the anthozoans, *P. f. fulvum* exhibits a unique mode of sexual reproduction and planulae development. This coral is oviparous, yet cleavage of the eggs takes place on the surface of the female colonies within a mucoid suspension. We term this peculiar mode of planula development as surface brooding. Brooding in marine invertebrates was defined by Dunn (1975) as "the retention of offspring by

parent through embryonic stages usually passed in the plankton," hence, *P. f. fulvum* is an external brooder. External brooding in anthozoans is uncommon. The group which is best known are actinians of the genus *Epiactis* (Chia, 1976), especially *E. prolifera* which broods its young on its lower column (Dunn, 1975). In this species the embryos are enveloped by the parent, and the ectoderm of the two are closely apposed. The intimate connnection between the offspring and the parent is obligatory and essential for their development. Dunn further suggests that this might serve a nutritional function.

External brooding has also been recorded in the octocoral species from the order Stolonifera: *Clavularia crassa* (Kowalewsky and Marion, 1883), *Cornularia komaii,* and *C. saganiensis* (Suzuki, 1971). In these species the fertilized eggs developed into planulae in an external brooding cavity formed by the tentacles. The eggs of the scleractian coral *Goniastea australensis* are expelled as masses embedded in mucus (Kojis and Quinn, 1981). They remain on the colony and after spawning is terminated, the eggs sink down to the bottom where planular development takes place. The results of the present work indicate that the brooding behavior of *P. f. fulvum* differs from that of other anthozoans with external brooding. Although no cellular connection exists between the embryos and the colonies, cleavage occurs on the external surface of the females. Thus, the embryos are protected from mechanical damage such as the erosive activity of sediment or wave action.

Membanaceous growth form is rare among the octocorals. The encrusting colonies of *P. f. fulvum* are characterized by a thin coenenchyme and short polyp cavities. Most eggs of soft corals are large in diameter (500–700 μm: Benayahu, 1982). It is therefore presumed, that if embryogenesis had been internal, the number of eggs per polyp would have been reduced even below the number of 18–24 oocytes due to small polyp size. We suggest that surface brooding maximizes fecundity and is an adaptation to the encrusting growth form. Egg production in *P. f. fulvum* is rather low, but this is compensated for by surface brooding which protects the offspring through embryogenesis. It is interesting to note that the three aforementioned external brooding Stolonifera species are also encrusting corals. Hence, the same reproductive strategy has been adopted by two different octocoral groups.

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