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Larval development and survivorship in the corals *Favia favus* and *Platygyra lamellina*

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Abstract

Two Red Sea faviid species, *Favia favus* and *Platygyra lamellina* spawn eggs and sperm once a year, during the summer. External fertilization occurs 0.5 h after spawning, and mobile gastrulae appear 20 h later. Four stages in the early ontogenesis of these corals are described. The slow development (2–3 months) to the polyp stage in broadcasting species is attributed to the lack of zooxanthellae in their planulae and their appearance in the primary polyp only at a later stage. Survivorship of one-month-old primary polyps is *ca* 0.21% and 0.25% in *F. favus* and *P. lamellina* respectively, from the populations of 2–9-day-old planulae. Despite these low rates of survival, both species form dense populations in the Gulf of Eilat.

Introduction

Sexual reproduction in corals results in free swimming planulae. The settlement and metamorphosis of planulae into primary polyps are crucial phases in the life history. Detailed information exists concerning the behaviour of planulae and their settlement, and growth of primary polyps in coral species which brood their larvae (see Fadlallah, 1983). However, little is known about the morphological changes and their duration that occur during the post-settlement period of those corals which spawn gametes (Babcock, 1985). Furthermore, little is known of the fate of gametes after their release. Studies on postlarval development in broadcasting species have usually ended prior to the settlement process (Szmant-Froelich *et al.*, 1980; Babcock & Heyward, 1986): hence, comparisons are lacking between brooding and broadcasting species. If questions of reproductive success and contribution to community structure are to be addressed, the survivorship rates of larval and postlarval stages must be examined.

This study reports on patterns of larval and postlarval development and survivorship in two spawning faviid corals, *Favia favus* (Forskål) and *Platygyra lamellina* (Ehrenberg). Both species are simultaneous hermaphrodites and spawn each summer in July–August, during 3–5 sequential nights at different phases of the moon: *F. favus* releases dark red eggs between the full moon and the last quarter; *P. lamellina* releases pink eggs at the new moon (Shlesinger & Loya, 1985). The aims of the study were: to assess the times required for embryogenesis, settlement, and metamorphosis into primary polyps; to describe morphological changes through the different stages; and to estimate the survivorship of mobile larvae, postlarval stages and primary polyps.

Material and methods

The study site is in front of the Marine Biological Laboratory, 10 km south of Eilat, Red Sea. The study took place during 1982–1985. Two days before the expected spawning periods of *F. favus* and *P. lamellina*, 10 mature colonies (20–30 cm diam.) of each species were removed from the reef and were transferred individually to the laboratory. Colonies were maintained separately in running seawater aquaria. After spawning had occurred, colonies were returned to the reef. Flow of seawater in the aquaria was stopped for 24 h immediately after spawning, although continuous aeration was provided; outlets of the aquaria were covered by plankton netting (100 μm) to prevent loss of eggs or larvae.

Both species spawned egg-sperm clusters. For the studies of embryogenesis and development of the larvae and postlarval stages (primary polyps), clusters of gametes from all colonies were cultured together in several aquaria immediately after being released. The aquaria were maintained under a natural day-night regime. Unfiltered seawater was pumped to the aquaria from 5 m depth. Planulae settled on different substrates provided (glass plates 10–25 cm diam., plastic petri dishes 10 cm diam., and pieces of dead coral). As coral spat were best detected on the plastic and glass substrates, only these were transferred to the reef later. Survivorship during the first 2 weeks was based on counts of planulae, which had settled on all artificial substrates including aquarium sides. After 2 weeks, postlarvae had already metamorphosed into primary polyps with a solid attachment to the substrate. At this stage they were placed on the coral reef for further growth and survivorship studies. Samples of the settlement substrates were periodically removed to the laboratory in seawater containers for studying spat development using a dissecting microscope. These substrates were returned to the reef within 30 min, with no adverse effects on the coral spat. Gametes and various embryonic stages for scanning electron microscope studies were preserved in 2.5% w/v glutaraldehyde and kept at 4 °C.

Results

Fertilization and embryogenesis

F. favus and *P. lamellina*, were observed spawning clusters of gametes which floated (Fig. 1A). Each cluster contained eggs (*ca* 350 μm diam.) and sperm in a condensed sphere (Fig. 1B–1E). The sperm formed local concentrations tightly attached to the eggs. No zooxanthellae were detected in the oocytes. Ten to 20 min after spawning, the gametes separated from the clusters and dispersed (Fig. 1C). After dispersal, the oocytes became spherical, and swelled to *ca* 700 μm diam. Simultaneously, a whitish cloud of sperm dispersed in the water. It was established that fertilization takes place at the earliest 20–30 min after spawning (Shlesinger & Loya, in prep.).

One hour after spawning, the endogenous red pigment of the oocytes (uniformly distributed in the unfertilized egg) had formed a dark red cap at the vegetal pole, similarly to that described for fertilized eggs of the ascidian *Boltenia villosa* (Simoncini *et al.*, 1988). Cleavage began *ca* 3 h after spawning. In both species furrow formation progressed equally on all sides of the embryo. The cleavage plane was initially radial, but shifted to a pseudospiral pattern (Mergner, 1971; Szmant-Froelich *et al.*, 1980; Babcock & Heyward, 1986) as development progressed. Blastocoels were observed at the morula stage (6–8 h after spawning). At this point many of the embryos broke apart and embryogenesis ceased. The remainder developed to bastulae 6–8 h later. Formation of a pharynx by invagination of the ectoderm was followed by creation of a gut cavity 24 h after spawning (gastrula stage, Fig. 1F). Gastrulae were spherical and exhibited slight rotating movements. The main change in the embryogenetic process from gastrula to planula was the further development of numerous cilia. Early planulae were spherical and became highly mobile within 48 h. Planulae of *F. favus* were red; those of *P. lamellina* were pink. The free swimming stages (gastrulae and 2–4 d planulae) did not possess zooxanthellae and lacked mesenteries (Fig. 1G).

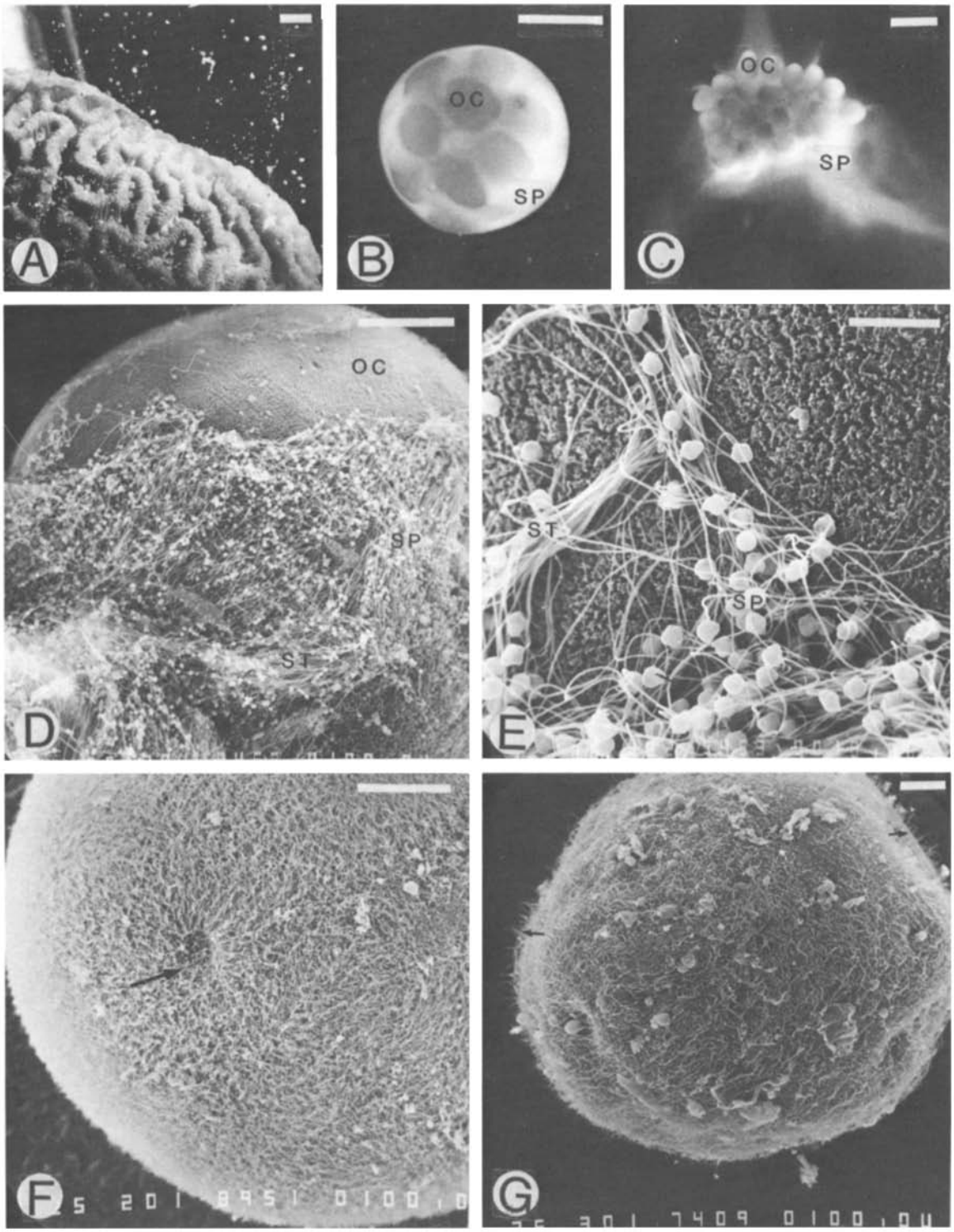

Fig. 1. A) *P. lamellina* during spawning; B) Intermingled cluster of oocytes (OC) and sperm (SP); C) Dispersal of cluster 10–20 min after spawning. Scanning electron micrographs of: D) Clusters of sperm around the oocyte; E) Magnification of spermatozoan tails (ST); F) Early planula – 48 h old, (arrow indicates oral pore); G) Planula at 3 d (arrows indicate cilia). Scale bars: A = 1 cm; B–C = 1 mm; D–G = 100 μm.

Up to this point no differences in developmental stages were observed between species. Subsequent developmental stages and differences between the two species are summarized in Table 1. Initiation of mesenteries was found one day before settlement and was completed by the time of settlement at the edwardsia stage (4 primary mesenteries, Fig. 2A). Although the edwardsia stage developed earlier in *F. favus*, further development into the halcampoides stages (6 primary mesenteries) was slower in *F. favus* than in *P. lamellina* (Table 1). One to 2 d later, calcareous secretion started with formation of a basal plate. The corallite wall progressed, growing upwards and building the circumference skeleton only (epitheca). Following this, 6 tentacle buds were first observed (Fig. 2B, 2C). Invasion by zooxanthellae occurred a few days later (Fig. 2D, Table 1). A complete primary polyp developed in *P. lamellina* 20–24 d, and in *F. favus* 26–30 d, after spawning.

At 1 m old, the diameter of the primary polyp was approximately 2.0 mm in both species, but they still lacked calcareous septa. First septal rudiments were observed only after the first month post spawning. Juvenile polyps at age 3 m were 3–4 mm diam. and had a fully developed skeleton with cycles of complete septa. First polyp budding was observed on the reef 7–9 m after spawning. The growth rates of colonies of the 2 species from primary polyps to 2 y old (*F. favus*) and 5 y old (*P. lamellina*) are illustrated in Fig. 2E–2J.

Table 1. Embryogenesis and morphological changes in larval and postlarval stages of *F. favus* and *P. lamellina*. Based on: 500 planulae, 150 primary polyps and 20 polyps with secondary septa, for each species.

Time (h, d) since spawning	Embryological and morphological changes	
	F. favus	*P. lamellina*
1 h	Gamete separation, fertilization	Gamete separation, fertilization
6–8 h	Morula	Morula
14–16 h	Blastula (dark red)	Blastula (pink)
20 h	Gastrula, appearance of cilia, oral pore	Gastrula, appearance of cilia, oral pore
2–4 d	Planula	Planula
5–6 d	Mesenteries formed	
7 d	Attachment to substrate, edwardsia stage	Mesenteries formed
8–9 d		Attachment to substrate, edwardsia stage
10–11 d		Halcampoides stage, basal plate development
12 d	Halcampoides stage	Epithecal development
14–15 d	Basal plate development	6 tentacle buds
16–18 d	Epithecal development	Appearance of zooxanthellae in polyp
20–24 d	6 tentacle buds	Complete primary polyp: 12 mesenteries, zooxanthellae, tentacles, corallite wall (circumference only)
26–30 d	Complete primary polyp: 12 mesenteries, zooxanthellae, tentacles, corallite wall (circumference only)	

Survivorship

Table 2 shows the survivorship of settled planulae in the laboratory. *Ca* 17% of the planulae of both species settled within 2–9 d. Planulae which failed to settle during this period continued to swim for up to 25 d and finally died. No significant differences were detected in the average survivorship rates within each age interval of the 2 species, until 1 m old (t-test, $P > 0.05$). It is estimated that only 0.21%–0.25% of the settled planulae developed to the primary polyp stage (Table 2). Unfortunately, the entire populations of *F. favus* and *P. lamellina*, which had settled on the artificial substrates and whose survivorship was detected between 1–6 m old, were wiped out by a storm. A different detailed study on survivorship of a young population of *F. favus* which settled *in situ* on artificial substrates indicated mortality rates of 33% at 0.5–1 y old, and 18% and 19% at age classes of 1–2 y and 2–3 y old, respectively (Shlesinger, 1985).

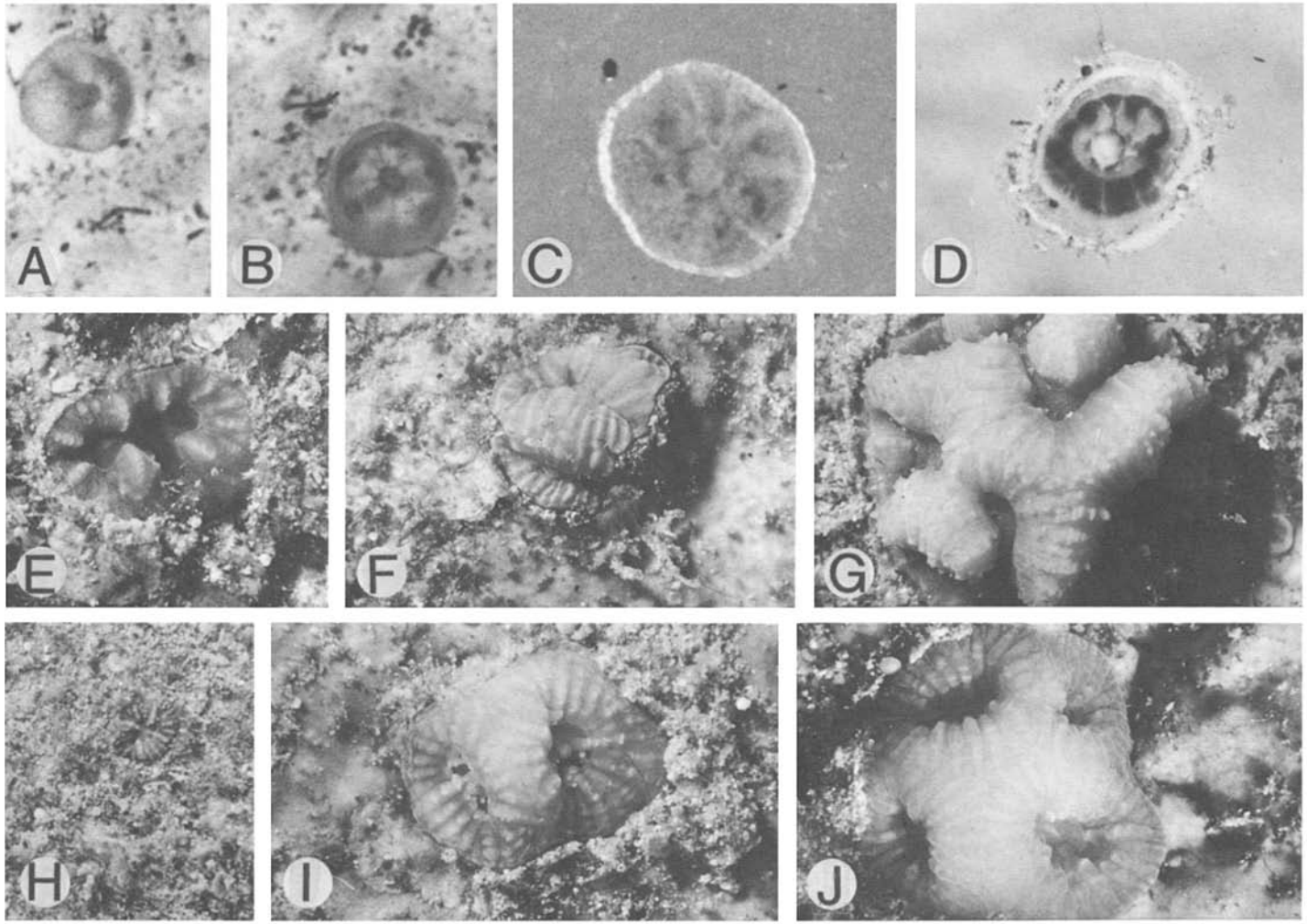

Fig. 2. Development of primary polyp and young colonies of *P. lamellina* (A–G) and *F. favus* (H–J). Measurements are diameters. A) Settlement at edwardsia stage (1 mm); B) Halcampoides stage (1.5 mm); C) Corallite wall formation (epitheca) at 15 d (2 mm); D) Primary polyp with zooxanthellae at 30 d (2 mm); E) Juvenile coral at 10 m (8 mm); F) and G) Young colonies at 3 y (23 mm) and 5 y (40 mm), respectively. H)–J) *F. favus* at 6 m (5 mm), 1 y (10 mm) and 2 y (25 mm).

Table 2. Survivorship of planulae which settled (P) and postlarval stages (PL) of *F. favus* and *P. lamellina*. Survivorship experiments were conducted independently for each age interval. Cumulative survivorship at the end of age interval was calculated since settlement.

Species	Age interval (d)	X	Y	Average survivorship (% ± SD)	Cumulative survivorship (%)
P. lamellina	2–9 (P)	40	8	17.1 ± 6.9	17.1
		120	9		
		63	15		
F. favus	2–9 (P)	60	9	17.6 ± 8.2	17.6
		340	80		
		450	120		
		200	11		
P. lamellina	10–15 (PL)	20	1	10.5 ± 5.5	1.79
		25	4		
F. favus	10–15 (PL)	40	2	11.2 ± 4.9	1.97
		100	17		
		51	6		
P. lamellina	16–30 (PL)	34	9	14.4 ± 10.9	0.25
		20	1		
		250	30		
F. favus	16–30 (PL)	20	1	10.9 ± 7.5	0.21
		48	3		
		320	69		

X = No. of P or PL at beginning of age interval in different experiments
Y = No. of PL at end of age interval in different experiments

Discussion

Little information is available on the larval development of gamete-spawning coral species (Babcock & Heyward, 1986; Heyward *et al.*, 1987) and almost nothing is known of the post-settlement and survivorship rates of their primary polyps (Babcock, 1985). Our observations on larval development of *F. favus* and *P. lamellina* (Table 1) are consistent with other reports for broadcasting coral species (Szmant-Froelich *et al.*, 1980; Kojis & Quinn, 1981; Babcock, 1984). Searching behavior and settlement occur within 6–9 d after spawning. A similar time range has been reported for other broadcasting species (Shlesinger & Loya, 1985; Babcock & Heyward, 1986), although 14–36 d had previously been suggested (Kojis & Quinn, 1981; Babcock, 1984; Harrison *et al.*, 1984). These differences may be due to different culture methods as discussed by Babcock & Heyward (1986).

The planulae of brooding coral species are characterized by the presence of mesenteries and zooxanthellae (Atoda, 1947a, 1947b, 1951; Rinkevich & Loya, 1979). In contrast, the early planulae of spawning species begin life without mesenteries, which are formed in some species only 4 d after spawning (Babcock & Heyward, 1986), or 5–7 d after spawning as in *F. favus* and *P. lamellina* (Table 1). In addition, most of the spawning species lack zooxanthellae in their eggs and planulae (Kojis & Quinn, 1982; Babcock, 1984, 1985; Shlesinger & Loya, 1985; Babcock & Heyward, 1986). Few species are known which spawn eggs containing zooxanthellae (2 *Montipora* species (see Babcock & Heyward, 1986);

and *Pocillopora verrucosa* (Ellis & Solander), pers. observ.). We found that invasion by zooxanthellae occurred only in the primary polyp, 11–19 d after settlement. This was also reported in primary polyps of some other broadcasting species (Babcock & Heyward, 1986; Heyward *et al.*, 1987).

The morphological differences between the planulae of brooding and broadcasting species, in addition to the presence or absence of zooxanthellae may account for the different time periods required for the settlement of brooding species (1–2 d; Fadlallah, 1983) and broadcasting species (4–7 d; Babcock & Heyward, 1986, or 6–10 d; Shlesinger & Loya, 1985).

Vandermeulen & Watabe (1973) and Le Tissier (1988) described the morphology and pattern of development of the skeleton of planulae of *Pocillopora damicornis* (L.). Formation of the skeleton starts with the basal plate and septal rudiments, and continues with the corallite wall and cycles of septa and costae. Le Tissier (1988) points out that although the rate of development of the larval skeleton may vary, complete maximum growth is attained 8 d after settlement.

Brooding species such as *P. damicornis* (see Atoda, 1947a; Vandermeulen & Watabe, 1973) and *Stylophora pistillata* (Esper) (see Atoda, 1947b) produce a complete corallite wall with 24 septa within 1–3 d (Atoda, 1951). Similar development was observed in *Seriatopora hystrix* (Dana) (see Atoda, 1951) and *Seriatopora caliendrum* (Ehrenberg) (see Shlesinger, 1985). Formation of the skeleton in the spawning species *F. favus* and *P. lamellina* is initiated at the basal plate but, in contrast to brooding species, it progresses slowly upwards to establish the circumferential skeleton (epitheca) only. This process forms a calcareous cup still lacking septa. Septal rudiments appear only after the first month of growth. Although considerable variation exists in the degree of skeletal development between spat, it takes about 2 more months to establish a fully developed corallite in these species.

If *F. favus* and *P. lamellina* are typical with regard to the time required for skeletal development of the primary polyp in spawning species, it is evident that this time is 2–3 orders of magnitude slower than in brooding species. Richmond (1982) showed that metabolites are translocated from the zooxanthellae of the planulae of *P. damicornis* to the animal portion of the larva. It is possible that this marked difference in time for skeletal formation is related, at least partially, to the existence of zooxanthellae in the planulae of brooding species.

Factors that affect settlement of planulae and survival of primary polyps are complex and may differ considerably between species. *F. favus* and *P. lamellina* form dense populations in the Gulf of Eilat and are among the most abundant corals in this area (Loya, 1972). Post-settlement survivorship of *P. lamellina* and *F. favus* in Eilat is *ca* 0.2% at 1 m old, i.e., *ca* 99.8% mortality. Babcock (1985) estimated the percent mortality of several coral species between 0–7.8 m old, with a maximum of 94% in *Platygyra sinensis* (Milne Edwards & Haime). At 2.7–9.3 m old, post-settlement mortalities of several species were estimated at 66%–86% (Babcock, 1985).

We estimate that single reproductive colonies (20 cm diam.) of *F. favus* and *P. lamellina* will each contribute 20–25 juvenile colonies (up to 1 m old) to the community per annum. This is based on the estimates that single mature colonies of this size in both species spawn *ca* 130000 oocytes; *ca* 10000 of the eggs develop into mature planulae 2–9 d old (Shlesinger & Loya, in prep.); and *ca* 0.21%–0.25% of the mature planulae settle and reach an age of 1 m old (Table 2). Clearly, additional mortality in different age classes reduces the populations of *F. favus* and *P. lamellina*. Further studies on reproduction, larval development, settlement and survivorship of juvenile colonies of coral species are needed for a better understanding of coral community structures.

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