

SYNCHRONOUS MASS SPAWNING OF *MONTASTRAEA ANNULARIS*
(ELLIS & SOLANDER) AND *MONTASTRAEA FAVEOLATA* (ELLIS &
SOLANDER) (FAVIIDAE: SCLERACTINIA) AT ROSARIO ISLANDS,
CARIBBEAN COAST OF COLOMBIA

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ABSTRACT

Montastraea annularis (Ellis & Solander, 1786) and *Montastraea faveolata* (Ellis & Solander, 1786), two hermaphrodite broadcasting species, are among the most important reef-building corals of the Caribbean. These species have recently been separated, but this separation has been questioned. Spawning of the two species was observed on the Caribbean coast of Colombia in 1997, 6 and 7 d after the full moons from August to October in *M. faveolata* and September to October in *M. annularis*. During three different nights in which mass spawning was observed, including the major event in September (approximately 90% of all colonies spawned), these species were synchronous and spawning started 2.5 h after sunset (40–50 min of time span). Additionally, the same spawning behavior was observed once on October 1998. Timing records of 17 colonies in 1998, during the birth stage, indicate that *M. annularis* colonies spawned longer (20:40–21:45) than *M. faveolata* (20:46–21:20). Previous observations and our findings suggest that there is a great predictability in the number of days after full moon and of hours after sunset (6–8 d, 2–4 h), which has been concordant in all the localities. The spawning length, whereas similar, has been variable (minutes to hours) among sites and years. A latent potential for hybridization between *M. annularis* and *M. faveolata*, as well as the variation in synchrony and time span, deserves additional investigation.

Mass spawning is the synchronous release of gametes by colonies of more than one broadcast-spawning coral species (Willis et al., 1985). Synchronous spawning ensures cross-fertilization in marine organisms without copulative mating behavior (Szmant, 1986), but multispecies spawning increases the potential of hybridization in sympatric species (Babcock, 1995; Kenyon, 1997; Szmant et al., 1997). The number of synchronous species, in mass-spawning events, is highly variable according to the geographical sites or biogeographical settings (Richmond and Hunter, 1990; Babcock, 1995). The largest known mass spawning event occurs in the tropical West Pacific Ocean along the Great Barrier Reef; more than a hundred species release gametes synchronously within a period of 5 d, and nearly 30 species spawn during the same night (Harrison et al., 1984; Babcock et al., 1986). In the Caribbean region, multispecies mass spawning has also been observed at several localities (e.g., Wyers et al., 1991; Gittings et al., 1992; Van Veghel, 1993), but with less synchrony and a greater partitioning of spawning periods throughout several months and lunar phases (Richmond and Hunter, 1990). However, there are relatively few studies that document these events by direct observations of several species at different geographical locations. In fact, many of the species-spawning periods have been inferred from the presence or absence of gonads in histological studies (Acosta and Zea, 1997).

Montastraea annularis (Ellis and Solander, 1786), *M. faveolata* (E. & S., 1786) and *M. franksi* (Gregory, 1895), three hermaphroditic broadcasting species, are among the most important reef-building corals of the Caribbean. These species have been recently sepa-

rated as valid (Weil and Knowlton, 1994) but the separation has been questioned by some authors who consider them as part of a polymorphic species complex (Van Veghel and Bak, 1993; Van Veghel, 1994). Spawning observations can be used to identify fertilization barriers (Knowlton et al., 1997) and they have added a new element of controversy to discussion of the *M. annularis* complex. In this paper we report the recurrent and overlapping mass spawning of *M. annularis* and *M. faveolata* at a coral reef in the southern Caribbean.

MATERIALS AND METHODS

STUDY AREA.—The study was carried out at the Isla Grande coral reef, in the Rosario archipelago (Fig. 1) off the Caribbean coast of Colombia (30 km southwest of Cartagena). This archipelago has been a National Natural Park since 1978. The studied area lies in the Intertropical Convergence Zone which is under trade wind influences that alternate from northwest to southeast. The annual average for seawater temperature, precipitation, and salinity are 27.5°C, 1013.1 mm, and 35‰, respectively (Sánchez, 1995). Tidal variation along the Caribbean coast of Colombia is semi-diurnal with a short range between 17 and 58 cm. The area chosen for spawning observations (10°11'04"N, 75°43'51"W; Fig. 1) is part of an 11 km fringing reef complex. Seaward, there is a sinuous fore-reef

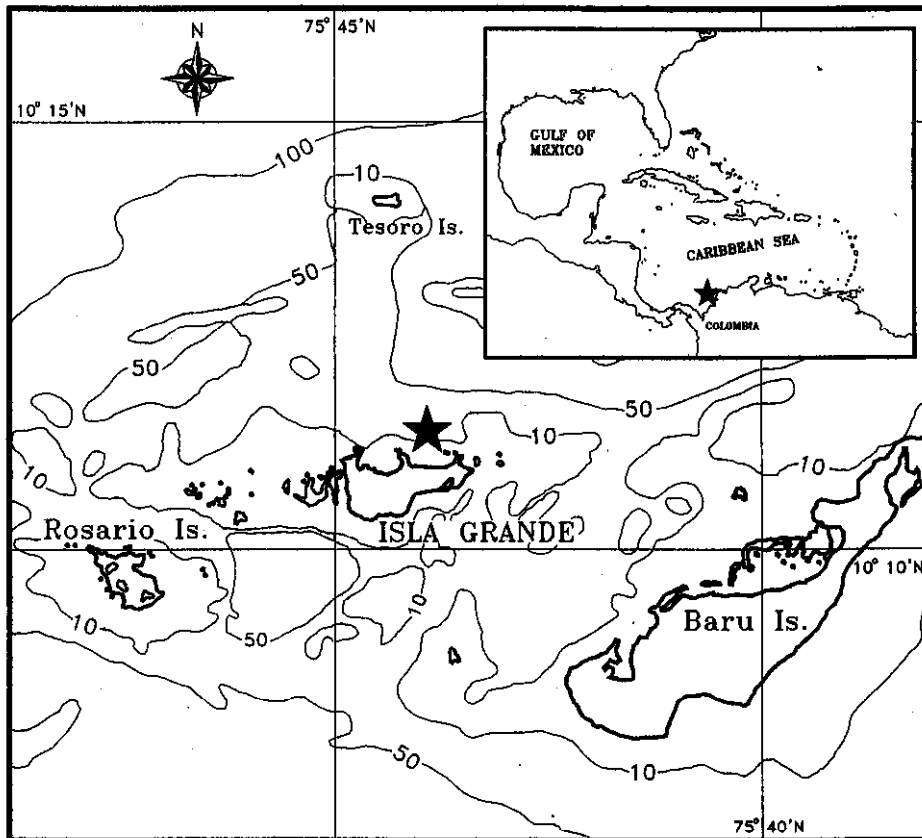


Figure 1. Rosario Islands (Caribbean coast of Colombia) showing the location of Isla Grande and the position of the spawning observations (stars).

terrace (50–200 m width) with dead *Acropora palmata* or *A. cervicornis* stands. The fore-reef terrace is irregularly crossed by a mid-depth (8–14 m) mixed coral zone, which contains numerous large massive corals (*M. annularis*, *M. faveolata*, and *Colpophyllia natans*) and coralline sand on the bottom.

A 150 m-long transect yellow polypropylene line was placed in this zone between 7 and 12 m in depth to guide nocturnal observations. Along the line, 96 colonies (genets recognized by skeletal coherence) of *M. annularis*, 74 of *M. faveolata*, 32 of *M. franksi* (mostly small colonies), and 12 of *M. cavernosa* were counted.

FIELD OBSERVATIONS.—Following the predictions by Szmant (1991), Van Veghel (1993), and Van Veghel (1994) on spawning of the *M. annularis* species complex, field observations took place during 5 to 7 d after the full moon of August, September and October 1997. Colonies were observed between 20:00 (or 1.5 to 2 h after sunset according to the month) and 23:00, except on nights with bad sea conditions. Diver pairs observed colonies 3 m away of each transect side, and additionally, HI8 video (Sony™) and underwater photographs (Nikon™ N90 and Ikelite™) were taken to detail the spawning behavior. Observations were made simultaneously by diver pairs along each side of the line in order to increase the surveyed area. Some eggs of *M. annularis* were collected during spawning and fixed in formalin (5% in seawater) in order to determine their sizes. *M. franksi*, the third sibling species of the “*annularis* complex”, has been previously observed spawning earlier than *M. annularis* and *M. faveolata* (Szmant et al., 1997; Knowlton et al., 1997; Knowlton and Van Veghel, pers. comm.). It is important to note that on the sampled site there was not an abundant population of *M. franksi*; at these islands it is more abundant in deeper water, down to 30 m on the slope (Sánchez, 1995). Therefore, our observations were focused mainly on *M. annularis* and *M. faveolata*.

RESULTS

Spawning of the two species was observed in 1997, 6 and 7 d after the full moons from August to October in *M. faveolata* and September to October in *M. annularis* (Table 1, Fig. 2). During three different nights in which mass spawning was observed in both species, including the major event in September (approximately 90% of all colonies spawned), these species were completely synchronous, and the estimated percentage of spawning colonies of each species was similar at each month (5–95%: Table 1). Spawning started

Table 1. Spawning by *Montastraea faveolata* and *Montastraea annularis* in 1997 along a 150 × 6-m line transect at Isla Grande, Colombia.

	August	September		October
Dates ^a	24	22	23	21
Days after full moon	6	6	7	6
Hours after sunset	3	2.5	2.5	2.7
Spawning time period ^b	21:40–22:25	21:00–21:50	21:15–22:00	21:00–21:40
<i>Montastraea faveolata</i>				
Colonies (%) ^c	10	90	20	5
<i>Montastraea annularis</i>				
Colonies (%)	–	95	35	5

^a On the 5th day after full moon spawning was never observed; on the 7th day after the full moons of August and October it was impossible to work due bad sea conditions; observations stopped after 7th day.

^b From appearance of egg-sperm bundles in polyps until their release.

^c Percentage (%) of colonies was visually estimated on the previously counted colonies in consensus among divers.

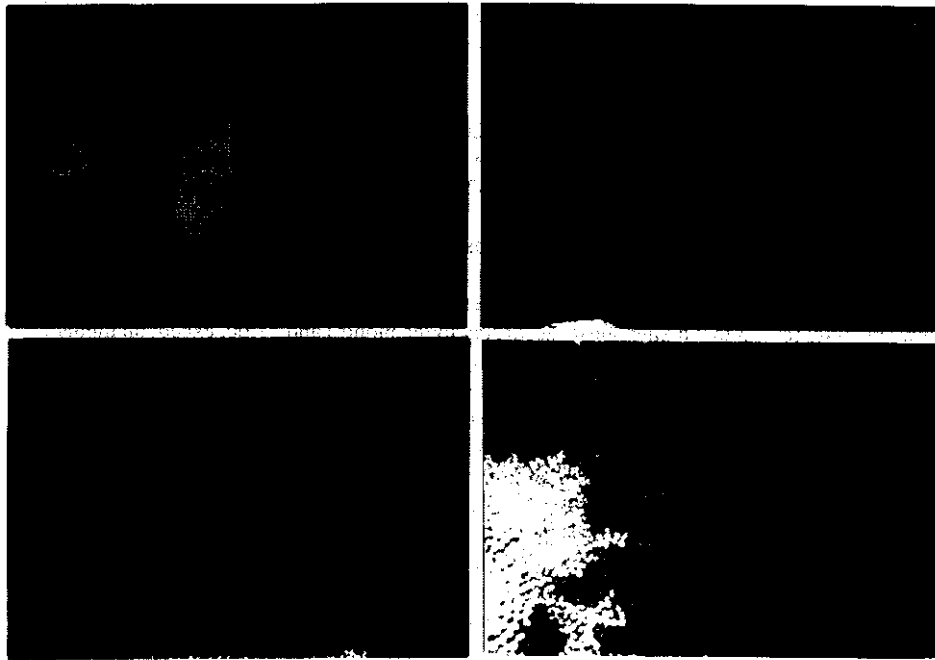


Figure 2. *Montastraea annularis* (A–B) and *M. faveolata* (C–D) during synchronous mass spawning at Isla Grande, Rosario Islands (Caribbean coast of Colombia, 22 September 1997). Photographs were taken a few seconds before (A and C) and after (B and D) the birth stage.

ca 2.5 h after sunset and lasted approximately 40–50 min. Spawning behavior was highly consistent with the observations of Van Veghel (1994) except for some details during the gliding stage noted in videos; bundles in *M. annularis* moved upward more rapidly than in *M. faveolata* (Fig. 2). *M. faveolata* bundles seemed to show some cohesion which prevented a quick separation from the mother colony. Although the setting stage was simultaneous in many colonies, birth and gliding stages started in a few colonies (or ramets) and then slowly began among neighboring colonies. During the major event in September, copious spawning resulted in spawning slicks (egg-sperm bundles white to pink in color) mixed in the surface, that formed rows parallel to the wind direction, which finally dissolved. Almost all polyps of even small ramets of *M. annularis*, both from the top and side of colony, spawned bundles (Fig. 2A,B). When colonies had regenerating polyps or recent injuries from grazing, only uninjured polyps spawned. Among *M. faveolata*, just one or two rows of marginal polyps did not clearly spawn bundles (Fig. 2C,D), while in *M. annularis* most of the marginal polyps spawned. Eggs taken directly from a ramet of *M. annularis* and fixed immediately after the dive, had a mean size of 321.7 μm after fixation (± 13.52 SD). Although our observations were primarily focused on these two species of *Montastraea*, other species were also inspected. Two male genets of *M. cavernosa* (3 and 2 ramets each) were observed releasing sperm (24 August, 20:45–21:00 and 22:30–22:50, respectively) and one of them was simultaneous with *M. faveolata*. The few *M. franksi* colonies at the site were never observed spawning at the times of our observations (always after 20:00 or 1.5–2 h after sunset). Although, we did not tag the colonies that spawned, using some spatial features along the transect we did note that

some colonies spawned at least during two consecutive months (August–September in *M. faveolata* and September–October in *M. annularis*).

During 1998 one of us (M. F. G.) observed the same spawning behavior of *M. annularis* and *M. faveolata* along the sampling transect (11 October starting ca 2.5 h after sunset). Timing records of 17 colonies spread along the transect, during the birth stage, indicate that *M. annularis* colonies spawned longer (20:40–21:45) than *M. faveolata* (20:46–21:20).

DISCUSSION

At Rosario Islands *M. annularis* and *M. faveolata* colonies spawned at similar times, a similar percentage of colonies of each spawned, and each spawned with similar intensity during the mass spawning events of 1997 and 1998. These species also have overlapping spawning in Panama (Knowlton et al., 1997) and Curaçao (Van Veghel, 1994). This suggests that *M. annularis* and *M. faveolata* spawn synchronously and, considering that they are sibling species (Knowlton et al., 1992; Weil and Knowlton, 1994), there is potential for hybridization among them. Although there is considerable evidence that support splitting the *M. annularis* species complex (Knowlton et al., 1992; Weil and Knowlton 1994; Lopez et al., 1999), other data and/or interpretations suggest it is one polymorphic species (Van Veghel and Bak, 1993; Van Veghel, 1993). For instance, Nei's unbiased genetic distance between *M. annularis* and *M. faveolata* is 0.24 in Panama (Knowlton et al., 1992) and about 0.13–0.16 in Curaçao (Van Veghel and Bak, 1993). Recently, Lopez et al. (1999) have found fixed differences between *M. annularis* and *M. faveolata*, from Panama, using more accurate DNA markers (AFLPs).

Despite their overlapping spawning events, it does not necessarily follow that interspecific fertilization occurs under natural conditions. In some free spawning marine invertebrates, species-specific gamete-binding protein receptors act as a fertilization barrier (Lessios and Cunningham, 1990; Vaquier and Lee, 1993; Metz and Palumbi, 1996). Reciprocal inter- and intra-specific crosses among gametes of the *M. annularis* complex have demonstrated inconstant hybridization potential among them (Knowlton et al., 1997; Szmant et al., 1997). Although, no clear evidence is available documenting *Montastraea* hybrids in the natural environment, there are individuals that are very hard to identify (i.e., Szmant et al., 1997). Similarly, there has been experimental evidence of multiple crosses among sympatric morphs of the Indo-Pacific corals genus *Platygyra*, which also overlap in their spawning timing in their natural environment (Miller and Babcock, 1997).

Across their species range and over time, there are differences in the monthly spawning periods of *M. annularis* and *M. faveolata*. These species have spawning periods that might vary from 3 to 5 mo each year along their geographical range. Spawning occurs between July and September in Northern latitudes ($>18^{\circ}\text{N}$: Gittings et al. 1992; Szmant 1986, 1991; Wyers et al. 1991; Szmant et al. 1997), and between August and November in the tropical Southwestern Caribbean ($9\text{--}18^{\circ}\text{N}$: Van Veghel, 1993, 1994; Knowlton et al., 1997; this paper). Van Veghel (1994) suggested the variation might reflect the difference in the moment of maximum sea water temperature in the wider Caribbean in relation to latitude, which triggers the initiation of the gametogenic cycle. He also remarked on the great predictability of spawning in the number of days after full moon and of hours after sunset (6–8 d; 2–3 h), which has been partially concordant in all the localities (i.e., Colombia 2.5–3.5 h vs Panama 3.5–4.5 h after sunset). Colombian Caribbean seawater temperature

and spawning periods have a similar course of variation as Curaçao. During 1984–1996, the temperature increased by March–April, decreased slightly during August, and exhibited the highest mean values in October and November (28.8° and 29.7°C, respectively; IDEAM, Colombia, Rosario Islands station). Less predictable variables have been the proportion and time span of spawning colonies of each species during each month. In August of 1997, colonies of *M. faveolata* spawned while *M. annularis* did not, and Knowlton et al. (1997) have made similar observations in Central America. The spawning time span, although similar, also varies different among sites. Mass spawning events seem to occur synchronously in both species (Van Veghel, 1994; this paper), but sometimes *M. faveolata* spawns earlier than *M. annularis* (Knowlton et al., 1997). We observed that spawning seemed to start contagiously between neighboring colonies. It would be interesting to see if the variation in synchrony or even time span might be related to some characteristics of local populations such as density and/or habitat setting. The latent potential for hybridization between *M. annularis* and *M. faveolata* deserves additional investigation.

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