

Primary Research Paper

## Coral mass- and split-spawning at a coastal and an offshore Venezuelan reefs, southern Caribbean

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### Abstract

This study aimed to evaluate potential differences in coral spawning behavior between a fringing coastal reef and an offshore reef in the southern Caribbean. For this, scleractinian and gorgonian colonies ( $N = 324$ ) of 21 species were mapped along eight transects, each 10-m long, at two study sites located in Morrocoy and Los Roques National Parks, Venezuela. Observations were made between 19:30 and 23:00 from August 23 to 30 and from September 26 to 30, 2002. Ninety one colonies belonging to six hard coral and seven octocoral species spawned or planulated during this period. We were unable to observe any signs of reproductive activity in 95 colonies of nine species different from those that reproduced. Despite the differences in environmental conditions between the two sites, we observed high synchrony in the spawning behavior of seven coral species common to both reefs. The most striking result was the ability of colonies of *Montastraea faveolata* and *Eusmilia fastigiata* to split spawn up to three times, either in consecutive nights or in different months.

### Introduction

In the Caribbean, the timing of coral reproduction is relatively well known for the commonest species. The spatial and temporal variability of their reproductive activity, however, is relatively less well established. Differences in spawning time were observed for *Montastraea franski* and *Montastraea faveolata*, between continental fringing reefs of Honduras and laboratory observations at insular reefs of Panama (Knowlton et al., 1997). Moreover, in the Great Barrier Reef (GBR, Australia), corals on inshore reefs spawn 1 month earlier than those on offshore reefs and this phenomenon is associated with the more rapid seasonal warming

of the shallower waters (Willis et al., 1985). Nevertheless, there are no comparative *in situ* studies between corals of inshore and offshore reefs within the same spawning season for the Caribbean.

The influence of the proximity to land may go beyond a difference in temperature between inshore and offshore reefs and it may include differences in disturbance. For instance, in 1996 a mass mortality event affected the largest coastal fringing reef of Venezuela, at Morrocoy National Park, while no consequences were detected on coral reefs of the Archipelago of Los Roques National Park, located 160 km from the mainland. In addition to long-term anthropogenic disturbances (e.g. Bone et al., 1993), during the 1996

event, coral cover in Morrocoy was reduced by 60–98% (Villamizar, 2000; Laboy-Nieves et al., 2001). Due to the lack of data for Los Roques, it is impossible to assess whether there is a significant difference in water temperature between these two localities, but their geography suggests that it may be the case. Sand keys at Morrocoy are <5 km from the mainland and form a network of shallow channels with a maximum depth of 20 m. By contrast, the Archipelago of Los Roques is on the top of an underwater mountain, surrounded by deep waters down to 1000 m, and is under the influence of oceanic currents (Méndez, 2002).

To evaluate differences in coral spawning behavior between an inshore and an offshore reef, we monitored coral colonies in two separate months during the 2002 spawning season. We report spawning times of six species of scleractinians and seven of gorgonians and made observations of split spawning within single colonies.

### Materials and methods

Corals were monitored in four transects at each of two study sites: Cayo Sombrero in Morrocoy (10°52' N, 68°16' W) and Dos Mosquises Sur in Archipelago of Los Roques (11°50'N, 65°45' W). Transects were established at 4–10-m depth, each transect being 10-m long and 2-m wide. Colonies of soft and hard corals were identified and mapped within the transects; outside the transects, we observed 33 unmapped colonies of species that were absent in the transects or that were observed spawning by chance.

Two groups of two divers took turns observing the corals between the hours of 19:30 and 23:00, from August 23 to 30 and from September 26 to 30, 2002. Our first day of recording was +2 days after the full moon of August and +5 in September. This timing was established according to previous records of coral spawning in the Caribbean.

### Results

Forty percent, or 91 out of 229 of colonies belonging to 13 species of hard and soft corals spawned or planulated at both localities (Table 1). Despite a smaller observation effort in September

than in August, 67% of these 91 colonies were observed spawning in September. No reproductive activity was observed in another eight hard coral and one octocoral species that comprised 95 colonies (Table 2). It is possible that some of the species in Table 2 spawned earlier than our first day of observation, as mature size bundles were present in *Acropora palmata* in July at Los Roques; or later in the year, as *Montastraea cavernosa* spawned in October at Curacao (27/10/02 = +6 after full moon; 2 female and 1 male colony; C. Bastidas and A. Cróquer, personal observations).

Seven of the 13 species that spawned were common to both study sites, spawning at similar times and dates (Table 1). In particular, *Montastraea annularis* (Ellis & Solander, 1786) and *M. faveolata*, for which the number of colonies observed was relatively large, displayed very similar timing. Furthermore, at both locations, these two species overlapped in spawning hours (Table 1). Despite these similarities, differences between the two localities occurred in August, when *M. annularis* spawned only at Los Roques and *Colpophyllia natans* (Houttuyn, 1772) spawned only at Morrocoy (Fig. 1a). We were unable to assess the spawning of *M. franski* at Los Roques in September, since bad weather prevented us from diving on the 7th night after the full moon, when spawning of this species occurred at Morrocoy. Furthermore, *Diploria strigosa* spawned more than an hour earlier in Morrocoy than in Los Roques. Octocoral species also showed this pattern (Table 1), but data are limited as only a few colonies were observed.

Split-spawning was observed in eight colonies of *M. faveolata*. One colony spawned three times (once in August and on two consecutive nights in September), and another seven colonies spawned twice: four colonies spawned once each month; one, in two consecutive nights of August; and two, in two consecutive nights of September. The *M. faveolata* colonies that spawned twice in a month did it so earlier during the second night.

Two colonies of *Eusmilia fastigiata* (Pallas, 1766) also showed split reproduction at Morrocoy. Gametes or zygotes were noticed at the tip of tentacles, as reported by de Graaf et al. (1999), the 7th night after the full moon of August at 22:50 h, and were released the 8th night by 20:00. In Sep-

Table 1. Number of colonies (left), spawning dates and hours (right) of corals at Morrocoy (M – solid line) and Los Roques (LR – dashed line) during August (A) and September (S) 2002

Species	No. colonies spawning/total observed colonies		
	M	LR	
<i>Montastraea faveolata</i>	30/44	10/48	
<i>Montastraea annularis</i>	4/10	5 + 2u/8 + 2u	A6,7; S6,7 A6,7; S6
<i>Montastraea franski</i>	5/8	0/1	S7 A6,7; S6
<i>Diploria strigosa</i>	4/14	1/8	S7
<i>Colpophyllia natans</i>	1/33	0/10	S7 S6
<i>Eusmilia fastigiata</i>	2u/3u	0/0	A8
<i>Pseudoplexaura</i> sp.	3 + 7u/4 + 7u	1/1	see text
<i>Plexaura flexuosa</i>	6u/6u	1/5	A6,7; S6,7 A7; S6
<i>Plexaura homomalla</i>	1u/2 + 1u	2/7	A6,7; S6,7 A7
<i>Eunicea calyculata</i>	1u/1u	0/0	A6,7 A6
<i>Eunicea tourneforti</i>	1u/1u	0/0	S7 S8
<i>Plexaurella</i> sp.	0/0	1u/1u	
<i>Pseudopterogorgia americana</i>	2u/2u	1u/1 + 1u	A6,7,8 A7,8
Total	67/136	24/95	

u – unmapped colonies. Scale at bottom right indicates hours. Letters and numbers above the lines indicate month and nights after the full moon, respectively. No line indicates either that the species was absent from the locality or that it was not observed spawning. Observations were not possible in LR on A8 and S7.

Table 2. Number of colonies of coral species that did not spawn at the reef localities of Los Roques (LR) and Morrocoy (M) during August and September 2002

Species	M	LR
<i>Acropora palmata</i> (Lamarck, 1816)	0	12
<i>Stephanocoenia intersepta</i> (Esper, 1795)	1 + 8u	0
<i>Madracis mirabilis</i> (Duchassaing & Michelotti, 1861)	14	17
<i>Montastraea cavernosa</i> (Linnaeus, 1766)	19	2
<i>Diploria labyrinthiformis</i> (Linnaeus, 1758)	2	3
<i>Meandrina meandrites</i> (Linnaeus, 1758)	2	0
<i>Siderastrea siderea</i> (Ellis & Solander, 1786)	10	2
<i>Dendrogyra cylindrus</i> (Ehrenberg, 1834)	0	1
<i>Gorgonia ventalina</i> (Linnaeus, 1758)	0	2
Total	56	39

Zero indicates that the species was absent from the mapped zone at that locality; u – unmapped colonies. For *M. mirabilis*, numbers are patches up to 3 m<sup>2</sup> each.

tember, these same two colonies again showed zygotes; first noticed at 20:15 on the 7th and still visible at 22:15 on the 8th night after full moon, our last day of observation.

In colonies of *M. faveolata*, *M. annularis*, and *M. franski*, spawning occurred in patches (Fig. 1b), taking up to 20 min for a single colony to spawn. Contrasting with this relatively short period of spawning for hard coral species, octocorals seemed to released their gametes slowly but continuously over several hours (Table 1, Fig. 1c).

Only at Morrocoy were abundant swarms of bioluminescent polychaetes of the genus *Odontosyllis* (Claparede, 1863) observed spawning at the water surface between 19:30 and 20:00, both in August and at lower densities in September. Furthermore, the polychaete *Hermodice carunculata* (Pallas, 1766) was commonly seen preying on corals only at this locality.

## Discussion

In contrast to coral spawning observations in the Great Barrier Reef (Australia), where corals on inshore reefs spawn one month earlier than those on offshore reefs (Willis et al., 1985), there were similar spawning dates for the seven species

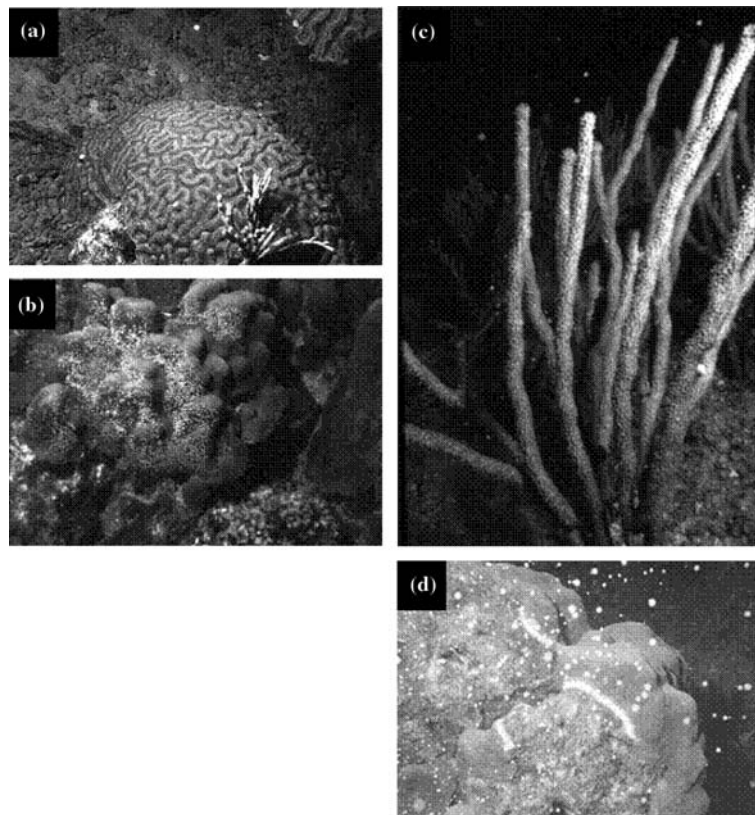


Figure 1. (a) *Colpophyllia natans* releasing bundles (Morrocoy Aug-02). (b) Patchy release of bundles in *Montastraea faveolata* (Morrocoy, Aug-02). (c) Spawning of *Eunicea tourneforti* (Morrocoy, Sep-02). (d) Spawning of *Montastraea faveolata* affected with yellow blotch (Morrocoy, Sep-02).

common to both coastal and offshore Venezuelan localities. The similarity in spawning dates and times for these species between localities suggested that the surviving colonies after the 1996 mortality event in Morrocoy are reproductively active. Egg size ranges of the different species were very similar to those found in the literature, when available, except for *Diploria strigosa* (Dana, 1846), the egg diameters (640–780  $\mu\text{m}$ ) of which were almost double those reported by Szmant (1986) and Wyers (1985). Even colonies affected by yellow blotch syndrome were able to spawn in Morrocoy (Fig. 1d). Furthermore, rough estimates of *in situ* fertilization rate using mesh bags on four colonies of *M. faveolata* at Morrocoy were relatively high (37–80%) compared with similar studies (Oliver & Babcock, 1992; Lasker et al., 1996); and fecundity (3.4–98.2 eggs/cm<sup>2</sup>) was in the lower limit of previous results (Szmant, 1991; van Veghel, 1994). However, preliminary analyses of egg and larva

concentrations in the surface waters of Morrocoy were one tenth of those in Los Roques (Bastidas, unpublished data). It remains to be investigated whether this difference is consistent through time, and if it is related to lower fecundity of colonies, lower coral cover and/or to smaller total area covered by reefs at Morrocoy.

Spawning times for *M. faveolata*, *M. annularis* and *M. franski* in Venezuela were very similar to previous reports for most localities in the Caribbean (Szmant, 1991; Wyers et al., 1991; Knowlton et al., 1997; Szmant et al., 1997; Sanchez et al., 1999). However, we observed timing differences in the spawning of *M. franski* and the other two species, which contrast with the absence thereof at Curaçao (van Veghel, 1994).

The August spawning observed in this study has been considered relatively rare in the southern Caribbean, where species are expected to spawn mostly in September and October (van Veghel,

1993, 1994; Sanchez et al., 1999; Mendes & Woodley, 2002). In contrast, the northern Caribbean, including Florida and Bermuda, have spawning events earlier in the year, mostly in July and August (Wyers et al., 1991; Szmant et al., 1997; Hagman et al., 1998; although see Gittings et al., 1992). Spawning of *M. faveolata* colonies during August and September support the idea that the spawning in August may occur occasionally in the Southern Caribbean, and that split spawning can occur not only for the population but also as an individual strategy, as it has been suggested by Willis et al. (1985) for other genera. Split spawning, or spawning over consecutive moon cycles has been associated with an early full moon during the peak of the gametogenesis (Willis et al., 1985), and may constitute a strategy to minimize the effects of a catastrophic event over a single reproductive event (Richmond & Hunter, 1990). Mostly, split spawning in *Montastraea* spp. has been considered a population strategy based on histological studies (Szmant, 1991; van Veghel, 1994; Mendes & Woodley, 2002) and direct observations (Sánchez et al., 1999). Further studies should focus on determining the extent to which split spawning could serve as a strategy to reduce the risk of failure in a single spawning at both the individual and the population levels.

Information on the spawning behavior of cnidarians other than scleractinians is scarce. Nevertheless, other organisms such as octocorals may largely contribute to the total mass of spawned eggs. This is likely the case in our study sites, given the cover of octocorals species in these reefs (10–20%), and their long lapse of spawning. For example, a single colony of *Plexaura homomalla* released gametes for up to 2 h, in clear contrast with the hard corals, for which a single colony spawned for a maximum of 20 min. Reports on plexaurids at localities with similar sunset hours suggest that spawning in this study may have started earlier than our first observations: in Curacao, *Plexaura* sp. at 18:55 (van Veghel, 1993); in Panama, *Pseudoplexaura porosa* (Houttuyn, 1772) at 18:15–20:15 (Kapela & Lasker, 1999), and *Plexaura kuna* (Lasker, Kim & Coffroth, 1996) at 18:30–18:50 (Brazeau & Lasker, 1989). Nevertheless, our observations suggest that some plexaurids may extend their reproductive activity until much later than has previously been reported.

As for hard corals, regional differences occur in spawning months for octocoral species. Histological studies of *Plexaura homomalla* and *P. flexuosa* from Florida indicated a peak of reproductive activity in June and July (Fitzsimmons-Sosa et al., 2004), whereas these species spawned in August and September at both Venezuelan localities. Moreover, *Pseudopterogorgia americana* apparently spawned in October and/or November in Florida (Fitzsimmons-Sosa et al., 2004), whereas our observations suggest that this species may start spawning earlier in the southern Caribbean.

### Conclusions

In this study we have reported the spawning behavior of thirteen hard coral and octocoral species of Venezuelan reefs. We found similar patterns of spawning among the seven coral species that were common to a coastal reef and an offshore island reef. Individual colonies of *Montastraea faveolata* were able to spawn more than once either on consecutive nights of the same month or in different months; and the monitored population of this species was able to split-spawn in August and in September during the 2002 event.

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