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NOTE

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Deepwater broadcast spawning by *Montastraea cavernosa*, *Montastraea franksi*, and *Diploria strigosa* at the Flower Garden Banks, Gulf of Mexico

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Abstract Broadcast spawning by corals is a tightly synchronized process characterized by co-ordinated gamete release within 30–60 min time windows once per year. In shallow water corals, annual water temperature cycles set the month, lunar periodicity the day, and sunset time the hour of spawning. This tight temporal regulation is critical for achieving high fertilization rates in a pelagic environment. Given the differences in light and temperature that occur with depth and the importance of these parameters in regulating spawn timing, it has been unclear whether deeper coral can respond to the same environmental cues that regulate spawning behaviour in shallower coral. In this report, a remotely operated vehicle was used to monitor coral spawning activity at the Flower Garden Banks at depths from 33 to 45 m. Three species *Montastraea cavernosa*, *Montastraea franksi*, and *Diploria strigosa* were documented spawning within this depth range. All recorded spawning events were within the same temporal windows as shallower conspecifics. These data indicate that deep corals at this location either sense the same environmental parameters, despite local attenuation, or communicate with shallower colonies that can sense such spawning cues.

Keywords Broadcast spawning · Reproductive strategies · Reef building · Mass spawning

Introduction

The mass spawning of coral at the Flower Garden Banks in the northwest Gulf of Mexico has been studied for over a decade (e.g. Gittings et al. 1992). Peak broadcast spawning is observed on the 7th and 8th evenings after the August full moon, and precise spawning windows have been defined for many species on these and adjacent evenings. The shallowest point on these reefs is approximately 15 m below sea level while the deepest point of coral growth is at approximately 43 m, where the reef meets extensive sand flats. *Montastraea cavernosa*, *Montastraea franksi*, and *Diploria strigosa* are three of the most common corals at the Flower Garden Banks, covering between them 31% of the reef (Gittings 1998; Pattengill-Semmens et al. 2000).

Coral spawning at the Flower Garden Banks is extremely consistent from year to year. On the peak spawning night six different species of hard coral broadcast spawn, along with a variety of other animals including sponges, worms, and brittle stars (Bright 1991; Gittings et al. 1992; Hagman et al. 1998a; Hagman and Vize 2003). The timing of broadcast spawning in the six major species of coral is predictable to within a few minutes from year to year (Vize et al. 2005). The timing of spawning is very similar to that at Caribbean reef sites, which were recently reviewed by Levitan et al. (2004).

Most coral spawning reports describe spawning activity at shallow depths of less than 10 m and there are no previous reports of spawning at depths below 30 m. Below 30 m, water temperature and light intensity are very different and corals adapt to these different conditions in a variety of ways (e.g. Brakel 1983; Gattuso et al. 1993). In this report a remotely operated vehicle was used to document spawning activity at the deepest part of the Flower Garden Banks reef. Both sexes of *M. cavernosa* and hermaphroditic *M. franksi* and *D. strigosa* were observed spawning at depths below 33 m on the 7th evening after the August full moon in the 1999 season. The timing of spawning activity was consistent with that on the reef cap at a depth of 20 m and at other Caribbean sites at even shallower depths. These observations indicate that despite very different local environments, deepwater corals broadcast spawn in synchrony with shallower corals.

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Results and conclusions

An S2 Phantom remote operated vehicle (ROV) equipped with an S-video camera and depth sensor was used to document spawning behaviour on the evening of September 2, 1999—seven evenings following the full moon of August 26. Sunset was at 19:34 h. At the Flower Garden Banks (FGB: latitude 27°59′, longitude 93°35′) the average time window for *M. cavernosa* mass broadcast spawning is 1:01–1:31 h post-sunset for males, 1:27–1:56 h post-sunset for females, for *M. franksi* 1:51–2:20 h post-sunset, and for *D. strigosa* 1:29–2:29 h post-sunset (Hagman et al. 1998a, b; Vize et al. 2005). The ROV was used to document the initiation of normal mass spawning on the reef cap by male *M. cavernosa* colonies at approximately 18 m depth beginning at 20:30 h. The ROV was briefly surfaced for technical adjustments and then flown to the base of the reef, reaching bottom at 21:15 h. Video was continuously recorded over the following 45 min at depths ranging from 33 to 42 m.

Six individual colonies were recorded spawning and unequivocally identified (Table 1). Video footage of spawning by three of these colonies has been posted online and can be viewed at http://www.xenbase.org/coral. Many additional colonies out of range of the video camera were also spawning, as evident from the large number of gamete packets drifting into the video field of view. Table 1 documents each of the recorded spawning events and lists time, depth, and comparison to FGB shallower water corals. The deepest recorded spawner was *M. cavernosa* at the deepest point of this part of the reef at 42 m. Each of the three species that spawns in this temporal window was recorded spawning at depths below 33 m.

Villinski (2003) recently compared a wide range of reproductive characteristics of a broadcast spawner, *Montastraea faveolata*, at two depths, 3 and 18 m. Villinski's data set showed similar fecundity, gamete size, and total lipid investment in gametogenesis at both depths. However, studies on two brooding corals, *Acropora palifera* and *Stylophora pistilata* observed that smaller numbers of planulae were produced at greater depths (Kojis and Quinn 1984; Rinkevich and Loya 1987). The lower numbers may be due to indirect effects of depth such as colony polyp density and may not be an accurate reflection of reproductive activity by individual polyps. Villinski (2003) found that colonies spawned at a depth of 18 m, but this was inferred from the absence of gametes in histological sections rather than by directly observing broadcast spawning behaviour and it is not known if this spawning was in synchrony with shallower coral.

The data presented in Table 1 indicate that spawning behaviour in two *Montastraea* species is similar between depths of 16 and 42 m and in *D. strigosa* between 16 and 33 m. All spawning events in the present study recorded below 33 m in depth were within the temporal windows identified for each species on the reef cap (Vize et al. 2005). These times were also within those reported at shallower depths for Caribbean sites. Examples include Bocas del Toro (1–12 m), Curaçao (13–17 m), San Blas islands (5–15 m), and Venezuela (4–10 m) (Levitan et al. 2004; Bastidas et al. 2005).

Although no quantitative data on gamete numbers in deepwater spawning is available from the video we recorded (see http://www.xenbase.org/coral), qualitatively gamete release was very robust and similar to hundreds of other releases documented at shallower depths at the Flower Garden Banks. One *M. franksi* colony at a depth of 39 m was observed to release many thousands of gamete packets. In a second *M. franksi* colony at a depth of 34 m, every visible polyp in the field of view released a gamete packet.

Despite the differences that exist between depths in terms of both light and temperature, and the well-characterized responses of corals to these factors (e.g. Brakel 1983; Gattuso et al. 1993), the data presented here indicate that in behavioural terms deep colonies participate in mass spawning events synchronously with shallower colonies, maximizing their likelihood of reproductive success. As light plays a central role in setting both the evening of spawning and the hour of spawn release in shallow water coral, deep coral must either be able to sense the same lunar and solar light cues (Harrison et al. 1984; Oliver et al. 1988; Jokiel et al. 1995; Levitan et al. 2004), or it may be that there is some other relationship between the behaviour of the shallow water corals and those at depth. Further observations of deepwater coral, especially in locations

Table 1 Deepwater coral spawning times at Flower Garden Banks. The spawning times for shallow water corals (16–20 m) at the same site are given for comparison. Calculation of shallow water spawn timing averages represent the average onset and cessation times over multiple seasons, while the range represents the earliest and latest events observed at this locale (Vize et al. 2005)

Species, sex	Deepwater spawning			Shallow water spawning (hours post-sunset)	
	Depth (m)	Time of spawning (h)	Hours post-sunset	Average	Range
Montastraea cavernosa, male	42	21:17	1:43	1:01–1:31	0:57–1:44
Montastraea franksi	39	21:19	1:45	1:51–2:20	1:22–2:35
M. cavernosa, male	37	21:20	1:46	1:01–1:31	0:57–2:00
M. cavernosa, female	35	21:25	1:51	1:27–1:56	1:04–2:05
Diploria strigosa	33	21:53	2:19	1:29–2:29	0:48–2:41
M. franksi	34	21:56	2:22	1:51–2:20	1:22–2:35

distant from any shallow water corals, may help further explain the coordination of spawning behaviour in deepwater systems.

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