

Tight Temporal Consistency of Coral Mass Spawning at the Flower Garden Banks, Gulf of Mexico, from 1997–2003

PETER D. VIZE, JOHN A. EMBESI, MIKE NICKELL, D. PAUL BROWN, AND DEREK K. HAGMAN

Mass spawning by the hard corals of the Flower Garden Banks National Marine Sanctuary has been studied for over a decade. In this report we present observations by a single set of experienced observers on spawning events extending over seven years, on spawning activity, lack of activity and coordination within and between species. This compilation shows that the spawning times of each species are extremely consistent during major events, with onset and hiatus often predictable to within seven minutes, and in some species to within two minutes. In addition to the extraordinary degree of temporal regulation, the other striking feature of the spawning schedule is the uniqueness of most spawning windows. With the exception of *Diploria strigosa*, each of the major spawning species—*Colpophyllia natans*, *Montastraea cavernosa*, *M. annularis*, *M. faveolata*, *M. franksi* and *Stephanocoenia intersepta*—has a unique window of time in which it and no other coral species releases gametes. Spawning times for the 2005–2008 seasons are predicted based on these findings.

Introduction.—Many different animals participate in late summer mass spawning events throughout the Caribbean and at the Flower Garden Banks (FGB) including hard corals (Bright, 1991; Gittings et al., 1992; Hagman et al., 1998a), brittle stars (Hagman and Vize, 2003), worms, and sponges (Harrison and Wallace, 1990; Gittings et al., 1992; van Veghel, 1993). Approximately 49% of the FGB reef above 45 m in depth is covered by live hard corals; of this, approximately 37% is *Montastraea franksi*, 13% *Diploria strigosa*, 13% *M. cavernosa*, 9% *M. faveolata*, 6% *Colpophyllia natans* (Gittings, 1998; Pattengill-Semmens et al., 2000), species that participate in the mass spawning described in this study. Less abundant but active mass spawners include *M. annularis* and *Stephanocoenia intersepta*. All but one of the above species spawn on the same night, seven or eight evenings after the August full moon.

The three major environmental factors regulating the timing of coral mass are annual cycling in water temperature, lunar periodicity, and time of sunset (Babcock et al., 1986; Oliver et al., 1988; Harrison and Wallace, 1990; Hagman et al., 1998a). Annual cycles of water temperature are believed to coordinate gonadal maturation, whereas the tight temporal regulation of the spawning event is controlled by the phases of the moon (e.g., Harrison and Wallace, 1990; Knowlton et al., 1997). The timing of mass spawning events by hard corals can be accurately predicted, once the reproductive cycle at any particular local has been linked to the lunar cycle. The same species may spawn

on different evenings and at different times in different locations, and spawn timing can be altered by falsifying sunset time (e.g., Levitan et al., 2004). However, at the same geographical location, species spawn in tight temporal windows irrespective of local variations in temperature, light, and depth, as evidenced by FGB hard corals below 40 m in depth spawning in synchrony with those on the reef cap (P. D. Vize, unpubl.). In general, temperature is proposed to set the month, lunar periodicity the day, and sunset time the hour of spawning activity.

Another potential key regulator of spawning behavior is chemical signaling, but although much circumstantial evidence supports the existence of such a process (e.g., Slattery et al., 1999), no hard data are yet available.

In this study, we describe observations on spawning behavior at the FGB over 7 yr. The presented data were all gathered by three experienced observers who performed extended surveys, rather than compiling larger numbers of reports from multiple divers over shorter survey windows. Also, times were adjusted for local variation in sunset times. The resulting data set demonstrates extraordinary temporal specificity, with most species having onset or cessation of spawning times consistent to within 7 min.

Methods.—Observations were made at either the East or the West bank of the FGB National Marine Sanctuary (NMS), Gulf of Mexico, using SCUBA. East bank mooring buoy 1 is located at latitude 27°54'N, longitude 93°35'W.

TABLE 1. *Montastraea cavernosa* spawning times in hours post sunset.^a

Date	Sunset	NAFM	Survey	Male			Female		
				Earliest	Latest	Number	Earliest	Latest	Number
28 July 1997	20:06	9	1:04–3:06						0
24 Aug. 1997	19:44	7	1:58–3:08						0
25 Aug. 1997	19:42	8	3:10–5:21						0
26 Aug. 1997	19:41	9	52 min						0
27 Aug. 1997	19:40	10	1:03–2:43						0
14 Aug. 1998	19:54	7	2:34–4:38						0
15 Aug. 1998	19:53	8	0:37–2:57						0
16 Aug. 1998	19:52	9	1:38–3:24						0
3 Sep. 1999	19:33	9	0:45–3:29	0:57	1:44	6	1:04	1:52	6
5 Sep. 1999	19:31	11	0:44–2:32						0
21 Aug. 2000	19:46	7	2:16–4:04						0
22 Aug. 2000	19:45	8	1:34–3:11						0
23 Aug. 2000	19:44	9	0:41–1:50						0
9 Aug. 2001	19:58	6	0:32–2:37						0
10 Aug. 2001	19:57	7	0:48–2:56	1:05	1:18	20	1:28	1:52	7
11 Aug. 2001	19:56	8	2:04–3:02						0
9 Sep. 2001	19:26	8	0:49–2:37	1:44	1:49	4	1:49	2:05	5
10 Sep. 2001	19:25	9	1:35–3:41						0
28 Aug. 2002	19:40	7	1:29–3:59						0
29 Aug. 2002	19:38	8	1:12–4:01	?		1			0
30 Aug. 2002	19:37	9	0:36–3:15						0
31 Aug. 2002	19:36	10	0:36–1:27						0
18 Aug. 2003	19:50	7	1:03–3:38	1:26	1:37	4	1:43	1:48	2
19 Aug. 2003	19:49	8	0:42–3:25						0
20 Aug. 2003	19:48	9	0:43–3:22						0

^a NAFM; nights after full moon.

Observation depths ranged from 17 to 22 m, which represent the reef cap at this site. The long bottom times at these depths were achieved using 44% nitrox as the breathing mixture and large-capacity tanks.

Sunset times were calculated for the coordinates of East FGB mooring buoy 1 (see above), using the U.S. Naval Observatory data services (<http://aa.usno.navy.mil>). The FGB time zone is U.S.A. central standard time zone, which is GMT – 6 hr and including local daylight savings time, amounts to GMT – 5 hr. All data time points are expressed in hours and minutes postsunset. Full moon data were also gathered from the U.S. Naval Observatory Web site. The time of the appearance of the full moon was included in the evening calculations, but late or early full moons were not.

Results.—Spawning times were recorded by one or more of the authors using SCUBA. Often, only a single pair of divers were recording at any one time. Spawning times for each of the major species are shown in Tables 1–5. Activity of each species was recorded for each night, even if negative. In the following sections, spawning activity is described for each species

in the order in which activity is observed on the reef.

Montastraea cavernosa males were recorded spawning on five separate evenings during 7 yr (Table 1). When this species spawns, it is the earliest active coral on the FGB reef. In one of the recorded years, only one colony was observed spawning, and the time was not noted, which is represented with a “?” in Table 1. Because only two data sets are available for this species with at least five colonies spawning, these were used in estimating the average spawning window, which is $1:01 \pm 4$ to $1:31 \pm 13$ ($n = 2$). This “five colony” rule is also used in following spawning window estimations where possible, but in each case, the choice of samples or exceptions is justified.

Females of the same species were observed spawning in only 4 of the 24 observation windows of which one evening only had two spawning colonies and was not used in window calculations. The average times for the other three evenings (Table 1) with greater than five spawners were $1:27 \pm 23$ to $1:56 \pm 9$ ($n = 3$).

The next species typically observed to spawn was the brain coral, *D. strigosa* (Table 2). Colonies of this species were observed spawning

TABLE 2. *Diploria strigosa* and *M. franksi* spawning times in hours post sunset.

Date	Sunset	NAFM	Survey	<i>D. strigosa</i>			<i>M. franksi</i>		
				Earliest	Latest	Number	Earliest	Latest	Number
28 July 1997	20:46	9	1:04–3:06			0			0
24 Aug. 1997	19:44	7	1:58–3:08	yes		?	yes		>10
25 Aug. 1997	19:42	8	3:10–5:21			0			0
26 Aug. 1997	19:41	9	52 min	2:01	?	5	yes		>1
27 Aug. 1997	19:40	10	1:03–2:43			0	2:10	2:10	1
14 Aug. 1998	19:54	7	2:34–4:38			0			0
15 Aug. 1998	19:53	8	0:37–2:57	1:22	?	6	2:07	?	6
16 Aug. 1998	19:52	9	1:38–3:24			0			0
3 Sep. 1999	19:33	9	0:45–3:29	1:47	?	>20			0
5 Sep. 1999	19:31	11	0:44–2:32	2:06	2:32	4			0
21 Aug. 2000	19:46	7	2:16–4:04			0			0
22 Aug. 2000	19:45	8	1:34–3:11			0			0
23 Aug. 2000	19:44	9	0:41–1:50			0			0
9 Aug. 2001	19:58	6	0:32–2:37			0	1:47	2:02	>1
10 Aug. 2001	19:57	7	0:48–2:56	<0.48	2:08	>50	1:43	2:13	>50
11 Aug. 2001	19:56	8	2:04–3:02			0	?	2:35	10
9 Sep. 2001	19:26	8	0:49–2:37	1:30	2:34	22	1:49	2:34	>50
10 Sep. 2001	19:25	9	1:35–3:41	1:50	2:41	50	1:52	2:29	50
28 Aug. 2002	19:40	7	1:29–3:59			0	1:50	2:20	20
29 Aug. 2002	19:38	8	1:12–4:01	1:17	2:22	30	1:44	2:27	50
30 Aug. 2002	19:37	9	0:36–3:15	1:03	1:03	1			0
31 Aug. 2002	19:36	10	0:36–1:27			0			0
18 Aug. 2003	19:50	7	1:03–3:38	2:10		2	1:51	2:24	50
19 Aug. 2003	19:49	8	0:42–3:25	1:41	2:41	15	2:23	?	20
20 Aug. 2003	19:48	9	0:43–3:22			0			0

TABLE 3. *Stephanocoenia intersepta* spawning times in hours post sunset.

Date	Sunset	NAFM	Survey	Male			Female		
				Earliest	Latest	Number	Earliest	Latest	Number
28 July 1997	20:06	9	1:04–3:06			0			0
24 Aug. 1997	19:44	7	1:58–3:08			0			0
25 Aug. 1997	19:42	8	3:10–5:21			0			0
26 Aug. 1997	19:41	9	52 min			0			0
27 Aug. 1997	19:40	10	1:03–2:43			0			0
14 Aug. 1998	19:54	7	2:34–4:38	2:36	3:06	5	2:36	3:06	3
15 Aug. 1998	19:53	8	0:37–2:57	2:18	2:18	1			0
16 Aug. 1998	19:52	9	1:38–3:24			0			0
3 Sep. 1999	19:33	9	0:45–3:29			0			0
5 Sep. 1999	19:31	11	0:44–2:32			0			0
21 Aug. 2000	19:46	7	2:16–4:04			0	yes		?
22 Aug. 2000	19:45	8	1:34–3:11			0	yes		?
23 Aug. 2000	19:44	9	0:41–1:50			0			0
9 Aug. 2001	19:58	6	0:32–2:37			0			0
10 Aug. 2001	19:57	7	0:48–2:56			0			0
11 Aug. 2001	19:56	8	2:04–3:02	2:24	2:24	1			1
9 Sep. 2001	19:26	8	0:49–2:37			0			0
10 Sep. 2001	19:25	9	1:35–3:41	2:51	2:58	3	2:52	2:59	3
28 Aug. 2002	19:40	7	1:29–3:59			0			0
29 Aug. 2002	19:38	8	1:12–4:01	2:41	2:57	10	2:52	2:59	3
30 Aug. 2002	19:37	9	0:36–3:15	2:23	2:53	12	2:43	2:53	2
31 Aug. 2002	19:36	10	0:36–1:27			0			0
18 Aug. 2003	19:50	7	1:03–3:38	3:00	?	2			0
19 Aug. 2003	19:49	8	0:42–3:25			0			0
20 Aug. 2003	19:48	9	0:43–3:22			0			0

TABLE 4. *Montastraea faveolata* and *M. annularis* spawning times in hours post sunset.

Date	Sunset	NAFM	Survey	<i>M. faveolata</i>			<i>M. annularis</i>		
				Earliest	Latest	Number	Earliest	Latest	Number
28 July 1997	20:06	9	1:04–3:06			0			0
24 Aug. 1997	19:44	7	1:58–3:08			0			0
25 Aug. 1997	19:42	8	3:10–5:21	3:18	3:48	5	3:48	4:18	3
26 Aug. 1997	19:41	9	52 min			0			0
27 Aug. 1997	19:40	10	1:03–2:43			0			0
14 Aug. 1998	19:54	7	2:34–4:38	3:06	3:36	4	3:36	4:06	3
15 Aug. 1998	19:53	8	0:37–2:57			0			0
16 Aug. 1998	19:52	9	1:38–3:24			0			0
3 Sep. 1999	19:33	9	0:45–3:29	3:08	?	2			0
5 Sep. 1999	19:31	11	0:44–2:32			0			0
21 Aug. 2000	19:46	7	2:16–4:04	3:14	3:44	3			0
22 Aug. 2000	19:45	8	1:34–3:11	3:15	3:45	4			0
23 Aug. 2000	19:44	9	0:41–1:50			0			0
9 Aug. 2001	19:58	6	0:32–2:37			0			0
10 Aug. 2001	19:57	7	0:48–2:56			0			0
11 Aug. 2001	19:56	8	2:04–3:02			0			0
9 Sep. 2001	19:26	8	0:49–2:37			0			0
10 Sep. 2001	19:25	9	1:35–3:41			0			0
28 Aug. 2002	19:40	7	1:29–3:59			0			0
29 Aug. 2002	19:38	8	1:12–4:01	3:17	?	3			0
30 Aug. 2002	19:37	9	0:36–3:15			0			0
31 Aug. 2002	19:36	10	0:36–1:27			0			0
18 Aug. 2003	19:50	7	1:03–3:38			0			0
19 Aug. 2003	19:49	8	0:42–3:25			0			0
20 Aug. 2003	19:48	9	0:43–3:22			0			0

TABLE 5. *Colpophyllia natans* spawning times in hours post sunset.

Date	Sunset	NAFM	Survey	Earliest	Latest	Number
28 July 1997	20:06	9	1:04–3:06			0
24 Aug. 1997	19:44	7	1:58–3:08			0
25 Aug. 1997	19:42	8	3:10–5:21			0
26 Aug. 1997	19:41	9	52 min			0
27 Aug. 1997	19:40	10	1:03–2:43	1:05	1:30	30
14 Aug. 1998	19:54	7	2:34–4:38			0
15 Aug. 1998	19:53	8	0:37–2:57			0
16 Aug. 1998	19:52	9	1:38–3:24			0
3 Sep. 1999	19:33	9	0:45–3:29			0
5 Sep. 1999	19:31	11	0:44–2:32	1:06	1:21	40
21 Aug. 2000	19:46	7	2:16–4:04			0
22 Aug. 2000	19:45	8	1:34–3:11			0
23 Aug. 2000	19:44	9	0:41–1:50	0:46	1:26	?
9 Aug. 2001	19:58	6	0:32–2:37			0
10 Aug. 2001	19:57	7	0:48–2:56			0
11 Aug. 2001	19:56	8	2:04–3:02			0
9 Sep. 2001	19:26	8	0:49–2:37			0
10 Sep. 2001	19:25	9	1:35–3:41			0
28 Aug. 2002	19:40	7	1:29–3:59			0
29 Aug. 2002	19:38	8	1:12–4:01			0
30 Aug. 2002	19:37	9	0:36–3:15			0
31 Aug. 2002	19:36	10	0:36–1:27	1:03	1:23	30
18 Aug. 2003	19:50	7	1:03–3:38			0
19 Aug. 2003	19:49	8	0:42–3:25			0
20 Aug. 2003	19:48	9	0:43–3:22			0

on 12 different evenings, but of these starting or ending times were sometimes missed, and one event had only four participants. In the remaining events (15–80 participants per evening), spawning times were $1:29 \pm 21$ ($n = 6$) to $2:29 \pm 21$ ($n = 5$). However, on the evening of 10 Aug. 2001, spawning was much earlier than typically observed, and if this event is not scored, the initiation time is raised to $1:37 \pm 20$ to $2:29 \pm 21$. The ending of *Diplora* spawning is quite different from that observed in other species. Early spawning occurs in large numbers, and individual observers may record over 30 spawning heads within 30 min. There is no abrupt end to spawning, however. Typically around the time when *M. franksi* begins to spawn, *D. strigosa* spawning becomes very rare, but occasional release by single individuals continues for sometime, and may outlast even the latest *M. franksi* spawners.

Montastraea franksi is the most abundant species and one of the most prolific spawners of the FGB reef, with eight events with more than 20 participants recorded during the 7-yr period described in this study (Table 2). On events in which 50 or more colonies were observed spawning (five evenings), the spawning window was from $1:51 \pm 16$ to $2:20 \pm 19$ ($n = 5$). If all samples where five or more were estimated, the range was $1:56 \pm 27$ to $2:21 \pm 19$. The average onset and cessation times were therefore very similar to those of more profligate activity, but the range slightly increased.

In the standard species progression at the FGB, the next species observed spawning is *S. intersepta*. Male colonies release sperm over a window of approximately 4–5 min, with the entire colony usually releasing sperm at around the same time. The number of spawners is not as high as for other species (Table 3), so all data with 3 ($n = 4$) or more male sightings were used in calculating spawning ranges, which were from $2:38 \pm 13$ to $2:59 \pm 7$.

Stephanocoenia intersepta female spawning proceeds in a wave that slowly traverses the coral head. With occasional pauses in the progression of the border of egg release, the total time is 2–3 min per coral colony. Female *S. intersepta* colonies were often observed spawning only when immediately adjacent to male colonies, which were actively releasing sperm. Female spawn times were from $2:46 \pm 10$ to $2:59 \pm 7$ ($n = 3$; Table 3). On two evenings, females were first observed either simultaneously spawning next to a male (14 Aug. 1998, 10 Sep. 2001) or next to a large group of spawning males some 11–20 min later (29 Aug. and 30 Aug., 2002). Each of these colo-

nies was tagged according to sex to allow further study of the potential linkage between spawning activity in the two sexes.

Montastraea faveolata forms the largest single coral heads at the FGB, sometimes measuring over 4 m across. Like *M. franksi*, entire *M. faveolata* heads release synchronously, generating a massive cloud of gamete packets. The spawning window for this species is based on small sample numbers, as often only a single diver was on station during this relatively late window (Table 4). The average spawning times were $3:13 \pm 7$ ($n = 6$) to $3:43 \pm 7$ ($n = 4$).

The latest (postsunset) spawning species observed at the FGB is *M. annularis*. Given its late spawning window and the relative scarcity of colonies (<1% coverage), observations for this species are few, and only three colonies were recorded spawning on each of the two evenings in which *M. annularis* was observed releasing packets (Table 4). Spawning times ranged from $3:42 \pm 6$ to $4:12 \pm 6$ ($n = 2$).

Two evenings after the major spawning night at the FGB, the hermaphrodite *C. natans* spawns and is the only species usually observed on this evening (Table 5). The spawning window is the shortest and most consistent recorded, $1:05 \pm 2$ to $1:25 \pm 5$ ($n = 3$) postsunset. This extraordinary consistency observed in three different years cannot be explained through signaling from other species, and if chemical modulation is involved in this species, it must be conspecific not heterospecific. One aberrant report from 2001 indicates a slightly earlier onset time, but individual release times or participant numbers were not recorded on this evening, so it is not included in range estimates.

The uniqueness of each species-spawning window observed during the course of a single, long observation period is not as obvious from the above data set as it is when witnessing the event in situ. This same data is therefore represented graphically in Figure 1 and in summation form in Table 6, and in both, this sequential activity is more obvious. The only species reported in this study that does not have a unique window is *D. strigosa*, but as explained above and represented by a gradation in intensity in Figure 1, this species does have a window in which it is the only major spawning species, and spawning frequency is greatly reduced after the onset of *M. franksi* spawning. *Montastraea cavernosa* females spawn in the peak *D. strigosa* window, but they are rare and most evenings have fewer than five spawners. Table 6 also shows estimates of predicted spawning

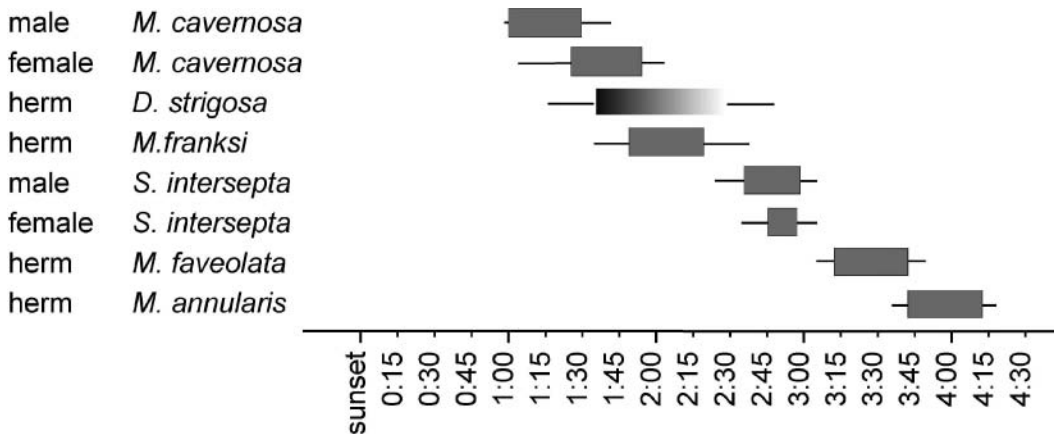


Fig. 1. Spawning times on the eighth evening after the August full moon. A graphical representation of the data in Tables 1–5. Peak spawning windows are shown in gray, and range with black bars. The *Diploria* profile is shown as a gradient, reflecting the strong bias toward spawning in the early portion of this window.

windows for peak spawning at the FGB in the years 2005–2008.

Discussion.—The tightness of the spawning windows described in this study over multiple seasons is extraordinary. The most consistent spawner is *C. natans*, which over 3 yr was uniform to within 2 min for onset times, and 5 min for spawning hiatus. At the other end of the spectrum was *D. strigosa*, which was the least consistent species temporally, with mean spawning ranges of $1:29 \pm 21$ ($n = 6$) to $2:29 \pm 21$.

Of the 18 onset or hiatus times determined in this study for nine species, nine were within 7 min or less from the average. Not only does this vastly improve on our ability to predict spawning events, it implies a level of tight temporal regulation that has not previously been detected. The use of a small number of observers over multiple seasons is much more consistent than are larger numbers of observ-

ers over shorter time spans, as has also been noted by others (e.g., Levitan et al., 2004).

In the two gonochoric species described in this study, male colonies were observed releasing sperm before any female egg release. Because this could be masked by averaging spawning times, the delay between gamete release in colonies of different sexes is displayed on a per evening basis in Table 7. As has been previously observed for this and other mass spawners, female *M. cavernosa* spawned later than males. Females initiated spawning 5–23 min after the first observed release by a male. No obvious association with nearby male colonies was observed for this species.

Stephanocoenia intersepta females often spawned only when immediately adjacent (<0.5 m) to a male colony actively releasing sperm. On the remaining two evenings, males released earlier than females, and only females close (within 2 m) to spawning males were observed to release eggs. Because we have previ-

TABLE 6. Peak spawning times and future coral spawning predictions.

Species	Postsunset	26 Aug. 2005	14 Sep. 2006	4 Sep. 2007	23 Aug. 2008
<i>Montastraea cavernosa</i> M	1:01–1:31	20:42–21:12	20:21–20:51	20:33–21:03	20:45–21:15
<i>Montastraea cavernosa</i> F	1:27–1:56	21:08–21:37	20:47–21:16	20:59–21:28	21:11–21:40
<i>Diploria strigosa</i>	1:29–2:29	21:10–22:10	20:49–21:49	21:01–22:01	21:13–22:13
<i>Montastraea franksi</i>	1:51–2:20	21:32–22:01	21:11–21:40	21:23–21:52	21:35–22:04
<i>Stephanocoenia intersepta</i> M	2:38–2:59	22:19–22:40	21:58–22:19	22:10–22:31	22:22–22:43
<i>Stephanocoenia intersepta</i> F	2:46–2:59	22:27–22:40	22:06–22:19	22:18–22:31	22:30–22:43
<i>Montastraea faveolata</i>	3:13–3:43	22:54–23:24	22:33–23:03	22:45–23:15	22:57–23:27
<i>Montastraea annularis</i>	3:42–4:12	23:23–23:53	23:02–23:32	23:14–23:44	23:26–23:56
<i>Colpophyllia natans</i> ^a	1:05–1:25	20:44–21:04 ^a	20:32–20:43 ^a	20:35–20:55 ^a	20:47–21:07 ^a
Sunset		19:41	19:20	19:32	19:44

^a *Colpophyllia natans* spawns two evenings later than the date shown.

TABLE 7. Delayed spawning by female gonochorics.

Date	Species	Minutes post male	Proximity to male (m)
3 Sep. 1999	<i>Montastraea cavernosa</i>	7	NA
10 Aug. 2001	<i>Montastraea cavernosa</i>	23	NA
9 Sep. 2001	<i>Montastraea cavernosa</i>	5	NA
18 Aug. 2003	<i>Montastraea cavernosa</i>	17	NA
14 Aug. 1998	<i>Stephanocoenia intersepta</i>	0	<0.5
10 Sep. 2001	<i>Stephanocoenia intersepta</i>	1	<0.5
29 Aug. 2002	<i>Stephanocoenia intersepta</i>	11	1–2
30 Aug. 2002	<i>Stephanocoenia intersepta</i>	20	1–2

ously found that eggs collected immediately on release from female *S. intersepta* show extraordinarily high rates of fertilization without the addition of any sperm (Hagman et al., 1998b), this observation may indicate that sperm directly triggers egg release. This remains to be confirmed experimentally.

The spawning times at the FGB, although extremely consistent at this site, differ somewhat from those at other locations in the northern Atlantic and Caribbean. Levitan et al. (2004) recently reviewed spawning times throughout the Caribbean for the *M. annularis* complex. These data and FGB data from Tables 2 and 4 are compared with those in Table 8. In general, the FGB times are consistent with other spawning times reported from throughout the Caribbean, but peak FGB windows are considerably briefer. Because spawning window lengths on any one evening are similar in duration to those of the window averages, our peak times may be more representative of normal activity. An exception to the close correlation between the data sets is observed for the Panama and Bahamas data for *M. faveolata*. These data shows onset times 30–40 min later than that of other locales and hiatus times 40–60 min later. Interestingly, *M. annularis* spawns earlier than *M. faveolata* in the Levitan et al. (2004) observations, but this is reversed at the FGB. Onset times for *M. franksi* are also a little different, about 20 min earlier in the Panama/Bahamas data. Fertilization studies indicate that this may be because of an increased need for temporal separation when species are ca-

pable of nonproductive cross-fertilization (Levitan et al., 2004). *Montastraea* species cannot cross-fertilize in some locations and correspondingly spawning times can be much closer (Szmant et al., 1997; Hagman et al., 1998b; Fukami et al., 2003; Levitan et al., 2004). Because of long-range dispersal, there is generally low intraspecific genetic variation in corals throughout the Caribbean (e.g., Lopez et al., 1999; Fukami et al., 2003); in the absence of variation, this flexibility in spawning timing implies that corals may adjust behavior to their local spawning environment, rather than evolving into a specific temporal niche at each geographical location. Data such as that documented in this study will help investigate the basis of this behavior.

Acknowledgments.—This study was supported by the FGBNMS, without whose generous support none of these studies would have been possible. FGBNMS staff who have helped include Steve Gittings, Emma Hickerson, Jennifer DeBose, and G. P. Schmahl. We are also grateful for the help of our field assistants including videographer Kaile Tsapis and diving support by Miles Dear, Randy Beckmann, Jerry Thomsen, Susan Vize, and Cat LaBlanche. Critical financial, equipment, and logistical support were provided by Ocean Management Systems (NY) and Austin Aquasports (TX). Operations at the FGB were carried out under permit numbers FGBNMS 2000-006-A1, FGBNMS-2001-012, FGBNMS-2001-015, and FGBNMS-2002-007.

TABLE 8. Comparison of FGB *Montastraea* data with other Caribbean studies.

	Literature average	Levitan et al. 2004	Present study average	Present study full range
<i>Montastraea franksi</i>	1:52–3:00	1:25–2:35	1:51–2:20	1:43–2:35
<i>Montastraea faveolata</i>	3:05–4:02	3:43–4:40	3:13–3:43	3:06–3:48
<i>Montastraea annularis</i>	3:17–4:15	3:04–4:22	3:42–4:12	3:36–4:18

LITERATURE CITED

- BABCOCK, R. C., G. D. BULL, P. L. HARRISON, A. J. HEYWARD, J. K. OLIVER, C. C. WALLACE, AND B. L. WILLIS. 1986. Synchronous spawning of 105 scleractinian coral species on the Great Barrier Reef. *Mar. Biol.* 90:379–394.
- BRIGHT, T. J. 1991. First direct sighting of star coral spawning. Texas Shores, Texas A&M Univ. Sea Grant Prog. 24(1):2.
- FUKAMI, H., M. OMORI, K. SHIMOIKE, T. HAYASHIBARA, AND M. HATTA. 2003. Ecological and genetic aspects of reproductive isolation by different spawning times in *Acropora* corals. *Mar. Biol.* 142:679–684.
- GITTINGS, S. R. 1998. Reef community stability on the Flower Garden Banks, Northwest Gulf of Mexico. *Gulf Mex. Sci.* 16:161–169.
- , G. S. BOLAND, K. J. DESLARZES, C. L. COMBS, B. S. HOLLAND, AND T. J. BRIGHT. 1992. Mass spawning and reproductive viability of reef corals at the East Flower Garden Bank, northwest Gulf of Mexico. *Bull. Mar. Sci.* 51:420–428.
- HAGMAN, D. K., S. R. GITTINGS, AND K. J. P. DESLARZES. 1998a. Timing, species participation, and environmental factors influencing annual mass spawning at the Flower Gardens Banks (Northwestern Gulf of Mexico). *Gulf Mex. Sci.* 16:170–179.
- , ———, AND P. D. VIZE. 1998b. Fertilization in broadcast-spawning corals of the Flower Gardens Banks National Marine Sanctuary. *Gulf Mex. Sci.* 16:180–187.
- , AND P. D. VIZE. 2003. Mass spawning by two brittle star species, *Ophioderma rubicundum* and *O. squamosissimum*, at the Flower Garden Banks, Gulf of Mexico. *Bull. Mar. Sci.* 72:871–876.
- HARRISON, P. L., AND C. V. WALLACE. 1990. Reproduction, dispersal and recruitment of scleractinian corals, p. 133–207. *In: Ecosystems of the world*. Vol. 25: coral reefs. Z. Dubinsky (ed.). Elsevier, Amsterdam, The Netherlands.
- KNOWLTON, N., J. L. MATE, H. M. GUZMAN, R. ROWAN, AND J. JARA. 1997. Direct evidence for reproductive isolation among the three species of the *Montastraea annularis* complex in Central America (Panama and Honduras). *Mar. Biol.* 127:705–711.
- LEVITAN, D. R., H. FUKAMI, J. JARA, D. KLINE, T. M. MCGOVERN, K. E. MCGHEE, C. A. SWANSON, AND N. KNOWLTON. 2004. Mechanisms of reproductive isolation among sympatric broadcast-spawning corals of the *Montastraea annularis* species complex. *Evolution* 58:308–323.
- LOPEZ, J. V., R. KERSANACH, S. A. REHNER, AND N. KNOWLTON. 1999. Molecular determination of species boundaries in corals: genetic analysis of the *Montastraea annularis* complex using amplified fragment length polymorphisms and a microsatellite marker. *Biol. Bull.* 196:80–93.
- OLIVER, J., R. C. BABCOCK, P. L. HARRISON, AND B. L. WILLIS. 1988. Geographic extent of mass coral spawning: clues to ultimate causal factors. *Proc. 6th Int. Coral Reef Symp.* 2:853–859.
- PATTENGILL-SEMMENS, C., S. R. GITTINGS, AND T. SHYKA. 2000. A rapid assessment of coral, fish and algae using the AGRRA protocol. *Mar. Sanctuaries Conservation Series*, MSD-00-3. p. 1–22.
- SLATTERY, M., G. A. HINES, J. STARMER, AND V. J. PAUL. 1999. Chemical signals in gametogenesis, spawning, and larval settlement and defense of the soft coral *Sinularia polydactyla*. *Coral Reefs* 18:75–84.
- SZMANT, A. M., E. WEIL, M. W. MILLER, AND D. E. COLON. 1997. Hybridization within the species complex of the scleractinian coral *Montastraea annularis*. *Mar. Biol.* 129:561–572.
- VAN VEGHEL, M. L. 1993. Multiple species spawning on Curacao reefs. *Bull. Mar. Sci.* 52:1017–1021.
- (PDV) DEPARTMENT OF BIOLOGICAL SCIENCES, UNIVERSITY OF CALGARY, ALBERTA, CANADA T2N 1N4; AND DEPARTMENT OF ZOOLOGY, UNIVERSITY OF TEXAS, AUSTIN, TEXAS 78712; (JAE) TEXAS PARKS AND WILDLIFE DEPARTMENT, ARTIFICIAL REEF PROGRAM, 1502 FM 517 EAST, DICKINSON, TEXAS 77539; AND (MN, DPB, DKH) DEPARTMENT OF BIOLOGICAL SCIENCES, UNIVERSITY OF CALGARY, ALBERTA, CANADA T2N 1N4. Send reprint requests to PDV. Date accepted: May 20, 2005.