



Expanding coral reproductive knowledge using remotely operated vehicles (ROV): broadcast-spawning observations of mesophotic corals at the Flower Garden Banks

Marie E. Strader¹ · Hannah E. Aichelman² · Carlos A. Tramonte² · Hayden E. W. Dickerson² · Brooke E. Benson² · Lauren I. Howe-Kerr³ · Emma L. Hickerson⁴ · Sarah W. Davies²

Received: 15 October 2020 / Revised: 15 December 2020 / Accepted: 18 December 2020 / Published online: 5 August 2021
© Senckenberg Gesellschaft für Naturforschung 2021

Abstract

Broadcast-spawning scleractinian corals undergo mass spawning annually, the timing of which is determined by a series of environmental and chemical cues. Flower Garden Banks reefs (FGB, NW Gulf of Mexico) have high coral cover compared to the rest of the Tropical Western Atlantic and exhibit highly synchronous coral spawning, although spawning observations have been largely limited to shallower depths (17–24 m). Using a remotely operated vehicle (ROV), we report observations of mesophotic (39–42 m) broadcast spawning of three major reef-building coral species at East FGB. We observed spawning of 20 *Montastraea cavernosa* colonies, an order of magnitude more than has been previously reported for this population at mesophotic depths. Spawning times of the three target species (*M. cavernosa*, *Orbicella franksi*, and *Pseudodiploria strigosa*) ranged from 45 min prior to sunset up to 1 h, 33 min after sunset, consistent with shallow conspecifics. We place these observations in the context of other spawning reports of the same species at the FGB and throughout the Tropical Western Atlantic. In addition, the ROV was directed to collect eight genetically unique fragments of gravid *Orbicella faveolata* and employed a novel gamete collection device designed to capture gametes from actively spawning colonies in situ. These data and collection techniques highlight the benefits of using ROV technology for coral-spawning research, particularly for mesophotic coral reef ecosystems, where gamete release occurs across time ranges exceeding limits imposed by recreational diving. Finally, our observations of overlap in the timing of spawning along the shallow to mesophotic continuum at the FGB suggest—at least for the corals monitored here—that the potential for cross fertilization across depths exists.

Keywords Coral spawning · *Montastraea cavernosa* · *Orbicella* spp. · Mesophotic coral reefs · Tropical Western Atlantic

Introduction

Population persistence is maintained by reproductive output and connectivity within metapopulations. Mesophotic coral

reefs (30–150 m), which are hypothesized to experience dampened effects of anthropogenic change, could act as a source of genetic material to maintain more threatened shallow water reefs (Bongaerts et al. 2010; Holstein et al. 2015; Laverick et al. 2018; Rocha et al. 2018). However, this hypothesis has been challenged as new data and observations paint a more complex picture.

First, mesophotic reefs vary substantially both spatially and temporally, with some reefs showing detrimental effects of anthropogenic change similarly to shallow reefs and higher sensitivities to temperature anomalies (Lesser et al. 2009; Smith et al. 2016; Frade et al. 2018; Shlesinger et al. 2018; Slattery et al. 2018; Weil 2019; de Oliveira et al. 2020). For example, mesophotic populations of *Orbicella* spp. have lower bleaching thresholds, making them more sensitive to high thermal anomalies, which can occur at these depths (Smith et al. 2016).

Communicated by B. W. Hoeksema

✉ Marie E. Strader
stradermarie@gmail.com

¹ Department of Biological Sciences, Auburn University, Auburn, AL, USA

² Department of Biology, Boston University, Boston, MA, USA

³ BioSciences at Rice, Rice University, 6100 Main St, Houston, TX, USA

⁴ Flower Garden Banks NMS, 4700 Ave. U, Bldg 216, Galveston, TX, USA

Second, depth gradients may vary in environmental cues that corals use to induce spawning, such as light intensity, light-color spectra, and temperature, which could drive differences in spawning times. Differences in current patterns could also cause delays in the mixing of mesophotic and shallow reef gametes. Spawning asynchrony can limit fertilization success, which reduces larval numbers and ultimately limits recruitment (Shlesinger and Loya 2019).

Third, independent of spawning synchrony, fecundity is reduced in some mesophotic corals due to limited nutrients and shifts in energy allocation away from reproduction (Gori et al. 2012; Prasetya et al. 2017b; Shlesinger et al. 2018), although fecundity is maintained in some mesophotic coral populations (Holstein et al. 2016). Therefore, it is necessary to understand variation in reproductive ecology across depth gradients and collect data across diverse mesophotic reefs globally in order to develop sustainable management plans for threatened species, such as reef-building corals in the Tropical Western Atlantic.

Currently, data on reproductive ecology of mesophotic coral subpopulations, including timing of spawning and reproductive output, remain sparse due to the difficulty of observing broadcast spawning at depth, especially for longer time periods. However, comparisons of coral reproductive traits between shallow and mesophotic reefs have been investigated in several systems. The mesophotic species *Acropora tenella* off the coast of Japan exhibits similar spawning times as shallow *Acropora*, but have longer gametogenesis cycles and lower fecundity overall (Prasetya et al. 2016, 2017a). Mesophotic populations of *Seriatopora hystrix* exhibit similar spawning times but reduced larval size and reproductive season compared to shallow conspecifics (Prasetya et al. 2017b), which is similar to what is observed in the gorgonian *Eunicella singularis* (Gori et al. 2012).

In the Tropical Western Atlantic, *Porites astreoides* exhibits similar fecundity in shallow and mesophotic populations (Holstein et al. 2016). Many of the studies examining reproductive differences between mesophotic and shallow water corals have used reproductive histology or taken colonies back to the lab for observation, which has the potential to misrepresent spawning behavior on the reef. Here, we report spawning observations taken from a remotely operated vehicle (ROV) of a mesophotic coral reef with high coral cover and compare these observations with spawning data at adjacent, shallower parts of the same reef and across the wider Tropical Western Atlantic basin.

The Flower Garden Banks (FGB) is unique in the Tropical Western Atlantic due to its high coral cover of multiple threatened species: 52% at the East FGB in 2019 (Gardner et al. 2003; Johnston et al. 2016, 2020). Coral spawning at the FGB is known to be predictable with regard to the number of days after the full moon when peak spawning is observed, as seen through decades of spawning observations (Gittings et al.

1992, 1994; Hagman et al. 1998; Vize et al. 2005; Vize 2006). Further, the FGB has been shown to be genetically connected to other Tropical Western Atlantic reefs (Lugo-Fernández et al. 2001; Rippe et al. 2017), and modeling work has suggested that its position in the NW Gulf of Mexico allows for potential dispersal events to the Florida Keys as well as northern Cuba (Davies et al. 2017; Limer et al. 2020).

While the FGB reef caps begin at 16 m depth, reef-building corals can extend as deep as 50 m (Schmahl et al. 2008). Studies of genetic diversity and biophysical models suggest high vertical connectivity among reefs at the FGB (Garavelli et al. 2018; Studivan and Voss 2018a, b); however, little data exists on the reproductive ecology of these deeper, mesophotic reefs. In 1999, spawning of six mesophotic colonies (including *Montastraea cavernosa*, *Orbicella franksi*, (formerly known as *Montastraea franksi*), and *Pseudodiploria strigosa* (formerly known as *Diploria strigosa*)) was observed at the FGB, ranging from 33 to 42 m depth (Vize 2006).

One of the major challenges of observing mesophotic coral spawning are physical SCUBA diving limitations that minimize depth and bottom time, thus making it logistically unfeasible to observe the full evening of coral spawning. To overcome this challenge, we leveraged remotely operated vehicle (ROV) technology for continuous monitoring of colonies between 39 and 42 m depth at East FGB. We documented the initial spawning time for three reef-building species, reported the proportion of each colony that spawned, and compared these values to long-term spawning data available for the FGB's shallower depths.

In addition, the ROV successfully collected gravid *Orbicella faveolata* fragments and gametes from actively spawning colonies, highlighting the potential use of ROV research for other experimental work at depth. Together, these observations, coupled with previous genetic connectivity work in this region (Studivan and Voss 2018b), provide further support for vertical connectivity between mesophotic and shallow water coral reefs at the FGB.

Materials and methods

Coral spawning observations were conducted via the ROV *Yogi* aboard the National Marine Sanctuary vessel R/V *Manta*, at East Flower Garden Bank within the Flower Garden Banks National Marine Sanctuary (27.904, -93.595). *Yogi* is equipped with multiple simultaneous camera feeds and sensors to allow live remote viewing while recording locally on the ship at native resolutions. Video footage was collected using an Insite Pacific Mini Zeus 4K Camera with a digital 4K resolution of 3840 × 2160p, which includes a 12× optical zoom lens with a 126° super wide-angle field of view down to a telephoto 11.9° narrow field of view. Another key

component to the *Yogi* ROV system is the on-ship control-room and satellite system used to control, process, record, display, and transmit the video and data back to shore.

Spawning observations took place on August 22, 2019, corresponding to eight nights after the full moon. Sunset was documented at 19:55 CDT, and video was recorded continuously from 16:29 to 21:57 (CDT). The video documented coral spawning behavior through an exploratory random diving path without a predefined transect at an average depth of 40 m. Originally, ROV dives were also planned for later into the evening on the eighth night after the full moon, as well as the ninth and tenth nights after the August full moon in 2019 (August 21–24); however, inclement weather limited these observations.

Dive recordings were reviewed post-cruise to identify video segments containing active coral spawning. Video analysis was conducted using Pro-Res videos from ROV *Yogi* on 23 unique coral colonies that were observed to spawn between 19:10 and 21:33 (CDT). Using continuous video broken up into 5-min segments, detailed information on exact times, depths, temperature, proportion of the coral colony spawning, and size of the spawning colony were measured, when possible. Colony sizes were calculated using two lasers mounted on the ROV, and set 10 cm apart, within the video frame (Supplemental Video 1). The proportion of the coral colony observed to spawn was determined by approximating the total percentage of observed polyps spawning within the time the video was focused on the colony and was placed under percentile bins ranging from 0 to 100% (0–25%, 25–50%, 50–75%, and 75–100%). It is worth noting that we cannot confirm whether or not spawning took place after the ROV left the colony as well as on nights before or after the spawning dive; so these data should be considered conservative estimates of spawning behavior.

Taxonomic identification was confirmed by at least three researchers during the live video streaming and later verified through video footage and audio recordings to ensure correct identification of target coral species. The criteria used to determine spawn from a colony was as follows: (1) hermaphroditic sperm and egg bundles being released from a colony source or (2) clouds of sperm or clumps of eggs originating from a male or female colony, respectively (Fig. 1). Time of gamete release was recorded both in real time and later during video analysis to corroborate timing measurements. In situ seawater temperatures and depth readings were relayed from the ROV instrumentation by the ROV pilot and recorded directly.

Results and discussion

The use of an ROV enabled novel observations of coral spawning at mesophotic depths over longer time periods than was previously documented at FGB (Vize 2006). We

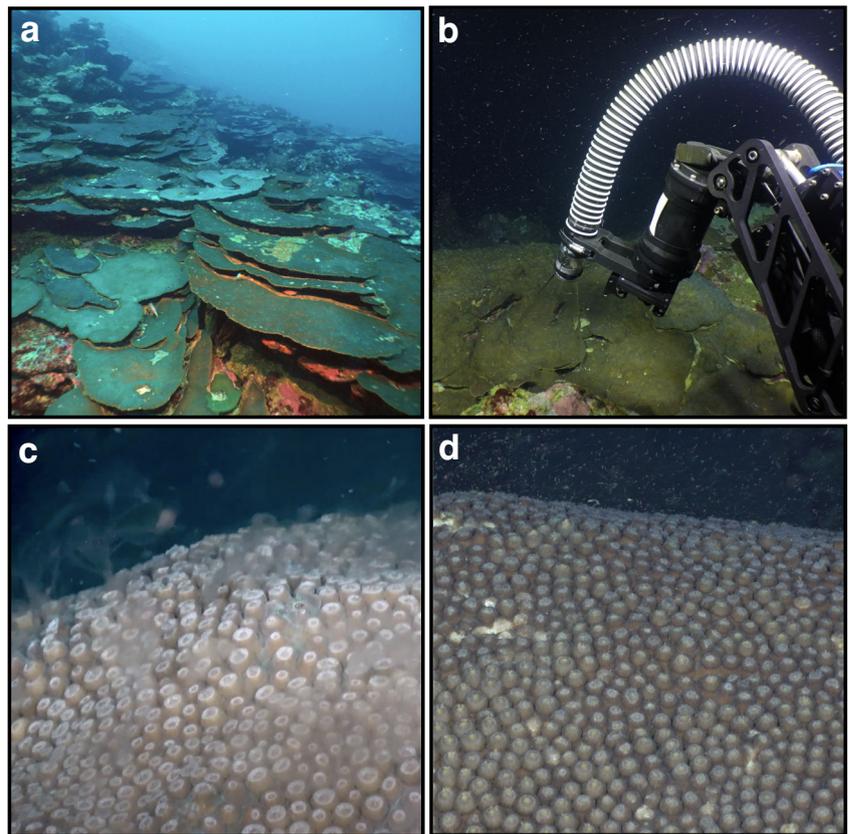
observed broadcast coral spawning behavior of three species: *Montastraea cavernosa*, *Pseudodiploria strigosa*, and *Orbicella franksi*. In total, spawning of 14 colonies of male *M. cavernosa*, six colonies of female *M. cavernosa*, two colonies of *O. franksi*, and one colony of *P. strigosa* were observed, with all colonies residing between 39 and 42 m depth (Table 1). We began observing the spawning of male *M. cavernosa* colonies at 19:10:43 CDT, 45 min prior to sunset (19:55:00), and spawning observations extended until 21:06:10 CDT (Fig. 2, Table 1).

In 57% of the male *M. cavernosa* colonies observed, > 50% of the colony area was observed to release sperm (Table 1). Male *M. cavernosa* colonies were observed to release sperm prior to female colonies, which is consistent with previous observations (Gittings et al. 1994; Hagman et al. 1998; De Graaf et al. 1999; Vize et al. 2005; Vize 2006) (Fig. 2). Female *M. cavernosa* colonies began spawning at 19:40:00 CDT, and the last observed colony spawned at 21:33:43 CDT, coinciding with the conclusion of the dive itself, suggesting that spawning may have continued. Of the female *M. cavernosa* colonies observed, only 33% exhibited spawning across > 50% of the colony. It is possible that the remaining females and males spawned either after our dive concluded or on different nights flanking the observation night.

The skewed sex ratio between males and females observed here could be due to several reasons: (1) Females at mesophotic depths spawn later in the night, and thus we missed peak female spawning due to the dive being aborted by adverse weather conditions; (2) the night we observed spawning may not have been the peak night for female release; and (3) environmental factors are influencing the sex ratios and/or differences in spawning patterns between males and females. However, based on previous work suggesting that *M. cavernosa* exhibit 1:1 sex ratios in shallow water (Soong 1991; Szmant 1991; Acosta and Zea 1997), we propose that the most likely scenario is that males generally begin spawning before females, and we therefore only observed peak male spawning. However, we cannot rule out that there could be differences in sex ratios at depth given that similar observations have been reported in other mesophotic coral reef ecosystems (Shlesinger et al. 2018).

In the Tropical Western Atlantic, peak spawning for *M. cavernosa* is the 6th and 7th night after the full moon (Johnston et al. 2014, 2020; Jordan 2018). Observations of *M. cavernosa* spawning across other Tropical Western Atlantic sites indicate that the earliest timing of spawning occurs 1 h to 30 min prior to sunset (Gittings et al. 1994; Jordan 2018) (Table 2), which corresponds to the onset of spawning in the mesophotic *M. cavernosa* at the FGB (Table 1, Fig. 2; Vize 2006). This result overlaps with what has been previously observed in conspecifics at shallower FGB depths (Fig. 2, Table 2). Overall, *M. cavernosa* exhibited

Fig. 1 Broadcast spawning of mesophotic (39–42 m) corals at FGB. **a** Plating colonies of *Orbicella* spp.; **b** ROV *Yogi* collecting gametes from a spawning *O. franksi* colony. Spawning of *Montastraea cavernosa*; **c** male; **d** female



a wide range of spawning times, consistent with other reported observations. Therefore, while the peak spawning dates at the FGB are highly predictable, the window of time within an evening when spawning is observed is relatively wide for *M. cavernosa*. Consequences of wide-spawning windows could be reduced fertilization and higher instances of non-random mating in this species compared to species with highly synchronous spawning times.

We also observed the onset of spawning activity for *O. franksi* and *P. strigosa*, with spawning times beginning at 21:17:10 and 21:19:39 CDT, respectively. These times are well within the range of spawning observations of conspecifics at the reef crest of the FGB as well as at other Tropical Western Atlantic reefs (Table 2). As we only observed a few spawning colonies of *P. strigosa* ($N = 1$) and *O. franksi* ($N = 2$), we cannot speculate about whether remaining colonies spawned after our observations on the eighth night or on subsequent nights. Another explanation for the lack of observations in these species is that they are less abundant at mesophotic depths compared to their abundance at the reef crest (Johnston et al. 2014, 2020). Further observations of spawning behavior of these species at mesophotic depths are warranted.

In addition to spawning observations captured live and video recorded, the ROV *Yogi* was specially equipped to sample both fragments of adult colonies as well as spawning

gametes (Fig. 1). The day prior to spawning observations, fragments from eight colonies of *O. faveolata* were collected from 38 to 48 m depth using a robotic sampling arm. These colonies were maintained on the deck of the RV *Manta* in flow-through seawater for the duration of the cruise. Spawning was observed in three of these fragments. The lack of spawning observed in the remaining fragments could be explained by the stress of collection or reduced fecundity of mesophotic colonies. Thus, future work should examine differences in fecundity between mesophotic and shallow conspecifics at the FGB, similarly to other mesophotic reefs worldwide (Gori et al. 2012; Holstein et al. 2015, 2016; Prasetya et al. 2016, 2017b). Six of these coral fragments survived and are maintained in husbandry in the Marine Invertebrate Research Facility at Boston University. In situ gamete collection via ROV was only minimally successful given that these collections were contaminated with other zooplankton in the water column that were attracted to the ROV by the artificial lighting (Supplemental Video 1). Future sampling efforts should attempt gamete collection under minimal lights.

Environmental parameters differ between the mesophotic coral habitats in this study and colonies existing on the shallower reef cap, particularly with regard to the intensity and spectrum of light available to deeper colonies (Kirk 2011). Temperature at the time of spawning (29–30 °C) at

Table 1 Mesophotic coral-spawn recordings at the East Flower Garden Banks National Marine Sanctuary on August 22, 2019, via ROV

Species ID	Sex	Depth (m)	Temp (°C)	Time (CDT)	Colony size (LxW, cm)	Proportion of colony spawned (%)
<i>M. cavernosa 1</i>	M	42	28.9	19:10:43	N/A	75–100%
<i>M. cavernosa 2</i>	M	39	30.1	19:35:41	N/A	75–100%
<i>M. cavernosa 3</i>	F	39	30.1	19:40:00	N/A	75–100%
<i>M. cavernosa 4</i>	M	39	30.1	19:57:40	110 × 67.5	25–50%
<i>M. cavernosa 5</i>	M	39	30.1	20:02:55	N/A	25–50%
<i>M. cavernosa 6</i>	M	39	30.1	20:08:00	N/A	50–75%
<i>M. cavernosa 7</i>	M	39	30.0	2:19:58	N/A	50–75%
<i>M. cavernosa 8</i>	M	39	30.0	20:26:23	40 × 30	0–25%
<i>M. cavernosa 9</i>	M	39	30.0	20:33:08	N/A	0–25%
<i>M. cavernosa 10</i>	F	39	30.0	20:37:33	N/A	0–25%
<i>M. cavernosa 11</i>	M	41	29.1	20:42:34	N/A	0–25%
<i>M. cavernosa 12</i>	M	41	29.1	20:43:52	140 × 60	75–100%
<i>M. cavernosa 13</i>	M	41	29.2	20:47:46	N/A	75–100%
<i>M. cavernosa 14</i>	F	41	29.2	20:48:31	N/A	N/A
<i>M. cavernosa 15</i>	M	41	29.2	20:52:11	N/A	25–50%
<i>M. cavernosa 16</i>	M	41	29.2	20:58:36	N/A	75–100%
<i>M. cavernosa 17</i>	M	41	29.2	21:06:10	N/A	50–75%
<i>M. cavernosa 18</i>	F	39	29.4	21:09:35	N/A	25–50%
<i>M. cavernosa 19</i>	F	39	29.4	21:13:30	N/A	75–100%
<i>P. strigosa 1</i>	H	39	29.4	21:17:10	N/A	75–100%
<i>O. franksi 1</i>	H	39	30.0	21:19:39	N/A	0–25%
<i>O. franksi 2</i>	H	40	30.0	21:26:59	N/A	25–50%
<i>M. cavernosa 20</i>	F	40	30.1	21:33:43	100 × 120	25–50%

Observations were 8 days after the full moon. Sunset was recorded at approximately 19:55 CDT. All coral colonies were examined through an exploratory random diving path without a predefined transect on the reef crest. Sex: *F* female, *M* male, *H* hermaphrodite. Times are reported in HH:MM:SS format

39–42 m depth (Table 1) was within the same range of temperatures recorded at 24 m (Johnston et al. 2020). We report overlapping spawning times between mesophotic and shallow conspecifics observed in previous years (Vize et al. 2005; Vize 2006; Johnston et al. 2014, 2020), suggesting that synchrony is possibly maintained across these depths despite

environmental differences. Future studies could investigate fecundity, larval viability, and fitness traits including survival and settlement, as it remains to be seen if this deeper FGB population cross-fertilizes with gametes sourced from the reef crest, and if these larvae contribute to maintenance of coral populations at the FGB. Regardless, our data on the

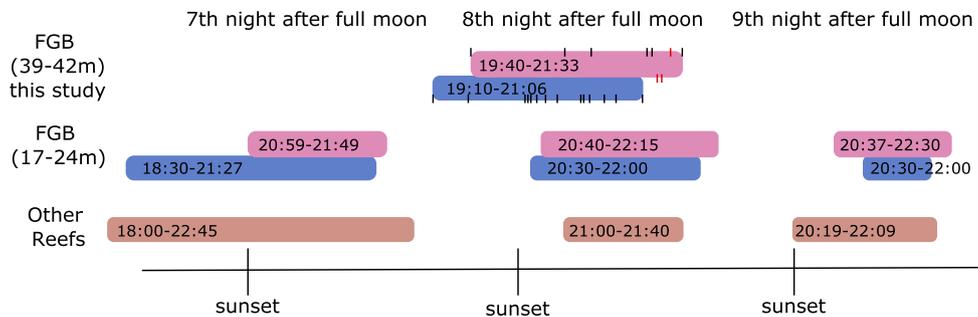


Fig. 2 Shallow and mesophotic coral spawning observations of *Montastraea cavernosa*. Data observed from this study, FGB (39–42 m), is put in context with decades of observations at shallower FGB reefs (17–24 m; FGBNMS data), and spawning observations of this species at other reefs (Bonaire (De Graaf et al. 1999), Bermuda (Wyers et al. 1991), the Bahamas (Gittings et al. 1994), Honduras (Gittings et al.

1994), Puerto Rico (Steiner 1995), and Florida (Gittings et al. 1994)). Tick marks for FGB (39–42 m) represent timing of observed mesophotic spawning from (Vize 2006) (red ticks, 1 female, 2 male colonies) and this study (black ticks). For FGB records, pink represents female colonies and blue represents male colonies

Table 2 Spawning records of reef-building Caribbean corals from the literature

Species	Time of day	Date	Sex	Hour after sunset	NAFM	Reef name	Number of individuals	Reference
<i>M. cavernosa</i>	20:45–22:00	1990–1988	M	N/A	8	Flower Garden Banks	N/A	Hagman et al. 1998
<i>M. cavernosa</i>	21:20–22:15	1991–1995, 1997	F	N/A	8	Flower Garden Banks	N/A	Hagman et al. 1998
<i>M. cavernosa</i>	21:20–21:45	1996/09/27	N/A	N/A	6	Belhem, Bonaire	7	De Graaf et al. 1999
<i>M. cavernosa</i>	20:19–22:09	1986/08/28	H	0:28–2:18	9	Northwest Reef Rim, Bermuda	4	Wyers et al. 1991
<i>M. cavernosa</i>	20:30	1989/08/23	N/A	N/A	7	El Mario, La Parguera, Puerto Rico	3	Steiner 1995
<i>M. cavernosa</i>	20:32	1994/08/28	N/A	0:38–1:28	7	Dry Tortugas	N/A	Gittings et al. 1994
<i>M. cavernosa</i>	N/A	1994/08/28	N/A	N/A	7	Lee Stocking Island, Bahamas	N/A	Gittings et al. 1994
<i>M. cavernosa</i>	18:00	1994/08/28	N/A	1:29–2:02	7	Roatan, Honduras	N/A	Gittings et al. 1994
<i>M. cavernosa</i>	N/A	1994/08/29	N/A	10:05–10:50	8	Saba, NA	N/A	Gittings et al. 1994
<i>M. cavernosa</i>	19:30–20:15	1996/09/02	N/A	N/A	5	Harbour Village, Bonaire	1	De Graaf et al. 1999
<i>M. cavernosa</i>	19:45–22:15	1996/10/02	N/A	N/A	5	Bari Reef, Bonaire	20	De Graaf et al. 1999
<i>M. cavernosa</i>	21:35–23:05	1996/10/03	N/A	N/A	6	Bari Reef, Bonaire	15	De Graaf et al. 1999
<i>M. cavernosa</i>	21:05–22:45	1996/09/04	N/A	N/A	7	Bari Reef, Bonaire	9	De Graaf et al. 1999
<i>M. cavernosa</i>	21:00–21:40	1996/09/05	N/A	N/A	8	Bari Reef, Bonaire	13	De Graaf et al. 1999
<i>M. cavernosa</i>	21:35	1996/11/02	N/A	N/A	7	Bari Village, Bonaire	1	De Graaf et al. 1999
<i>M. cavernosa</i>	21:17	1999/09/02	M	1:43	7	Flower Garden Banks	1	Vize 2006
<i>M. cavernosa</i>	21:20	1999/09/02	M	1:45	7	Flower Garden Banks	1	Vize 2006
<i>M. cavernosa</i>	21:25	1999/09/02	F	1:46	7	Flower Garden Banks	1	Vize 2006
<i>M. cavernosa</i>	20:30–21:17	1999/09/03	M	0:57–1:44	9	Flower Garden Banks	6	Vize et al. 2005
<i>M. cavernosa</i>	20:37–21:25	1999/09/03	F	1:04–1:52	9	Flower Garden Banks	6	Vize et al. 2005
<i>M. cavernosa</i>	21:02–21:15	2001/08/10	M	1:05–1:18	7	Flower Garden Banks	20	Vize et al. 2005
<i>M. cavernosa</i>	21:25–21:49	2001/08/10	F	1:28–1:52	7	Flower Garden Banks	7	Vize et al. 2005
<i>M. cavernosa</i>	21:10–21:15	2001/09/09	M	1:44–1:49	8	Flower Garden Banks	4	Vize et al. 2005
<i>M. cavernosa</i>	21:15–21:31	2001/09/09	F	1:49–2:05	8	Flower Garden Banks	5	Vize et al. 2005
<i>M. cavernosa</i>	21:16–21:27	2003/08/18	M	1:26–1:37	7	Flower Garden Banks	4	Vize et al. 2005
<i>M. cavernosa</i>	21:33–21:38	2003/08/18	F	1:43–1:48	7	Flower Garden Banks	2	Vize et al. 2005
<i>O. faveolata</i>	21:50–23:00	1989/08/23	H	N/A	7	El Mario, La Parguera, Puerto Rico	N/A	Steiner 1995
<i>O. faveolata</i>	23:15–00:40	1992, 1994–1995, 1997–1998	H	N/A	8	Flower Garden Banks	N/A	Hagman et al. 1998
<i>O. faveolata</i>	21:40–22:25	1997/08/24	H	3	6	Isla Grande, Colombia	N/A	Sánchez et al. 1999
<i>O. faveolata</i>	23:00–23:30	1997/08/25	H	3:18–3:48	8	Flower Garden Banks	5	Vize et al. 2005
<i>O. faveolata</i>	21:00–21:50	1997/09/22	H	2.5	6	Isla Grande, Colombia	N/A	Sánchez et al. 1999
<i>O. faveolata</i>	21:15–22:00	1997/09/23	H	2.5	7	Isla Grande, Colombia	N/A	Sánchez et al. 1999
<i>O. faveolata</i>	21:00–21:40	10/21/97	H	2.7	6	Isla Grande, Colombia	N/A	Sánchez et al. 1999
<i>O. faveolata</i>	23:00–23:30	1998/08/14	H	3:06–3:36	7	Flower Garden Banks	4	Vize et al. 2005
<i>O. faveolata</i>	22:41–?	1999/09/03	H	3:08–?	9	Flower Garden Banks	2	Vize et al. 2005
<i>O. faveolata</i>	23:00–23:30	2000/08/21	H	3:14–3:44	7	Flower Garden Banks	3	Vize et al. 2005
<i>O. faveolata</i>	23:00–23:30	2000/08/22	H	3:15–3:45	8	Flower Garden Banks	4	Vize et al. 2005
<i>O. faveolata</i>	22:55–?	2002/08/29	H	3:17–?	8	Flower Garden Banks	3	Vize et al. 2005
<i>O. faveolata</i>	N/A	2014/08/17	H	N/A	7	Grecian Rocks, Florida	N/A	Miller et al. 2018
<i>O. faveolata</i>	N/A	2015/08/07	H	N/A	7	Horseshoe, Florida	N/A	Miller et al. 2018
<i>O. faveolata</i>	N/A	2015/09/05	H	N/A	7	Horseshoe, Florida	N/A	Miller et al. 2018
<i>O. franki</i>	21:00–22:30	1991–1998	H	N/A	8	Flower Garden Banks	N/A	Hagman et al. 1998
<i>O. franki</i>	21:50	1997/08/27	H	2:10	10	Flower Garden Banks	1	Vize et al. 2005

Table 2 (continued)

Species	Time of day	Date	Sex	Hour after sunset	NAFM	Reef name	Number of individuals	Reference
<i>O. franki</i>	22:00-?	1998/08/15	H	2:07-?	8	Flower Garden Banks	6	Vize et al. 2005
<i>O. franki</i>	21:19-21:56	1999/09/02	H	1:51-2:22	7	Flower Garden Banks	2	Vize 2006
<i>O. franki</i>	21:45-22:02	2001/08/09	H	1:47-2:02	6	Flower Garden Banks	> 1	Vize et al. 2005
<i>O. franki</i>	21:40-22:10	2001/08/10	H	1:43-2:13	7	Flower Garden Banks	> 50	Vize et al. 2005
<i>O. franki</i>	?-22:31	2001/08/11	H	?-2:35	8	Flower Garden Banks	10	Vize et al. 2005
<i>O. franki</i>	21:15-22:00	2001/09/09	H	1:49-2:34	8	Flower Garden Banks	> 50	Vize et al. 2005
<i>O. franki</i>	21:17-21:54	2001/09/10	H	1:52-2:29	9	Flower Garden Banks	50	Vize et al. 2005
<i>O. franki</i>	21:30-22:00	2002/08/28	H	1:50-2:20	7	Flower Garden Banks	20	Vize et al. 2005
<i>O. franki</i>	21:22-22:05	2002/08/29	H	1:44-2:27	8	Flower Garden Banks	50	Vize et al. 2005
<i>O. franki</i>	21:41-22:14	2003/08/18	H	1:51-2:24	7	Flower Garden Banks	50	Vize et al. 2005
<i>O. franki</i>	22:12	2003/08/19	H	2:23-?	8	Flower Garden Banks	20	Vize et al. 2005
<i>P. strigosa</i>	20:30-22:30	1991-1998	H	N/A	8	Flower Garden Banks	N/A	Hagman et al. 1998
<i>P. strigosa</i>	20:30	1987/08/16	H	N/A	7	El Mario, La Parguera, Puerto Rico	1	Steiner 1995
<i>P. strigosa</i>	18:00	1994/08/28	H	2:10	7	Roatan, Honduras	N/A	Gittings et al. 1994
<i>P. strigosa</i>	20:45	1996/09/04	H	N/A	7	Leonora's Reef, Bonaire	1	De Graaf, 1999
<i>P. strigosa</i>	21:42-?	1997/08/26	H	2:01-?	9	Flower Garden Banks	5	Vize et al. 2005
<i>P. strigosa</i>	21:15-?	1998/08/15	H	1:22-?	8	Flower Garden Banks	6	Vize et al. 2005
<i>P. strigosa</i>	21:53	1999/09/02	H	2:19	7	Flower Garden Banks	1	Vize et al. 2006
<i>P. strigosa</i>	21:20-?	1999/09/03	H	1:47-?	9	Flower Garden Banks	> 20	Vize et al. 2005
<i>P. strigosa</i>	21:37-22:03	1999/09/05	H	2:06-2:32	11	Flower Garden Banks	4	Vize et al. 2005
<i>P. strigosa</i>	< 20:45-22:05	2001/08/10	H	< 0:48-2:08	7	Flower Garden Banks	> 50	Vize et al. 2005
<i>P. strigosa</i>	19:56-22:00	2001/09/09	H	1:30-2:34	8	Flower Garden Banks	22	Vize et al. 2005
<i>P. strigosa</i>	21:15-22:06	2001/09/10	H	1:50-2:41	9	Flower Garden Banks	50	Vize et al. 2005
<i>P. strigosa</i>	20:55-22:00	2002/08/29	H	1:17-2:22	8	Flower Garden Banks	30	Vize et al. 2005
<i>P. strigosa</i>	20:40	2002/08/30	H	1:03	9	Flower Garden Banks	1	Vize et al. 2005
<i>P. strigosa</i>	22:00	2003/08/18	H	2:10	7	Flower Garden Banks	2	Vize et al. 2005
<i>P. strigosa</i>	21:30-22:30	2003/08/19	H	1:41-2:41	8	Flower Garden Banks	15	Vize et al. 2005

Sex: F female, M male, H hermaphrodite. NAFM night after full moon. Dates presented in YYYY-MM-DD format

reproductive ecology of reef-building corals at mesophotic depths highlight overlapping spawning windows, and together with genetic and biophysical data (Garavelli et al. 2018; Studivan and Voss 2018a, b), further support the notion that corals across these depths have the potential to interbreed and should be managed as a single population.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12526-020-01159-4>.

Acknowledgments We are grateful to Global Foundation for Ocean Exploration (GFOE) engineers and scientists including Dave Lovalvo, Melissa Ryan, Todd Gregory, Jeff Laning, Roland Brian, Joshua Carlson, and Karl McLetchie, who through a grant awarded to GFOE from NOAA's Office of National Marine Sanctuaries made these observations possible, and to the FGB National Marine Sanctuary staff and crew of the R/V *Manta* for ship time and permitting: Marissa Nuttall, Justin Blake, and G.P. Schmahl. We are also grateful for additional collaborators Drs. Joshua Voss, Mercer Brugler, and Shirley Pomponi and anonymous reviewers who have ameliorated the manuscript during its development.

Funding This study was supported by the National Oceanic and Atmospheric Administration NOAA-NOS-ONMS-2018-2005606.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable guidelines for the care and use of animals were followed by the authors.

Sampling and field studies All observational field studies were obtained through permit: FGBNMS-2018-006-A1.

Data availability All data generated during the study are included in the published article.

Authors' contributions SWD conceived and designed the research. MES, HEA, BEB, LIH, ELH, and SWD contributed observations and wrote the manuscript. CAT and HEWD reviewed video footage and compiled data for Tables 1 and 2. All authors read and approved the manuscript.

References

- Acosta A, Zea S (1997) Sexual reproduction of the reef coral *Montastrea cavernosa* (Scleractinia: Faviidae) in the Santa Marta area, Caribbean coast of Colombia. *Mar Biol* 128:141–148. <https://doi.org/10.1007/s002270050077>
- Bongaerts P, Ridgway T, Sampayo EM, Hoegh-Guldberg O (2010) Assessing the “deep reef refugia” hypothesis: focus on Caribbean reefs. *Coral Reefs* 29:1–19. <https://doi.org/10.1007/s00338-009-0581-x>
- Davies SW, Strader ME, Kool JT et al (2017) Modeled differences of coral life-history traits influence the refugium potential of a remote Caribbean reef. *Coral Reefs* 36:913–925. <https://doi.org/10.1007/s00338-017-1583-8>
- De Graaf M, Geertjes GJ, Videler JJ (1999) Observations on spawning of scleractinian corals and other invertebrates on the reefs of Bonaire (Netherlands Antilles, Caribbean). *Bull Mar Sci* 64:189–194
- de Oliveira MD, Thé J, Araújo D et al (2020) Why do mesophotic coral ecosystems have to be protected? *Sci Total Environ* 726:138456. <https://doi.org/10.1016/j.scitotenv.2020.138456>
- Frade PR, Bongaerts P, Englebert N et al (2018) Deep reefs of the Great Barrier Reef offer limited thermal refuge during mass coral bleaching. *Nat Commun* 9:3447. <https://doi.org/10.1038/s41467-018-05741-0>
- Garavelli L, Studivan MS, Voss JD et al (2018) Assessment of mesophotic coral ecosystem connectivity for proposed expansion of a marine sanctuary in the Northwest Gulf of Mexico: larval dynamics. *Front Mar Sci* 5:174. <https://doi.org/10.3389/fmars.2018.00174>
- Gardner TA, Côté IM, Gill JA et al (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:958–960. <https://doi.org/10.1126/science.1086050>
- Gittings SR, Boland GS, Deslarzes KJP et al (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
- Gittings SR, Boland GS, Merritt CRB et al (1994) Mass spawning by reef corals in the Gulf of Mexico and Caribbean Sea. Flower Garden Banks Fund Technical Series Report No.94-03
- Gori A, Viladrich N, Kotta M et al (2012) Reproductive cycle and trophic ecology in deep versus shallow populations of the Mediterranean gorgonian *Eunicella singularis* (Cap de Creus, northwestern Mediterranean Sea). *Coral Reefs* 31:823–837. <https://doi.org/10.1007/s00338-012-0904-1>
- Hagman DK, Gittings SR, Deslarzes KJP (1998) Timing, species participation, and environmental factors influencing annual mass spawning at the Flower Garden Banks (northwest Gulf of Mexico). *Gulf Mex Sci* 16:170–179. <https://doi.org/10.18785/goms.1602.06>
- Holstein DM, Smith TB, Gyory J, Paris CB (2015) Fertile fathoms: deep reproductive refugia for threatened shallow corals. *Sci Rep* 5:12407. <https://doi.org/10.1038/srep12407>
- Holstein DM, Smith TB, Paris CB (2016) Depth-independent reproduction in the reef coral *Porites astreoides* from shallow to mesophotic zones. *PLoS One* 11:e0146068. <https://doi.org/10.1371/journal.pone.0146068>
- Johnston MA, Nuttall MF, Eckert RJ, Embesi JA (2014) Long-term monitoring at East and West Flower Garden Banks National Marine Sanctuary: 2013 annual report. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Flower Garden Banks National Marine Sanctuary, Galveston, TX. 59 pp.
- Johnston MA, Embesi JA, Eckert RJ et al (2016) Persistence of coral assemblages at East and West Flower Garden Banks, Gulf of Mexico. *Coral Reefs* 35:821–826. <https://doi.org/10.1007/s00338-016-1452-x>
- Johnston MA, O'Connell K, Blakeway RD, et al (2020) Long-term monitoring at East and West Flower Garden Banks: 2019 annual report. Marine Sanctuaries Conservation Series ONMS-2020. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Flower Garden Banks National Marine Sanctuary, Galveston, TX. 93 pp.
- Jordan AC (2018) Patterns in Caribbean coral spawning. Masters thesis. Nova Southeastern University
- Kirk JTO (2011) Light and photosynthesis in aquatic ecosystems, Cambridge. <https://doi.org/10.1017/CBO9780511623370>
- Laverick JH, Piango S, Andradi-Brown DA et al (2018) To what extent do mesophotic coral ecosystems and shallow reefs share species of conservation interest? A systematic review. *Environ Evid* 7:15. <https://doi.org/10.1186/s13750-018-0127-1>

- Lesser MP, Slattery M, Leichter JJ (2009) Ecology of mesophotic coral reefs. *J Exp Mar Biol Ecol* 375:1–8. <https://doi.org/10.1016/j.jembe.2009.05.009>
- Limer BD, Bloomberg J, Holstein DM (2020) The influence of eddies on coral larval retention in the Flower Garden Banks. *Front Mar Sci* 7:372. <https://doi.org/10.3389/fmars.2020.00372>
- Lugo-Fernández A, Deslarzes KJP, Price JM et al (2001) Inferring probable dispersal of Flower Garden Banks coral larvae (Gulf of Mexico) using observed and simulated drifter trajectories. *Cont Shelf Res* 21:47–67. [https://doi.org/10.1016/S0278-4343\(00\)00072-8](https://doi.org/10.1016/S0278-4343(00)00072-8)
- Miller MW, Baums IB, Pausch RE et al (2018) Clonal structure and variable fertilization success in Florida Keys broadcast-spawning corals. *Coral Reefs* 37:239–249. <https://doi.org/10.1007/s00338-017-1651-0>
- Prasertia R, Sinniger F, Harii S (2016) Gametogenesis and fecundity of *Acropora tenella* (Brook 1892) in a mesophotic coral ecosystem in Okinawa, Japan. *Coral Reefs* 35:53–62. <https://doi.org/10.1007/s00338-015-1348-1>
- Prasertia R, Sinniger F, Harii S (2017a) First record of spawning in the mesophotic *Acropora tenella* in Okinawa, Japan. *Galaxea J Coral Reef Stud* 19:5–6. https://doi.org/10.3755/galaxea.19.1_5
- Prasertia R, Sinniger F, Hashizume K, Harii S (2017b) Reproductive biology of the deep brooding coral *Seriatopora hystrix*: implications for shallow reef recovery. *PLoS One* 12:e0177034. <https://doi.org/10.1371/journal.pone.0177034>
- Rippe JP, Matz MV, Green EA et al (2017) Population structure and connectivity of the mountainous star coral, *Orbicella faveolata*, throughout the wider Caribbean region. *Ecol Evol* 7:9234–9246. <https://doi.org/10.1002/ece3.3448>
- Rocha LA, Pinheiro HT, Shepherd B et al (2018) Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. *Science* 361:281–284. <https://doi.org/10.1126/science.aaq1614>
- Sánchez JA, Alvarado EM, Gil MF et al (1999) Synchronous mass spawning of *Montastraea annularis* (Ellis & Solander) and *Montastraea faveolata* (Ellis & Solander) (Faviidae: Scleractinia) at Rosario Islands, Caribbean coast of Colombia. *Bull Mar Sci* 65:873–879
- Schmahl GP, Hickerson EL, Precht WF (2008) Biology and ecology of coral reefs and coral communities in the Flower Garden Banks Region, Northwestern Gulf of Mexico. In: Riegl BM, Dodge RE (eds) *Coral Reefs of the USA*. Springer Netherlands, Dordrecht, pp 221–261
- Shlesinger T, Grinblat M, Rapuano H et al (2018) Can mesophotic reefs replenish shallow reefs? Reduced coral reproductive performance casts a doubt. *Ecology* 99:421–437. <https://doi.org/10.1002/ecy.2098>
- Shlesinger T, Loya Y (2019) Breakdown in spawning synchrony: a silent threat to coral persistence. *Science* 365:1002–1007. <https://doi.org/10.1126/science.aax0110>
- Slattery M, Moore S, Boye L et al (2018) The Pulley Ridge deep reef is not a stable refugia through time. *Coral Reefs* 37:391–396. <https://doi.org/10.1007/s00338-018-1664-3>
- Smith TB, Gyory J, Brandt ME et al (2016) Caribbean mesophotic coral ecosystems are unlikely climate change refugia. *Glob Chang Biol* 22:2756–2765. <https://doi.org/10.1111/gcb.13175>
- Soong K (1991) Sexual reproductive patterns of shallow-water reef corals in Panama. *Bull Mar Sci* 49:832–846
- Steiner SC (1995) Spawning in scleractinian corals from SW Puerto Rico (West Indies). *Bull Mar Sci* 56:899–902
- Studivan MS, Voss JD (2018a) Population connectivity among shallow and mesophotic *Montastraea cavernosa* corals in the Gulf of Mexico identifies potential for refugia. *Coral Reefs* 37:1183–1196. <https://doi.org/10.1007/s00338-018-1733-7>
- Studivan MS, Voss JD (2018b) Assessment of mesophotic coral ecosystem connectivity for proposed expansion of a marine sanctuary in the Northwest Gulf of Mexico: population genetics. *Front Mar Sci* 5:174. <https://doi.org/10.3389/fmars.2018.00152>
- Szmant AM (1991) Sexual reproduction by the Caribbean reef corals *Montastrea annularis* and *M. cavernosa*. *Mar Ecol Prog Ser* 74:13–25. <https://doi.org/10.3354/meps074013>
- Vize PD (2006) Deepwater broadcast spawning by *Montastraea cavernosa*, *Montastraea franksi*, and *Diploria strigosa* at the Flower Garden Banks, Gulf of Mexico. *Coral Reefs* 25:169–171. <https://doi.org/10.1007/s00338-005-0082-5>
- Vize PD, Embesi JA, Nickell M et al (2005) Tight temporal consistency of coral mass spawning at the Flower Garden Banks, Gulf of Mexico, from 1997 to 2003. *Gulf Mex Sci* 23:107–114. <https://doi.org/10.18785/goms.2301.08>
- Weil E (2019) Disease Problems. In: Loya Y et al (eds) *Mesophotic coral ecosystems, coral reefs of the world* 12. Springer Nature, Switzerland, pp 779–800
- Wyers SC, Barnes HS, Smith SR (1991) Spawning of hermatypic corals in Bermuda: a pilot study. *Hydrobiologia* 216–217:109–116. <https://doi.org/10.1007/BF00026450>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.