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A coral spawning calendar for Sesoko Station, Okinawa, Japan

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Abstract Sesoko Station, Okinawa, has been the site of many significant advances in coral reproductive research and it continues to be a preferred destination for both Japanese and international researchers. Consequently, there are decades of spawning observations, which we present and explore here with the aim of making it easier to predict when species spawn at Sesoko Station. The data include over 700 spawning observations from 87 species of reef-building hermatypic corals. Almost all spawning occurred between dusk and dawn, with most spawning activity concentrated in the 2 to 4 hours after sunset. Some phylogenetic patterns were evident: most *Acropora* species spawn on or around the 6th full moon after December 21st (the northern hemisphere winter solstice); spawning in common species of merulinids and *Porites* appears to be concentrated around the 7th full moon and spawning in the fungiids around the 8th and subsequent full moons. The night of peak spawning with respect to the night of the full moon varied considerably among years in common *Acropora* species, but was dependent on the calendar date of the full moon in May or June. Therefore, despite an extended spawning season of over three months and considerable variation in the calendar date of spawning in many species among years, the month and night of spawning are reasonably predictable for many species enhancing the value of Sesoko Station as a site for coral reproductive research.

Keywords Coral reefs, Phenology, Reproduction, Multi-species synchronous spawning

Introduction

Most scleractinian corals broadcast spawn their gametes for external fertilization (Harrison and Wallace 1990; Baird et al. 2009). In general, each colony spawns once per year, often in high synchrony with nearby conspecifics. These multi-specific spawning events are an excellent opportunity for scientists to access coral propagules for experiments. The time of spawning is often predictable in terms of the month of the year, the day relative to the full moon and the time of day, however, there is considerable annual variation at most temporal scales that has yet to be fully explored. Being able to accurately predict spawning dates and times is essential for planning field trips to conduct coral spawning work and for managing human activities that affect coral reproduction, such as dredging (Baird et al. 2011; Styan and Rosser 2012).

The Tropical Biosphere Research Center (TBRC) of the University of the Ryukyus, based on Sesoko Island in the prefecture of Okinawa (hereafter referred to as Sesoko Station), was opened in 1971. Sesoko Station has been the site of many significant advances in coral reproductive research and it continues to be a preferred destination for both Japanese and international researchers. The first records for coral spawning times at Sesoko Station are those of Heyward et al. (1987). Other landmark studies on coral reproductive biology and larval ecology from Sesoko include the first records of daytime spawning (Kinzie 1993), the first records of a single colony being able to both brood and broadcast spawn propagules (Sakai 1997), the first evidence to suggest that individuals of some fungiids can change sex (Loya and Sakai 2008), some of the first work to explore the timing of the acquisition of zooxanthellae in the early life-history of corals (Harii et al. 2009), the effect of increased temperature on pre-competent periods in coral planulae (Figueiredo et al. 2014) and evidence of the first naturally occurring coral hybrids in the Indo-Pacific (Morita et al. 2019). Sesoko Station is also the site of some of the most exhaustive and detailed observation of coral spawning *in situ*. In particular, Dr Satoshi Nojima spent up to 4 hours a night on the reef in front of Sesoko Station every night for over 30 days in 1993 to record coral spawning, a feat which was recently repeated by Dr Takuma Mezaki.

Many interesting and important questions can be addressed with data on the timing of coral spawning. Spawning times are a useful line of evidence in taxonomic studies. For example, if two putative species spawn at different times they are likely to be different species (Wolstenholme 2004; Furukawa et al. 2020). Effective conservation and management of coral reefs is also dependent on knowing when corals spawn. For example, potentially damaging activities, such as dredging, can be prohibited at times that corals are known or predicted to spawn (Baird et al. 2011; Jones et al. 2015). Coral spawning is also a significant attraction for tourists in many parts of the world. Knowing when corals spawn is also fundamental to understanding and predicting patterns of connectivity, given that currents vary seasonally in many parts of the world (Hock et al. 2019).

The aim of this paper is to provide a spawning calendar and some predictive tools to allow researchers to better manage human activities and plan field trips to Sesoko Station.

Materials and methods

Site description: The fringing reefs of Sesoko Island, Okinawa, Japan (26°38′42″N 127°51′52″E). For a description of the reef see Sakai and Yamazato (1987).

Source of data: The data are a subset of the dataset published by Baird et al. (2021). We included all data from sites around Sesoko. The only changes were that the open nomenclature status of two species *(Acropora* cf. *hyacinthus* and *Acropora* aff. *hyacinthus*) were dropped because at this location they appear to be one species.

Data exploration: The date of coral spawning is usually expressed in days relative to the date of the nearest full

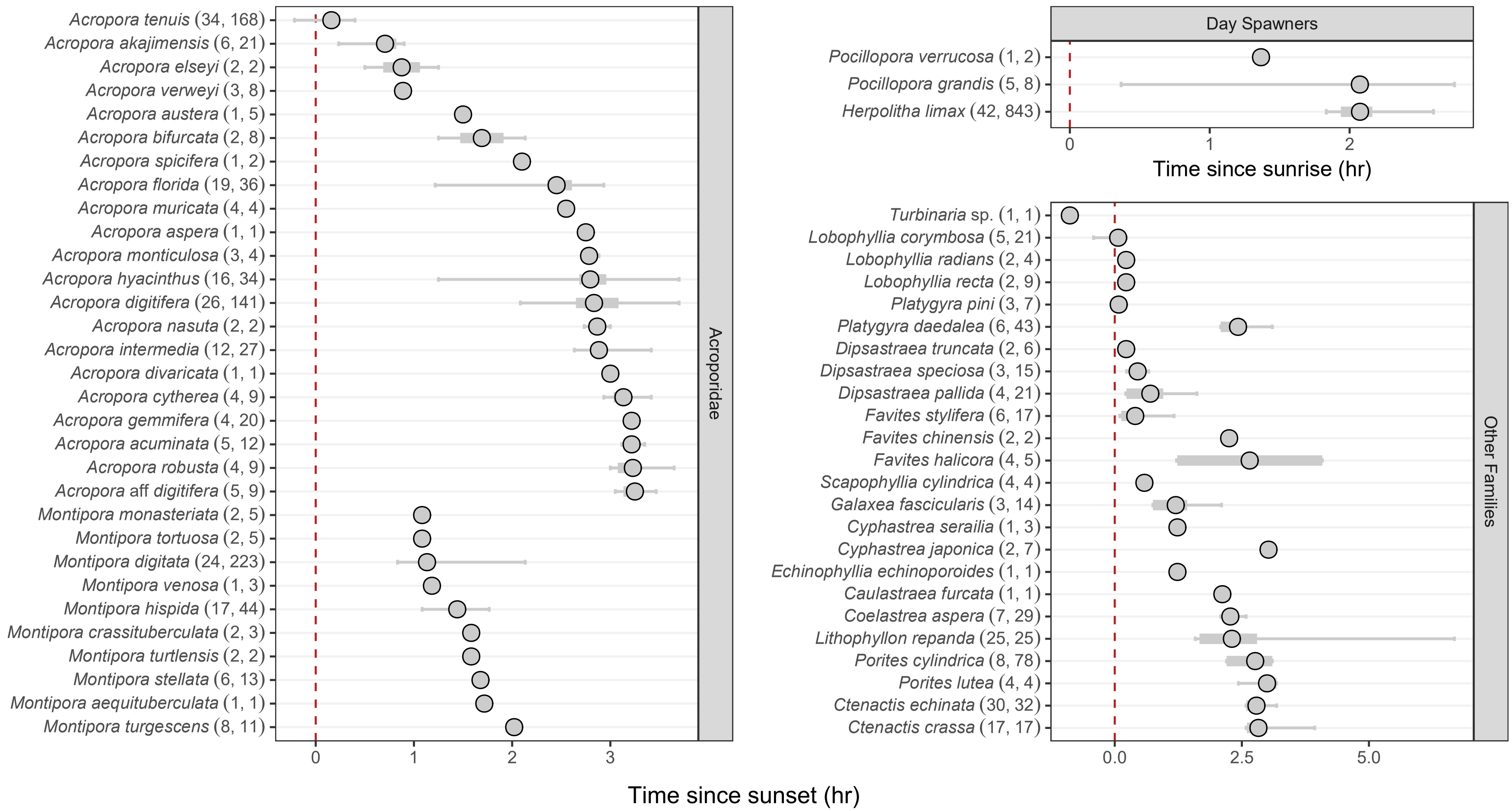

Fig. 1 The time of coral spawning relative to sunset or sunrise. The grey filled circle is the mean observed start time and the bars are the range of start times, showing the minimum and maximum (thin bars) and the 25th to 75th percentiles (thick bars). Within the brackets after each species, the first value represents the total number of records (e.g., nights when timing was noted) and the second value represents the total number of colonies observed to spawn (note: if the number of colonies was not recorded then at least one colony was assumed to have spawned).

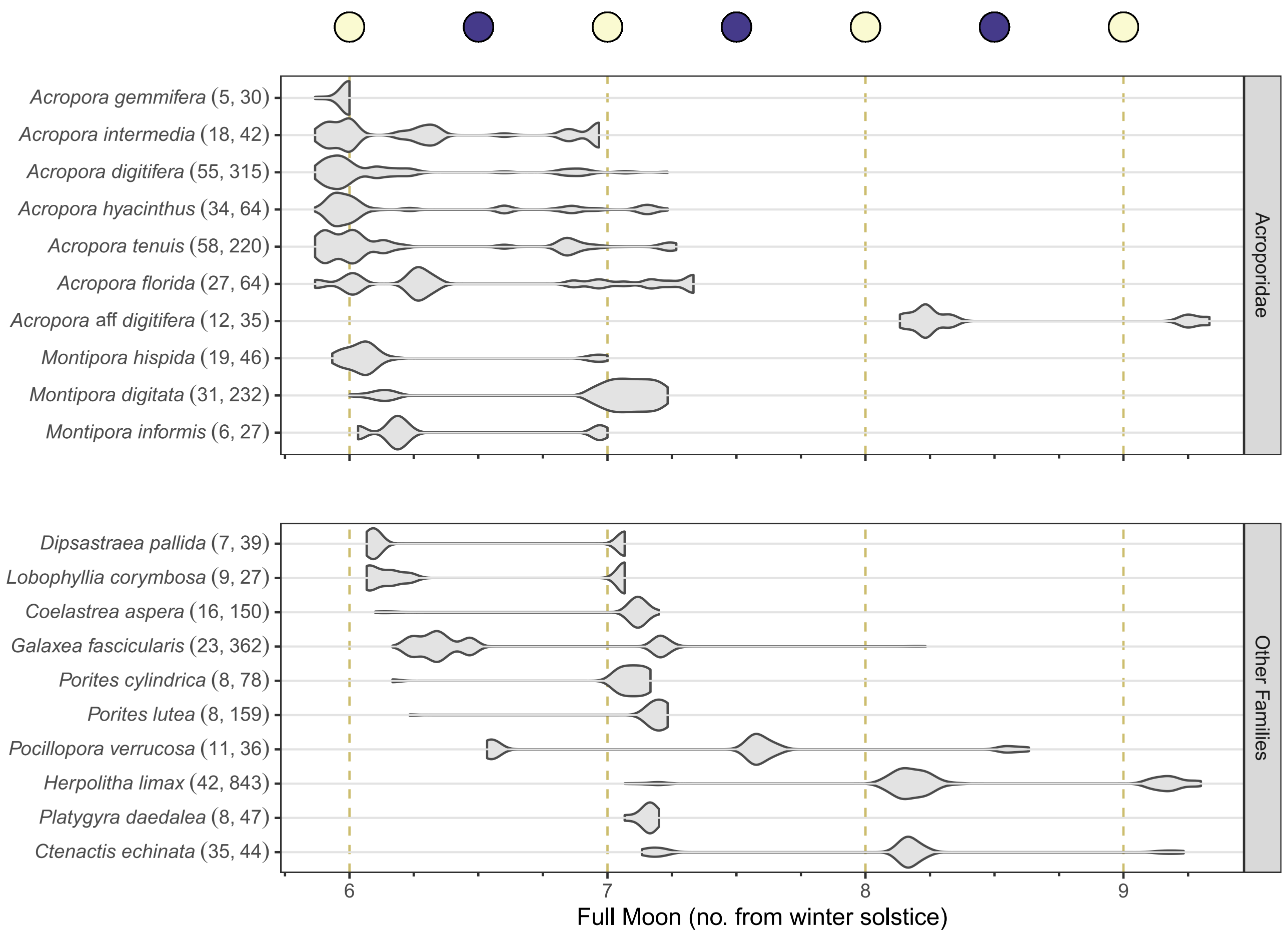

Fig. 2 A spawning calendar for some common coral species at Sesoko Island. The x-axis divides the year into lunar months with full moon 1 defined as the first full moon on or after December 21st of the previous calendar year. Full and new moons are represented as pale and dark circles, respectively. Within the brackets after each species name, the first value represents the total number of records (e.g., nights when spawning was observed) and the second value represents the total number of colonies observed to spawn (note: if the number of colonies was not recorded then at least one colony was assumed to have spawned). Violin contours show the probability density of spawning being observed at a specific date in the lunar calendar. A daily breakdown of the total number of colonies observed to spawn for each species, including rare species not shown here, can be found in the spawning calendar table in the electronic supplementary materials. All years of data are pooled.

moon. For the purpose of our spawning calendar, full moons were numbered consecutively from December 21 (the typical date of the northern hemisphere winter solstice). This resulted in full moon 1 in the lunar year being the first full moon on or after December 21 in the previous calendar year to spawning. This is in contrast to the Gregorian calendar which has spawning commencing in May in some years and June in others. Coral spawning relative to the lunar calendar was visualized for the 20 species with the greatest number of spawning observations. Probability density curves, presented as violin plots, were computed for each taxon to show the distribution of spawning observations through time. This required a decision on the smoothing bandwidth parameter value (standard deviation of the smoothing kernel). A value of 0.03 avoided over-smoothing, whilst still clearly showing dates without spawning observations. Observations with no spawning times recorded were removed from the analysis of spawning times relative to sunset resulting in a different number of observations for the same species between Fig. 1 & 2.

Results

Spawning times relative to sunset

Of the 58 species for which there are observations on the diel timing of spawning at Sesoko, most observations

Table 1 Summary of diel spawning times of 58 species on the fringing reefs of Sesoko Island, Okinawa, Japan. The # colonies column indicates the total number of colonies observed (note: if the number of colonies was not recorded then at least one colony was assumed to have been observed).

Night spawners			**All times decimal hours relative to sunset**					
Taxon	Observations	# colonies	Min_start	Mean_start	Max_start	Min_end	Mean_end	Max_end
Acropora acuminata	5	12	3.12	3.22	3.35	3.93	3.93	3.93
Acropora aff. *digitifera*	5	9	3.05	3.25	3.47			
Acropora akajimensis	6	21	0.23	0.71	0.90			
Acropora aspera	1	1	2.75	2.75	2.75			
Acropora austera	1	5	1.50	1.50	1.50			
Acropora bifurcata	2	8	1.25	1.69	2.13	2.13	2.13	2.13
Acropora cytherea	4	9	2.93	3.13	3.42	3.57	3.57	3.57
Acropora digitifera	24	128	2.08	2.84	3.70	2.08	3.53	4.25
Acropora divaricata	1	1	3.00	3.00	3.00	4.25	4.25	4.25
Acropora elseyi	2	2	0.50	0.88	1.25			
Acropora florida	19	36	1.22	2.45	2.93	2.62	2.86	3.32
Acropora gemmifera	4	20	3.18	3.22	3.25			
Acropora hyacinthus	15	32	1.25	2.80	3.70	3.70	3.70	3.70
Acropora intermedia	12	27	2.63	2.88	3.42	2.63	3.14	4.08
Acropora monticulosa	3	4	2.72	2.78	2.88	4.25	4.25	4.25
Acropora muricata	4	4	2.52	2.55	2.58			
Acropora nasuta	2	2	2.73	2.87	3.00	3.48	3.87	4.25
Acropora robusta	4	9	3.00	3.23	3.65	4.25	4.25	4.25
Acropora spicifera	1	2	2.10	2.10	2.10			
Acropora tenuis	34	168	−0.22	0.16	0.40	0.07	0.48	0.90
Acropora verweyi	3	8	0.85	0.89	0.92			
Caulastraea furcata	1	1	2.12	2.12	2.12	2.12	2.12	2.12
Coelastrea aspera	7	29	2.08	2.27	2.58	2.33	3.31	3.68
Ctenactis crassa	17	17	2.58	2.83	3.93	3.93	5.18	5.55
Ctenactis echinata	30	32	2.58	2.79	3.18	3.18	4.99	5.55
Cyphastrea japonica	2	7	2.88	3.03	3.17	3.17	3.17	3.17
Cyphastrea serailia	1	3	1.23	1.23	1.23			
Dipsastraea pallida	4	21	0.22	0.70	1.62	0.98	1.30	1.62
Dipsastraea speciosa	2	11	0.23	0.45	0.67	0.67	0.67	0.67
Dipsastraea truncata	2	6	0.22	0.23	0.23			
Echinophyllia echinoporoides	1	1	1.23	1.23	1.23			
Favites chinensis	2	2	2.25	2.25	2.25	3.58	3.58	3.58
Favites halicora	4	5	1.22	2.65	4.08			
Favites stylifera	6	17	0.10	0.40	1.17	0.10	0.49	1.17
Galaxea fascicularis	3	14	0.75	1.20	2.10	2.08	2.09	2.10
Lithophyllon repanda	25	25	1.58	2.30	6.68	7.68	7.68	7.68
Lobophyllia corymbosa	5	21	−0.42	0.07	0.23	−0.42	−0.04	0.15
Lobophyllia radians	2	4	0.22	0.23	0.23			
Lobophyllia recta	2	9	0.22	0.23	0.23			
Montipora aequituberculata	1	1	1.72	1.72	1.72			
Montipora crassituberculata	2	3	1.58	1.58	1.58			
Montipora digitata	24	223	0.83	1.13	2.13	1.58	2.11	3.17
Montipora hispida	17	44	1.08	1.44	1.77	2.10	2.10	2.10
Montipora monasteriata	2	5	1.08	1.08	1.08			
Montipora stellata	6	13	1.65	1.68	1.72			
Montipora tortuosa	2	5	1.08	1.08	1.08			
Montipora turgescens	8	11	1.98	2.02	2.07			
Montipora turtlensis	2	2	1.58	1.58	1.58			
Montipora venosa	1	3	1.18	1.18	1.18	3.18	3.18	3.18
Platygyra daedalea	6	43	2.08	2.43	3.10	2.58	3.41	3.85
Platygyra pini	3	7	0.00	0.08	0.23	1.08	1.08	1.08
Porites cylindrica	8	78	2.20	2.76	3.10	4.60	4.60	4.60
Porites lutea	4	4	2.43	3.00	3.18			
Scapophyllia cylindrica	4	4	0.58	0.58	0.58			
Turbinaria sp.	1	1	−0.88	−0.88	−0.88			
	359	**1180**						
Day spawners			**All times decimal hours relative to sunrise**					
Taxon	Observations	# colonies	Min_start	Mean_start	Max_start	Min_end	Mean_end	Max_end
Herpolitha limax	42	843	1.83	2.07	2.60	3.30	4.50	4.78
Pocillopora grandis	5	8	0.37	2.07	2.75	3.25	4.75	5.25
Pocillopora verrucosa	1	2	1.37	1.37	1.37	1.87	1.87	1.87
	48	**853**						

are concentrated in the first 4 hours after sunset (Table 1; Fig. 1; ESM). In contrast, *Herpolitha limax*, *Pocillopora grandis* and *P. verrucosa* start to spawn between 1 and 2 h after sunrise (Table 1; Fig. 1). The majority of *Acropora* spp. spawn between 2.5 and 3.5 hours after sunset (ESM). The exceptions are a few *Acropora* spp. that spawn within one hour of sunset, including *A. tenuis* and *A. akajimensis*. Some *Acropora* spp. have a large range of spawning times, e.g. *A. digitifera*, *A. hyacinthus* and *A. florida* (Fig. 1; ESM). *Montipora* spp. spawn between 1 and 3.5 hours after sunset, with most species spawning 1−2 hours after sunset (Table 1; Fig. 1; ESM). The majority of non-acroporid taxa spawn within 2 hours of sunset (ESM).

Lunar moon and night of spawning

The vast majority of spawning observations in the 87 taxa occur on or around full moons (ESM). The only species that does not follow this trend is *Pocillopora verrucosa* which spawns on the new moon (Fig. 2). For the *Acropora* spp., the majority of spawning observations are concentrated around the 6th moon following the winter solstice (ESM). Nonetheless, for species with greater than approximately 20 observations, spawning also occurred around the 7th moon following the winter solstice (ESM). In all species, spawning occurred over a considerable range of nights (ESM) and the night of peak spawning in some *Acropora* species is affected in part by the date of the full moon (Fig. 3). For example, if the 6th full moon falls before May 30 the *Acropora* tend to spawn on the nights after the full moon, whereas, if it falls after May 30 the *Acropora* tend to spawn on nights prior to the full moon (Fig. 3). One species, *A.* aff. *digitifera* (previously referred to as *Acropora* sp_1; e.g. Hayashibara and Shimoike (2002)) spawns two months later than the other *Acropora* species following the 8th moon after the winter

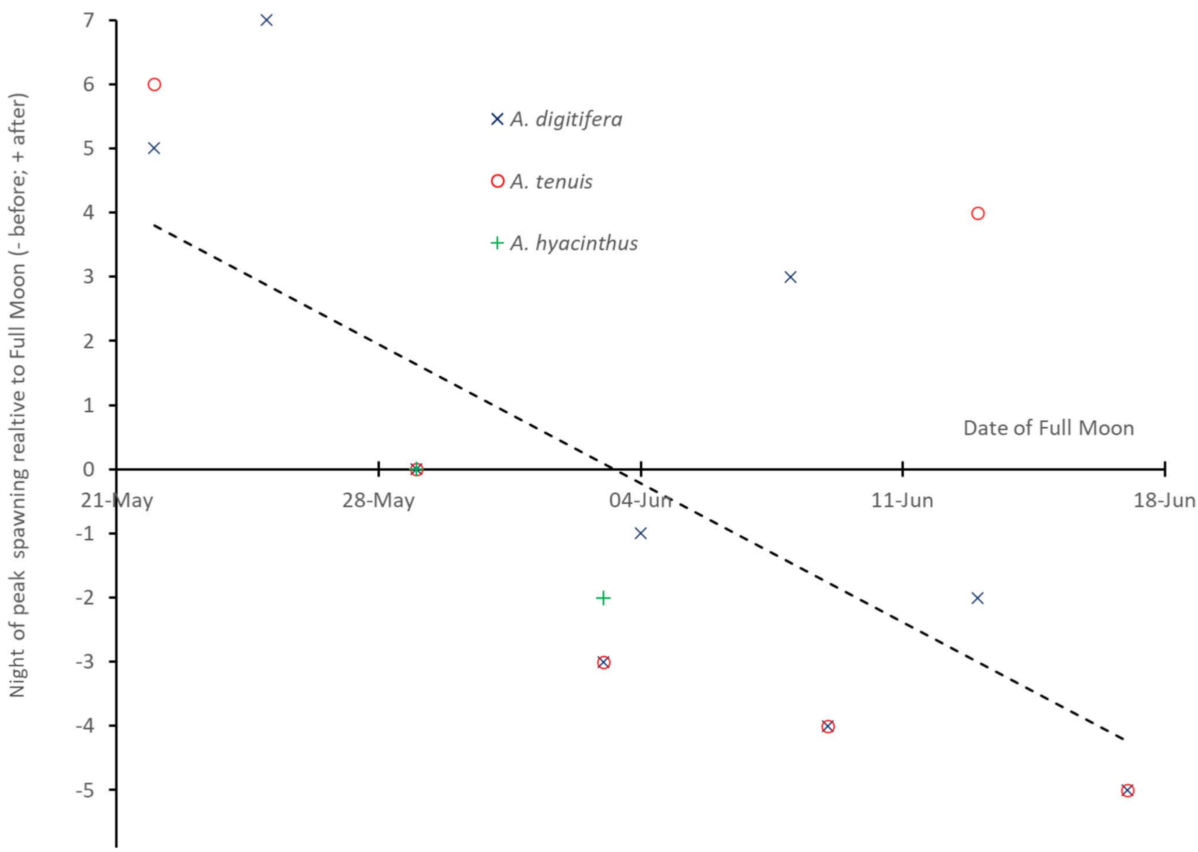

Fig. 3 The night of peak spawning in three species of the genus *Acropora* as a function of the calendar date of the full moon at Sesoko Station. The x-axis is the calendar date of the full moon, and the y-axis is the night of peak spawning in *Acropora tenuis*, *A. digitifera* and *A. hyacinthus* relative to the full moon. Peak spawning was defined as the night on which the highest proportion of *Acropora* colonies were observed to spawn. The dashed line is the trend line of all the points.

solstice.

Some *Acropora* spp. have two peaks in spawning observations within the 6th month after the winter solstice. For example, *A. intermedia* and *A. florida* have a peak in spawning observations just before the 6th moon and another approximately a week later.

The *Montipora* spp. have very similar patterns with respect to the lunar month to the *Acropora*, with most spawning observations concentrated around the 6th full moon and fewer on the 7th full moon (ESM). In contrast, spawning observations for the two *Porites* spp. are concentrated around the 7th full moon (ESM). In addition to *A.* aff. *digitifera* mentioned above, the only other species with spawning observations later in the lunar year are four fungiid spp. (Fig. 2, ESM 1) that spawn following moons 7, 8 and 9 plus some *Galaxea* colonies following the 8th full moon (ESM).

Discussion

The vast majority of spawning observations in Sesoko occur at night. These results are similar to observations from other regions in the Indo-Pacific, including the Great Barrier Reef (Harrison et al. 1984; Babcock et al. 1986) and the Red Sea (Shlesinger and Loya 1985; Bouwmeester et al. 2015), however, this in part reflects the fact that people are generally only looking for spawning at night. Species known to release gametes during the day include *Pavona* sp. (Plathong et al. 2006) and *Porites rus* (Bronstein and Loya 2011). Even with all the coral reproductive research at Sesoko over a 30 year period, there are still data on the night of spawning for only 87 species and data on the time of spawning for 58 species of the approximately 143 species recorded at Sesoko (Sakai and Yamazato 1987). Furthermore, the number of observations for many species is low. More work is needed at other times of the day to determine when these other species are spawning, in particular, species that are not from families well represented in the spawning observations to date, such as the Agariciidae and Coscinaraeidae.

Interestingly, there are no spawning observations before the 6th moon following the 21 December. While there are 114 records of spawning between 20th and 31st May (out of 711 records in total) all of these are from -3 to +6 days from the 6th full moon after the 21 December. Clearly, a lunar calendar commencing on 21 December is a better predictor of the month of coral spawning than the Gregorian calendar at Sesoko. Whether or not this predictive tool works in other locations in which there is annual variation in the first month of spawning, such as the GBR, needs to be tested.

Phylogeny appears to have an effect on the lunar month of spawning. Most acroporid and lobophylliid corals spawn on the 6th moon after 21 December; pocilloporids and poritids around the 7th and fungiids on the 8th moon after the winter solstice. Phylogeny also appears to influence the night of spawning within the mass spawning period on the Great Barrier Reef (Willis et al. 1985). Further research is required to identify whether there are similar patterns in other regions and to identify the causes of such patterns.

The night of peak spawning (defined as the night on which the most colonies were observed to spawn within a species) varied considerably among years in some species. For example, peak spawning of *A. tenuis* occurred anywhere from 5 days before to 6 days after the closest full moon (Fig. 3). A similar range in spawning nights was also evident in the *Acropora* spp. in Taiwan (Lin and Nozawa 2017). A similar range in spawning nights is not seen at sites on the Great Barrier Reef, such as Lizard Island or Orpheus Island (Baird et al. 2021). However, the night of spawning is associated with the calendar date of the full moon (Fig. 3) with spawning occurring earlier relative to the full moon the later the calendar date of the full moon. This pattern has recently been shown to be influenced, in part, by environmental conditions in the weeks and months prior to spawning, in particular, cumulative sea temperatures (Sakai et al. 2020).

Some caveats apply to these data, in particular, the value of the observed data to make predictions will be strongly dependent on the number of observations. However, the fact that the variability in these data increases with the number of observations suggests that making accurate predictions might always be difficult, particularly for variables such as the night of spawning. Furthermore, it remains to be tested whether the patterns observed at Sesoko apply in other parts of the world. For example, it would not be wise to predict the night of spawning for a given species on the Great Barrier Reef based on these data from Sesoko. Further research is required to test the generality of the patterns identified at Sesoko.

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Electronic supplementary material

ESM can be downloaded from the J-STAGE website: https://doi.org/10.3755/galaxea.G2021_S10O