Coral Reefs
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BRIEF REPORT

Patterns of coral spawning in the Palm Islands, Great Barrier Reef

Hanaka Mera[1] · Alasdair J. Edwards[2] · James R. Guest[2] · Liam Lachs[2] · Kate M. Quigley[1,3] · Bette L. Willis[1] · Andrew H. Baird[1]

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Abstract Scleractinian reproductive biology has been a focus of research since the discovery of multi-species synchronous spawning in the early 1980s; however, predicting when colonies will spawn on the Great Barrier Reef remains problematic. Here, we combine over 30 years of direct coral spawning observations that include colonies from 128 species from 44 genera in 10 families with 20 years of data on the stage of gamete maturity in colonies of *Acropora* (hereafter, colony reproductive condition) from the Palm Island group on the Great Barrier Reef to explore patterns within and among species. We find the lunar month counted from the southern hemisphere winter solstice better predicts the first month of spawning in the Palm Islands than the Gregorian month: spawning was never observed before the 5th lunar month. Direct observations suggest that most coral spawning in the Palm Islands occurs in the 5th and 6th lunar months over a 12-day interval starting one day before the full moon, between 30 min before and 5 h after sunset. Split spawning was also a frequent occurrence in *Acropora* populations. Some *Acropora* spp. had colonies that spawned in four or five different lunar months, a pattern that might be affected by taxonomic uncertainty. The range in spawning start times was considerably greater among colonies maintained in the laboratory vs those in the field, suggesting that spawning times are affected by handling. This work highlights the importance of a systematic approach to documenting spawning times to improve our understanding of spawning synchrony and seasonality.

Keywords Multi-species synchronous spawning · Split spawning · Scleractinia · Great Barrier Reef · Reproduction · Coral reefs

Introduction

The majority of hermatypic scleractinian corals reproduce sexually by broadcast spawning gametes for external fertilisation (Baird et al. 2009a; Harrison 2011). Spawning is often synchronous within populations, and there is also considerable overlap in the timing of spawning with populations of other species at a given location (Harrison et al. 1984; Baird et al. 2009a). Predicting when corals spawn is essential to various disciplines and industries including experimental biology, tourism, reef restoration and environmental management (Baird et al. 2011; Styan and Rosser 2012; Omori 2019; Randall et al. 2020). Hence, understanding both the local and broad scale geographical patterns of coral spawning and the environmental cues and underlying molecular mechanisms that induce coral spawning is an area of ongoing research (Keith et al. 2016; Lin and Nozawa 2017; Sakai et al. 2020; Lin et al. 2021).

Multi-species synchronous coral spawning was first documented on the central Great Barrier Reef (GBR) in Australia in the 1980s (Harrison et al. 1984; Babcock et al. 1986), including at sites around Orpheus Island Research Station on Goolboddi (in the Palm Island group, Queensland, ~ 20 km offshore). Harrison et al. (1984) originally

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✉ Hanaka Mera
hanaka.mera@my.jcu.edu.au

[1] College of Science and Engineering, James Cook University, 1 James Cook Drive, Townsville, QLD 4811, Australia

[2] School of Natural and Environmental Sciences, Newcastle University, Newcastle upon Tyne NE1 7RU, UK

[3] Minderoo Foundation, Perth, WA 6000, Australia

posited that “spawning can be predicted to occur at characteristic hours, four to five nights after one or two full moons in spring, from October to December”. Subsequent direct observations of coral spawning have generally confirmed these predictions for many scleractinian species within the region (Willis et al. 1985, 1997; van Oppen et al. 2002). However, deciding which of these one or two months to conduct field trips to best capture coral spawning is an ongoing challenge (Willis et al. 1985; Baird et al. 2009a) because the distance of most reefs from shore dictates that most spawning research on the GBR occurs on live-aboard vessels or island research station. Recent research from Okinawa suggests that predicting the first month of the spawning season can be improved by using a lunisolar calendar (Baird et al. 2022). This is not surprising, given that a calendar based on the cycles of the sun and moon is more likely to capture the features of the natural environment that organism use to time cycles of reproduction than the arbitrary nature of the Gregorian calendar. However, the utility of a lunisolar calendar for predicting a reproductive phenomenon has not been explored on the GBR, nor indeed is such test common in the phenology literature (Andreatta and Tessmar-Raible 2020; Ritter and Tessmar-Raible 2024). In addition, other lines of evidence suggest an extended reproductive season of up to six months, both on the GBR and in other well studied regions such as Japan (Wallace 1985; Wolstenholme 2004; Baird et al. 2009b, 2012). Here, we combine over 30 years of coral spawning observations with 20 years of data on colony reproductive condition sensu Baird et al. (2002) from the Palm Island group on the GBR to improve predictions of spawning timing and explore patterns within and among species.

Methods

Coral spawning observations

We extracted data from the Indo-Pacific Coral Spawning Database (Baird et al. 2021) to explore patterns of coral spawning in the Palm Island group in the central GBR, Queensland, Australia. This resulted in a total of 748 spawning observations from at least 1512 colonies between years 1982 and 2018 (Supplementary Data Table S1). We used full moon dates listed in the Coral Spawning Database (Baird et al. 2021) sheet "Full moon dates 1970_2030" for time zone "10" which corresponds to Australian Eastern Standard Time (AEST). Daily sunset and moonrise time data were obtained from Geoscience Australia "Geodetic Calculators" website (Geoscience Australia 2021), with the location criteria set as “Orpheus Island National Park” (18° 37′ S, 146° 29′ E). Observed genera were matched to families based on information at World Register of Marine Species database (Hoeksema and Cairns 2021).

Determining reproductive condition of Acropora colonies

To further explore the month of spawning, we used colony reproductive condition data from Bouwmeester et al. (2021) for the Palm Island group plus additional data collected in an identical manner between 2018 and 2020 in the Palm Island group. (All data are presented in Supplementary Data Table S2.) Colonies of *Acropora* were identified to the species level in the field or from photographs following Wallace (1999). Colonies were categorised into three reproductive conditions based on the colour of oocytes exposed by breaking branches following Baird et al. (2002): pigmented oocytes indicate that a colony is likely to spawn following the next full moon; white oocytes indicate the colony is likely to spawn on the 2nd full moon after sampling; and the absence of oocytes suggests the colony has recently spawned or is unlikely to spawn during the next three lunar cycles.

Data exploration

To test whether predicting the first month of the spawning season could be improved by using a lunisolar calendar as opposed to the Gregorian calendar, each spawning observation was assigned a lunar month, where lunar month 1 in a given year commenced on the date of the first full moon following the southern hemisphere winter solstice. The dates of past winter solstice were obtained from timeanddate.com website (accessed 11 May 2025). Similarly, the month of spawning as inferred from colony reproductive condition was explored using both the Gregorian calendar month and the lunar month. The night of spawning relative to the nearest full moon was explored for both in situ (i.e. in the field) and ex situ (i.e. laboratory) observations. The relationship between peak spawning day, defined as the day when the greatest number of colonies were recorded to spawn within the same lunar cycle, and the date of the nearest full moon was explored using linear regressions for selected taxa. Observations with times of first spawning were further explored in relation to the time of sunset using AEST. All data visualisations and summaries were performed in R v4.1.0 (R Core Team 2021) with base and additional packages including *lubridate* v1.9.3 (Grolemund and Wickham 2011), *tidyverse* v1.3.2 (Wickham et al. 2019) and *patchwork* v1.1.2 (Pedersen 2022).

Results

Comparing the Gregorian and lunisolar calendars to infer the month of spawning in coral assemblages

Spawning was observed for 128 species from 44 genera in 10 families. Most observations were from colonies within the family Acroporidae (46.6%), followed by colonies within the families Merulinidae (25.8%) and Poritidae (8.3%). Most observations (99.1%) occurred in the 5th and 6th lunar months (28.2% and 70.9%, respectively). In the Gregorian calendar, these same observations occurred in the months of October, November and December, with 75.3% of observations in November and 23.5% in December (Fig. 1a, b).

Direct spawning observations were spread over three months using both calendars. However, the spawning season on Orpheus Island always began in the 5th lunar month (Fig. 1b, d), in contrast to commencing in either October or November using the Gregorian calendar (Fig. 1a, c). The inferred month of *Acropora* spawning based on colony reproductive condition also indicated, with one exception out of 674 observations, that spawning began in the 5th lunar month (Fig. 1f): 50% of *A. longicyathus* colonies were inferred to spawn in October in 2017, corresponding to the 4th lunar month. Colony reproductive condition also indicated that some *Acropora* colonies spawned between January and March or the 8th and 10th lunar months (Fig. 1e, f).

Lunar month of spawning for *Acropora* spp.

Based on samples of colony reproductive condition, 26 common species of *Acropora* had at least some colonies that were predicted to have spawned in either lunar month 5 or 6 (Fig. 2). Some species were predicted to have spawned only early in the reproductive season, i.e. lunar months 5 and 6, including *A. cytherea, A. florida, A. hyacinthus, A. intermedia, A. millepora, A. muricata, A. papillare, A. pulchra, A. robusta, A. sarmentosa, A. selago* and *A. tenuis.* All species, except *A. microphthalma* and *A. subulata,* were predicted to have spawned in more than one lunar month. *Acropora cerealis, A. gemmifera, A. humilis, A. valenciennesi* and *A. valida* were predicted to have spawned in four different lunar months, whereas *A. digitifera, A. divaricata* and *A. nasuta* were predicted to have spawned in five different lunar months.

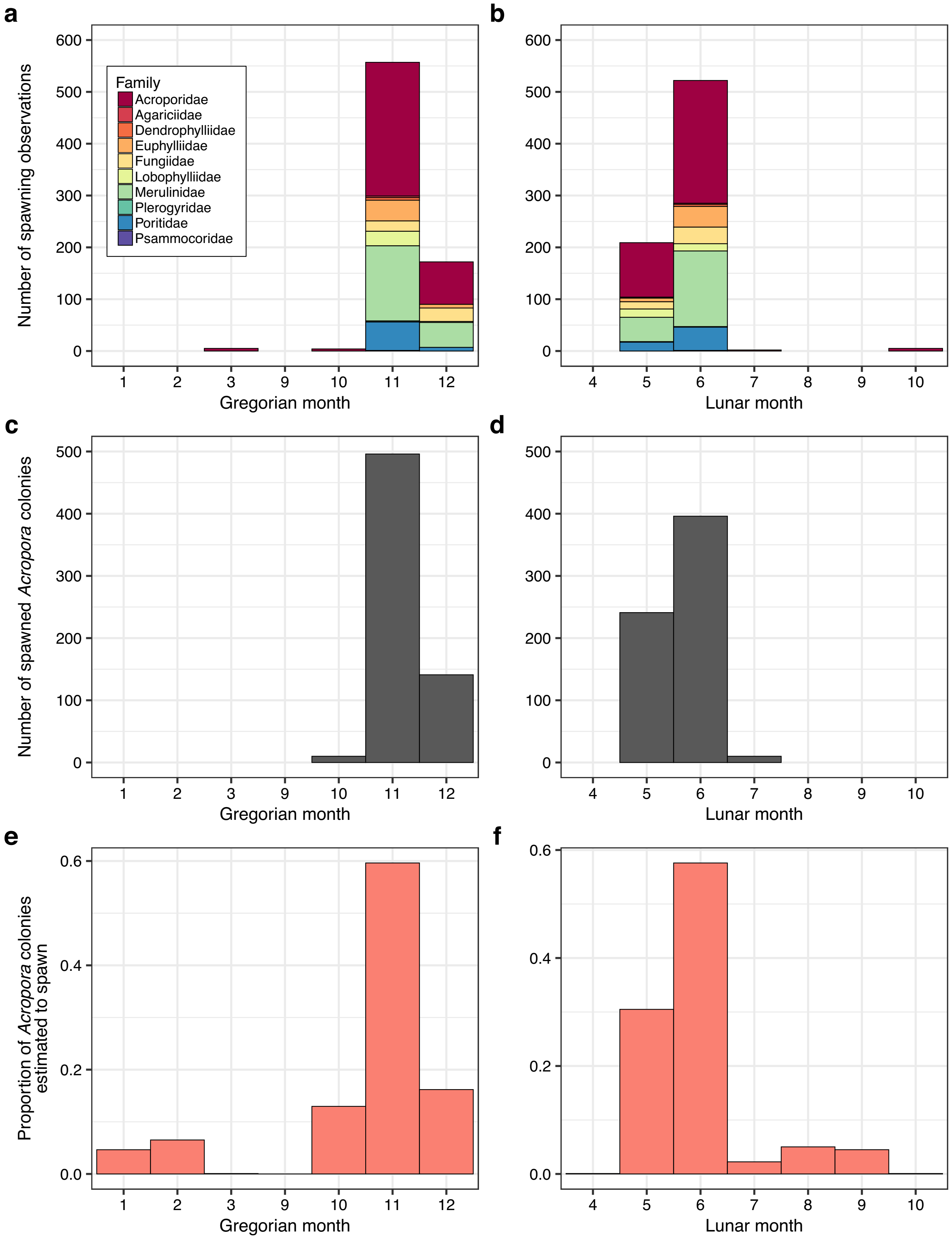
Split spawning

At the *Acropora* assemblage level and based on samples of colony reproductive condition, spawning was split over more than one lunar month in every year examined except 2019, when there was only one survey late in the season (Fig. 3a). The distribution of spawning among months varied from year to year. For example, in 1999, over 60% of *Acropora* colonies spawned in lunar month 6 compared to less than 10% in month 7. In contrast, in 2009 and 2010, spawning was comparatively evenly split between months 5 and 6. The lunar month of peak spawning also varied among years. For example, in 1999, 2006, 2010, 2012 and 2018 peak spawning occurred in lunar month 6, whereas in 2009, 2016 and 2017 peak spawning occurred in lunar month 5. In years when sampling was conducted every month during the spawning season (i.e. lunar month 4 to 10), e.g. 2006 and 2020, some spawning was inferred to have occurred in most months. The total estimated proportion of *Acropora* colonies spawning rarely reached 100% and was particularly low in 2020, when less than 50% of *Acropora* colonies were inferred to have spawned throughout the season despite sampling in every month.

In the four species of *Acropora* with sufficient data to examine temporal patterns, the total proportion of colonies predicted to spawn varied among years, but was generally consistent among these four species. For example, this proportion was relatively high in 1999, 2006 and 2018 but low in 2019 and 2020 (Fig. 3a). Spawning was split between lunar months in six of the ten years examined in *A. nasuta*, four of the ten years in *A. hyacinthus* and *A. millepora*, and two of the ten years in *A. spathulata* (Fig. 3b). The peak month of *Acropora* spawning varied among years but was generally consistent among the four species.

Day of spawning

Most direct spawning observations occurred a few nights before or after the full moon. Only two species, *Lobophyllia vitiensis* and *Oulophyllia bennettae*, were observed to spawn around the new moon (Supplementary Data Table S1). Spawning day relative to the date of the nearest full moon varied among families (Fig. 4). For example, the day of spawning ranged from − 1 to + 10 d relative to the full moon across five genera in the family Acroporidae, + 2 to + 8 d across 17 genera in the Merulinidae, and + 3 to + 6 d in two genera of Euphyllidae (Fig. 4a, b, e). Peak spawning days also varied among families. The earliest peak spawning occurred in the family Poritidae (+ 3 d) followed by corals in the families Acroporidae and Euphylliidae (+ 4 d), then Fungiidae, Lobophylliidae and Merulinidae (+ 5 d; Fig. 4). Variations were also seen within each family; for example, in the family Fungiidae, *Heliofungia* spawned on + 2 and + 5 to + 7 nights after full moon, whereas *Lithophyllon* ranged from + 4 to + 10 nights after full moon (Fig. 4c). Similarly, in the Family Lobophylliidae, *Lobophyllia* spawned


a
Number of spawning observations
600
500
400
300
200
100
0
Family
Acroporidae
Agariciidae
Dendrophylliidae
Euphylliidae
Fungiidae
Lobophylliidae
Merulinidae
Plerogyridae
Poritidae
Psammocoridae
1
2
3
9
10
11
12
Gregorian month
b
600
500
400
300
200
100
0
4
5
6
7
8
9
10
Lunar month
c
Number of spawned *Acropora* colonies
500
400
300
200
100
0
1
2
3
9
10
11
12
Gregorian month
d
500
400
300
200
100
0
4
5
6
7
8
9
10
Lunar month
e
Proportion of *Acropora* colonies estimated to spawn
0.6
0.4
0.2
0.0
1
2
3
9
10
11
12
Gregorian month
f
0.6
0.4
0.2
0.0
4
5
6
7
8
9
10
Lunar month

◂**Fig. 1** Month of coral spawning in terms of the Gregorian calendar months (**a**, **c**, **e**) and lunisolar calendar months (**b**, **d**, **f**). **a**, **b** Number of spawning observations per family; **c**, **d** number of *Acropora* colonies observed spawning; **e**, **f** proportion of *Acropora* colonies inferred to spawn based on colony reproductive condition. Data are pooled for all years

between + 4 and + 7 d after full moon, whereas the remaining genera spawned only 1 or 2 d (Fig. 4d). Peak spawning day differed by 2 d for the two major genera *Montipora* and *Acropora* in the family Acroporidae (+ 2 and + 4 d, respectively; Fig. 4a), as did peak spawning day for *Porites* and *Goniopora* in the family Poritidae (+ 3 and + 5 d, respectively; Fig. 4f).

Peak spawning as a function of the date of the full moon

Peak spawning day as a function of the date of the nearest full moon showed contrasting patterns between the four most frequently recorded *Acropora* species. For *A. hyacinthus* and *A. spathulata*, there were negative linear trends ($R^2 = 0.41$ and 0.80, respectively), indicating that peak spawning occurred closer to the full moon later in the calendar year, whereas there was no trend in the other two species (Fig. 5).

Time of spawning

Exact or approximate starting time of spawning were recorded for 536 observations and were restricted to a window from 16:00 to 23:37 AEST. Overall, spawning start times ranged from 2.5 h before to 5 h after sunset, with a mean of 2.2 h after sunset. Species in which some colonies spawned before sunset included *Acropora tenuis*, *A. pulchra*, *M. digitata*, *Galaxea fascicularis*, *Lithophyllon concinna*, *Pachyseris speciosa* and *Lobophyllia* sp. (Fig. 6).

Large variations in spawning start time were evident in some taxa. For example, *G. fascicularis* (family Euphylliidae) had a start time from 0.5 h before to 3.4 h after sunset, with 25th and 75th percentiles of 0.1 and 2.6 h after sunset, respectively. In contrast, *A. tenuis* had a similar number of observations as *G. fascicularis*; however, both percentiles were relatively closer to the mean. Some species in families Merulinidae and Lobophylliidae also had a wide range of spawning start times (e.g. *Coelastrea aspera, Favites abdita, Echinophyllia orpheensis*; Fig. 6).

In situ vs ex situ observations

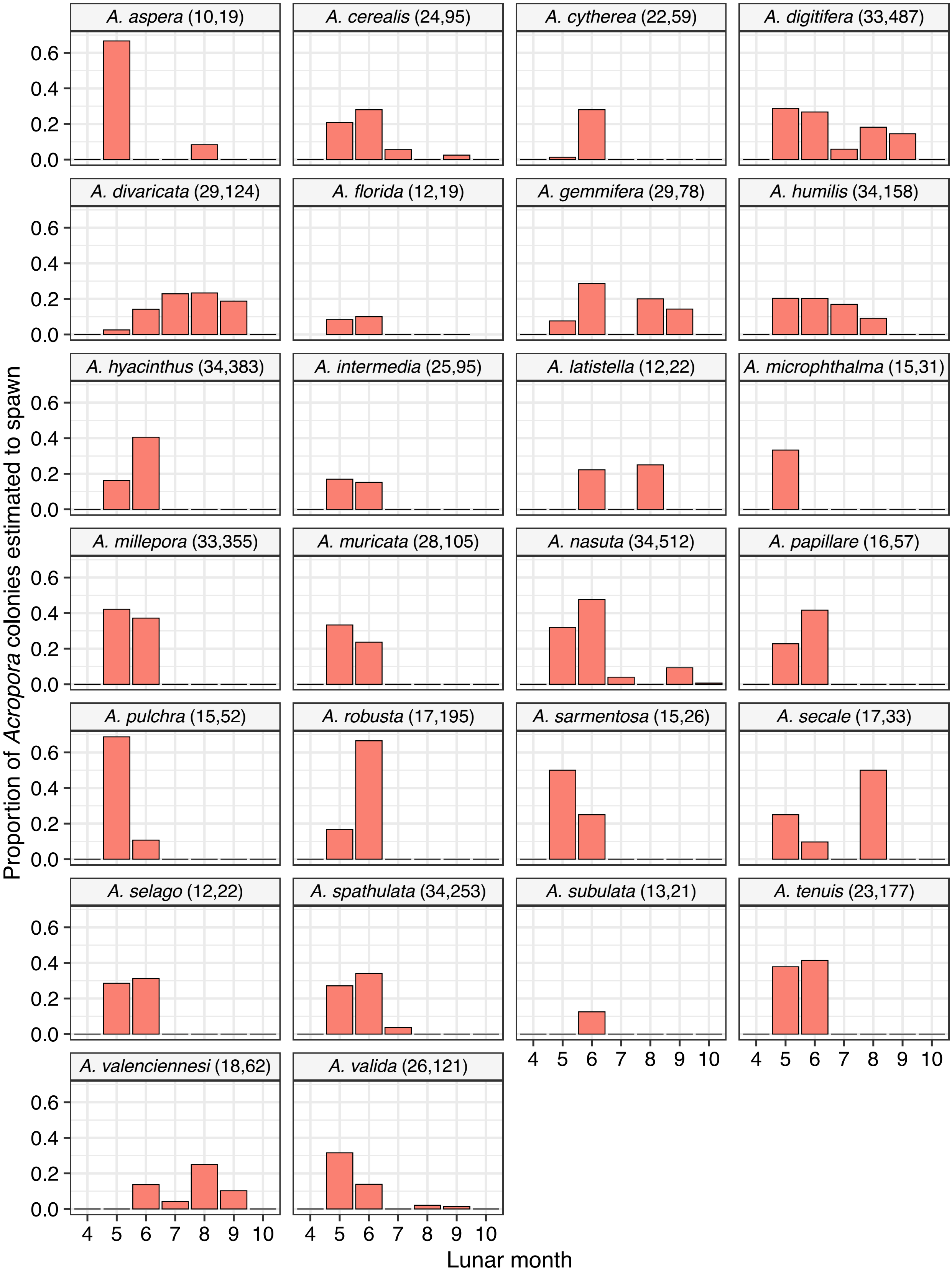
In situ records across all taxa were significantly fewer than ex situ ones (198 out of 748 observations). Peak spawning days were the same for both sets of records for the Acroporidae and Merulinidae, with spawning peaking on + 3 and + 4 d relative to the date of the nearest full moon, respectively (Fig. 7a, b). However, the range in spawning days differed for both families, with a range of -1 and + 3 to + 5 d in situ and − 1 to + 10 d ex situ for Acroporidae and + 2 and + 4 to + 6 d in situ and + 3 to + 8 d ex situ for Merulinidae (Fig. 7a, b). For the four frequently recorded *Acropora* spp., there was similarly a greater range in spawning days ex situ compared to in situ (Fig. 7c).

The time that spawning commenced in five commonly recorded species often varied by over an hour among colonies (Fig. 8). While the mean start time did not differ greatly among colonies maintained in the laboratory vs those in the field, the range in start time was greater for colonies maintained in the laboratory, except for *A. spathulata*, which only had one ex situ observation with spawning start time (Fig. 8).

Discussion

This study expands considerably on previously understood patterns of spawning times in broadcast spawning scleractinian corals within the Palm Island group. We confirm that most coral spawning occurs early in the austral summer (e.g. Harrison et al. 1984; Willis et al. 1985); however, we also demonstrate that many species of *Acropora* spawn outside of this window, with some spawning occurring in every month up to at least the 9th lunar month (e.g. Wallace 1985; Baird et al. 2002, 2009b; Wolstenholme 2004). We show that a lunisolar calendar is a better predictor of the first month of the spawning season, with no spawning inferred prior to the 5th lunar month after the southern winter solstice (June 21st). We also confirm differences in the night of peak spawning relative to the full moon among different taxa. Finally, we show that the range of spawning start times is considerably greater among colonies maintained in the laboratory vs those in the field, suggesting that spawning times are affected by handling.

Broadcast spawning of scleractinians in the Palm Island group almost invariably starts in the 5th lunar month, based on a lunisolar calendar commencing from the southern winter solstice. This result is similar to the pattern found for corals at Sesoko, Okinawa, Japan, where spawning almost invariably starts in the 6th lunar month after the northern hemisphere winter solstice (December 21st; Baird et al. 2022). This improved capacity to predict the first month of the spawning season is valuable when planning research and restoration activities; for example, corals are highly unlikely


A. aspera (10,19)
A. cerealis (24,95)
A. cytherea (22,59)
A. digitifera (33,487)
A. divaricata (29,124)
A. florida (12,19)
A. gemmifera (29,78)
A. humilis (34,158)
A. hyacinthus (34,383)
A. intermedia (25,95)
A. latistella (12,22)
A. microphthalma (15,31)
A. millepora (33,355)
A. muricata (28,105)
A. nasuta (34,512)
A. papillare (16,57)
A. pulchra (15,52)
A. robusta (17,195)
A. sarmentosa (15,26)
A. secale (17,33)
A. selago (12,22)
A. spathulata (34,253)
A. subulata (13,21)
A. tenuis (23,177)
A. valenciennesi (18,62)
A. valida (26,121)
0.0
0.2
0.4
0.6
4
5
6
7
8
9
10
Proportion of Acropora colonies estimated to spawn
Lunar month

◂**Fig. 2** Predicted lunar month of spawning in 26 common *Acropora* spp. based on colony reproductive condition. The numbers in parentheses next to species name indicate the total number of observations and colonies across all years pooled. Species with limited number of observations are excluded. Open nomenclature has been removed from taxon names

to spawn in October in the Palm Islands if only four full moons have passed since the winter solstice.

The length of the spawning season in the Palm Islands appears to be variable among *Acropora* species and among years. Estimates of the month of spawning based on the reproductive condition of *Acropora* spp. suggest that species fall into two broad groups: species that only spawn early in the breeding season (i.e. during lunar months 5–7) and species that spawn throughout the season (Fig. 2). Even among the early season spawning *Acropora* species, spawning was regularly split between consecutive months. Clearly, split spawning occurs frequently in populations and assemblages of *Acropora* (e.g. Baird et al. 2002, 2009b; Wolstenholme 2004; Guest et al. 2005). However, the prevalence of split spawning in these data might be a real phenomenon, or it might be a result of the current taxonomic framework (Cowman et al. 2020; Bridge et al. 2023). For example, unpublished molecular and morphological data suggest that colonies we identified as *A. digitifera* belong to two different species: one that spawns in November/December and one that spawn in February/March (pers. comm. AH Baird). An ongoing research initiative revising the taxonomy of *Acropora* on the GBR should help resolve the causes of extended spawning seasons in *Acropora* (see https://coralprojectphoenix.org).

Differences in the day of peak spawning were apparent between taxonomic groups, expanding on early studies of family and generic differences in the days of spawning on the GBR (Willis et al. 1985; Babcock et al. 1986). Similar patterns in peak spawning days for Acroporidae and Merulinidae have been observed in different regions, including Okinawa, Japan, and Lyudao, Taiwan (Hayashibara et al. 1993; Lin and Nozawa 2017). A correlation between the day of peak spawning and the calendar date of the full moon was evident for two of the four *Acropora* taxa examined in detail. These two species spawned closer to the date of full moon later in the calendar year, possibly because gametes have had longer to mature (Baird et al. 2022). This information is potentially useful in deciding when to bring corals into the laboratory from the field for spawning experiments. A similar pattern between the day of peak spawning and the calendar date of the full moon was evident in some species of *Acropora* spp. at Sesoko, Japan (Baird et al. 2022). However, more work is required to determine the generality of these results across a wider range of species and locations.

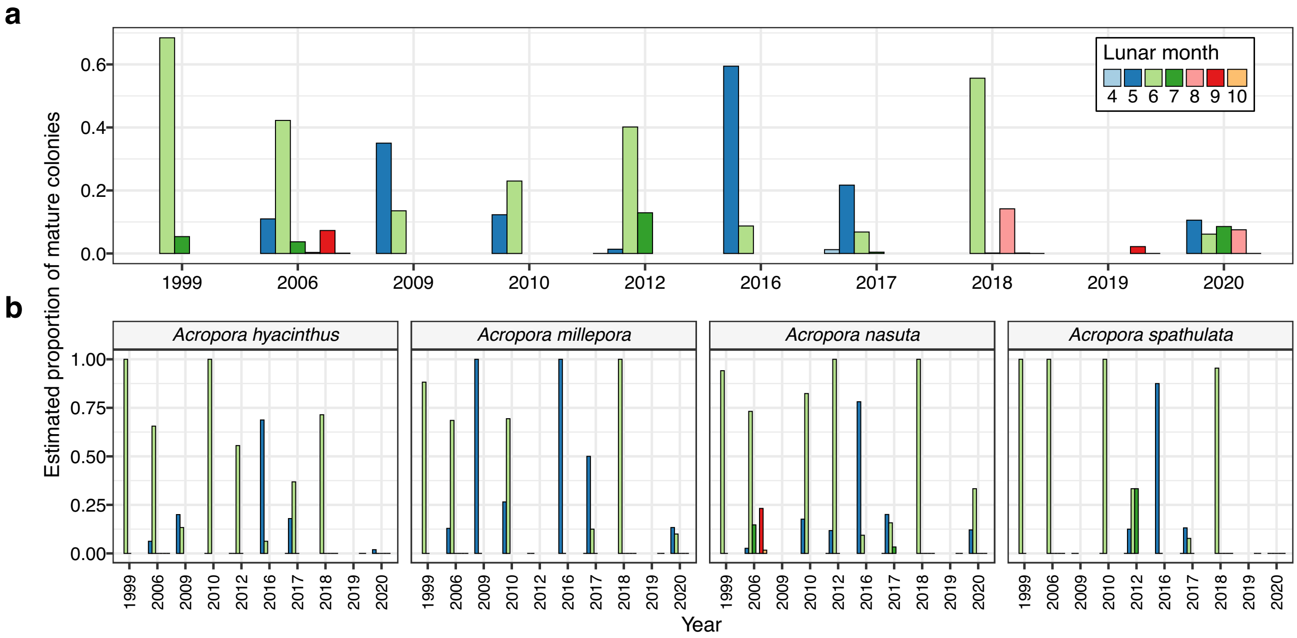


Fig. 3 Lunar month of spawning predicted from colony reproductive condition in **a** all *Acropora* spp. from all sites sampled in the Palm Islands and **b** four common *Acropora* spp. from two frequently visited sites (Pelorus Island south-east and Orpheus Island Little Pioneer Bay)

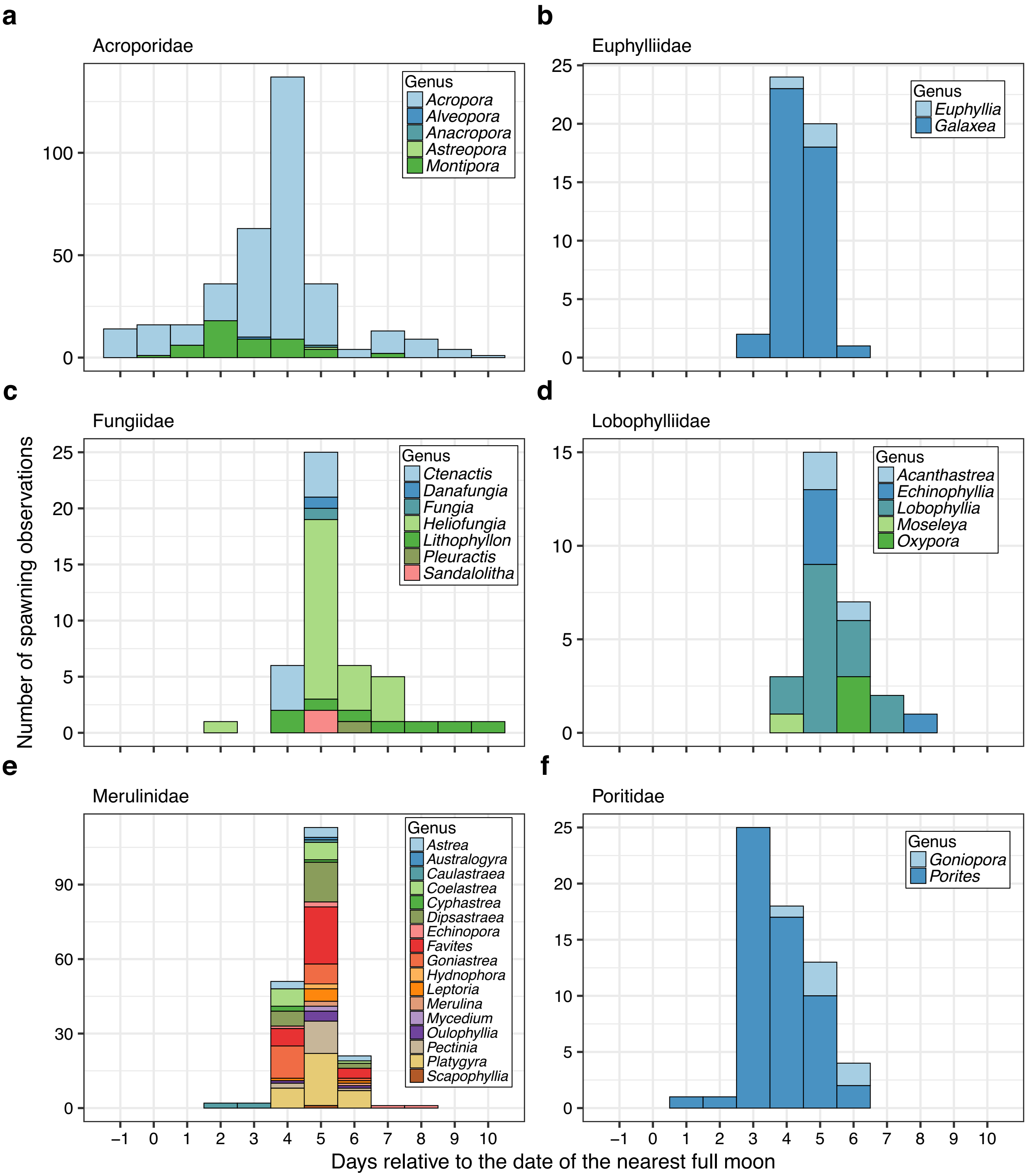


Fig. 4 Summary of the day of spawning observed relative to the date of the nearest full moon by family and genus. Each panel represents family **a** Acroporidae, **b** Euphylliidae, **c** Fungiidae, **d** Lobophylliidae, **e** Merulinidae and **f** Poritidae. All years' data are pooled

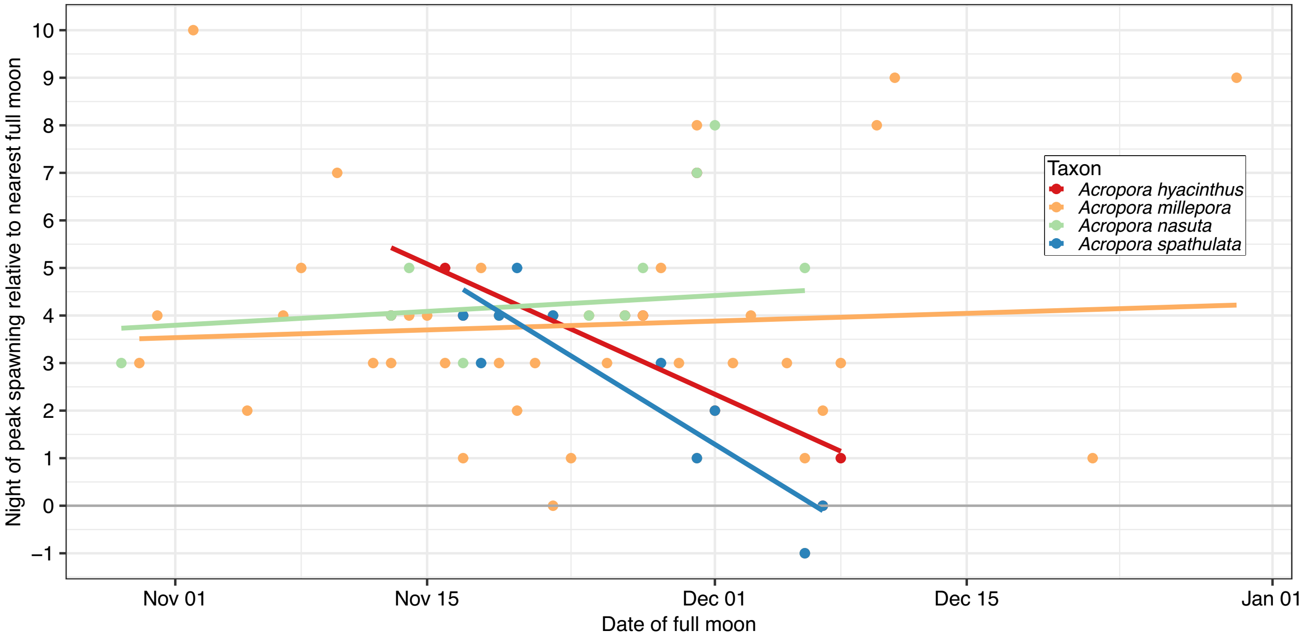
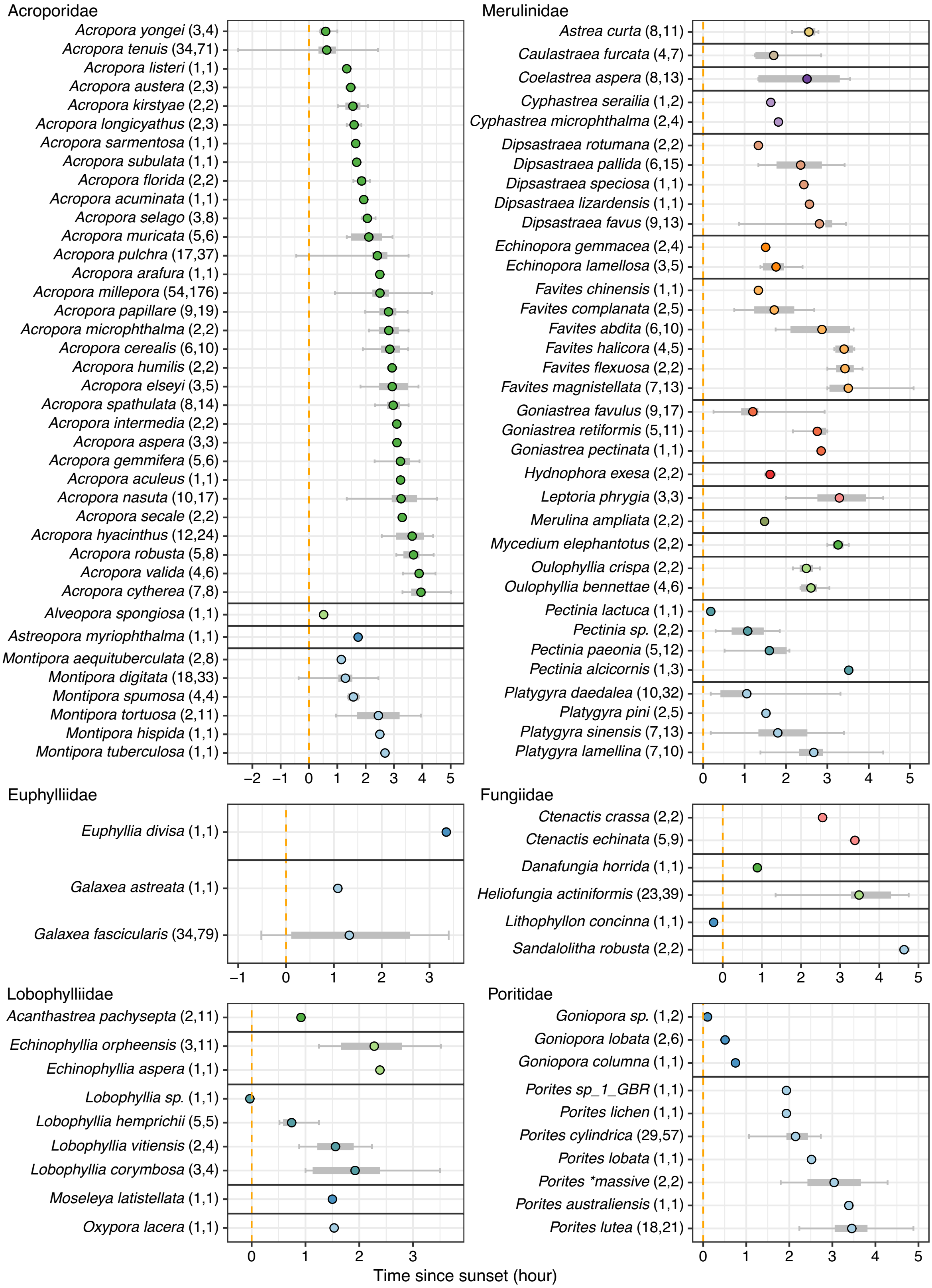


Fig. 5 Relationship between the day of peak spawning relative to the nearest full moon and the timing of each full moon. The coloured trend lines correspond to the four most frequently recorded *Acropora* species. All years' data are pooled

Spawning start times varied widely among taxa. For example, within *Acropora,* some species spawn early in the evening, such as *A. tenuis,* whereas others, such as *A. cytherea,* spawn 4 h after sunset (Fig. 6). Such differences in spawning times might be sufficient to limit interspecific breeding even if the gametes were compatible (Levitan et al. 2004). However, the wide range in start times within some taxa might also be the result of the current taxonomic framework. For example, *Galaxea fascicularis* sensu Veron 2000, in which spawning start times varied by 2 h in situ and nearly 4 h ex situ (Fig. 8), includes at least three genetically distinct lineages within its putative geographical range (Wepfer et al. 2020; Bonito et al. 2021). Similarly, *Coelastrea aspera,* which also had a wide range in spawning start times, includes at least two lineages within its putative geographical range (Mitsuki et al. 2021). We recommend that future records be accompanied by voucher specimens deposited to museums or photographic records uploaded to open-source online repositories to overcome ongoing challenges with scleractinian taxonomy (Kitahara et al. 2016; Voolstra et al. 2021) and amend identifications where needed.

The range and variation in both the day and the start time of spawning were greater in the laboratory than in the field, suggesting both aspects are affected by handling. In particular, colonies in the laboratory might not have access to the necessary cues to synchronise spawning, including sunset, moon light or any potential chemical cues (see also Neely et al. 2020). Rigorous surveys both in situ and ex situ across a wide range of taxa, ideally with repeated surveys from the same colony (e.g. Boch et al. 2011), will help quantify the effect of handling on coral spawning times, as well as improve our understanding of endogenous mechanisms and exogenous cues for synchrony. For example, annual variation in the night of spawning can be explained, to some extent, by sea surface temperature and wind speed in the weeks preceding spawning (Sakai et al. 2020). Furthermore, periods of darkness and light conditions (e.g. intensity, colour spectrum) are important proximate cues for spawning (Boch et al. 2011; Lin et al. 2021). Changes in environmental conditions introduced ex situ might therefore contribute to the


Acroporidae
Acropora yongei (3,4)
Acropora tenuis (34,71)
Acropora listeri (1,1)
Acropora austera (2,3)
Acropora kirstyae (2,2)
Acropora longicyathus (2,3)
Acropora sarmentosa (1,1)
Acropora subulata (1,1)
Acropora florida (2,2)
Acropora acuminata (1,1)
Acropora selago (3,8)
Acropora muricata (5,6)
Acropora pulchra (17,37)
Acropora arafura (1,1)
Acropora millepora (54,176)
Acropora papillare (9,19)
Acropora microphthalma (2,2)
Acropora cerealis (6,10)
Acropora humilis (2,2)
Acropora elseyi (3,5)
Acropora spathulata (8,14)
Acropora intermedia (2,2)
Acropora aspera (3,3)
Acropora gemmifera (5,6)
Acropora aculeus (1,1)
Acropora nasuta (10,17)
Acropora secale (2,2)
Acropora hyacinthus (12,24)
Acropora robusta (5,8)
Acropora valida (4,6)
Acropora cytherea (7,8)
Alveopora spongiosa (1,1)
Astreopora myriophthalma (1,1)
Montipora aequituberculata (2,8)
Montipora digitata (18,33)
Montipora spumosa (4,4)
Montipora tortuosa (2,11)
Montipora hispida (1,1)
Montipora tuberculosa (1,1)
−2 −1 0 1 2 3 4 5
Merulinidae
Astrea curta (8,11)
Caulastraea furcata (4,7)
Coelastrea aspera (8,13)
Cyphastrea serailia (1,2)
Cyphastrea microphthalma (2,4)
Dipsastraea rotumana (2,2)
Dipsastraea pallida (6,15)
Dipsastraea speciosa (1,1)
Dipsastraea lizardensis (1,1)
Dipsastraea favus (9,13)
Echinopora gemmacea (2,4)
Echinopora lamellosa (3,5)
Favites chinensis (1,1)
Favites complanata (2,5)
Favites abdita (6,10)
Favites halicora (4,5)
Favites flexuosa (2,2)
Favites magnistellata (7,13)
Goniastrea favulus (9,17)
Goniastrea retiformis (5,11)
Goniastrea pectinata (1,1)
Hydnophora exesa (2,2)
Leptoria phrygia (3,3)
Merulina ampliata (2,2)
Mycedium elephantotus (2,2)
Oulophyllia crispa (2,2)
Oulophyllia bennettae (4,6)
Pectinia lactuca (1,1)
Pectinia sp. (2,2)
Pectinia paeonia (5,12)
Pectinia alcicornis (1,3)
Platygyra daedalea (10,32)
Platygyra pini (2,5)
Platygyra sinensis (7,13)
Platygyra lamellina (7,10)
0 1 2 3 4 5
Euphylliidae
Euphyllia divisa (1,1)
Galaxea astreata (1,1)
Galaxea fascicularis (34,79)
−1 0 1 2 3
Fungiidae
Ctenactis crassa (2,2)
Ctenactis echinata (5,9)
Danafungia horrida (1,1)
Heliofungia actiniformis (23,39)
Lithophyllon concinna (1,1)
Sandalolitha robusta (2,2)
0 1 2 3 4 5
Lobophylliidae
Acanthastrea pachysepta (2,11)
Echinophyllia orpheensis (3,11)
Echinophyllia aspera (1,1)
Lobophyllia sp. (1,1)
Lobophyllia hemprichii (5,5)
Lobophyllia vitiensis (2,4)
Lobophyllia corymbosa (3,4)
Moseleya latistellata (1,1)
Oxypora lacera (1,1)
0 1 2 3
Poritidae
Goniopora sp. (1,2)
Goniopora lobata (2,6)
Goniopora columna (1,1)
Porites sp_1_GBR (1,1)
Porites lichen (1,1)
Porites cylindrica (29,57)
Porites lobata (1,1)
Porites *massive (2,2)
Porites australiensis (1,1)
Porites lutea (18,21)
0 1 2 3 4 5
Time since sunset (hour)

◂**Fig. 6** Summary of the start times of spawning per taxon relative to sunset. The circle indicates the mean observed start time, thin grey lines indicate the range between minimum and maximum, and thick grey bars indicate the range between 25 and 75th percentiles. The numbers in parentheses next to taxon name indicate the total number of observations and colonies across all available years. The circles are coloured to reflect different genera within each family. Observations without spawning start time records were removed from this analysis

increase in the range of observed spawning times (Craggs et al. 2017).

Despite over 30 years of direct spawning observations, we still have records for only a fraction of the approximately 320 species listed as occurring in the north and central GBR (Veron 2000). Various taxa are known to spawn around the day of the new moon or during daytime in other regions (e.g. Plathong et al. 2006; Mangubhai et al. 2007; Bouwmeester et al. 2011; Schmidt-Roach et al. 2012, 2014; Suzuki 2012). Future efforts to determine when the remaining species are breeding may reveal significant variations to the standard spring nocturnal timing typically studied on the GBR.

In conclusion, the utility of direct spawning observations is restricted by the fact that observers rarely record negative observations. For example, the spawning observations in the database are largely restricted to the months when researchers expect corals to spawn in the Palm Islands, i.e. lunar months 5 and 6. Similarly, observations in the coral spawning database cannot address questions of synchrony, because they do not specify the proportion of colonies spawning in the field and only mature colonies are generally brought back to the laboratory. Nonetheless, the direct spawning observations have allowed us to establish that a lunisolar calendar is a better predictor of the first month of the spawning season than the Gregorian calendar. The direct spawning observations have also allowed us to highlight differences in the night of peak spawning among families and to infer that handling of corals affects variation in the night and time of spawning. All this information can help plan field work and improve experimental practice. The coral reproductive condition data allowed us to determine that many species spawn outside the typical times researchers are in the field; indeed, there are some colonies of *Acropora* spawning every month from lunar month 5 to 9. Extended reproductive seasons and broad ranges in spawning times in some species suggest that these species might in fact be species complexes (Rassmussen et al. 2025), and that the taxonomic framework

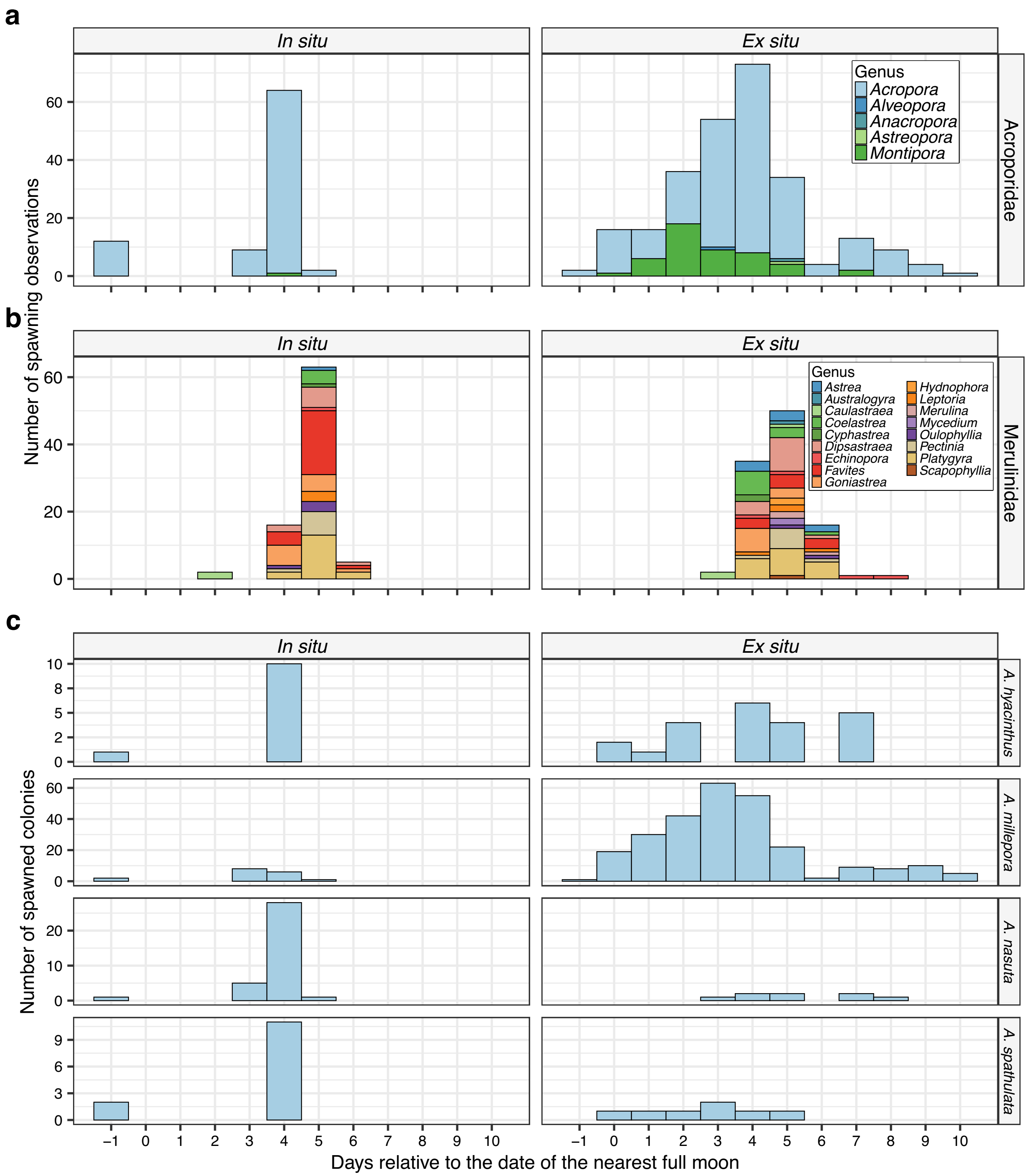


Fig. 7 Day of spawning as a function of whether colonies were observed in the field (in situ) or maintained in the laboratory (ex situ). **a** Family Acroporidae, **b** Merulinidae and **c** the four most frequently recorded *Acropora* species. All years' data are pooled

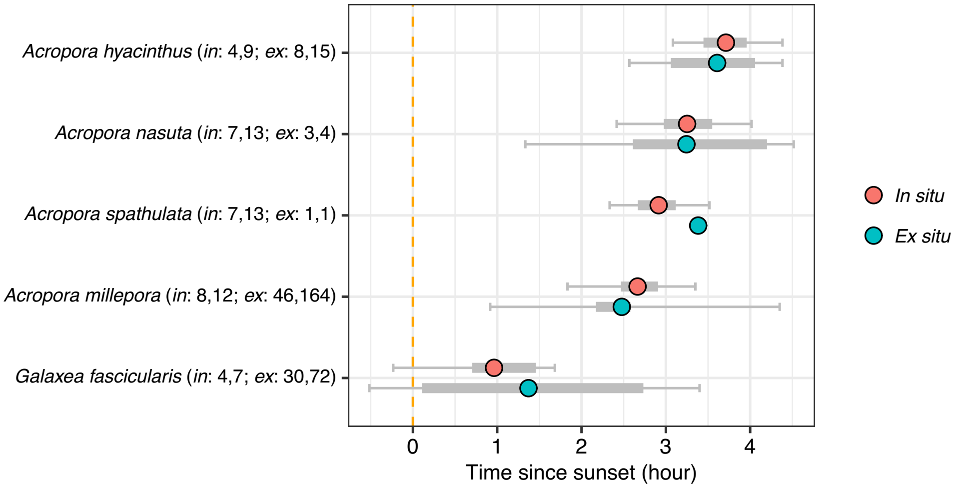


Fig. 8 Start times of spawning relative to sunset for colonies maintained in the laboratory (ex situ) vs those in the field (in situ) for five frequently recorded taxa. The numbers in parentheses indicate the total number of observations and colonies with spawning start time records across all available years per situations

underpinning these species identifications also requires further revision.

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Author contributions H.M. and A.H.B. conceptualised the study, A.H.B. carried out the fieldwork for extra data collection, A.J.E. and L.L. prepared the data and code for analyses, and H.M. and A.H.B. revised the code and analysed the results. H.M. wrote the first draft of the manuscript, and A.H.B., A.J.E., J.R.G., L.L., K.M.Q. and B.L.W. critically revised the manuscript. All authors contributed to the finalisation of the manuscript.

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Data availability Data are provided within the manuscript or supplementary information files.

Declarations

Conflict of interest The authors declare no competing interests.

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