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# Multi-specific coral spawning and monsoonal transitions: assemblage-level observations from Baa Atoll, Maldives

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Coral reefs support a vast diversity of marine life but are increasingly threatened by anthropogenic activities. To assess changes in community composition and the recovery potential of coral reefs in a changing climate, documenting sexual reproduction and understanding its environmental drivers are essential. Here, we report the exact timing and reproductive strategies for 375 individual coral colonies across 28 species from 10 genera between February 2024 and April 2025 at a near-shore reef in Baa Atoll, Maldives. We identify two peak periods of multi-specific spawning, coinciding with the monsoonal transition seasons. We note variations in spawning patterns within and between taxa, documenting the occurrence of extended breeding via asynchronous spawning of colonies within a species and split-spawning of individual colonies across lunar months and bi-annual seasons. Our results show that larger spawning events in a given month are significantly correlated with lower wind speeds, higher sea surface temperatures, and higher levels of solar insolation. These findings highlight the influence of environmental cues on the timing and extent of coral reproduction and provide the first detailed spawning records for several non-Acropora genera in the Maldives, contributing a critical baseline for future research.

## KEYWORDS

coral, spawning, monsoon, reproduction, coral reef, synchrony

## Introduction

Corals are autogenic ecosystem engineers; the complex structures they build support a vast diversity of marine life and provide key services such as fisheries, coastal protection, tourism and recreational activities (Grafeld et al., 2017; Graham and Nash, 2013; Woodhead et al., 2019). Globally, coral reefs are threatened by anthropogenic stressors such as ocean acidification, pollution and climatic changes (Emslie et al., 2024; Frölicher et al., 2018; Hoegh-Guldberg, 1999; Hughes et al., 2017, 2003; Kleypas et al., 1999; Spalding and Brown, 2015). Ocean warming events are a particularly prevalent threat to coral reefs, as elevated sea surface temperatures (SST) can disrupt the reproductive cycles and spawning synchrony of corals (Paxton et al., 2016; Shlesinger and Loya, 2019) and can

cause bleaching-induced mortality on large scales (Baker et al., 2008; Bruno and Selig, 2007; Hughes et al., 2018; Perry and Morgan, 2017a). Whilst coral bleaching can reduce a colony's immediate growth rates, reproductive output, and larval supply, studies have shown coral reefs have the capacity to recover from mass bleaching events (Cantin and Lough, 2014; Donati et al., 2025; Gilmour et al., 2013; Gold and Palumbi, 2018; Gouezo et al., 2019; Graham et al., 2024; Pisapia et al., 2016). Reef recovery and repopulation is driven by the growth and reproduction of surviving colonies and the successful settlement of recruits (Adjeroud et al., 2017; Gilmour et al., 2013; Johnston et al., 2020). Hence, understanding the reproductive patterns of coral at the colony level is key for assessing how communities restructure following disturbances and for evaluating impacts on ecosystem function.

Reef-building corals reproduce by brooding or, for most species, via broadcast spawning events in which gametes are released into the water column for external fertilisation at the surface (Harrison, 2011). The success of broadcast reproductive events is dependent on synchronous release of gametes between colonies to enable cross-fertilisation (Levitan, 2004; Oliver and Babcock, 1992; Willis et al., 1985). The timing and extent of synchronous broadcast spawning events can vary greatly within and between taxa and biogeographic regions (Baird et al., 2022, 2009; Gouezo et al., 2020; Harrison, 2011; Harrison and Wallace, 1990; Mangubhai and Harrison, 2008; Moritz et al., 2025; Sheridan et al., 2025). An expansion of research on coral spawning in recent years has revealed reproductive patterns ranging from the highly synchronised mass spawning of over 100 different coral species as documented on the Great Barrier Reef (Babcock et al., 1986; Harrison et al., 1984; Oliver et al., 1988; Willis et al., 1985), to temporal reproductive isolation of 24 coral species studied in the Gulf of Eliat (Shlesinger et al., 1998; Shlesinger and Loya, 1985). Between these two extremes are records of multi-specific spawning (Monfared et al., 2023), asynchronous spawning (Gouezo et al., 2020), and extended breeding seasons (Mangubhai and Harrison, 2008) in other regions (summarised in Harrison, 2011). It has been hypothesised that there is a breakdown of spawning synchrony at low latitudes due to weaker fluctuations in environmental conditions that enable protracted breeding seasons (Oliver et al., 1988), as supported by studies on Kenyan reefs (Mangubhai and Harrison, 2008). However, synchronous spawning has been recorded in other equatorial regions (Gilmour et al., 2016; Gouezo et al., 2020; Monfared et al., 2023; Sheridan et al., 2025; Sola et al., 2016; Wijayanti et al., 2019).

The timing of sexual reproduction of reef-building corals has been linked to various environmental factors such as sea temperature (Keith et al., 2016; Lin and Nozawa, 2023; Nozawa, 2012; Monfared et al., 2023; Sheridan et al., 2025), solar insolation (Penland et al., 2004; van Woessik et al., 2006), regional wind fields (van Woessik, 2010), moon phase, sunrise (Bronstein and Loya, 2011; Moritz et al., 2025), and sunset (Baird et al., 2022; Lin and Nozawa, 2017). Whilst knowledge of coral reproduction has expanded in recent years, fundamental background information on the timing of spawning events is limited in some regions. Elucidating our understanding of spawning patterns across vast

geographic scales is key for assessing the reproductive phylogeny of scleractinian corals and hence the impacts of climatic changes and the potential for recovery of coral reef ecosystems.

The Maldivian archipelago is considered the world's seventh largest reef system (MEE, 2015). With 80% of all land area lying less than 1 metre above sea level, the islands that comprise the Maldives rely heavily on the 2,041 distinct coral reefs identified for protection, and provision for the population (Dhunya et al., 2017; Dryden et al., 2020; Naseer and Hatcher, 2004). In the Maldives, observations of asynchronous coral spawning in diverse assemblages over multiple lunar phases have been reported (Harrison and Hakeem, 2007). Monfared et al. (2023) noted extended breeding seasons of 22 species of *Acropora* over an 8 month period, detailing peak multi-specific spawning events coinciding with the transitional monsoon period, and asynchronous spawning between *Acropora* species and between colonies of the same species over multiple lunar phases. Further, Sheridan et al. (2025) assessed the degree of spawning synchrony of *Acropora* and found that larger, multi-specific spawning events occur more frequently than single species spawning events. These studies reported exact timings of *Acropora* spawning and correlated earlier spawning events relative to the full moon with lower tide depths, wind speeds, daily precipitation and higher sea surface temperatures.

However, to date, knowledge of spawning patterns and exact spawning times of non-*Acropora* corals is comparatively limited. Increasingly, restoration initiatives are utilising sexual reproduction for reef replenishment, including larval propagation, assisted fertilisation and selective breeding (Dela Cruz and Harrison, 2020; Harrison, 2024a, 2024b; Humanes et al., 2021; Koch et al., 2022; Pollock et al., 2017; Randall et al., 2020). Such techniques rely on accurately predicting when corals will spawn; advancing knowledge on the months of spawning and exact time of spawning for each region is pivotal for success and optimization of these initiatives. With both asexual and sexual restoration methods practised widely across the Maldives, understanding reproductive patterns of corals at the assemblage level is key for managing reef recovery via restorative intervention and for predicting the extent of community shifts following bleaching events. This study provides key baseline data for restoration initiatives utilising sexual reproduction. Here, we document the exact timing and sexual reproductive strategies for 375 individual colonies of 10 different genera of corals between February 2024 and April 2025. Data collection occurred before, during, and following the fourth global bleaching event confirmed by the International Coral Reef Initiative (International Coral Reef Initiative, 2024). This study describes two peak seasons for multispecific spawning events in Baa Atoll [as first identified for *Acropora* by Monfared et al. (2023)], as well as taxon-specific differences in reproductive synchronicity, noting instances of annual and bi-annual spawning, split spawning of individual colonies of various genera over multiple days in a lunar month and over multiple lunar months in a year. To date, this study is the first to report exact spawning times of non-*Acropora* genera in the Maldives.

## Materials and methods

### Survey site

Coral spawning surveys were conducted from February 2024 to April 2025 on a near-shore reef on the southern side of Landaa Giraavaru, a resort island in Baa Atoll, Maldives (5.2862°N, 73.1121°E). The “House Reef” site, approximately 1,300m<sup>2</sup> in area, was chosen for surveys based on accessibility from the shore and due to the higher diversity of coral genera present on this reef in comparison to other sites. The depth range of colonies surveyed was 1m–4m.

### Reproductive maturity assessments

To inform for which lunar months nightly surveys would be undertaken, reproductive maturity of colonies at the survey site was assessed. For colonies of *Acropora*, an approximately 5cm fragment was removed from the colony base using scissors; for *Galaxea*, a single polyp was excised similarly to check for the presence or absence of gametes (Baird et al., 2002; Craggs, Personal Communication, August 26, 2024; Monfared et al., 2023). Maturity assessments of *Acropora* colonies coincided with ongoing coral restoration activities to reduce negative ecological impacts, and between four and seven randomly selected *Galaxea* colonies were surveyed in the week prior to the full moon each month.

Additional opportunistic reproductive maturity assessments were conducted on colonies of *Astrea*, *Cyphastrea*, *Goniastrea* and *Leptoria* at restoration sites. Small fragments from these colonies were removed using a hammer and a fine chisel, and examined for the presence of gametes using a microscope (Adonstar AD407 Digital Microscope) (Craggs, Personal Communication, August 26, 2024; Whiting, Personal Communication, June 21, 2024). Fragmentation of these genera for maturity assessments did not take place between March 2024 and June 2024 to avoid causing stress to colonies during the ongoing coral bleaching event (International Coral Reef Initiative, 2024; Reefscapers, 2024). From June 2024 onwards, only a proportion of colonies that remained healthy throughout the bleaching event were fragmented. Other genera later identified spawning were not fragmented to assess reproductive maturity due to time constraints, and as some had very small polyps that made positive gamete identification difficult.

Colonies with gametes identified were noted and mapped on a slate for observer reference, but not tagged at this stage; reproductive maturity data was used only to inform when field surveys should take place and was not included in analysis.

### Spawning surveys

As spawning events are typically documented in accordance with the lunar cycle (Babcock et al., 1994; Komoto et al., 2023), nightly surveys to check for signs of coral spawning were conducted

around the full and new moons. Upon observation of mature gametes in any species, nightly surveys would take place from two days prior to the full moon (FM) (FM-2) until seven days after the full moon (FM + 7), and from two days prior to the new moon (NM) (NM-2), until two days after the new moon (NM + 2) to check for signs of coral spawning. Therefore, resulting surveys occurred in March, April, October, November, and December 2024, and in March and April 2025. As spawning has been observed over multiple lunar phases (Mangubhai and Harrison, 2008; Gouezo et al., 2020), opportunistic surveys (where weather and staffing constraints allowed) in months where no mature gametes had been observed took place. Where possible, “full surveys” from FM-2 until FM + 7 and from NM-2 until NM + 2 took place, but if not possible “short surveys” from FM-1 until FM + 4 took place. Such opportunistic “full surveys” occurred in February, May, and September 2024. Opportunistic “short surveys” took place in June 2024 and in January 2025.

Nightly surveys were conducted by a minimum of two observers via SCUBA or freediving from 19:00–20:30 local time, to encompass known spawning periods of *Acropora* (Monfared et al., 2023) and anticipated spawning times of massive and encrusting genera (Baird et al., 2021). Observers would swim along a course routinely taken on the reef and check colonies in which mature gametes had been noted, as well as other corals from various genera for “setting” (mature gametes visible in the mouth of the polyp prior to release) or spawning (Monfared et al., 2023). If observed, divers would remain in the water until the release of gametes was complete for all colonies. Accurate time of spawning onset was obtained by placing surveyors in a specified area of the routinely taken course and ensuring setting colonies were frequently checked to document the moment of gamete release. In the event that a colony was observed setting but spawning onset was not recorded, the colony was fragmented the following day. If a loss of gametes was recorded then we would deduce that the colony had spawned (Monfared et al., 2023).

During nightly surveys, spawning colonies were temporarily tagged with numbered cloth ties (tied on to nearby stable substrate) for ease of identification the following day. The following data was collected for each colony *in-situ* using dive slates: cloth tie number, colony ID (if a permanent identification tag was already present on the spawning colony), time at which setting was first observed, exact time of spawning onset, depth, genus, species (if known), location on the reef relative to coral frames planted for restoration activities (each with GPS coordinates noted), and reproduction type (hermaphroditic/gonochoric, specifying egg/sperm release where known). Where time constraints allowed, pictures of spawning colonies were also taken with a digital camera for reference (Olympus Tough TG-6 digital camera) (Figure 1).

### Spawning and environmental condition database

The following day, colonies spawning the night prior were located and temporary cloth ties were removed. If a colony

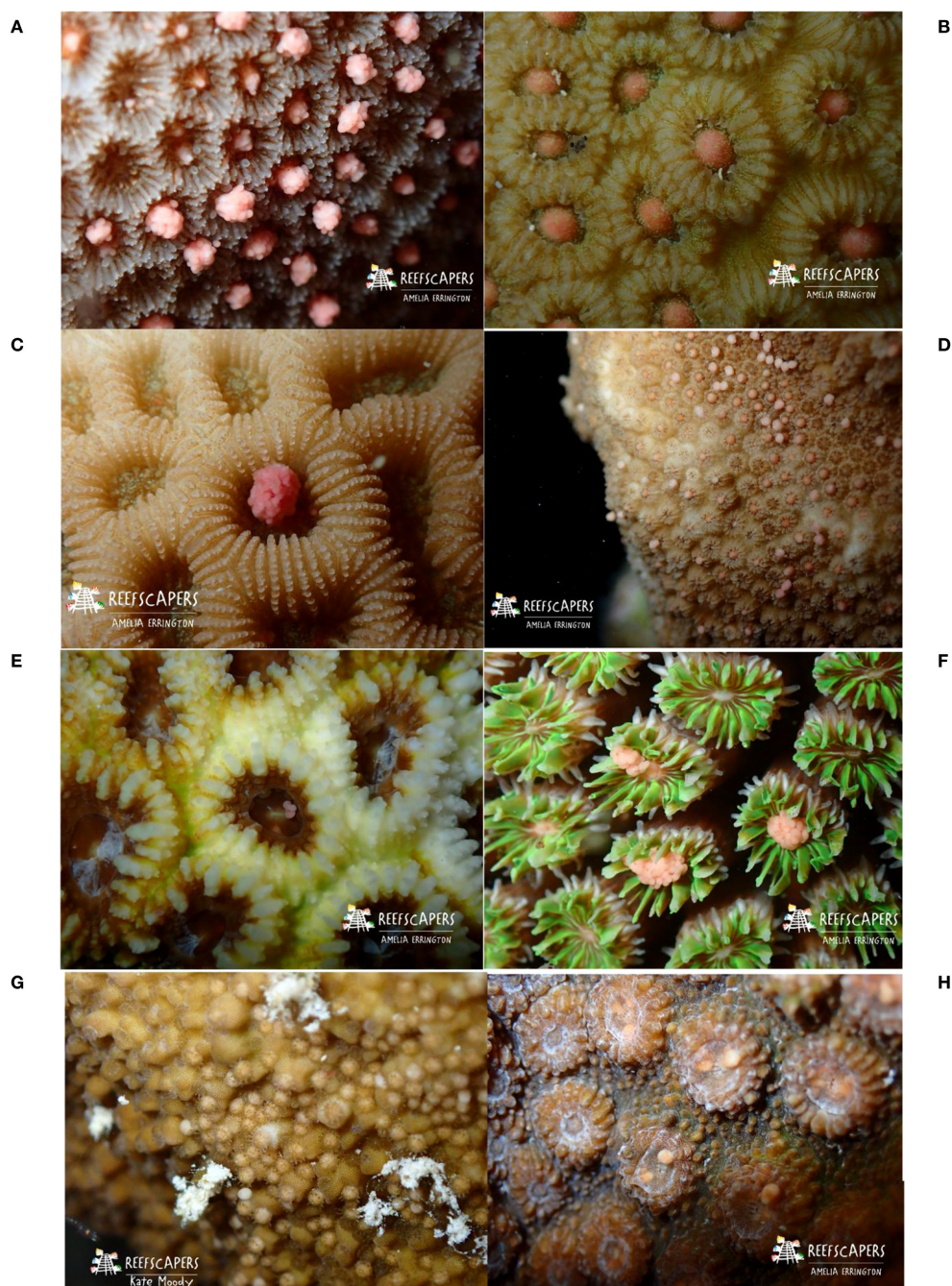


FIGURE 1

Images to show setting and spawning in various coral species. (A) Spawning in *Goniastrea retiformis*. Photograph by Amelia JF Errington. (B) Setting in *Astrea curta*. Photograph by Amelia JF Errington. (C) A bundle ready for release in *Goniastrea pectinata*. Photograph by Amelia JF Errington. (D) Spawning in *Cyphastrea microphthalma*. Photograph by Amelia JF Errington. (E) Spawning in *Dipsastrea matthai*. Photograph by Amelia JF Errington. (F) Bundles of eggs ready for release in *Galaxea fascicularis*. Photograph by Amelia JF Errington. (G) Setting and onset of spawning in *Montipora tuberculosa*. Photograph by Kate P Moody. (H) Spawning in *Echinopora* spp. Photograph by Amelia JF Errington.

already had a permanent identification (ID) tag, no further information would be collected. Colonies recorded spawning for the first time were given a permanent ID tag with a unique colony ID for future monitoring of spawning events at the individual colony level. Five high-quality pictures of each colony would be taken: ID tag in-shot with the colony, and a wide-shot, mid-shot, close-up and scaled-shot of the colony for positive identification to

genus level (and species where possible) using the Indo-Pacific Coral Finder (Kelley, 2022) and Corals of the World (Veron et al., 2025). These images were stored in a photo ID database for reference. Genetic testing would be required to confirm species identification but was not done for this study.

The unique colony ID was input into a spawning database along with the data collected from the night of spawning so reproductive

patterns of individual colonies could be followed over time. Additional data input included the date of spawning, the day of spawning relative to the nearest full moon, and the lunar month of spawning (eg the March 2024 full moon (FM) was on 25th March, but spawning was recorded on April 1st (FM + 7); for these colonies, lunar month of spawning was recorded as March). The environmental factors solar radiation and wind speed were obtained using a weather station located on Landaa Giraavaru (Gill Instruments GMX 500 Maximet). Moon phase (Moon Giant, 2025), average daily sea surface temperature (SST) (Sea Temperatures, 2025), sunset time, and depth of the low tide closest to sunset (Tideschart, 2025) on days where spawning occurred were gathered for Baa Atoll. The day of spawning relative to the full moon was recorded and spawning time in minutes after sunset for each colony was calculated. Average monthly SST, wind speed and solar insolation were calculated across all days of each calendar month for the duration of the study.

## Statistical analysis

To assess whether environmental factors such as sea surface temperature (SST), wind speed, and solar insolation influence the occurrence of coral spawning, a generalized linear model (GLM) with a binomial distribution and logit link was fitted. Spawning occurrence was used as a binary response variable, coded as 1 if spawning of any species/genus occurred in a given month and 0 if it did not. Univariate models were fitted separately for each predictor variable: average SST, average wind speed, and average solar insolation, each measured during the month preceding the spawning event. Model fit was assessed using residual deviance, Akaike Information Criterion (AIC), and pseudo- $R^2$  statistics.

To examine whether environmental variables influence the proportion of colonies spawning each month, beta regression was fitted. The monthly proportion was calculated as the number of colonies of any genus/species to spawn in a given month divided by the total number of spawning events recorded throughout the study period of all species/genera combined. Three univariate beta regressions were conducted using average SST, wind speed, and solar insolation (per lunar month) as explanatory variables. Model diagnostics, including Pearson residual plots, Q-Q plots, and pseudo- $R^2$ , indicated that beta regression assumptions were adequately met. Multicollinearity among predictors was assessed, and a strong negative correlation between SST and wind speed ( $r = -0.71$ ) was identified, which prevented multivariable modeling. Final model selection was based on AIC values.

## Results

A total of 449 observations of spawning from 375 individual colonies of 10 different genera (*Acropora* (N = 162), *Astrea* (N = 9), *Astreopora* (N = 16), *Cyphastrea* (N = 21), *Dipsastrea* (N = 20), *Echinopora* (N = 1), *Galaxea* (N = 60), *Goniastrea* (N = 134), *Montipora* (N = 25) and *Porites* (N = 2)) were recorded at Landaa

Giraavaru, Baa Atoll, between February 2024 and April 2025 (Table 1). The majority of studied coral species (99.3% of colonies observed) released gametes in multi-specific spawning events during two peak seasons; in March and April (N = 326) and between October and December (N = 120) (Figure 2).

All colonies recorded spawning released gametes approximately one to three hours after sunset (Figure 3) within a few days of the full moon (Figure 4). Depending on the taxa, spawning occurred as a single event or extended spawning patterns (via asynchronous spawning amongst colonies of a species and/or split spawning of individual colonies) was observed.

Neither SST ( $p = 0.200$ ) nor wind speed ( $p = 0.071$ ) were statistically significant predictors of the probability of spawning occurrence in the binomial GLM (Table 2). However, solar insolation was a significant predictor ( $p = 0.047$ ), with a positive association ( $\beta = 2.079 \pm 1.046$ ), indicating that higher solar insolation increased the likelihood of spawning occurring in a given month.

In the beta regression analysis, all three environmental variables (average SST, wind speed, and solar insolation) were found to significantly influence the proportion of colonies spawning per month (Figure 5). Average wind speed had the strongest effect ( $\beta = -0.709 \pm 0.219$ ,  $p = 0.001$ ), with a negative association, suggesting that higher wind speeds were associated with a lower proportion of colonies spawning (Table 3). SST also showed a significant positive effect ( $\beta = 0.701 \pm 0.304$ ,  $p = 0.021$ ), indicating increased spawning with higher SST. Solar insolation was similarly positively associated with the proportion of spawning events ( $\beta = 0.585 \pm 0.250$ ,  $p = 0.019$ ).

## Species-specific spawning patterns observed

Spawning patterns differed within and between species of *Acropora*. Some species spawned in both peak seasons (*A.gemmifera*, *A.humilis*, *A.plantaginea* and *A.secale*) via asynchronous spawning of different colonies or via individual colonies undergoing multiple gametogenic cycles in a year. Some species spawned only in March/April (*A.aspera*, *A.digitifera*, *A.hyacinthus*, *A.millepora*, *A.muricata*, *A.nasuta* and *A.samoensis*) and some species spawned only between October and December (*A.polystoma*, *A.rosaria* and *A.squarrosa*).

Colonies of *Galaxea fascicularis* (N = 60) exhibited varied spawning patterns. We commonly noted individual colonies spawning over consecutive days and months in a year. Asynchronous spawning within the population was also documented, as some colonies spawned only in March/April (29%) and some only between October and December (39%). Bi-annual spawning was also recorded as some colonies (32%) spawned in both peak seasons. This species exhibits pseudogynodioecious reproduction; we noted that, for the duration of this study, colonies first recorded spawning one gender would spawn the same gender in future reproductive events.

Colonies of *Goniastrea retiformis* were observed spawning in both peak seasons. In contrast to many other genera, spawning was noted in only one month of each peak season; in March 2024 (N = 55),

TABLE 1 A summary of spawning records from Baa Atoll, showing the number of colonies, years and month of spawning, day of spawning relative to full moon and earliest time of spawning onset for each species.

| Genus             | Species              | Number of colonies recorded spawning | Spawned years | Months of spawning                        | Day of spawning relative to full moon (+)/(-) | Earliest time of spawning onset | Reproduction type |
|-------------------|----------------------|--------------------------------------|---------------|-------------------------------------------|-----------------------------------------------|---------------------------------|-------------------|
| <i>Acropora</i>   | <i>aspera</i>        | 7                                    | 2024          | April                                     | -2                                            | 20:05:00                        | Hermaphroditic    |
| <i>Acropora</i>   | <i>cytherea</i>      | 1                                    | 2025          | April                                     | +3                                            | 20:22:00                        | Hermaphroditic    |
| <i>Acropora</i>   | <i>digitifera</i>    | 19                                   | 2024, 2025    | April                                     | -2, -1, +5                                    | 20:32:00                        | Hermaphroditic    |
| <i>Acropora</i>   | <i>gemmifera</i>     | 6                                    | 2024          | April                                     | -2, -1                                        | 19:57:00                        | Hermaphroditic    |
| <i>Acropora</i>   | <i>humilis</i>       | 10                                   | 2024, 2025    | April, November                           | -2, -1, +3, +6                                | 20:08:00                        | Hermaphroditic    |
| <i>Acropora</i>   | <i>hyacinthus</i>    | 3                                    | 2024, 2025    | April                                     | -2, -1, +5                                    | 20:42:00                        | Hermaphroditic    |
| <i>Acropora</i>   | <i>millepora</i>     | 31                                   | 2024, 2025    | April                                     | -2, -1, +3, +4                                | 20:26:00                        | Hermaphroditic    |
| <i>Acropora</i>   | <i>muricata</i>      | 2                                    | 2024          | April                                     | -2, -1                                        | 20:29:00                        | Hermaphroditic    |
| <i>Acropora</i>   | <i>nasuta</i>        | 16                                   | 2024          | April                                     | -2, -1                                        | 21:00:00                        | Hermaphroditic    |
| <i>Acropora</i>   | <i>plantaginea</i>   | 27                                   | 2024          | March, October, November                  | +2, +6, +14                                   | 19:27:00                        | Hermaphroditic    |
| <i>Acropora</i>   | <i>polystoma</i>     | 6                                    | 2024          | November                                  | +6                                            | 19:57:00                        | Hermaphroditic    |
| <i>Acropora</i>   | <i>rosaria</i>       | 5                                    | 2024          | October                                   | +13, +14                                      | 19:54:00                        | Hermaphroditic    |
| <i>Acropora</i>   | <i>samoensis</i>     | 13                                   | 2024          | April                                     | -2, -1                                        | 20:27:00                        | Hermaphroditic    |
| <i>Acropora</i>   | <i>secale</i>        | 14                                   | 2024          | March, November                           | +5, +6                                        | 19:57:00                        | Hermaphroditic    |
| <i>Acropora</i>   | <i>squarrosa</i>     | 2                                    | 2024          | November                                  | +6                                            | 19:57:00                        | Hermaphroditic    |
| <i>Astrea</i>     | <i>curta</i>         | 9                                    | 2024, 2025    | March                                     | +4, +5, +6, +7                                | 19:45:00                        | Hermaphroditic    |
| <i>Astreopora</i> | <i>myriophthalma</i> | 16                                   | 2024          | December                                  | +2, +3, +4, +5                                | 19:12:00                        | Hermaphroditic    |
| <i>Cyphastrea</i> | <i>chalcidium</i>    | 2                                    | 2024          | March                                     | +5                                            | 19:26:00                        | Hermaphroditic    |
| <i>Cyphastrea</i> | <i>microphthalma</i> | 19                                   | 2024, 2025    | March, April                              | +4, +5, +6, +7                                | 19:28:00                        | Hermaphroditic    |
| <i>Dipsastrea</i> | <i>matthai</i>       | 19                                   | 2024, 2025    | March, April                              | +5, +6, +7                                    | 19:55:00                        | Hermaphroditic    |
| <i>Echinopora</i> | <i>spp.</i>          | 1                                    | 2024          | March                                     | +5                                            | 20:16:00                        | Hermaphroditic    |
| <i>Galaxia</i>    | <i>fascicularis</i>  | 60                                   | 2024, 2025    | March, April, October, November, December | +3, +4, +5                                    | 19:09:00                        | Gonochoric        |
| <i>Goniastrea</i> | <i>pectinata</i>     | 5                                    | 2024, 2025    | March                                     | +2, +3                                        | 19:29:00                        | Hermaphroditic    |
| <i>Goniastrea</i> | <i>retiformis</i>    | 129                                  | 2024, 2025    | March, April, November                    | -1, 0, + 1, +2, +3, +4, +6                    | 19:51:00                        | Hermaphroditic    |
| <i>Montipora</i>  | <i>efflorens</i>     | 3                                    | 2024          | September                                 | -1, 0                                         | 19:33:00                        | Hermaphroditic    |
| <i>Montipora</i>  | <i>monasteriata</i>  | 17                                   | 2024, 2025    | March, April, November                    | +2, +4, +5, +6, +7                            | 19:26:00                        | Hermaphroditic    |
| <i>Montipora</i>  | <i>peltiformis</i>   | 5                                    | 2024          | November, December                        | +3, +4                                        | 19:23:00                        | Hermaphroditic    |
| <i>Porites</i>    | <i>lobata</i>        | 2                                    | 2025          | March                                     | +4                                            | 19:05:00                        | Gonochoric        |

November 2024 (N = 11), and April 2025 (N = 68). No split-spawning over consecutive lunar months was noted, and release of gametes only once per year was recorded for each colony. In some colonies, spawning would occur over consecutive days over the full moon period.

*Cyphastrea microphthalma*, *Cyphastrea chalcidium*, *Dipsastrea matthai*, *Echinopora* spp., *Goniastrea pectinata* and *Porites lobata* released gametes in multi-specific spawning events in March/April. Spawning of *Astreopora myriophthalma* colonies occurred as a multi-species event following the December full moon.

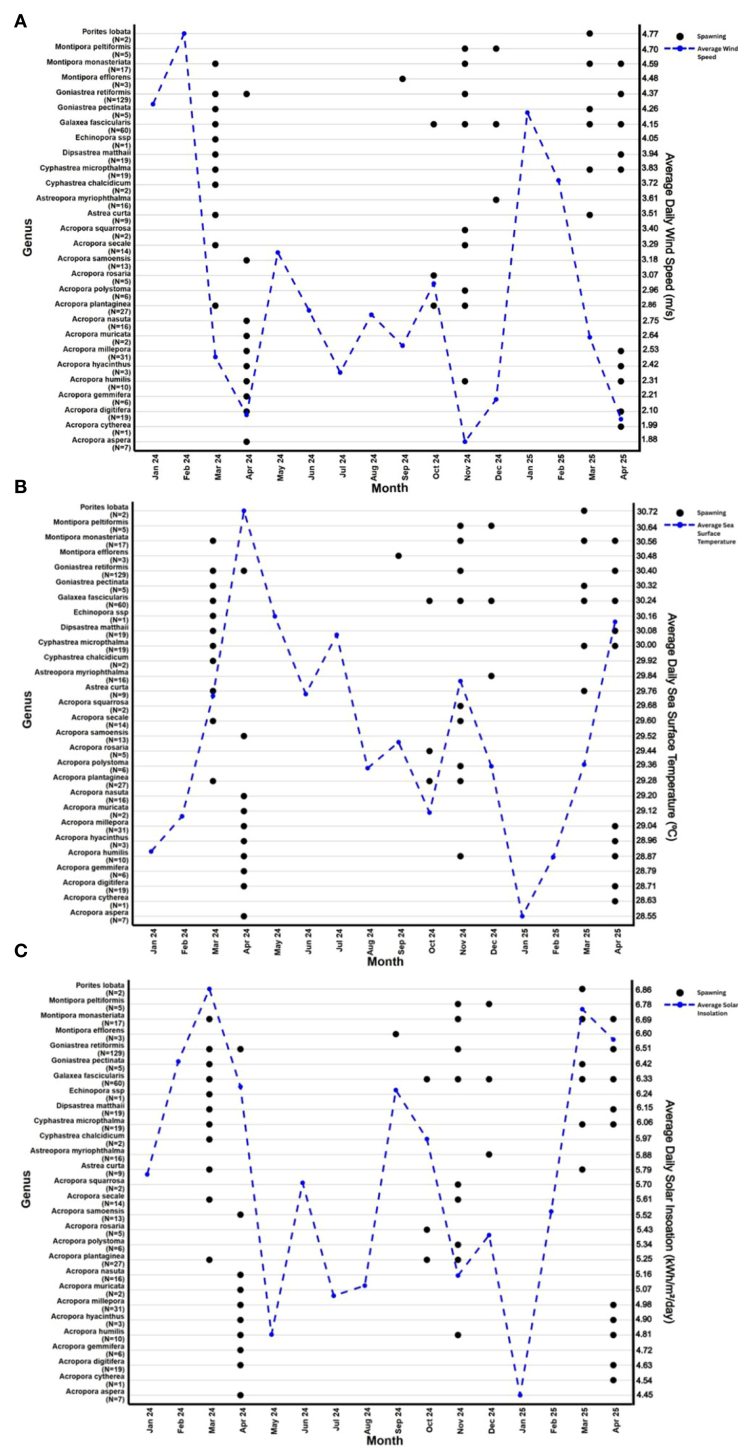


FIGURE 2

Monthly coral spawning observations by genus overlaid with daily averages of environmental variables. Back circles refer to months in which spawning occurred for each genus. Blue circles indicate the monthly average values of environmental factors, wind speed (m/s) (A), sea surface temperature (°C) (B) and solar insolation levels (kWh/m<sup>2</sup>/day) (C). The number of spawning observations for each genus is shown on the y-axis as N = X.

*Montipora* species were observed spawning in multiple months of the year, with inter-specific spawning asynchrony noted but synchronised spawning within species. Colonies of *M. monasteriata* (N = 17) spawned predominantly in March/April, with only one

colony recorded spawning in November. Colonies of *M. peltiformis* (N = 5) spawned in November and December. Colonies of *Montipora efflorens* (N = 3) released gametes outside of the identified peak spawning seasons, spawning in September 2024 as a singular event.

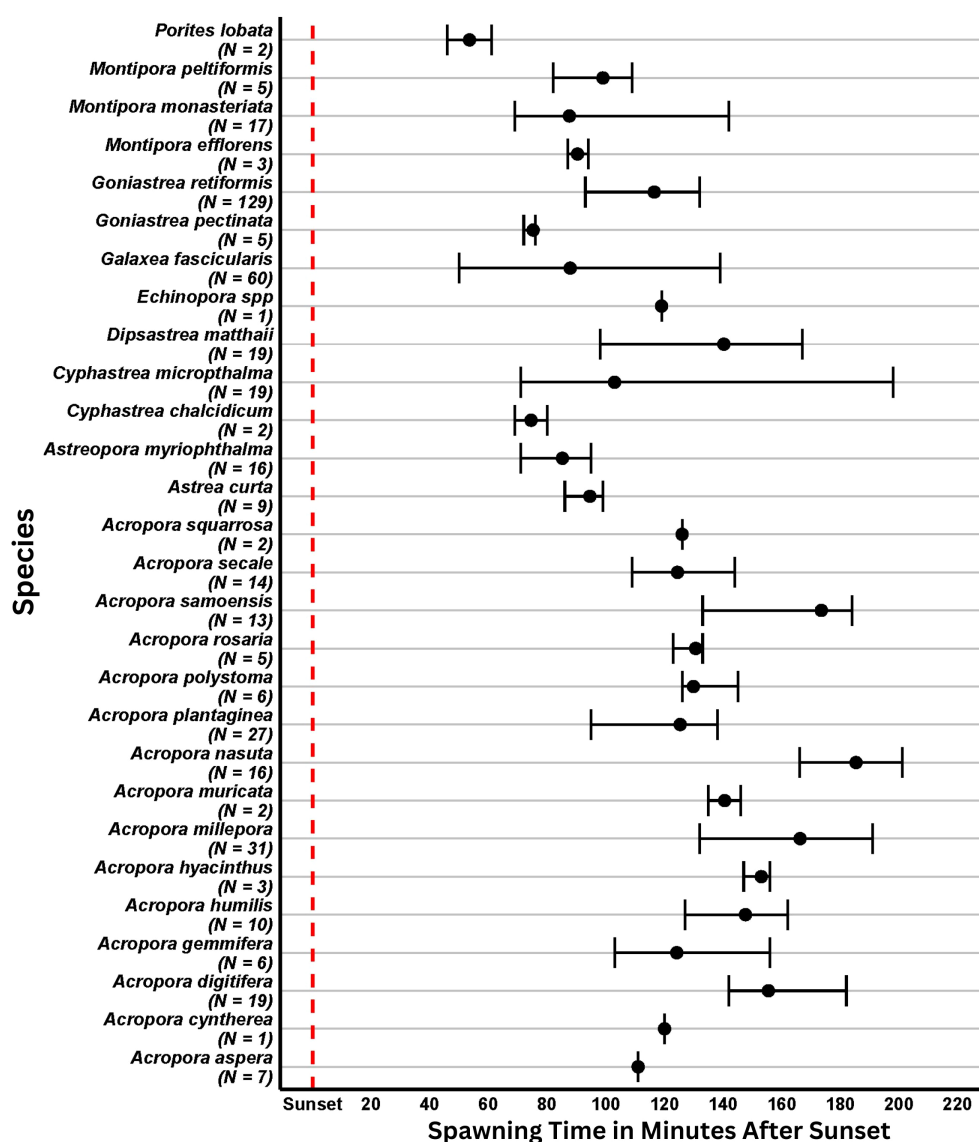


FIGURE 3

The spawning time relative to sunset for various coral species. The black circles represent the mean observed spawning time for each species recorded. The associated error bars display the range of time spawning was observed across all individual colonies of that species. The number of spawning colonies for each species was totaled and placed under the y-axis labels, in the form of (N=X).

## Multi-specific spawning

Multispecific spawning events coincided with sharp seasonal declines in average wind speed (Figure 2A), which occurred consistently each year in March and November. Multispecific spawning events also occurred in April during periods of declining wind speeds (2.50 to 2.08 m/s). A smaller multispecies spawning event was noted in December during a period of increasing wind speed (1.88 to 2.19 m/s).

Solar insolation levels revealed two main peaks a year; in March and a smaller peak in September. Multi-specific spawning events occurred during these peaks and were additionally observed during the subsequent months, occurring during periods where solar insolation declined (Figure 2C). There was no coral spawning

observed during the months containing the lowest solar insolation levels or during periods when solar insolation was increasing towards that of dual maxima.

SST rises and falls in a biannual cycle, with distinct peaks in April and November (Figure 2B). The largest multispecific spawning events coincided with sharp rises and/or peaks in SST in March, April and November. Spawning was also observed in the months surrounding these maxima, extending from October through to December.

## Discussion

The results of this study expand on previous observations of *Acropora* coral spawning in the Maldives (Monfared et al., 2023;

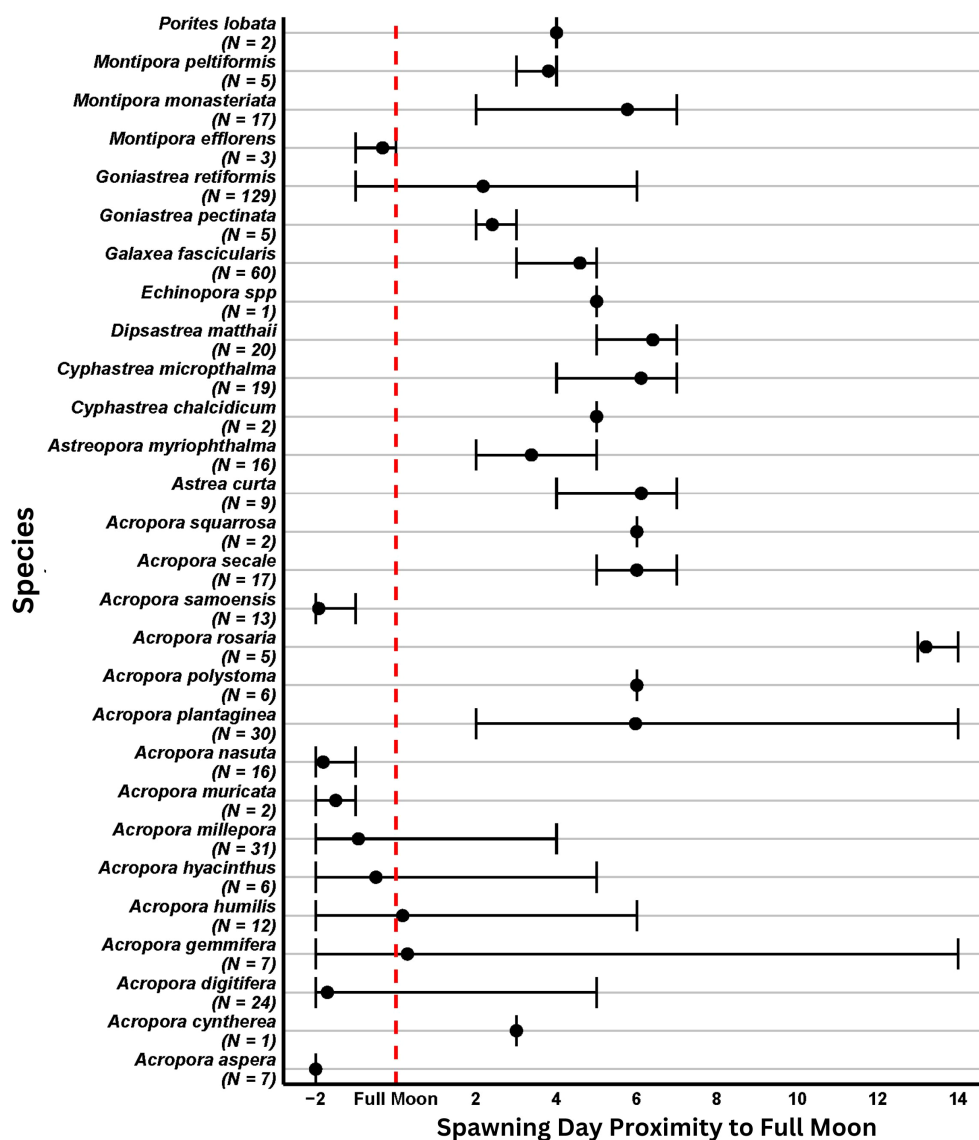


FIGURE 4

The spawning day relative to the closest full moon. The black circles represent the mean observed day that spawning occurred per species. The associated error bars indicate the range of days in which colonies of each species spawned relative to the nearest full moon. The number of colonies recorded spawning for the duration of this study is noted in the y axis (N=x).

Sheridan et al., 2025) and provide new information about the exact time of spawning onset and months of spawning for 13 species of 12 genera of non-*Acropora* corals in this region. We support the identification of two peak spawning seasons in the Maldives by Monfared et al. (2023) in March and April and between October and December, in which large, multispecific spawning events occur. We note variations in spawning patterns within and between taxa, documenting the occurrence of extended breeding via asynchronous spawning of colonies within a species and split-spawning of individual colonies across lunar months. We also note the occurrence of spawning as an annual or bi-annual event for individual colonies, demonstrating that the number of annual reproductive cycles and degree of spawning synchrony varies among taxa in this region. Our data suggests varied and complex patterns of reproduction and provides crucial foundational

observations of coral spawning in the Maldives, a data-deficient region where little is known about the reproduction of non-*Acropora* corals.

Varied spawning patterns were observed between taxa in this study. *Goniastrea retiformis* colonies spawned in only one peak season per year. Temporal segregation between March/April and November spawning cohorts, coupled with a single gametogenic cycle annually may reduce gamete encounter rates and the chance of successful fertilisation (Shlesinger and Loya, 2019). Conspecific coral populations that spawn in different seasons may become reproductively isolated and experience limited gene flow, which over time can lead to genetic divergence (Rosser, 2015; Rosser et al., 2020). While our single-year dataset limits long-term inferences, these findings warrant further investigation into the genetic structure of *G. retiformis* populations in the Maldives. Region-

**TABLE 2** Results of binomial generalised linear models to explore the influence of environmental conditions (sea surface temperature, wind speed and solar insolation) on the occurrence of coral spawning.

| Environmental factor | Estimate ( $\pm$ SE) | Z value | P value      | R <sup>2</sup> (McFadden) | AIC    |
|----------------------|----------------------|---------|--------------|---------------------------|--------|
| Wind Speed (m/s)     | -3.816 $\pm$ 2.113   | -1.806  | 0.071        | 0.470                     | 15.671 |
| SST (°C)             | 1.35 $\pm$ 1.050     | 1.280   | 0.200        | 0.086                     | 24.270 |
| Solar Insolation     | 2.079 $\pm$ 1.046    | -1.987  | <b>0.047</b> | 0.260                     | 20.400 |

Shown are regression coefficients ( $\beta \pm$  SE), test statistics (z), p-values, McFadden's pseudo-R<sup>2</sup>, and AIC for each univariate model. Results are given in bold. Significance was found at  $p < 0.05$ .

wide data collected over extended time periods is needed to assess the degree of temporal segregation and potential for genetic divergence in this population.

Contrastingly, spawning of individual colonies over bi-annual spawning seasons was noted in *Galaxea fascicularis* and some colonies of *Acropora humilis*, *A. plantaginea* and *A. secale*. Split-spawning, where coral colonies release gametes over consecutive lunar months, was commonly noted in colonies *G. fascicularis*, for some species of *Acropora*, and for *Cyphastrea microphthalma*. This reproductive strategy has been widely documented across multiple taxa and regions (Baird et al., 2022, 2009; Bastidas et al., 2005; Bauman et al., 2011; Foster et al., 2018; Hock et al., 2019; Kongiandtre et al., 2010; Moritz et al., 2025; Willis et al., 1985). Split-spawning may lead to multiple smaller or staggered spawning events, reducing reproductive synchrony and gamete encounter rates, and increasing the vulnerability of gametes released to predation (Oliver and Babcock, 1992). However, whilst large spawning events maximise gamete encounter rates, at high gamete densities polyspermy can reduce fertilisation success (Leviton, 2004); as such, split-spawning may increase local fertilisation success by preventing gamete saturation. Further, by releasing gametes over multiple days following the full moon and in consecutive lunar months, the risk of total reproductive failure in a single event is reduced (Babcock et al., 1986; Harrison et al., 1984). Split-spawning can enable corals to realign reproductive timing with favourable environmental conditions, particularly when lunar cycles may cause spawning to occur outside optimal windows (Foster et al., 2018; Hock et al., 2019). Split-spawning is often associated with suboptimal environmental conditions in the lead-up to the full moon, or when thermal or photic thresholds are not met synchronously across coral populations (Baird et al., 2009; Harrison et al., 1984; Keith et al., 2016; Nozawa et al., 2015; Sweeney et al., 2011). Foster et al. (2018) noted that years with slower seasonal rises in SST showed increased incidences of split spawning, suggesting strong environmental cues may drive more synchronised spawning in a single lunar cycle. As such, corals in tropical regions where seasonal changes are less distinct may show less synchronised spawning. Split-spawning has been documented on the Great Barrier Reef (GBR) and in Western Australia most commonly when the full moon falls in the first half of the month (Baird et al., 2011; Gilmour et al., 2009; Willis et al., 1985), but can also occur when the full moon falls in the second half of the month (Babcock et al., 1986; Foster et al., 2015). Our study shows that split-spawning occurs in *G. fascicularis* and *Acropora* when the full moon

falls in both the first and second half of the month, supporting observations of no consistent relationship between split-spawning and full moon timing. Long-term studies have shown that split-spawning is not an annual feature but rather occurs periodically (Foster et al., 2018), but recent research on daytime spawning corals has documented individual colonies of *Porites rus* spawning over five consecutive months each year (Moritz et al., 2025); as such, more data collected over extended time periods would be needed to identify the extent, environmental drivers, and impact on successful fertilisation of split-spawning in this region.

It has been hypothesised that equatorial reefs exhibit extended breeding seasons due to weaker environmental seasonality enabling multiple spawning events in a year (Oliver et al., 1988). Whilst the results of some studies support this hypothesis (Mangubhai and Harrison, 2008), others at similar latitudes have countered it (Baird et al., 2002; Chelliah et al., 2015; Guest et al., 2005b; Monfared et al., 2023; Gouezo et al., 2020; Novriansyah et al., 2023; Penland et al., 2004; Sola et al., 2016; Wijayanti et al., 2019). Bouwmeester et al. (2021) used data from 90 sites across the Indo-Pacific and found no correlation between latitude and reproductive synchrony, indicating that other factors drive reproductive synchronicity. In the Maldives, Monfared et al. (2023) noted that *Acropora* corals spawn over an extended period of eight months of the year. Further analysis of the degree of spawning synchrony found that *Acropora* corals in the Maldives spawn most frequently and in greater numbers during multispecific spawning events than they do in single species events, with 95.1% of colonies in Baa Atoll and 96.7% of colonies in North Male Atoll spawning during multispecific events (Sheridan et al., 2025). Our study concurs with these findings and reveals that previously unstudied genera at the same site in Baa Atoll also follow similar patterns, indicating similar environmental drivers of spawning.

The timing of peak spawning seasons in the Maldives coincide with the transition between the southwest and northeast monsoon, characterised by a reversal in wind direction and current (Aleem, 2013; Litster, 2016; Schott et al., 2009; Su et al., 2021). Similar patterns have been noted on other equatorial reefs (Wijayanti et al., 2019) and a global analysis spanning seven regions by van Woessik (2010) revealed that regional periods of low wind speeds were often tightly coupled with mass spawning events. Transitional periods of reduced wind intensity offer evolutionary advantages for coral reproduction by increasing successful fertilisation (Babcock et al., 1994) and enhancing larval retention, ultimately supporting local recruitment and population resilience (Elmhirst et al., 2009).

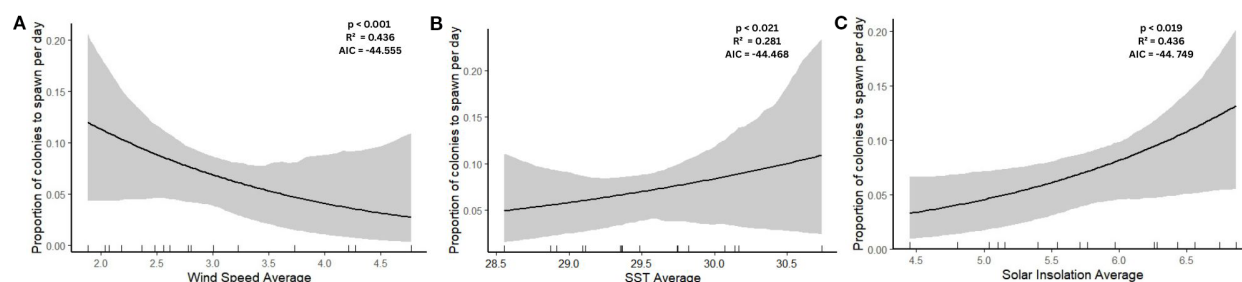


FIGURE 5

Effect of environmental conditions on the proportion of colonies to spawn per month based on the results of beta regression model. The explanatory variables included in the model are average monthly (A) wind speed (m/s), (B) sea surface temperature (SST) (°C) and (C) daily solar insolation (kWh/m<sup>2</sup>/day). The black line indicates the relationship between the environmental variables and proportion of colonies to spawn. The grey shading indicates the 95% confidence interval. Rug marks along the x-axis displays the distribution of observed data points. P-values, AIC and R<sup>2</sup> are exhibited within each panel.

However, low current (induced or not by wind) may limit the dispersal of larvae to other reef systems, reducing larval exchange between reef systems and genetic mixing, impacting metapopulation resilience (Cowen et al., 2000; Jones et al., 2009). As an archipelago comprising approximately 1,192 islands spread across 26 geographic atolls (Maldives National Statistical Bureau, 2020), more research from different regions is needed to assess the extent of larval dispersal and genetic connectivity in the Maldives.

In this study, while wind speed was not a significant predictor of the occurrence of spawning in a given month, it had the strongest influence on the proportion of colonies spawning each month. The largest multispecific spawning events observed occurred in March, April and November (annually); periods that displayed abrupt drops in average wind speed. Notably, these months coincided with the transitional periods between monsoon seasons in the Maldives. The Hulhangu (Southwest) monsoon occurs from May to September, while the Iruvai (Northeast) monsoon occurs from December to February (Aleem, 2013). These results are consistent with equatorial studies conducted in Palau (Penland et al., 2004), the Karimunjawa Archipelago in Indonesia (Wijayanti et al., 2019), Singapore (Guest et al., 2005a) and in Baa and North Malé Atolls in the Maldives (Monfared et al., 2023; Sheridan et al., 2025), all of which documented large multispecific coral spawning during the inter-monsoonal periods. These transition phases mark distinct and pronounced environmental shifts that may act as major spawning cues for gamete release in regions where wind conditions are rarely calm (van Woesik, 2010), and where changes in SST and solar insolation are less pronounced than in reefs at higher latitudes.

The duration of the gamete release is understood to be correlated with sustained periods of low wind speeds (van Woesik, 2010). A study on Kenyan reefs at a similar latitude to this study (4°S) found no evidence of a main spawning period to be during the inter-monsoon season; instead, a protracted breeding season of approximately 8 months was observed (Mangubhai and Harrison, 2008). This may be linked to Kenya's less sharply defined seasonal wind transitions, with spawning occurring predominantly during the Northeast monsoon (December to March), when conditions are relatively calm and stable. Whilst our study concurs with findings of two peak spawning seasons in the Maldives coinciding with monsoonal transitions, we consider that extensive surveys of spawning in *Acropora* in this region revealed asynchronous spawning occurring outside of these peaks during the Northeast monsoon (Monfared et al., 2023; Sheridan et al., 2025). These patterns suggest that where there is no abrupt drop in wind speed, the persistence of calm conditions over a sustained period of time may too serve as a cue for coral spawning.

Monsoonal transitions are typically associated with rapid increases in sea surface temperature (SST), which have been identified as a key driver of coral spawning across various temporal and vast geographic scales (Keith et al., 2016; Novriansyah et al., 2023). SST has been shown to influence both gametogenic development and the timing of gamete release, with several studies correlating earlier or more synchronous spawning events with higher SSTs (Howells et al., 2014; Lin and Nozawa, 2023; Moritz et al., 2025; Nozawa, 2012; Monfared et al., 2023; Sun et al., 2024). Moritz et al. (2025) noted that at both large scales and at the individual colony level, increases in temperature

TABLE 3 Results of beta regression models testing the effects of environmental conditions (sea surface temperature, wind speed and solar insolation) on the proportion of colonies to spawn each month.

| Environmental factor | Estimate ( $\pm$ SE) | Z value | P value      | R <sup>2</sup> (McFadden) | AIC     |
|----------------------|----------------------|---------|--------------|---------------------------|---------|
| Wind Speed (m/s)     | -0.709 $\pm$ 0.219   | -3.238  | <b>0.001</b> | 0.436                     | -44.555 |
| SST (°C)             | 0.701 $\pm$ 0.304    | 2.308   | <b>0.021</b> | 0.281                     | -44.468 |
| Solar Insolation     | 0.585 $\pm$ 0.250    | 2.338   | <b>0.019</b> | 0.2793                    | -47.749 |

Significant results are given in bold. Proportion of colonies spawning per month (response) was calculated as the total number of colonies spawning each month divided by the total number of colonies recorded spawning for the duration of this study. Model fit was evaluated using McFadden's pseudo-R<sup>2</sup> and AIC. Significance was found at  $p < 0.05$ .

induced earlier spawning. The role of SST as a spawning cue appears to vary by region and species. As such, peak spawning months could be inferred from rapid rises in SST, but not months where few colonies spawned. [Sheridan et al. \(2025\)](#) noted that while change in SST was a significant predictor of the number of colonies to spawn within a month, it did not significantly predict the month in which spawning occurred. Our study suggests that SST influences the intensity of spawning rather than the timing, as a higher proportion of colonies spawning in a given month were significantly correlated with higher average monthly SSTs. [Sheridan et al. \(2025\)](#) also found that *Acropora* species differed in their response to SST changes indicating that thermal cues alone do not universally regulate spawning patterns. In Palau, [Gouezo et al. \(2020\)](#) recorded spawning over an extended period of nine months with no consistent correlation between SST and the timing of reproductive events, suggesting that temperature alone may not serve as a universal proximate cue. These studies underscore the complexity of coral reproductive cues and highlight the need for further research to understand the interplay of various environmental factors influencing coral spawning.

Solar insolation cycles play an important role in entraining the endogenous reproductive rhythms of corals on broad seasonal scales ([Mangubhai and Harrison, 2008](#); [Gouezo et al., 2020](#); [van Woesik et al., 2006](#)). Studies have shown that in some equatorial regions the rate of change of solar insolation is a reliable predictor of coral spawning, with gamete release often occurring after the peak of solar insolation maxima, during the subsequent fall ([Mangubhai and Harrison, 2008](#); [Gouezo et al., 2020](#); [van Woesik et al., 2006](#); [Penland et al., 2004](#)). Our study found that solar insolation significantly influenced both the likelihood of spawning occurrence and the proportion of colonies spawning in a given month. This dual influence underscores its importance as a key environmental cue. Studies have demonstrated that a combination of increased solar irradiance and high SST can result in oxidative stress to coral tissues ([Yakovleva et al., 2009](#); [Hoegh-Guldberg and Jones, 1999](#)). As such, timing spawning to occur after peak solar insolation may serve as an evolutionary advantage to improve larval viability and reduce post-spawning stress on parent colonies. These studies highlight the complex interplay of multiple environmental factors influencing scleractinian coral spawning.

## Conclusion

This study provides new insights into the timing, synchrony, and species-specific patterns of coral spawning in the Maldives, offering the first detailed records for several non-*Acropora* genera in this region. We found that larger spawning events in a given month were significantly correlated with lower wind speeds, higher sea surface temperatures, and increased solar insolation, highlighting the influence of environmental conditions on both the occurrence and extent of coral reproduction. Because more frequent and severe bleaching events can damage the reproductive fitness of corals, studying the successful

reproduction and recruitment of surviving colonies is central to maintaining coral populations and restoring reef structure and function. Understanding when and how corals reproduce is critical for evaluating the potential of coral populations to recover following disturbance. With restoration initiatives in the Maldives increasingly utilising sexual reproduction (e.g. larval propagation and assisted fertilisation), these findings serve as an important baseline for reef managers, researchers, and restoration practitioners. However, as this study is based on a single year of observations from one atoll, caution must be taken in extrapolating trends across space and time. Long-term, region-wide monitoring is needed to identify the environmental drivers of coral spawning and assess how spawning patterns may shift under future climate scenarios.

## Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

## Author contributions

AE: Data curation, Methodology, Writing – review & editing, Supervision, Conceptualization, Writing – original draft, Investigation, Software, Project administration, Funding acquisition, Visualization, Resources, Formal analysis, Validation. KM: Writing – review & editing, Validation, Conceptualization, Methodology, Supervision, Investigation, Funding acquisition, Software, Formal analysis, Resources, Writing – original draft, Visualization, Data curation, Project administration. TL: Writing – original draft, Writing – review & editing.

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## Conflict of interest

Authors AE, KM, and TL were employed by Reefscapers.

## Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2025.1646721/full#supplementary-material>

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