Coral spawning patterns of *Acropora* across two Maldivian reef ecosystems (#85212)

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Coral spawning patterns of *Acropora* across two Maldivian reef ecosystems

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Understanding coral reproductive biology at ~~a~~ local and regional scale is crucial to elucidate our knowledge ~~on~~ characteristics that regulate populations and communities ~~over time~~. The lack of published data on coral spawning patterns ~~here~~ in the Maldives hinders our understanding of coral reproductive biology at a local and regional scale and limits our ability to assess shifts in reproductive phenology over time. Here we document baseline environmental cues, spawning patterns, exact timings and oocyte development of restored and wild *Acropora* inhabiting shallow water reefs across two Maldivian Atolls. A total of 1,200 colonies were recorded spawning across the two sites between September 2021 and April 2023. These colonies represent 22 species of *Acropora*, with coral spawning observed over an extended period of eight months. This research details exact spawning times of multi-specific spawning, asynchronous spawning and 'split spawning' of *Acropora,* across multiple lunar phases; and highlights the need to consider restored colonies when discussing the sexual reproductive patterns of Maldivian *Acropora* in the future. Overall, corals spawned 2.3577 days earlier in North Male Atoll compared with Baa Atoll. Earlier spawning events were significantly correlated with lower tide depths and lower wind speeds, which ~~can help to explain~~ inter-atoll and inter-annual variations in spawning date. This study contributes to understanding sexual reproductive cycles of *Acropora* in the Maldives; knowledge which is vital for effective management of a critically endangered ecosystem in a changing climate.

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Abstract

Understanding coral reproductive biology at a local and regional scale is crucial to elucidate our knowledge on characteristics that regulate populations and communities over time. The lack of published data on coral spawning patterns here in the Maldives hinders our understanding of coral reproductive biology at a local and regional scale and limits our ability to assess shifts in reproductive phenology over time. Here we document baseline environmental cues, spawning patterns, exact timings and oocyte development of restored and wild *Acropora* inhabiting shallow water reefs across two Maldivian Atolls. A total of 1,200 colonies were recorded spawning across the two sites between September 2021 and April 2023. These colonies represent 22 species of *Acropora*, with coral spawning observed over an extended period of eight months. This research details exact spawning times of multi-specific spawning, asynchronous spawning and 'split spawning' of *Acropora,* across multiple lunar phases; and highlights the need to consider restored colonies when discussing the sexual reproductive patterns of Maldivian *Acropora* in the future. Overall, corals spawned 2.3577 days earlier in North Male Atoll compared with Baa Atoll. Earlier spawning events were significantly correlated with lower tide depths and lower wind speeds, which can help to explain inter-atoll and inter-annual variations in spawning date. This study contributes to understanding sexual reproductive cycles of *Acropora* in the Maldives; knowledge which is vital for effective management of a critically endangered ecosystem in a changing climate.

Introduction

Scleractinian corals are structural architects that form the foundation of coral reef ecosystems~~,~~ predominantly made from three-dimensional (3D) calcium carbonate structures (Baird et al., 2015; Jamodiong et al., 2018) ~~that~~ support 25% of all known marine inhabitants (Bourne & Webster, 2013). Reef building corals have a bipartite life history; initially as planktonic larvae that allows connectivity among reefs before becoming sessile during the adult stage (Mayorga-Adame, Batchelder & Spitz, 2017). This early planktonic stage is a critical component to sustaining coral reef ecosystems, which have been on the decline over the past three decades due to numerous anthropogenic pressures including climate change, pollution and overfishing (Hughes et al., 2017, 2018).

Coral reproduction is a fundamental process that ~~retains~~ coral reef functions and structure (Baird et al., 2015), and has evolved to improve survival by taking place during favourable conditions that maximise fertilisation, gamete density and predator satiation (Foster, Heyward & Gilmour, 2018). Understanding of coral ~~reproduction~~ timings is crucial to elucidate our knowledge ~~on~~ characteristics that regulate populations and communities, particularly through recruitment ~~rates~~ and ecosystem connectivity (Kool, Moilanen & Treml, 2013; Done, Gilmour & Fisher, 2015). Furthermore, sexual reproduction increases genetic diversity of offspring, improving the adaptation and resilience of the next generation (Otto & Lenormand, 2002), which in turn has important implications ~~on~~ coral reef management and conservation (Richmond, 1997; Guest, 2008).

The first documentation of multi-specific synchronous spawning took place in the 1980s on the Great Barrier Reef (Harrison et al., 1984). This phenomenon led to the increased effort to document coral spawning across a wide geographic region (Harrison, 2011). ~~Research~~

discovered that multi-specific coral spawning is probably a characteristic of all speciose coral assemblages, occurring at both high and low latitudes (Guest et al., 2005; Baird, Guest & Willis, 2009; Bauman, Baird & Cavalcante, 2011; Chelliah et al., 2015; Bouwmeester et al., 2015; Gouezo et al., 2020) and has revealed that the dominant spawning pattern of coral species is classified as hermaphroditic broadcast (Harrison, 2011). Local and regional environmental conditions have been shown to regulate the seasonal timing of gametogenic cycles either as ultimate factors or proximate cues (Babcock et al., 1986; Harrison & Wallace, 1990) and typically include sea surface temperature (Keith et al., 2016; Sakai et al., 2020), wind speed (van Woesik, 2010; Keith et al., 2016; Sakai et al., 2020), precipitation (Hayashibara et al., 1993; Mendes & Woodley, 2002) and lunar phase (Brady, Hilton & Vize, 2009; Boch et al., 2011), among others.

Located in the Indian Ocean lies the Maldives (3.2028° N, 73.2207° E), in which coral reef ecosystems were subject to two mass bleaching events in 1998 and 2016 (Cowburn et al., 2019). Coral coverage decreased from 40-60% to less than 8% after the 1998 bleaching event (Morri et al., 2015; Pisapia et al., 2016). Despite this disturbance, Maldivian reefs showed resilience and recovered up to 40% in 2015 (Pisapia et al., 2016). However, in 2016, another mass bleaching event extirpated many reef building corals ~~such as~~ the genus *Acropora* (Pisapia, Burn & Pratchett, 2019). Coral bleaching has been shown to decrease reproductive potential of survivors (Leinbach et al., 2021), reduce gamete numbers (Ward, Harrison & Hoegh-Guldberg, 2000), and lead to a long-term impact on reproduction over multiple spawning periods (Levitan et al., 2014). To alleviate these impacts on coral reef ecosystems, restoration initiatives that manipulate asexual propagation were implemented not only in the Maldives but worldwide (Boström-Einarsson et al., 2020; Montano et al., 2022). As the persistence of coral populations ~~rely~~ on the success of natural recruitment through reproduction, (Richmond, Tisthammer & Spies, 2018) it is imperative we understand reproductive ~~rates~~ to predict population recovery following disturbance in the Maldives.

Although coral spawning is a well-known phenomenon where patterns in the Indo-Pacific have been collated from both the literature and unpublished observations (Baird et al., 2021), little remains documented about the extent of spawning synchronicity in the Maldives, the world's seventh largest coral reef ecosystem, comprising 3.14 % of global reefs (Dhunya, Huang & Aslam, 2017). Published reports from the Maldives include observations on coral slicks in South Ari Atoll (Loch et al., 2002), and spawning of *Pocillopora verrucosa* (Sier & Olive, 1994). Mentions of *A. hyacinthus* and *A. digitifera* spawning during March and April were stated in personal communications (Clark & Edwards, 1999) and a published report by Harrison & Hakeem, (2007) revealed patterns of asynchronous spawning over multiple lunar cycles. Informal records of slick formations and the inference of spawning are mentioned during March-April and in the last quarter of the year ("Marine Research Centre - Coral Spawn Slick Formation"). Blog posts reveal coral spawning observations in April-May 2012 at Gili Lankanfushi, North Male Atoll, ("We have witnessed the elusive coral spawning event this week ! – Gili Lankanfushi Maldives," 2012) and also in December 2014 ("Coral Spawning – Gili Lankanfushi Maldives," 2014), whilst Newsletters from Laamu Atoll ~~publicise~~ spawning information over multiple months since 2021 ("Blue & Green Laamu Newsletter — MUI By Six Senses Laamu," 2021). Yet exact timings and species information is not readily available. The lack of published data to distinguish the onset of gametogenesis in-situ and exact spawning times to amalgamate regional spawning patterns hinders our understanding of coral reproductive biology at a regional scale and limits our ability to assess shifts in reproductive phenology over time. The Maldives territory is 99% water spanning across 26 atolls and is home to 258 species of hermatypic corals (Dhunya, Huang & Aslam, 2017). While informal spawning research has been documented through blogs and newsletters, peer-reviewed literature remains scarce. Moreover, the impact of coral restoration activities on the natural spawning cycle of *Acropora* has not been documented in this region.

Asexual propagation techniques can be limited by species availability and constrained genotypic diversity of clonal fragments (Oppen et al., 2017). However, the successful out planting of vast numbers of coral can lead to 'spawning hubs' that reproduce sexually resulting in a mass supply of coral larvae released back into the environment (Horoszowski-Fridman, Izhaki & Rinkevich, 2011; Montoya Maya et al., 2016). Moreover, if donor colonies are the remnants of preceding mass bleaching events, coral propagation improves the likelihood of bleaching-resistant genotypes within populations which can be passed onto new recruits improving ecosystem resilience (Montoya Maya et al., 2016). Reefscapers Pvt Ltd (hereafter referred to as: Reefscapers) utilises asexual propagation through their coral frame technique by attaching coral fragments, of varying species and genera onto metal frames, which have been previously coated with resin and sand, using cable ties (Morand, Dixon & Le Berre, 2022). Each frame is given a unique reference code. Due to the high mortality of branching species following the 2016 coral bleaching event (Pisapia, Burn & Pratchett, 2019; Bessell-Browne et al., 2021), propagation efforts were predominantly focused on increasing ~~coral~~ coverage of the coral genus *Acropora*.

In this study we document baseline environmental cues, spawning patterns, exact spawning timings, and oocyte development of naturally occurring and restored *Acropora* inhabiting shallow water reefs across two islands, over a two-year period (October 2021 – April 2023). This information will be critical to begin to understand coral spawning synchronicity of Maldivian Reefs at a local and regional scale and will help to direct conservation and management strategies in a changing environment.

Materials & Methods

Study Sites

Research surveys took place around two resort islands with long-term restorative projects run by Reefscapers situated in two different Maldivian Atolls: Landaa Giraavaru located in Baa Atoll (5.2862° N, 73.1121° E) a UNESCO Biosphere Reserve since 2011 and Furana Fushi (4.2500° N, 73.5458° E), located in North Male Atoll, Maldives, since 2020 (Figure 1). Landaa Giraavaru is 0.18km^2 in area in a small sand cay situated on the western front of the Maldivian atoll chains (Hein et al., 2020). Furana Fushi is located 8.5km north of Male, the Maldives capital city.

Coral colonies were surveyed up to an 11m depth around the 'house reef', with particular focus on the southern near-shore reef of Landaa Giraavaru. At Furana Fushi, surveys were conducted up to a 6m depth at two shallow, near-shore reef sites and two lagoon sites. The most severely affected taxa from the 2016 coral bleaching event, *Acropora* (Pisapia, Burn & Pratchett, 2019; Bessell-Browne et al., 2021), were the main focus of this study. Survey sites were chosen based on *Acropora* coverage and diversity of reef type, which were: i) Wild – naturally occurring colonies, ii) Relocated – colonies moved from another site and transplanted directly onto the reef, iii) Frame – colonies asexually propagated as small fragments onto Reefscapers human-made structures, and iv) Pyramid – relocated colonies transplanted directly onto Reefscapers human-made structures in their entirety (i.e. not asexually propagated). Pyramid and relocated colonies are only located at Furana Fushi and were relocated from Gulhifalhu in 2020. The pyramids have been in-situ since June 2020.

Surveys

Identification of Gravid Colonies

Reproductive maturity surveys were conducted in-water for *Acropora* from September 2021 – April 2023, by a minimum of two observers in each location. Surveys coincided with coral restoration activities to reduce negative ~~impact~~ on coral colonies. To identify gravid colonies, observers fragmented a 1-2 inch section of a coral colony from the base using scissors to identify the presence of gametes (Harrison et al., 1984). Reproductive stages were tracked and classified into three distinct categories based on oocyte colouration: i) white – immature (Figure 2A), ii) pale – close to maturity (Figure 2B), and iii) pigmented – mature (Figure 2C), following Baird, Marshall & Wolstenholme, (2000). Upon observation of gametes, the species, location, reef type and oocyte category of gravid colonies were recorded in a central database. Gravid colonies were thereafter sampled bi-monthly to track changes in colouration. If sampling bi-monthly was not possible (due to adverse weather, staffing constraints, access to location etc.), colonies were sampled monthly. Coral species were identified using Corals of the World (Veron & Stafford-Smith, 2000). Genetic testing would need to be carried out to confirm species identification.

Observing coral spawning and bundles

Upon observation of gravid colonies with mature gametes within the skeletal tissue, nightly surveys took place over a period of six hours (16:30 – 22:30) around the full moon and new moon. The times of bundle appearance/setting and spawning time vary among *Acroporid* species (Fukami et al., 2003); thus observers entered the water prior to the sunset and remained checking for bundling for up to two hours after sunset. Surveys around full moon began two days prior and continued for up to eight days after, whilst new moon surveys took place two days prior for up to four days after, from September 2021 - April 2023 at all sites. Surveyors utilised a combination of conventional SCUBA and free diving at both locations.

Observers were checking for ‘bundling’, tightly packed egg and sperm bundles that ‘set’ in the coral polyp mouth prior to being released (Figure 2D) in previously identified gravid colonies. These bundles are buoyant due to the lipid components and thus float to the surface upon release (Arai et al., 1993). During nightly surveys, all timings were recorded on slates in situ by observers. Bundle appearance and spawning time (defined as the first gamete release; Figure 2E), were recorded for individual colonies.

The sunset time was recorded for both study sites utilising ‘Time and Date’ webpage (Steffen Thorsen, 1995a,b), to later calculate the individual colony spawning and bundling time after sunset, as sunset can be associated with spawning behaviour (Babcock et al., 1986; Brady, Hilton & Vize, 2009; Sweeney et al., 2011; Keith et al., 2016) and a useful indicator for predicting spawning (Baird et al., 2022). Data and information on colonies that were not previously recorded as gravid but were observed to spawn were also collected. In addition, the ~~tide~~ depth of the ~~closest~~ low tide to sunset (m) was collected (“Baa Atholhu’s Tideschart.com”; “Male Tideschart.com”). In the case of logistical constraints preventing night surveys, due to adverse weather, staffing numbers or site access, colonies were sampled daily and checked for absence of gametes the following morning to ensure exact spawning dates.

Statistical Analysis

General linear models (GLMs) were used to investigate potential variations in spawning date relative to the nearest full moon and spawning time after sunset between Atolls and annually for all observed colonies, and for individual species. To identify whether potential inter-Atoll or inter-annual variations in spawning date could be explained by environmental conditions, general linear mixed models (GLMMs) were constructed. These GLMMs used the ~~date~~ of spawning relative to the nearest full moon as the response variable for all data, and two ~~additional models were constructed isolating each Atoll~~. Four environmental parameters were chosen as explanatory variables that reportedly influence the date of coral spawning: sea surface temperature (Keith et al., 2016; Sakai et al., 2020), wind speed (van Woesik, 2010; Keith et al., 2016; Sakai et al., 2020), precipitation (Hayashibara et al., 1993; Mendes & Woodley, 2002) and tide depth (Jamodiong et al., 2018). Average daily sea surface temperatures were obtained from ("Baa Atoll Sea Temperature"; "Male Sea Temperature"). Total daily precipitation (mm) and average daily wind speed (mph) were obtained from windy.app ("Windy.app – Live wind map & weather forecast"). When testing for collinearity between the environmental parameters, average daily wind speed was strongly correlated with average daily sea surface temperature ($r = 0.680$). Therefore, average daily sea surface temperature was excluded from the final models because although variations in sea surface temperatures (SSTs) have been documented to influence gametogenic cycles, SSTs can be a poor predictor of coral spawning events in the tropics (Penland et al., 2004). The differences in reef type and spawning month were included as random intercepts. Type III tests of variance were performed on the models to determine the significance of each explanatory variable on the response variables. GLMs were used to assess correlations between spawning date relative to the nearest full moon, and spawning time after sunset and reef type, for *A. humilis, A. digitifera,* and *A. millepora* in Baa Atoll. Only two reef types were recorded for these species: wild and frame colonies. These species and Atoll were chosen for this analysis due to ~~sample size limitations~~; in North Male Atoll there were too few wild colonies observed spawning for statistical analyses, and in Baa Atoll the number of wild colonies ~~to spawn~~ was too small for all other species. All statistical analysis were conducted using R Studio Version 2022.12.0 (R Core Team, 2022).

Results

In total, 1,200 colonies were recorded spawning across the two sites between 1 October 2021 and 30 April 2023: 501 frame, 593 pyramid, 2 relocated and 104 wild (Table 1). These colonies represent 22 species of *Acropora*: 17 confirmed species were recorded in Baa Atoll and 19 confirmed species in North Male Atoll (Table 1). Fourteen species were recorded spawning in both atolls. Coral spawning was recorded in eight months of the year: January (N = 1), February (N = 2), March (N = 66), April (N = 553), May (N = 2), October (N = 53), November (N = 444), and December (N = 79). Furthermore, spawning was recorded on 46 days throughout the study period; 24 days of which recorded spawning of more than one species. The highest number of species recorded spawning on the same day was 14, which occurred on 5 April 2023 in North Male Atoll. All coral spawning was recorded across multiple lunar phases (Figure 3A) and after sunset (Figure 3B). Thirty-six colonies were recorded spawning around the new moon. Fourteen colonies spawned over more than one consecutive day within one spawning season and included: six *A. tenuis*, two *A. rosaria*, one *A. millepora* and five *A. nasuta*. One colony of *A. gemmifera* and two colonies of *A. tenuis* in the North Male Atoll were witnessed spawning immature (white) gametes (see Figure 2F).

Oocyte Development

Of the 1,200 colonies documented spawning in this study, 503 were first identified with immature oocytes across 16 species. On average, immature oocytes were identified 94.5 days before spawning.

Inter-Annual Variation

The timing of coral spawning varied annually. When considering all species together, corals spawned 8.795 minutes (GLM; $SE = 3.276$, $t = -2.685$, $p = 0.00737$) and 1.4656 days (GLM; $SE = 0.1934$, $t = -7.578$, $p < 0.001$) earlier relative to full moon each year. However, when looking at species-specific spawning, annual variation in spawning time is only significant in three species: *A. hempricii*, *A. humilis*, and *A. tenuis* (Table 2), although the effect of year on spawning time on *A. tenuis* was small, with spawning occurring only 1.9277 minutes later each year (Table 2). All species spawned earlier each year in relation to date of spawning proximity to full moon (Table 2); but for *A. gemmifera, A. plantaginea*, *A. samoensis* and *A. squarrosa* this relationship was not statistically significant based on univariate GLMs (Table 2).

Inter-Atoll Variation

Overall, corals spawned 2.3577 days earlier in North Male Atoll compared with Baa Atoll (GLM; $SE = 0.2116$, $t = -11.14$, $p < 0.001$). This pattern is true of all species, excluding *A. plantaginea* (Table 3). Furthermore, corals in North Male Atoll spawned 26.113 minutes earlier (GLM; $SE = 3.636$, $t = -7.177$, $p < 0.001$). However, at individual species level this trend is largely not significant, except in the case of *A. secale* ($p < 0.001$) which spawns on average 7.619 minutes earlier in North Male (Table 3). Contrastingly, *A. plantaginea* spawned on average 7.026 minutes earlier in Baa atoll ($p < 0.001$; Table 3).

Environmental predictors of spawning

Earlier spawning events relative to full moon were significantly correlated with lower tide depths ($p < 0.001$) and lower wind speeds ($p < 0.001$) for both atolls (Table 4). Total daily precipitation was not significantly correlated with the proximity of spawning to the full moon when considering both sites together ($p = 0.770$; Table 4), but when looking at the individual Atolls, earlier spawning events relative to full moon were also significantly correlated with lower precipitation in North Male ($p < 0.001$; Table 4). The main difference when looking at predictors of spawning at Atoll-scale was the relationship between total daily precipitation (Table 4). In North Male Atoll, earlier spawning events relative to full moon were significantly correlated with lower precipitation ($p < 0.001$; Table 4), and the inverse relationship is true in the Baa Atoll, although not statically significant ($p = 0.064$; Table 4). However, the effect of precipitation on spawning date is small for both atolls (North Male - 0.263 days; Baa - 0.243 days; Table 4).

Reef type variations

There is no significant difference in the spawning date proximity to full moon between wild and frame colonies of *A. digitifera* (GLM; $SE = 0.129$, $t = -0.883$, $p = 0.381$), *A. humilis* (GLM; SE =

356, t = 1.005, p = 0.318), or *A. millepora* (GLM; SE = 125, t = -1.805, p = 0.077) in Baa Atoll. There is also no significant difference in the spawning time after sunset between wild and frame colonies of *A. humilis* (GLM; SE = 6.810, t = 0.553, p = 0.582) and *A. millepora* (GLM; SE = 6.205, t = -0.577, p = 0.567) in Baa Atoll. However, wild colonies of *A. digitifera* spawned 3.911 minutes earlier than frame colonies in Baa Atoll, which was statistically significant (GLM; SE = 1.823, t = -2.145, p = 0.037).

Discussion

The results from this study expand our limited knowledge on the exact spawning times of 22 *Acropora* spp. across two Maldivian atolls and identify two peak spawning periods each year. The first season: March - April, and the second season: October - December. Similar patterns have been observed in Western Australia (Rosser & Gilmour, 2008; Rosser, 2013; Gilmour, Speed & Babcock, 2016) and Indonesia (Permata et al., 2012; Wijayanti et al., 2019), with peak spawning events inferred from recruitment studies in Sri Lanka during March – April (Kumara, Cumaranatunga & Souter, 2007). In addition, this study demonstrates spawning events occur in the Maldives over an extended period of eight months of the year (Table 1), which has similarly been seen in other equatorial reefs (Gouezo et al., 2020).

In North Male Atoll, more species were observed spawning in the first season (16 species) compared to the second seasons (six species), but in Baa Atoll, nine species were observed during each season (Table 1). The climate in the Maldives experiences a wet season, accompanied with the west to northwest winds associated with the *hulhangu* monsoon, from April to November; and a dry season known as the *iruvai* monsoon associated with winds from the east-northeast from December to March (Kench & Brander, 2006). The transition period of the *hulhangu* monsoon takes place between March and April (Aleem, 2013), which appears to be associated with the largest number of multi-species spawning observed in North Male Atoll. In comparison, the *iruvai* transitional period from October to November (Aleem, 2013), signifying the end of the wet season, appears to show fewer species spawning in North Male Atoll. In contrast, nine species were observed spawning in each transitional period in Baa Atoll. Multi-specific spawning events have also been observed to take place during monsoonal transition periods in Indonesia (Wijayanti et al., 2019; Indrayanti et al., 2019). The bi-annual monsoon change strongly influences environmental parameters such as winds and currents in the North of the Maldives, in comparison to the South of the Maldives, which is less affected by monsoon changes and influenced by the equatorial currents (Su, Wijeratne & Pattiaratchi, 2021). This highlights that inter-atoll differences could be observed in spawning patterns across the North-to-South Atoll chain of the Maldives and may be linked to the different effects of the monsoon, as well as intra-atoll variations further influenced by local environmental factors. This emphasises the need to document and record coral spawning patterns across the Maldives and will help to expand our understanding of inter- and intra-atoll connectivity.

At both sites surveyed in this study, colonies of *Acropora* utilised multiple spawning events: i) 14 colonies spawned sections of their branches over consecutive days; ii) several species utilsied ‘split spawning’ and spawned in consecutive months within the same season; iii) two colonies spawned over two lunar phases within the same month and; iv) one colony was observed spawning in two consecutive spawning seasons. Corals utilise variations in spawning synchrony as a mechanism for reproductive isolation and to reduce interbreeding (Gilmour, Speed & Babcock, 2016). For one colony to spawn during two spawning seasons within one year remains rare, but has been documented in *A. tenuis*, *A. cytherea* and *A. florida* (Gilmour, Speed & Babcock, 2016). Utilising multiple spawning events, either over multiple days in the same month, multiple months in the same season, or two consecutive seasons, can have individual advantages; namely to: i) increase the likelihood of successful fertilisation; or ii) minimise the effects of a single catastrophic event on reproductive success (Harrison et al., 1984; Babcock et al., 1986; Richmond & Hunter, 1990), or iii) to help realign reproduction events to favourable environmental conditions (Hock et al., 2019), particularly in instances of multi-specific spawning events or events in which the number of conspecific colonies spawning is high. Despite potential advantages, such mechanisms of 'split' spawning in *Acropora* corals occur periodically in the Maldives, which concurs with research from Australia (Foster, Heyward & Gilmour, 2018). This could be explained by the date of where the full moon falls in the lunar month each year. Foster, Heyward & Gilmour, (2018) identified that split spawning took place regularly on Scott Reef when the full moon occurs in the first week of the typical spawning month or the last week of the previous month. However, in some documented cases, conspecific spawning in different seasons has the potential to impede gene flow and result in genetic divergence (Rosser, 2015; Rosser et al., 2020). Further research into the genetic structure of *Acropora* corals in the Maldives would be beneficial to distinguish the true extent of species-specific spawning across and within atolls over time.

Although both Atolls experienced two peak spawning seasons in this study with similarities within those seasons in terms of species composition, differences observed between North Male and Baa Atolls in spawning seasonality, date, and time suggest the potential for further inter-atoll variation in *Acropora* coral spawning across the Maldives. Although we found local environmental factors are likely driving variation in spawning date relative to full moon events, our results show considerable inter-atoll differences in spawning seasonality within populations of the same species, with four species experiencing differences in spawning season between atolls. Therefore, we can hypothesise that across the Maldives there is variation between other atolls in *Acropora* spawning seasonality and synchrony. Some inter-atoll variability observed in spawning patterns can likely be explained by species composition at our study sites. Some species present at Landaa Giraavaru are not present at sampled sites in Furana Fushi, for example *A. rosaria*. Other species such as *A. retusa* are present at Furana Fushi but were not observed with gametes or spawning.

The date of spawning relative to the full moon ~~was significantly~~ varied annually for nine species. Although this study did not attempt to establish a causal relationship between environmental conditions and coral spawning, the results of our linear mixed models demonstrate that the proximity of coral spawning to the full moon is significantly correlated with various environmental conditions. Thus, temporal and geographic variability can be expected based on local factors influencing the night of spawning. However, whether regional environmental conditions are influencing spawning seasonality across Maldivian Atoll chains year-on-year remains to be explored.

Across multiple spawning events and both Atolls, we recorded *A. tenuis* spawning, on average, 21.2 minutes after sunset, and earlier than other species during nights of multi-specific spawning (Figure 3B). *A. tenuis* has also been observed spawning soon after sunset in Australia and Japan

(Harrison et al., 1984; Hayashibara et al., 1993; Fukami et al., 2003). Shifting spawning time could be a mechanism to reduce the risk of hybridisation for broadcast spawners during mass, multi-specific spawning events (Palumbi, 1994; Knowlton et al., 1997; Fukami et al., 2003). Therefore, *A. tenuis* could be spawning earlier than other species to ensure fertilisation only between conspecifics. Additionally, the mechanism to shift spawning time could also explain inter-annual variations in spawning time experienced by three species of *Acropora* in this study, due to the high number of species recorded spawning on the same night. During multi-specific spawning events, species can stagger their gamete release times through the evening to prevent hybridisation (Fukami et al., 2003; Levitan et al., 2004; van Woesik, 2010). On average, *Acropora* species observed spawning in this study first released gamete bundles over 100 minutes after sunset, with exception of *A. tenuis* and *A. valida* (Figure 3B). Fukami et al., (2003) also observed *A. austera* spawning earlier than other mass-spawning species, which was not the case in our study where *A. austera* spawned, on average, 101.8 minutes after sunset. However, our average is based on 3 colonies, which could be anomalous.

This study provides the first insight into restored and wild colony spawning behaviour of *Acropora* in the Maldives. The date of coral spawning in Baa Atoll showed no significant relationship between reef type (frame and wild) of *A. millepora*, *A. humilis* and *A. digitifera*. Due to a low sample size in wild colonies affected by previous bleaching events (Pisapia, Burn & Pratchett, 2019), this analysis could only be conducted on three species. Despite these sample size limitations, our study provides a preliminary trend indicating that restoration activities may not impact the natural spawning cycle of *Acropora* at our study site*;* and there is potential for cross-fertilisation. Furthermore, there was no significant relationship between spawning time between frame and wild colonies of *A. millepora* and *A. humilis*, highlighting the potential for cross-fertilisation to increase genetic diversity. Although for *A. digitifera* a statistically significant difference in spawning time between frame and wild colonies was found, the substantive difference in initial release time between these reef types was small (3.[illegible] minutes), and would likely not prevent the potential for cross-fertilisation. A critical aim of coral restoration is to increase coral cover, diversity, and fecundity. Given the rate of decline of *Acropora* in the Maldives and subsequent popularity in restorative activities, the ability for frame colonies to reproduce sexually and fertilise with wild conspecifics can improve the resilience of reef ecosystems. Zayasu & Suzuki, (2019), found greater genetic diversity in an artificial population of *A. yongei* compared with wild colonies, showcasing the ability of restoration efforts to improve resilience of coral reefs to future stressors. The preliminary findings of spawning patterns based on reef type in this study demonstrate the need to consider restored colonies when discussing sexual reproductive patterns of *Acropora* in the Maldives.

Conclusion

This research details for the first time exact spawning times of *Acropora* across two Maldivian atolls indicating observations on multi-specific spawning, asynchronous spawning and 'split spawning' across multiple lunar phases. It is clear that the Maldives experiences two distinct spawning seasons throughout the year, but spawning events can occur over an extended period of eight months. Inter-atoll variations in spawning date are likely explained by local environmental factors, however further research into coral reproductive patterns of multiple study sites within atolls and across the Maldives needs to be conducted to ascertain regional disparities and seasonal variations. The preliminary findings of spawning patterns based on reef type in this study demonstrate the need to consider restored colonies when discussing the sexual reproductive patterns of Maldivian *Acropora* in the future.

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Table 1(on next page)

The number of colonies to spawn and months of spawning per *Acropora* spp. in each atoll and reef type.

1

Species	**No. colonies**		**Months of spawning**		**Reef Type (No. colonies)**	
	Baa	**North Male**	**Baa**	**North Male**	**Baa**	**North Male**
A. aspera	4	2	October, November	April	F = 4	P = 2
A. austera	0	5	*NA*	April	*NA*	P = 5
A. clathrata	0	1	*NA*	April	*NA*	P = 1
A. cytherea	0	85	*NA*	March, April	*NA*	P = 85
A. digitifera	56	3	March, April	April	F = 37 W = 19	F = 3
A. gemmifera	4	13	March, April	January, March, April, November	F = 2 W = 2	F = 1 P = 12
A. globiceps	2	0	October, November	*NA*	W = 2	*NA*
A. hempricii	0	16	*NA*	March, April	*NA*	F = 1 P = 15
A. humilis	82	48	March, April, October, November	March, April, May, November	F = 64 W = 18	F = 5 P = 43
A. hyacinthus	1	17	April	March, April	W = 1	F = 2 P = 15
A. latistella	0	2	*NA*	April	*NA*	F = 1 P = 1
A. millepora	56	20	March, April	March, April	F = 29 W = 27	F = 1 P = 19
A. muricata	3	50	April	April	F = 3	F = 11 P = 39
A. nasuta	9	14	March, April	March, April	F = 4 W = 5	P = 14
A. plantaginea	141	34	October, November, December	November, December	F = 133 W = 8	F = 31 P = 3
A. retusa	2	0	November	*NA*	F = 2	*NA*
A. rosaria	7	0	November	*NA*	F = 6 W = 1	*NA*
A. samoensis	6	7	April	March, April, November, December	F = 6	F = 2 P = 5
A. secale	48	158	March, April, October, November	October, November, December	F = 42 W = 6	F = 28 P = 120 R = 2 W = 8
A. squarrosa	6	2	November	November	F = 6	P = 2
A. tenuis	60	231	November, December	March, April, November, December	F = 56 W = 4	F = 18 P = 210 W = 3
A. valida	3	1	February,	April	F = 3	P = 1

			May			

Reef types are recorded as F – Frame, W – Wild, R – Relocated, and P – Pyramid.

Table 2(on next page)

Results of general linear models to explore the relationship between spawning date relative to full moon and year; and spawning time after sunset and year, for *Acropora* spp.

Significant results are given in bold. Values less than 0.001 (highly significant) are denoted as < 0.001.

Species	**Response**		**Explanatory**		**Response**		**Explanatory**	
	Spawn date relative to full moon (day)		Year		Spawning time after sunset (minutes)		Year	
	Estimate	**SE**	**t value**	**p**	**Estimate**	**SE**	**t value**	**p**
Intercept	7079.667	291.8506	24.26	< **0.001**	-884.5	17187.0	-0.051	0.964
A. aspera	-3.500	0.1443	-24.25	< **0.001**	0.5	8.5	0.059	0.958
Intercept	11098.378	480.507	23.1	< **0.001**	5305.766	8512.917	0.623	0.535
A. cytherea	-5.486	0.238	-23.1	< **0.001**	-2.530	4.209	-0.601	0.549
Intercept	2582.000	607.755	4.248	< **0.001**	1939.765	3788.279	0.512	0.611
A. digitifera	-1.275	0.301	-4.242	< **0.001**	-0.882	1.873	-0.471	0.640
Intercept	-1316.182	2956.621	-0.445	0.663	29014.73	27602.16	1.051	0.312
A. gemmifera	0.652	1.462	0.446	0.662	-14.27	13.65	-1.046	0.315
Intercept	10892.692	607.404	17.93	< **0.001**	-44356.0	11526.281	-3.848	**0.002**
A. hempricii	-5.385	0.300	-17.93	< **0.001**	22.0	5.698	3.861	**0.002**
Intercept	4000.600	689.850	5.799	< **0.001**	27415.633	7371.479	3.719	**< 0.001**
A. humilis	-1.977	0.341	-5.795	< **0.001**	-13.484	3.645	-3.699	**< 0.001**
Intercept	4829.014	1001.297	4.823	< **0.001**	9722.800	14167.182	0.686	0.495
A. millepora	-2.386	0.495	-4.819	< **0.001**	-4.725	7.004	-0.675	0.503
Intercept	8885.075	1637.466	5.426	< **0.001**	21670.38	30844.91	0.703	0.490
A. nasuta	-4.392	0.810	-5.425	< **0.001**	-10.63	15.25	-0.697	0.494
Intercept	4664.248	4175.892	1.117	0.266	-5645.196	7332.731	-0.770	0.442
A. plantaginea	-2.306	2.065	-1.117	0.266	2.858	3.627	0.788	0.432
Intercept	3.000	3031	0.001	0.999	-59190.45	30969.14	-1.911	0.0824
A. samoensis	< 0.001	1.498	0.000	1.000	29.35	15.31	1.917	0.0816
Intercept	5005.841	1830.254	2.735	**0.00679**	3928.970	3004.961	1.307	0.193
A. secale	-2.475	0.9052	-2.734	**0.00680**	-1.882	1.486	-1.266	0.207
Intercept	3103.200	3589.505	0.865	0.421	-6945.000	4057.215	-1.712	0.185
A. squarrosa	-1.533	1.776	-0.864	0.421	3.500	2.007	1.744	0.180
Intercept	4001.663	539.370	7.419	< **0.001**	-3879.035	755.853	-5.132	**< 0.001**
A. tenuis	-1.978	0.267	-7.418	< **0.001**	1.9277	0.3737	5.159	**< 0.001**

Table 3(on next page)

Results of general linear models to explore the relationship between spawning date relative to full moon and atoll; and spawning time after sunset and atoll, for *Acropora* spp.

Significant results are given in bold. Values less than 0.001 (highly significant) are denoted as < 0.001.

Species	**Response**		**Explanatory**		**Response**		**Explanatory**	
	Spawn date relative to full moon (day)		Atoll		Spawning time after sunset (minutes)		Atoll	
	Estimate	**SE**	**t value**	**p**	**Estimate**	**SE**	**t value**	**p**
Intercept	-4.500	0.750	6.000	**0.004**	126.000	12.020	10.482	**0.009**
A. aspera	-5.500	1.299	-4.234	**0.013**	1.00	17.00	0.059	0.958
Intercept	4.286	0.062	69.62	**< 0.001**	*Timing not recorded.**			
A. digitifera	-4.952	0.273	-18.14	**< 0.001**				
Intercept	4.000	1.232	3.247	**0.005**	164.33	13.470	12.196	**< 0.001**
A. gemmifera	-3.385	1.409	-2.402	**0.030**	-16.08	15.060	-1.068	0.305
Intercept	4.110	0.160	25.70	**< 0.001**	149.099	2.658	56.091	**< 0.001**
A. humilis	-3.881	0.263	-14.74	**< 0.001**	-8.401	4.328	-1.941	0.055
Intercept	4.339	0.184	23.65	**< 0.001**	168.025	4.025	41.74	**< 0.001**
A. millepora	-3.789	0.358	-10.60	**< 0.001**	-6.975	6.972	-1.00	0.321
Intercept	4.333	0.293	14.82	**< 0.001**	159.000	9.342	17.020	**< 0.001**
A. muricata	-4.793	0.301	-15.92	**< 0.001**	-8.600	9.618	-0.894	0.375
Intercept	4.667	0.678	6.884	**< 0.001**	174.778	11.664	14.98	**< 0.001**
A. nasuta	-3.952	0.869	-4.549	**< 0.001**	8.079	14.950	0.54	0.595
Intercept	0.809	0.522	1.55	0.123	131.489	0.934	140.730	**< 0.001**
A. plantaginea	3.692	1.183	3.12	**0.002**	7.026	2.096	3.353	**< 0.001**
Intercept	4.333	0.923	4.696	**< 0.001**	182.830	10.75	17.006	**< 0.001**
A. samoensis	-2.476	1.257	-1.969	0.075	-30.260	14.65	-2.065	0.0633
Intercept	4.458	0.487	9.157	**< 0.001**	130.419	0.771	169.168	**< 0.001**
A. secale	-3.977	0.556	-7.154	**< 0.001**	-7.619	0.894	-8.524	**< 0.001**
Intercept	4.500	0.514	8.76	**< 0.001**	132.000	1.269	103.995	**< 0.001**
A. squarrosa	-4.500	1.027	-4.38	**0.005**	-3.500	2.007	-1.744	0.18
Intercept	2.317	0.313	7.400	**< 0.001**	20.250	0.456	44.414	**< 0.001**
A. tenuis	-2.196	0.351	-6.248	**< 0.001**	-0.237	0.501	-0.472	0.637

*In the North Male Atoll, *A. digitifera* was recorded spawning through absence of gamete surveys. Therefore, the exact spawning date was obtained but not the spawning time.

Table 4(on next page)

General linear mixed models assessing the influence of local environmental factors on the spawning date relative to full moon for *Acropora* spp.

Model 1 assessed all species and both Atolls, whereas Models 2 and 3 investigate each Atoll independently. Significant results are denoted in bold. Values less than 0.001 (highly signficant) are denoted as < 0.001.

Response	**Explanatory: fixed effects**	**Estimate**	**SE**	**X^2**	**p-value**
Proximity of spawning to full moon	Total daily precipitation	0.020	0.068	0.085	0.770
	Tide depth	41.594	1.785	542.970	**< 0.001**
	Average daily wind speed	0.127	0.030	18.511	**< 0.001**
	Random effects	**Variance**	**SD**		
	Spawning month	4.618	2.149		
	Structure	0.602	0.776		

Response	**Explanatory: fixed effects**	**Estimate**	**SE**	**X^2**	**p-value**
Proximity of spawning to full moon in the North Male Atoll	Total daily precipitation	0.263	0.052	25.143	**< 0.001**
	Tide depth	15.956	1.649	93.602	**< 0.001**
	Average daily wind speed	0.221	0.023	91.782	**< 0.001**
	Random effects	**Variance**	**SD**		
	Spawning month	4.027	2.007		
	Structure	3.893	1.973		

Response	**Explanatory: fixed effects**	**Estimate**	**SE**	**X^2**	**p-value**
Proximity of spawning to full moon in the Baa Atoll	Total daily precipitation	-0.243	0.131	3.422	0.064
	Tide depth	57.052	3.130	332.158	**< 0.001**
	Average daily wind speed	0.044	0.059	0.541	0.462
	Random effects	**Variance**	**SD**		
	Spawning month	7.307	2.703		
	Structure	*0 **	*0 **		

* In Model 3, the variance of Structure was 0, and as such this variable was removed

Figure 1

Location of study sites in the Maldives: Landaa Giraavaru, Baa Atoll, and Furana Fushi, North Male Atoll.

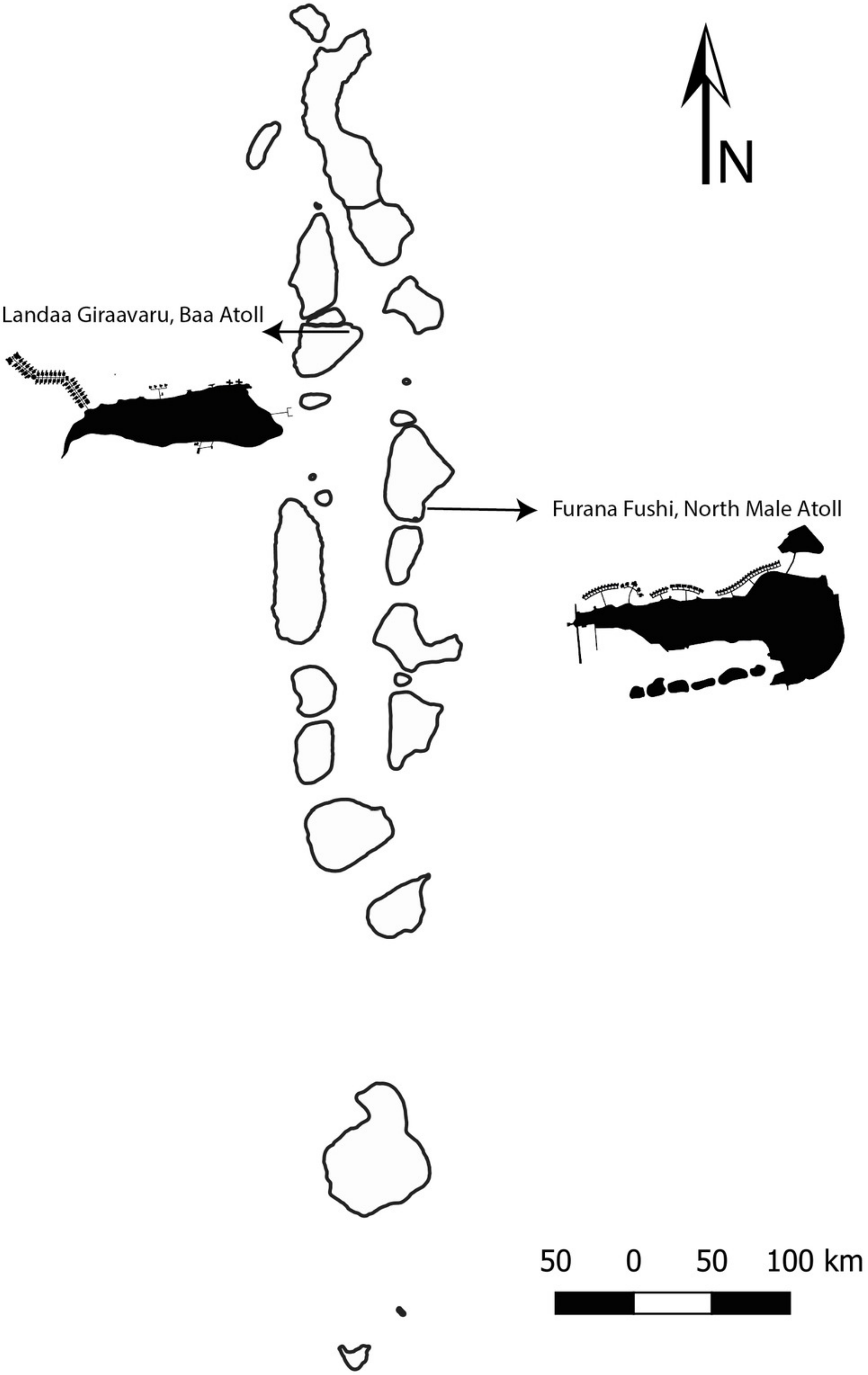

N
Landaa Giraavaru, Baa Atoll
Furana Fushi, North Male Atoll
50 0 50 100 km

Figure 2

Stages of sexual reproduction in *Acropora*, Maldives.

Figure 2A-C: Development of oocyte colouration from white (immature; Figure 2A), to pale (Figure 2B), to pigmented (mature; Figure 2C). Photographs by Margaux A A Monfared.

Figure 2D otograph to show moment of gamete bundle release, defined as the spawning time per colony. Photograph by Simon P Dixon.

Figure 2E: Observed gamete 'bundling' in *A. secale* prior to spawning. The presence of 'bundling' as shown in this image is what observers were looking for during nightly surveys. Photograph by Kate Sheridan.

Figure 2F: A colony of *A. gemmifera* spawning white oocytes. Photograph by Kate Sheridan.

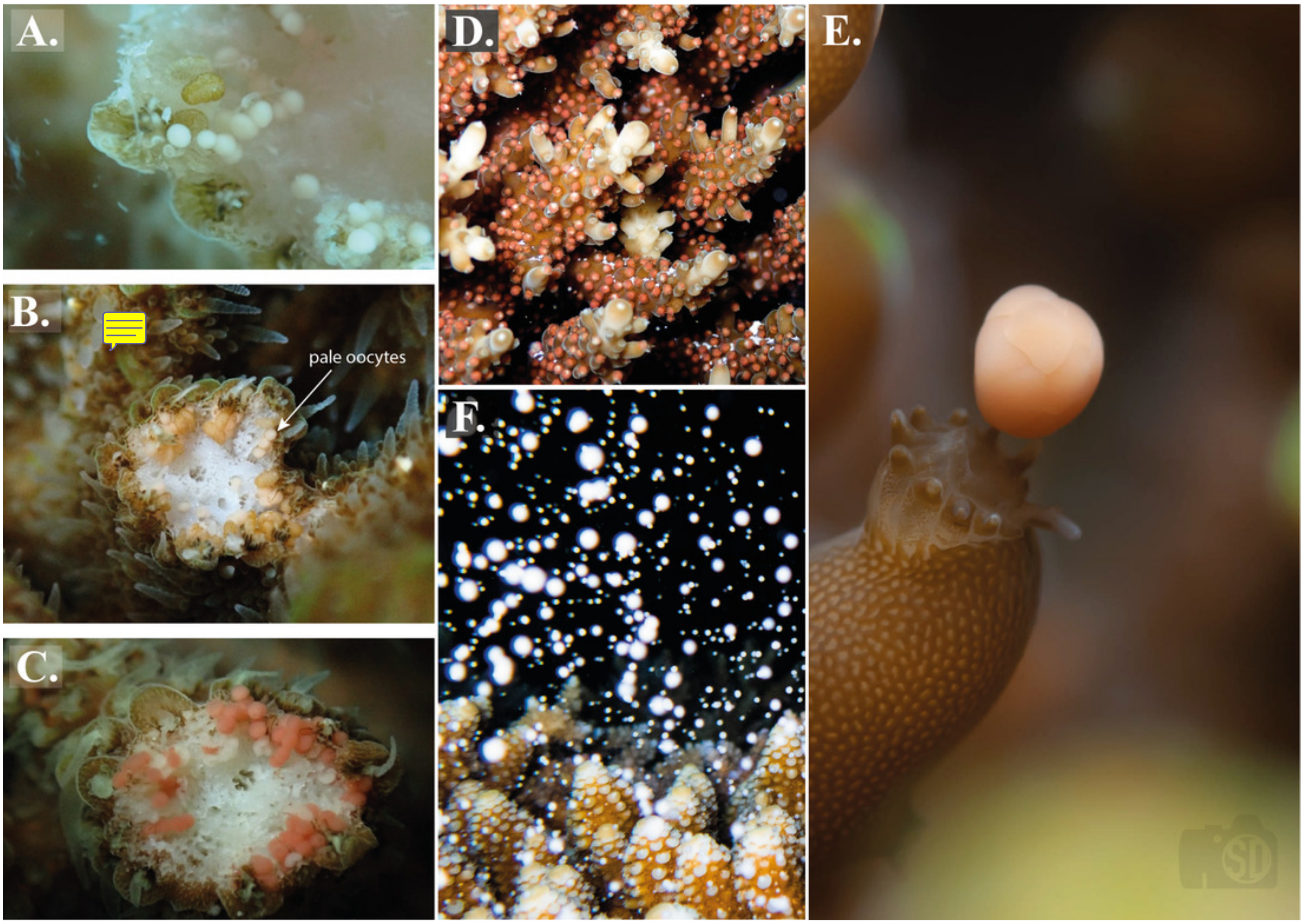
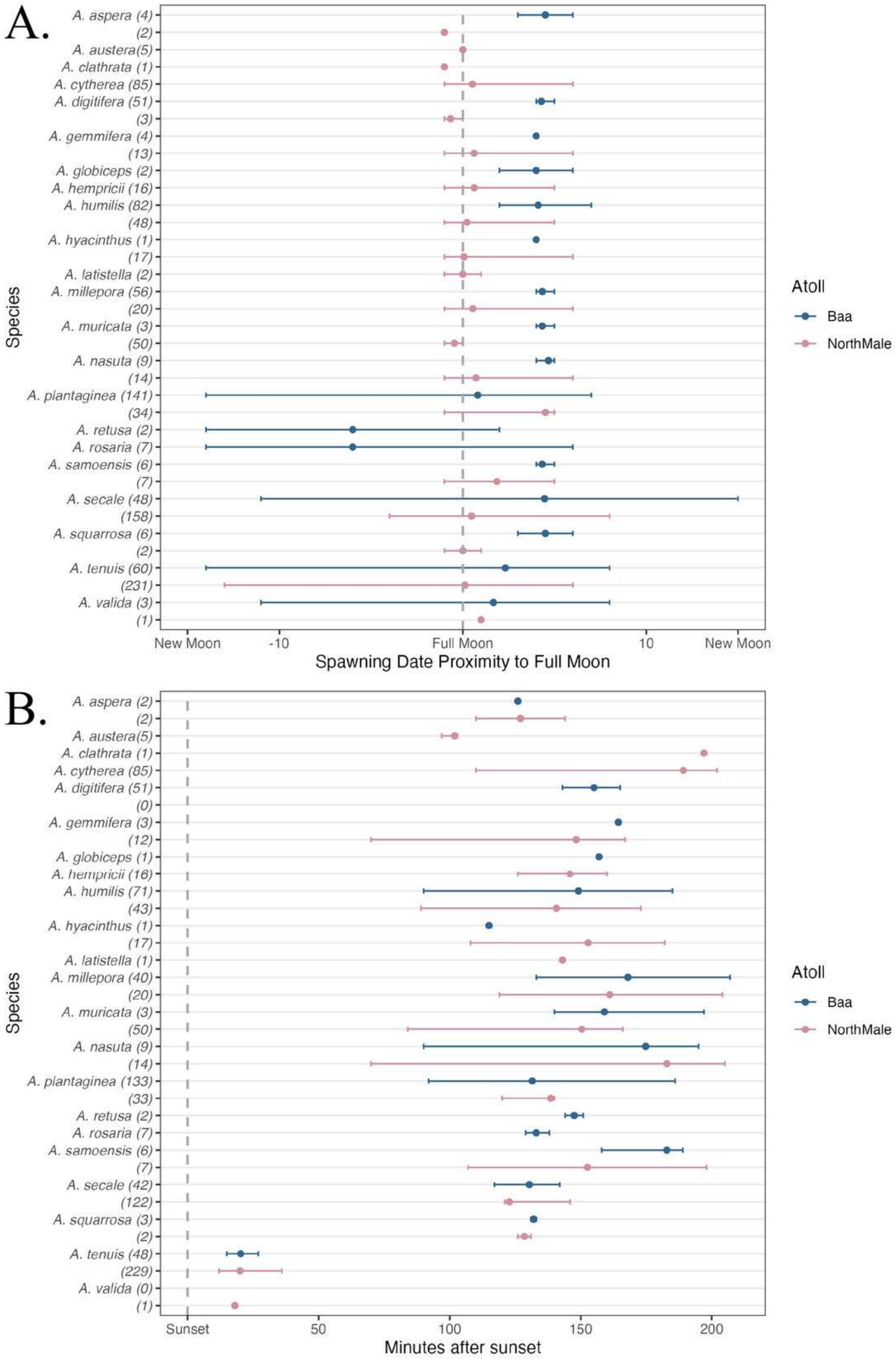


Figure 3

Spawning date and time of *Acropora* spp.

Figure 3A: The date of coral spawning of *Acropora* spp. relative to the nearest full moon. The filled circles are the mean observed spawning date, and the bars are the range, per species. Observations from Baa Atoll are given in blue, and North Male Atoll in pink. Within the brackets after each species, the total number of colonies to spawn of that species is given.

Figure 3B: The time of coral spawning of *Acropora* spp. after to sunset. The filled circles are the mean observed spawning time after sunset, and the bars are the range, per species. Observations from Baa Atoll are given in blue, and North Male Atoll in pink. Within the brackets after each species, the number of colonies within that species of which an exact spawning time was recorded.


A.
A. aspera (4)
(2)
A. austera(5)
A. clathrata (1)
A. cytherea (85)
A. digitifera (51)
(3)
A. gemmifera (4)
(13)
A. globiceps (2)
A. hempricii (16)
A. humilis (82)
(48)
A. hyacinthus (1)
(17)
A. latistella (2)
A. millepora (56)
(20)
A. muricata (3)
(50)
A. nasuta (9)
(14)
A. plantaginea (141)
(34)
A. retusa (2)
A. rosaria (7)
A. samoensis (6)
(7)
A. secale (48)
(158)
A. squarrosa (6)
(2)
A. tenuis (60)
(231)
A. valida (3)
(1)
Species
New Moon
-10
Full Moon
10
New Moon
Spawning Date Proximity to Full Moon
Atoll
Baa
NorthMale
B.
A. aspera (2)
(2)
A. austera(5)
A. clathrata (1)
A. cytherea (85)
A. digitifera (51)
(0)
A. gemmifera (3)
(12)
A. globiceps (1)
A. hempricii (16)
A. humilis (71)
(43)
A. hyacinthus (1)
(17)
A. latistella (1)
A. millepora (40)
(20)
A. muricata (3)
(50)
A. nasuta (9)
(14)
A. plantaginea (133)
(33)
A. retusa (2)
A. rosaria (7)
A. samoensis (6)
(7)
A. secale (42)
(122)
A. squarrosa (3)
(2)
A. tenuis (48)
(229)
A. valida (0)
(1)
Species
Sunset
50
100
150
200
Minutes after sunset
Atoll
Baa
NorthMale