Daytime broadcast spawning in cryptic *Pocillopora* species at Mo'orea, French Polynesia

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Github: https://github.com/hputnam/Pocillopora_Spawning_Moorea
OSF: https://osf.io/5geqd/

Abstract

Knowledge of when corals release gametes is fundamentally important for understanding reef ecology and evolution, but further research is needed to document patterns at the species level and in a broader range of taxa. In Mo'orea (17°32′S 149°50′W), French Polynesia, when corals were decimated by crown-of-thorns and a cyclone between 2007-2010, *Pocillopora spp.* recruitment primarily drove reef recovery over the following decade. Furthermore, recent research has identified that the Pocillopora community is composed of six morphologically-cryptic species. Spawning times at the genetically-verified species level at Mo'orea are undocumented in the scientific literature. To address this gap, we conducted in situ surveys of *Pocillopora spp.* over a total of 89 days during September 2022 - January 2023 and October 2023 - January 2024. For corals observed spawning, we used molecular analysis of mtORF and PocHistone markers to identify corals to species. We documented the synchronized lagoon level spawning of *P. meandrina* 2-3 days following the full moon in December 2022 (06:16-06:32, 06:21-06:35), and of a few colonies in October of 2023 (06:22-06:38) and a single colony in November 2022 (06:32). In contrast, sister species *P. verrucosa* and *P. tuahiniensis* spawned around the new moons in November and December of 2023. These species' spawning overlapped one day after the new moon, but *P. verrucosa* tended to release on the new moon and earlier in the day (~05:45 - 06:15), whereas *P. tuahiniensis* tended to release 1 - 3 days after the new moon and later in the day (~06:30 - 06:50), We observed only one colony of *P. cf. effusa* spawning (+3 days after new moon ~06:30 - 06:50). Collectively, these first reported observations provide an initial documentation of *Pocillopora* spawning in Mo'orea (to our knowledge), expanding on indigenous knowledge and increasing capacity to study the essential, yet environmentally sensitive, process of coral reproduction for critical reef building species in French Polynesia.

Introduction

Natural disturbances can trigger new ecological trajectories and states and for a community (Knowlton 2015), with enduring ecological legacy effects (Cuddington 2011; Kopecky et al. 2023). However, natural disturbances such as storms and predator outbreaks have now combined with Anthropogenic disturbances, like increasing heat waves (Oliver et al. 2021), to degrade marine ecosystems, in particular coral reefs. Reef-building scleractinian corals are the ecosystem engineers that create 3D structure and provide vital resources to millions of people through critical ecosystem services, such as fisheries, food security, economic enhancement via tourism and biopharmaceuticals, indigenous cultural resources, and coastal protection from storms (Costanza et al. 2014). Consequently, natural maintenance of reef ecosystems relies on replenishment via coral reproduction and knowledge of coral reproductive timing and spawning are essential for coral breeding and seeding in active reef restoration efforts.

Coral reef construction is based on the productive symbiotic relationship between the cnidarian host and symbiotic dinoflagellates (Symbiodiniaceae), which is susceptible to dysbiosis in response to relatively small environmental perturbations (e.g., 1°C over mean summer maxima (Lesser 2011)). Of particular concern in the Anthropocene is coral bleaching, or the coral-dinoflagellate symbiotic disruption driven by marine heatwaves that often results in substantial mortality of corals (Hughes et al. 2018) and cascading negative consequences for reef function (Courtney et al. 2018; Hughes et al. 2019). In French Polynesia, coral bleaching in 2002 contributed to reduced coral cover (Pérez-Rosales et al. 2021), with >50% of corals surveyed showing bleaching in Mo'orea, French Polynesia (Penin et al. 2007). In Mo'orea in 2019, surveys of coral bleaching of the dominant genera, *Acropora* and *Pocillopora*, revealed 89% and 46% bleaching/partial mortality, respectively, for these species (Burgess et al. 2021; Speare et al. 2022). Further, bleaching has just occurred in Mo'orea in March - May 2024. Therefore, without coral replenishment through reproduction, reef maintenance is threatened under current and future climate conditions in Mo'orea, and we also see evidence of these threats and degradation worldwide (Hughes et al. 2019; Reimer et al. 2024).

On multiple Polynesian islands, the genus *Pocillopora* has become the dominant space holder following a crown-of-thorns seastar outbreak in 2007 and a major cyclone, Oli, in 2010 (Pérez-Rosales et al. 2021). For example in Mo'orea, French Polynesia, when coral cover was reduced by nearly ~90% due to crown-of-thorns outbreaks and between 2007 and 2009 and cyclone Oli in 2010 (Holbrook et al. 2018), *Pocillopora spp.* were responsible for rapid reef recovery (Adjeroud et al. 2007; Edmunds 2018; Holbrook et al. 2018). *Pocillopora spp.* are early colonizing species (Grigg and Maragos 1974) due to high fecundity (Sier and Olive 1994; Tsounis and Edmunds 2016) and high recruitment (Adjeroud et al. 2007). Further, with their complex branching morphologies, *Pocillopora*

spp. provide extensive reef organism habitat (Stella et al. 2010; Pisapia et al. 2020). In light of this, it is essential that we quantify and describe the process of *Pocillopora spp.* spawning in French Polynesia, which undoubtedly exists in indigenous knowledge, but has yet to be reported in this region in the scientific literature.

A major impediment to quantifying and describing spawning patterns in corals, including *Pocillopora* spp., is the presence of morphologically cryptic species that potentially mislead understanding if species-level observations were made based on morphology. At Mo'orea, there are five morphologically-cryptic species of *Pocillopora* that necessitate the use of genetic markers to verify observations at the species level (Johnston et al 2021), plus *P. acuta*. Existing literature on *Pocillopora spp*. indicates they are hermaphroditic and primarily reproduce sexually via broadcast spawning (the release of both sperm and eggs into the water column). However, *P. damicornis*, and *P. acuta* can produce asexual larvae (Yeoh and Dai 2010; Combosch and Vollmer 2013) and reproduce sexually by brooding fertilized eggs internally or by broadcast spawning (Ward 1992; Schmidt-Roach et al. 2014). The release of sperm, eggs, and larvae (depending on the species) typically occurs after sunrise. While not all past studies conducted genetic species identification, there are reports (Table 1) of spawning near the full moon for morphologically identified *P. meandrina* in Australia (Schmidt-Roach et al. 2012) and Hawai'i (Apprill et al. 2009; Schmidt-Roach et al. 2014), and for morphologically identified *P. grandis* in Japan (Kinzie 1993; Hirose et al. 2000, 2001). In contrast, observations of morphologically identified *P. verrucosa* spawning have been made primarily during the new moon (but see (Schmidt-Roach et al. 2012)) in the Red Sea in Saudi Arabia, Sudan (Bouwmeester et al. 2011, 2021), and Eilat (Shlesinger and Loya 1985), as well as in South Africa (Kruger and Schleyer 1998) and in Japan (Kinzie 1993; Hirose et al. 2000, 2001; Baird et al. 2022). As lunar phase outliers, morphologically identified *P. meandrina* have been reported spawning on the new moons in Australia (Schmidt-Roach et al. 2012) and Taiwan (Lin and Nozawa 2017; Mulla et al. 2021).

In this study, we conducted *in situ* surveys of *Pocillopora spp* spawning over a total of 89 days in the lagoon of the north shore of Mo'orea French Polynesia. On each day, observations lasted for ~2-3 hours following sunrise for several days around the full and new moons (where logistics and conditions allowed) for the months of September - January in 2022-2023 and in 2023-2024. Corals observed spawning were genetically identified to species. Collectively, this allowed for clear documentation of spawning of *P. meandrina*, *P. verrucosa*, and *P. tuahiniensis*, as well as a possible indication of *P. cf. effusa* timing.

Methods

In order to describe spawning times to the species level, we completed *in situ* visual and photographic documentation of *Pocillopora* spp. spawning and confirmed successful embryo development, as well as analyzed samples for species level genetic identification.

Spawning observations and sample collection

For this work, we followed the lunar calendar dates set by the United States Astronomical Applications Department (https://aa.usno.navy.mil/data/MoonPhases). The spawning observation site was located on the north shore lagoon reef in Mo'orea (-17.475757, -149.808062), which was selected for high Pocilloporidae cover (Edmunds 2022) and capacity for safe low light small boat transit from the UC Richard B. Gump South Pacific Research Station. All observations were made while snorkeling in ~3m, with a minimum of two observers in the water. Observers were positioned to simultaneously visualize multiple morphologies with the intention of observing all five species (*P. c.f. effusa*, *P. grandis, P. meandrina*, *P. verrucosa*, and *Pocillopora tuahiniensis sp. nov.*) that have been documented in the lagoon reefs of Mo'orea (Burgess et al in Press Evolutionary Applications). Coral spawning observations were documented as follows: (1) photographs of each colony were taken during or following spawning (Canon G7X MarkII); (2) colonies were tagged and geolocated via GPS (Garmin GPSMAP 64); (3) biopsies were collected from each tagged colony in sterile Whirlpaks (Fig. 1-4); and (4) where possible, gametes were collected from the water next to the colonies. Samples were returned to the Gump South Pacific Research Station and biopsies from the tagged colonies were preserved. To confirm successful fertilization occurred, collected gametes were examined with a compound microscope (LEICA DM500)(e.g., Fig. 1).

Pocillopora species genetic identification

In order to determine the species of *Pocillopora* spawning, DNA was extracted from each sample using the Quick-DNA™ Miniprep Plus Kit (Zymo Research Cat # D4069) or Chelex 100 Resin (Bio-Rad Cat #142-1253). For the Quick-DNA extractions, DNA was extracted according to the manufacturer's instructions for samples stored in DNA/RNA Shield, including the addition of Proteinase K (20mg mL^{-1}). For the Chelex extractions, 10 µL of DNA Shield was placed into 100 µL of 10% Chelex solution and incubated at 55°C for 60 minutes followed by 95°C for 20 minutes. The sample was centrifuged at 4,000 rpm for 2 minutes and the supernatant DNA moved to a new tube. To identify *Pocillopora spp.* we amplified the mitochondrial open reading frame (mtORF) region using the primers of Flot et al. (Flot et al. 2008) FatP6.1 (5′-TTTGGGSATTCGTTTAGCAG-3′) and RORF (5′-SCCAATATGTTAAACASCATGTCA-3′). For the Quick-DNA extractions, PCR mixes contained 12.5 µL of EmeraldAmp GT PCR Master Mix (TaKaRa Bio USA Inc. Cat # RR310B), 0.3 µL of each of the forward and reverse primers (10 µM), 1 µL of template DNA, and 10.9 µL of deionized water to 25 µL final volume per sample. For the Chelex

extractions, PCR mixes contained 5 µL BioMix Red (Bioline Ltd., London, UK Cat # BIO-25006), 0.13 µL of each of the forward and reverse primers (10 µM), 0.1 µL Recombinant Albumin (New England Biolabs Cat # B9200S), 1 µL of template DNA, and 3.64 µL of deionized water to 10 µL final volume per sample. Sample DNAs were amplified with the polymerase chain reaction (PCR) profile of a single denaturation step of 60s at 94 °C, followed by 30s at 94 °C for denaturation, 30s at 53 °C for annealing, and extension of 75s at 72 °C for 30 cycles (2022 samples) or 40 cycles (2023 samples); thermocycling was followed by final incubation at 72 °C for 5 min. The products were then assessed with a 1.5% or 2% agarose gel in TAE for 45 mins at 100 V or 30 mins at 90 V to verify bands of ~1000bp. The PCR products from the Quick-DNA extractions (2022 samples) were cleaned with Qiagen MinElute PCR Purification Kit (Qiagen Cat # 28004) according to the manufacturer's instructions. The PCR products from the Chelex extractions (2023 samples) were cleaned with Exo-CIP Rapid PCR Cleanup (New England Biolabs Cat # E1050L) according to the manufacturer's instructions. Sanger sequencing was completed with forward primers at the URI Genomics and Sequencing center using Applied Biosystems BigDye Terminator v3.1 chemistry (2022 samples) and at the Florida State University Core Facility using the Applied Biosystems 3730 Genetic Analyzer with Capillary Electrophoresis (2023 samples). Sequences were aligned using Geneious Alignment in GENEIOUS PRIME 2020.2.4. Pairwise alignment of 723bp from the 72 sample sequences along with the 16 reference sequences (https://osf.io/5geqd/) was completed using Clustal Omega (Sievers et al. 2011) in GENEIOUS PRIME 2020.2.4. Tree building was conducted with a Jukes-Cantor genetic distance model (Jukes and Cantor 1969) and no outgroup. The phylogenetic tree was generated via Neighbor-Joining estimation (Saitou and Nei 1987) with the NJ function from the package phangorn (Schliep 2011) in R (Team 2013) followed by Ward's hierarchical agglomerative clustering method (ward.D (Murtagh and Legendre 2014). Raw sequence data and alignment fasta files are archived here: https://osf.io/5geqd/ (Harnay et al. 2023)

Where mtORF sequencing identified samples as Haplotype 1 (containing both *P. grandis* and *P. meandrina*), DNAs were also PCR amplified with the histone 3 region using the primers of Johnston et al. (Johnston et al. 2018) (PocHistoneF: 5′-ATTCAGTCTCACTCACTCACTCAC-3′ and PocHistoneR: 5′-TATCTTCGAACAGACCCACCAAAT-3′) including *P. grandis* as a positive control. PCR mixes were made following the methods above (but with PocHistone primers). Thermal cycling included a denaturation step of 60 s at 94 °C, followed by 30 cycles (2022 samples) or 40 cycles (2023 samples) of 30 s at 94 °C, 30 s at 53 °C, and 60 s at 72 °C; and an elongation step at 72 °C for 5 min. PCR products were then used for Restriction Fragment Length Polymorphism (RFLP) with *Xho*I (NEB R0146S) in rCutSmart buffer (NEB B6004S) according to Johnston et al. 2018 (Johnston et al. 2018) (with a volume exception as follows for 2023 samples; 5 µL of PCR product were then digested with

0.5µL of XhoI restriction enzyme (New England BioLabs, Ipswich, MA, USA), 0.8 µL of 10X CutSmart buffer, and 2.7µL of deionized water, for a final volume of 9µL). Restriction digest products were viewed on a 2% agarose gel in 1X TAE after running for ~90-110 min at 70V with a GeneRuler 100 bp DNA Ladder (Thermo Fisher Cat SM0241) or Quick-Load Purple 100 bp DNA Ladder (New England Biolabs Cat #N0467S). A single band at 669 bp indicates the species is *P. meandrina*, while two bands at 382 and 287 bp indicate the species identification is *P. grandis*. Raw sequence data, alignment fasta files, and gel images are archived here: https://osf.io/5geqd/ (Harnay et al. 2023)

Importantly, the use of mtORF and PocHistone + *Xho*I digestion RFLP (Johnston et al. 2018) has previously been validated as suitable species-level markers based on multiple genome-wide datasets and analyses (Johnston et al 2021) (*Pocillopora meandrina* = mtORF haplotype 1 and a single *Xho*I digestion RFLP band, mtORF haplotype 8; *P. grandis* = mtORF haplotype 1 and two *Xho*I digestion RFLP bands; *P. tuahiniensis* = mtORF haplotype 10; *P. verrucosa* = mtORF haplotype 3; *P.* cf. *effusa* = mtORF haplotype 2 and 11).

Results

Full Moon Observations

In our observations of full moon spawning (October 2023, November 2022 and December 2022, Table 2) of 19 colonies, *Pocillopora meandrina* was the only identified species (Table 3) (Fig. 5). Sequencing of the mtORF (Table 3,4; Fig. 6) indicated 16 samples as Haplotype 1). The three remaining samples were identified as *P. meandrina* mtORF lineage Haplotype 8a, which is genetically indistinguishable in nuclear DNA from Haplotype 1 (Johnston et al. 2022a) (Fig. 6). The PocHistone RFLP of haplotype 1 samples confirmed them as *Pocillopora meandrina* (see repository for all gel images; https://osf.io/5geqd/).

Gametes of *P. meandrina* were released early in the morning in 2022, at ~06:15-06:40, ~ 70-80 minutes after sunrise local time. We documented split-spawning (spawning of the species in multiple consecutive months) in *P. meandrina*, with one colony spawning November 10 (06:32, 3 days after the full moon), what appeared to be reef-wide spawning December 9th (06:16-06:32; full moon+2 days), and fewer colonies than December 9 2022, but more than November 10 2022, releasing on the December 10 2022 (06:21-06:35; full moon+3 days) (Fig. 5). In 2023, we conducted observations from full moon (October 28) to full moon+7 (November 4), but the only day we observed *P. meandrina* gamete release was at full moon +2 (October 30), again early in the morning, ~60 minutes after local sunrise, between 06:22 - 06:38. Spawning was not observed in our surveys around the full moon days of 24 - 27 November 2023 (full moon -2 to full moon), nor on

26 - 27 of December 2023 (full moon to +1), nor on 25 - 28 of January 2024 (full moon to +3) (Table 2).

New Moon Observations

In our new moon spawning observations (November 2023, December 2023) of 53 colonies, 56.6% were identified as *P. tuahiniensis sp. Nov.* (Fig. 2), 41.5% as *P. verrucosa* (Fig. 3) and 1.9% as *P. cf. effusa* (Fig. 4). There was only a single colony identified as *P. cf. effusa* (Haplotype 11; Fig. 6).

P. verrucosa gametes were released earliest of all species detected, at 5:45-6:20, ~45-65 min after sunrise local time. We observed spawning in 2023 on the new moon and 1 day after the new moon of November 12-13. We observed first the release of sperm followed by eggs. Initially, only a few colonies released gametes and after a short time (1-2min) many colonies within our observers' views began releasing as well.

During the new moon, *P. tuahiniensis* (Johnston and Burgess 2023) was observed spawning later in the day than *P. verrucosa* (Fig. 5). On the morning of November 13, 2023 (+1 after the new moon) the first *P. tuahiniensis* colony was observed spawning at ~06:04-6:19 local time, then a second colony was observed between ~06:33-06:44 local time. The following day (November 14 2023, +2 after the new moon), 17 colonies of *P. tuahiniensis* spawned between ~06:26-06:50 local time. At +3 after the new moon (November 14 2023), nine colonies of the *P. tuahiniensis* observed spawning at ~06:31-06:50 local time were sampled. The next month (December 14 2023 +2 days after the new moon), two colonies of *P. tuahiniensis* spawned at ~06:56-07:05.

The least abundant species detected by mtORF sequencing during the new moon (Table 3, Fig. 6) was a single colony of *P. cf.effusa* identified as Haplotype 11 (Johnston et al. 2022b) (Fig. 6). The *P. cf.effusa* observation fell within the November sampling window of ~06:30 - 06:50 on the new moon+3 days (Fig. 4).

Discussion

The Pocilloporid species diversity documented to date in Mo'orea includes *P. meandrina*, *P. verrucosa, P. grandis*, *P. c.f. effusa* (Burgess et al. 2021) *P. tuahiniensis (Johnston et al. 2022b; Johnston and Burgess 2023)*, and *P. acuta* (primarily occurring on the fringing reefs). Multiple recruitment studies in Mo'orea indicate the density of Pocilloporidae recruits peaks between December - April each year (Gleason 1996; Adjeroud et al. 2007; Edmunds et al. 2010). Therefore, we focused our examination of *Pocillopora spp.* spawning in the months of October - February in 2022 and 2023, resulting in the clear description of the timing of spawning for *P. meandrina*, *P. verrucosa,* and *P. tuahiniensis*, and the start of documentation for *P. cf. effusa* (Figs. 5,6).

Pocillopora meandrina

During our observations of *P. meandrina*, gametes were released early in the morning at ~06:15-06:40, which was ~ 70-80 minutes after sunrise local time. This information aligned with the range of (morphologically identified) *Pocillopora spp.* spawning in the literature of ~45-180 minutes after sunrise between different locations around the world, such as Australia (~45 minutes after sunrise (Schmidt-Roach et al. 2012)), Okinawa, Japan (~95 to 120 minutes after sunrise (Kinzie 1993; Hirose et al. 2000, 2001; Baird et al. 2022)), Hawai'i (~120 minutes after sunrise (Schmidt-Roach et al. 2014)), and the Red Sea (~180 minutes after sunrise (Bouwmeester et al. 2011, 2021)). We documented split-spawning (spawning in multiple consecutive months) in *P. meandrina*, with one colony spawning November 10th (06:32, full moon+3days) and reef-wide spawning December 9th (06:16-06:32; full moon+2days) and December 10th (06:21-06:35; full moon+3days). Split spawning is in line with spawning observations of (morphologically identified) *P. meandrina* in Hawai'i (Fiene-Severns 1998; Kolinski and Cox 2003), and the congeners (morphologically identified) of *P. verrucosa* and *P. grandis* (previously *P. eydouxi*) in Japan (Kinzie 1993).

In December, most of the *P. meandrina* colonies observed had synchronized spawning, based on the observation that on December 9 (Full+2), from 6:16 am to 6:32am, a large number of *P. meandrina* colonies were observed spawning both eggs and sperm turning the water of the lagoon cloudy and producing surface slicks (Fig 1A). Personal communications from other scientists in the region confirmed that *Pocillopora spp.* were spawning on forereef sites in Tetiaroa Dec 9th ~06:30 (Camille Gâche, Pers Comm) and Rangiroa Dec 9th ~06:20 (Camille Leonard, Pers Comm). On December 10 (Full+3), from 6:21 to 6:35, we observed a second day of synchronized spawning, but with a lower abundance of colonies releasing. Our results corroborate those from Japan (Kinzie 1993) and Hawai'i (Fiene-Severns 1998; Kolinski and Cox 2003) that *Pocillopora spp.* can spawn across multiple days within a month.

Across our observation period of October 2023 - January 2024, we were unable to access the observation site for all months and all desired days around the full moon (-2 to +5) where we hypothesized *P. meandrina* spawning could be occurring based on our 2022 observations, the Pocilloporid recruitment window of November to March from Mo'orea (Adjeroud et al. 2007; Edmunds et al. 2010), and from the hypothesized timing of *Pocillopora spp* from emerging histological data (Putnam Unpublished Data). Given that recruitment continues through March (Adjeroud et al. 2007; Edmunds et al. 2010), it is possible that: 1) *P. meandrina* also spawns around the full moons of January and February, 2) that pelagic larval duration (PLD) can extend over 1-2 months; and/or 3) that connected populations of *Pocillopora meandrina* (e.g., throughout French Polynesia) may

spawn at different times, or PLD varies in those populations. Alternatively, the recruitment data of *Pocillopora spp* could represent multiple species spawning across different months, and have yet only been identified to genus on the recruitment tiles. These competing hypotheses identify high priorities for further research as marine heatwaves both drive mass mortality (Hughes et al. 2018; Speare et al. 2022) and also can impact reproductive timing (Shlesinger and Loya 2019), amount/quality (Baird and Marshall 2002; Johnston et al. 2020), and recruitment (Edmunds 2017; Hughes et al. 2019).

Pocillopora verrucosa

In Mo'orea (17.53S latitude), *P. verrucosa* gametes were released ~5:45-6:20 local time, ~45-65 min after sunrise local time, earlier than morphologically identified *P. verrucosa* in several other regions of the world. While morphologically identified *P. verrucosa* spawning at the island of Okinawa, Japan (26.60N latitude) occurs within the same time range as Mo'orea at ~1h after sunrise (Kinzie 1993, Hirose et al. 2000), closer to the equator at the island of Ishigaki, Japan (24.42N latitude) morphologically identified *P. verrucosa* was observed to spawn ~3h after sunrise (Suzuki 2012). Similarly to Ishigaki Japan, in the Red Sea morphologically identified *P. verrucosa* spawning has been documented at ~3h after sunrise (~08:45) on reefs in Bara Musa Saqir Reef in Sudan (19.048300 latitude) and Al Jadir Reef in Saudi Arabia (19.787700 latitude) (Bouwmeester et al. 2021). The same diel timing of morphologically identified *P. verrucosa* spawning ~08:40 - 09:20 was also documented in the central Red Sea Thuwal, (22.22N latitude)(Bouwmeester et al. 2011) and Al Fahal (22.22N latitude) and Dreams Beach Reef (21.756786 latitude) (Bouwmeester et al. 2015) Furthermore, in Lyudao Taiwan (22.66N latitude), morphologically identified *P. verrucosa* spawning was observed much later in the morning, ~5 h after sunrise (09:30 to 10:30) (Lin and Nozawa 2017; Mulla et al. 2021).

Further work on the clarification of the diel timing of spawning and development of Pocilloporid symbiotic larvae will be essential. Both spawning (Baird et al. 2009; Keith et al. 2016) and development (Negri et al. 2007; Randall and Szmant 2009; Woolsey et al. 2013) are temperature dependent. Additionally, symbiotic larvae are light dependent with respect to metabolism (Kopp et al. 2016; Huffmyer et al. 2023) and phototaxis swimming (Mulla et al. 2021), resulting in the potential for UV damage to host and symbiont. For example, embryo developmental abnormalities increase with increasing temperature (Bassim et al. 2002) and symbiotic larvae accumulate more DNA damage from UV than aposymbiotic larvae (Nesa et al. 2012; Baird et al. 2021). Therefore understanding the diel timing of release will be essential for quantifying the amount of irradiance and diel solar warming *Pocillopora* larvae will experience in the critical first 8 hours of development to the swimming stage.

P. verrucosa only spawned in association with the new moon in (new moon and new moon +1day). Similarly, in the Red Sea (Sudan region), morphologically identified *P. verrucosa* spawning was observed to take place -1 day before the new moon, and in Saudi Arabia at -2 days before the new moon (Bouwmeester et al. 2011, 2015, 2021). Conversely, morphologically identified *P. verrucosa* spawning has been reported +0 and +1 days after full moon on the GBR (Schmidt-Roach et al. 2012) and 1–3 days following the full moon in Lyudao Taiwan (Lin and Nozawa 2017; Mulla et al. 2021). These reports are outliers from the broader geographical pattern we are seeing in Mo'orea and the reports of new moon morphologically identified *P. verrucosa* spawning in the Red Sea (Bouwmeester et al. 2011, 2015, 2021), indicating further species identification is essential. Therefore we propose a broad geographic distribution of *P. verrucosa* spawning associated with the new moon. It is critical that future studies identify Pocillopora based on now-established genetic markers (Johnston and Burgess 2023) and genomic data (Johnston et al. 2022a).

Pocillopora tuahiniensis

At the same site where we observed the spawning of *P. meandrina* and *P. verrucosa* species, we also observed the spawning of *Pocillopora tuahiniensis sp. Nov. (Johnston and Burgess 2023)*. *P. verrucosa* and *P. tuahiniensis* are sister species and overlap in their distribution at Mo'orea, across habitats and depth (Johnston et al. 2022b). *P. verrucosa* has a much broader geographic distribution across the Indo-Pacific (Gelin 2017 and Oury 2023 refs) compared to *P. tuahiniensis*, though the latter has also been documented within a subset of the range of the former (French Polynesia (Forsman et al. 2013; Edmunds et al. 2016; Gélin et al. 2017; Oury et al. 2021), Ducie Island, and in Rapa Nui (Armstrong et al. 2023; Voolstra et al. 2023). The close phylogenetic relationship between *P. tuahiniensis* and *P. verrucosa* and their overlap in geographic ranges, strongly suggests that the temporal separation in gamete release, in terms of both the day after new moon and the minutes after sunrise on overlapping lunar days, provides a mechanism to maintain species boundaries (preventing gene flow) between these species.

In our observations *P. verrucosa* spawning (~05:55 - 06:20) was temporally offset from its sister species *P. tuahiniensis* (~06:30 - 06:50). (Johnston and Burgess 2023) described recently *Pocillopora tuahiniensis* as a sister taxa to *P. verrucosa*. Our results are consistent with a linkage between genetic divergence and the temporal divergence in spawning time we observed here. *Pocillopora spp.* embryo development is some of the most rapid of corals described to date, where fertilization is proposed to occur within 15 minutes (Mulla et al. 2021), cleavage occurs within 30 - 40 minutes, and full development to the swimming larval stage occurs by 8 hours post fertilization (Hirose et al. 2000). Given this rapid fertilization and cleavage and the quick dissipation of the clouds of egg

and sperm following spawning, the ~30 minute offset between spawning in these two species appears to be one line of evidence that would minimize the potential for cross fertilization. Genome-wide analyses of these species show no evidence of hybridization (Johnston et al. 2022a), further supporting that the timing offset of spawning between *P. verrucosa* and *P. tuahiniensis* is acting as a temporal barrier for speciation.

Pocillopora cf. effusa

P. cf. effusa is less abundant in the lagoon than on the fore reef (Burgess et al in Press Evolutionary Applications). In addition, this species recently suffered a significant loss of abundance due to bleaching at Mo'orea in 2019 (Burgess et al. 2021). Within this context, observations of *P. cf.effusa* in the lagoon are likely to be rare. Indeed, only a single colony of *P. cf.effusa* was observed spawning +3 day after the November 2023 new moon (15 November) at ~06:31-06:50. Because this was a single observation, it could indicate spawning at different times when observers were not present, or multiple months as we observed with the other *Pocillopora* species in our study. Alternatively, it could be due to low abundance at our observation site, or accidental assignment of adjacent colony spawning to *P. cf.effusa*. Therefore, it is necessary to conduct additional sampling with extended time of day, days in a month, and additional months in future studies to concretely assign the timing of spawning for *P. cf.effusa* as well as for *P. grandis*, which has not yet been reported.

Larvae contain zooxanthellae and development is rapid

For all *Pocillopora* species we observed, once spawning commenced, the water quickly became cloudy with eggs and sperm (e.g., Fig. 1A, B, C). Eggs appeared to be neutrally or negatively buoyant, which has been reported by (Schmidt-Roach et al. 2012; Suzuki 2012; Mulla et al. 2021), as we observed they did not rise quickly to the surface like the eggs of Acroporidae. Following release, the gametes were rapidly dispersed by the waves and current. From our collections, eggs (~90µm) and developing embryos (~120µm) that were observed at ~10:00am via compound microscopy contained zooxanthellae, which have been shown to enter the eggs in the ~6 days prior to spawning in *Pocillopora* in Japan (Hirose et al. 2001). By 14:00 (~7.5 hours post fertilization, hpf) larvae were actively swimming, matching the timing of development in the morphologically identified *P. verrucosa* and *P. eydouxi* in Japan, where ciliated swimming larvae were documented 8 hpf (Hirose et al. 2000). The rapid development of Pocilloporidae larvae with vertically transmitted Symbiodiniaceae that can provide nutritional supplementation (Kopp et al. 2016) helps to ensure high recruitment success (Gleason 1996; Adjeroud et al. 2007; Edmunds et al. 2010). This combination of traits supports the capacity of *Pocillopora spp.* to promote rapid recovery following disturbances on the reefs of Mo'orea, if enough adult colonies are available under future climate change conditions (Speare et al. 2022) and gametogenesis is not severely impaired by mass bleaching events (Johnston et al. 2020).

Documentation is not always discovery

Although we are the first to report scientific documentation of *Pocillopora meandrina, P. verrucosa* and *P. tuahiniensis* spawning in French Polynesia, we also want to acknowledge the likelihood that that the timing of coral spawning for multiple taxa has been known by local Polynesians for decades to centuries. Merging of traditional ecological knowledge, citizen science, and scientific monitoring and documentation is poised to greatly expand our understanding of reproduction in French Polynesia, which will be critical to reef recovery and maintenance under climate change.

Acknowledgements

As guests, we recognize and give thanks for the land and water resources of Polynesia, in particular Mo'orea, and to the traditional owners of the land, both past and present. Māuruuru roa. With respect to the spelling of Tahitian words, we endeavored to followed the Te Fare Vanā'a transcription system that is adhered to by a large segment of the Tahitian community, but also recognize other community members follow the Raapoto transcription system where the island name of Moorea is, for example, spelled without the 'eta (i.e., Moorea).

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Data Availability: DOI 10.17605/OSF.IO/5GEQD (Harnay et al. 2023)

Author Contributions: Funding HMP, SCB; Conceptualization PEH, HMP; Field work PEH, HMP; Molecular Analysis HMP, AT, SCB; Writing PEH, HMP, AT, SCB

Conflict of interest statement: The authors have no conflict of interest.

Figures:

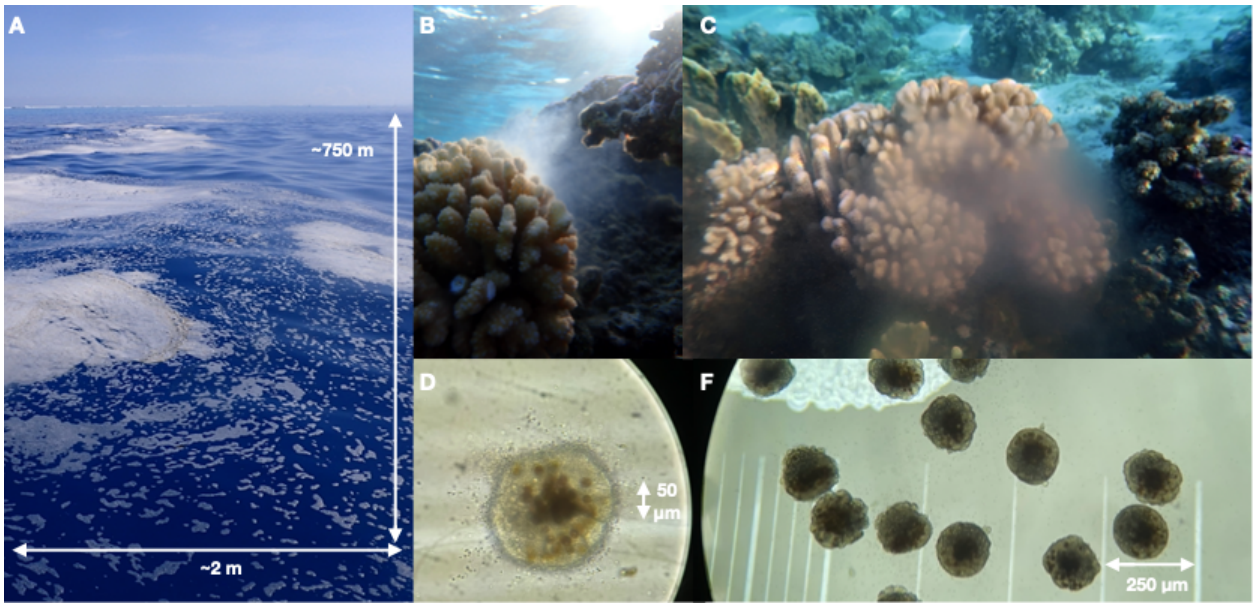

Figure 1. A) Slick of sperm and egg on the surface of the water in the lagoon was observed after spawning with the image showing ~ 750m distance between the fore reef and the observer. **B)** *Pocillopora meandrina* spawning **C)** eggs and sperm in the lagoon. Samples of the gametes were collected from the seawater revealing the **D)** presence of symbiotic eggs surrounded by sperm followed by **F)** embryos at ~4 hours post spawning and swimming embryos at 14:00, ~8 hours post spawning. More images and videos are archived here: https://osf.io/5geqd/ (Harnay et al. 2023)

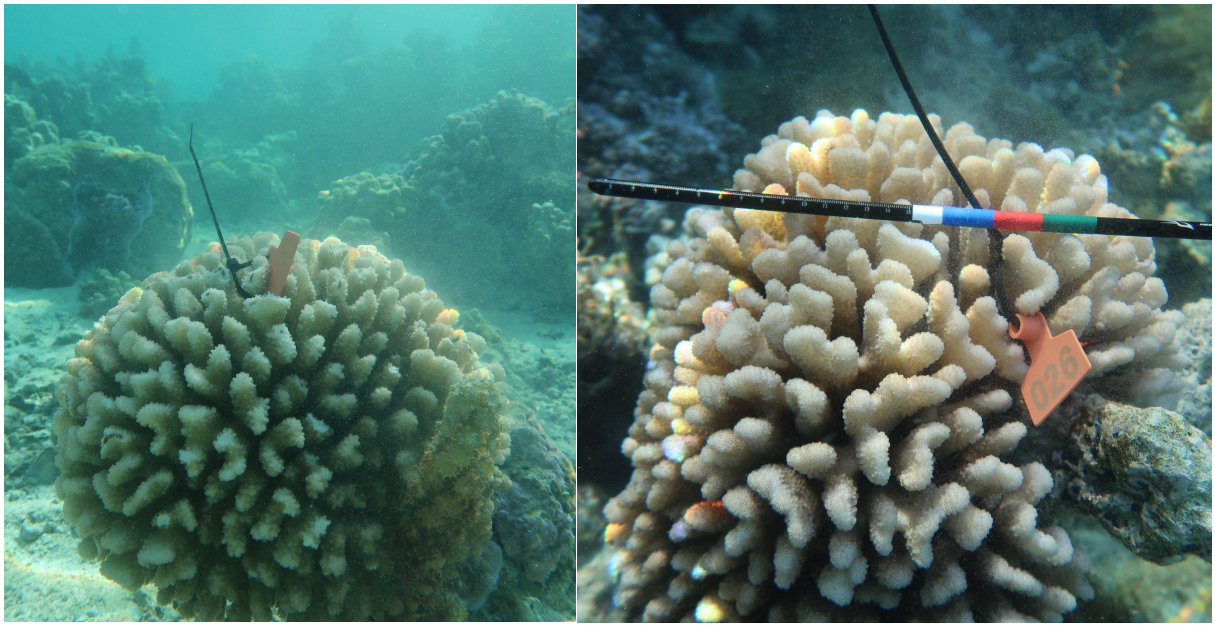

Figure 2. Examples of *Pocillopora tuahiniensis* colonies that were tagged during spawning of eggs and sperm in the lagoon. More images and videos are archived here: https://osf.io/5geqd/ (Harnay et al. 2023)

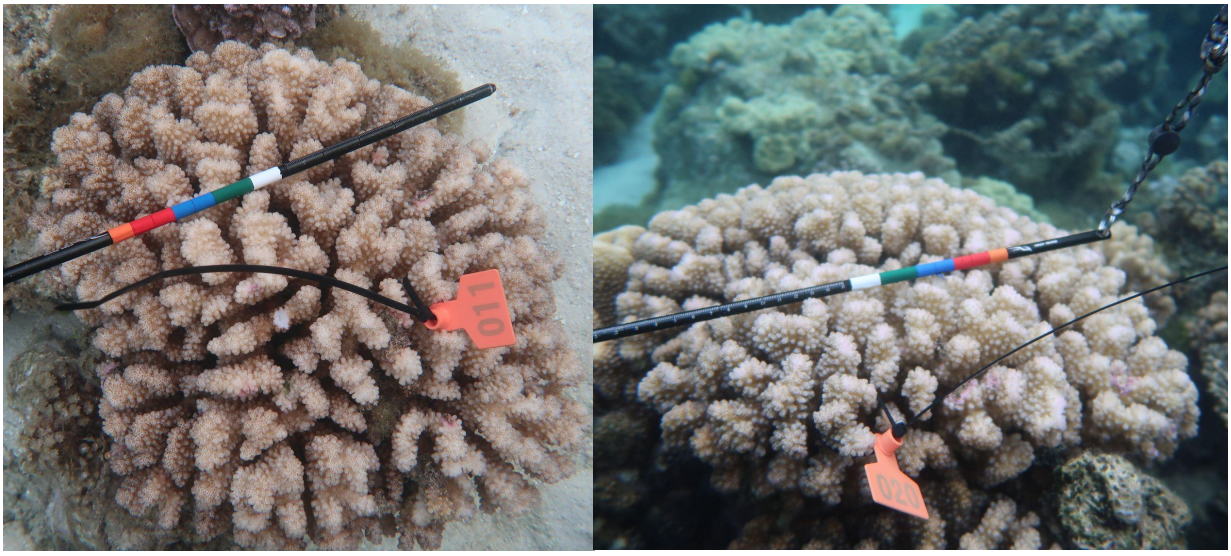

Figure 3. Examples of *Pocillopora verrucosa* colonies that were tagged during spawning. More images and videos are archived here: https://osf.io/5geqd/ (Harnay et al. 2023)

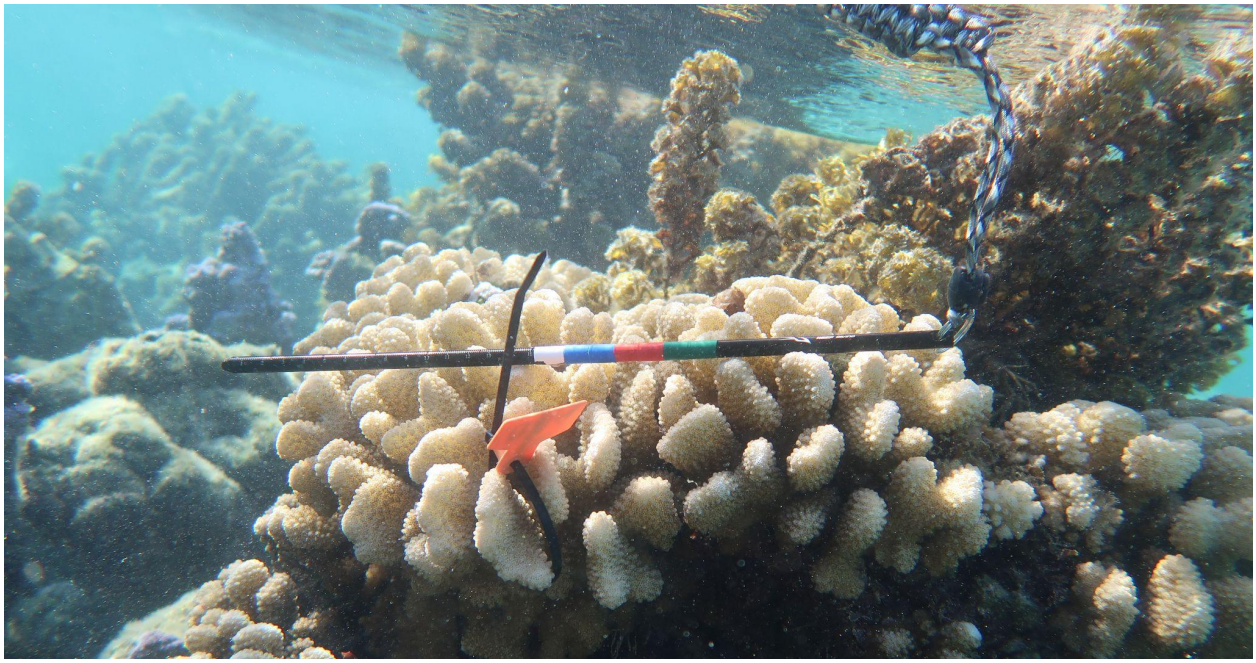

Figure 4. *Pocillopora cf. effusa* colony that was tagged during spawning of eggs and sperm in the lagoon. More images and videos are archived here: https://osf.io/5geqd/ (Harnay et al. 2023)

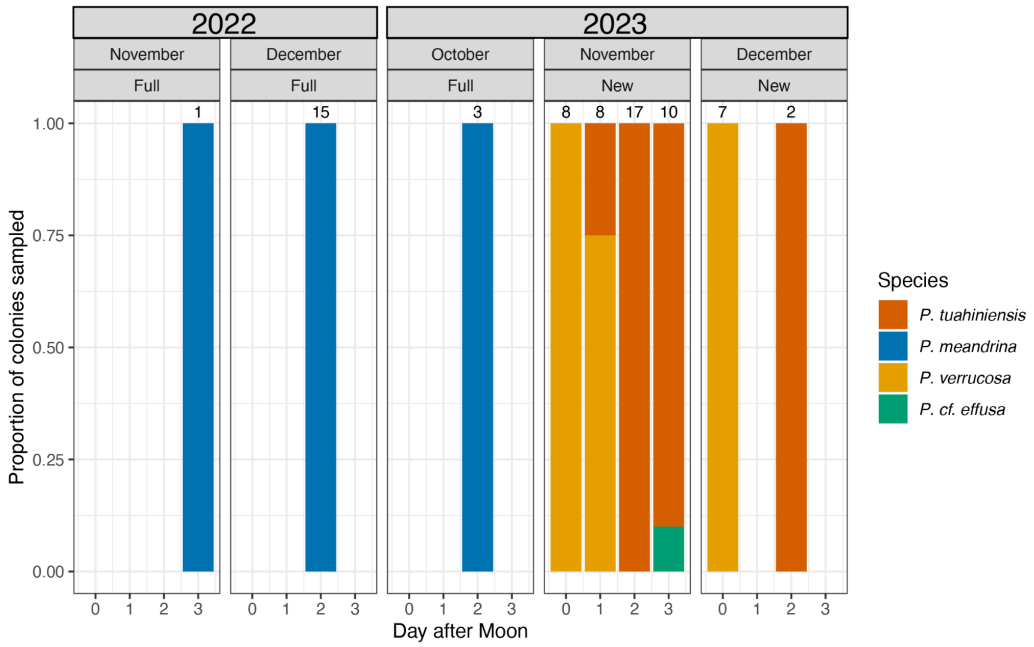

Figure 5. Proportion of spawning corals from which tissue was sampled (i.e., not the proportion of corals that spawned) as a function of day after new or full moon in November and December 2022 and October through December 2023 (sample size is indicated on the top of each bar.

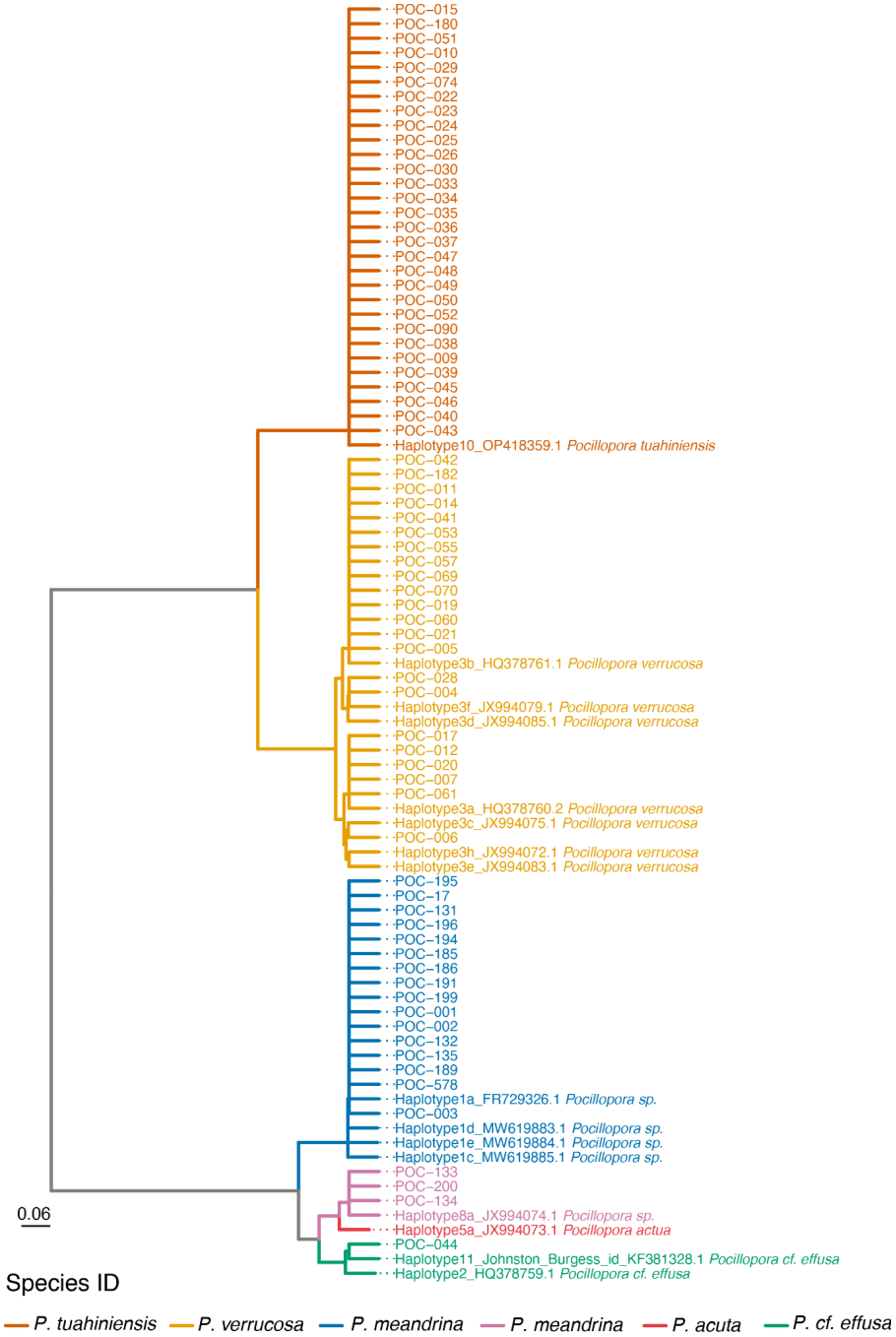

Figure 6. Haplotype identification via mtORF for spawning colonies in 2022 and 2023 generated from hierarchical clustering of Jukes-Cantor genetic distance (Jukes and Cantor 1969) from 71 collected samples, 15 reference samples, and no outgroup. The gene tree is based on mtORF to visualize species delimitation and does not reflect exact phylogeny (see (Johnston et al. 2022a)). Species colors are added based on unambiguous mtORF haplotypes, or following unambiguous PocHistone RFLP results. Raw sequence data, alignments, gel images, and reference fasta files are archived here: https://osf.io/5geqd/ (Harnay et al. 2023).

Tables

Table 1. *Pocillopora spp* spawning times reported from the literature based on observations or histological evidence.

Reference	Location	Species	Identification	Evidence	Date	Moon	Lunar Day	Local Time
(Glynn et al. 1991)	Caño Island, Costa Rica	*P. elegans*	Morphological	Histology	1985-1989	Full	NA	NA
(Glynn et al. 1991)	Pearl Islands, Panama	*P. elegans*	Morphological	Histology	1984, 1985, 1989	Full	NA	NA
(Glynn et al. 1991)	Uva Island, Panama	*P. elegans*	Morphological	Histology	1984-1990	Full	NA	NA
(Glynn et al. 1991)	Santa Cruz Island, Galapagos	*P. elegans*	Morphological	Histology	1985-1989	Full	NA	NA
(Kinzie 1993)	Okinawa, Japan	*P. grandis (P. eydouxi)*	Morphological	Spawning Observed	May - August 1992	Full	Full Moon +1 to 5	08:00 – 10:50
(Hirose et al. 2000)	Okinawa, Japan	*P. grandis (P. eydouxi)*	Morphological	Spawning Observed	June - July 1998	Full	Few days after full moon	NA
(Schmidt-Roach et al. 2012)	Lizard Island, Australia	*P. grandis (P. eydouxi)*	Morphological	Spawning Observed	11-12 November 2011	Full	Full moon +1-2	NA
(Fiene-Severns 1998)	Molokini, Hawai‘i	*P. meandrina*	Morphological	Spawning Observed	April-May; 1991, 1994-1998	Full	Full moon +2-5	07:20
(Schmidt-Roach et al. 2012)	Lizard Island, Australia	*P. meandrina*	Morphological	Spawning Observed	11-12 November 2011	Full	Full moon +1-2	06:25
(Fadlallah 1985)	Yanbu, Saudi Arabia	*P. verrucosa*	Morphological	Histology	May June	New	NA	NA

(Shlesinger and Loya 1985)	Eilat, Israel	*P. verrucosa*	Morphological	Spawning Observed	July - August 1981-1982	New	NA	NA
(Kinzie 1993)	Okinawa, Japan	*P. verrucosa*	Morphological	Spawning Observed	May – July 1992	New	New Moon +1 to 6	07:00 – 07:11
(Sier and Olive 1994)	Maldives	*P. verrucosa*	Morphological	Histology	March - April 1991	NA	NA	NA
(Tomascik 1997)	Karimunjawa Islands, Indonesia	*P. verrucosa*	Morphological	not provided	October November 1995	NA	NA	NA
(Kruger and Schleyer 1998)	South Africa	*P. verrucosa*	Morphological	Histology	January-February 1993	New	NA	NA
(Hirose et al. 2000)	Okinawa, Japan	*P. verrucosa*	Morphological	Spawning Observed	June - July 1998	New	Few days after new moon	NA
(Romatzki 2008)	Sulawesi, Indonesia	*P. verrucosa*	Morphological	Histology	March, August 2006-2007	New	NA	NA
(Bouwmeester et al. 2011)	Thuwal, Saudi Arabia	*P. verrucosa*	Morphological	Spawning Observed	31 May 2011	New	New moon - 1	8:40 - 9:15
(Schmidt-Roach et al. 2012)	Lizard Island, Australia	*P. verrucosa*	Morphological	Spawning Observed	11-12 November 2011	Full	Full moon +1-2	NA
(Suzuki 2012)	Ryukyu Islands, Japan	*P. verrucosa*	Morphological	Spawning Observed	18 June 2011	Full	NA	09:00
(Bouwmeester et al. 2015)	Dreams Beach Reef, Saudi Arabia	*P. verrucosa*	Morphological	Spawning Observed	May 2011, May 2012	New	New moon - 1	8:40 - 9:20
(Lin and Nozawa 2017)	Lyudao, Taiwan	*P. verrucosa*	Morphological	Spawning Observed	April - June 2011 - 2015	Full	Full +1 +2 +3	09:50– 11:00
(Mulla et al. 2021)	Lyudao, Taiwan	*P. verrucosa*	Morphological	Spawning Observed	21 April 2019	Full	Full +2 +3	9:30 and 10:00

This study	Mo'orea, French Polynesia	*P. meandrina*	Genetic	Spawning Observed	October 2023, November 2022, December 2022	Full	Full +2 +3	6:16-6:38
This study	Mo'orea, French Polynesia	*P. verrucosa*	Genetic	Spawning Observed	November, December 2023	New	New +1 +2	5:56-6:19
This study	Mo'orea, French Polynesia	*P. tuahiniensis*	Genetic	Spawning Observed	November, December 2023	New	New +1 +2 +3	6:26-6:50
This study	Mo'orea, French Polynesia	*P. cf effusa*	Genetic	Spawning Observed	November 2023	New	New +3	NA

Table 2. *Pocillopora spp* spawning observation timeline from September 2022 to January 2023. Moon phase dates were reported based on the website https://aa.usno.navy.mil/data/MoonPhases. Sunrise and sunset times were reported for the location of Mo'orea using this website https://www.timeanddate.com/sun/@4034185
NOR: No Data Recorded indicates no observers were present in the field.
- - - indicates no additional notes

Date YYYYMMDD	Sunrise Time	Lunar Phase	Spawn	Observation Start Time	Observation Stop Time	Spawning Timing and Notes
20220925	5:46 AM	New	NDR	NDR	NDR	- - -
20220926	5:45 AM	New+1	No	05:30 AM	7:00 AM	- - -
20220927	5:44 AM	New+2	No	05:40 AM	8:00 AM	- - -
20220928	5:43 AM	New+3	No	05:45 AM	08:15 AM	- - -
20221007	5:36 AM	Full-2	No	05:45 AM	08:00 AM	- - -
20221008	5:35 AM	Full-1	No	06:00 AM	08:05 AM	- - -
20221009	5:34 AM	Full	NDR	NDR	NDR	- - -
20221010	5:34 AM	Full +1	NDR	NDR	NDR	- - -
20221011	5:33 AM	Full +2	NDR	NDR	NDR	- - -
20221012	5:32 AM	Full +3	NDR	NDR	NDR	- - -
20221106	5:18 AM	Full-2	No	6:00 AM	7:45 AM	- - -
20221107	5:17 AM	Full-1	No	6:10 AM	8:00 AM	- - -
20221108	5:17 AM	Full	NDR	NDR	NDR	Bad weather with lightning precluded in water observations
20221109	5:15 AM	Full+1	No	5:50 AM	8:00 AM	- - -
20221110	5:15 AM	Full+2	Yes	05:45 AM	08:25 AM	Spawn at 06:32
20221111	5:14 AM	Full+3	No	6:00 AM	7:40 AM	- - -
20221205	5:16 AM	Full -2	NDR	NDR	NDR	- - -
20221206	5:16 AM	Full -1	NDR	NDR	NDR	- - -
20221207	5:16 AM	Full	No	06:00 AM	07:28 AM	- - -
20221208	5:16 AM	Full+1	No	06:20 AM	07:52 AM	- - -
20221209	5:17 AM	Full+2	Yes	06:05 AM	08:00 AM	Spawn at 06:16 to 06:32
20221210	5:17 AM	Full+3	Yes	06:00 AM	07:45 AM	Spawn at 06:21 to

						06:35
20230104	5:29 AM	Full -2	NDR	NDR	NDR	- - -
20230105	5:30 AM	Full -1	NDR	NDR	NDR	- - -
20230106	5:29 AM	Full	NDR	NDR	NDR	Bad weather with lightning precluded in water observations
20230107	5:30 AM	Full+1	No	06:09 AM	07:37 AM	Bad weather and strong current reduced in water time
20230108	5:30 AM	Full+2	No	06:10 AM	07:18 AM	Bad weather and strong current reduced in water time
20230109	5:33 AM	Full+3	No	06:10 AM	06:37 AM	Bad weather, waves and current precluded water work past ~06:40
20230110	5:33 AM	Full +4	NDR	NDR	NDR	- - -
20230111	5:34 AM	Full +5	NDR	NDR	NDR	- - -
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20231026	5:23 AM	Full -2	NDR	NDR	NDR	- - -
20231027	5:23 AM	Full -1	NDR	NDR	NDR	- - -
20231028	5:22 AM	Full	No	6:00 AM	7:30 AM	- - -
20231029	5:22 AM	Full +1	No	6:07 AM	8:00 AM	- - -
20231030	5:21 AM	Full +2	Yes	6:00 AM	8:00 AM	06:22 - 06:38
20231031	5:21 AM	Full +3	No	6:08 AM	8:02 AM	- - -
20231101	5:20 AM	Full +4	No	6:18 AM	7:40 AM	- - -
20231102	5:20 AM	Full +5	No	6:04 AM	7:12 AM	- - -
20231103	5:19 AM	Full +6	No	6:10 AM	7:30 AM	Low visibility
20231104	5:19 AM	Full +7	No	6:02 AM	7:30 AM	Low visibility
20231110	5:17 AM	New -2	NDR	NDR	NDR	- - -
20231111	5:17 AM	New -1	NDR	NDR	NDR	- - -
20231112	5:16 AM	New	Yes	5:52 AM	7:30 AM	06:00 - 06:17 AM
20231113	5:16 AM	New +1	Yes	5:49 AM	7:08 AM	6:04 - 6:19 AM *P. verrucosa*
20231113	5:16 AM	New +1	Yes	5:49 AM	7:08 AM	6:33 - 6:44 AM *P. tuahiniensis*

20231114	5:16 AM	New +2	Yes	5:50 AM	7:18 AM	6:26 - 6:50 AM
20231115	5:15 AM	New +3	Yes	5:55 AM	7:30 AM	6:31 - 6:50 AM
20231116	5:15 AM	New +4	No	5:54 AM	7:24 AM	lot of wind and wave at the water surface but good visibility
20231117	5:15 AM	New +5	No	5:57 AM	7:04 AM	lot of wind
20231124	5:14 AM	Full -2	No	6:00 AM	7:00 AM	- - -
20231125	5:14 AM	Full -1	No	5:50 AM	7:10 AM	- - -
20231126	5:14 AM	Full	No	5:49 AM	7:09 AM	- - -
20231127	5:15 AM	Full +1	NDR	NDR	NDR	Big swell, high current. Visibility zero
20231128	5:15 AM	Full +2	NDR	NDR	NDR	- - -
20231129	5:15 AM	Full +3	NDR	NDR	NDR	- - -
20231130	5:15 AM	Full +4	NDR	NDR	NDR	- - -
20231201	5:15 AM	Full +5	NDR	NDR	NDR	- - -
20231210	5:17 AM	New -2	No	6:02 AM	6:57 AM	- - -
20231211	5:17 AM	New -1	No	6:06 AM	7:03 AM	- - -
20231212	5:18 AM	New	Yes	5:45 AM	7:00 AM	5:56 - 6:17 AM
20231213	5:18 AM	New +1	NDR	NDR	NDR	Huge Storm, too dangerous to monitor
20231214	5:18 AM	New +2	Yes	6:06 AM	7:05 AM	6:33 - 6:42 AM
20231215	5:19 AM	New +3	Yes	6:06 AM	7:00 AM	6:34 - 6:36 AM No colony clearly identified
20231216	5:19 AM	New +4	NDR	NDR	NDR	- - -
20231217	5:20 AM	New +5	NDR	NDR	NDR	- - -
20231224	5:23 AM	Full -2	NDR	NDR	NDR	- - -
20231225	5:24 AM	Full -1	NDR	NDR	NDR	- - -
20231226	5:24 AM	Full	No	6:00 AM	7:05 AM	- - -
20231227	5:25 AM	Full +1	No	6:01 AM	7:35 AM	- - -
20231228	5:25 AM	Full +2	NDR	NDR	NDR	- - -
20231229	5:26 AM	Full +3	NDR	NDR	NDR	- - -
20231230	5:26 AM	Full +4	NDR	NDR	NDR	- - -
20231231	5:27 AM	Full +5	NDR	NDR	NDR	- - -

20240109	5:33 AM	New -2	NDR	NDR	NDR	- - -
20240110	5:33 AM	New -1	NDR	NDR	NDR	- - -
20240111	5:34 AM	New	NDR	NDR	NDR	- - -
20240112	5:34 AM	Newl +1	No	6:05 AM	7:05 AM	Strong current, the day before big storm and rain
20240113	5:35 AM	New +2	No	5:45 AM	7:05 AM	Strong current
20240114	5:36 AM	New +3	No	5:40 AM	7:00 AM	Strong current
20240115	5:36 AM	New +4	NDR	NDR	NDR	- - -
20240116	5:37 AM	New +5	NDR	NDR	NDR	- - -
20240123	5:41 AM	Full -2	NDR	NDR	NDR	- - -
20240124	5:42 AM	Full -1	NDR	NDR	NDR	- - -
20240125	5:42 AM	Full	No	6:02 AM	6:15 AM	High wind impossible to monitor longer because of the swell and the current
20240126	5:43 AM	Full +1	No	5:55 AM	7:05 AM	- - -
20240127	5:44 AM	Full +2	No	5:50 AM	7:10 AM	- - -
20240128	5:44 AM	Full +3	No	5:50 AM	7:10 AM	- - -
20240129	5:45 AM	Full +4	NDR	NDR	NDR	- - -
20240130	5:45 AM	Full +5	NDR	NDR	NDR	- - -

Table 3. *Pocillopora* spawning samples collected from corals observed spawning in 2022 and 2023.

Sample ID	mtORF Sanger ID Haplotype	PocHistone RFLP ID	Species ID	Collection Date YYYYMMDD
POC-578 (Tag 192)	Haplotype 1	*P. meandrina*	*P. meandrina*	20221110
POC-131	Haplotype 1	*P. meandrina*	*P. meandrina*	20221209
POC-132	Haplotype 1	*P. meandrina*	*P. meandrina*	20221209
POC-133	Haplotype 8	*NA*	*P. meandrina*	20221209
POC-134	Haplotype 8	*NA*	*P. meandrina*	20221209
POC-135	Haplotype 1	*P. meandrina*	*P. meandrina*	20221209
POC-176	Haplotype 1	*P. meandrina*	*P. meandrina*	20221209
POC-185	Haplotype 1	*P. meandrina*	*P. meandrina*	20221209
POC-186	Haplotype 1	*P. meandrina*	*P. meandrina*	20221209
POC-189	Haplotype 1	*P. meandrina*	*P. meandrina*	20221209
POC-191	Haplotype 1	*P. meandrina*	*P. meandrina*	20221209
POC-194	Haplotype 1	*P. meandrina*	*P. meandrina*	20221209
POC-195	Haplotype 1	*P. meandrina*	*P. meandrina*	20221209
POC-196	Haplotype 1	*P. meandrina*	*P. meandrina*	20221209
POC-199	Haplotype 1	*P. meandrina*	*P. meandrina*	20221209
POC-200	Haplotype 8	*NA*	*P. meandrina*	20221209

POC-002	Haplotype 1	*P. meandrina*	*P. meandrina*	20231030
POC-001	Haplotype 1	*P. meandrina*	*P. meandrina*	20231030
POC-003	Haplotype 1	*P. meandrina*	*P. meandrina*	20231030
POC-011	Haplotype 3	*NA*	*P. verrucosa*	20231112
POC-012	Haplotype 3	*NA*	*P. verrucosa*	20231112
POC-014	Haplotype 3	*NA*	*P. verrucosa*	20231112
POC-017	Haplotype 3	*NA*	*P. verrucosa*	20231112
POC-019	Haplotype 3	*NA*	*P. verrucosa*	20231112
POC-020	Haplotype 3	*NA*	*P. verrucosa*	20231112
POC-004	Haplotype 3	*NA*	*P. verrucosa*	20231112
POC-005	Haplotype 3	*NA*	*P. verrucosa*	20231112
POC-022	Haplotype 10	*NA*	*P. tuahiniensis*	20231113
POC-047	Haplotype 10	*NA*	*P. tuahiniensis*	20231113
POC-007	Haplotype 3	*NA*	*P. verrucosa*	20231113
POC-021	Haplotype 3	*NA*	*P. verrucosa*	20231113
POC-028	Haplotype 3	*NA*	*P. verrucosa*	20231113
POC-041	Haplotype 3	*NA*	*P. verrucosa*	20231113
POC-042	Haplotype 3	*NA*	*P. verrucosa*	20231113
POC-006	Haplotype 3	*NA*	*P. verrucosa*	20231113
POC-015	Haplotype 10	*NA*	*P. tuahiniensis*	20231114
POC-023	Haplotype 10	*NA*	*P. tuahiniensis*	20231114
POC-024	Haplotype 10	*NA*	*P. tuahiniensis*	20231114
POC-025	Haplotype 10	*NA*	*P. tuahiniensis*	20231114
POC-026	Haplotype 10	*NA*	*P. tuahiniensis*	20231114
POC-029	Haplotype 10	*NA*	*P. tuahiniensis*	20231114
POC-030	Haplotype 10	*NA*	*P. tuahiniensis*	20231114
POC-033	Haplotype 10	*NA*	*P. tuahiniensis*	20231114
POC-038	Haplotype 10	*NA*	*P. tuahiniensis*	20231114
POC-045	Haplotype 10	*NA*	*P. tuahiniensis*	20231114
POC-046	Haplotype 10	*NA*	*P. tuahiniensis*	20231114
POC-048	Haplotype 10	*NA*	*P. tuahiniensis*	20231114
POC-050	Haplotype 10	*NA*	*P. tuahiniensis*	20231114
POC-051	Haplotype 10	*NA*	*P. tuahiniensis*	20231114
POC-009	Haplotype 10	*NA*	*P. tuahiniensis*	20231114
POC-010	Haplotype 10	*NA*	*P. tuahiniensis*	20231114
POC-180	Haplotype 10	*NA*	*P. tuahiniensis*	20231114
POC-044	Haplotype 11	*NA*	*P. cf. effusa*	20231115
POC-034	Haplotype 10	*NA*	*P. tuahiniensis*	20231115
POC-035	Haplotype 10	*NA*	*P. tuahiniensis*	20231115

POC-036	Haplotype 10	*NA*	*P. tuahiniensis*	20231115
POC-037	Haplotype 10	*NA*	*P. tuahiniensis*	20231115
POC-039	Haplotype 10	*NA*	*P. tuahiniensis*	20231115
POC-040	Haplotype 10	*NA*	*P. tuahiniensis*	20231115
POC-043	Haplotype 10	*NA*	*P. tuahiniensis*	20231115
POC-049	Haplotype 10	*NA*	*P. tuahiniensis*	20231115
POC-052	Haplotype 10	*NA*	*P. tuahiniensis*	20231115
POC-053	Haplotype 3	*NA*	*P. verrucosa*	20231212
POC-055	Haplotype 3	*NA*	*P. verrucosa*	20231212
POC-057	Haplotype 3	*NA*	*P. verrucosa*	20231212
POC-060	Haplotype 3	*NA*	*P. verrucosa*	20231212
POC-061	Haplotype 3	*NA*	*P. verrucosa*	20231212
POC-069	Haplotype 3	*NA*	*P. verrucosa*	20231212
POC-070	Haplotype 3	*NA*	*P. verrucosa*	20231212
POC-182	Haplotype 3	*NA*	*P. verrucosa*	20231212
POC-090	Haplotype 10	*NA*	*P. tuahiniensis*	20231214
POC-074	Haplotype 10	*NA*	*P. tuahiniensis*	20231214

Table 4. Reference mtORF sequences and their accession numbers used for sequence alignment and tree building. Raw sequence data, fasta files, and alignment are archived at https://osf.io/5geqd/ (Harnay et al. 2023)

Haplotype ID	Accession Number	Species	Citation
Haplotype 1a	FR729326	*Pocillopora meandrina* or *P. grandis*	(Flot et al. 2010)
Haplotype 1c	MW619885	*Pocillopora meandrina* or *P. grandis*	(Burgess et al. 2021)
Haplotype 1d	MW619883	*Pocillopora meandrina* or *P. grandis*	(Burgess et al. 2021)
Haplotype 1e	MW619884	*Pocillopora meandrina* or *P. grandis*	(Burgess et al. 2021)
Haplotype 2	HQ378759	*Pocillopora cf. effusa*	(Pinzón and LaJeunesse 2011)
Haplotype 3a	HQ378760	*Pocillopora verrucosa*	(Pinzón and LaJeunesse 2011)
Haplotype 3b	HQ378761	*Pocillopora verrucosa*	(Pinzón and LaJeunesse 2011)
Haplotype 3c	JX994075	*Pocillopora verrucosa*	(Pinzón et al. 2013)
Haplotype 3d	JX994085	*Pocillopora verrucosa*	(Pinzón et al. 2013)
Haplotype 3e	JX994083	*Pocillopora verrucosa*	(Pinzón et al. 2013)
Haplotype 3f	JX994079	*Pocillopora verrucosa*	(Pinzón et al. 2013)
Haplotype 3h	JX994072	*Pocillopora verrucosa*	(Pinzón et al. 2013)
Haplotype 5a	JX994073	*Pocillopora acuta*	(Pinzón et al. 2013)
Haplotype 8a	JX994074	*Pocillopora meandrina*	(Pinzón et al. 2013)
Haplotype 10	OP418359	*P. tuahiniensis*	(Johnston and Burgess 2023)
Haplotype 11	KF381328	*Pocillopora cf. effusa*	Forsman et al 2013 (KF381328) (Johnston et al. 2022b) full sequence

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