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

Harnay P[1], Turner AM[2], Burgess SC[2], and Putnam HM[3*]

[1] University of Haifa, The Leon H. Charney School of Marine Sciences, Department of Marine Biology, Haifa Israel
[2] Florida State University, Department of Biological Science, 319 Stadium Drive, Tallahassee, Florida 32306-4296 USA
[3] University of Rhode Island, College of the Environment and Life Sciences, Department of Biological Sciences, 120 Flagg Rd. Kingston, RI 02881 USA
*corresponding author: hputnam@uri.edu

Data, Code, Image Archive: https://osf.io/5geqd/

Abstract

Knowledge of coral gamete release is fundamental to reef ecology and evolution, but cryptic species complicate reproduction studies. In Mo'orea, French Polynesia, when corals were decimated by crown-of-thorns and a cyclone between 2007-2010, recruitment of six cryptic species of *Pocillopora spp.* primarily drove decadal reef recovery. Broadcast spawning for these genetically-verified species at Mo'orea is, however, undocumented in the scientific literature. We conducted *in situ* surveys over 58 days during September 2022-January 2023, October 2023-January 2024, and October 2024-December 2024. To identify the *Pocillopora spp.* we used molecular analysis of mtORF and PocHistone markers. *P. meandrina* and *P. grandis* spawned 2-3 days following the full moons of October-December. In contrast, *P. verrucosa* and *P. tuahiniensis* spawned at the new moons in November-December, with *P. verrucosa* spawning on lunar days 0-1, and *P. tuahiniensis* spawning on lunar days 1-3. Diel offset in the timing of spawning following sunrise was present in both moon phases indicating a temporal speciation barrier. *P. verrucosa* spawned ~45 min after sunrise, whereas *P. tuahiniensis* spawned ~73 min after sunrise. Similarly, *P. grandis* spawned ~40 minutes after sunrise, whereas *P. meandrina* spawned ~65 minutes after sunrise. Only one colony of *P. effusa* spawned (lunar day 3 new moon ~06:30-06:50), requiring further confirmation of the timing for this low abundance species. Collectively, these first spawning reports provide an initial scientific documentation of *Pocillopora* spawning at the genetically-verified species level in Mo'orea, increasing capacity to study the essential process of coral reproduction for critical reef building species.

Résumé

La connaissance de la libération des gamètes chez les coraux est fondamentale pour comprendre l'écologie et l'évolution des récifs, mais la présence d'espèces cryptiques complique les études sur la reproduction. À Mo'orea, en Polynésie française, lorsque les coraux ont été décimés par des étoiles de mer couronne d'épines et un cyclone entre 2007 et 2010, le recrutement de six espèces cryptiques de *Pocillopora spp*. a principalement contribué à la récupération des récifs au cours de la décennie suivante. Toutefois, la reproduction par émission synchronisée des gamètes (broadcast spawning) de ces espèces génétiquement vérifiées à Mo'orea n'a pas encore été documentée dans la littérature scientifique. Nous avons mené des observations in situ sur 58 jours entre septembre 2022 et janvier 2023, d'octobre 2023 à janvier 2024, puis d'octobre à décembre 2024. Pour identifier les espèces de *Pocillopora spp.*, nous avons utilisé une analyse moléculaire des marqueurs mtORF et PocHistone. *P. meandrina* et *P. grandis* ont pondu 2 à 3 jours après les pleines lunes d'octobre à décembre. En revanche, *P. verrucosa* et *P. tuahiniensis* ont pondu lors des nouvelles lunes en novembre et décembre, *P. verrucosa* aux jours lunaires 0 à 1, et *P. tuahiniensis* aux jours lunaires 1 à 3. Un décalage journalier dans le moment de la ponte après le lever du soleil a été observé pour les deux phases lunaires, indiquant une barrière temporelle de spéciation. *P. verrucosa* a pondu environ 45 minutes après le lever du soleil, tandis que *P. tuahiniensis* a pondu environ 73 minutes après. De manière similaire, *P. grandis* a pondu environ 40 minutes après le lever du soleil, alors que *P. meandrina* a pondu environ 65 minutes après. Une seule colonie de *P. effusa* a pondu (jour lunaire 3, nouvelle lune, entre ~06:30 et 06:50), ce qui nécessite une confirmation supplémentaire du moment de reproduction pour cette espèce peu abondante. Collectivement, ces premières observations de ponte constituent une première documentation scientifique de la reproduction des *Pocillopora* au niveau des espèces génétiquement vérifiées à Mo'orea, augmentant la capacité à étudier ce processus essentiel de reproduction chez des espèces clés pour la construction des récifs.

Introduction

Natural disturbances can trigger new ecological trajectories and states 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 (Kayal et al. 2012) 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 therefore the knowledge of coral reproductive timing and spawning is essential for basic coral biology and ecology, as well as coral selective breeding (van Oppen et al. 2015) and recruitment seeding (Doropoulos et al. 2019) 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, Kerry, and Simpson 2018) and cascading negative consequences for reef function (Courtney et al. 2018; Hughes et al. 2019). In French Polynesia, coral bleaching in 2002 resulted in >50% of corals surveyed showing bleaching in Mo'orea (Penin et al. 2007), and contributed to reduced coral cover (Pérez-Rosales et al. 2021). In Mo'orea in 2019, surveys of coral bleaching of the dominant genera revealed 89% of *Acropora* and 46% of *Pocillopora* had signs of bleaching and partial mortality (Speare et al. 2022). Additionally, another study of *Pocillopora* bleaching in April 2019 showed 72% of *Pocillopora* colonies bleached (Burgess et al. 2021). Further, bleaching occurred again in Mo'orea in March - May 2024 (MCR LTER pers comm). 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 (*Acanthaster planci*) outbreak in 2007 (Kayal et al. 2012) 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 between 2007 and 2009 and cyclone Oli in 2010 (Holbrook

et al. 2018), *Pocillopora spp.* were responsible for rapid reef recovery (Adjeroud, Penin, and Carroll 2007; Holbrook et al. 2018; Edmunds 2018). *Pocillopora spp.* are early colonizing species (Grigg and Maragos 1974) due to high fecundity (Sier and Olive 1994) and high recruitment (Adjeroud, Penin, and Carroll 2007). Further, with their complex branching morphologies, *Pocillopora spp.* provide extensive reef organism habitat (Stella, Jones, and Pratchett 2010; Pisapia et al. 2020). The Pocilloporid species diversity documented in Mo'orea and validated with genetics includes *P. meandrina*, *P. verrucosa, P. grandis*, *P. effusa, P. tuahiniensis (*Johnston and Burgess 2023; Johnston et al. 2022; Burgess et al. 2021; Burgess, Turner, and Johnston 2024), and *P. acuta* (primarily occurring on the fringing reefs; (Burgess, Turner, and Johnston 2024)). In light of this, it is essential that we quantify and describe the process of *Pocillopora* spp*.* spawning in French Polynesia, in order to understand and forecast the ecological dynamics of the reef in the future of increasing environmental disturbances.

A major impediment to quantifying and describing spawning patterns in corals, including *Pocillopora* spp., is the presence of cryptic species. Genetic identification to the species level in Mo'orea has clarified taxonomic differences in niche preference across reef zones and around the island (Burgess, Turner, and Johnston 2024), and also identified differential thermal sensitivity and mortality of *P. effusa* compared to other taxa in the 2019 coral bleaching event in Mo'orea (Burgess et al. 2021). Existing literature on reproduction in *Pocillopora* spp. (Baird, Guest, and Willis 2009; Schmidt-Roach et al. 2012) 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). For *Pocillopora spp.*, 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* (previously called *P. eydouxi*) in Japan (Hirose, Kinzie, and Hidaka 2001; Kinzie 1993; Hirose, Kinzie, and Hidaka 2000). 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, Berumen, and Baird 2011; Bouwmeester et al. 2021), and Eilat (Shlesinger and Loya 1985), as well as in South Africa (Kruger and Schleyer 1998) and in Japan (Hirose, Kinzie, and Hidaka 2001; Kinzie 1993; Hirose, Kinzie, and Hidaka 2000; Baird et al. 2022). As lunar phase outliers, visually 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), but these were not genetically confirmed.

Multiple recruitment studies in Mo'orea indicate the density of Pocilloporidae recruits peaks between December - April each year (Gleason 1996; Adjeroud, Penin, and Carroll 2007; Edmunds, Leichter, and Adjeroud 2010). Therefore, we focused our examination of *Pocillopora spp.* spawning in the months of October - January. In this study, we conducted *in situ* surveys of *Pocillopora* spp*.* spawning over a total of 58 days in the lagoon of the north shore of Mo'orea French Polynesia (Table S1). 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, October - January in 2023-2024, and October - December in 2024. Corals observed spawning were genetically identified to species (Table S2). Collectively, this allowed for clear documentation of the lunar and diel timing of spawning of *P. grandis, P. meandrina*, *P. verrucosa*, and *P. tuahiniensis*, as well as a possible indication of *P. effusa* timing.

Methods

In order to describe the lunar and diel spawning times to the species level, we completed *in situ* visual and photographic/video 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) covering approximately an area of 400m^2, 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 goal of observing five common lagoon species (*P. effusa*, *P. grandis, P. meandrina*, *P. verrucosa*, and *P. tuahiniensis*) (Burgess, Turner, and Johnston 2024). 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 using plastic bottles. After collecting eggs and sperm from different colonies, the bottles used for collection were poured into larger

reservoirs (~5L bottles) to facilitate genetic mixing, as well as fertilization as soon as possible directly on a boat. Samples were returned to the Gump South Pacific Research Station and biopsies from the tagged colonies were preserved in DNA/RNA Shield stabilization solution (Zymo Research Corporation, Cat # R1100). To confirm successful fertilization occurred, collected gametes were viewed with a compound microscope (LEICA DM500)(e.g., Fig. 1).

Pocillopora species genetic identification

The use of mtORF sequencing and PocHistone PCR plus *Xho*I digestion for Restriction Fragment Length Polymorphism (RFLP) has previously been validated as suitable species-level markers based on multiple genome-wide datasets and analyses (Johnston, Forsman, and Toonen 2018; Johnston, Cunning, and Burgess 2022). Through these methods, the following *Pocillopora* species have been defined as: *P. meandrina* = mtORF haplotype 1 followed by a single *Xho*I digestion RFLP band of the PocHistone amplification product, or mtORF haplotype 8a and haplotype 9; *P. grandis* = mtORF haplotype 1 followed two or three *Xho*I digestion RFLP bands of the PocHistone amplification product; *P. tuahiniensis* = mtORF haplotype 10; *P. verrucosa* = mtORF haplotype 3; and *P. effusa* = mtORF haplotypes 2 and 11.

In order to determine the species of *Pocillopora* spawning, DNA was extracted from each sample using the Quick-DNA Miniprep Plus Kit (Zymo Research Corporation 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 Zymo 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 species tree was generated via Neighbor-Joining estimation (Saitou and Nei 1987) with the Neighbor-Joining 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).

When 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, Forsman, and Toonen 2018) (PocHistoneF: 5′-ATTCAGTCTCACTCACTCACTCAC-3′ and PocHistoneR: 5′-TATCTTCGAACAGACCCACCAAAT-3′), including a previously identified *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 (New England BioLabs, NEB R0146S) in rCutSmart buffer (New England BioLabs, NEB B6004S) according to Johnston et al. (Johnston, Forsman, and Toonen 2018) (with a volume exception as follows for 2023 samples; 5 µL of PCR product were digested with 0.5µL of *Xho*I restriction enzyme, 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 NEB 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* (Johnston, Forsman, and Toonen 2018). Colonies observed spawning in 2024 were previously tagged and extracted with the Chelex methods as described above, amplified with the 2022 methods and sequenced as follows. The PCR product was cleaned by mixing 3µl of 3M sodium acetate and 3x volume of ice cold 100% ethanol with the PCR product and holding it in the -80°C freezer for 30 min. The samples were then spun for 30 minutes at 12,000 rpm, the supernatant discarded, and the DNA pellet rinsed with ice cold 70% ethanol, spun for 5 minutes at 12,000 rpm, and left to dry at room temperature until all ethanol evaporated. Sanger sequencing was completed with forward primers at the URI Genomics and Sequencing center using Applied Biosystems BigDye Terminator v3.1 chemistry. Raw sequence data, alignment fasta files, and gel images are archived here: https://osf.io/5geqd/ (Harnay et al. 2023)

Results

Full Moon Observations

In our observations of full moon spawning, *Pocillopora meandrina* and *P. grandis* were observed releasing eggs and sperm (Table S1-2; Fig. 2). We witnessed gamete release in *P. grandis* on lunar days 2 and 3 after the full moon in the months of November and December in 2024 (Fig. 4). Spawning occurred between 36 and 42 minutes after sunrise (Fig. 5). Observations of *P. meandrina* conducted between 2022 and 2024 revealed spawning on lunar day 1 to 3 after the full moon between October and December (Fig. 4), with the largest events occurring in December. Gamete release occurred later in the morning after *P. grandis*, between 59 and 77 minutes after sunrise (Fig. 5).

New Moon Observations

In our new moon spawning observations, colonies were predominantly identified as *P. verrucosa* and *P. tuahiniensis* (Fig. 3). *P. verrucosa* spawning was observed spawning in November and December 2023 and 2024, on lunar days 0 and +1 (Fig. 4), between 38 and 55 minutes after sunrise (Fig. 5). *Pocillopora tuahiniensis*, spawning was observed in 64 to 77 minutes after sunrise (Fig. 5), also in November and December of 2023 and 2024, but from day +1 to +3 (Fig. 4).

The least abundant species detected by mtORF sequencing during the new moon (Table S2) was a single colony of *P. effusa* identified as Haplotype 11 (Johnston et al.

2022). The *P. effusa* observation occurred in November 2023 sampling window of ~06:30 - 06:50 on the new moon lunar day 3. This species was not included in the figures because of the small sample size (n=1), and therefore we do not have enough observations for this species to demonstrate a clear spawning pattern. See repository for image; https://osf.io/5geqd/).

Larvae contain zooxanthellae and development

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 in the collection bottles and in the water the gametes were rapidly dispersed by the waves and current. Eggs (~90µm) and developing embryos (~120µm) that were observed at ~10:00 via compound microscopy contained zooxanthellae. By 14:00 (~7.5 hours post fertilization, hpf) larvae were actively swimming.

Discussion

Multiple recruitment studies in Mo'orea indicate the density of Pocilloporidae recruits peaks between December - April each year (Gleason 1996; Adjeroud, Penin, and Carroll 2007; Edmunds, Leichter, and Adjeroud 2010). Therefore, we focused our examination of *Pocillopora* spp. spawning between the month of October and January during the years 2022, 2023 and 2024, resulting in the clear description of the timing of spawning for *P. meandrina*, *P. verrucosa, P. tuahiniensis*, *P. grandis* and the start of documentation for *P. effusa*.

Pocillopora meandrina

During our observations of *P. meandrina*, gametes were released early in the morning at ~06:15-06:40, which was ~ 60-85 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 (Hirose, Kinzie, and Hidaka 2001; Kinzie 1993; Hirose, Kinzie, and Hidaka 2000; Baird et al. 2022)), Hawai□i (~120 minutes after sunrise (Schmidt-Roach et al. 2014)), and the Red Sea (~180 minutes after sunrise (Bouwmeester, Berumen, and Baird 2011; Bouwmeester et al. 2021)). We documented split-spawning (spawning in multiple consecutive months) in *P. meandrina*, with one colony spawning November 10th (06:32, full moon lunar day 3) and reef-wide spawning December 9th (06:16-06:32; full moon lunar day 2) and December 10th (06:21-06:35; full moon lunar day 3), which could be seen as surface slicks (Fig. 1A). Split spawning across multiple months 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 2022, most of the *P. meandrina* colonies observed had synchronized spawning, based on the observation that on December 9 (Full+2), from 6:16 to 6:32, 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 10th 2022 (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) when 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, Penin, and Carroll 2007; Edmunds, Leichter, and Adjeroud 2010), and from the hypothesized timing of *Pocillopora* spp. spawning from emerging histological data (Putnam Unpublished Data). Given that pocilloporid recruitment continues through March (Adjeroud, Penin, and Carroll 2007; Edmunds, Leichter, and Adjeroud 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 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, Kerry, and Simpson 2018; Speare et al. 2022) and also can impact reproductive timing (T. Shlesinger and Loya 2019), amount/quality (Johnston et al. 2020; A. H. Baird and Marshall 2002), and recruitment (Peter J. Edmunds 2017; Hughes et al. 2019).

Pocillopora grandis

Given the complexity of identification, very little observational literature on spawning in *P. grandis* (Previously named *P. eydouxi*) has been recorded *(Smith et al. 2008; Schmidt-Roach et al. 2012; Hirose, Kinzie, and Hidaka 2000)*. The first observations with visual identification in Okinawa Japan made by (Hirose, Kinzie, and Hidaka 2000),

indicated spawning a few days after the full moon, which is in line with our findings. A second study on the Great Barrier Reef in Australia identified *P. grandis* both visually and by mtORF haplotype (Schmidt-Roach et al. 2012), but not to the species level with PocHistone (Johnston, Forsman, and Toonen 2018). The Australia study reported spawning on full moon and full moon +1, which matches our observations in Mo'orea (Fig. 4). However, in Australia both *P. meandrina* and *P. grandis* were reported with the same diel timing (06:25), whereas we documented distinctly different diel timing, with *P. grandis* spawning first and *P. meandrina* 25 minutes later (Fig. 5). This paucity of data across the broad geographic distribution of *P. grandis* indicates further study is necessary in multiple areas of the world to enable capacity to complete location specific differences, and their proximate environmental causes, in lunar and diel timing.

Pocillopora verrucosa

P. verrucosa in Mo'orea only spawned in association with the new moon on lunar day 0 and 1 . 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. 2021; Bouwmeester, Berumen, and Baird 2011; Bouwmeester et al. 2015). Conversely, morphologically identified *P. verrucosa* spawning has been reported on full moon lunar day 0 and 1 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, Berumen, and Baird 2011; Bouwmeester et al. 2021; Bouwmeester et al. 2015), suggest species differences are present.

When considering diel timing of release, in Mo'orea (17.53S latitude), *P. verrucosa* gametes were released ~5:45-6:20 local time, ~38 to 55 min after sunrise local time, closer to sunrise than morphologically identified *P. verrucosa* in several other regions of the world (Table 1). These findings suggest two hypotheses. First, that there are latitudinal differences in diel/lunar spawning times and second that there are different cryptic *Pocillopora spp.* that can't be compared in the absence of genetic identification in other studies. While spawning of morphologically identified *P. verrucosa* 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), morphologically identified *P. verrucosa* closer to the equator at the island of Ishigaki, Japan (24.42N latitude) 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 (19.05N latitude) and Al Jadir Reef in Saudi Arabia (19.79 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)(JBouwmeester, Berumen, and Baird 2011) and Al Fahal (22.22N latitude) and Dreams Beach Reef (21.76 latitude) (Bouwmeester et al. 2015). Lastly, morphologically identified *P. verrucosa* in Lyudao Taiwan (22.66N latitude), the reports of ~5 h after sunrise (09:30 to 10:30) (Lin and Nozawa 2017; Mulla et al. 2021). Peak spawning time occurring later in the season further from the equator has been documented in multiple corals (Howells et al. 2014), but the lunar data mismatch of our genetically identified *P. verrucosa* as new moon and two other morphologically identified *P. verrucosa* as full moon spawners (Schmidt-Roach et al. 2012; Lin and Nozawa 2017), suggests species identification could explain these different patterns instead.

Previously morphologically identified *P. verrucosa* in the Red Sea is actually *P. favosa* (Oury et al. 2025). The identification of *P. favosa* could explain the several hour difference in time of gamete release (<2h after sunrise in Mo'oera, versus 3 - 4 hours after sunrise in the Red Sea) and indicates that no global spawning conclusions should be made for *P. verrucosa* due to the genetic differences within the morphological group. Further, not every coral observed spawning in the GBR report (Schmidt-Roach et al. 2012) was identified genetically, and none of the corals in the Taiwan observations (Lin and Nozawa 2017; Mulla et al. 2021) were identified genetically. Therefore it is highly likely that contrasting results by reef location are due to species identity. Therefore we propose a broad geographic distribution of *P. verrucosa* spawning associated with the new moon based on genetic species identification. Despite the greater amount of studies of spawning in *P. verrucosa*, comparisons of latitudinal drivers can not yet be made in the absence of genetic identification. In the future latitudinal associated drivers in spawn timing (e.g., (Howells et al. 2014)) should also be tested in spawning *Pocillopora spp.* It is essential that studies identify *Pocillopora* based on now-established genetic markers (Johnston and Burgess 2023) and/or genomic data (Johnston, Cunning, and Burgess 2022).

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 (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. 2022). *P. verrucosa* has a much broader geographic distribution across the Indo-Pacific (Gelin 2017 and Oury 2023 refs) compared to *P. tuahiniensis*; the latter has been documented within a subset of the range of the former (French Polynesia (Oury, Gélin, and Magalon 2021; Edmunds et al. 2016; Gélin et al. 2017; Forsman et al. 2013)), 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 and distributions within reefs, 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) by ~28 minutes. Our results are consistent with a linkage between genetic divergence and the temporal divergence in diel spawning time we observed here. Further, *Pocillopora* spp*.* embryo development is some of the most rapid of corals described to date, where fertilization can occur within 15 minutes (Mulla et al. 2021), cleavage within 30 - 40 minutes, and full development to the swimming larval stage by 8 hours post fertilization (Hirose, Kinzie, and Hidaka 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 between species. Genome-wide analyses of these species show no evidence of hybridization (Johnston, Cunning, and Burgess 2022), further supporting that the timing offset of spawning between *P. verrucosa* and *P. tuahiniensis* is acting as a temporal barrier for speciation.

Pocillopora effusa

P. effusa is less abundant in the lagoon than on the fore reef (Burgess, Turner, and Johnston 2024). 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. effusa* in the lagoon are likely to be rare. Indeed, only a single colony of *P. effusa* was observed spawning on lunar day 3 after the November 2023 new moon (15 November) at ~06:31-06:50. Because this was a single observation, it could indicate that spawning is occurring 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 of colonies at our observation site, or accidental assignment of adjacent colony spawning to *P. 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. effusa*.

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 within collection bottles, which has been reported by (Suzuki

2012; Schmidt-Roach et al. 2012; Mulla et al. 2021), as we observed they did not rise quickly to the surface like the larger, lipid rich egg bundles 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 ~10:00 on the day of release 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, Kinzie, and Hidaka 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, Kinzie, and Hidaka 2000). The rapid development of Pocilloporidae larvae with vertically transmitted Symbiodiniaceae that can provide nutritional supplementation (Kopp et al. 2016; Huffmyer et al. 2025) could affect recruitment success (Adjeroud, Penin, and Carroll 2007; Gleason 1996; Edmunds, Leichter, and Adjeroud 2010). Rapid development of symbiotic larvae could influence the capacity of *Pocillopora* spp*.* to promote rapid recovery following disturbances on the reefs of Mo'orea, provided there is enough adult colonies (Speare et al. 2022) and that gametogenesis is not severely impaired by heatwaves and mass bleaching events (Johnston et al. 2020).

Further work on the clarification of the diel timing of spawning, development, and settlement of spawned Pocilloporid symbiotic larvae will be essential. Both spawning (Keith et al. 2016; Baird, Guest, and Willis 2009) and development (Woolsey, Byrne, and Baird 2013; Negri, Marshall, and Heyward 2007; Randall and Szmant 2009) 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, Sammarco, and Snell 2002) and symbiotic larvae accumulate more DNA damage from UV than aposymbiotic larvae (Baird et al. 2021; Nesa et al. 2012). 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.

Pocillopora spp. can dominate coral reefs (Pérez-Rosales et al. 2021) and facilitate rapid reef recovery (Holbrook et al. 2018). Cryptic *Pocillopora* species, however, exhibit differences in their thermal sensitivity (Burgess et al. 2021). Here, we have documented differences in their timing of spawning in terms of month, lunar phase, and time of day. Future work can now build on these findings to determine key aspects such as thermal tolerance of larval development and early life stages, pelagic larval duration, and

settlement preferences, which will improve ecological forecasting capabilities for tropical reefs throughout the Indo-Pacific.

Acknowledgements

As guests, we recognize and give thanks for the land and water resources of French Polynesia, in particular Mo'orea, and to the traditional owners of the land, both past and present for the resources studied in this work. Māuruuru roa. With respect to the spelling of Tahitian words, we endeavored to follow the Te Fare Vāna'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). The samples collected herein are resources of the people and government of French Polynesia and have been supplied under the Direction de l'environnement DIREN Permit Number 10626 (06 November 2023) and exported under Convention on International Trade in Endangered Species CITES export permit FR24987000029-E.

Although we are the first to report scientific documentation of *Pocillopora meandrina, P. verrucosa*, *P. tuahiniensis* and *P. grandis* 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.

En tant qu'invités, nous reconnaissons et exprimons notre gratitude envers les ressources terrestres et aquatiques de la Polynésie française, en particulier de Mo'orea, ainsi qu'envers les propriétaires traditionnels de ces terres, passés et presents pour les ressources étudiées dans ce travail. Māuruuru roa. En ce qui concerne l'orthographe des mots tahitiens, nous avons fait notre possible pour suivre le système de transcription Te Fare Vāna'a, auquel adhère une grande partie de la communauté tahitienne, tout en reconnaissant que d'autres membres de la communauté suivent le système de transcription Raapoto où le nom de l'île de Moorea, par exemple, est orthographié sans le 'eta (c'est-à-dire Moorea). Les échantillons collectés ici sont des ressources du peuple et du gouvernement de la Polynésie française et ont été fournis sous le permis de la Direction de l'environnement DIREN numéro 10626 (06 novembre 2023) et exportés sous le permis d'exportation de la Convention sur le commerce international des espèces de faune et de flore sauvages menacées d'extinction CITES FR24987000029-E.

Bien que nous soyons les premiers à rapporter une documentation scientifique sur la ponte de *Pocillopora meandrina*, *P. verrucosa*, *P. tuahiniensis* et *P. grandis* en Polynésie française, nous tenons également à reconnaître qu'il est probable que le calendrier de reproduction de plusieurs taxons de coraux soit connu des Polynésiens depuis des décennies, voire des siècles. La combinaison des savoirs écologiques traditionnels, de la science participative et du suivi et de la documentation scientifiques est en passe d'élargir considérablement notre compréhension de la reproduction en Polynésie française, ce qui sera essentiel pour la restauration et le maintien des récifs face au changement climatique.

We are thankful for observer support from Ariana Huffmyer, Danielle Becker, Chloé Gilligan, Erica Atkins, Danielle Barnes, Holly Moeller, Arnaud Fabregues, Guillaume Iwankow, Lucy Gorman, Ross Cunning, Shayle Matsuda, Tali Mass, Keisha Bahr, Cody Clements, Kelly Speare, and Raine Detmer and for the staff of the UC Richard B. Gump South Pacific Research Station for facilitating our research. We appreciate discussions with and feedback from Peter Edmunds and Ariana Huffmyer. This research was funded by the U.S. National Science Foundation Grants EF-1921465 and OCE-2348674 to HMP and OCE-1829867 to SCB and supported by resources from NSF-OCE 2224354 to the Mo'orea Coral Reef LTER, as well as a generous gift from the Gordon and Betty Moore Foundation.

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 PEH, HMP, AT, SCB; Writing PEH, HMP, AT, SCB

Statements and Declarations

Competing Interests: The authors have no competing interests.

Figures:

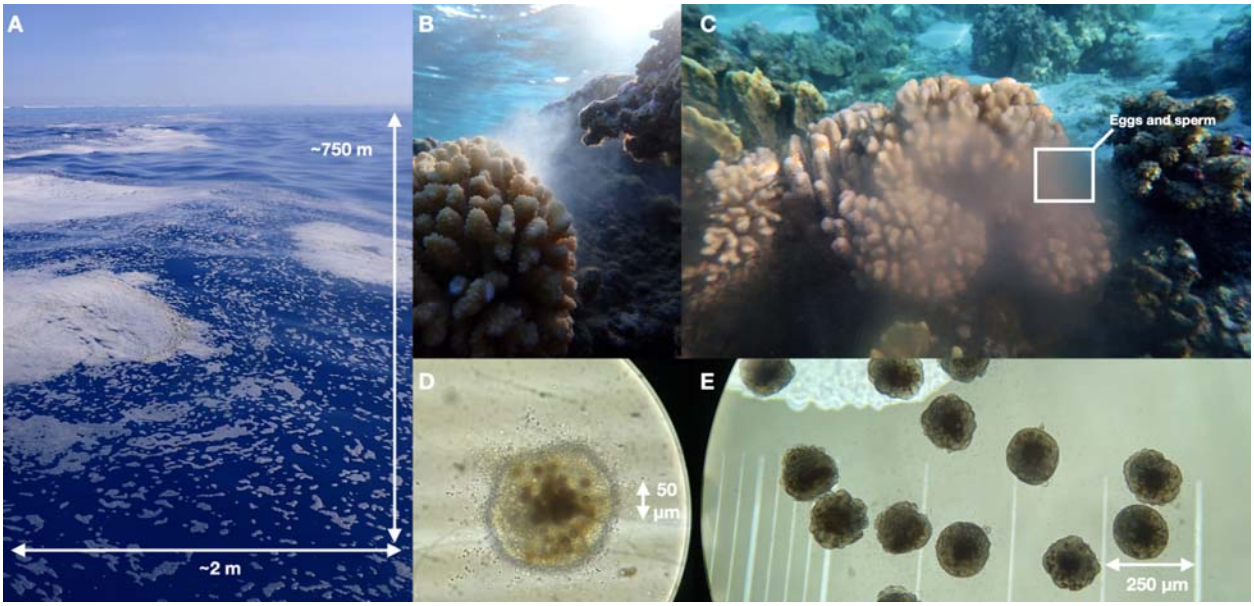

Figure 1. A) Slick of sperm and egg on the surface of the water in the lagoon was observed after *Pocillopora meandrina* spawning, with the image showing ~ 750m distance between the fore reef and the observer. **B)** and **C)** Spawning of *P. meandrina* colonies in the lagoon. **D)** Brightfield microscopy image of eggs (brown circle) and sperm (gray dots) surrounding the egg. **E)** Embryos at a multi-cell stage were visible at ~4 hours post spawning. More images and videos are archived here: https://osf.io/5geqd/ (Harnay et al. 2023)

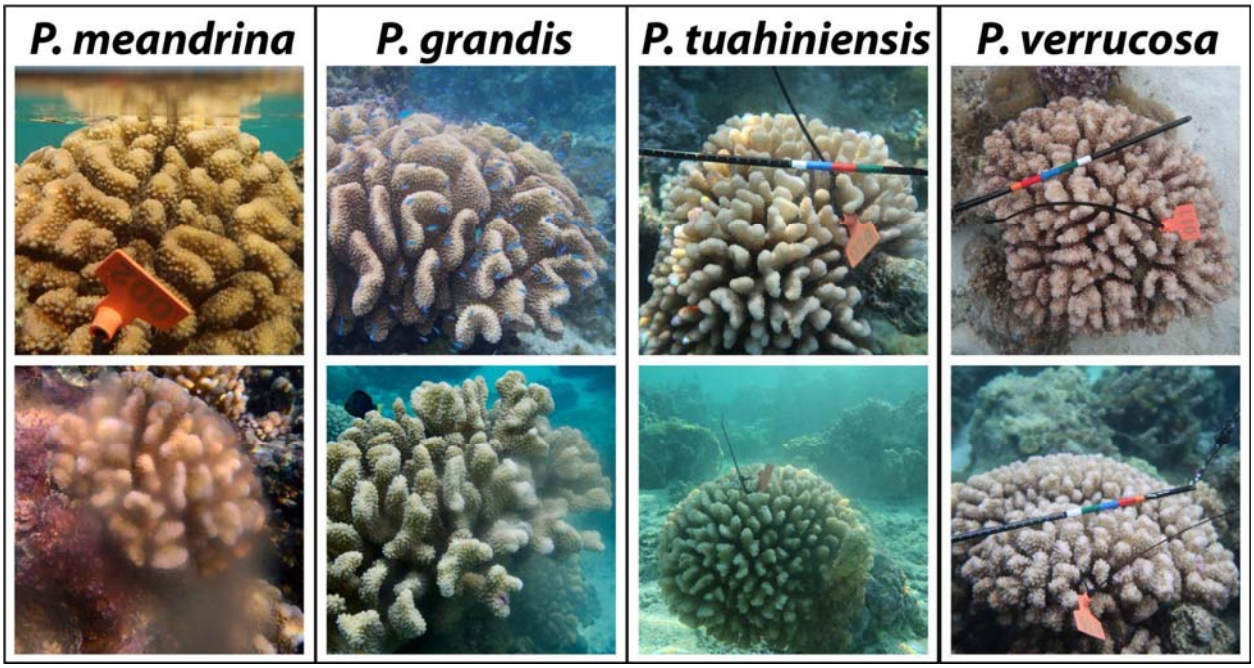

Figure 2. Examples of *Pocillopora* colonies that were tagged and observed spawning eggs and sperm in the lagoon.

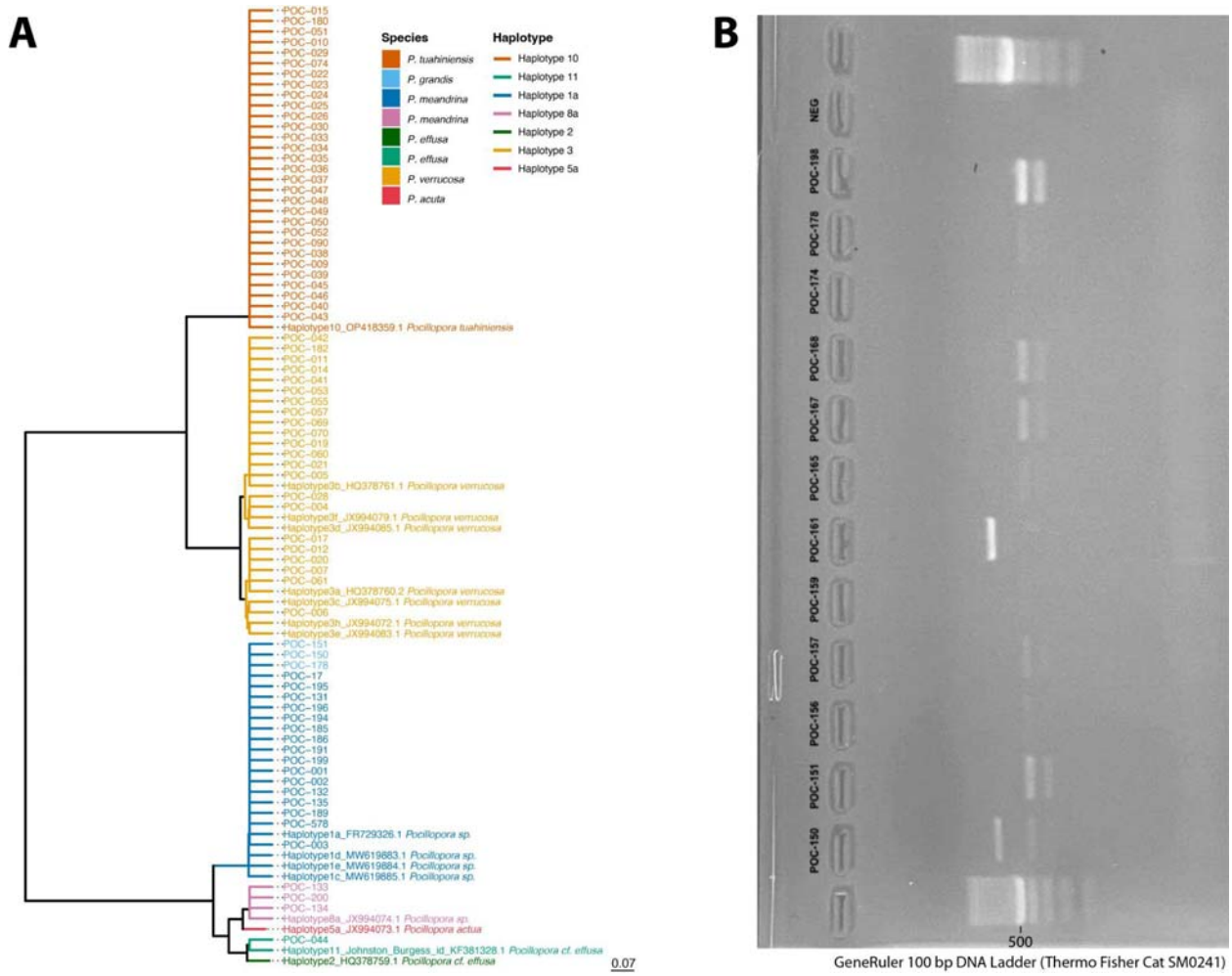

Figure 3. Haplotype identification via mtORF for spawning colonies in 2022, 2023, and 2024 generated from hierarchical clustering of Jukes-Cantor genetic distance (Jukes and Cantor 1969) from 75 collected samples, 16 reference samples, and no outgroup. The gene tree is based on mtORF to visualize species delimitation and does not reflect exact phylogeny (see (Johnston, Cunning, and Burgess 2022)). 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).

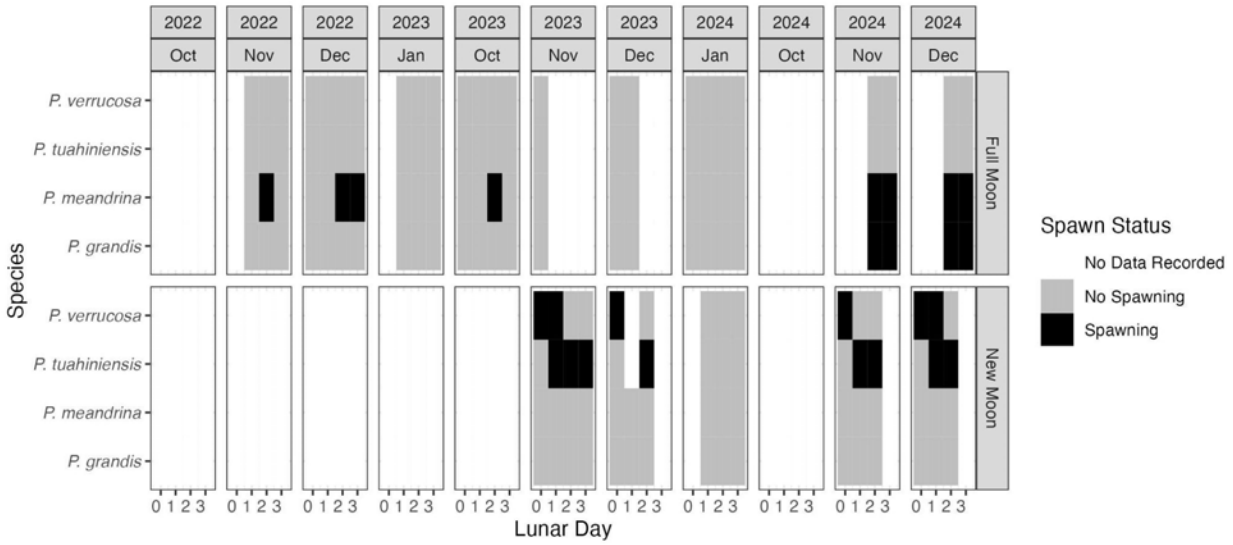

Figure 4. Lunar timing of spawning on day 0 (full or new moon) and the following 3 days during the months surveyed from October 2022 to December 2024.

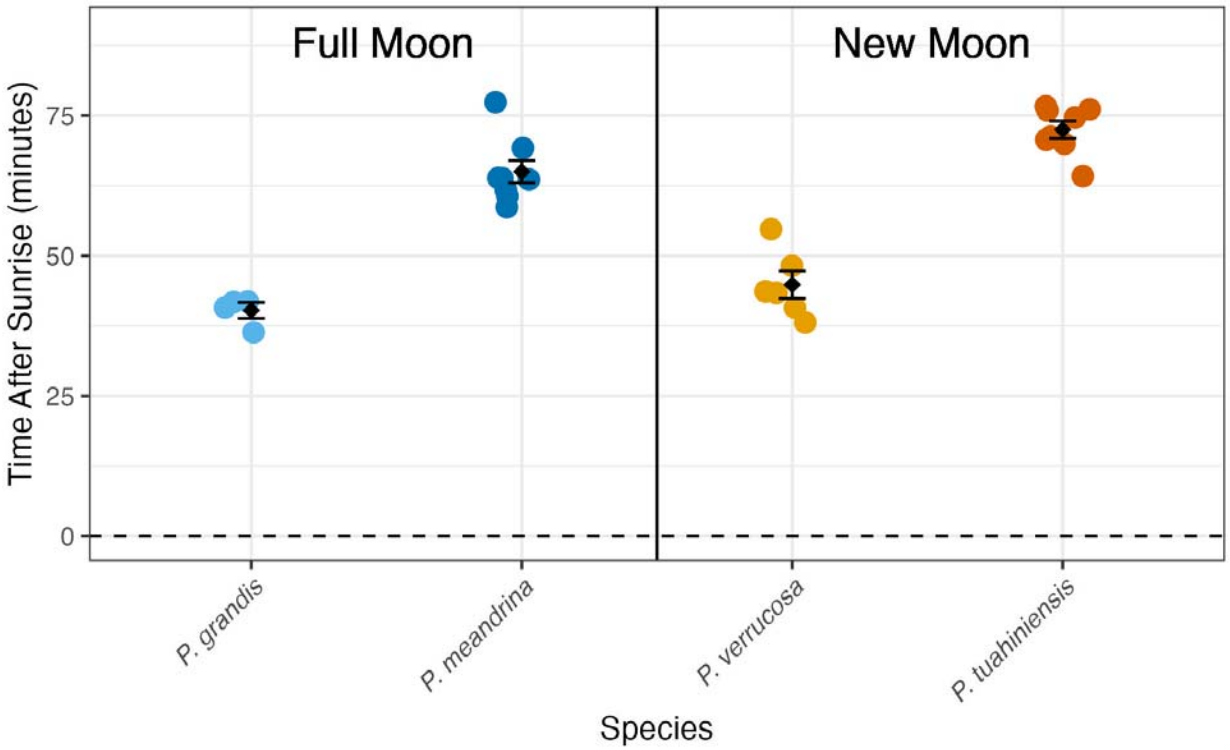

Figure 5. Diel timing of spawning (minutes after sunrise) for *P. grandis* and *P. meandrina* around the full moon and for *P. verrucosa* and *P. tuahiniensis* around the new moon. Colored circles indicate an individual coral, while black diamonds indicate the mean value ± standard error of the mean.

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 (*previously *P. eydouxi)*	Morphological	Spawning Observed	May - August 1992	Full	Full Moon +1 to 5	08:00 – 10:50
(Hirose, Kinzie, and Hidaka 2000)	Okinawa, Japan	*P. grandis (*previously *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 (*previously *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, Kinzie, and Hidaka 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, Berumen, and Baird 2011)	Thuwal, Saudi Arabia	*P. verrucosa (now P. favosa)*	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 (now P. favosa)*	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. grandis*	Genetic	Spawning Observed	November, December 2024	Full	Full +2 +3	5:55-6:12
This study	Mo'orea, French Polynesia	*P. verrucosa*	Genetic	Spawning Observed	November, December 2023	New	New +1 +2	5:56-6:25
This study	Mo'orea, French Polynesia	*P. tuahiniensis*	Genetic	Spawning Observed	November, December 2023	New	New +1 +2 +3	6:19-6:58
This study	Mo'orea, French Polynesia	*P. effusa*	Genetic	Spawning Observed	November 2023	New	New +3	06:30-06:50

Table 2. 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*	*(Flot, Couloux, and Tillier 2010)*

		or *P. grandis*	
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 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 effusa*	Forsman et al 2013 (KF381328) (Johnston et al. 2022) full sequence

Supplementary material:

Table S1. *Pocillopora* spp. spawning observation timeline from September 2022 to December 2024. 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
NDR: No Data Recorded indicates no observers were present in the field.
- - - indicates no additional notes

** Indicates species were identified from previously tagged and sequenced colonies

Table S2. *Pocillopora* spawning sample numbers and genetic species identification collected from corals observed spawning in 2022, 2023, and 2024.

References Cited

Adjeroud, Mehdi, Lucie Penin, and Andrew Carroll. 2007. "Spatio-Temporal Heterogeneity in Coral Recruitment around Moorea, French Polynesia: Implications for Population Maintenance." *Journal of Experimental Marine Biology and Ecology* 341 (2): 204–18.

Apprill, Amy, Heather Q. Marlow, Mark Q. Martindale, and Michael S. Rappé. 2009. "The Onset of Microbial Associations in the Coral *Pocillopora meandrina*." *The ISME Journal* 3 (6): 685–99.

Armstrong, Eric J., Julie Lê-Hoang, Quentin Carradec, Jean-Marc Aury, Benjamin Noel, Benjamin C. C. Hume, Christian R. Voolstra, et al. 2023. "Host Transcriptomic Plasticity and Photosymbiotic Fidelity Underpin *Pocillopora* Acclimatization across Thermal Regimes in the Pacific Ocean." *Nature Communications* 14 (1): 3056.

Baird, A. H., and P. A. Marshall. 2002. "Mortality, Growth and Reproduction in Scleractinian Corals Following Bleaching on the Great Barrier Reef." *Marine Ecology Progress Series* 237:133–41.

Baird, Andrew H., Alasdair J. Edwards, James R. Guest, Saki Harii, Masayuki Hatta, Liam Lachs, Hanaka Mera, et al. 2022. "A Coral Spawning Calendar for Sesoko Station, Okinawa, Japan." *Galaxea, Journal of Coral Reef Studies* 24 (1): 41–49.

Baird, Andrew H., James R. Guest, and Bette L. Willis. 2009. "Systematic and Biogeographical Patterns in the Reproductive Biology of Scleractinian Corals." *Annual Review of Ecology, Evolution, and Systematics* 40 (Volume 40, 2009): 551–71.

Baird, Andrew H., Irina M. Yakovleva, Saki Harii, Frederic Sinniger, and Michio Hidaka. 2021. "Environmental Constraints on the Mode of Symbiont Transmission in Corals." *Journal of Experimental Marine Biology and Ecology* 538 (May):151499.

Bassim, K., P. Sammarco, and T. Snell. 2002. "Effects of Temperature on Success of (self and Non-Self) Fertilization and Embryogenesis in *Diploria strigosa* (Cnidaria, Scleractinia)." *Marine Biology* 140 (3): 479–88.

Bouwmeester, J., A. H. Baird, C. J. Chen, J. R. Guest, K. C. Vicentuan, and M. L. Berumen. 2015. "Multi-Species Spawning Synchrony within Scleractinian Coral Assemblages in the Red Sea." *Coral Reefs* 34 (1): 65–77.

Bouwmeester, Jessica, Michael Lee Berumen, and Andrew Hamilton Baird. 2011. "Daytime Broadcast Spawning of *Pocillopora verrucosa* on Coral Reefs of the Central Red Sea." *Galaxea, Journal of Coral Reef Studies* 13 (1): 23–24.

Bouwmeester, Jessica, Darren J. Coker, Tane H. Sinclair-Taylor, and Michael L. Berumen. 2021. "Broadcast Spawning of *Pocillopora verrucosa* across the Eastern and Western Coast of the Central Red Sea." *Ecosphere* 12 (1). https://doi.org/10.1002/ecs2.3340.

Burgess, Scott C., Erika C. Johnston, Alex S. J. Wyatt, James J. Leichter, and Peter J. Edmunds. 2021. "Response Diversity in Corals: Hidden Differences in Bleaching

Mortality among Cryptic *Pocillopora* Species." *Ecology* 102 (6): e03324.

Burgess, Scott C., Alyssa M. Turner, and Erika C. Johnston. 2024. "Niche Breadth and Divergence in Sympatric Cryptic Coral Species (*Pocillopora Spp.*) across Habitats within Reefs and among Algal Symbionts." *Evolutionary Applications* 17 (8): e13762.

Combosch, David J., and Steven V. Vollmer. 2013. "Mixed Asexual and Sexual Reproduction in the Indo-Pacific Reef Coral *Pocillopora damicornis*." *Ecology and Evolution* 3 (10): 3379–87.

Costanza, Robert, Rudolf de Groot, Paul Sutton, Sander van der Ploeg, Sharolyn J. Anderson, Ida Kubiszewski, Stephen Farber, and R. Kerry Turner. 2014. "Changes in the Global Value of Ecosystem Services." *Global Environmental Change: Human and Policy Dimensions* 26 (May):152–58.

Courtney, T. A., E. H. De Carlo, H. N. Page, K. D. Bahr, A. Barro, N. Howins, R. Tabata, G. Terlouw, K. S. Rodgers, and A. J. Andersson. 2018. "Recovery of Reef□scale Calcification Following a Bleaching Event in Kāne'ohe Bay, Hawai'i." *Limnology and Oceanography Letters* 3 (1): 1–9.

Cuddington, Kim. 2011. "Legacy Effects: The Persistent Impact of Ecological Interactions." *Biological Theory* 6 (3): 203–10.

Doropoulos, Christopher, Jesper Elzinga, Remment ter Hofstede, Mark van Koningsveld, and Russell C. Babcock. 2019. "Optimizing Industrial□scale Coral Reef Restoration: Comparing Harvesting Wild Coral Spawn Slicks and Transplanting Gravid Adult Colonies: Industrial-Scale Coral Reef Restoration." *Restoration Ecology* 27 (4): 758–67.

Edmunds, Peter J. 2017. "Unusually High Coral Recruitment during the 2016 El Niño in Mo'orea, French Polynesia." *PloS One* 12 (10): e0185167.

———. 2018. "Implications of High Rates of Sexual Recruitment in Driving Rapid Reef Recovery in Mo'orea, French Polynesia." *Scientific Reports* 8 (1): 1–11.

———. 2022. "MCR LTER: Coral Reef: Long-Term Population and Community Dynamics: Corals, Ongoing since 2005." EDI. https://doi.org/10.6073/pasta/913b1532594fcaf02de7671ed940b4c5.

Edmunds, Peter J., James J. Leichter, Erika C. Johnston, Eric J. Tong, and Robert J. Toonen. 2016. "Ecological and Genetic Variation in Reef-Building Corals on Four Society Islands." *Limnology and Oceanography* 61 (2): 543–57.

Edmunds, P. J., J. J. Leichter, and M. Adjeroud. 2010. "Landscape-Scale Variation in Coral Recruitment in Moorea, French Polynesia." *Marine Ecology Progress Series* 414 (September):75–89.

Fadlallah, Y. H. 1985. "Reproduction in the Coral *Pocillopora verrucosa* on the Reefs Adjacent to the Industrial City of Yanbu (Red Sea, Saudi Arabia)." In *Proc 5th Int Coral Reef Cong*, 4:313–18.

Fiene-Severns, P. 1998. "A Note on Synchronous Spawning in the Reef Coral *Pocillopora meandrina* at Molokini Islet, Hawai'i." 42. Edited by Cox Ef Krupp Da Pl. University Hawai□i . https://www.researchgate.net/profile/Paul-Jokiel/publication/242253947_Reproduction_in_Reef_Corals_Results_of_the_1997_Edwin_W_Pauley_Summer_Program_in_Marine_Biology/links/53dc33b70cf2cfac99290077/Reproduction-in-Reef-Corals-Results-of-the-1997-Edwin-W-Pauley-Summer-Program-in-Marine-Biology.pdf.

Flot, Jean-François, Arnaud Couloux, and Simon Tillier. 2010. “Haplowebs as a Graphical Tool for Delimiting Species: A Revival of Doyle’s ‘Field for Recombination’ Approach and Its Application to the Coral Genus *Pocillopora* in Clipperton.” *BMC Evolutionary Biology* 10 (1): 372.

Flot, Jean-François, Hélène Magalon, Corinne Cruaud, Arnaud Couloux, and Simon Tillier. 2008. “Patterns of Genetic Structure among Hawaiian Corals of the Genus *Pocillopora* Yield Clusters of Individuals That Are Compatible with Morphology.” *Comptes Rendus Biologies* 331 (3): 239–47.

Forsman, Zac H., Erika C. Johnston, Andrew J. Brooks, Thomas C. Adam, and Robert J. Toonen. 2013. “Genetic Evidence for Regional Isolation of *Pocillopora* Corals from Moorea.” *Oceanography* 26 (3): 153–55.

Gélin, P., B. Postaire, C. Fauvelot, and H. Magalon. 2017. “Reevaluating Species Number, Distribution and Endemism of the Coral Genus *Pocillopora* Lamarck, 1816 Using Species Delimitation Methods and Microsatellites.” *Molecular Phylogenetics and Evolution* 109 (April):430–46.

Gleason, Mary G. 1996. “Coral Recruitment in Moorea, French Polynesia:the Importance of Patch Type and Temporal Variation.” *Journal of Experimental Marine Biology and Ecology* 207 (1): 79–101.

Glynn, P. W., N. J. Gassman, C. M. Eakin, J. Cortes, D. B. Smith, and H. M. Guzman. 1991. “Reef Coral Reproduction in the Eastern Pacific: Costa Rica, Panama, and Galapagos Islands (Ecuador).” *Marine Biology* 109 (3): 355–68.

Grigg, Richard W., and James E. Maragos. 1974. “Recolonization of Hermatypic Corals on Submerged Lava Flows in Hawaii.” *Ecology* 55 (2): 387–95.

Harnay, Pierrick, Scott Burgess, Alyssa Turner, and Hollie Putnam. 2023. “*Pocillopora* Spawning Moorea.” OSF. https://doi.org/10.17605/OSF.IO/5GEQD.

Hirose, M., R. A. Kinzie 3rd, and M. Hidaka. 2000. “Early Development of Zooxanthella-Containing Eggs of the Corals *Pocillopora verrucosa* and *P. eydouxi* with Special Reference to the Distribution of Zooxanthellae.” *The Biological Bulletin* 199 (1): 68–75.

Hirose, M., R. Kinzie, and M. Hidaka. 2001. “Timing and Process of Entry of Zooxanthellae into Oocytes of Hermatypic Corals.” *Coral Reefs* 20 (3): 273–80.

Holbrook, Sally J., Thomas C. Adam, Peter J. Edmunds, Russell J. Schmitt, Robert C. Carpenter, Andrew J. Brooks, Hunter S. Lenihan, and Cheryl J. Briggs. 2018. “Recruitment Drives Spatial Variation in Recovery Rates of Resilient Coral Reefs.” *Scientific Reports* 8 (1): 7338.

Howells, E. J., D. Abrego, G. O. Vaughan, and J. A. Burt. 2014. “Coral Spawning in the Gulf of Oman and Relationship to Latitudinal Variation in Spawning Season in the Northwest Indian Ocean.” *Scientific Reports* 4 (1): 7484.

Huffmyer, Ariana S., Kevin H. Wong, Danielle M. Becker, Emma Strand, Tali Mass, and Hollie M. Putnam. 2025. “Shifts and Critical Periods in Coral Metabolism Reveal Energetic Vulnerability during Development.” *Current Biology: CB* 35 (12): 2858–71.e6.

Hughes, Terry P., James T. Kerry, Andrew H. Baird, Sean R. Connolly, Tory J. Chase, Andreas Dietzel, Tessa Hill, et al. 2019. “Global Warming Impairs Stock–Recruitment Dynamics of Corals.” *Nature* 568 (7752): 387–90.

Hughes, Terry P., J. T. Kerry, and T. Simpson. 2018. “Large-Scale Bleaching of Corals

on the Great Barrier Reef." *Ecology* 99 (2): 501.
Johnston, Erika C., and Scott C. Burgess. 2023. "*Pocillopora tuahiniensis*: A New Species of Scleractinian Coral (Scleractinia, Pocilloporidae) from French Polynesia." *Zootaxa* 5369 (1): 117–24.
Johnston, Erika C., Chelsie W. W. Counsell, Tayler L. Sale, Scott C. Burgess, and Robert J. Toonen. 2020. "The Legacy of Stress: Coral Bleaching Impacts Reproduction Years Later." *Functional Ecology* 34 (11): 2315–25.
Johnston, Erika C., Ross Cunning, and Scott C. Burgess. 2022. "Cophylogeny and Specificity between Cryptic Coral Species (*Pocillopora Spp.*) at Mo'orea and Their Symbionts (Symbiodiniaceae)." *Molecular Ecology* 31 (20): 5368–85.
Johnston, Erika C., Zac H. Forsman, and Robert J. Toonen. 2018. "A Simple Molecular Technique for Distinguishing Species Reveals Frequent Misidentification of Hawaiian Corals in the Genus *Pocillopora*." *PeerJ* 6 (February):e4355.
Johnston, Erika C., Alex S. J. Wyatt, James J. Leichter, and Scott C. Burgess. 2022. "Niche Differences in Co-Occurring Cryptic Coral Species (*Pocillopora Spp.*)." *Coral Reefs* 41 (3): 767–78.
Jukes, T. H., and C. R. Cantor. 1969. "Evolution of Protein Molecules." In *Mammalian Protein Metabolism*, edited by H. N. Munro. Vol. 3. Elsevier.
Kayal, Mohsen, Julie Vercelloni, Thierry Lison de Loma, Pauline Bosserelle, Yannick Chancerelle, Sylvie Geoffroy, Céline Stievenart, et al. 2012. "Predator Crown-of-Thorns Starfish (Acanthaster Planci) Outbreak, Mass Mortality of Corals, and Cascading Effects on Reef Fish and Benthic Communities." *PloS One* 7 (10): e47363.
Keith, Sally A., Jeffrey A. Maynard, Alasdair J. Edwards, James R. Guest, Andrew G. Bauman, Ruben van Hooidonk, Scott F. Heron, et al. 2016. "Coral Mass Spawning Predicted by Rapid Seasonal Rise in Ocean Temperature." *Proceedings. Biological Sciences / The Royal Society* 283 (1830). https://doi.org/10.1098/rspb.2016.0011.
Kinzie, R. A. 1993. "Spawning in the Reef Corals *Pocillopora verrucosa* and *P. eydouxi* at Sesoko Island, Okinawa." *Galaxea* 11:93–105.
Knowlton, Nancy. 2015. "Thresholds and Multiple Stable States in Coral Reef Community Dynamics1." *Integrative and Comparative Biology* 32 (6): 674–82.
Kolinski, Steven P., and Evelyn F. Cox. 2003. "An Update on Modes and Timing of Gamete and Planula Release in Hawaiian Scleractinian Corals with Implications for Conservation and Management." *Pacific Science* 57 (1): 17–27.
Kopecky, Kai L., Adrian C. Stier, Russell J. Schmitt, Sally J. Holbrook, and Holly V. Moeller. 2023. "Material Legacies Can Degrade Resilience: Structure-Retaining Disturbances Promote Regime Shifts on Coral Reefs." *Ecology* 104 (4): e4006.
Kopp, Christophe, Isabelle Domart-Coulon, Dominique Barthelemy, and Anders Meibom. 2016. "Nutritional Input from Dinoflagellate Symbionts in Reef-Building Corals Is Minimal during Planula Larval Life Stage." *Science Advances* 2 (3): e1500681.
Kruger, A., and M. H. Schleyer. 1998. "Sexual Reproduction in the Coral *Pocillopora verrucosa* (Cnidaria: Scleractinia) in KwaZulu-Natal, South Africa." *Marine Biology* 132 (4): 703–10.
Lesser, Michael P. 2011. "Coral Bleaching: Causes and Mechanisms." In *Coral Reefs: An Ecosystem in Transition*, edited by Zvy Dubinsky and Noga Stambler, 405–19.

Dordrecht: Springer Netherlands.
Lin, Che-Hung, and Yoko Nozawa. 2017. “Variability of Spawning Time (lunar Day) in *Acropora* versus Merulinid Corals: A 7-Yr Record of *in situ* Coral Spawning in Taiwan.” *Coral Reefs* 36 (4): 1269–78.
Mulla, Aziz J., Che-Hung Lin, Shunichi Takahashi, and Yoko Nozawa. 2021. “Photo-Movement of Coral Larvae Influences Vertical Positioning in the Ocean.” *Coral Reefs* 40 (4): 1297–1306.
Murtagh, Fionn, and Pierre Legendre. 2014. “Ward’s Hierarchical Agglomerative Clustering Method: Which Algorithms Implement Ward’s Criterion?” *Journal of Classification* 31 (3): 274–95.
Negri, A. P., P. A. Marshall, and A. J. Heyward. 2007. “Differing Effects of Thermal Stress on Coral Fertilization and Early Embryogenesis in Four Indo Pacific Species.” *Coral Reefs* 26 (4): 759–63.
Nesa, Badrun, Andrew H. Baird, Saki Harii, Irina Yakovleva, and Michio Hidaka. 2012. “Algal Symbionts Increase DNA Damage in Coral Planulae Exposed to Sunlight.” *Zoological Studies* 51 (1): 6.
Oliver, Eric C. J., Jessica A. Benthuysen, Sofia Darmaraki, Markus G. Donat, Alistair J. Hobday, Neil J. Holbrook, Robert W. Schlegel, and Alex Sen Gupta. 2021. “Marine Heatwaves.” *Annual Review of Marine Science* 13 (January):313–42.
Oppen, Madeleine J. H. van, James K. Oliver, Hollie M. Putnam, and Ruth D. Gates. 2015. “Building Coral Reef Resilience through Assisted Evolution.” *Proceedings of the National Academy of Sciences of the United States of America* 112 (8): 2307–13.
Oury, Nicolas, Michael L. Berumen, Gustav Paulay, and Francesca Benzoni. 2025. “One Species to Rule Them All: Genomics Sheds Light on the *Pocillopora* Species Diversity and Distinctiveness around the Arabian Peninsula.” *Coral Reefs* 44 (3): 983–98.
Oury, Nicolas, Pauline Gélin, and Hélène Magalon. 2021. “High Connectivity within Restricted Distribution Range in *Pocillopora* Corals.” *Journal of Biogeography* 48 (7): 1679–92.
Penin, Lucie, Mehdi Adjeroud, Muriel Schrimm, and Hunter Stanton Lenihan. 2007. “High Spatial Variability in Coral Bleaching around Moorea (French Polynesia): Patterns across Locations and Water Depths.” *Comptes Rendus Biologies* 330 (2): 171–81.
Pérez-Rosales, Gonzalo, Simon J. Brandl, Yannick Chancerelle, Gilles Siu, Elodie Martinez, Valeriano Parravicini, and Laetitia Hédouin. 2021. “Documenting Decadal Disturbance Dynamics Reveals Archipelago-Specific Recovery and Compositional Change on Polynesian Reefs.” *Marine Pollution Bulletin* 170 (September):112659.
Pinzón, Jorge H., and Todd C. LaJeunesse. 2011. “Species Delimitation of Common Reef Corals in the Genus Pocillopora Using Nucleotide Sequence Phylogenies, Population Genetics and Symbiosis Ecology.” *Molecular Ecology* 20 (2): 311–25.
Pinzón, Jorge H., Eugenia Sampayo, Evelyn Cox, Leonard J. Chauka, Chaolun Allen Chen, Christian R. Voolstra, and Todd C. LaJeunesse. 2013. “Blind to Morphology: Genetics Identifies Several Widespread Ecologically Common Species and Few Endemics among Indo-Pacific Cauliflower Corals (*Pocillopora*, Scleractinia).” *Journal of Biogeography* 40 (8): 1595–1608.

Pisapia, Chiara, Jessica Stella, Nyssa J. Silbiger, and Robert Carpenter. 2020. "Epifaunal Invertebrate Assemblages Associated with Branching Pocilloporids in Moorea, French Polynesia." *PeerJ* 8 (June):e9364.

Randall, Carly J., and Alina M. Szmant. 2009. "Elevated Temperature Affects Development, Survivorship, and Settlement of the Elkhorn Coral, *Acropora palmata* (Lamarck 1816)." *The Biological Bulletin* 217 (3): 269–82.

Reimer, James Davis, Raquel S. Peixoto, Sarah W. Davies, Nikki Traylor-Knowles, Morgan L. Short, Rafael A. Cabral-Tena, John A. Burt, et al. 2024. "The Fourth Global Coral Bleaching Event: Where Do We Go from Here?" *Coral Reefs* , May. https://doi.org/10.1007/s00338-024-02504-w.

Romatzki, S. 2008. "Reproduction Strategies of Stony Corals (Scleractinia) in an Equatorial, Indonesian Coral Reef. Contributions for the Reef-Restoration." Accessed March 27, 2024. https://media.suub.uni-bremen.de/handle/elib/2634.

Saitou, N., and M. Nei. 1987. "The Neighbor-Joining Method: A New Method for Reconstructing Phylogenetic Trees." *Molecular Biology and Evolution* 4 (4): 406–25.

Schliep, Klaus Peter. 2011. "Phangorn: Phylogenetic Analysis in R." *Bioinformatics* 27 (4): 592–93.

Schmidt-Roach, Sebastian, Erika Johnston, Silvia Fontana, Christopher P. Jury, and Zac Forsman. 2014. "Daytime Spawning of *Pocillopora* Species in Kaneohe Bay, Hawai'i." *Galaxea, Journal of Coral Reef Studies* 16 (1): 11–12.

Schmidt-Roach, Sebastian, Karen J. Miller, Erika Woolsey, Gabriele Gerlach, and Andrew H. Baird. 2012. "Broadcast Spawning by *Pocillopora* Species on the Great Barrier Reef." *PloS One* 7 (12): e50847.

Shlesinger, T., and Y. Loya. 2019. "Breakdown in Spawning Synchrony: A Silent Threat to Coral Persistence." *Science*. https://science.sciencemag.org/content/365/6457/1002.abstract?casa_token=FyHHFcrvEXYAAAAA:jMAY6yeLOtoj2d01OSP8djUXB8gNET2dVnIt71kAfi9c5v8pO4ZDa667-p18uX1gpkD4OMkt9e5znuA.

Shlesinger, Y., and Y. Loya. 1985. "Coral Community Reproductive Patterns: Red Sea versus the Great Barrier Reef." *Science* 228 (4705): 1333–35.

Sier, C. J. S., and P. J. W. Olive. 1994. "Reproduction and Reproductive Variability in the Coral *Pocillopora verrucosa* from the Republic of Maldives." *Marine Biology* 118 (4): 713–22.

Sievers, Fabian, Andreas Wilm, David Dineen, Toby J. Gibson, Kevin Karplus, Weizhong Li, Rodrigo Lopez, et al. 2011. "Fast, Scalable Generation of High-Quality Protein Multiple Sequence Alignments Using Clustal Omega." *Molecular Systems Biology* 7 (1): 539.

Smith, L. W., H. H. Wirshing, A. C. Baker, and C. Birkeland. 2008. "Environmental versus Genetic Influences on Growth Rates of the Corals *Pocillopora eydouxi* and *Porites lobata* (Anthozoa: Scleractinia)1." *Pacific Science* 62 (1): 57–69.

Speare, Kelly E., Thomas C. Adam, Erin M. Winslow, Hunter S. Lenihan, and Deron E. Burkepile. 2022. "Size-Dependent Mortality of Corals during Marine Heatwave Erodes Recovery Capacity of a Coral Reef." *Global Change Biology* 28 (4): 1342–58.

Stella, J. S., G. P. Jones, and M. S. Pratchett. 2010. "Variation in the Structure of

Epifaunal Invertebrate Assemblages among Coral Hosts." *Coral Reefs* 29 (4): 957–73.

Suzuki, Go. 2012. "Simultaneous Spawning of *Pocillopora* and *Goniopora* Corals in the Morning Time." *Galaxea, Journal of Coral Reef Studies* 14 (1): 115–16.

Team, R. Core. 2013. "R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria." *URL Http://www. R-Project. Org/. (3. 3. 1) Software Vienna, Austria: R Foundation for Statistical Computing*.

Tomascik, Tomas. 1997. *The Ecology of the Indonesian Seas Part 1*. Periplus Editions (HK) Limited.

Voolstra, Christian R., Benjamin C. C. Hume, Eric J. Armstrong, Guinther Mitushasi, Barbara Porro, Nicolas Oury, Sylvain Agostini, et al. 2023. "Disparate Genetic Divergence Patterns in Three Corals across a Pan-Pacific Environmental Gradient Highlight Species-Specific Adaptation." *Npj Biodiversity* 2 (1): 1–16.

Ward, S. 1992. "Evidence for Broadcast Spawning as Well as Brooding in the Scleractinian Coral *Pocillopora damicornis*." *Marine Biology* 112 (4): 641–46.

Woolsey, E. S., M. Byrne, and A. H. Baird. 2013. "The Effects of Temperature on Embryonic Development and Larval Survival in Two Scleractinian Corals." *Marine Ecology Progress Series* 493 (November):179–84.

Yeoh, Shang-Ru, and Chang-Feng Dai. 2010. "The Production of Sexual and Asexual Larvae within Single Broods of the Scleractinian Coral, *Pocillopora damicornis*." *Marine Biology* 157 (2): 351–59.