Pocillopora meandrina daytime broadcast spawning in Moorea, French Polynesia

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Abstract

Pocillopora are abundant branching corals that create 3-dimensional reef structure. In French Polynesia, when corals were decimated by crown-of-thorns, bleaching, and a cyclone between 2007-2010, *Pocillopora* recruitment primarily drove recovery by 2016, yet spawning times are undocumented. To address this, we surveyed *Pocillopora* in Moorea between September 2022-January 2023. We documented split-spawning around the full moons, 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). Molecular analysis (n=16) identified 100% as *P. meandrina*, with 13 as Haplotype 1a and 3 as Haplotype 8a, suggesting *P. verrucosa, P. grandis,* and Haplotype 10 spawn on the new moon or in later months. These observations provide initial documentation of *Pocillopora* spawning in Moorea (to our knowledge), expanding on indigenous knowledge and increasing capacity to study *Pocillopora* reproduction, connectivity, and adaptation.

Introduction

Natural disturbances can trigger a new successional state (Knowlton 2015) and trajectory for the community, 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, such as increasing heatwaves (Oliver et al. 2021), to degrade marine ecosystems, in particular coral reefs. Reef-building, or 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).

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 Moorea, French Polynesia (Penin et al. 2007). In Moorea in 2019, surveys of coral bleaching of the dominant genera, *Acropora* and *Pocillopora*, revealed 89% and 46% bleaching/partial mortality, respectively for these species (Speare et al. 2022). Therefore, without coral replenishment through reproduction, reef maintenance is threatened under current and future climate conditions.

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 Moorea, French Polynesia, when coral cover was reduced by nearly ~90% due to crown-of-thorns outbreaks, bleaching, and successive cyclones between 2006 and 2010 (Holbrook et al. 2018), *Pocillopora spp.* were responsible for rapid reef recovery (Adjeroud et al. 2007; Holbrook et al. 2018). *Pocillopora spp.* are early successional species (Grigg and Maragos 1974) due to high fecundity (Sier and Olive 1994; Tsounis and Edmunds 2016) and recruitment (Adjeroud et al. 2007). Further, with their complex branching morphologies, *Pocillopora spp.* provide extensive reef habitat (Stella et al. 2010). In light of this, it is essential that we quantify and describe the process of *Pocillopora spp.* spawning in French Polynesia, which has yet to be reported in the scientific literature.

Existing literature on *Pocillopora spp*. indicates they primarily reproduce sexually via spawning, excluding *P. damicornis*, and *P. acuta*, which can (a)sexually brood (Yeoh and Dai 2010), but can also spawn (Ward 1992; Schmidt-Roach et al. 2014). While not all past studies conducted genetic species identification, there are reports of spawning near the full moon for *P. meandrina* in Australia (Schmidt-Roach et al. 2012), Hawai□i (Apprill et al. 2009; Schmidt-Roach et al. 2014) and for *P. grandis* in Japan (Kinzie 1993; Hirose et al. 2000, 2001). In contrast, observations of *P. verrucosa* spawning have been made during the new moon 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). In light of this, we monitored *Pocillopora spp.* colonies for signs of spawning in the lagoon of the north shore of Mo'orea French Polynesia, with observations for each month from September 2022 to January 2023 on 3-5 days around the full (and new moons where possible) starting ~45 min after sunrise (~06:00 in Moorea) for ~ 2 hours (Table 1).

Methods

In order to describe spawning times to the species level, we completed visual and photographic documentation of *Pocillopora* spawning, embryo development, and species level genetic identification.

Spawning observations and sample collection

The spawning observation site was located on the north shore lagoon reef in Moorea (-17.475757, -149.808062), which was selected for high Pocilloporidae cover (Edmunds 2022) and capacity for safe low light transit from the UC Richard B. Gump South Pacific Research Station. All observations were made while snorkeling at ~1-3m, with a minimum of two observers in the water. Observers were positioned to simultaneously visualize multiple morphologies (e.g., *P. meandrina*, *P. verrucosa*, *P. grandis*). Coral spawning observations were documented as follows: (1) spawning was filmed and photographs of each colony were taken (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; and (4) where possible, gametes were collected from the water next to the colonies with 50 mL falcon tubes. Samples were returned to the Gump South Pacific Research Station and biopsies from the tagged colonies were fixed in DNA/RNA Shield (Zymo Research Cat # R1100-250). To determine if successful fertilization occurred, collected gametes were placed in a MyTemp Mini Digital incubator (Benchmark H2200-HC) set at ambient seawater temperature (~28°C). Development through the swimming stage was monitored with a compound microscope (LEICA DM500).

Pocillopora species genetic identification

Samples (n=16, Table 2) were transported to the University of Rhode Island, USA, under CITES FR2398700017-E. DNA was extracted with Quick-DNA™ Miniprep Plus Kit (Zymo Research Cat # D4069) according to the manufacturer's instructions for samples stored in DNA/RNA Shield, including the addition of 20µl of Proteinase K (20mg mL^{-1}). Samples were eluted in 50µl of kit Elution Buffer warmed to 65°C and DNA was assessed with a 1.5% agarose gel in 1x TAE buffer run for 45 mins at 100 V and stained with Biotium GelGreen (Fisher Cat NC9728313). To identify *Pocillopora spp.* we amplified the mitochondrial open reading frame (mtORF) region using the primers of Flot et al. (2008) FatP6.1 (5′-TTTGGGSATTCGTTTAGCAG-3′) and RORF (5′-SCCAATATGTTAAACASCATGTCA-3′). 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. Samples were amplified with the polymerase chain reaction (PCR) profile of a single denaturation step of 60s at 94 °C, followed by 30 cycles of 30s at 94 °C for denaturation, 30s at 53 °C for annealing, and extension of 75s at 72 °C; thermocycling was followed by final incubation at 72 °C for 5 min. The products were then assessed with a 1.5% agarose gel in TAE for 45 mins at 100 V to identify bands of ~1000bp. PCR products were cleaned with Qiagen MinElute PCR Purification Kit (Qiagen Cat. 28004) according to the manufacturer's instructions. Sanger sequencing was completed in both forward and reverse at the URI Genomics and Sequencing center using Applied Biosystems BigDye Terminator v3.1 chemistry. Sequences were analyzed using Geneious Alignment in GENEIOUS PRIME 2020.2.4. Pairwise alignment of the 16 sample sequences with the reference sequences (Table 3; https://osf.io/5geqd/) was completed using Clustal Omega (Sievers et al. 2011) and Tree building was completed via a Neighbor-Joining tree (Saitou and Nei 1987) with Jukes-Cantor genetic distance model (Jukes and Cantor 1969) and no outgroup.

Where mtORF sequencing identified samples as Haplotype 1a (containing both *P. grandis* and *P. meandrina*), DNAs were also amplified with the histone 3 region using the primers of Johnston et al. (2018) (PocHistoneF: 5′-ATTCAGTCTCACTCACTCACTCAC-3′ and PocHistoneR: 5′-TATCTTCGAACAGACCCACCAAAT-3′). *P. acuta* (Sample H2, Figure 2B) and *P. grandis* (POC-198, Figure 2B) were used as positive amplification and restriction enzyme controls, respectively. PCR mixes were made following methods above (but with PocHistone primers). Thermal cycling included a denaturation step of 60 s at 94 °C, followed by 30 cycles 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 with *Xho*I (NEB R0146Sk) according to Johnston et al. (2018) and viewed on a 2% agarose gel in 1X TAE after running for ~110 min at 70V

with a GeneRuler 100 bp DNA Ladder (Thermo Fisher Cat SM0241). A lack of cutting indicates the species is *P. meandrina*, while two bands at 287, 382 bp indicates the species identification is *P. grandis* (Fig. 2B). Raw sequence data, alignments, and fasta files are archived here: https://osf.io/5geqd/ DOI 10.17605/OSF.IO/5GEQD

Results and Discussion

Species specific spawning

Pocillopora meandrina spawning was clearly documented from our observations (Table 1) and genetic identification of 16 spawning colonies (Table 2). Of these 16, mtORF sequencing (Table 1, Figure 2A) indicated 13 samples as Haplotype 1a (Haplotype 1, also identified as PSH 9 from Gelin et al. 2017, which contains *P. meandrina* and *P. grandis*) followed by histone 3 region identification as *P. meandrina*. The three remaining samples were identified as *P. meandrina* lineage Haplotype 8a. The presence of Pocilloporid species diversity in Moorea, including *P. meandrina*, *P. verrucosa, P. grandis*, and Haplotype 10, ((Burgess et al. 2021); proposed as *P. tuahiniensis,* Johnston and Burgess in revision) indicate additional spawning research should be focused on the new moon in Moorea and over additional months, or times of day. Multiple studies indicate recruitment of Pocilloporidae peaks between December - April each year (Gleason 1996; Adjeroud et al. 2007; Edmunds et al. 2010). This broad window and the documentation that *Pocillopora verrucosa* (morphologically identified) spawns in the new moon in all other locations reported to date (Shlesinger and Loya 1985; Kinzie 1993; Kruger and Schleyer 1998; Hirose et al. 2000, 2001; Bouwmeester et al. 2011, 2021; Baird et al. 2022) indicates additional work remains in the area of species-specific *Pocillopora spp.* gametogenesis, spawning, development, and recruitment in French Polynesia.

Synchronized reef-wide spawning of Pocillopora meandrina *occurs in Moorea*

In Moorea, *P. meandrina* gametes were released early in the morning at ~06:15-06:35 local time, which was ~ 70-80 minutes after sunrise local time. This information supports a synchronization of *Pocillopora spp.* spawning 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)). Split-spawning and species-specific windows are both possible in Moorea. While only one colony of *P. meandrina* was observed spawning during the month of November (November 10 Full +2 at 6:32 am), *P. meandrina*, *P. verrucosa,* and *P. grandis* spawning has also been documented at similar latitude on the Great Barrier Reef in November (Schmidt-Roach et al. 2012).

In December, most of the colonies observed had synchronized spawning. Indeed, on December 9 (Full+2), from 6:16 am to 6:32am, a large number of colonies were observed spawning both eggs and sperm turning the water of the lagoon cloudy. In addition to the observations made in the lagoon, waves of eggs and sperm appeared to be arriving from the forereef, indicating simultaneous spawning between the two environments (lagoon and forereef), but this was not documented by our team of observers. 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 reef-wide spawning, but with a lower abundance of colonies. Our results corroborate those from Japan and Hawai□i that *Pocillopora spp.* can spawn across multiple days (Kinzie 1993; Fiene-Severns 1998).

Larvae contain zooxanthellae and development is rapid

Once spawning commenced on 10 December 2022, the water quickly became cloudy with eggs and sperm (Fig. 1A, B). Both appeared to be negatively buoyant and rapidly dispersed by the waves and current. Eggs (~90µm) and developing embryos (~120µm) that were observed at ~10:00am via compound microscopy contained zooxanthellae (Fig. 1C, D, E). 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 vertical transmission 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 Moorea, if enough adult colonies are available under future conditions (Speare et al. 2022).

Documentation is not always discovery

Although we are the first to report scientific documentation of *Pocillopora meandrina* spawning in French Polynesia, it is most likely that coral spawning of many species 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.

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Figures:

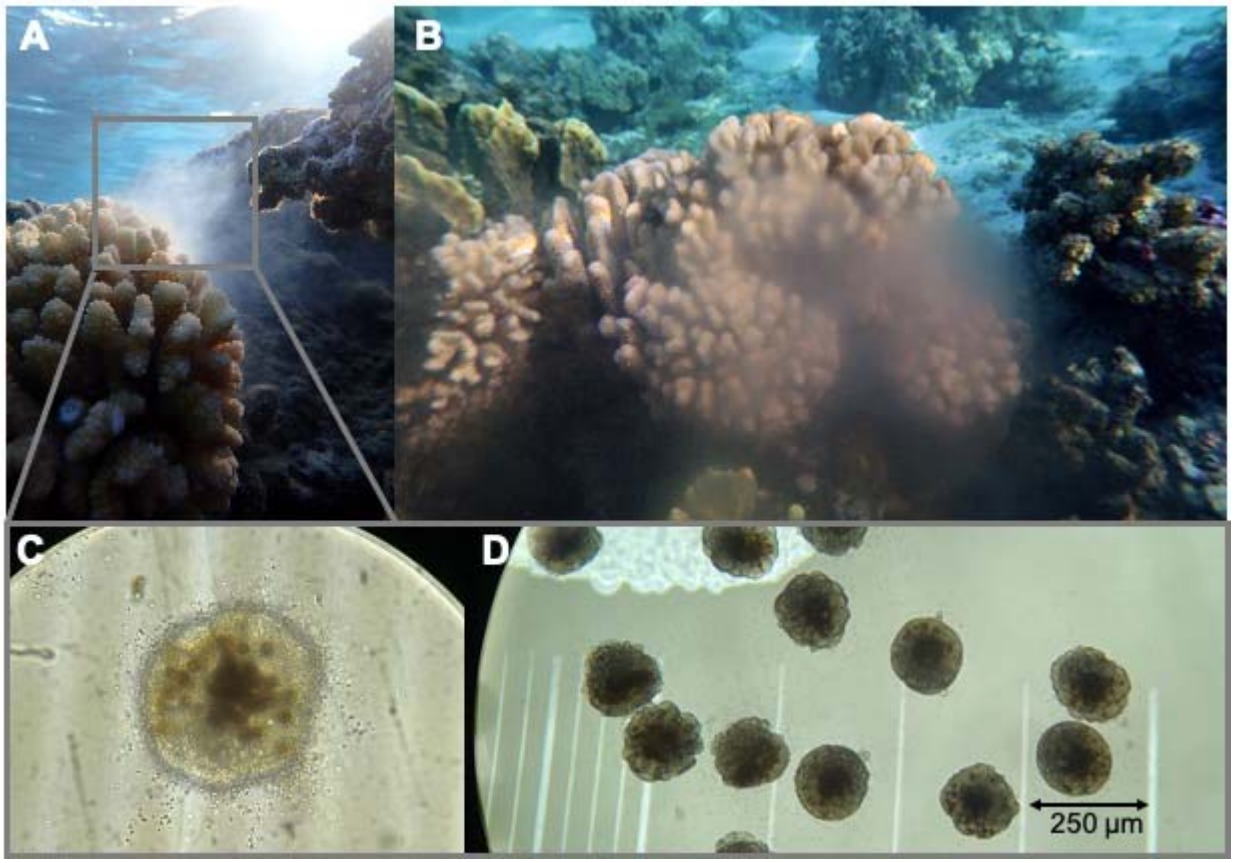

Figure 1. *Pocillopora meandrina* spawning of **A, B)** eggs and sperm on the lagoon. Samples of the gametes were collected from the seawater revealing the **C)** interaction of symbiotic eggs and sperm followed by **D)** later stage cell division of embryos at ~4 hours post spawning. Swimming embryos were documented at 14:00, ~7.5 hours post spawning. More images and videos are archived here: https://osf.io/5geqd/ DOI 10.17605/OSF.IO/5GEQD

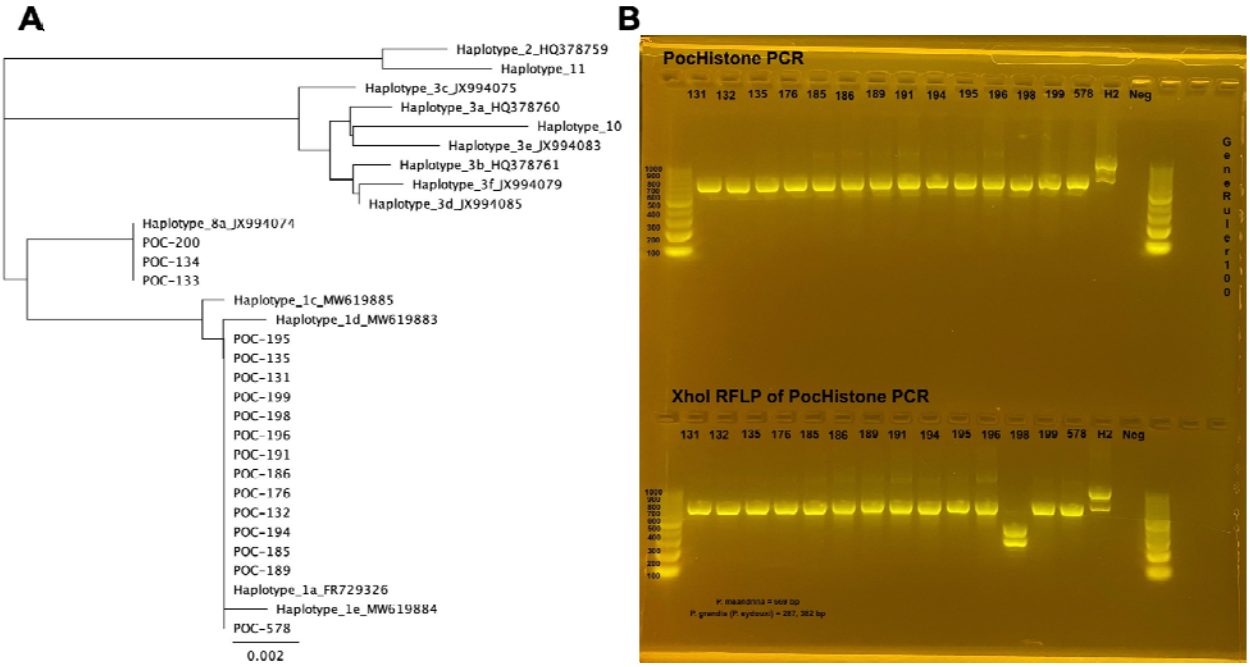

Figure 2. A) Neighbor-Joining tree (Saitou and Nei 1987) with Jukes-Cantor genetic distance model (Jukes and Cantor 1969) and no outgroup in GENEIOUS PRIME 2020.2.4. **B)** PocHistone PCR using the primers of Johnston et al. (2018) shown in the upper row and restriction digest of the PocHistone PCR using *Xho*I indicating *P. meandrina* in samples with a single band of 669 bp and a positive control of *P. grandis* in sample 198 with double bands of 287, 382 bp. Raw sequence data, alignments, and reference fasta files are archived here: https://osf.io/5geqd/ DOI 10.17605/OSF.IO/5GEQD

Table 1. *Pocillopora spp* spawning observation timeline from September 2022 to January 2023. Sunrise and sunset times were reported based on this link.

Date	Sunrise Time	Lunar Phase	Spawn	Start Time	Stop Time	Notes
26 Sept 2022	5:45:00 AM	New+1	No	05:30	7:00	NA
27 Sept 2022	5:44:00 AM	New+2	No	05:40	8:00	NA
28 Sept 2022	5:43:00 AM	New+3	No	05:45	08:15	NA
07 Oct 2022	5:36:00 AM	Full-2	No	05:45	08:00	NA
08 Oct 2022	5:35:00 AM	Full-1	No	06:00	08:05	NA
06 Nov 2022	5:18:00 AM	Full-2	No	6:00	7:45	NA
07 Nov 2022	5:17:00 AM	Full-1	No	6:10	8:00	NA
08 Nov 2022	5:17:00 AM	Full	NA	NA	NA	Bad weather with lightning precluded in water observations
09 Nov 2022	5:15:00 AM	Full+1	No	5:50	8:00	NA
10 Nov 2022	5:15:00 AM	Full+2	Yes	05:45	08:25	Spawn at 06:32, 1 colony
11 Nov 2022	5:14:00 AM	Full+3	No	6:00	7:40	NA
07 Dec 2022	5:16:00 AM	Full	No	06:00	07:28	NA
08 Dec 2022	5:16:00 AM	Full+1	No	06:20	07:52	NA
09 Dec 2022	5:17:00 AM	Full+2	yes	06:05	08:00	Spawn at 06:16 to 06:32
10 Dec 2022	5:17:00 AM	Full+3	yes	06:00	07:45	Spawn at 06:21 to 06:35

11 Dec 2022	5:17:00 AM	Full+3	NA	NA	NA	Bad weather with lightning precluded in water observations
06 Jan 2023	5:29:00 AM	Full	NA	NA	NA	Bad weather with lightning precluded in water observations
07 Jan 2023	5:30:00 AM	Full+1	No	06:09	07:37	Bad weather and strong current reduced in water time
08 Jan 2023	5:30:00 AM	Full+2	No	06:10	07:18	Bad weather and strong current reduced in water time
09 Jan 2023	5:31:00 AM	Full+3	No	06:10	06:37	Bad weather, waves and current precluded water work past ~06:40

Table 2. *Pocillopora* spawning samples collected from corals observed spawning in November and December 2022.

Sample ID	**mtORF Sanger ID Haplotype**	**mtORF Citation**	**PocHistone RFLP ID**	**Species ID**	**Collection Date**
POC-578 (Tag 192)	Haplotype 1a	PSH 9 (Gélin et al. 2017)	*P. meandrina*	*P. meandrina*	10 November 2022
POC-131 (Tag 131)	Haplotype 1a	PSH 9 (Gélin et al. 2017)	*P. meandrina*	*P. meandrina*	09 December 2022
POC-132 (Tag 132)	Haplotype 1a	PSH 9 (Gélin et al. 2017)	*P. meandrina*	*P. meandrina*	09 December 2022
POC-133 (Tag 133)	Haplotype 8a	PSH 6 (Gélin et al. 2017)	*NA*	*P. meandrina*	09 December 2022
POC-134 (Tag 134)	Haplotype 8a	PSH 6 (Gélin et al. 2017)	*NA*	*P. meandrina*	09 December 2022

POC-135 (Tag 135)	Haplotype 1a	PSH 9 (Gélin et al. 2017)	*P. meandrina*	*P. meandrina*	09 December 2022
POC-176 (Tag 176)	Haplotype 1a	PSH 9 (Gélin et al. 2017)	*P. meandrina*	*P. meandrina*	09 December 2022
POC-185 (Tag 185)	Haplotype 1a	PSH 9 (Gélin et al. 2017)	*P. meandrina*	*P. meandrina*	09 December 2022
POC-186 (Tag 186)	Haplotype 1a	PSH 9 (Gélin et al. 2017)	*P. meandrina*	*P. meandrina*	09 December 2022
POC-189 (Tag 189)	Haplotype 1a	PSH 9 (Gélin et al. 2017)	*P. meandrina*	*P. meandrina*	09 December 2022
POC-191 (Tag 191)	Haplotype 1a	PSH 9 (Gélin et al. 2017)	*P. meandrina*	*P. meandrina*	09 December 2022
POC-194 (Tag 194)	Haplotype 1a	PSH 9 (Gélin et al. 2017)	*P. meandrina*	*P. meandrina*	09 December 2022
POC-195 (Tag 195)	Haplotype 1a	PSH 9 (Gélin et al. 2017)	*P. meandrina*	*P. meandrina*	09 December 2022
POC-196 (Tag 196)	Haplotype 1a	PSH 9 (Gélin et al. 2017)	*P. meandrina*	*P. meandrina*	09 December 2022
POC-199 (Tag 199)	Haplotype 1a	PSH 9 (Gélin et al. 2017)	*P. meandrina*	*P. meandrina*	09 December 2022
POC-200 (Tag 200)	Haplotype 8a	PSH 6 (Gélin et al. 2017)	*NA*	*P. meandrina*	09 December 2022

Table 3. 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/ DOI 10.17605/OSF.IO/5GEQD

Haplotype ID	**Accession Number**	**Species**	**Citation**
Haplotype 1a	FR729326	*Pocillopora meandrina or P. grandis*	(Flot et al. 2010)
Haplotype 1c	MW619885	*Pocillopora meandrina*	(Burgess et al. 2021)
Haplotype 1d	MW619883	*Pocillopora meandrina*	(Burgess et al. 2021)
Haplotype 1e	MW619884	*Pocillopora meandrina*	(Burgess et al. 2021)
Haplotype 2	HQ378759	*Pocillopora verrucosa*	(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 8a	JX994074	*Pocillopora meandrina*	(Pinzón et al. 2013)
Haplotype 10	*KF381330*	*Pocillopora sp.* Proposed as *P. tuahiniensis*	*(Johnston et al. 2022)* (Johnston and Burgess in revision)
Haplotype 11	KF381328	*Pocillopora* sp.	(Johnston et al. 2022)

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