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Spawning Asynchrony of the Endangered Acropora cervicornis: Are Light Pollution and Abnormally Warm Temperatures the Culprits?

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HALMOS COLLEGE OF ARTS AND SCIENCES

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By

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Abstract

The persistence of reefs relies on mature corals spawning synchronously to maximize fertilization and produce larvae to replenish local populations. Corals synchronize the release of gametes by responding to temperature, sun, and moon light cycles; however, abnormalities in these patterns can disrupt synchrony. This study is the first to describe regional asynchronous spawning of *Acropora cervicornis* by quantifying gamete development and spawning times among two reefs, an *in situ* nursery off Fort Lauderdale, and an *in situ* nursery in the Florida Keys. While *A. cervicornis* in the Florida Keys synchronously spawned within the predicted window of 2-5 days after the full moon both years, corals off Fort Lauderdale spawned 7-10 days before the full moon in 2022 and 1-9 days after the full moon in 2023. Additionally, *A. cervicornis* in Fort Lauderdale also spawn an hour longer than those in the Keys. While regional asynchrony cannot be explained by temperature differences, it remains unclear if light pollution or turbidity drive regional asynchrony. Regardless, it is likely that corals in this region are not receiving the moon light cue for spawning causing asynchronism in both the spawning day and hour of *A. cervicornis* in Fort Lauderdale. This results in dramatically reduced fertilization success and, consequently, lowers coral recruitment and the ability of reef populations to replenish themselves. A reduction in sexual reproduction and therefore reef connectivity and recruitment will reduce the genetic diversity needed for populations to remain resilient to future disturbances such as marine heat waves.

Keywords: reproduction, histology, *Acropora cervicornis*, synchronization

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Introduction

Coral reefs are highly productive and diverse habitats that provide important ecosystem services to over 500 million people (Moberg & Folke, 1999; Wilkinson, 2008). Despite only covering 0.2% of the ocean floor (Reaka-Kudla, 1997), nearly 25% of marine organisms are supported by coral reefs, making it one of the most diverse ecosystems on this planet (McAllister, 1995). In addition to providing a physical habitat for marine species, corals provide a structure that protects coastlines from storm surges and flooding. Indeed, by dissipating up to 97% of incident wave energy (Ferrario et al., 2014), coral reefs across the United States provide $1.8 billion in coastal protection (Storlazzi et al., 2019). In Florida, coral reefs support an $8.5 billion economy through tourism as well as commercial and recreational fisheries (NOAA Coral Reef Conservation Program, 2020).

Despite their importance, half of the world's coral reefs have been lost since the 1950s (Eddy et al., 2021) due to anthropogenic threats from climate change, most notably warming (Baker et al., 2008; Hughes et al., 2017; Hughes et al., 2018a; Hughes et al., 2018b; Souter et al., 2021), ocean acidification (Hoegh-Guldberg, 2011; Veron et al., 2009) though perhaps to a lesser extent (Bahr et al., 2016; Jiang et al., 2018; McCulloch et al., 2012; Pandolfi et al., 2011), and local sources of pollution (Hoegh-Guldberg et al., 2017), that have the potential to eliminate 60% of remaining coral reefs by 2030 (Hughes et al., 2003). In the Caribbean, coral cover has declined by more than 80% since the 1970s (Jackson et al., 2014) due to repeat bleaching events (Baker et al., 2008; Souter et al., 2021), coral diseases (Aronson & Precht, 2001b; Gladfelter, 1982; Hayes et al., 2022; Walton et al., 2018), and a loss of herbivores (Lessios et al., 1984) leading to a shift to an algae-dominated ecosystem (Souter et al., 2021).

Reef coral populations can recover from disturbances through both asexual reproduction (i.e. budding and fragmentation; Tunnicliffe 1981; Highsmith 1982; Edmunds and Whitman 1991) and sexual reproduction (i.e. forming new genotypes through genetic recombination, (Randall et al., 2020)). However, asexual reproduction through fragmentation results in genetic clones of the parent colony; therefore, this method does not contribute to the increase in genetic diversity. On the other hand, sexual reproduction increases genetic diversity (Baums, 2008; van Oppen et al., 2015, 2017) and thus might contribute to the increase in population's resistance to stressors, such as disease events, ocean acidification, and temperature-induced bleaching events (Barton et al., 2017; Edwards, 2010). When corals sexually reproduce, the larvae produced can

disperse and recruit to a reef, replenishing it and thus allowing it to recover from previous disturbance events.

Chronically disturbed reefs often see little to no recruitment (Bak & Engel, 1979; Bauman et al., 2015; Dustan, 1977; van Woesik et al., 2014), likely because environmental stressors can reduce coral fecundity, gamete quantity and quality, negatively affect larval development and settlement and/or cause asynchronous spawning that prevent fertilization. In disturbed areas, coral colonies tend to be smaller and have reduced fecundity; i.e. adult corals may be allocating energy towards survival and growth, rather than toward producing gametes (Tanner, 1995). Even when corals reach sexual maturity, environmental stressors, such as warming-induced bleaching, often result in a reduction in gamete quantity and/or quality even after the colony has appeared to recover (Cetz-Navarro et al., 2015; Johnston et al., 2020; Leinbach et al., 2021; Levitan et al., 2014). Furthermore, elevated temperatures may cause developmental abnormalities of larvae Randall & Szmant, 2009), resulting in larval mortality (Figueiredo et al., 2014; Pitts et al., 2020; Randall & Szmant, 2009), reduced settlement (Humanes et al., 2017; Randall & Szmant, 2009b; Pitts et al. 2020), and increased mortality of juvenile corals (Edmunds, 2004; Randall & Szmant, 2009). Low coral recruitment can also be caused by reduced fertilization during spawning events. Most coral species reproduce by broadcast spawning, in which colonies synchronously release gametes into the water column that get fertilized by gametes released by nearby corals. Low coral cover may result in genetically distinct individuals of the same species being too spatially isolated for their gametes to ever meet, reducing fertilization success (Nozawa et al., 2015; Oliver & Babcock, 1992). This consequently results in a strong allee effect, in which the population size is further reduced due a decrease in an individual's fitness (i.e. reduced fertilization success due to mate limitation; Courchamp et al. 1999). Furthermore, asynchronous spawning can occur, resulting in corals releasing their gametes at different times (Fogarty and Marhaver 2019; Shlesinger and Loya 2019; Neely et al. 2020). Evidence suggests that fertilization success drops drastically within the first few hours of gamete release, as sperm loses mobility (Levitan et al., 2011). Thus, coral spawning asynchrony – which may be triggered by abnormal environmental cues—can greatly impact the persistence of a species.

Coral spawning is synchronized at multiple time scales: month, day, hour, and even minutes (Fogarty & Marhaver, 2019). Proximate cues, such as temperature affect the month in

which corals spawn (de Putron & Smith, 2011; Nozawa, 2012; Sola et al., 2016; van Woesik et al., 2006). Like other marine species, most corals typically spawn during the spring and summer months when food abundance for their offspring is the highest (Baird et al., 2009; Fadlallah, 1982; Forrest & Miller-Rushing, 2010). The month in which most corals spawn seems to coincide with the highest rate of increase in temperature though, rather than the highest temperature (Keith et al., 2016). Elevated temperatures can negatively affect fertilization (Humanes et al., 2017; Schutter et al., 2015), larval survival (Pitts et al., 2020; Randall & Szmant, 2009), development (Chua et al., 2013; Figueiredo et al., 2014; Humanes et al., 2017; Schutter et al., 2015), and settlement success (Humanes et al., 2017; Randall & Szmant, 2009). Alternatively, other proximate cues for the spawning month include wind speeds (R van Woesik, 2010) and rainfall (Mendes & Woodley, 2002). Indeed, several studies indicate that the peak spawning month corresponds to periods of mild to moderate winds, as higher windspeeds generate waves that can be harmful to the fertilization process (Keith et al., 2016; Sola et al., 2016; van Woesik, 2010). Similarly, the peak spawning month was correlated with periods of low rainfall, as heavy rains can dilute the surface waters and inhibit fertilization (Sola et al., 2016). However, neither wind speeds nor rainfall appear to be strong of cues of spawning, rather they just correlate with the seasons of spawning which is cued by the rate of temperature change (Keith et al., 2016).

On a finer scale, the lunar cycle, along with irradiance ultraviolet radiation (UVR) and photosynthetically active radiation (PAR), are expected to play a role in the day in which spawning occurs. Indeed, coral spawning occurs during specific lunar phases, particularly around the full moon (Babcock et al., 1986a; Harrison, 2011; C. H. Lin & Nozawa, 2017). Spawning during this lunar phase is associated with reduced currents which may enhance fertilization (Wolstenholme et al., 2018). Additionally, there is evidence that altering the ultraviolet radiation (UVR) and photosynthetically active radiation (PAR) can impact spawning behavior (Jokiel et al., 1985; Torres et al., 2008). Indeed, corals transplanted to deeper waters experienced a 2-3 week delay in the release of gametes compared to control shallow water corals (Torres et al., 2008).

The length of day and sunset and moonrise times may impact the hour of spawning (Ayalon et al., 2021; Brady et al., 2009; Takeshi Hayashibara et al., 2004; Kaniewska et al., 2015). *Ex situ* corals exposed to an earlier sunset time than control corals exhibited a significant

shift in spawning time, indicating that reproductive behavior is under the direct control of light (Brady et al., 2009). Indeed, the period of darkness between sunset and moonrise is an important cue for spawning behavior (Lin et al., 2021). Coral colonies exposed to constant light or darkness fail to spawn, while corals exposed to ambient light spawn nearly synchronously with those *in situ* (Craggs et al., 2017; Kaniewska et al., 2015). Recently, unsynchronized gamete release was documented for several genera, including *Montipora, Favites, Acropora, Dipsastraea, Goniastrea, Galaxea, Acanthastrea, Platygyra, Cyphastrea,* and *Porites,* with corals spawning 1-3 days earlier than normal due to exposure to artificial light at night (Ayalon et al., 2021; Davies et al., 2023).

While sunset time may trigger setting, i.e. the presence of gametes in the mouths of corals, the synchronized release of gametes at the scale of minutes may be regulated by other factors, such as cellular cascades, pheromones, and genotype (Kaniewska et al., 2015; Levitan et al., 2011). Levitan et al. (2011) observed the spawning of three *Orbicella* species and found that colonies of the same genotype spawn within minutes of each other and at significantly different times than other genotypes. While this provides evidence for genetic influences on spawning time, it was also found that neighboring colonies spawn more synchronously than colonies further away, regardless of genotype, indicating that there may be a pheromonal cue that synchronizes the release of gametes at the scale of minutes. Spawning synchronously at this fine time scale maximizes fertilization success and may prevent predation due to predator satiation (Harrison et al., 1984). Synchronous, multi-species spawning, also termed mass-spawning (Baird et al., 2001; Baird & Guest, 2009; Guest et al., 2002; Hanafy et al., 2010; Hayashibara et al., 1993), may be explained by species requiring similar environmental conditions for successful reproduction and/or other benefits such as predator satiation (Westneat & Resing, 1988).

Recent studies have found that some areas are experiencing a lack of intra-specific spawning synchrony, from the month of spawning (Shlesinger and Loya 2019; Ayalon et al. 2021) to the day (Shlesinger and Loya 2019; Davies et al. 2023) and hour of spawning (Neely et al., 2020). Evidence of this mismatch may be attributed to variations in environmental parameters, such as sea temperature (Shlesinger and Loya, 2019), and night light pollution (Shlesinger and Loya 2019; Neely et al. 2020; Ayalon et al. 2021; Davies et al. 2023), or hormonal cues (Shlesinger and Loya 2019; Neely et al. 2020). This lack of synchrony can lead to low rates of fertilization due to sperm dilution (Levitan et al., 2011), further exacerbating reef

degradation associated with climate change by preventing the recruitment of juvenile corals which may be better suited to an ever-changing environment (Fogarty & Marhaver, 2019; Shlesinger & Loya, 2019).

The staghorn coral, *Acropora cervicornis,* is a historically abundant and ecologically important reef-builder in Florida's Coral Reef. However, for the last twenty years it has been considered a critically endangered species (Aronson & Precht, 2001a) due to mass mortality events caused by outbreaks of white-band disease (Aronson & Precht, 2001b) and climate-induced stressors that caused corals to bleach (Muller et al., 2018). *Acropora cervicornis* is a simultaneous hermaphroditic broadcast-spawning coral with an annual reproduction cycle (Szmant, 1986). Each year, oogenesis begins in September or October, i.e., ten to eleven months before spawning, and spermatogenesis begins around April or May, i.e. three to four months before spawning (Szmant, 1986). Throughout its distribution in the wider Caribbean, spawning of *A. cervicornis* historically occurred 0-7 days after the full moon (DAFM) in late July or early August (Marhaver et al., 2023; Vermeij et al., 2022), with peak spawning in the Upper Keys occurring 4-5 DAFM (Miller, 2013, 2014; Miller et al., 2015), between 150-210 minutes after sunset (MAS; Vargas-Ángel et al. 2006; Miller 2013; Vermeij et al. 2022; Marhaver et al. 2023). However, some coral populations of *A. cervicornis* off Fort Lauderdale have in the past 4 years been observed to spawn up to 2 weeks before the full moon (Figueiredo's lab observations); the population in the Florida Keys the species still spawns in synchrony with the wider Caribbean.

This study aims to describe the (a)synchronicity of the spawning of *Acropora cervicornis* off Fort Lauderdale (relative to the Florida Keys), and to determine if it can be explained by light pollution and rising sea temperatures. Gamete development and spawning synchrony will be compared through histological analyses and direct observations across two reefs and an *in situ* nursery off Fort Lauderdale, along with an *in situ* nursery in the Florida Keys, which experience varying levels of light pollution and temperature. We hypothesize that northern sites with higher nighttime light pollution and higher variation in sea surface temperatures will spawn asynchronously, before the full moon. Conversely, we hypothesize that corals in the Florida Keys which experience low to no nighttime light pollution and less variation in sea surface temperatures will spawn a few days after the full moon, as it has been historically recorded for this species. As a critically endangered species, sexual reproduction with synchronized spawning is vital to the species' persistence and the health of coral reefs. Determining the time of spawning

of staghorn corals, *Acropora cervicornis*, in Southeast Florida will inform researchers and restoration practitioners of when gametes can be collected for assisted fertilization; fertilized embryos can then be released back on the water to "seed" the reefs or brought to a land-based coral nursery for rearing until these corals reach a size suitable to be outplanted on the reef for restoration. Similarly, quantifying the effects of light pollution and abnormal temperature on spawning (a)synchrony across reefs will further inform on the effects of climate change on the persistence of corals, as well as assist reef managers in developing regulations to minimize light pollution to protect the future of this endangered species.

Methodology

Site Selection:

Acropora cervicornis corals were monitored for the presence/absence of eggs and oocytes/spermaries developmental stage in four sites (3 colonies per site). Three sites were located in Fort Lauderdale, FL, between Port Everglades (26°05.34'N; 80°06.26'W) and Hillsboro Inlet (26°15.28'N; 80°04.51'W), approximately 0.5 miles offshore in approximately 5–7 m depth (Fig. 1). Two sites are expected to experience higher water temperatures and nighttime light irradiance from land-based light pollution, and the other site is expected to experience lower light irradiance and less daily temperature variation. The fourth site is the Coral Restoration Foundation's in-water nursery in Monroe County, FL (24.983000 N, -80.437500 W), approximately 5 miles offshore in 7-9 m depth (Fig. 1).

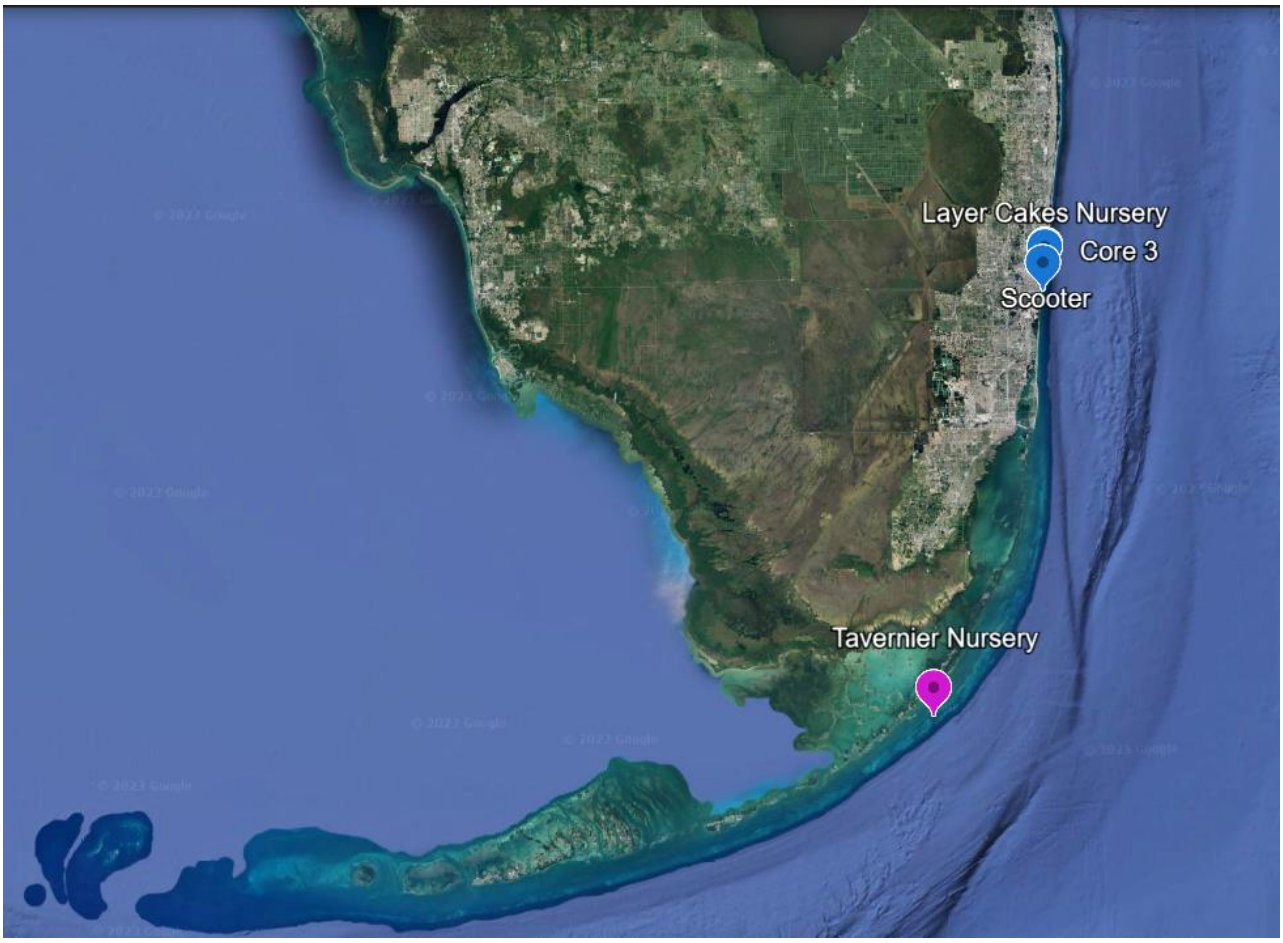

Figure 1: Map of Study Sites. Two reef sites and one *in situ* nursery were located approximately 0.5 miles off Fort Lauderdale (blue) and one *in situ* nursery was located 5 miles offshore in the Florida Keys (pink).

Tissue Sampling

Repeat tissue samples were collected from tagged colonies in both Fort Lauderdale and Monroe County by divers using cutters over the course of a month to determine the gametogenesis stage and spawning time. Corals were initially sampled two weeks before the July full moon in 2023 to confirm whether corals were fecund. Corals were then sampled once a week until the gametes were determined to be mature based on increased pigmentation approximately two weeks before the August 2023 full moon. Tissue samples were sampled approximately every other day for two weeks before and following the August 2023 full moon, during which the late stages of oogenesis, spermatogenesis, and gamete release can be observed. Tissue samples were collected at a minimum of 5 cm from an apical tip where it is more fecund, then placed in a labeled falcon tube and submerged in a Z-fix® seawater solution (20% Z-fix

concentrate: 80% artificial seawater) upon surfacing from each dive and later stored at 3°C (St. Gelais et al., 2016).

Colony Collection and Spawning Observation:

Three coral colonies selected for sampling at each site were a minimum of 30 cm in total linear extension to maximize chances of being reproductive (Soong & Lang, 1992). Upon measuring and tagging coral colonies, ODYSSEY Loggers were installed on metal stakes near coral colonies and recorded information on water temperature and light intensity every 5 minutes for the length of the study (Fig. 2). To ensure accurate measurements throughout the observation period, the ODYSSEY PAR logger had a wiper programmed to clean the PAR probe every 12

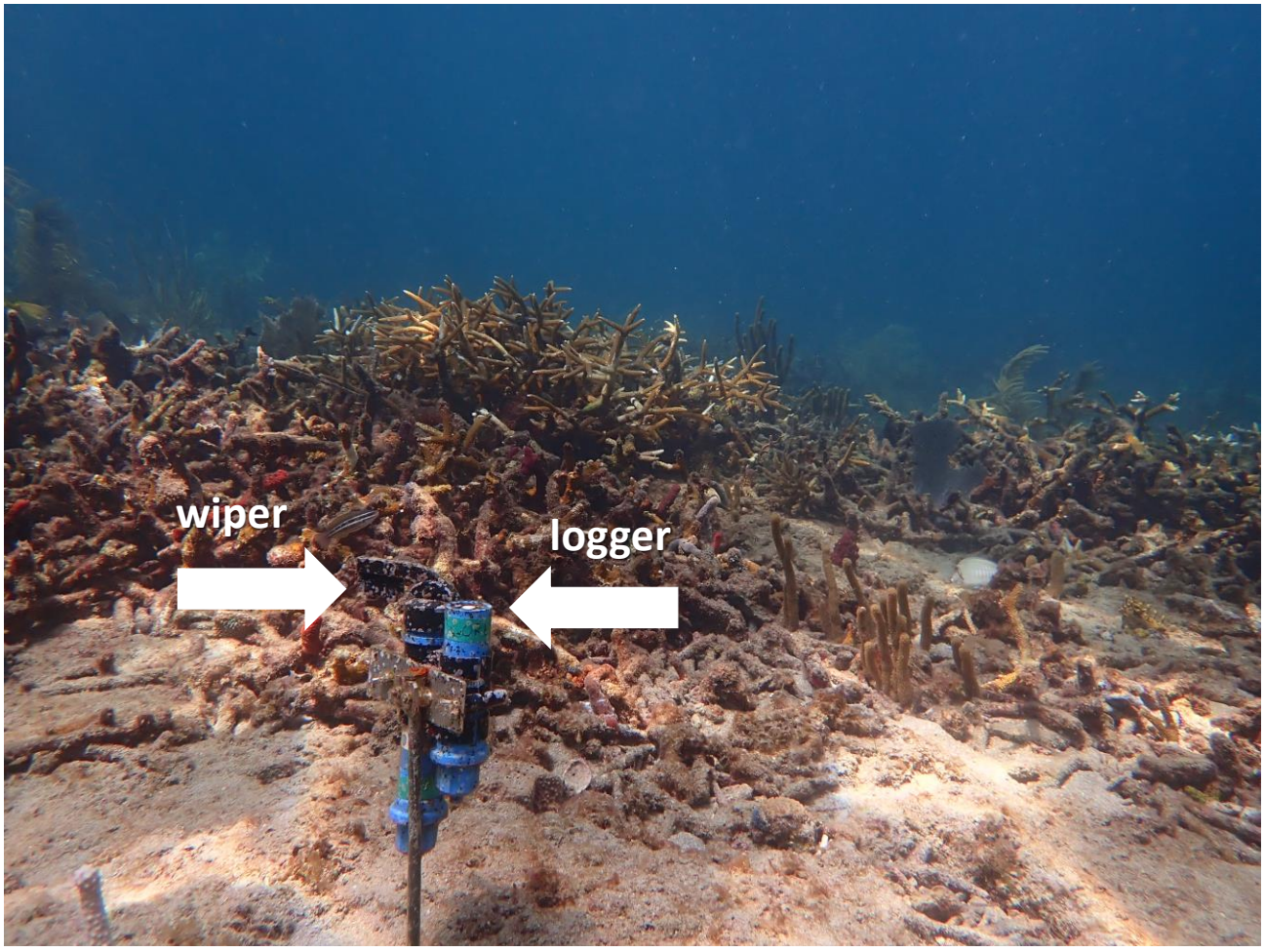

Figure 2: Logger installation. Odyssey loggers were installed at each site to measure photosynthetically active radiation and temperature.

An additional portion of tagged colonies from Fort Lauderdale were collected and temporarily housed for 2-3 weeks at Nova Southeastern University's land-based outdoor coral

nursery to monitor spawning *ex situ* (Fig. 3). Upon arrival, colonies were placed into temporary holding containers and acclimated to artificial seawater from the aquaria by performing small-volume water replacements for 30 minutes. To prevent any contamination, colonies were dipped in a 0.1% concentration of ReVive Coral Cleaner Dip (320mL ReVive: 30L saltwater) for 15 minutes and the remaining pests were manually removed. Corals were then suspended using monofilament in a recirculating fiberglass tank measuring 3.05 m × 1.07 m × 0.61 m. Water was recirculated through mechanical (filter socks and a carbon filter, Two Little Fishies PhosBan Carbon Reactor 150), chemical (Red Sea RSK 900 Reefer Internal Protein Skimmer), and biological (Brightwell Aquatics Xport BIO Bricks) filtration, and a UV sterilizer, as well as a Phosphate reactor (Two Little Fishies PhosBan Phosphate Reactor 550), and a calcium reactor (AquaMaxx cTech T-2 Calcium Reactor). The raceway was equipped with a chiller (Tecumseh 60Hz Chiller model AJA4512YXDXC) and two titanium heaters (Finnex 800W Titanium Heater model W/HC-H20M) that maintain water within the tank at a temperature of 28°C. Water was completely recirculated in the system approximately every 30 minutes. Flow in the tank was achieved with two gyres (CoralVue IceCap 2K Gyre Flow Pump) located at both the inflow and outflow ends of the system, providing an additional 2,000 GPH per gyre. Four small circulation pumps (Aqueon Circulation Pump 1250) provided perpendicular water movement throughout the system at a flow rate of 1250 GPH each, for a total flow rate in the tank of approximately 13,000 GPH. Photosynthetically active radiation (PAR) in the recirculating system was maintained between 500 – 600 μmol photons $m^{-2}s^{-1}$ during the day and a 70% shade cloth was placed over the system during the evening to reduce artificial night lights and maintain PAR between 0-0.1

μmol photons $m^{-2}s^{-1}$.

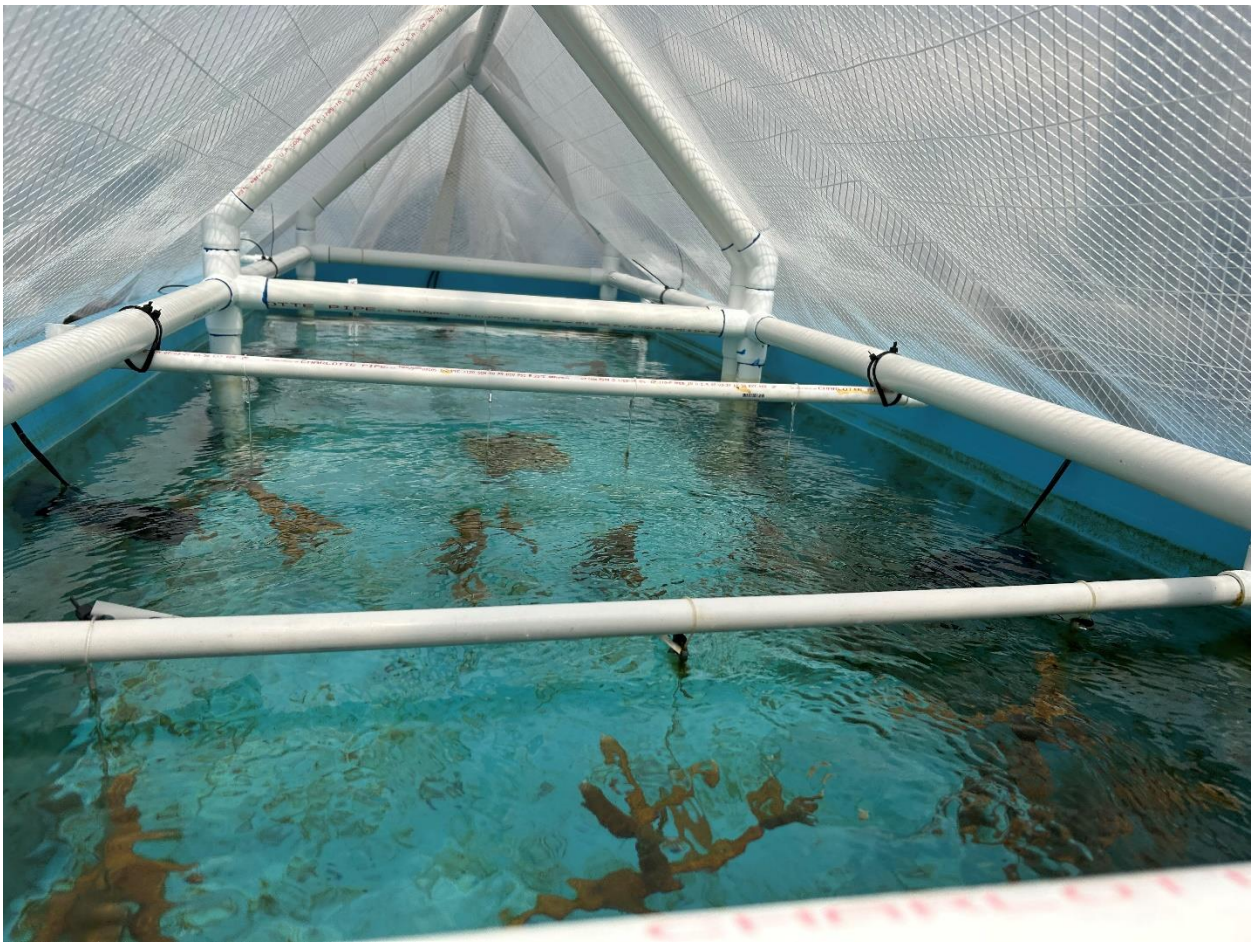

Figure 3: Experimental aquaria set up.

Beginning 2 weeks before the 2023 August full moon, colonies at Nova Southeastern University were monitored for spawning from 9 pm-12 am, approximately 45-225 minutes after sunset (MAS). The system was closed, and gyres and wavemakers were shut off to aid in spawning observations and gamete collection. Additionally, to reduce the effects of artificial lights, observations were conducted using red lights only. Colonies from Monroe County were monitored on August 5, 2023, 4 days after the full moon (DAFM). Colonies were individually tented and monitored for spawning *in situ* via SCUBA using red lights (Fig. 4). When these colonies spawned, data about the site, colony, and timing of setting and spawning were recorded. Gamete bundles were collected and mixed for fertilization.

Figure 4: *In situ* spawning observations at Coral Restoration Foundation's nursery in the Florida Keys.

Histological Preparation

To prepare the samples for histological analyses after fixation, samples were decalcified using a buffered 10% hydrochloric acid solution for approximately 48 h, after which they were rinsed in reverse osmosis water and stored in 70 % Ethanol (Soong, 1991). To prepare the

samples for embedding, tissues will be dehydrated using successively higher concentrations of ethanol (two solutions of 80%, 95%, and three solutions of 100%) followed by three solutions of xylene and then infiltrated with paraffin via a Sakura Tissue Tek II histology processor (Fig 5; Peters and Pilson 1985; Soong 1991; Lueg et al. 2012). Slides were prepared with cross and longitudinal sections taken from three different depths (~300µm apart, 5 µm thick) from each colony. Slides were placed on a hotplate for 20min before entering a 56˚C oven until staining. Slides were stained with Hematoxylin and Eosin (H&E) to aid in locating reproductive structures (Appendix I) and photos were taken using an Olympus DP21 camera attached to an Olympus BX43F light microscope.

Figure 5: Histoprocessing Equipment. (A) Sakura Tissue Tek automated tissue processor. (B) Sakura Tissue Tek TEC embedding station (C) Leica tissue sectioning station.

The developmental stages of gametocytes were categorized based on established methods (Szmant, 1991; Vargas-Ángel et al., 2006) considering both the size and coloration of gametocytes, with Stage 1 consisting of small, pale primary gametocytes and Stage 4 consisting of mature ova or sperm (Table 1). Additionally, oocytes were measured using ImageJ, and diameters were calculated using the following equation from Tan et al. (2020):

$$Geometric\ mean = \sqrt{Maximum\ length\ \times\ Width\ perpendicular\ to\ maximum\ length}$$

The timing of coral spawning on the reefs was deduced by histological samples showing the absence of gametocytes following spawning months (July and August) and therefore was only determined at the resolution of days.

Table 1: Developmental classification of oocytes and spermaries.

Stage	Oocytes	Spermaries
I	Enlarged interstitial cells with large nuclei in mesoglea of mesentery	Small clusters of interstitial cells near or entering mesoglea
II	Accumulation of a small amount of cytoplasm around nuclei	Clusters of spermatocytes with distinct spermary boundary; large nuclei
III	Oocytes of variable size; main period of vitellogenesis	Spermatocytes are smaller with smaller nuclei; the number of cells within spermary much larger
IV	Oocytes full size with indented nucleus; chromatin dispersed	Spermatocytes with little cytoplasm; tails not evident
V	As in stage IV but with condensed chromatin	Spermatozoa with tails; ready to spawn

Data Analysis

All statistical tests were performed using R version 4.3.1. Data analysis included descriptive analyses of egg development stage change over time and spawning time for all colonies at all sites. Because linearity and normality assumptions were not met, a generalized additive model was used to test whether temperature and PAR significantly differed across date and time of day, as well as between sites. For analyses, the date and time of day were combined and represented in Julian time (e.g., 7/1/2023 at 23:00 is 182.96 in Julian time). Variance in spawning day was used to assess intra and inter-regional spawning asynchrony. To determine whether spawning day was significantly different between regions, a survival analysis was conducted using a Mantel-Haenszel test. An additional survival analysis was conducted using a Mantel-Haenszel test to determine whether spawning day differed significantly between years within regions. To determine whether spawning hours were significantly different between regions, a two-tailed Mann-Whitney Wilcoxon test was conducted.

Results

Temperature Variations

Temperature significantly changed over time ($F_{8.8}$= 3686.3, p<2x10^{-16}), with time explaining 74.2% of the variance in temperature ($R^2_{adj.}$=0.742; Fig. 6) from mid-June through mid-August. Temperatures at Core 3 ranged from 27.19-31.19°C. Temperatures at Layer Cakes Nursery ranged from 27.25-31.25°C. Temperatures at Scooter ranged from 27.56-31.31°C. Temperatures at Tavernier Nursery ranged from 29.94-31.69°C.

The temperature significantly differed among sites (F_3=1152; p<2x10^{-16}; Fig. 6). Layer Cakes had significantly higher temperatures than Core 3 (t_3=8.462; p<2x10^{-16}). Scooter had significantly higher temperatures than Layer Cakes (t_3= 46.095; p<2x10^{-16}). Temperatures at Scooter were also significantly higher than at Core 3 (t_3= 54.621; p<2x10^{-16}). Temperatures in Tavernier Nursery were not significantly different from Core 3 (t=1.058; p=0.29), Layer Cakes Nursery (t=1.053; p=0.292), or Scooter (t=1.027; p=0.305). The mean temperature at Core 3 was 29.4°C, whereas the mean temperature at Scooter was 29.66°C, 30.79°C at Tavernier Nursery, and 29.45°C at Layer Cakes Nursery.

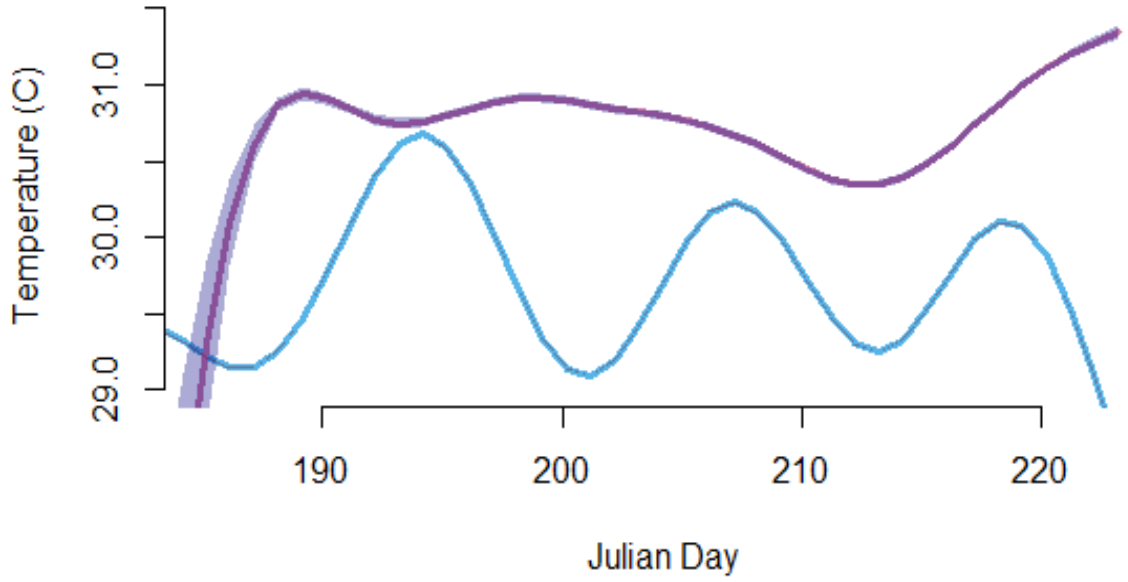

Figure 6: Regional variations in temperature between Fort Lauderdale (blue) and the Florida Keys (pink).

Photosynthetically Active Radiation Variations

PAR significantly changed over time ($F_{8.5768}$= 19.934, p<2x10^{-16}; Fig. 7), with time explaining 8.21% of variance in PAR (R^2_{adj}=0.0816). PAR at Core 3 ranged from 0-963.4 μmolm^{-2}s^{-1}, at Layer Cakes ranged from 0-699.04 μmolm^{-2}s^{-1}, at Scooter ranged from 0-1095.08 μmolm^{-2}s^{-1}, and at Tavernier Nursery ranged from 0-1966.05 μmolm^{-2}s^{-1}. Across all

sites, PAR values measured 0 $\mu molm^{-2}s^{-1}$ between 30 minutes after sunset and 30 minutes before sunrise throughout the study, regardless of moon phase.

PAR significantly differed among sites (F_3=235.4; p<$2x10^{-16}$; Fig. 7). Layer Cakes had significantly lower PAR than Core 3 (t= -17.203; p<$2x10^{-16}$). Scooter had significantly higher PAR than Core 3 (t_3= 8.507; p=$2x10^{-16}$). PAR at Scooter was also significantly higher than at Layer Cakes Nursery (t_3= 25.70; p=$2x10^{-16}$). PAR at Tavernier Nursery was significantly higher than at Core 3 (t_3=4.522 p=$6.14x10^{-6}$), Layer Cakes Nursery (t_3=4.53, p=$5.92x10^{-6}$), and Scooter (t_3=4.518, p=$6.25x10^{-6}$). The mean PAR at Core 3 was 161.12 $\mu molm^{-2}s^{-1}$, whereas at Scooter was 185.47 $\mu molm^{-2}s^{-1}$, 419.31 $\mu molm^{-2}s^{-1}$ at Tavernier Nursery, and 111.95 $\mu molm^{-2}s^{-1}$ at Layer Cakes. PAR in the Keys was much lower than average between 204-216 julian days, however, this was not a result of biofouling as the wiper operated as normal and is likely a reflection of storms and increased cloud coverage in the area during that time.

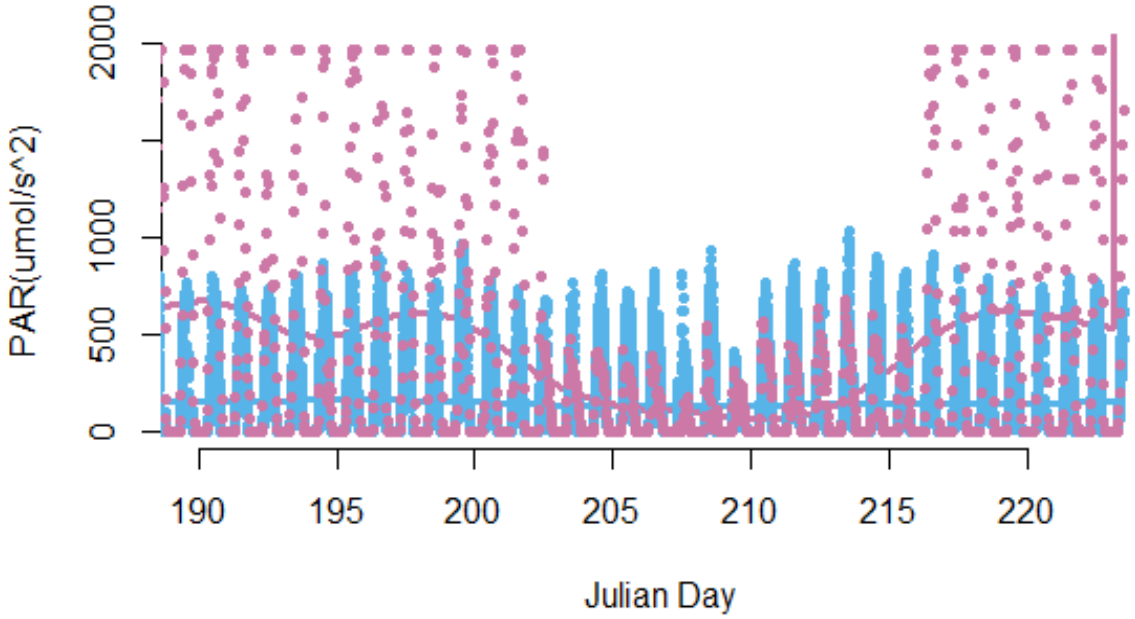

Figure 8: Variation in photosynthetically active radiation (PAR) over time in Fort Lauderdale (blue) and the Florida Keys (pink).

Gamete Development

In the initial field sampling (mid-June), gametes lacked pigmentation (Fig. 8a), indicating they were not fully mature yet. Histological analyses revealed Stage III oocytes, with a mean (±SE) diameter of (368.55 ± 68.18 µm) and Stage II-III spermaries (54.98 ± 9.45 µm) across all sites in Fort Lauderdale (Fig. 8b). Initial samples in the Keys were collected one week later,

however, gametes were also unpigmented and upon histological analyses contained Stage III oocytes (323.88 ± 101.25 μm) and Stage III spermaries (65.88 ± 7.04 μm). Two weeks before the early August full moon, gametes in the field became noticeably more pigmented (Fig. 8c). Histological analyses revealed a mixture of Stage III/IV oocytes, with a mean diameter of (426.48 ± 90.16 μm), and a mixture of Stage IV/V spermaries (85.95± 18.22 μm) across all Fort Lauderdale sites (Fig. 8d). In the Keys, the mean diameter of Stage III/IV oocytes was 401.87± 50.64 μm and Stage III/IV spermaries was 89.61 ± 20.00 μm, thus were not significantly different from those in Fort Lauderdale ($t_{9.8402}$ = 0.65887, p = 0.2625, and $t_{26.182}$ = -0.526, p = 0.3017, respectively).

At Core 3 (Fort Lauderdale), gametes were absent 3 DAFM in the two (of the three) tagged colonies. The other colonies at all three sites still contained Stage III/IV oocytes (375.68 ± 71.90 μm). Six DAFM, a single colony from Layer Cakes Nursery no longer had gametes, thus must have spawned between 3-5 DAFM. Histological analyses from the remaining corals revealed a mixture of stage III-V oocytes (455.18 ± 61.64 μm). Eight DAFM, two colonies from Scooter, and an additional 2 colonies in Layer Cakes Nursery no longer had gametes, suggesting a larger spawn occurred 6-7 DAFM. Ten DAFM, a single colony from Scooter no longer had gametes, suggesting it spawned 8-9 DAFM. The remaining two colonies from Core 3 and Layer Cakes Nursery were never cleared of gametes during the field sampling period (last day 10 DAFM before sunset). However, histology of these colonies shows preliminary evidence of oocyte necrosis and resorption (Fig. 8e), suggesting they never spawned. In the Keys, corals were observed spawning in the field 4 DAFM. Samples 7 DAFM revealed an absence of gametes.

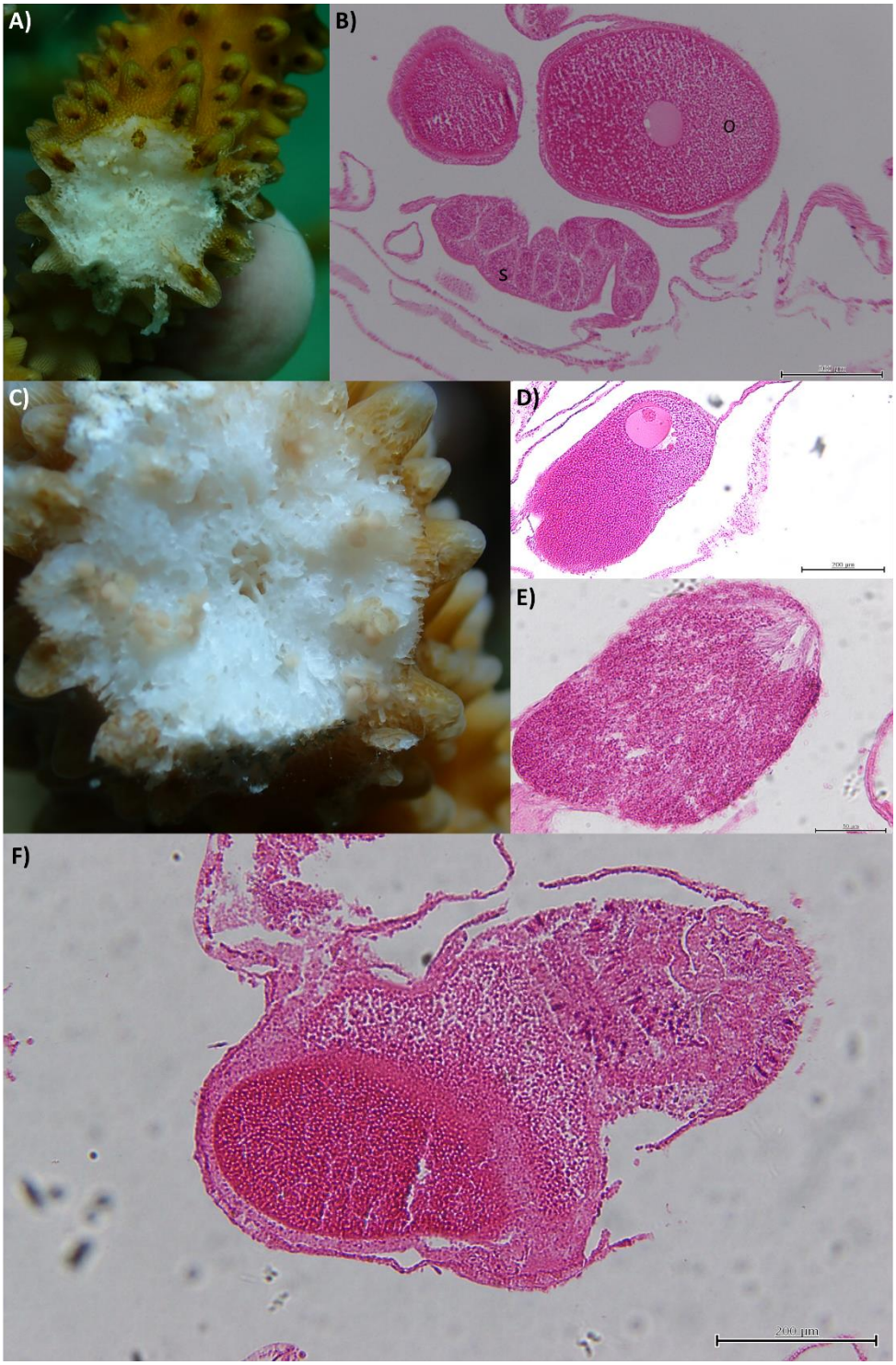

Figure 8: (A) Fort Lauderdale gametes 1.5 months prior to spawning lack pigmentation. (B) Histology reveals Stage III oocytes and spermaries. (C) Fort Lauderdale gametes 1.5 weeks prior to spawning gain pigmentation. Histology reveals (D) Stage IV oocytes and (E) spermaries. (F) Oocyte necrosis was observed in some colonies two weeks after the full moon.

Spawning Observations

In 2022, *ex situ* corals in Fort Lauderdale were observed to spawn between 8-12 days before the full moon in August, whereas colonies in the Keys spawned *in situ* between 2-5 DAFM. However, corals still spawned within the expected time window (120-226 minutes after sunset; MAS), regardless of region or whether observations occurred *in situ* or *ex situ*. In 2023, *ex situ* corals from Fort Lauderdale sites spawned 0-8 DAFM between 180-258 MAS. However, many colonies observed *ex situ* never spawned, despite having mature gametes. In the Keys, *in situ* spawning was only observed 4 DAFM between 151-191 MAS. Similarly, to corals in Fort Lauderdale, about half of the colonies were never observed to spawn.

Spawning time was significantly different between years in Fort Lauderdale (χ^2=150, p<0.001), with corals from 2022 spawning 8-12 days before the full moon, while corals in 2023 spawned 1-9 DAFM. In contrast, spawning time in the Keys was not significantly different between years (χ^2=0, p=0.9), with corals from 2022 spawning 2-5 days after the full moon, while corals in 2023 spawned 4 DAFM. However, it is possible that some colonies may have spawned on nights prior to this but were not observed due to weather conditions.

Acropora cervicornis in Fort Lauderdale and the Florida Keys do not spawn synchronously (χ^2=21.5, p<0.001). In 2022, corals in Fort Lauderdale spawned significantly earlier than corals in the Keys (χ^2=288, p<0.001) and the two regions also spawned at significantly different times in 2023 (χ^2=13.7, p<0.001; Fig. 9). The variance in spawning in Fort Lauderdale was much greater than that in the Keys in both 2022 (2.4 days in Fort Lauderdale vs. 0.99 days in the Keys) and 2023 (7.4 days in Fort Lauderdale vs. 0 days in the Keys; Fig. 10). Additionally, spawning time in Fort Lauderdale was significantly longer than in the Keys (W = 754.5, p,<0.001), with Fort Lauderdale spawning between 120-258 MAS while the Keys spawned between 151-191 MAS (Fig. 10). While the best fit generalized additive model suggested that spawning day was significantly affected by the number of days after the full moon (χ^2=59.4, p<0.01) and the weekly rate of change in PAR (χ^2=13.28, p<0.001), with these factors combined accounting for 40% of the variance in spawning day (R^2= 0.40), model validation revealed this model was not a good enough fit for the data.

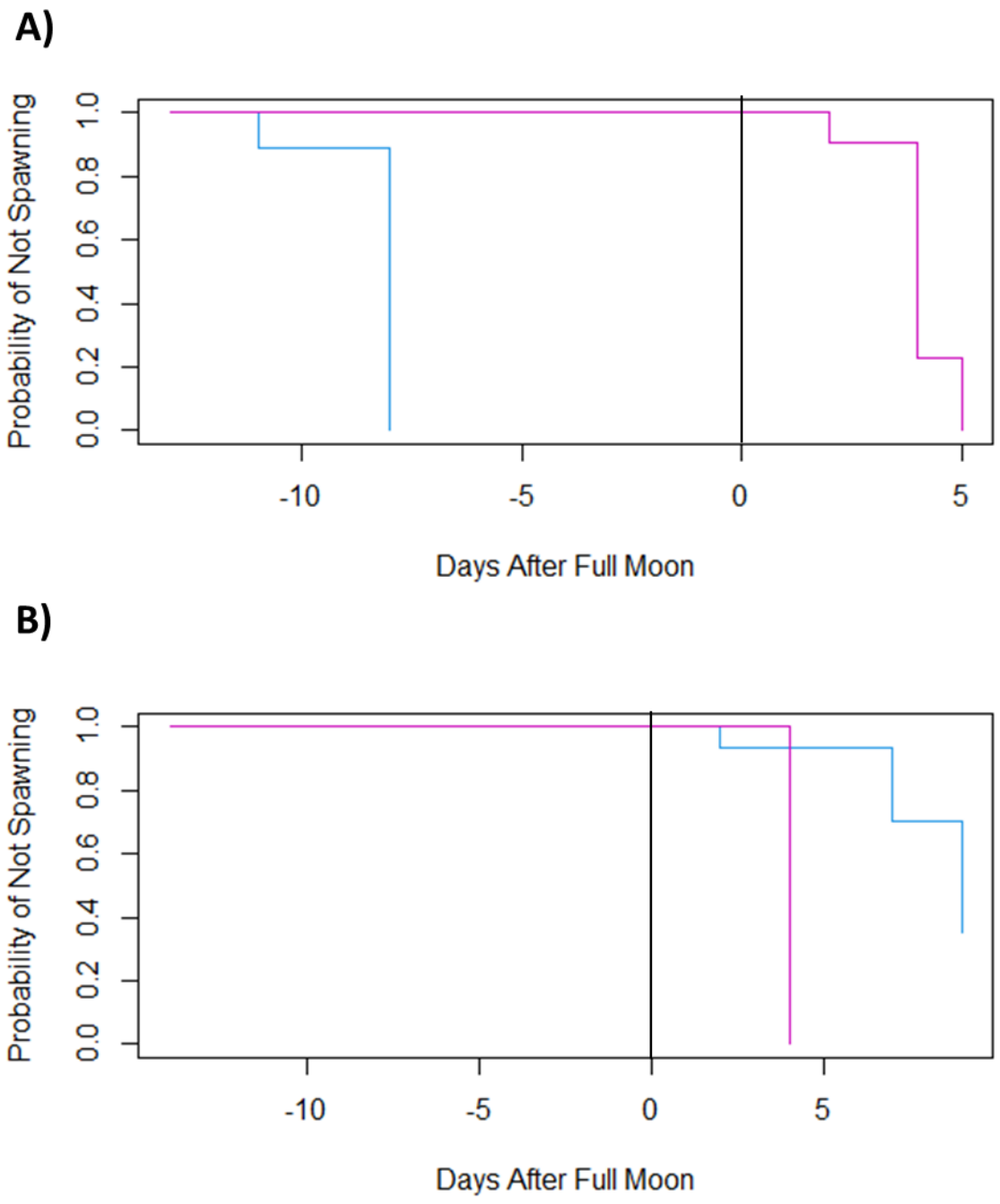

Figure 9: Survival analyses reveal regional spawning asynchrony both in (A) 2022 and (B) 2023. Fort Lauderdale is indicated by the blue line, whereas the Keys is indicated by a pink line. The black vertical line indicates the night of the full moon.

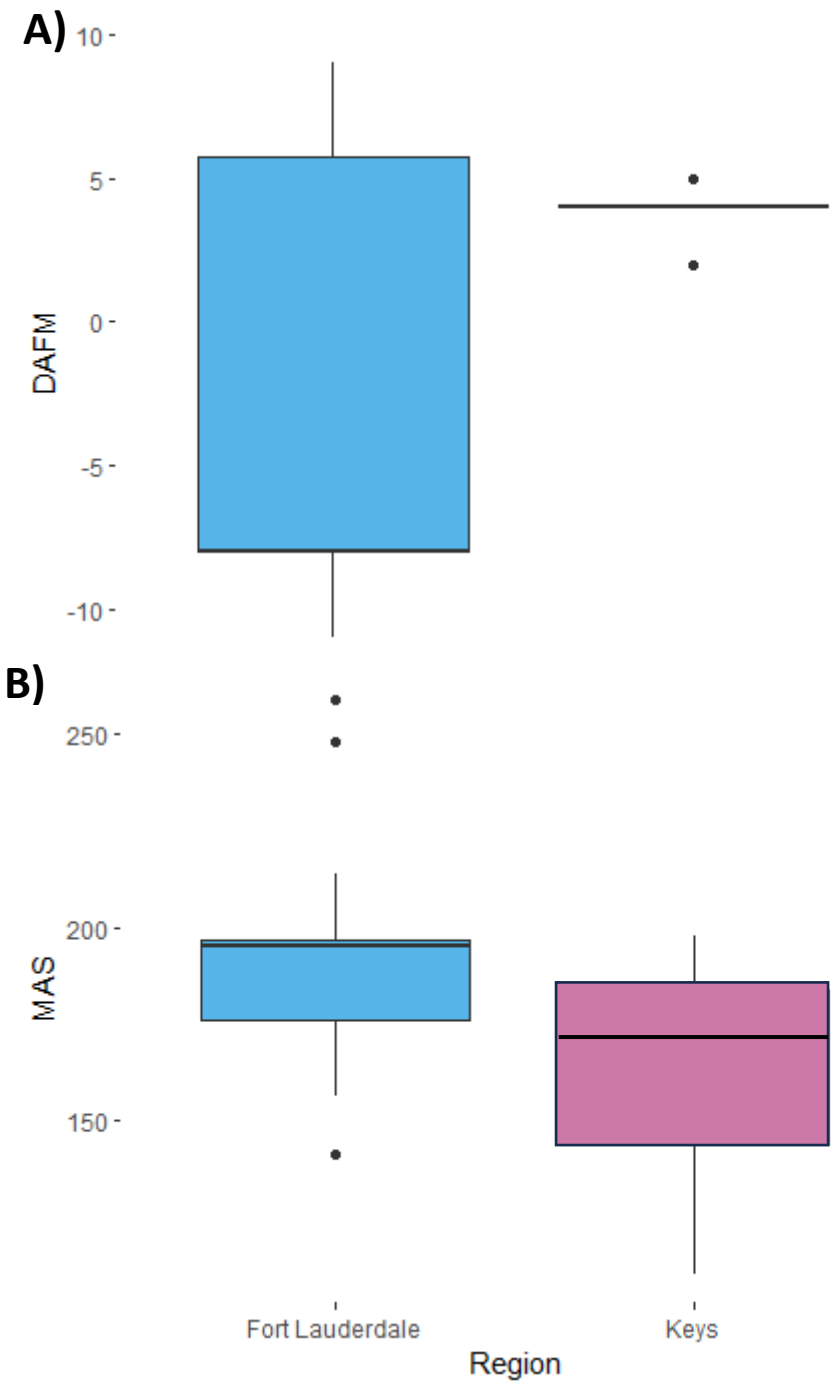

Figure 10: Spawning times differ between Fort Lauderdale (blue) compared to the Keys (pink) both in (A) DAFM and (B) MAS.

Discussion

This study is the first to report the asynchronous spawning of *Acropora cervicornis*. Specifically, off Fort Lauderdale, FL, the northern portion of Florida's Coral Reef, *A. cervicornis* corals spawn several days apart from populations in the Florida Keys and historically throughout the Caribbean. While *A. cervicornis* in the Florida Keys reliably and synchronously spawned within the predicted window of 2-5 DAFM (Vargas-Ángel et al., 2006) in both 2022 and 2023, *A. cervicornis* off Fort Lauderdale, FL spawned 7-10 days before the full moon in 2022 and 1-9 days after the full moon in 2023. Additionally, even within Fort Lauderdale, FL region, there was asynchronous spawning across sites and years. Temperature was found not to explain the differences in day of spawning between regions or sites within region. We were not able to determine if this asynchrony was caused by light pollution or turbidity, or a confounding factor such as the presence of exogenous sex steroids disrupting a coral's hormonal cues (Fogarty and Marhaver 2019; Shlesinger and Loya 2019), but our observations seem to suggest that the corals in this region are not receiving the moonlight cue for spawning.

Temperatures do not explain the discrepancy in spawning times between Fort Lauderdale and the Keys. Differences in water temperature between sites seem better explained by differences in depth between sites, regardless of region. Indeed, in Fort Lauderdale, the shallowest site had the highest mean temperature, whereas the deepest site had the lowest mean temperature. In Tavernier Nursery in the Florida Keys, depth is comparable to that of Layer Cakes Nursery in Fort Lauderdale and their temperatures are not significantly different. While temperature can vary between latitudes (Nozawa et al., 2015; Woolsey et al., 2015), or be affected by oceanographic patterns, such as the Florida Current (Fratantoni et al., 1998; Kourafalou & Kang, 2012; Lee & Mayer, 1977; Walker & Gilliam, 2013), several areas in the Caribbean experience different temperatures but still report synchronous spawning among regions (Hudson et al., 2020; Marhaver et al., 2023; Vermeij et al., 2022). Across the Indo-Pacific, other *Acropora* species also exhibit latitudinal synchrony, despite differences in temperature (Bouwmeester et al., 2021). There is extensive evidence that the temperature only affects the month in which corals spawn (de Putron & Smith, 2011; Nozawa, 2012; Sola et al., 2016; van Woesik et al., 2006), particularly the month that coincides with the highest rate of increase in temperature within each region (Keith et al. 2016); absolute temperature is not relevant to spawning synchrony (Keith et al. 2016).

The daytime light irradiance levels (PAR) differed greatly between Fort Lauderdale and the Florida Keys but is not likely the cause of the spawning asynchrony between regions. Light irradiance typically decreases with depth (Kirk, 1977), for example, in Fort Lauderdale, the shallowest site had the highest mean PAR, whereas the deepest site had the lowest mean PAR. Still, Tavernier Nursery in the Florida Keys is at the same depth as the Layer Cakes Nursery in Fort Lauderdale, but its daytime light irradiance was approximately 2.75 times greater than in Fort Lauderdale. Light irradiance at sea surface is known to decrease from the equator towards the pole (Campbell & Aarup, 1989); however, the one-degree latitudinal difference between Fort Lauderdale and the Keys is too small to justify the differences found. The regional discrepancy in daytime light levels is likely attributed to higher levels of turbidity in Fort Lauderdale's nearshore reef compared to the Upper Keys (Florida Department of Environmental Protection 2023), as turbidity boosts light attenuation at an exponential rate (Kirk, 1977). Regardless, published spawning data does not support the hypothesis that differences in daylight time irradiance determine the regional spawning asynchrony. Sites with varying depths, light availability, and latitude still document synchronous spawning at the scale of days (Harrison et al., 1984; Levitan et al., 2011). Additionally, Keith et al. (2016) conclude light availability is not a reliable predictor of spawning month due to variances in turbidity and cloud coverage. However, they acknowledge that light availability at night is vital to spawning synchrony at the day and hour time scales (Bosch et al., 2014). Moreover, daytime light irradiance certainly does not explain the spawning asynchrony between sites and years within Fort Lauderdale.

It is unclear whether turbidity or night light pollution explain the phenomenon of regional spawning asynchrony; both mask the moonlight and could prevent corals from receiving that spawning cue. Given that the differences in daytime PAR levels between regions are likely due to turbidity, it is very likely that turbidity also dims the moonlight, potentially preventing it from reaching the corals. Nighttime light pollution may mask the fluctuating light levels from the lunar cycle, which are vital to predicting the days in which the species will spawn (Fogarty & Marhaver, 2019). Indeed, recent studies have documented unsynchronized gamete release for several genera when exposed to artificial light at night via sky glow (Ayalon et al., 2021; Davies et al., 2023). Since the equipment used to measure light at reef depth, Odyssey, regardless of region, was not able to capture any light starting approximately 30 minutes after sunset, it seems less likely that coastal night light pollution is the culprit of the observed spawning asynchrony.

As for the turbidity, in both regions, nighttime light irradiance measurements remained zero regardless of moon phase, i.e., the equipment used was also unable to capture the full moon light at reef depth (~0.01-0.02 $\mu molm^{-2}s^{-1}$; Jokiel et al. 1985). It is not clear whether the Odyssey PAR Loggers do not have a fine enough resolution to measure light from the full moon at reef depth or if turbidity levels are decreasing moonlight levels to a point below the equipment resolution. In other studies conducted in a hyper-turbid environment, the Odyssey PAR Logger was also unable to capture moonlight levels (Chow et al., 2019; Law & Huang, 2023). To our knowledge, no studies have reported measurements with this instrument in no-low turbidity environments, but measurements made in lab detected low irradiance (0.04 $\mu molm^{-2}s^{-1}$). Because spawning is asynchronous between regions, but also between years within Fort Lauderdale, it is more likely that the higher turbidity in Fort Lauderdale is the culprit. Fort Lauderdale reefs are in a heavily urbanized area, experiencing high levels of turbidity which could prevent moon light from reaching the corals; we hypothesize the spawning is solely regulated by the annual temperature and sunlight cycles. The spawning asynchrony cannot be explained by genotypes because corals from this species collected in Fort Lauderdale and held in aquaria systems where they are exposed to lights that mimic the temperature, sun and moon light cycles consistently spawn synchronously 2-6 DAFM (Fogarty et al., 2012) as in the Florida Keys and throughout the Caribbean. In the Florida Keys, turbidity, albeit lower than in Fort Lauderdale, may dim moonlight levels below the light meter resolution but still be detectable by the corals.

Spawning asynchrony at the scale of day and hour can be caused by lack of moonlight cue and/or lower pheromone concentration resulting from the lower coral density. The lunar cycle (moon phase and moonrise relative to sunset time) typically predicts the day and hour corals spawn (Babcock et al., 1986b; Harrison, 2011; Lin & Nozawa, 2017). *Acropora cervicornis* typically spawn 2-7 days after the full moon, between 150-210 MAS (Marhaver et al., 2023; Miller, 2013; Vargas-Ángel et al., 2006; Vermeij et al., 2022). Corals from Fort Lauderdale brought *ex situ* prior to the expect spawning window spawned within the expected hours in both years (2022: 120-226 MAS; 2023: 180-258 MAS); however, there was a larger variance than what had been reported 21 years ago in this region (180-210 MAS; Vargas-Angel et al. 2006). While corals still receive the vital cue of sunset to predict the hour of spawning, the inability to detect moonrise may explain the variance in spawning time (Ayalon et al., 2021;

Brady et al., 2009; Hayashibara et al., 2004; Kaniewska et al., 2015). However, this variance in *ex situ* spawning times may be a result of heavy night light pollution due to close proximity to Port Everglades – a trend that has been exhibited in *Dendrogyra cylindrus* (Neely et al., 2020). Additionally, a decline in coral density in the region (Goergen et al., 2020) may result in a low concentration of pheromones that can regulate spawning to the minute (Levitan et al., 2011). The increased range in spawning hour may result in a lack of fertilization, as success drastically reduces within the first few hours of gamete release, as sperm loses mobility (Levitan et al., 2011).

Within Fort Lauderdale, corals at different sites did not spawn on the same night, nor on the same nights relative to the full moon between years. Because this species tends to primarily reproduce through asexual fragmentation (Neigel & Avise, 1983; Tunnicliffe, 1981), we assume that there is genetic homogeneity within each site, with corals from different sites being genetically distinct (Drury et al., 2017). Discrepancies in spawning time among sites are thus likely driven by genetic differences. Indeed, corals at Scooter and Core 3 spawned each year within one night but days apart from each other. In contrast, Layer Cakes Nursery in Fort Lauderdale houses multiple genotypes and had a more prolonged spawning window; the Tavernier Nursery in the Keys also houses multiple genotypes, but the great majority was observed spawning on the same day. It is possible that sites within Fort Lauderdale are not spawning synchronously year to year due to a lack of lunar cue; currently, it is not possible to discern whether this is driven by high turbidity. Spawning time is regulated by a hierarchy of cues that have a progressively finer resolution (Fogarty & Marhaver, 2019). Temperature and irradiance cue the month in which corals spawn (de Putron & Smith, 2011; Keith et al., 2016; Nozawa, 2012; Sola et al., 2016; van Woesik et al., 2006), while the lunar cycle cues the days in which corals spawn (Babcock et al., 1986a; Harrison, 2011; Lin & Nozawa, 2017). If corals cannot receive the lunar cue, it is possible that spawning will be prompted by the higher-level cue (i.e., the month of the fastest rate of temperature change; Keith et al. 2016) and will not have the tight synchrony needed to optimize fertilization. Though spawning times of *A. cervicornis* in Fort Lauderdale have only been systematically studied in the last two years, data collected over the last four years indicates that, regardless of the time of the month of the full moon, this species always spawns between late July and mid-August. Yet, other regions consistently observe spawning 2-7 DAFM, regardless of the full moon occurring early or late in the month (Hudson et

al., 2020; Marhaver et al., 2023; Miller et al., 2015; Vermeij et al., 2022). Thus, it is likely that, in this region, this species is only responding to the temperature cue that synchronizes spawning to the month, rather than the lunar cue which synchronizes spawning to the day. Similarly, it is hypothesized that the reproduction mode of this genus fits an hourglass biological clock model (Lin et al., 2021; Lin & Nozawa, 2017), in which spawning time is maintained solely by fluctuations in environmental cues rather than entrained (Lin et al., 2013; Rensing et al., 2001). Indeed, there is evidence that this genus exhibits inconsistent spawning days from year to year in the Indo-Pacific, presumably due to fluctuations in temperature and light (Lin and Nozawa 2017). Therefore, the inconsistencies in the spawning time of *Acropora cervicornis* across years in Fort Lauderdale may also be due to fluctuations in light due to a lack of lunar cue.

While it is still unclear what is driving the spawning asynchrony in *Acropora cervicornis* in Fort Lauderdale, we hypothesize that corals are not receiving the final cue (i.e. light cue of the full moon) needed to accurately synchronize the day of spawning. Future studies should measure night light through more sophisticated underwater instrumentation intended for deep sea research (Tamir et al., 2017, 2019) or extrapolate underwater night light pollution through sky glow measurements (Doron et al., 2007). Additionally, it is also possible that light spectrum, rather than light intensity is a more appropriate metric to measure the impact of light pollution and turbidity on spawning synchrony (Sweeney et al., 2011; Tamir et al., 2017). If heavily urbanized areas emit enough artificial light that shifts the spectrum of light normally experienced at night, the cues that synchronize the day and hour in which corals spawn may be lost (Tamir et al. 2017). A shift in light spectrum combined with dimming effects turbidity may substantially mask lunar cues that are vital to synchronizing spawning to the day and hour. Furthermore, the potential of exogenous sex steroids disrupting the hormonal cues of gametogenesis and gamete release ought to be further explored. Armoza-Zvuloni found that reproduction patterns were inhibited in corals located on reefs near sewage outlets which had high concentrations of progesterone, testosterone, and estradiol (Armoza-Zvuloni et al., 2012). Sites in Fort Lauderdale are located close to shore and may experience increased concentrations of exogenous sex steroids compared to corals in the Keys which are several miles offshore; thus asynchronous spawning may be exacerbated by hormonal disruptions.

Regardless of the cause, asynchronous spawning has massive implications for the persistence of this species in Fort Lauderdale. A lack of synchrony results in dramatically reduced fertilization success (Levitan et al. 2011) and consequently lowers recruitment (Randall & Szmant, 2009b; Humanes et al., 2017) and the ability of populations to replenish themselves. Additionally, the inability to reliably predict the spawning day of *A. cervicornis* in Fort Lauderdale may prevent gamete collection from the field to sexually propagate corals for reef restoration (Randall et al. 2020). A reduction in sexual reproduction and therefore reef connectivity and recruitment, will reduce the genetic diversity needed for populations to remain resilient to future disturbances such as marine heat waves.

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APPENDIX 1: Histologic Staining Protocols

Harris Hematoxylin and Eosin Staining Protocol (modified):

I. Deparaffinize

3 Xylene:	3 minutes each
3 100 % EtOH:	3 minutes each
1 95 % EtOH:	2 minutes
1 80 % EtOH:	2 minutes
1 DI Water:	2 minutes

II. Stain

Harris Hematoxylin:	2 minutes
Running Tap Water Wash:	≥ 2 minutes
0.25 % Acid Alcohol:	2 dips
DI Water:	several dips
0.25 % Ammonium Hydroxide:	2 minutes
DI Water:	1 minute
95 % EtOH:	2 minutes
Eosin:	2 30 second dips
95 % EtOH:	2 minutes

III. Dehydrate and Clear

3 100 % EtOH:	3 minutes each
3 Xylene:	3 minutes each

IV. Coverslip